



## Effects of climate on the growth of Swiss uneven-aged forests: Combining >100 years of observations with the 3-PG model

David I. Forrester<sup>\*</sup>, Amanda S. Mathys, Golo Stadelmann, Volodymyr Trotsiuk

Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

### ARTICLE INFO

#### Keywords:

Climate change  
Continuous cover  
Maestra model  
Mixed-species forest  
Plenter forest  
Single-tree selection

### ABSTRACT

Stand-level process-based models have rarely been applied to uneven-aged forests that contain many size classes and negative exponential shaped size distributions. However, the relative simplicity of such models, in terms of parameterisation, use and interpretation, could make them valuable tools for studying and managing such forests. In particular, the effects of climate change on the stand-level growth of forests with negative exponential shaped size distributions has received very little attention compared with even-aged forests. The first objective of this study was to validate 3-PG, a stand-level process-based model, for five types of uneven-aged forests in Switzerland; (1) *Fagus sylvatica* dominated, (2) *Picea abies* dominated, (3) mixtures of *Picea abies* and *Abies alba*, (4) mixtures of *Picea abies*, *Abies alba* and *Fagus sylvatica*, and (5) mixtures of *Larix decidua*, *Pinus cembra* and *P. abies*. The second objective was to use 3-PG to examine how climate change has influenced the growth of these forests since the 1930s.

3-PG predictions of biomass, biomass partitioning in above- and belowground components, and light absorption were validated using inventory data from 23 plots, which had been monitored for an average of 81 years (15 to 112 years). For all species and size classes (2–3 per species), 3-PG produced accurate predictions of root biomass, stem biomass and outputs derived from it such as mean diameter, basal area and height, which were all highly correlated with the observed values ( $R^2 > 0.86$ ). The slope of predicted versus observed values was often not significantly different to 1 (averaged 1.13) and the bias averaged  $-1.2\%$ .

3-PG simulations to examine the effects of climate change without the confounding effects of stand structure and management, showed that the growth of the five forests types has, on average, increased by 17% since the 1930s. The growth was mainly influenced by temperature, while in the case of *A. alba*, growth was largely influenced by vapour pressure deficit. The accelerated growth rates imply that thinning intensities also need to increase to prevent high stand densities from inhibiting regeneration in these uneven-aged forests. This study shows that 3-PG can be used to predict the growth dynamics of uneven-aged mixed-species forests, and to our knowledge, this is the first time a stand-level process-based forest growth model has been used and validated for such forests.

### 1. Introduction

A wide range of forest growth models have been developed over the past few decades (Vanclay, 1994; Fontes et al., 2010; Weiskittel et al., 2011; Burkhart and Tomé, 2012; Pretzsch et al., 2015), many of which can be used for uneven-aged forests (Peng, 2000), including TREE-BGC (Korol et al., 1995), BALANCE (Grote and Pretzsch, 2002), and SILVA (Pretzsch et al., 2002). They vary greatly in terms of the spatial (tree level, cohort level, stand level) and temporal resolution (minutes, days, months, years, multi-year time steps), and the degree to which they rely

on statistical equations versus equations describing ecophysiological processes, e.g. photosynthesis, transpiration, light absorption. In this study, the term cohort indicates different groups of trees in terms of species and size classes. Despite this variability of models, very few models for uneven-aged forests are process-based with a stand (or cohort) level resolution. This contrasts with a widespread use of stand-level process-based models for even-aged forests, both by researchers and foresters (e.g. Battaglia et al., 2007; Gupta and Sharma, 2019).

While empirical and/or tree-level models have proven to be very useful, there are also important reasons for considering stand-level

<sup>\*</sup> Correspondence author.

E-mail address: [david.forrester@wsl.ch](mailto:david.forrester@wsl.ch) (D.I. Forrester).

<https://doi.org/10.1016/j.foreco.2021.119271>

Received 19 February 2021; Received in revised form 9 April 2021; Accepted 13 April 2021

Available online 12 May 2021

0378-1127/© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

process-based models for uneven-aged forests. With regards to the empirical versus process-based aspect, empirical models are limited to the conditions represented in the data sets from which they were developed, and may be less reliable when extrapolated to new climates, site conditions, species combinations, and silviculture (Battaglia and Sands, 1998; Peng, 2000; Landsberg, 2003). In contrast, models based on general, fundamental ecophysiological processes can potentially provide robust extrapolations to novel conditions (Weiskittel et al., 2010). For some types of uneven-aged forests (e.g. single-tree selection forests in central Europe, also known as plenter forests) there is limited data available to develop empirical models for past and present climatic conditions, let alone for future climatic conditions.

With regards to model resolution, while tree-level models can be useful for examining patterns resulting from tree-level interactions, those models typically require more calculations (and computing power), and as a consequence, can propagate error to the stand level (Grimm, 1999). This is exacerbated when processes that significantly influence tree-level growth are difficult to model at the tree level (e.g. mortality), or are ignored or inadequately represented e.g. micro-site heterogeneity, plasticity in tree architecture and crown or root positioning (García, 2016; Lee and García, 2016).

Stand- or cohort-level models can replace complex and non-linear tree-level processes with simpler and lower resolution calculations. This is useful when the desired output resolution is the cohort or stand level, rather than the tree level. It is also consistent with the fact that many of the main processes that drive forest growth can be modelled at the stand level or cohort level (i.e. age classes, size classes, or species) (Pretzsch et al., 2015). Given that stand-level models can accurately predict the growth of mixed-species forests (Forrester et al., 2017a; Bouwman et al., 2021), it is plausible that they may also accurately predict the growth of uneven-aged forests. The use of stand-level models can also simplify parameterisation and input data requirements, and may be easier for users to understand and interpret.

The term “uneven-aged” is broadly applied to forests with more than one age class, and can include a wide range of structures along a continuum from stands containing two age classes, each with unimodal diameter distributions, to stands with many age classes such as those with negative exponential shaped diameter distributions. The latter is an extreme example that provides a good test for a forest growth model and is the focus of this study. Stands with negative exponential shaped diameter distributions can result from thinning or other disturbances that remove single trees or small groups of trees at frequent enough intervals to maintain many size classes within a small area (e.g. <1 ha) (Schütz, 2001; Boncina, 2011), and hence they are often referred to as single-tree selection forests, or plenter forests. These forests provide a regular harvest of different sized trees and are also used in central Europe to maintain a continuous structure on steep slopes to reduce the risk of rock fall, erosion, avalanche and landslides (Brang et al., 2006).

Process-based models are useful for isolating the effects of different factors on stand growth, such as stand density, temperature, soil water availability, etc. For example, stand volume growth of several species in central Europe has increased by about 10 to 30% during the past few decades, with possible causes including rising temperatures, extended growing season lengths, nitrogen deposition, and increased atmospheric CO<sub>2</sub> concentrations (Spiecker et al., 1996; Pretzsch et al., 2014; Hilmers et al., 2019). However, few studies have examined whether there have also been long-term changes in stand growth of plenter forests, and these indicate that, in some cases, growth may have accelerated since in the 1980s (Spiecker, 1986, 1991; Zingg, 1996; O’Hara et al., 2007). A difficulty in their interpretation is that stand growth is strongly dependent on stand structure (e.g. size distribution, stand density, tree size-growth relationships, species composition) (Forrester, 2019), which

continuously changes, even in plenter forests (O’Hara et al., 2007). Therefore changes in climate can be confounded with changes in structure. When the change in growth is caused by changes in climate, then the thinning intensity or frequency needs to increase to maintain an appropriate range of stand density for sufficient regeneration.

The first objective of this study was to examine whether a process-based stand-level model (3-PG; Physiological Processes Predicting Growth; Landsberg and Waring, 1997) could predict the growth and yield, biomass partitioning, and light absorption in five types of plenter forests in Switzerland. The light absorption was considered because we assumed that this process is an important driver of interactions between different tree sizes and species in these types of forests. The second objective, was to use 3-PG to examine whether the growth of these forests has changed since the 1930s in response to climate change, and if so, which climatic variables were responsible.

## 2. Methods

### 2.1. Model description

The 3-PG model is a relatively simple stand-level model with a monthly time step. It was originally developed for even-aged evergreen monospecific forests (Landsberg and Waring, 1997), but recent developments such as 3-PG<sub>mix</sub> have broadened its applicability to deciduous species, and mixed-species forests (Forrester and Tang, 2016), and therefore potentially to uneven-aged forests, including plenter forests. These, and many other studies provide detailed descriptions of 3-PG. Of importance for this study, are the growth modifiers that reduce the species-specific potential light-use efficiency based on limitations imposed by temperature, frost, vapour pressure deficit, soil moisture, soil fertility, atmospheric CO<sub>2</sub> and stand age. Each of these limitations is quantified using a growth modifier, which with the exception of the CO<sub>2</sub>, can take values between 0 (no growth) and 1 (unlimited growth). The CO<sub>2</sub> growth modifier can also take values of >1. These growth modifiers indicate which factors are most limiting to growth, and hence how this changes within and between years.

3-PG requires species-specific parameters that describe their physiology and morphology. These were obtained from parameter sets developed using Bayesian calibration for central European tree species (Forrester et al., 2021). This calibration was based on empirical data from nearly 2500 forest plots as well as a literature review. For a more detailed description, published parameter sets and information about measurements needed to calculate each parameter, see Forrester (2020). In this study, 3-PG was run using the *r3PG* package (Trotsiuk et al., 2020) in R 3.6.1 (R Core Team, 2019) with *settings = list(light\_model = 2, transp\_model = 2, phys\_model = 2, height\_model = 2, correct\_bias = 1, calculate\_d13c = 0)*. These settings make use of the modifications included in the 3-PG<sub>mix</sub> version of 3-PG that was developed specifically for mixed-species forests (Forrester and Tang, 2016). An example R script for simulating a plenter forest containing two species, each with three size classes, is provided as supplementary material.

### 2.2. Modifications considered for 3-PG

Preliminary tests of 3-PG indicated that 3-PG sometimes overestimated the biomass and absorption of photosynthetically active radiation (APAR) of the largest size classes within some stands, but underestimated that of the smallest size classes. The mortality of the smallest size classes was also underestimated for some stands. Therefore, three 3-PG modifications were tested in order to prevent this. The first was based on an assumption that the APAR of shorter size classes was underestimated because their leaf area was underestimated. Leaf area is

**Table 1**

Summaries of plot and site characteristics averaged across all measurements for the 23 plots used in this study. The mean annual precipitation and temperature are for the years 1930 to 2018.

Plot	Longitude/ Latitude	Plot area (ha)	Elevation (m)	Precipitation (mm year <sup>-1</sup> )	Mean annual temperature (°C) (minimum/ maximum)	Forest type (dominant species)	Number of inventories (first and last)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Volume (m <sup>3</sup> ha <sup>-1</sup> )	Number of trees (ha <sup>-1</sup> )
1015001	7.66/46.86	1.78	947	1420	6.9 (3.1, 11.6)	<i>A. alba</i> & <i>P. abies</i>	19 (1905, 2017)	39.7	552	552
1015002	7.65/46.86	1.24	931	1420	6.9 (3.1, 11.6)	<i>A. alba</i> & <i>P. abies</i>	19 (1905, 2017)	34.0	456	456
1015003	7.65/46.86	1.01	937	1420	6.9 (3.1, 11.6)	<i>A. alba</i> & <i>P. abies</i>	12 (1905, 1964)	34.2	460	460
1019000	7.6/46.81	1.99	575	1048	9 (4.8, 13.9)	<i>A. alba</i> & <i>P. abies</i>	17 (1908, 1999)	37.7	462	462
1027000	7.69/46.88	1.99	861	1369	7.2 (3.4, 12)	<i>A. alba</i> & <i>P. abies</i>	17 (1912, 2012)	33.3	645	645
1028000	7.69/46.87	1.18	920	1437	6.8 (3, 11.5)	<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	17 (1912, 2012)	33.9	548	548
1030001	7.77/46.96	1.14	910	1430	7.1 (3.3, 11.8)	<i>A. alba</i> & <i>P. abies</i>	10 (1914, 1990)	49.1	398	398
1030002	7.77/46.96	1.84	888	1430	7.1 (3.3, 11.8)	<i>A. alba</i> & <i>P. abies</i>	10 (1914, 1990)	45.7	441	441
1030003	7.77/46.96	0.59	883	1430	7.1 (3.3, 11.8)	<i>A. alba</i> & <i>P. abies</i>	10 (1914, 1990)	45.7	625	625
1031000	7.66/46.95	1.26	920	1430	6.9 (3.1, 11.6)	<i>A. alba</i> & <i>P. abies</i>	16 (1918, 2013)	39.9	614	614
1033000	9.86/46.49	0.99	1810	989	2.5 (-1.9, 7.6)	<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	12 (1921, 2019)	35.5	513	513
1034000	9.85/46.49	1.00	1810	992	2.5 (-1.9, 7.5)	<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	12 (1921, 2019)	39.6	579	579
1041000	7.21/46.48	1.49	1294	1507	5.5 (1.7, 10.2)	<i>A. alba</i> & <i>P. abies</i>	14 (1928, 2013)	33.3	471	471
1042000	7.21/46.48	1.99	1185	1453	6 (2.2, 10.8)	<i>A. alba</i> & <i>P. abies</i>	14 (1928, 2013)	35.6	528	528
1046000	7.73/46.8	2.00	930	1379	7.1 (3.2, 11.9)	<i>A. alba</i> & <i>P. abies</i>	14 (1931, 2012)	40.8	468	468
2035000	6.56/46.88	1.98	983	1431	6.9 (3.3, 11.2)	<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	17 (1913, 2016)	37.7	502	502
2047000	7.76/46.84	2.47	1060	1521	6.3 (2.5, 11)	<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	13 (1931, 2011)	39.2	562	562
5003000	10.21/46.66	0.25	1880	931	1.9 (-2.7, 7)	<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	6 (1946, 2013)	57.2	594	594
6002000	8.26/47.37	3.06	470	1084	9.1 (5.1, 13.8)	<i>F. sylvatica</i>	4 (1999, 2018)	31.2	350	350
6003000	8.56/47.25	11.00	640	1363	8.2 (4.4, 12.7)	<i>F. sylvatica</i>	4 (2000, 2015)	34.6	276	276
21293001	7.75/46.73	1.53	1370	1615	4.7 (1.1, 9.5)	<i>P. abies</i>	10 (1925, 1997)	32.9	398	398
21293002	7.75/46.73	0.49	1405	1625	4.6 (1, 9.4)	<i>P. abies</i>	10 (1925, 1997)	33.8	484	484
21294000	6.22/46.56	2.00	1340	1783	5.1 (1.8, 9.2)	<i>P. abies</i>	11 (1925, 2014)	28.5	586	586

calculated by 3-PG as the product of foliage biomass and specific leaf area (SLA, m<sup>2</sup> kg<sup>-1</sup>). Since SLA is generally higher when light availability is lower (i.e. for shorter size classes), an underestimate in SLA might lead to an underestimate in leaf area and hence underestimates of APAR and growth. Therefore, the relationship between age and SLA used by 3-PG was modified to allow SLA to depend on the light availability at the height of the given size class.

Secondly, an assumption of the light calculations used by 3-PG is that the canopy is homogeneous in terms of the horizontal distribution of species and tree sizes. However, in uneven-aged forests, smaller trees (that survive) may be growing in small canopy gaps where the light availability is higher than the average light availability at that height. Therefore, the second modification tested whether this caused the underestimate in APAR, and hence growth, by examining whether the bias in APAR was correlated with the Clark and Evans aggregation index (Clark and Evans, 1954), which quantifies the aggregation of trees in terms of whether the trees are located randomly (index = 1), more evenly (index > 1), or in an aggregated arrangement (aggregation < 1).

The third modification tested was to correct the mortality, which was underestimated for the smallest cohorts of *F. sylvatica* monocultures leading to an overestimate in the number of trees and hence an underestimate in mean tree diameter and height (for a given stand biomass). The density-dependent mortality rates were increased by calculating an adjusted wSx1000 parameter value that declined with declining relative height (height of the size class divided by the mean stand height). This was based on a study that examined the effect of relative height on the slope of the relationship between the number of trees and the mean tree diameter (both log-transformed) (Forrester et al., 2021). The relative height was found to reduce the intercept of the linear relationship between log(tree density) and log(mean diameter) such that a large decrease in relative height (from 1 to 0.51) would reduce the mean diameter of a fully stocked stand with 1000 trees ha<sup>-1</sup> (cf. wSx1000) to 59% of what it would be if relative height = 1. This was averaged across many species so that it could be used for any species without additional parameters. The minimum wSx1000 when relative height ≤ 0.51 was wSx1000 × 0.59. When relative height > 1, the wSx1000 was used

without adjustment. When relative height was between 0.51 and 1, the adjusted wSx1000 was calculated assuming a linear relationship between relative height and wSx1000.

### 2.3. Data collection

To validate 3-PG, growth and yield data were used from 23 plots of temperate coniferous, broadleaved and mixed forests within the Experimental Forest Management (EFM) plot network in Switzerland (Forrester et al., 2019a). Most plots had been monitored for >60 years, with the exception of two *F. sylvatica* dominated plots that were only measured for 15–19 years. These were included because no other plots of this forest type were available. Five species compositions were included; (1) *Fagus sylvatica* dominated, (2) *Picea abies* dominated, (3) mixtures of *Picea abies* and *Abies alba*, (4) mixtures of *Picea abies*, *Abies alba* and *Fagus sylvatica*, and (5) mixtures of *Larix decidua*, *Pinus cembra* and *P. abies* (Table 1). Most plots were in plenter forests, except for three unmanaged forests, which each had negative exponential shaped size distributions (plots 5003000, 6,002,000 & 6003000). The measurements, at approximately 8-year intervals, were timed to coincide with thinning operations, which resulted in accurate records of trees that were thinned or died. The boundaries of each plot were georeferenced to provide accurate estimates of plot areas. The plot areas vary due to contrasting goals that drove the establishment of each plot.

The diameter at 1.3 m ( $d$ , cm) was measured for all trees with  $d \geq 8$  cm. Tree heights and height to the lowest main-crown live branch were measured for a sample of trees (the 100 largest- $d$  trees and 20% of the rest). The height and live-crown length were then predicted for all other trees using plot-, year- and species-specific regressions as described in Forrester et al. (2019a).

Monthly mean daily maximum and minimum temperatures, precipitation, solar radiation and frost days were interpolated (after Thornton et al. (1997)) from data collected by the Federal Office of Meteorology and Climatology MeteoSwiss from 1930 (100 m spatial resolution). Atmospheric CO<sub>2</sub> data were obtained from NOAA (2013). When plots were measured before 1930, the long-term average climate was used for those early years. Site-specific plant available soil water was retrieved from the European soil database derived data (Panagos et al., 2012). No direct empirical information about the soil fertility was available, so the fertility rating (FR) of each site was adjusted to values that gave satisfactory model performance (Landsberg et al., 2005). At a single site, each species usually had a different FR (Table A1).

### 2.4. Estimation of individual tree light absorption

Measurement of light absorption by individual species within mixtures or different size classes within uneven-aged forests is very difficult and rarely attempted. A common alternative approach is to estimate individual tree light absorption with a tree-level model that uses measurements of tree locations, tree heights, crown architecture and topography. Therefore, to validate 3-PG predictions of light absorption, the 3-PG outputs for each size class and species were compared with predictions from a 3D tree-level model Maestra (Grace et al., 1987; Wang and Jarvis, 1990; Medlyn, 2004; Duursma and Medlyn, 2012). Maestra has been validated in several mixed and monospecific forests (Wang and Jarvis, 1990; Charbonnier et al., 2013; le Maire et al., 2013; Forrester et al., 2018; Forrester et al., 2019b). In these studies, Maestra provided accurate predictions of APAR without any calibration (or ‘tuning’) and was therefore used for this study. Maestra calculates the absorption of photosynthetically active radiation (APAR) from the crown architecture (crown width and length, leaf area and leaf angle distributions), species-specific differences in leaf optical properties and

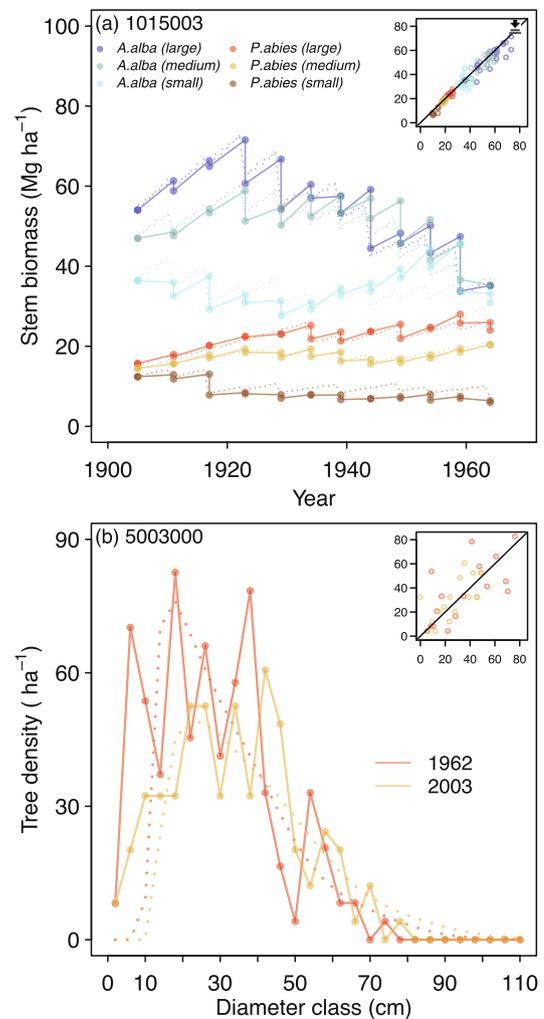


Fig. 1. An example of the stem biomass development (a; plot 1015003) and size distributions (b; plot 5003000) that were measured (solid lines and circles) or predicted by 3-PG (dotted lines). Three size cohorts were simulated for each species in (a). The insets show the predicted (x-axes) vs. observed (y-axes) stem biomass (a) or tree density (b).

leaf area density distributions. Shading by neighbouring trees is calculated by representing the canopy as an array of tree crowns with locations defined by x and y coordinates such that the slope and aspect are considered in both the x and y directions. Parameter values were obtained from the literature by Forrester (2019). The APAR of evergreen species was the total annual APAR (GJ tree<sup>-1</sup> year<sup>-1</sup>), while for deciduous species, growing season APAR was used where the growing season for each species was calculated as a function of altitude (Dittmar and Elling, 2006; Vitasse et al., 2009; Čufar et al., 2012; Pellerin et al., 2012; Cornelius et al., 2013; Schuster et al., 2014). The APAR was calculated for all inventories where tree locations had been recorded, which was usually from the 1970s until present. It was not possible to calculate APAR for one plot (6002000) due to an incomplete tree location data set.

### 2.5. Procedure for simulating forests used for validation

All trees that existed in the first inventory for each plot were assigned to a size class by dividing all trees of a given species into two or three size classes that each contained the same basal area (m<sup>2</sup> ha<sup>-1</sup>) at the first

Table 2

Statistical information, describing the relationships between the stem biomass ( $\text{Mg ha}^{-1}$ ) or light absorption ( $\text{GJ m}^{-2} \text{ year}^{-1}$ ) predicted by 3-PG and the same variables predicted using allometric equations (biomass) or the Maestra model (light absorption), for each size cohort, species, and the total stand. The statistical information includes the mean observed (O) and predicted (P) values, the relative average error (e%), the relative mean absolute error (MAE%), the square root of the mean square error (RMSE), the slope of the relationship forced through the origin, the P-value for the test of whether the slope of the relationship is significantly different from 1, and the  $R^2$  values. Foliage growth and root growth are not considered due to the low reliability of calculating those variables using allometric equations. Statistical information for root biomass, diameter, basal area, and height are shown in Table A2.

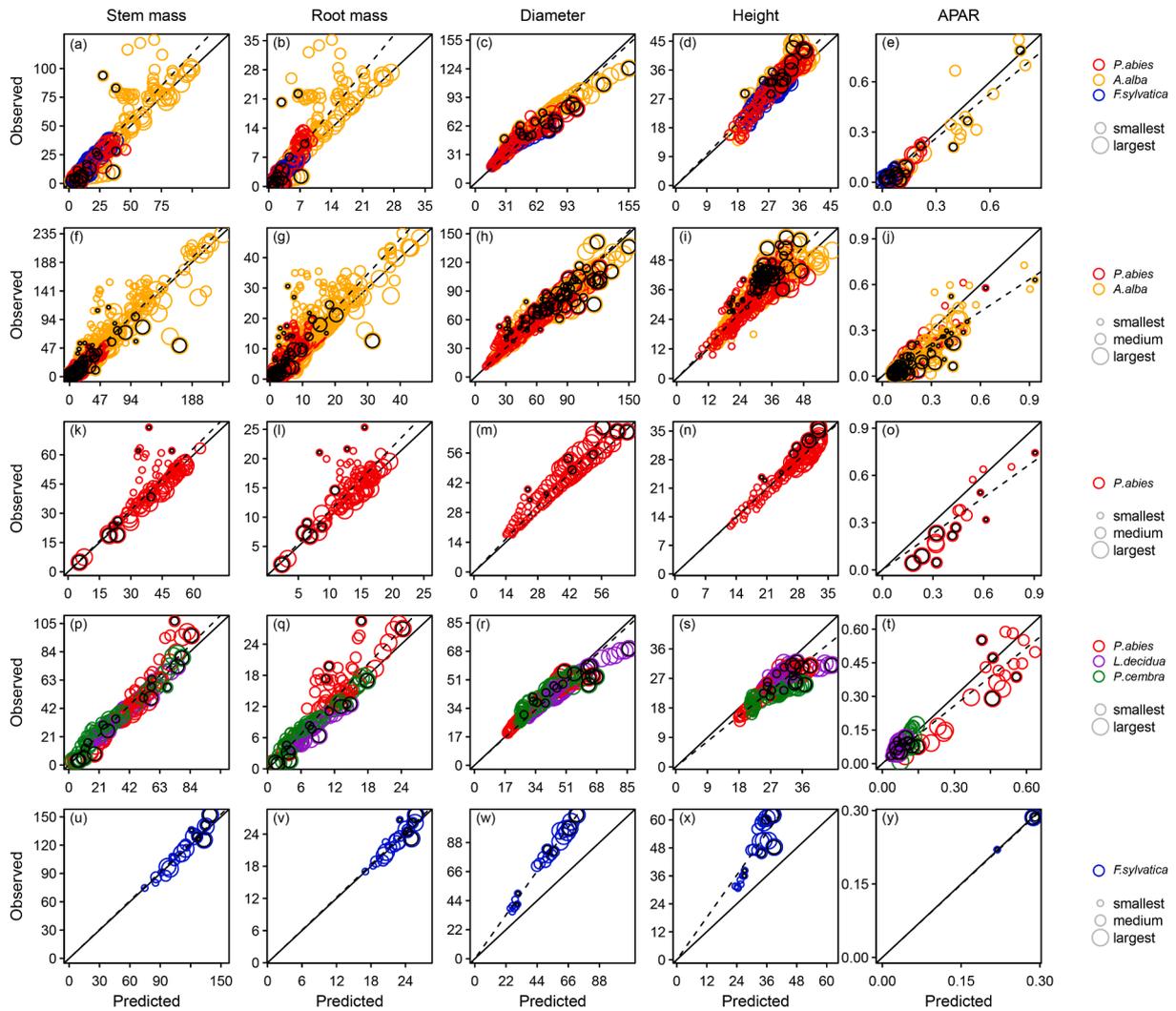
Forest type	Species	Size cohort	Mean O/P	e%	MAE%	RMSE	Slope	P-value	$R^2$
<b>Stem biomass (<math>\text{Mg ha}^{-1}</math>)</b>									
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Largest	11.3/15.3	35.6	35.6	29	0.8	0.017	0.94
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Medium	15.5/21	35	35.1	102	0.73	0.03	0.87
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Smallest	47.4/21.9	-53.7	53.7	854	1.98	< 0.001	0.95
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Largest	6.6/7.7	17.2	25	5	0.92	0.344	0.95
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Medium	14.7/16.1	9.9	14.5	11	0.88	0.027	0.98
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Smallest	25.8/21.1	-18.3	29.4	85	1.17	0.195	0.92
<i>A. alba</i> & <i>P. abies</i>	Total stand	Total stand	137.2/96.2	-29.9	29.9	1940	1.35	0.004	0.97
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Largest	6.1/16.6	170.2	170.2	232	0.3	0.009	0.91
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Smallest	67.9/29.4	-56.7	56.7	2128	2.34	0.127	0.91
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Largest	6.6/11.7	75.9	75.9	28	0.63	0.14	0.89
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Smallest	14.2/16.6	16.6	36.2	40	0.76	0.159	0.96
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	4.8/9.7	100.9	100.9	26	0.51	0.013	0.98
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	15/14.2	-4.9	8.3	2	1.06	0.307	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	Total stand	Total stand	182.4/97.5	-46.5	46.5	7285	1.86	0.013	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Largest	49.3/53	7.4	7.4	20	0.94	0.198	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Smallest	42.4/38	-10.2	10.2	23	1.1	0.122	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Largest	35.9/36.3	0.9	21.9	75	1.1	0.406	0.98
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Smallest	71.5/60.7	-15	17.1	376	1.21	0.33	0.96
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Largest	29.5/32	8.4	10.9	13	1.00	0.983	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Smallest	28.7/31	7.9	16.8	41	0.86	0.135	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	Total stand	Total stand	257.4/251	-2.5	7.7	595	1.06	0.342	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	138.8/136.3	-1.8	7.3	109	1.02	0.834	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Medium	135/130.6	-3.2	3.2	23	1.03	0.271	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	131.1/124.2	-5.3	6.3	116	1.05	0.572	0.99
<i>F. sylvatica</i>	Total stand	Total stand	404.9/391.1	-3.4	3.4	205	1.04	0.165	0.99
<i>P. abies</i>	<i>P. abies</i>	Largest	35.9/36.3	0.9	21.9	75	1.1	0.406	0.98
<i>P. abies</i>	<i>P. abies</i>	Medium	71.5/60.7	-15	17.1	376	1.21	0.33	0.96
<i>P. abies</i>	<i>P. abies</i>	Smallest	25.8/21.1	-18.3	29.4	85	1.17	0.195	0.92
<i>P. abies</i>	Total stand	Total stand	109.5/85.3	-22.1	22.1	706	1.25	0.192	0.98
<b>Absorption of photosynthetically active radiation (<math>\text{GJ m}^{-2} \text{ year}^{-1}</math>)</b>									
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Largest	0.02/0.1	349.6	349.6	0.0063	0.2	< 0.001	0.8
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Medium	0.06/0.1	84.9	84.9	0.0024	0.55	< 0.001	0.95
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Smallest	0.32/0.44	39	47.1	0.0271	0.72	0.004	0.94
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Largest	0.04/0.11	213.8	213.8	0.0076	0.29	< 0.001	0.8
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Medium	0.1/0.16	59	64.1	0.0058	0.62	0.005	0.87
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Smallest	0.24/0.31	31.2	33.1	0.0106	0.76	0.006	0.96
<i>A. alba</i> & <i>P. abies</i>	Total stand	Total stand	0.71/1.08	53.7	53.7	0.1636	0.65	< 0.001	0.97
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Largest	0.03/0.08	182.1	182.1	0.0034	0.34	0.041	0.75
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Smallest	0.45/0.55	20.5	23.2	0.0158	0.88	0.476	0.96
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Largest	0.05/0.11	113.3	113.3	0.0041	0.51	0.308	0.79
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Smallest	0.11/0.15	36.2	36.5	0.0027	0.8	0.419	0.9
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	0.02/0.03	29.5	57	0.0003	0.67	0.435	0.67
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	0.05/0.04	-19.5	19.5	0.0002	1.28	0.035	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	Total stand	Total stand	0.69/0.89	28.4	28.4	0.0399	0.8	0.097	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Largest	0.09/0.08	-15.5	15.5	0.0002	1.18	< 0.001	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Smallest	0.07/0.06	-17.7	19.6	0.0005	1.23	0.359	0.95
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Largest	0.14/0.23	62.8	62.8	0.0112	0.63	0.004	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Smallest	0.47/0.48	1.5	22.7	0.0161	0.95	0.82	0.93
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Largest	0.07/0.1	34.5	34.5	0.0008	0.73	0.052	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Smallest	0.09/0.1	8.5	14.8	0.0002	0.91	0.431	0.98
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	Total stand	Total stand	0.87/1.01	15.7	27.5	0.0617	0.84	0.318	0.96
<i>P. abies</i>	<i>P. abies</i>	Largest	0.14/0.23	62.8	62.8	0.0112	0.63	0.004	0.99
<i>P. abies</i>	<i>P. abies</i>	Medium	0.47/0.48	1.5	22.7	0.0161	0.95	0.82	0.93
<i>P. abies</i>	<i>P. abies</i>	Smallest	0.24/0.31	31.2	33.1	0.0106	0.76	0.006	0.96
<i>P. abies</i>	Total stand	Total stand	0.74/1.31	78.2	78.2	0.3634	0.57	0.067	0.92

inventory. Two size classes were used in plots containing three species, while three size classes were used in plots containing one or two species. In some plots, up to 10% of the basal area consisted of other species, but these species were not included in the simulation, and their basal area was allocated to that of the dominant species.

3-PG does not directly simulate regeneration. However, it generally took a longer period than the simulation length for regeneration of any species to develop a density of a similar size (number of trees and basal area) as the smallest of the initial 2 or 3 size classes. Furthermore, this regeneration had a negligible influence on the growth of other size

classes. Therefore, no new size classes were added to the simulations.

The model was initialised with cohort-specific stem biomass, foliage biomass, root biomass, age, and tree density ( $\text{trees ha}^{-1}$ ) in the first inventory (Fig. 1). Stem, root and foliage biomass were calculated for each tree using equations developed for European forests (Forrester et al., 2017b), and summed to obtain stand-level  $\text{Mg dry matter ha}^{-1}$ . To define the thinning treatments, 3-PG requires, for each cohort, the age and the retained tree density (not retained basal area, volume, mean tree size), which were obtained from the inventory data. Therefore, the simulated thinning was based on the plenter thinning except that it was



**Fig. 2.** Comparison of observed and predicted stem biomass ( $Mg\ ha^{-1}$ ; a,e,i), root biomass ( $Mg\ ha^{-1}$ ; b,f,j), mean diameter (cm; c,g,k), mean height (m; d,h,i) and absorbed photosynthetically active radiation (APAR,  $GJ\ m^{-2}\ year^{-1}$ ; a,b,c) for five forest types. The APAR “observations” were calculated using the Maestra model. The simulations ran for 15 to 112 years (first and last inventories shown in Table 1), and the final year for each simulation (used for statistics in Table 2 & A2) contains a black circle within the relevant coloured circle. The smallest, medium and largest indicate different size classes. The solid lines are 1:1 lines and the dashed lines are lines fitted to the data that pass through the origin.

applied to several size classes as opposed to many individual trees. To increase the precision of thinning inputs, the 3-PG also allows an additional thinning related input, which is the fraction of mean single-tree foliage, stem or root biomass lost per thinned tree of the given cohort. These were calculated for each plot, inventory and cohort as the ratio of the proportion of stand foliage, stem, or root biomass of thinned trees and the proportion of the number of trees lost due to thinning (Landsberg et al., 2005; Forrester, 2020).

2.6. Evaluation of model performance

Even if total stand outputs are accurately predicted, this provides no evidence that the model is accurate for different cohorts; over prediction of small or young cohorts could be compensated by under prediction of large or old cohorts, or vice versa. Therefore, each cohort, as well as the total stand, were considered.

The predictions and observations were compared for the final inventory of each plot. The mean number of years since the simulation began was 79.5 years, the maximum was 112 years, and the minimum was 15 years. The predictions were compared with observations by calculating the relative average error (average bias, e%, Eq. (1)), and the

relative mean absolute error (MAE%, Eq. (2)).

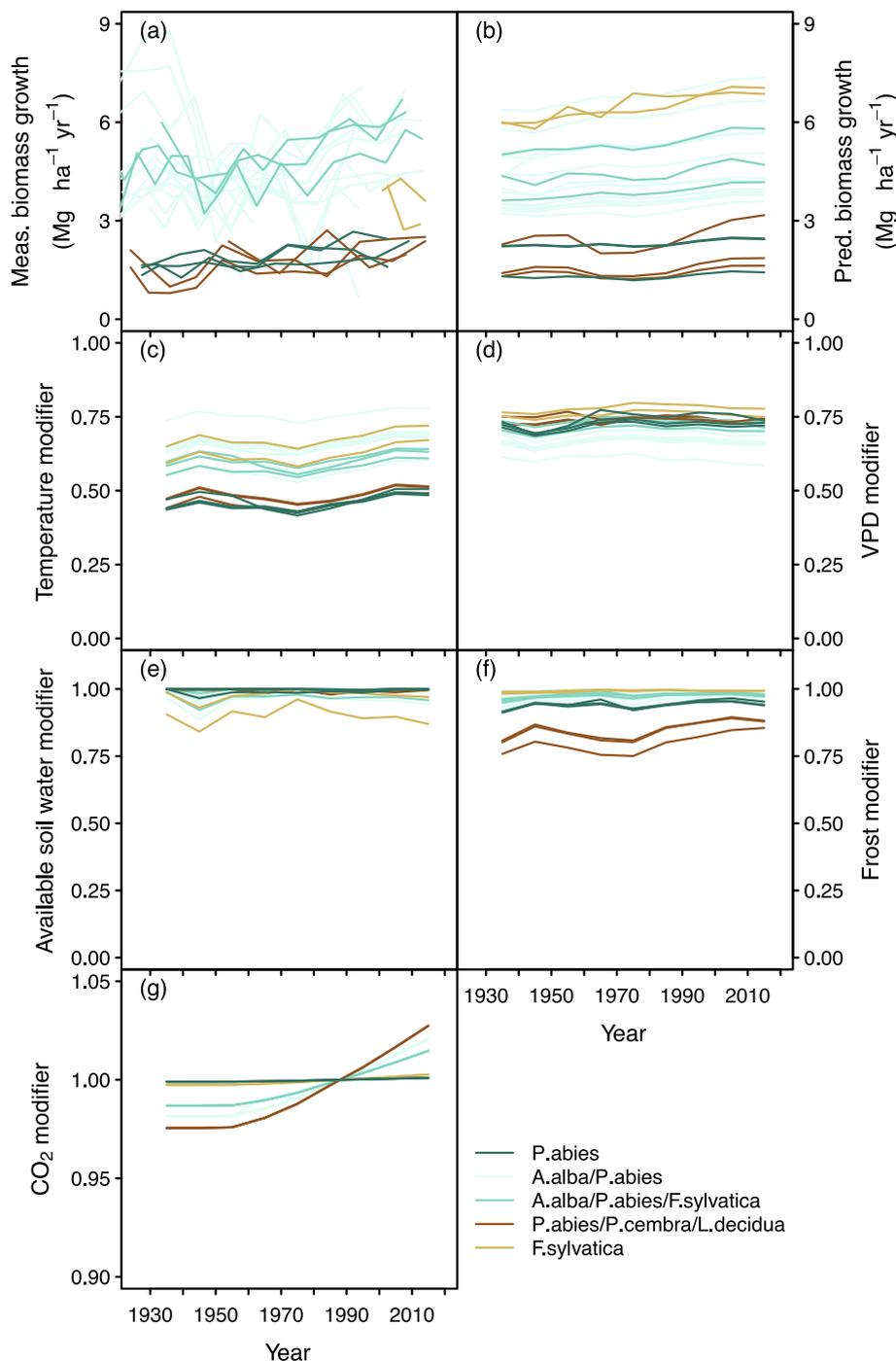
$$e\% = \frac{100 P - O}{O} \tag{1}$$

$$MAE\% = \frac{100 ((\sum_{i=1}^n |P_i - O_i|)/n)}{O} \tag{2}$$

where  $O_i$  are the observed values,  $P_i$  are the predicted values from 3-PG, and  $O$  and  $P$  are the means. All statistical analyses were performed using R 3.6.1 (R Core Team, 2019).

2.7. 3-PG simulations to examine the effect of climate (1930–2018)

After validating 3-PG, the second objective was to examine how the growth of the 23 plots could have been influenced by changes in climate since 1930. For each plot, a separate simulation was conducted for each decade (1930–1939, 1940–1949 ... 2000–2009, 2010–2018). The only input that varied between decades was the actual climate; for each decade, the same stand structure and thinning was used as input. This was the structure recorded the first time the plot was measured, and the simulated thinning treatment was the actual thinning done during the



**Fig. 3.** Measured stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric  $\text{CO}_2$  (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and  $>1$  (only for  $\text{CO}_2$  modifier) indicates enhanced growth. All simulated data (c–g) are for the growing season only. The same patterns for individual species are shown in Figs. A1-5.

first decade when that plot was monitored.

### 3. Results

#### 3.1. Validation

For all species and size cohorts, 3-PG produced accurate predictions of root biomass, stem biomass and outputs derived from it such as mean diameter, basal area and height, which were all highly correlated with the observed values ( $R^2 > 0.86$ , Tables 2 & A2; Fig. 2). Some cohorts were predicted poorly, such as the larger *A. alba* cohort of one of the mixtures, or the smallest *P. abies* cohorts in the *P. abies* monocultures (Fig. 2). But on average, the slope was close to 1 (averaged 1.13) and the  $e\%$  was nearly 0 (averaged  $-1.2\%$ ).

While the APAR predictions were also highly correlated with the values predicted using the Maestra model (mean  $R^2 = 0.74$ , Table 2, Fig. 2), they were less precise and more biased than the biomass and tree size variables. On average, 3-PG overestimated APAR (compared with Maestra) (average  $e\% = 0.59$ , average MAE = 68, Slope = 0.74). Predictions of leaf area index were consistent with expectations for these forest types, and changed very little through time (Fig. A6).

#### 3.2. Modifications made to 3-PG

The three modifications made to 3-PG to improve the growth, APAR or mortality predictions of the smallest size classes all had negligible effects on predictions. The first modification, to improve APAR, did result in a higher SLA and leaf area of the smallest size classes but did not

**Table 3**

The percent increase in stem biomass increment in the 2010s compared with the 1930s and 1960s as predicted using 3-PG. Stand density and thinning were held constant for each plot and decade and hence these temporal changes were only due to changes in climate.

Forest type (dominant species)	Species	Change (%) since	
		1930s	1960s
<i>F. sylvatica</i>	Total stand	16	12
<i>A. alba</i> & <i>P. abies</i>	Total stand	14	7
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	Total stand	13	8
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	Total stand	33	46
<i>P. abies</i>	Total stand	10	8
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	7	2
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	3	1
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	12	18
<i>P. abies</i>	<i>P. abies</i>	10	8
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	16	8
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	15	9
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	51	66
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	103	165
<i>F. sylvatica</i>	<i>F. sylvatica</i>	16	12
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	11	13

increase APAR or growth, because APAR could not increase much due to the lower light availability at the level of the shortest size classes. The second modification, to adjust the APAR of smaller size classes in relation to an aggregation index was also not useful because there was no significant correlation between the bias of APAR predictions and the aggregation index. The third modification to increase mortality as the dominance of a size class declines, as defined by its relative height, did not lead to additional mortality in the *F. sylvatica* monocultures and was therefore not retained in the model. Since the three modifications had so little influence on the outputs, the results are not shown.

### 3.3. Effect of climate on stem biomass growth (1930–2018)

There was a general trend of increasing simulated stem biomass growth from the 1930s to the 2010s (Fig. 3; Table 3). The fluctuations within this general trend were often due to growing season temperature limitations (1930s and 1970s). There were also fluctuations due to frost during the growing season for *P. abies*/*P. cembra*/*L. decidua* mixtures (1930s and 1970s) and due to soil water limitations during the growing season for one of the *F. sylvatica* plots (6002000). *A. alba*, in contrast to all other species, was also limited by vapour pressure deficit in both forest types where it occurred. This vapour pressure deficit limitation was similar or even slightly more extreme than the temperature limitation for *A. alba* (Fig. A1). Biomass growth of *A. alba*, *L. decidua*, and *P. cembra* increased slightly (up to 5%) with increasing CO<sub>2</sub> from about the 1990 s, whereas CO<sub>2</sub> had very little influence on *F. sylvatica* or *P. abies* (Figs. 3 & A1–A5). Despite large differences in productivity between sites, which were typically much larger than differences due to inter-decadal climatic variability, the increases and decreases in growth due to climate often occurred in the same decades for different sites.

## 4. Discussion

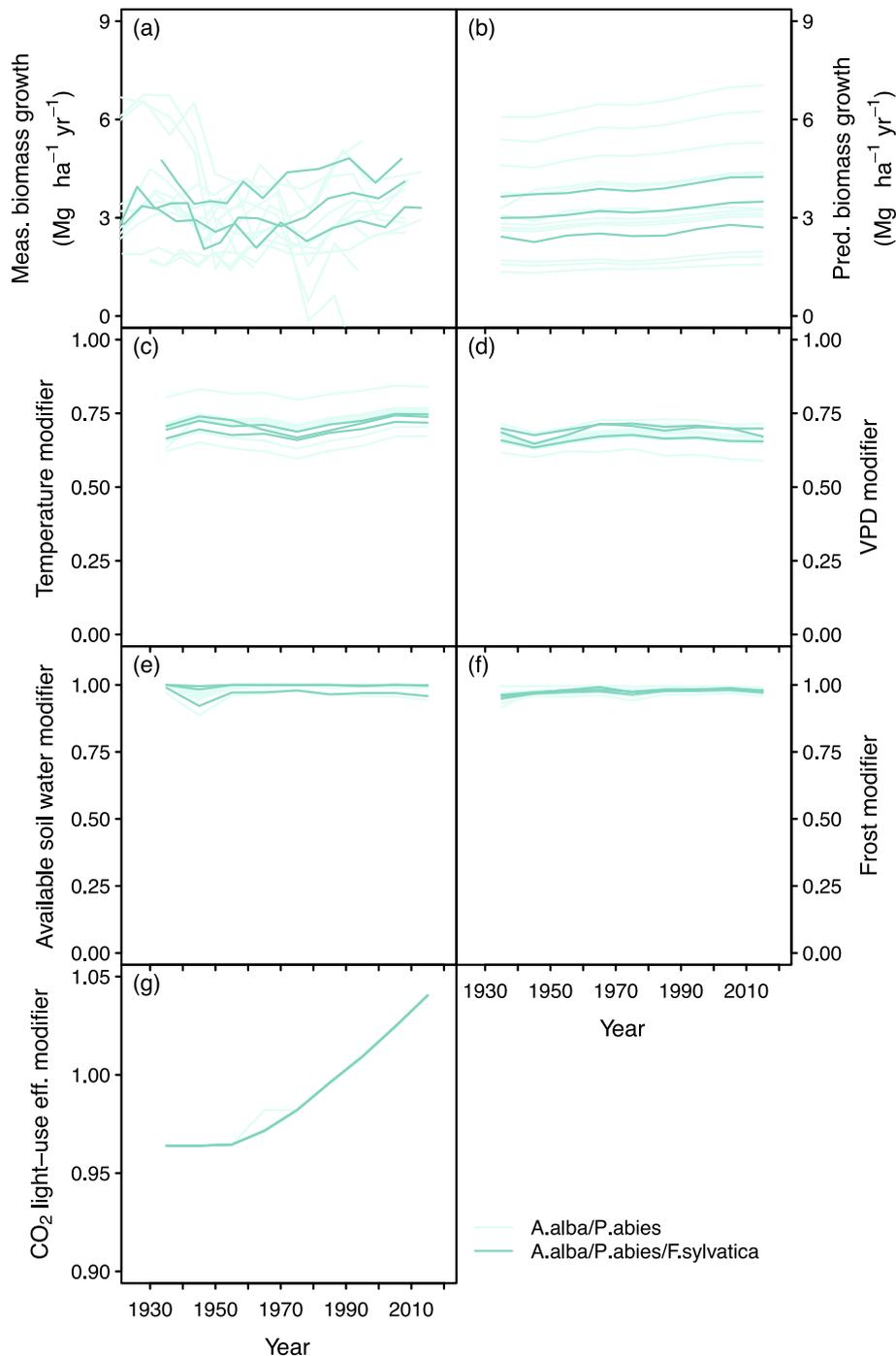
3-PG accurately predicted the growth, biomass partitioning, and light absorption of different size cohorts and species within five types of forests. Several studies have suggested that tree-level models are required to realistically examine the effects of silviculture on forest growth (Seidl et al., 2005; Jonard et al., 2020). However, we know of no studies that have demonstrated this by comparing tree- and stand-level model predictions for uneven-aged forests, and our results suggest that the accuracy of 3-PG is relatively high.

Few studies about tree-level models report results at the tree level. This suggests that stand-level dynamics are often the main interest, even when using tree-level models. Similarly, few studies about tree-level models validate tree-level outputs (Korol et al., 1995; Grote and Pretzsch, 2002; Brunner et al., 2006; Simioni et al., 2016; Jonard et al., 2020), as opposed to stand-level outputs. Validation of tree-level outputs is necessary to determine whether different tree sizes are predicted accurately or whether some sizes are under predicted while others are over predicted, thereby giving a false impression that the model is performing well. By considering multiple size classes and species, we showed that 3-PG can predict the growth of different sizes and species within uneven-aged mixed-species forests.

The predictions of 3-PG were relatively accurate despite the fact that 3-PG does not account for several processes that strongly influence individual tree growth, e.g. spatial locations of trees (Biging and Dobbertin, 1992), or the spatial and temporal heterogeneity of micro-sites (Schume et al., 2004; Hodge, 2006; Gómez-Aparicio and Canham, 2008; Boyden et al., 2012; Uriarte et al., 2015; Christina et al., 2017) and hence spatial distributions of resources that strongly influence tree growth. The accuracy of stand-level process based models for stands that do not have uniform spatial distributions of tree locations or tree sizes suggests that these complex processes can be simplified at the stand level without losing much accuracy. This avoids a potential problem faced by tree-level models with regards to processes that strongly influence tree-level growth, and are therefore important to consider at the tree level, but which are difficult to model at the tree level. For example, the spatial locations of trees relative to the spatial heterogeneity of micro-sites can strongly influence tree growth but these are not necessarily simple to model, and their effects are further complicated because of the plasticity of tree crown (and root) positioning relative to the base of the tree trunk (Stiell, 1982; Umeki, 1997; Brisson, 2001; Longuetaud et al., 2013; Lee and García, 2016), and the complexity of predicting where individual trees are actually competing for resources within the canopy volume and soil rooting volume (e.g. Schume et al., 2004; Zapater et al., 2011; Christina et al., 2017).

A potential problem for stand-level models is processes that significantly influence stand-level growth, but are difficult to model at the stand level. While many tree interactions depend on tree sizes or spatial locations of trees (Forrester, 2019), it is not clear which of these have effects that cannot be summarised at the stand level, and the results of this study indicate that there may be few such processes in these forests. One example of a potentially problematic situation for stand-level models is interactions for light that depend on tree size where the mean size of species or age class A is larger than that of B, but some individuals of B are still larger than some individuals of A. In this case, the larger individuals of B are likely to be successful (grow faster and survive) at the expense of smaller individuals of A, even though the mean sizes of A (as modelled at the stand level) are larger than B. This could distort interactions for light and may require stand level models to predict size distributions (an example using 3-PG is Landsberg et al., 2005) to correct for such distortions.

It is important to note that we are not suggesting that tree-level models cannot be more accurate than stand-level models when predicting stand growth or associated physiological processes (e.g. water balance, carbon balance), but we are suggesting that tree-level models have not yet been shown to be more accurate at the stand level for forests such as those examined in this study. For tree-level models to be more accurate, the improvements in accuracy resulting from the higher resolution would need to be greater than the error associated with the additional calculations at the tree level that are required to account for all factors that significantly influence individual tree growth and mortality, or there would need to be a tree-level process that strongly



**Fig. A1.** Measured *A. alba* stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric CO<sub>2</sub> (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and >1 (only for CO<sub>2</sub> modifier) indicates enhanced growth. All simulated data (c-g) are for the growing season only.

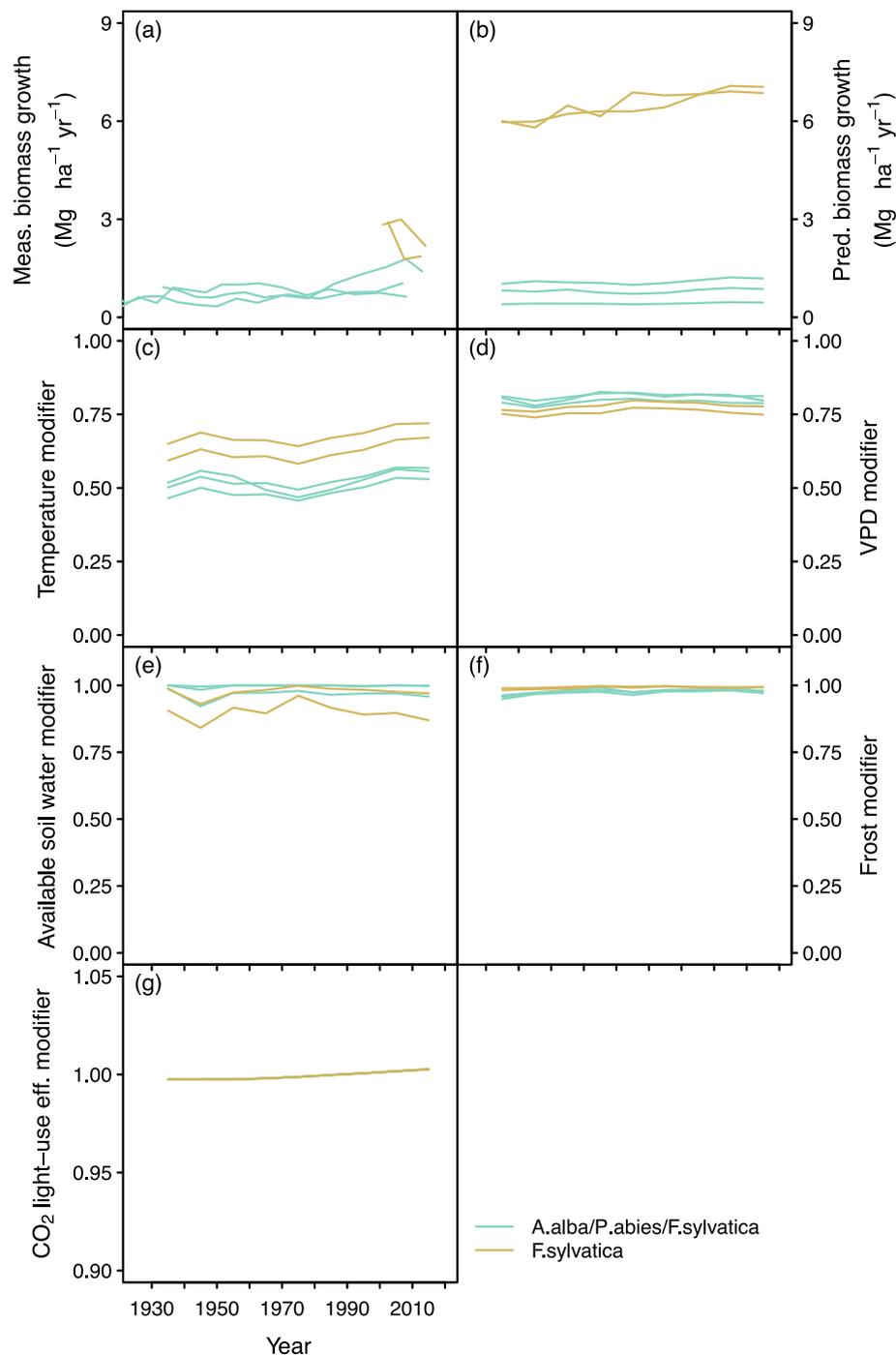
influences stand growth but cannot be modelled accurately at the stand level.

#### 4.1. Effects of climate change on growth since the 1930s

There was a general trend of increasing simulated stem biomass growth since the 1930s for all species compositions. The increase in total stand biomass growth averaged 16% since the 1960s, which is similar to a 10–30% increase in volume growth for monospecific even-aged *P. abies* or *F. sylvatica* forests in Germany for the same period (Pretzsch et al., 2014), but contrasts with no change in stand volume

growth since the 1970s in mountain forests containing *F. sylvatica*, *P. abies*, and *A. alba* in Europe (Hilmers et al., 2019). In our study, the most growth-limiting climatic factor was usually temperature, except for *A. alba* which was strongly limited by vapour pressure deficit. Similarly, the growth increase in monospecific even-aged *P. abies* or *F. sylvatica* forests in Germany was largely due to temperature, and extended growing seasons (Pretzsch et al., 2014). There was also a minor positive effect of increasing atmospheric CO<sub>2</sub> from the 1990s for *A. alba*, *L. decidua*, and *P. cembra*.

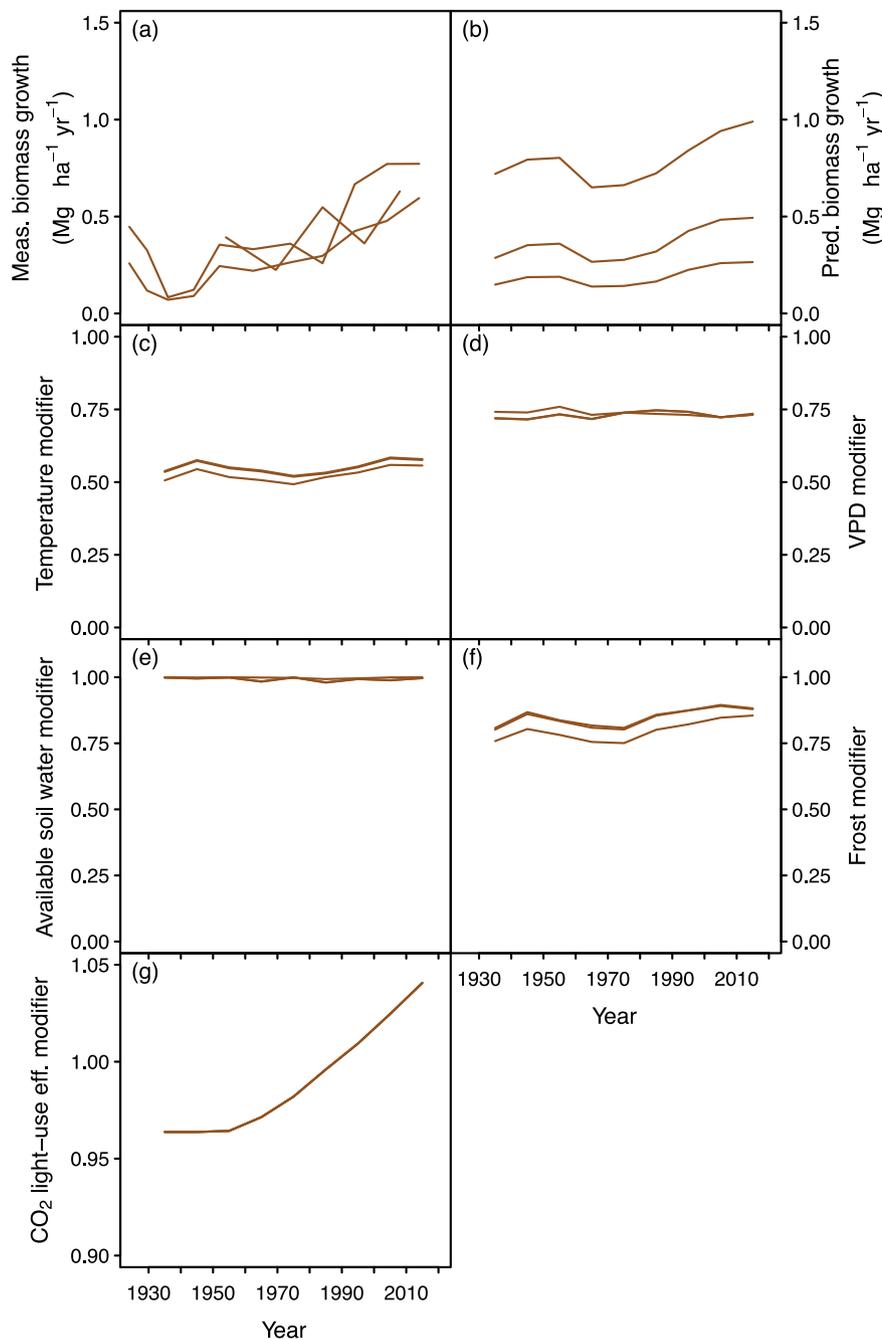
Few studies have focused on the long-term stand growth response to climate of plenter forests. In mixed *A. alba*/*P. abies* plenter forests in



**Fig. A2.** Measured *F. sylvatica* stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric CO<sub>2</sub> (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and >1 (only for CO<sub>2</sub> modifier) indicates enhanced growth. All simulated data (c–g) are for the growing season only.

southwestern Germany, stand volume growth dropped during the 1970s but increased again during the 1980s (Spiecker, 1986, 1991). In those forests, individual tree growth was strongly correlated with precipitation during the growing season. In contrast, soil water availability was less important in the Swiss forests of this study. Only one *F. sylvatica* plot in the north west of Switzerland was water limited in the 1940s (6002000), although after almost no water limitation in the 1970s the stand has become progressively more water limited since.

The comparison of stand growth responses to climate between this study and others is complicated by potential confounding effects of stand structural characteristics including stand density, species composition, size distributions, and size-growth relationships, which can all strongly influence stand growth (Forrester, 2019) and can continuously change, even in plenter forests (O'Hara et al., 2007). Distinguishing different structural and climatic effects is not only important for understanding forest ecology but also for management. When the increase



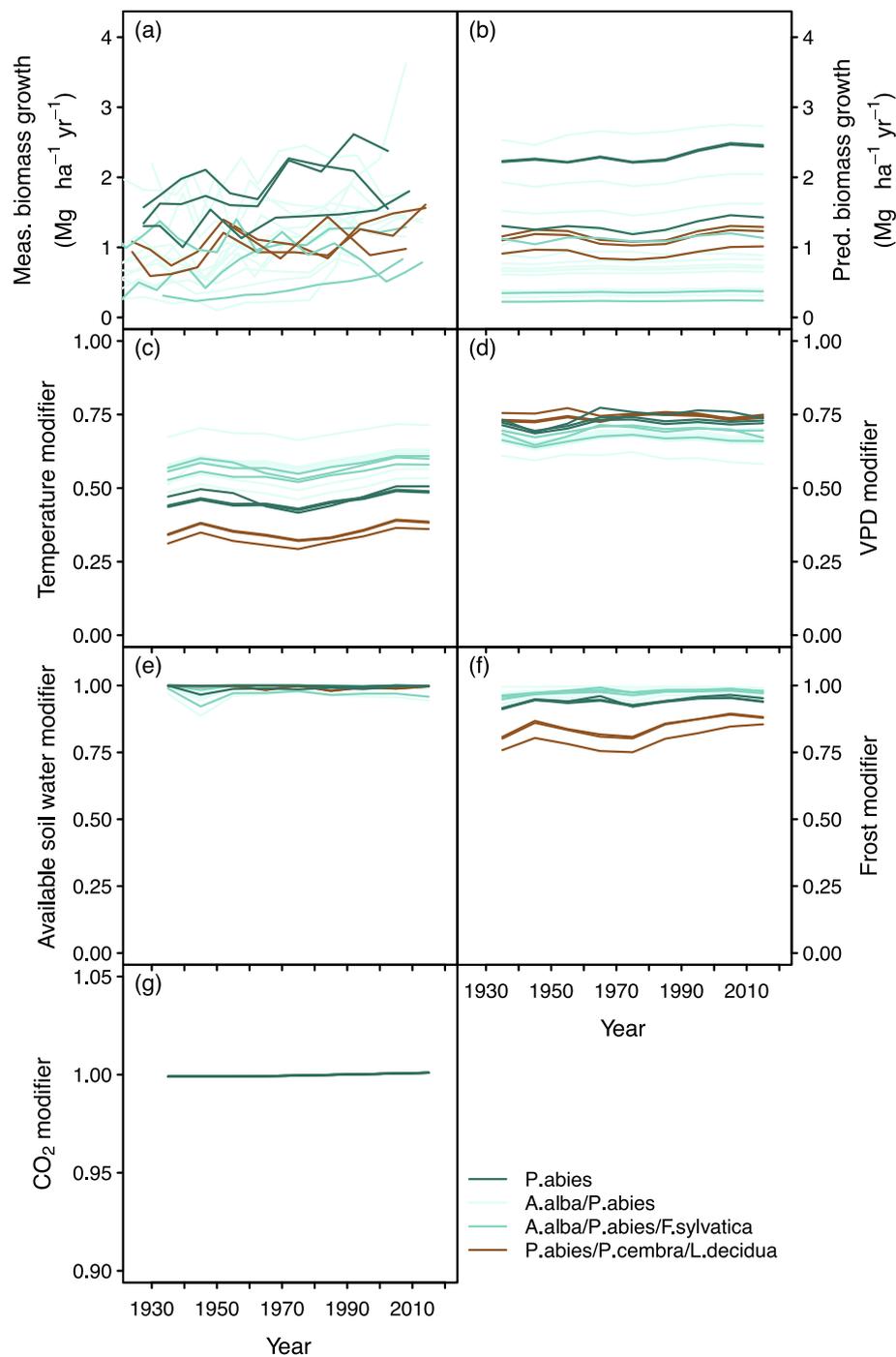
**Fig. A3.** Measured *L. decidua* stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric CO<sub>2</sub> (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and >1 (only for CO<sub>2</sub> modifier) indicates enhanced growth. All simulated data (c-g) are for the growing season only.

in growth is caused by changes in climate, then the thinning intensity or frequency needs to be increased to maintain an appropriate range of stand density for regeneration. Process-based models such as 3-PG may be used to distinguish the effects of different factors, such as stand structure, climate and edaphic characteristics, to determine whether modifications in thinning intensity or frequency might be required in the future.

#### 4.2. Unresolved inaccuracies of predictions

There were several species-cohort combinations where predictions were significantly different to the observations (P-values in Table 2) indicating biased predictions. In the two *F. sylvatica* dominated plots, 3-

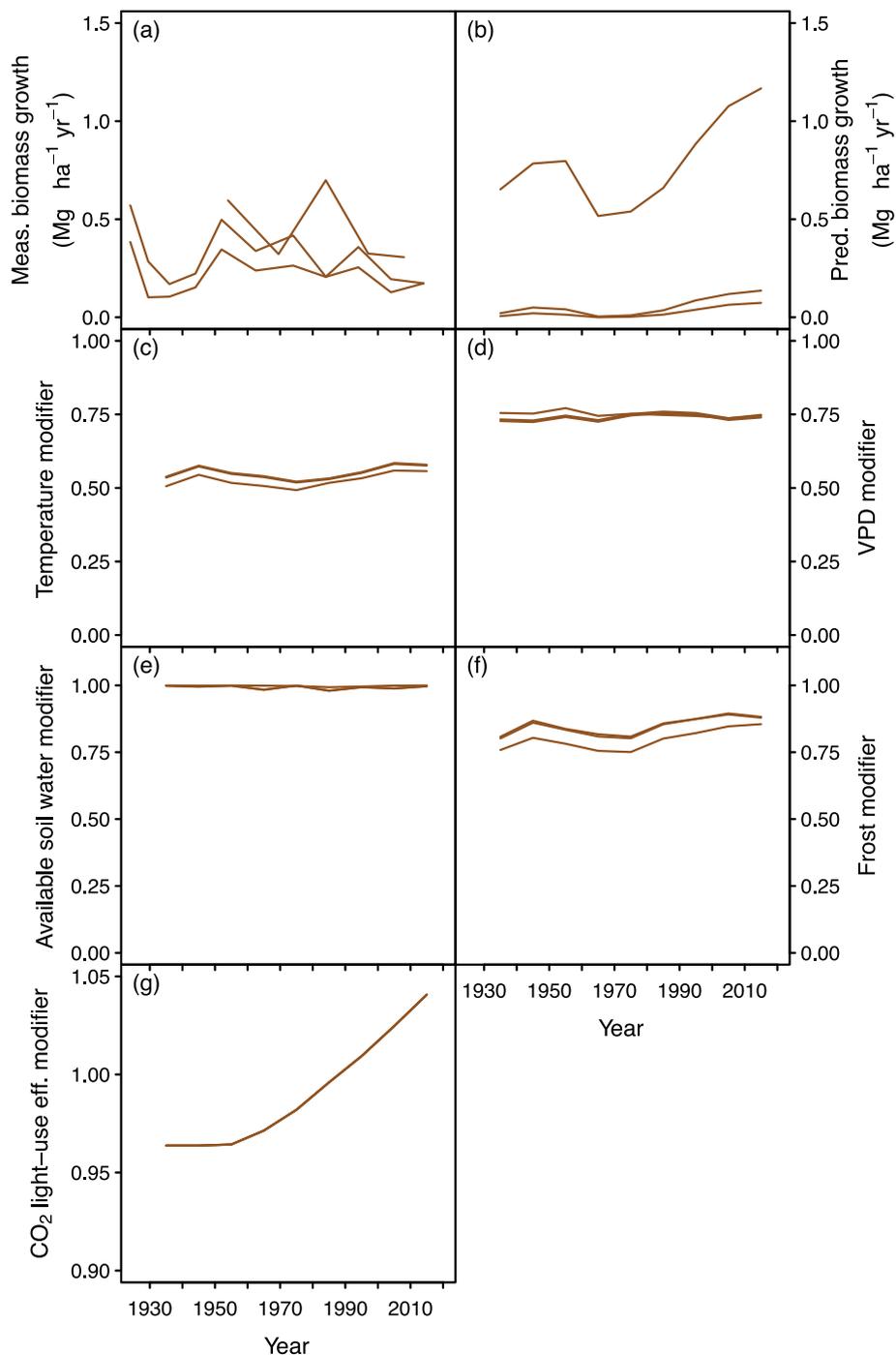
PG underestimated the mean diameter and mean height. This resulted from underestimates of mortality, which indirectly led to higher mean tree sizes for a given stand stem biomass. This issue was not solved by modifying the self-thinning calculations to be dependent on relative height, and thereby to account for shading as well as stand density. Furthermore, changes in climate (or density-independent mortality) do not appear to be large enough to have caused this underestimated mortality (Forrester et al., 2021). Thomas et al. (2017) found that different self-thinning parameters were required for different *Pinus taeda* experiments when using Bayesian inference to calibrate 3-PG. Similarly, values of self-thinning parameters calculated from many published studies, based on large data sets, did not always correspond well to those obtained using Bayesian calibration of 3-PG for several central European



**Fig. A4.** Measured *P. abies* stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric CO<sub>2</sub> (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and >1 (only for CO<sub>2</sub> modifier) indicates enhanced growth. All simulated data (c–g) are for the growing season only.

species, including *F. sylvatica* (Forrester et al., 2021). This suggests that the self-thinning parameters of 3-PG may quantify more than the self-thinning relationship and that improvements to 3-PG may be possible in relation to quantifying the carrying capacity of a site (Forrester et al., 2021).

3-PG underestimated the growth of the smallest cohorts in some of the plots containing *A. alba* or *P. abies*. This did not appear to result from an underestimation of light absorption by the shorter cohorts because the modifications made to improve this did not resolve the problem. Further work will be required to determine what could have caused this



**Fig. A5.** Measured *P. cembra* stem biomass growth (a), simulated stem biomass growth (mean for each decade) (b), and the growth limitation caused by temperature (c), vapour pressure deficit (d), soil water availability (e), frost (f), and atmospheric CO<sub>2</sub> (g), where 1 indicates no limitation, 0 indicates extreme limitation where no growth occurs, and >1 (only for CO<sub>2</sub> modifier) indicates enhanced growth. All simulated data (c–g) are for the growing season only.

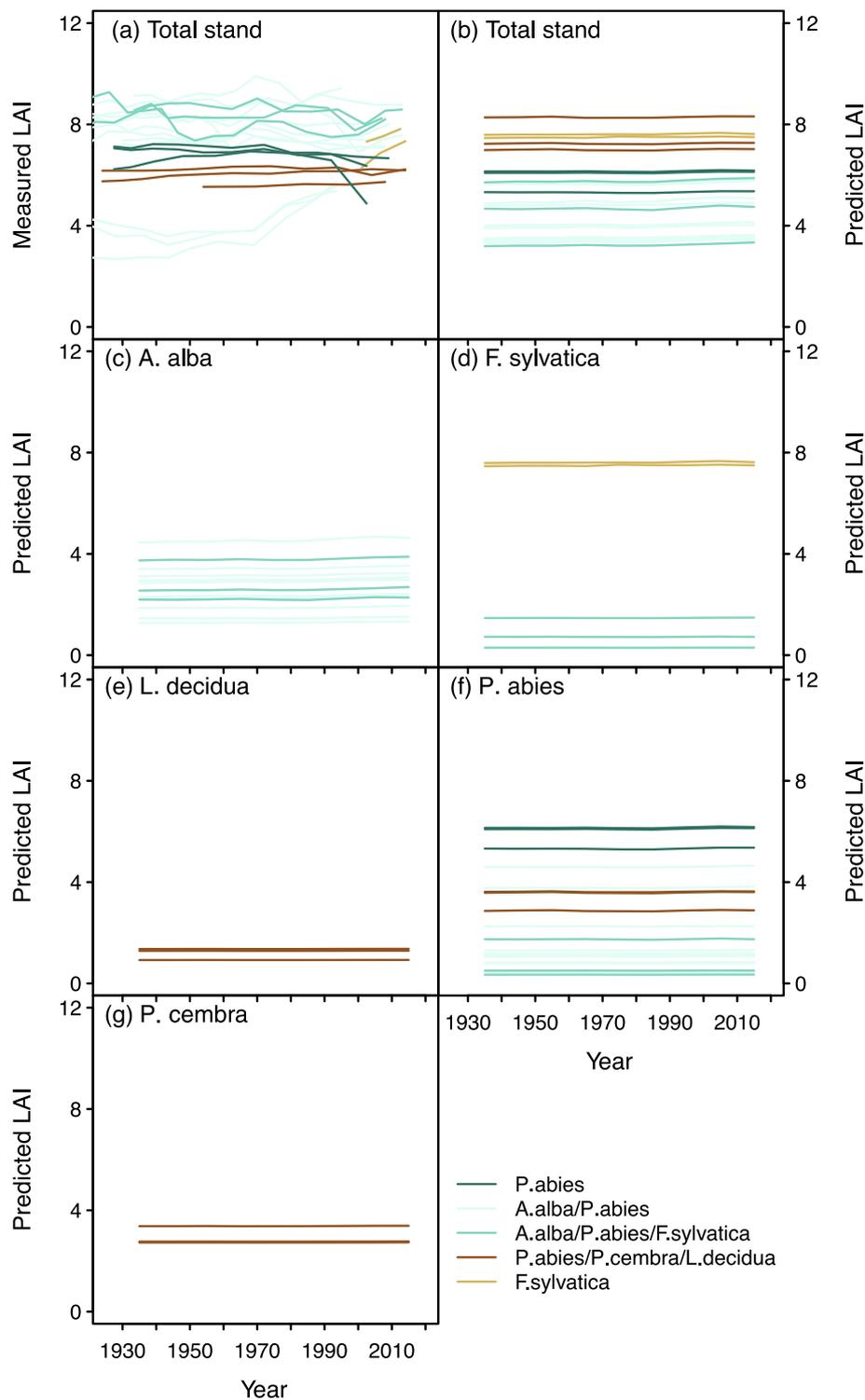
underestimate of growth.

### 5. Conclusions

3-PG accurately predicted the biomass, biomass partitioning, and APAR of different species and tree size classes within forests of five different species compositions. Accuracy may be increased by improving

the density-dependent mortality calculations and identifying the cause of the underestimated growth of the smallest cohorts in some of the plots containing *A. alba* or *P. abies*.

Few studies have examined the long-term influence climate change has had on the growth of plenter forests, and this is often hampered by confounding effects of changes in stand structure and management. 3-PG was used to remove these confounding effects and to show that the



**Fig. A6.** Estimated total stand leaf area index (LAI) using allometric equations (a), simulated total stand LAI (mean for each decade) (b), and simulated LAI of each species in the stands where they occurred (c-g).

growth of all five types of forests has increased since the 1930s. The growth was largely influenced by temperature, and in the case of *A. alba*, was largely influenced by vapour pressure deficit.

**CRedit authorship contribution statement**

**David I. Forrester:** Conceptualization, Data curation, Methodology, Formal analysis, Writing - original draft. **Amanda S. Mathys:** Conceptualization, Writing - review & editing. **Golo Stadelmann:**

**Table A1**Soil water availability, soil texture, species-specific soil fertility values (FR and  $f_{NO}$ ), the first year of the validation simulations, and the ages of each cohort at the first year of the simulation.

Plot	Maximum available soil water (mm)	Soil texture	FR					fNO					1 <sup>st</sup> year of simulation	Ages at beginning of simulation (oldest/intermediate/youngest cohorts; years)						
			<i>Aalb</i>	<i>Fsyl</i>	<i>Ldec</i>	<i>Pabi</i>	<i>Pcem</i>	<i>Aalb</i>	<i>Fsyl</i>	<i>Ldec</i>	<i>Pabi</i>	<i>Pcem</i>		<i>Aalb</i>	<i>Fsyl</i>	<i>Ldec</i>	<i>Pabi</i>	<i>Pcem</i>		
1,015,001	161	Clay loam	0.8			0.5		0.6			0.05			1905	144/109/ 30				121/70/ 30	
1,015,002	161	Clay loam	0.5			0.4		0.6			0.05			1905	142/117/ 30				92/61/30	
1,015,003	161	Clay loam	0.5			0.45		0.6			0.05			1905	118/99/ 30				106/82/ 30	
1,019,000	161	Clay loam	0.6			0.5		0.6			0.05			1908	168/113/ 30				119/90/ 30	
1,027,000	161	Clay loam	0.5			0.6		0.6			0.05			1912	135/103/ 30				102/78/ 30	
1,028,000	161	Clay loam	0.75	0.5		0.35		0.05	0.05		0.05			1912	139/96	160/120			95/62	
1,030,001	161	Clay loam	0.4			1		0.05			0.05			1914	153/92/ 40				123/59/ 40	
1,030,002	161	Clay loam	1			0.35		0.6			0.05			1914	145/92/ 40				158/89/ 40	
1,030,003	161	Clay loam	1			0.3		0.05			0.05			1914	101/72/ 40				101/65/ 40	
1,031,000	171	Clay loam	0.4			0.7		0.6			0.05			1918	148/125/ 30				92/59/30	
1,033,000	144	Sandy loam			0.2	0.9	0.2			0.3	0.05	0.3		1921				172/ 127	233/159	198/ 131
1,034,000	144	Sandy loam			0.45	0.9	0.4			0.05	0.05	0.05		1921				154/ 107	190/139	269/ 147
1,041,000	133	Sandy loam	0.8			0.6		0.6			0.05			1928	148/113/ 40				158/116/ 40	
1,042,000	133	Sandy loam	1			0.65		0.05			0.05			1928	132/106/ 40				117/91/ 40	
1,046,000	169	Clay loam	0.8			0.5		0.6			0.05			1931	150/126/ 50				152/131/ 50	
2,035,000	117	Sandy loam	1	0.8		0.75		0.05	0.05		0.05			1913	158/116	88/78			131/107	
2,047,000	161	Clay loam	1	0.8		0.55		0.05	0.05		0.05			1931	181/135	116/84			155/102	
5,003,000	119	Sandy			0.7	1	0.8			0.6	0.6	0.6		1946			340/ 250		312/182	383/ 207
6,002,000	150	Sandy		0.8						0.6				1999				111/76/ 20		
6,003,000	160	Clay loam		0.8						0.6				2000				119/115/ 20		
21,293,001	151	Sandy loam						0.6					0.05	1925					194/160/ 80	
21,293,002	151	Sandy loam						0.6					0.05	1925					199/153/ 80	
21,294,000	116	Sandy loam					0.3						0.05	1925					205/151/ 70	

Table A2

Statistical information, describing the relationships between predicted and observed root mass, diameter, basal area and height for each size cohort, species, and the total stand. The statistical information includes the mean observed (O) and predicted (P) values, the relative average error (e%), the relative mean absolute error (MAE %), the square root of the mean square error (RMSE), the slope of the relationship forced through the origin, the P-value for the test of whether the slope of the relationship is significantly different from 1, and the R<sup>2</sup> values. Foliage growth and root growth are not considered due to the low reliability of calculating those variables using allometric equations. Statistical information for stem mass and APAR are shown in Table 2.

Forest type	Species	Size cohort	Mean O/P	e%	MAE%	RMSE	Slope	P-value	R <sup>2</sup>
<b>Root biomass (Mg ha<sup>-1</sup>)</b>									
A. alba & P. abies	A. alba	Largest	2.6/3	17.5	23.3	1	0.94	0.381	0.96
A. alba & P. abies	A. alba	Medium	2.6/2.7	3.9	13.9	0	0.96	0.389	0.99
A. alba & P. abies	A. alba	Smallest	13.3/3.6	-72.8	72.8	135	3.37	0.003	0.82
A. alba & P. abies	P. abies	Largest	2.1/1.9	-9.3	28.6	1	1.21	0.045	0.96
A. alba & P. abies	P. abies	Medium	4/3.3	-19.3	23.4	1	1.23	0.007	0.98
A. alba & P. abies	P. abies	Smallest	8.8/4.2	-52.5	53	37	2.01	0.008	0.86
A. alba & P. abies	Total stand	Total stand	41.3/16.5	-60	60	718	1.86	0.055	0.75
A. alba, P. abies & F. sylvatica	A. alba	Largest	1.6/3.3	108.8	109	8	0.37	0.025	0.87
A. alba, P. abies & F. sylvatica	A. alba	Smallest	16.5/4.7	-71.4	71.4	183	3.23	0.182	0.81
A. alba, P. abies & F. sylvatica	P. abies	Largest	2.1/3.1	44.7	71.1	3	0.68	0.438	0.68
A. alba, P. abies & F. sylvatica	P. abies	Smallest	4.3/3.4	-21.1	29.1	2	1.25	0.17	0.98
A. alba, P. abies & F. sylvatica	F. sylvatica	Largest	0.7/1.2	66.5	66.5	0	0.55	0.1	0.86
A. alba, P. abies & F. sylvatica	F. sylvatica	Smallest	2.6/1.7	-35.5	39.8	2	1.64	0.073	0.98
A. alba, P. abies & F. sylvatica	Total stand	Total stand	45.6/17.1	-62.5	62.5	815	2.52	0.036	0.97
L. decidua, P. abies & P. cembra	L. decidua	Largest	10.3/12.4	20	20	5	0.84	0.097	0.99
L. decidua, P. abies & P. cembra	L. decidua	Smallest	9/8.9	-1	4.4	0	1.01	0.872	0.99
L. decidua, P. abies & P. cembra	P. abies	Largest	10.5/9.8	-6.2	11.1	3	1.1	0.074	0.99
L. decidua, P. abies & P. cembra	P. abies	Smallest	21.8/12.8	-41.5	41.5	86	1.71	0.002	0.99
L. decidua, P. abies & P. cembra	P. cembra	Largest	6.5/7.9	21.5	21.5	2	0.92	0.464	0.98
L. decidua, P. abies & P. cembra	P. cembra	Smallest	6.8/7.3	6.7	17.6	2	0.89	0.266	0.99
L. decidua, P. abies & P. cembra	Total stand	Total stand	64.9/59	-9	9	49	1.1	0.086	0.99
F. sylvatica	F. sylvatica	Largest	25.4/25.4	0.2	7.3	3	1.00	0.991	0.99
F. sylvatica	F. sylvatica	Medium	25.2/24.8	-1.6	1.7	0	1.02	0.515	0.99
F. sylvatica	F. sylvatica	Smallest	25.4/23.4	-7.8	7.8	7	1.08	0.46	0.99
F. sylvatica	Total stand	Total stand	76/73.7	-3	3	6	1.03	0.149	0.99
P. abies	P. abies	Largest	10.5/9.8	-6.2	11.1	3	1.1	0.074	0.99
P. abies	P. abies	Medium	21.8/12.8	-41.5	41.5	86	1.71	0.002	0.99
P. abies	P. abies	Smallest	8.8/4.2	-52.5	53	37	2.01	0.008	0.86
P. abies	Total stand	Total stand	38.6/26	-32.7	32.7	167	1.47	0.038	0.99
<b>Diameter (d; cm)</b>									
A. alba & P. abies	A. alba	Largest	92.4/107.9	16.7	18.3	394	0.85	0.003	0.99
A. alba & P. abies	A. alba	Medium	86.9/91.2	5	11.3	150	0.92	0.227	0.98
A. alba & P. abies	A. alba	Smallest	48.7/33.3	-31.6	31.6	265	1.45	< 0.001	0.98
A. alba & P. abies	P. abies	Largest	81.4/83.6	2.8	11.1	149	0.95	0.368	0.98
A. alba & P. abies	P. abies	Medium	73.1/70.4	-3.6	6.1	28	1.03	0.299	0.99
A. alba & P. abies	P. abies	Smallest	54/45.4	-15.9	16.8	156	1.14	0.119	0.96
A. alba & P. abies	Total stand	Total stand	64/68.7	7.4	15.3	167	0.92	0.189	0.97
A. alba, P. abies & F. sylvatica	A. alba	Largest	104.8/126.3	20.5	20.5	528	0.82	0.014	0.99
A. alba, P. abies & F. sylvatica	A. alba	Smallest	62.1/47.7	-23.1	23.1	227	1.24	0.189	0.98
A. alba, P. abies & F. sylvatica	P. abies	Largest	76.3/94	23.2	23.2	323	0.81	0.019	0.99
A. alba, P. abies & F. sylvatica	P. abies	Smallest	58/54.4	-6.3	12.8	60	1.06	0.589	0.99
A. alba, P. abies & F. sylvatica	F. sylvatica	Largest	63.7/75.6	18.7	18.7	164	0.84	0.063	0.99
A. alba, P. abies & F. sylvatica	F. sylvatica	Smallest	51.1/49.9	-2.4	6.7	12	1.02	0.701	0.99
A. alba, P. abies & F. sylvatica	Total stand	Total stand	52.2/72.8	39.5	39.5	486	0.71	0.025	0.99
L. decidua, P. abies & P. cembra	L. decidua	Largest	62.4/71.3	14.3	14.3	108	0.87	0.078	0.99
L. decidua, P. abies & P. cembra	L. decidua	Smallest	47.3/46.5	-1.7	2.8	3	1.02	0.605	0.99
L. decidua, P. abies & P. cembra	P. abies	Largest	53.8/59.8	11.1	18.1	103	0.89	0.322	0.98
L. decidua, P. abies & P. cembra	P. abies	Smallest	35.3/31.8	-9.9	9.9	14	1.11	0.058	0.99
L. decidua, P. abies & P. cembra	P. cembra	Largest	51.8/62.3	20.1	20.1	152	0.83	0.118	0.99
L. decidua, P. abies & P. cembra	P. cembra	Smallest	40.2/37.3	-7.4	11.4	27	1.07	0.484	0.99
L. decidua, P. abies & P. cembra	Total stand	Total stand	48.5/51.5	6.2	6.2	10	0.94	0.028	0.99
F. sylvatica	F. sylvatica	Largest	103.9/69.5	-33.1	33.1	1188	1.5	0.022	0.99
F. sylvatica	F. sylvatica	Medium	81.9/53.5	-34.7	34.7	815	1.53	0.097	0.99
F. sylvatica	F. sylvatica	Smallest	45.3/30.2	-33.4	33.4	245	1.5	0.159	0.99
F. sylvatica	Total stand	Total stand	77/51.1	-33.7	33.7	684	1.51	0.076	0.99
P. abies	P. abies	Largest	53.8/59.8	11.1	18.1	103	0.89	0.322	0.98
P. abies	P. abies	Medium	35.3/31.8	-9.9	9.9	14	1.11	0.058	0.99
P. abies	P. abies	Smallest	54/45.4	-15.9	16.8	156	1.14	0.119	0.96
P. abies	Total stand	Total stand	51.8/44.8	-13.5	13.5	67	1.15	0.182	0.99
<b>Basal area (m<sup>2</sup> ha<sup>-1</sup>)</b>									
A. alba & P. abies	A. alba	Largest	1.3/1.7	26.9	28.1	0	0.86	0.051	0.96
A. alba & P. abies	A. alba	Medium	1.9/2.5	31.3	31.4	1	0.76	0.042	0.88
A. alba & P. abies	A. alba	Smallest	7.2/4	-44.4	44.4	13	1.69	< 0.001	0.97
A. alba & P. abies	P. abies	Largest	1.1/1.2	11.5	28.4	0	1.01	0.883	0.93
A. alba & P. abies	P. abies	Medium	2.4/2.6	4.6	14.3	0	0.92	0.196	0.97
A. alba & P. abies	P. abies	Smallest	4.7/3.7	-20.7	28.5	3	1.24	0.081	0.93
A. alba & P. abies	Total stand	Total stand	22.6/14.8	-34.4	34.4	74	1.44	0.006	0.95
A. alba, P. abies & F. sylvatica	A. alba	Largest	0.7/1.6	137.4	137.4	2	0.34	0.016	0.89
A. alba, P. abies & F. sylvatica	A. alba	Smallest	9.4/4.8	-48.5	48.5	31	2.01	0.09	0.95

(continued on next page)

Table A2 (continued)

Forest type	Species	Size cohort	Mean O/P	e%	MAE%	RMSE	Slope	P-value	R <sup>2</sup>
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Largest	0.9/1.7	79	79	1	0.61	0.109	0.9
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Smallest	2.5/2.8	12.1	28.4	1	0.82	0.187	0.97
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	0.4/0.7	74.5	74.5	0	0.59	0.037	0.96
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	1.4/1.3	-7.5	11	0	1.1	0.086	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	Total stand	Total stand	25.4/12.6	-50.5	50.5	181	1.92	0.122	0.94
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Largest	5.1/7.4	45.3	45.3	7	0.67	0.03	0.98
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Smallest	4.8/5.9	23	28.1	3	0.75	0.153	0.96
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Largest	5.6/6.1	9.5	9.5	1	0.98	0.8	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Smallest	13.6/11.7	-13.5	13.5	6	1.17	0.132	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Largest	3.6/4.8	35.1	35.1	3	0.77	0.008	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Smallest	4.2/5.2	23.9	34	4	0.71	0.072	0.97
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	Total stand	Total stand	36.8/41.2	11.9	11.9	34	0.88	0.03	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	11.2/10.7	-4.5	6	1	1.05	0.562	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Medium	11.9/11.3	-4.6	4.6	0	1.05	0.212	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	13.2/13.7	4.1	8.2	1	0.96	0.684	0.99
<i>F. sylvatica</i>	Total stand	Total stand	36.3/35.8	-1.4	1.4	0	1.01	0.269	0.99
<i>P. abies</i>	<i>P. abies</i>	Largest	5.6/6.1	9.5	9.5	1	0.98	0.8	0.99
<i>P. abies</i>	<i>P. abies</i>	Medium	13.6/11.7	-13.5	13.5	6	1.17	0.132	0.99
<i>P. abies</i>	<i>P. abies</i>	Smallest	4.7/3.7	-20.7	28.5	3	1.24	0.081	0.93
<i>P. abies</i>	Total stand	Total stand	22.1/16	-27.8	27.8	42	1.35	0.115	0.98
<b>Height (m)</b>									
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Largest	41.4/34.3	-17.1	19.2	81	1.2	0.011	0.98
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Medium	40.6/31.8	-21.7	21.7	88	1.27	< 0.001	0.99
<i>A. alba</i> & <i>P. abies</i>	<i>A. alba</i>	Smallest	29.5/21.6	-26.8	26.8	67	1.36	< 0.001	0.99
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Largest	42.6/34.8	-18.4	18.4	69	1.22	< 0.001	0.99
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Medium	41.1/32.9	-19.7	19.7	69	1.24	< 0.001	0.99
<i>A. alba</i> & <i>P. abies</i>	<i>P. abies</i>	Smallest	34.5/27.8	-19.5	19.5	52	1.23	< 0.001	0.99
<i>A. alba</i> & <i>P. abies</i>	Total stand	Total stand	35.1/29.9	-14.7	16.2	44	1.17	0.01	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Largest	41.5/34.2	-17.5	17.5	65	1.21	0.087	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>A. alba</i>	Smallest	32.2/24.6	-23.6	23.6	58	1.3	0.021	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Largest	40.9/36.1	-11.7	11.7	23	1.13	0.008	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>P. abies</i>	Smallest	33.2/30.2	-9.2	9.2	12	1.1	0.128	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	32.4/30.9	-4.4	4.4	3	1.05	0.136	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	30.9/27.5	-11	11	15	1.12	0.122	0.99
<i>A. alba</i> , <i>P. abies</i> & <i>F. sylvatica</i>	Total stand	Total stand	28.7/30	4.6	4.6	3	0.96	0.162	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Largest	31.4/37.3	18.9	18.9	63	0.83	0.169	0.98
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>L. decidua</i>	Smallest	28.8/31	7.5	7.5	11	0.93	0.299	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Largest	30.5/35.9	17.6	17.6	32	0.85	0.03	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. abies</i>	Smallest	24/26.3	9.7	9.7	10	0.91	0.253	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Largest	25.6/34.9	36.5	36.5	90	0.73	0.009	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	<i>P. cembra</i>	Smallest	23/27.6	20.1	20.1	26	0.83	0.055	0.99
<i>L. decidua</i> , <i>P. abies</i> & <i>P. cembra</i>	Total stand	Total stand	27.2/32.2	18.2	18.2	31	0.84	0.078	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Largest	55.2/38.7	-30	30	325	1.43	0.264	0.98
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Medium	52.8/34.8	-34.1	34.1	363	1.52	0.196	0.99
<i>F. sylvatica</i>	<i>F. sylvatica</i>	Smallest	37.2/27.1	-27.2	27.2	103	1.37	0.065	0.99
<i>F. sylvatica</i>	Total stand	Total stand	48.4/33.5	-30.8	30.8	245	1.45	0.195	0.99
<i>P. abies</i>	<i>P. abies</i>	Largest	30.5/35.9	17.6	17.6	32	0.85	0.03	0.99
<i>P. abies</i>	<i>P. abies</i>	Medium	24/26.3	9.7	9.7	10	0.91	0.253	0.99
<i>P. abies</i>	<i>P. abies</i>	Smallest	34.5/27.8	-19.5	19.5	52	1.23	< 0.001	0.99
<i>P. abies</i>	Total stand	Total stand	29.8/27.4	-8	8	6	1.09	0.037	0.99

Conceptualization, Writing - review & editing. **Volodymyr Trotsiuk:** Conceptualization, Writing - review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

This work would not be possible without the long-term commitment of WSL and many scientists and technicians who collect the data, document all the events occurring in the plots and design the network. This contribution is gratefully acknowledged. In particular, we would like to thank Jens Nitzsche and Hubert Schmid, who contribute to the current management and development of the EFM project. Carlos Gonzalez-Benecke and an anonymous reviewer provided useful

constructive criticism of the manuscript, for which we are very grateful.

#### Appendix A

See Figs. A1–A6 and Tables A1 and A2.

#### Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119271>.

#### References

- Battaglia, M., Sands, P.J., 1998. Process-based forest productivity models and their application in forest management. *For. Ecol. Manage.* 102, 13–32.
- Battaglia, M., Almeida, A.C., O'Grady, A.P., Mendham, D., 2007. Process-based models in Eucalyptus plantation management: reality and perspectives. *Boletín del CIDEU*, 3. pp. 189–205. ISSN 1885-5237.

- Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science* 38, 695–720.
- Bončina, A., 2011. History, current status and future prospects of unevenaged forest management in the Dinaric region: an overview. *Forestry* 84, 467–478.
- Bouwman, M., Forrester, D.I., Ouden, J.D., Nabuurs, G.-J., Mohren, G.M.J., 2021. Species interactions in mixed stands of *Pinus sylvestris* and *Quercus robur* in the Netherlands: competitive dominance shifts in favor of *P. sylvestris* under projected climate change. *For. Ecol. Manage.* 481, 118615.
- Boyden, S., Montgomery, R., Reich, P.B., Palik, B., 2012. Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. *Ecol. Appl.* 22, 1578–1588.
- Brang, P., Schönenberger, W., Frehner, M., Schwitter, R., Thormann, J.-J., Wasser, B., 2006. Management of protection forests in the European Alps: an overview. *For. Snow Landscape Res.* 80, 23–44.
- Brisson, J., 2001. Neighborhood competition and crown asymmetry in *Acer saccharum*. *Can. J. For. Res.* 31, 2151–2159.
- Brunner, A., Hahn, K., Biber, P., Skovsgaard, J.P., 2006. Conversion of Norway spruce: a case study in Denmark based on silvicultural scenario modelling. In: Hasenauer, H. (Ed.), *Sustainable Forest Management: Growth models for Europe*. Springer, Berlin, Heidelberg, pp. 343–371.
- Burkhardt, H.E., Tomé, M., 2012. *Modeling Forest Trees and Stands*. Springer, Dordrecht p.
- Charbonnier, F., Maire, G.I., Dreyer, E., Casanoves, F., Christina, M., Dauzat, J., Eitel, J. U.H., Vaast, P., Vierling, L.A., Roupsard, O., 2013. Competition for light in heterogeneous canopies: Application of MAESTRA to a coffee (*Coffea arabica* L.) agroforestry system. *Agric. For. Meteorol.* 181, 152–169.
- Christina, M., Nouvellon, Y., Laclau, J.-P., Stape, J.L., Bouillet, J.-P., Lambais, G.R., Maire, G.I., 2017. Importance of deep water uptake in tropical eucalypt forest. *Functional Ecol.* 31, 509–519.
- "count(./sb:host[1]/child:\*/sb:date)"> Clark, P.J., Evans, F.C., . Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35, 445–453.
- Cornelius, C., Estrella, N., Franz, H., Menzel, A., 2013. Linking altitudinal gradients and temperature responses of plant phenology in the Bavarian Alps. *Plant Biology* 15, 57–69.
- Čufar, K., Luis, M.D., Saz, M.A., Črepinšek, Z., Kajfež-Bogataj, L., 2012. Temporal shifts in leaf phenology of beech (*Fagus sylvatica*) depend on elevation. *Trees* 26, 1091–1100.
- Dittmar, C., Elling, W., 2006. Phenological phases of common beech (*Fagus sylvatica* L.) and their dependence on region and altitude in Southern Germany. *Eur. J. Forest Res.* 125, 181–188.
- Duursma, R.A., Medlyn, B.E., 2012. MAESPA: a model to study interactions between water limitation, environmental drivers and vegetation function at tree and stand levels, with an example application to [CO<sub>2</sub>] × drought interactions. *Geosci. Model Dev.* 5, 919–940.
- Fontes, L., Bontemps, J.D., Bugmann, H., van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., Skovsgaard, J.P., 2010. Models for supporting forest management in a changing environment. *Forest Systems* 19, 8–29.
- Forrester, D.I., Tang, X., 2016. Analysing the spatial and temporal dynamics of species interactions in mixed-species forests and the effects of stand density using the 3-PG model. *Ecol. Model.* 319, 233–254.
- Forrester, D.I., Ammer, C., Annighöfer, P.J., Avdagic, A., Barbeito, I., Bielik, K., Brazaitis, G., Coll, L., Río, M.d., Drössler, L., Heym, M., Hurt, V., Löf, M., Matović, B., Meloni, F., Ouden, J.d., Pach, M., Pereira, M.G., Ponette, Q., Pretzsch, H., Skrzyszewski, J., Stojanović, D., Svoboda, M., Ruiz-Peinado, R., Vacchiano, G., Verheyen, K., Zlatanov, T., Bravo-Oviedo, A., 2017a. Predicting the spatial and temporal dynamics of species interactions in *Fagus sylvatica* and *Pinus sylvestris* forests across Europe. *For. Ecol. Manage.* 405, 112–133.
- Forrester, D.I., Tachauer, L.H.H., Annighöfer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G.W., 2017b. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *For. Ecol. Manage.* 396, 160–175.
- Forrester, D.I., Ammer, C., Annighöfer, P.J., Barbeito, I., Bielik, K., Bravo-Oviedo, A., Coll, L., Río, M.d., Drössler, L., Heym, M., Hurt, V., Löf, M., Ouden, J.d., Pach, M., Pereira, M.G., Plaga, B., Ponette, Q., Skrzyszewski, J., Sterba, H., Svoboda, M., Zlatanov, T., Pretzsch, H., 2018. Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. *J. Ecol.* 106, 746–760.
- Forrester, D.I., 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *For. Ecol. Manage.* 447, 139–157.
- Forrester, D.I., Nitzsche, J., Schmid, H., 2019a. The Experimental Forest Management project: An overview and methodology of the long-term growth and yield plot network. Swiss Federal Institute of Forest, Snow and Landscape Research WSL. Available from <https://www.wsl.ch/en/projects/long-term-growth-and-yield-data.html>. 77 p.
- Forrester, D.I., Rodenfels, P., Haase, J., Härdtle, W., Leppert, K.N., Niklaus, P.A., Oheimb, G.v., Scherer-Lorenzen, M., Bauhus, J., 2019b. Tree species interactions increase light absorption and growth in Chinese subtropical mixed-species plantations. *Oecologia* 191, 421–432.
- Forrester, D.I., 2020. 3-PG User Manual (available from <https://sites.google.com/site/davidforrestersite/home/projects/3PGmix/3pgmixdownload>). Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland. 70 p.
- Forrester, D.I., Baker, T.G., Elms, S.R., Hobi, M.L., Ouyang, S., Wiedemann, J.C., Xiang, W., Zell, J., Pulkkinen, M., 2021. Self-thinning tree mortality models that account for vertical stand structure, species mixing and climate. *For. Ecol. Manage.* 487, 118936.
- Forrester, D.I., Hobi, M.L., Mathys, A.S., Stadelmann, G., Trotsiuk, V., 2021. Calibration of the process-based model 3-PG for major central European tree species. *Eur. J. For. Res.* <https://doi.org/10.1007/s10342-021-01370-3> (in press).
- García, O., 2016. Cohort aggregation modelling for complex forest stands: Spruce-aspens mixtures in British Columbia. *Ecol. Model.* 343, 109–122.
- Gómez-Aparicio, L., Canham, C.D., 2008. Neighborhood models of the effects of invasive tree species on ecosystem processes. *Ecol. Monogr.* 78, 69–86.
- Grace, J.C., Jarvis, P.G., Norman, J.M., 1987. Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand J. For. Sci.* 17, 193–209.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* 115, 129–148.
- Grote, R., Pretzsch, H., 2002. A model for individual tree development based on physiological processes. *Plant Biol.* 4, 167–180.
- Gupta, R., Sharma, L.K., 2019. The process-based forest growth model 3-PG for use in forest management: a review. *Ecol. Model.* 397, 55–73.
- Hilmer, T., Avđagić, A., Bartkovic, L., Bielik, K., Binder, F., Bončina, A., Dobor, L., Forrester, D.I., Hobi, M., Ibrahimspahic, A., Jaworski, A., Klopčič, M., Matović, B., Nagel, T., Petráš, R., Río, M.d., Stajić, B., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H., 2019. The productivity of mixed mountain forests consisting of *Fagus sylvatica*, *Picea abies* and *Abies alba* across Europe. *Forestry* 92, 512–522.
- Hodge, A., 2006. Plastic plants and patchy soils. *J. Exp. Bot.* 57, 401–411.
- Jonard, M., André, F., de Coligny, F., de Wergifosse, L., Beudez, N., Davi, H., Ligot, G., Ponette, Q., Vincke, C., 2020. HETEROFOR 1.0: a spatially explicit model for exploring the response of structurally complex forests to uncertain future conditions – Part 1: Carbon fluxes and tree dimensional growth. *Geosci. Model Dev.* 13, 905–935.
- Korol, R.L., Running, S.W., Milner, K.S., 1995. Incorporating intertree competition into an ecosystem model. *Can. J. For. Res.* 25, 413–424.
- Landsberg, J., 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. *Can. J. For. Res.* 33, 385–397.
- Landsberg, J., Mäkelä, A., Sievänen, R., Kukkola, M., 2005. Analysis of biomass accumulation and stem size distributions over long periods in managed stands of *Pinus sylvestris* in Finland using the 3-PG model. *Tree Physiol.* 25, 781–792.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- le Maire, G., Nouvellon, Y., Christina, M., Ponzi, F.J., Gonçalves, J.L.M., Bouillet, J.-P., Laclau, J.-P., 2013. Tree and stand light use efficiencies over a full rotation of single- and mixed-species *Eucalyptus grandis* and *Acacia mangium* plantations. *For. Ecol. Manage.* 288, 31–42.
- Lee, M.J., García, O., 2016. Plasticity and extrapolation in modeling mixed-species stands. *Forest Sci.* 62, 1–8.
- Longuetaud, F., Piboule, A., Wernsdorfer, H., Collet, C., 2013. Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. *Eur. J. Forest Res.* 132, 621–634.
- Medlyn, B.E., 2004. A MAESTRO Retrospective. In: Mencuccini, M., Moncrieff, J., McNaughton, K., Grace, J. (Eds.), *Forests at the Land-Atmosphere Interface*. CABI Publishing, Wallingford UK, pp. 105–122.
- NOAA, 2013. National Oceanic and Atmospheric Administration, Department of Commerce, USA, 2013. National Climatic Data Center [online] Available at: <http://www.ncdc.noaa.gov>.
- O'Hara, K.L., Hasenauer, H., Kindermann, G., 2007. Sustainability in multi-aged stands: an analysis of long-term planter systems. *Forestry* 80, 163–181.
- Panagos, P., Liedekerke, M.V., Jones, A., Montanarella, L., 2012. European Soil Data Centre: Response to European policy support and public data requirements. *Land Use Policy* 29, 329–338.
- Pellerin, M., Delestrade, A., Mathieu, G., Rigault, O., Yoccoz, N.G., 2012. Spring tree phenology in the Alps: effects of air temperature, altitude and local topography. *Eur. J. Forest Res.* 131, 1957–1965.
- Peng, C., 2000. Growth and yield models for uneven-aged stands: past, present and future. *For. Ecol. Manage.* 132, 259–279.
- Pretzsch, H., Biber, P., Dursky, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Manage.* 162, 3–21.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 4967.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015. Representation of species mixing in forest growth models. A review and perspective. *Ecol. Model.* 313, 276–292.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

- Schume, H., Jost, G., Hager, H., 2004. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *J. Hydrol.* 289, 258–274.
- Schuster, C., Estrella, N., Menzel, A., 2014. Shifting and extension of phenological periods with increasing temperature along elevational transects in southern Bavaria. *Plant Biol.* 16, 332–344.
- Schütz, J.P., 2001. Der Plenterwald und weitere Formen strukturierter und gemischter Wälder. Parey, Berlin, Germany.
- Seidl, R., Lexer, M.J., Jäger, D., Hönninger, K., 2005. Evaluating the accuracy and generality of a hybrid patch model. *Tree Physiol.* 25, 939–951.
- Simioni, G., Marie, G., Huc, R., 2016. Influence of vegetation spatial structure on growth and water fluxes of a mixed forest: Results from the NOTG 3D model. *Ecol. Model.* 328, 119–135.
- Spiecker, H., 1986. Das Wachstum der Tannen und Fichten auf Plenterwald-Versuchsflächen des Schwarzwaldes in der Zeit von 1950 bis 1984. *Allgemeine Forst und Jagdzeitung* 157, 152–164.
- Spiecker, H., 1991. Zur Dynamik des Wachstums von Tannen und Fichten auf Plenterwald Versuchsflächen des Schwarzwaldes. *Allgemeine Forst und Jagdzeitung* 21, 1076–1080.
- Spiecker, H., Mielikäinen, K., Köhl, M., Skovsgaard, J.P., 1996. Growth Trends in European Forests. Springer-Verlag, Heidelberg, p. 372.
- Stiell, W.M., 1982. Growth of clumped vs equally spaced trees. *The Forestry Chronicle* 58, 23–25.
- Thomas, R.Q., Brooks, E.B., Jersild, A.L., Ward, E.J., Wynne, R.H., Albaugh, T.J., Dinon-Aldridge, H., Burkhart, H.E., Domec, J.-C., Fox, T.R., Gonzalez-Benecke, C.A., Martin, T.A., Noormets, A., Sampson, D.A., Teskey, R.O., 2017. Leveraging 35 years of Pinus taeda research in the southeastern US to constrain forest carbon cycle predictions: regional data assimilation using ecosystem experiments. *Biogeosciences* 14, 3525–3547.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251.
- Trotsiuk, V., Hartig, F., Forrester, D.I., 2020. r3PG – an R package for simulating forest growth using the 3-PG process-based model. *Methods Ecol. Evol.* 11, 1470–1475.
- Umeki, K., 1997. Effect of crown asymmetry on size-structure dynamics of plant populations. *Ann. Bot.* 79, 631–641.
- Uriarte, M., Turner, B.L., Thompson, J., Zimmerman, J.K., 2015. Linking spatial patterns of leaf litterfall and soil nutrients in a tropical forest: a neighborhood approach. *Ecol. Appl.* 25, 2022–2034.
- Vanclay, J.K., 1994. Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests. CAB International, Wallingford, UK, p. 312.
- Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.-Y., Louvet, J.-M., Kremer, A., Michalet, R., 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agric. For. Meteorol.* 149, 735–744.
- Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model - MAESTRO. *Agric. For. Meteorol.* 51, 257–280.
- Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Johnson, G.P., 2010. A hybrid model for intensively managed Douglas-fir plantations in the Pacific Northwest, USA. *Eur. J. Forest Res.* 129, 325–338.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. John Wiley & Sons, Chichester, UK, p. 415.
- Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., Granier, A., 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using <sup>18</sup>O soil water labelling. *Trees* 25, 885–894.
- Zingg, A., 1996. Diameter and Basal Area Increment in Permanent Growth and Yield Plots in Switzerland. In: Spiecker, H., Mielikäinen, K., Köhl, M., Skovsgaard, J.P. (Eds.), Growth Trends in European Forests. Springer, Berlin; Heidelberg, pp. 239–265.