Modelling the growth of *Pinus sylvestris* L. monocultures in Sweden depending on the absorbed light

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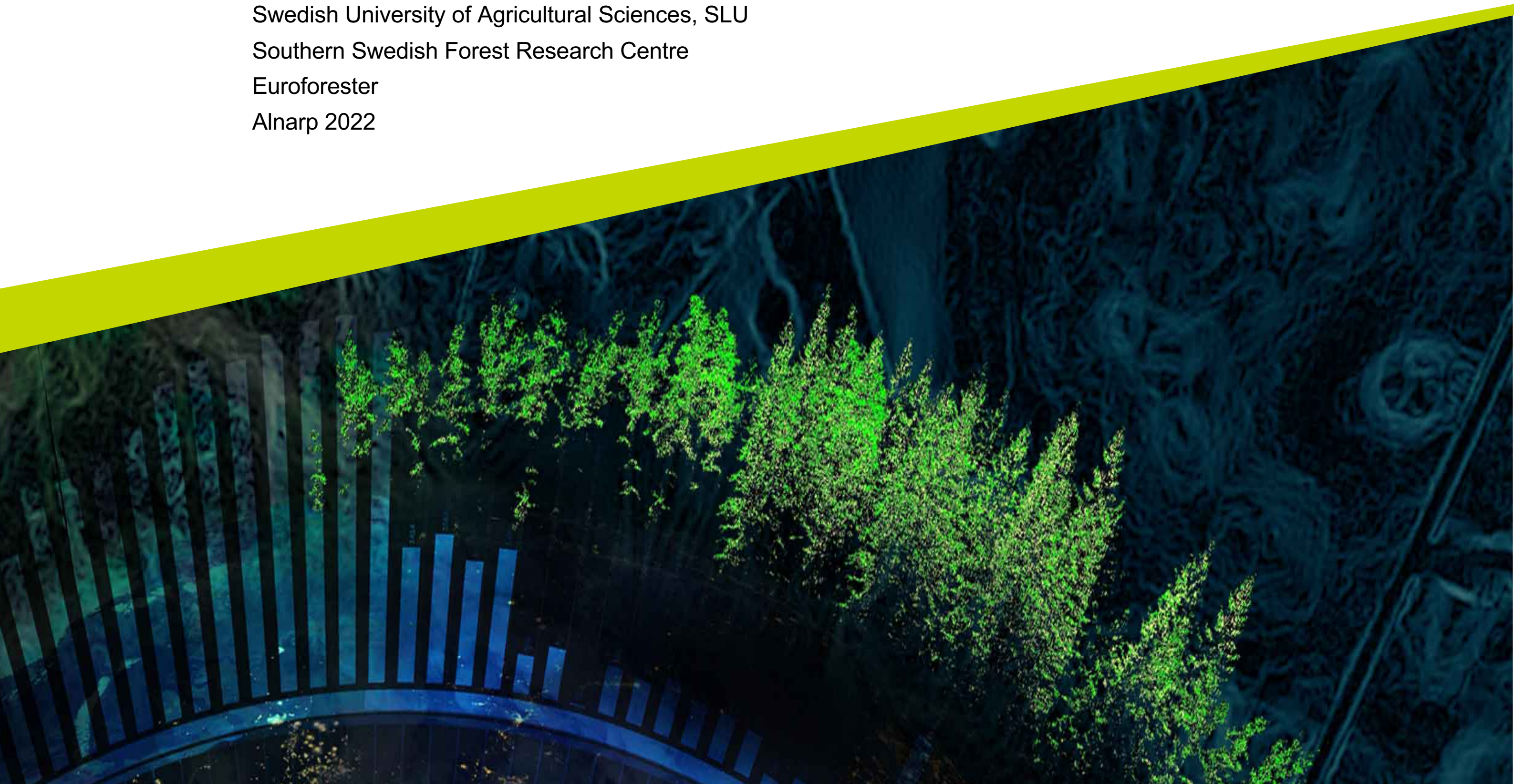

Modelling the growth of *Pinus sylvestris* L. monocultures in Sweden depending on the absorbed light

Modellera tillväxt hoss tallskogar i Sverige beroende av absorberat ljus

Mateusz Grzeszkiewicz

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Abstract

Stand growth models are an important aid in contemporary sustainable forest management as a major planning and decision-making tool. However, climate change influencing growth conditions worldwide is a challenge to commonly used empirical models as they do not provide enough flexibility, which can result in inaccurate predictions and thus wrong decisions and sub-optimal results. Climate sensitive models based on plant physiology are a solution that provides greater adaptability, but they are computationally demanding and require often unavailable input data, and therefore they are rarely used in practice. For this reason, simple growth models for Scots pine (*Pinus sylvestris* L.) monocultures based on the concept of Light-Use Efficiency (LUE) were developed in this thesis. They use the yearly sums of absorbed photosynthetically active radiation (APAR), readily available climate data (annual precipitation and mean air temperature), and basic stand characteristics (age, number of trees, and site index) to predict the annual stem volume increment. For model fitting and validation, stand data from a long-term thinning and fertilization experiment established in Sweden and climate data from the Swedish Meteorological and Hydrological Institute were used. Two approaches differing in the method of data preparation were analysed. Model 1 (M_1) was based on averaged variables and Model 2 (M_2) used variables from the beginning of the measurement periods. Both models fit reasonably well with the data, but the RMSE exceeded 20% and they proved to provide reliable estimates for only the part of the productivity range included in this study. The unsatisfactory performance can be attributed to the change of the dependent variable in the LUE model to stem volume increment, the lack of good quality APAR data, and the low degree of model hybridization.

Keywords: climate change, forest modelling, light use efficiency, photosynthetically active radiation, Scots pine

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Abbreviations

APAR	Absorbed Photosynthetically Active Radiation
fAPAR	Fraction of Absorbed Photosynthetically Active Radiation
LAI	Leaf Area Index
LUE	Light-Use Efficiency
M_1	Model 1 (based on averaged variables)
M_2	Model 2 (based on initial variables)
PAI	Periodic Annual Volume Increment
PAR	Photosynthetically Active Radiation
SI	Site Index

1. Introduction

1.1 Forest production and climate change

The productive function of the forest is an important element of sustainable forest management, supplying a variety of products, contributing to economic development, and fulfilling social functions by providing employment (Tegegne et al. 2018). Moreover, forests play an essential role in mitigating climate change by capturing atmospheric carbon dioxide in tree biomass (Lorenz & Lal 2010; Lundmark et al. 2014). However, climate change also poses challenges for forests. Reports show that the rise in temperature is progressing much faster than ever in recorded history and is already impacting extreme weather events. Depending on the scenario, the average global temperature is projected to increase between 1.4 and 4.4 degrees by the end of the 21st century, likely leading to changes in rainfall patterns (IPCC 2021). Changes in growth conditions will significantly affect forest productivity, but the exact impact is uncertain and differs from region to region (Lindner et al. 2014; Reyer 2015).

Due to the significant influence of climate change on forest productivity, it is necessary to consider its impact when forecasting the expected forest growth. The ability to accurately predict growth is indispensable in modern forestry. The forecasts support management decisions such as choosing silvicultural system, species composition, planting density, thinning strategy, and optimizing rotation lengths. At the estate level, it helps to determine the size of the harvest, schedule treatments and update the inventory data. Forecasts also facilitate planning at regional and national level and policy-making (Weiskittel et al. 2011). Accurate estimates are essential to making sound management decisions that ensure sustainable forest resource management (Goude 2021). Various models are used to simulate forest growth, but they differ in flexibility and the possibility of maintaining the accuracy of predictions in the face of climate change (Weiskittel et al. 2011).

1.2 Models used in forestry

The simplest and most prevalent models are empirical, usually stand-based models which predict the development of basic stand characteristics such as basal area, height, and volume. They are often derived from large data sets of stand measurement, using exclusively statistical methods without attempts to deeply describe the underlying processes (Landsberg & Sands 2011; Weiskittel et al. 2011). Within the range of environmental conditions and stand characteristics for which the models were developed, they allow for accurate growth predictions (Pinjuv et al. 2006; Landsberg & Sands 2011). However, their utility outside these conditions remains limited (Miehle et al. 2009). An alternative approach is to use process-based models that consist of mathematically expressed physiological processes, such as photosynthesis, respiration and transpiration, and incorporate the effects of environmental factors, to simulate forest development (Landsberg 2003). While adaptable to varying conditions, process-based models are usually highly complex and require seldom available input data (Weiskittel et al. 2011). In addition, many processes have not yet been sufficiently understood, whereas the sensitivity of the outputs to the uncertainties in the input data, parameterization and model structure increases with complexity (Mäkelä et al. 2000; Schmid et al. 2006; Landsberg & Sands 2011). Hybrid models, which consist of mechanistic elements and statistical relations, combine the strengths of empirical and process-based models (Landsberg & Sands 2011; Weiskittel et al. 2011). Although some studies indicate only a slight improvement in precision compared to empirical models (Dzierzon & Mason 2006; Pinjuv et al. 2006), their unquestionable advantage is greater flexibility and adaptability to changing growth conditions (Taylor et al. 2009).

1.3 Linking growth and light absorption

A key discovery that laid the foundation for developing various process-based (e.g., McMurtrie et al. 1990; Kirschbaum 1999) and hybrid models (e.g., Landsberg & Waring 1997; Peng et al. 2002; Mason et al. 2011) was the Light-Use Efficiency (LUE) concept (Waring et al. 2016). It is a simple model of the dependence of plant growth on photosynthetically active radiation (PAR), the part of the spectral band with a wavelength of 400-700 nm used by plants for photosynthesis that has been absorbed by foliage (APAR) (Landsberg & Sands 2011). LUE is usually expressed as dry biomass production per APAR unit (Waring et al. 2016). Monteith (1977) was the first to show a strong linear relationship between APAR and the accumulation of dry matter of agricultural plants. Subsequently, based on his findings, Jarvis and Laverenz (1983) analysed the application of this model to forests (as cited in Waring et al. 2016).

The use of LUE to predict hourly or daily production is limited as it is highly variable at short intervals. Yet, averaged over longer periods, LUE becomes substantially linear (Waring et al. 2016). The advantage of using APAR is that other factors influencing plant growth are also indirectly considered. Soil nutrient content, water availability, and temperature significantly influence leaf area production and, thus, the amount of light absorbed (Cannell 1989).

Estimates of LUE values for total or above-ground dry biomass production of different tree species range from 0.2 to 3.3 g MJ^{-1}, with lower values mainly found in temperate and boreal forests and higher in tropical eucalyptus plantations (Landsberg & Sands 2011). Many studies have shown that LUE also varies depending on climatic factors and site properties, including temperature (Waring 2000), water availability (Stape et al. 2008; Garbulsky et al. 2010) and soil fertility (Wang et al. 1991; Gower et al. 1992; Martin & Jokela 2004; Campoe et al. 2013).

Temperature is one of the main factors influencing the metabolic processes of plants. It affects the rate of photosynthesis, which decreases with departure from optimal conditions and ceases beyond certain thresholds (Kolari et al. 2007; Landsberg & Sands 2011). Air temperature also influences the atmospheric vapour pressure and thus the rate of transpiration. If soil water availability is too low to compensate for the losses, stomata close and stomatal conductance decreases, reducing the CO_2 uptake (Landsberg & Sands 2011). Soil fertility affects photosynthesis efficiency, which depends on the nitrogen content in the leaves, and the carbon allocation to the roots, influencing the above-ground biomass LUE (Cannell 1989; Landsberg & Sands 2011; Waring et al. 2016). LUE also changes together with the stand development. After an initial, short increase, it declines with the tree age (Saldarriaga & Luxmoore 1991; Martin & Jokela 2004). This can be explained by a decrease in xylem hydraulic conductance with height increment and a growing proportion of respiring to photosynthesizing tissues (Mencuccini & Grace 1996). To account for the influence of environmental factors, many models use modifiers ranging from 0 to 1 depending on the deviation from the optimal conditions to calculate a utilizable APAR (e.g., Landsberg & Waring 1997; Mäkelä et al. 2008; Goude et al. 2022).

The absorbed PAR (APAR), which is key in all LUE-based models, is highly variable and depends on many factors: cloud cover, latitude, the time of day and year affect the amount of radiant energy reaching the earth's surface (Landsberg & Sands 2011). On the other hand, the radiation absorption is influenced by the foliage area, optical properties and orientation of leaves, foliage clumping and stand structure (Binkley et al. 2013).

There are several methods of APAR estimation that differ in accuracy and labour intensity. Direct methods are based on measuring the difference between the irradiance above and below the canopy using solar radiation sensors (Fitter et al. 1980; Pierce & Running 1988). This can be done continuously over extended periods (Cannell et al. 1987; Wang et al. 1991; Mäkelä et al. 2008) or instantaneously to estimate the fraction of PAR absorbed (fAPAR) and calculate the APAR using constant measurements of total incident PAR (Pierce & Running 1988; Runyon et al. 1994). fAPAR can also be measured by both a plant canopy analyzer (Ahl et al. 2004) and hemispherical photography (Weiss & Baret 2017).

The most prevalent methods to estimate APAR are light interception models (e.g., Medlyn 2004) and simple functions such as Beer's Law (Monsi & Saeki 2005). The latter is better suited for practical use as it requires no parameterization. Beer's Law describes the logarithmic increase in radiation absorption with the leaf area index (LAI), assuming that the canopy is closed, uniform and the leaves are distributed randomly (Waring et al. 2016). LAI refers to the projected leaf area (Weiskittel et al. 2011) or half of the total leaf area per unit area of ground for non-flat leaves (Chen & Black 1992). It can be estimated by direct measurement of foliage harvested by destructive sampling (Mason et al. 2012; Goude et al. 2019) or litter collection (Martin & Jokela 2004). LAI can also be estimated indirectly using optical instruments (Mason et al. 2012; Goude et al. 2019), which provide a quick and less labour-intensive assessment but cause underestimation if the leaves are clumped (Chen et al. 1997; Goude et al. 2019). Additionally, Goude et al. (2019) demonstrated how the LAI of Scots pine and Norway spruce stands could be successfully estimated using correlation functions with basal area. In the future, rapidly developing remote sensing may become an affordable and accessible method of obtaining detailed LAI and APAR data (Dash & Ogutu 2016).

1.4 The Swedish context

Sweden's forested area ranks first in Europe, amounting to almost 28 million ha (Forest Europe 2020), of which 84% is productive forest land. One of the most fundamental production tree species is Scots pine (*Pinus sylvestris* L.), whose share in the growing stock on forest land amounts to 39.4 % (SLU 2021). Scots pine is a shade-intolerant pioneer species, undemanding to site properties, both in terms of fertility and moisture conditions, while being highly resistant to both drought and frost (Larsen et al. 2005; Houston Durrant et al. 2016). It is characterized by a medium growth rate, which in the conditions of northern Sweden reaches about 5-10 m^3 ha^{-1} $year^{-1}$ of mean annual increment depending on the site productivity (Nilsson et al. 2012).

Simulations indicate that by the end of the 21st century, the average annual temperature in Sweden may increase from 2.3 to 5.5 degrees (RPC4.5) (SMHI 2022a). Predicted changes in precipitation patterns also forecast increased rainfall in winter and decreased in summer, excluding only the northern parts of the country (Blenkinsop & Fowler 2007). This significantly exacerbates the need for wider use of models incorporating climate variables in practical forestry.

Relatively little research has been done on applying climate-sensitive hybrid and process-based models for Swedish conditions. The existing studies include a modification of the BIOMASS process-based model (McMurtrie et al. 1990) for boreal conditions to investigate the effects of climatic factors on Norway spruce productivity (Bergh et al. 1998) and simulate the impact of climate change on the production of several tree species and its economic implications (Bergh et al. 2010). The same model accompanied other models to measure the impact of intensive silviculture on forest production and its potential contribution to climate change mitigation (Poudel et al. 2012). ForSAFE is another detailed process-based model designed to assess the long-term impact of environmental changes on Swedish forests. It consists of four sub-models that simulate forest growth, soil chemistry, decomposition process and soil hydrology, and includes feedback mechanisms between them (Wallman et al. 2005).

On the other hand, Subramanian (2016) developed a less complex hybrid model merging the 3-GP (Landsberg & Waring 1997) and the empirical Heureka-Regwise (Wikström et al. 2011) models, but the parameterization was performed for only one region. The only hybrid growth model parameterized for all Sweden was developed by Goude et al. (2022). It is based on the Schumacher (1939) empirical equation with time replaced by a potentially usable light sum (Mason et al. 2007), obtained by correcting PAR with climate and site modifiers (Landsberg & Waring 1997). Still, physiological-based modelling of forest growth remains an open field for further research. Moreover, according to Landsberg (2003), hybrid models may become the main aid tools used in future forest management due to their flexibility and practical values.

1.5 Thesis aim

Despite being significantly simplified compared to those based solely on the mechanistic approach, the existing hybrid models are still more computationally demanding than the popular empirical models and require often unavailable data. Therefore, with a view to practical application, this study aimed to develop a simple model based on the data from an extensive long-term experiment using empirical methods with a limited application of any mechanistic equations. It was based upon the Light-Use Efficiency concept due to its simplicity, strong correlation of APAR with growth and wide application. For practical reasons, the dependent variable was changed from biomass production to stem volume increment. The stem volume is well known, widely used, and easy to calculate with good accuracy, whereas the volume increment remains the crucial variable for the economy in forestry. The inclusion of readily available climatic variables and basic stand characteristics was intended to improve the explanatory power of the model and its sensitivity to changes in growing conditions, while maintaining the ease of its use in practice.

This thesis aims to address the following research questions:

1. Could estimates of absorbed photosynthetically active radiation predict stem volume growth in boreal Scots pine stands?
2. Does the inclusion of climate and stand variables in the model improve prediction accuracy?

2. Materials and methods

2.1 Stand and climate data

This thesis was based on data collected from a thinning and fertilization experiment ("GG-experiment") established in 1966-1983 in Sweden (Nilsson et al. 2010). The aim of the research was to evaluate the influence of various types, intervals, timing and intensity of thinning and the effect of fertilization on the growth and yield of Scots pine and Norway spruce monocultures. The investigated treatment regimens included various thinning grades, from light (20-25% of basal area removed) to very heavy (60-70% of basal area removed), delaying the first treatment, thinning carried out from below or from above, and two types of fertilization. The experimental design consisted of blocks, one per site, covering most of the country's latitudinal gradient, divided into plots of approximately 0.1 ha. Stand data were collected at the beginning of the experiment, at each thinning and irregularly between them. More detailed information on the design and the treatments studied can be found in Nilsson et al. (2010).

From the available data set, 205 plots for Scots pine were selected, which covered 48 sites between 56 ° and 67 ° latitude (Fig. 1). All treatments were included except for thinning from above and fertilization, as they affect the site index estimates from the dominant height (Weiskittel et al. 2011). The selection produced 1217 measurement periods that spanned the years 1966 – 2016. The data set used in this thesis contained measurements of stands age between 26 to 95 years (mean = 57) collected at unequal time intervals from 1 to 14 years. The stand characteristics included: basal area, stand density, and top height, ranging between 6.0 – 51.6 m^2 ha^{-1} (mean = 21.8 m^2 ha^{-1}), 150 – 4000 trees ha^{-1} (mean = 969 trees ha^{-1}), and 9.0 – 28.3 m (mean = 17.8 m), respectively (Table 1). The experimental plots were also characterized by a large diversity of the site fertility and stand growth. The site index (SI), expressed as the predicted dominant height at the age of 100, ranged from 17 to 33 m with a mean value of 24 m. The periodic annual volume increment (PAI) ranged between 1.9 and 19.5 m^3 ha^{-1} $year^{-1}$, on average amounted to 7.1 m^3 ha^{-1} $year^{-1}$ (Table 1).

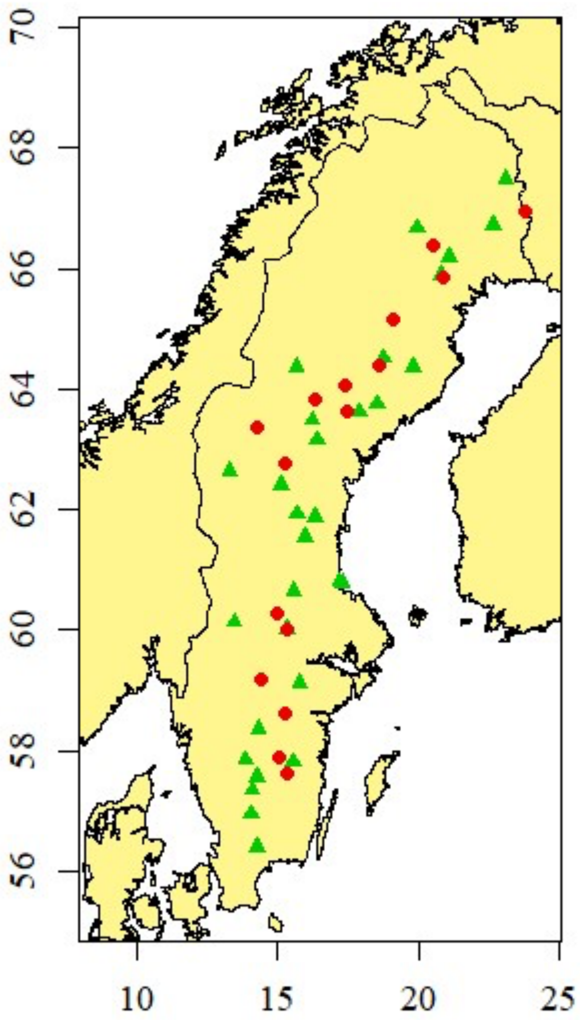

Figure 1. The map of the location of experimental sites in Sweden. The sites randomly selected for model fitting are marked with green/triangles, and for model validation with red/circles.

Climate data for each site covering the duration of the experiment were obtained from the Swedish Meteorological and Hydrological Institute (SMHI). The data set consisted of climate variables estimated with a meteorological model calibrated using observational data from meteorological stations, which was done in the framework of the UERRA project (Niermann et al. 2018, SMHI 2022b). It included monthly sums of precipitation, global radiation, and PAR, as well as average monthly values of minimum, maximum, daily and day-time temperatures. The data was provided in raster files with a spatial resolution of 11 km. Each experimental plot was assigned climate data from the nearest pixel.

The mean annual air temperatures at the experimental sites, averaged over period 1966 – 2016, ranged from 0.9 °C in the north to 7.1°C in the south and showed high variability between years and sites located at a similar latitude (Fig. 2c). The lowest mean annual temperature recorded in a single year was -2.2 °C, and the highest was 9.4 °C. Similarly, average yearly PAR sums decreased with latitude from 1783 to 1379 MJ m^{-2} $year^{-1}$ (Fig. 2b), with extreme values being 1238 and 2028 MJ m^{-2} $year^{-1}$. The amount of precipitation did not show a marked trend with a north-south gradient, but there was considerable variation between years (Fig. 2a). The smallest annual rainfall during the period 1966 – 2016 within the experimental sites was 349 mm while the greatest reached 1248 mm.

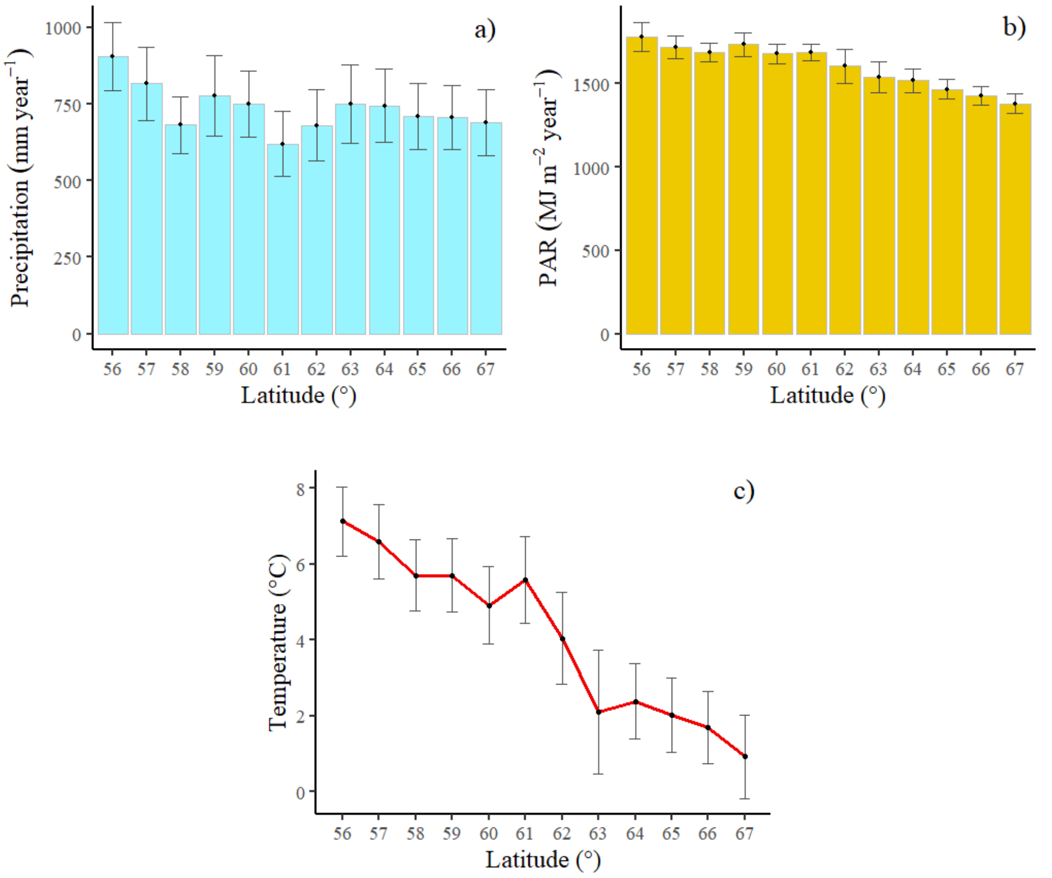

*Figure 2. The experimental sites average values for 1 ° latitudinal bands and period 1966 - 2016: yearly sums of precipitation **(a)** and photosynthetically active radiation **(b)** and annual mean air temperatures **(c)**. The vertical lines represent ±1 standard deviation.*

2.2 Data preparation

The entire data processing and the subsequent model fitting and evaluation were performed using the R (version 4.1.2) statistical program (R Core Team 2021). The preparatory work consisted in calculating the climatic conditions prevailing at individual sites in each distinguished period and estimating the amount of radiation absorbed by the canopy of stands.

To estimate the amount of radiation potentially usable for photosynthesis, the monthly PAR sums were first modified by the influence of temperature. A mechanistic approach was used, as the response of photosynthesis to temperature variation is distinctly non-linear (Landsberg & Sands 2011), and therefore a linear model could misrepresent its effect. The modifier was calculated with the following function derived from the 3GP model (Landsberg 1998, as cited in Waring 2000):

$$f_T = \left(\frac{T_{mean} - T_{min}}{T_{opt} - T_{min}}\right) \times \left(\frac{T_{max} - T_{mean}}{T_{max} - T_{opt}}\right)^{\left(\frac{T_{max} - T_{opt}}{T_{opt} - T_{min}}\right)} \qquad (1)$$

where T_{mean} was the average monthly day-time temperature (°C) that, according to previous studies, provides greater accuracy than daily means (Mason et al. 2011, Goude et al. 2022). T_{opt}, T_{max} and T_{min} referred to the optimal, maximum, and minimum temperatures that determine the rate of photosynthesis, the values of which were assumed at 20, 40, and -2 °C, respectively (adopted from Goude et al. 2022). f_T takes values from 0 to 1 for T_{mean} in the range of T_{min} to T_{max} and 0 for T_{mean} outside the threshold values.

LAI was estimated from the basal area using the correlation function ($R^2 = 0.68$, RMSE = 0.057 m^2 m^{-2}) developed by Goude et al. (2019) for Scots pine stands in Sweden:

$$\text{LAI} = 0.651 + 0.088 \times \text{BA} \qquad (2)$$

where BA is the basal area of stands (m^2 ha^{-1}).

Absorption of radiation by canopy was estimated from the annual sums of the modified PAR and stands' LAI using Beer's Law (Monsi & Saeki 2005):

$$\text{APAR} = \text{PAR} \times \left(1 - e^{-k \times \text{LAI}}\right) \qquad (3)$$

where k refers to the light extinction coefficient which depends on the canopy properties influencing the light penetration efficiency. In this study, k = 0.5 was assumed, which is the mean value for both deciduous and coniferous forests, commonly used in process-based models (Landsberg & Sands 2011; Weiskittel et al. 2011).

In order to exclude the impact of considerable mortality on the inter-periodic changes in LAI and stand growth, the periods in which the mortality exceeded 30% of the total basal area were removed. Preliminary analysis showed that further lowering the threshold did not result in significant improvement in the accuracy of the models (R^2 gain <1%, RMSE gain <0.01%).

Due to irregular measurement intervals, it was impossible to determine precisely the temporal resolution of the constructed model, and thus it was necessary to adopt certain assumptions. Consequently, two approaches were analyzed that differ in assumptions and thus in the method of data processing.

2.2.1 Model 1

Model 1 (M_1) assumed that the differences in the stands' PAI were best explained by both the mean climatic conditions and the averaged values of stand parameters in each period. Given that M_1 is based on annual average variables, the temporal resolution was therefore set to one year.

In this approach, the age of stands and the top height were averaged for each period between measurements. LAI was calculated using Equation 2 based on the residual basal area after the treatment and the remaining and removed basal area at the next revision, and subsequently averaged. Monthly precipitation and modified PAR values were summed for each period and then averaged to annual sums. The same method was used for rainfall totals during the summer months (June to August). APAR estimates were computed with Equation 3 from the mean LAI and annual PAR. It was assumed that both SI and the residual stand density were relatively constant in each period, thus the unaltered values from the measurement events were used in the subsequent model fitting and validation.

2.2.2 Model 2

Model 2 (M_2) assumed that the variation in climatic conditions on a given site in particular periods was relatively small, and the growth of the stand in the following years could be predicted based on measurements made in the year of the revision only. Therefore, the period for which M_2 simulates the annual volume increment is longer than in the case of M_1, since it depends on the measurement intervals, which averaged seven years.

The data set for M_2 consisted of the initial values of stand age, top height, SI, and residual stand density at the beginning of each period. LAI was computed with Equation 2 based on the residual basal area measured in the year of revision. The values of total precipitation, rainfall in the summer months and the modified PAR were summed up in the period of 1 year from the time of every measurement. Using Equation 3 APAR was then calculated from the previously obtained LAI estimates and PAR sums.

The data preparation process and methods used are presented graphically in the Figures 3 and 4.

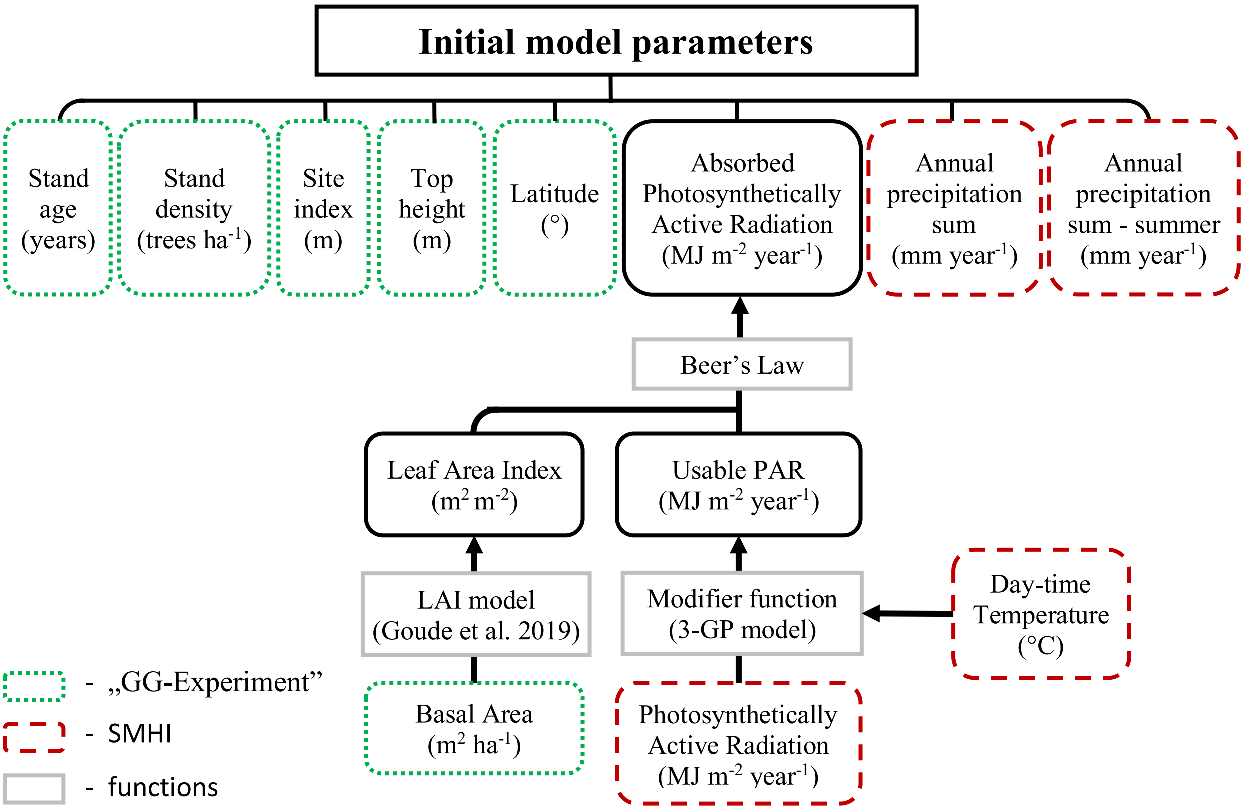

Figure 3. The diagram of the data sources for the stand and climate variables included in the initial models and the functions used. The green/dotted boxes represent the variables derived from the thinning and fertilization experiment ("GG – Experiment"), the red/dashed boxes - variables from the Swedish Meteorological and Hydrological Institute (SMHI), the black/solid boxes - variables computed with functions, and the functions are marked with the grey/solid boxes.

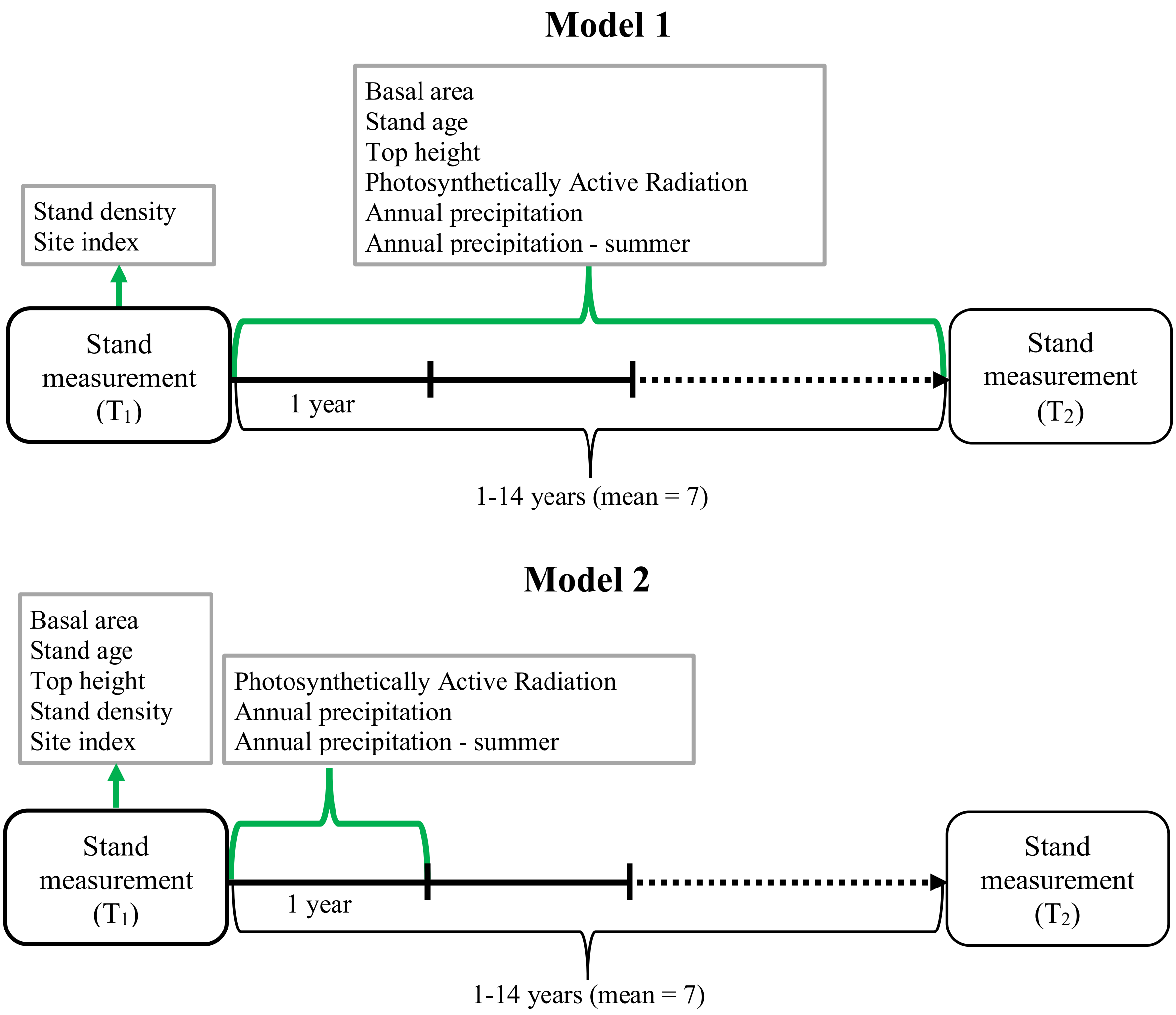

Figure 4. The diagrams representing two methods of data processing: Model 1 was based on averaged variables and Model 2 was based on variables from the beginning of the measurement periods. The timeline reflects the period between two following measurements of a given measurement plot. The green curly brackets indicate the period for which the variables were averaged, and the green arrows show the point in time from which the variables were taken.

2.3 Materials

Table 1 presents the summary of the climate variables for both data processing methods and the stand data, which were used in the subsequent fitting and validation of the models.

Table 1. Summary of the stand and site characteristics, and climate variables. Climate variables were calculated according to two analysed methods: as periodic averages and as values in the first year from the time of measurement (values in brackets).

Variable	Mean	Median	Range
Stand and site			
Basal area (m^2 ha^{-1})	21.8	20.4	6.0 – 51.6
Stand density (trees ha^{-1})	969	710	150 – 4000
PAI (m^3 ha^{-1} $year^{-1}$)	7.1	6.6	1.9 – 19.5
Top height (m)	17.8	17.8	9.0 – 28.3
SI (m)	24.4	24.6	17.2 – 33.0
Age (years)	57	56	26 – 95
Climate			
Mean annual temperature (°C)	4.0	4.3	-0.9 – 7.5
	(4.4)	(4.8)	(-1.4 – 8.5)
Mean annual day-time temperature (°C)	5.1	5.6	-0.3 – 8.4
	(5.6)	(6.0)	(-0.8 – 9.3)
Modified PAR (MJ m^{-2} $year^{-1}$)	1177	1232	797 – 1497
	(1317)	(1341)	(685 – 1730)
APAR (MJ m^{-2} $year^{-1}$)	847	849	439 – 1276
	(912)	(915)	(428 – 1462)
Precipitation (mm $year^{-1}$)	741	735	522 – 943
	(801)	(789)	(381 – 1148)
Precipitation in summer (mm $year^{-1}$)	256	258	146 – 374
	(284)	(289)	(96 – 641)

2.4 Model fitting and evaluation

Both datasets, including stand data from 205 measurement plots within 48 experimental sites (4 plots per site on average), were randomly divided. 32 sites were assigned for model fitting and 16 for validation (Fig. 1) which corresponded to 663 and 350 measurement periods, respectively. The model was fitted with the “lmer” function (“lme4” package; Bates et al. 2015). The linear mixed-effects model was chosen with regard to the experimental design to avoid pseudo-replication. For the variables for which heteroscedasticity was detected, a log transformation was applied to meet the basic assumptions of the statistical analysis. The transformation bias was corrected according to Baskerville (1972), and the correction factor should also be applied in the future use of these models. The p-values of the model parameters were calculated using the t-test and the Satterthwaite's method for estimating the degrees of freedom (“lmerTest” package; Kuznetsova et al. 2017). The pseudo-coefficients of determination for the fixed effects (R^2) and the entire model (R_c^2) were obtained using "r.squaredGLMM" function ("MuMIn" package; Bartoń 2022) and the root mean square error was calculated as follows:

$$\mathrm{RMSE} = \sqrt{\sum_{i=1}^{N}(y_i - f_i)^2/N} \tag{4}$$

$$\mathrm{RMSE\%} = \mathrm{RMSE}/\left(\sum_{i=1}^{N} f_i/N\right) \times 100 \tag{5}$$

where y_i are the observed values, f_i are the fitted values, and N is the number of observations. RMSE was computed using back-transformed values. Additionally, the variance inflation factor (VIF) was used to detect autocorrelation ("car" package; Fox & Weisberg 2019). The variables for which VIF was greater than 10 were considered significantly autocorrelated.

The models were built by manually simplifying the initial models using a stepwise approach. The removal of a given parameter was determined by whether: 1) there was a significant autocorrelation, 2) the parameter estimate was consistent with scientific knowledge, and 3) it significantly improved the model (p-value <0.05). Since the thesis aimed to construct a model based on the LUE concept, APAR was the key variable that could not be removed. Variables corresponding to the location and the main factors influencing LUE, namely latitude, age and structure of the stand, climatic conditions, and site fertility were also included, but disregarded where proved insignificant. The initial models were therefore as follows:

$$\mathrm{PAI} = \mathrm{APAR} + \mathrm{Age} + \mathrm{N} + \mathrm{H_{top}} + \mathrm{SI} + \mathrm{P_t} + \mathrm{P_s} + \mathrm{Lat} \tag{6}$$

where PAI was periodic annual volume increment (m^3 ha^{-1} $year^{-1}$), APAR was absorbed photosynthetically active radiation (MJ m^{-2} $year^{-1}$), Age was stand age (years), N was stand density (trees ha^{-1}), H_{top} was top height (m), SI was site index from top height (m), P_t was annual sum of precipitation (mm $year^{-1}$), P_s was annual sum of precipitation during summer months (mm $year^{-1}$), and Lat was latitude (°). In addition, the models accounted for the random effect of sites and the nested random effect of plots.

The models were validated by applying them to previously extracted datasets that were not used in the fitting process. Subsequently, the analysis of residuals was performed and the RMSE values were calculated according to the Equation 4 and 5 and the R^2 values were computed as follows:

$$R^2 = 1 - \frac{\sum_{i=1}^{N}(y_i - f_i)^2}{\sum_{i=1}^{N}(y_i - \bar{y})^2} \tag{7}$$

where y_i are the observed values, f_i are the predicted values, and $\bar{y}$ is the mean of the y_i values.

3. Results

3.1 Model fitting

The final models consisted of APAR, age and density of stand, site index, and total annual precipitation variables (Table 2). Top height was removed due to high autocorrelation (VIF > 10) with stand age and SI, while its correlation with PAI was much lower than in the case of the other two variables. Although the remaining variables were significant for the models, latitude and sum of rainfall during summer were not retained, as they displayed a correspondingly positive and negative relationship with PAI, which was inconsistent with the expectations based on plant physiology. Moreover, the random variability between treatments within the sites was 0 and therefore the nested random effect of plots was removed.

Table 2. Estimated parameters for the fitted PAI models: APAR (MJ m^{-2} $year^{-1}$), both stand age (years) and density (trees ha^{-1}), site index (m) and annual precipitation sum (mm $year^{-1}$); standard errors, p-values, pseudo-coefficients of determination for both the fixed effects (R^2) and the entire model (R_c^2), absolute (m^3 ha^{-1} $year^{-1}$) and relative (%) RMSE. Model 1 was based on averaged variables and Model 2 used variables from the beginning of the measurement periods.

Response variable	Parameters	Estimates	St. Error	p-value	R^2 (R_c^2)	RMSE (RMSE%)	Random variance
Model 1							
Log (PAI)	Intercept	-2.238e+00	2.668e-01	1.07e-15	0.72	1.64	
	APAR	6.564e-04	1.577e-04	5.22e-05	(0.83)	(21.9 %)	
	Age	-5.115e-03	1.198e-03	3.27e-05			
	Log (Density)	2.095e-01	2.645e-02	3.52e-13			
	SI	8.499e-02	8.027e-03	< 2e-16			
	Precipitation	5.043e-04	1.600e-04	0.00171			
	Site (random)						0.02186
Model 2							
Log (PAI)	Intercept	-1.089e+00	2.651e-01	4.72e-05	0.56	1.85	
	APAR	7.860e-04	1.037e-04	1.58e-13	(0.73)	(25.7 %)	
	Age	-5.039e-03	1.141e-03	1.21e-05			
	Log (Density)	1.877e-01	2.381e-02	1.82e-14			
	SI	3.997e-02	8.412e-03	3.76e-06			
	Precipitation	3.834e-04	8.044e-05	2.31e-06			
	Site (random)						0.02644

Both models fit reasonably well with the model data. Having compared the model based on average values (M_1) with the model based on the values from the beginning of the measurement periods (M_2), the former outperformed the latter, having a higher share of explained variance, 72 % compared to 56 %, and bearing a slightly lower error (Table 2). However, further analysis of residuals found M_1 biased positively and M_2 negatively for high PAI values. Moreover, M_2 tends to overestimate the dependent variable for the least productive stands (Fig. 5). The effect of APAR on PAI, taking into account the influence of other parameters, was greater in M_2 compared to M_1 (Fig. 6).

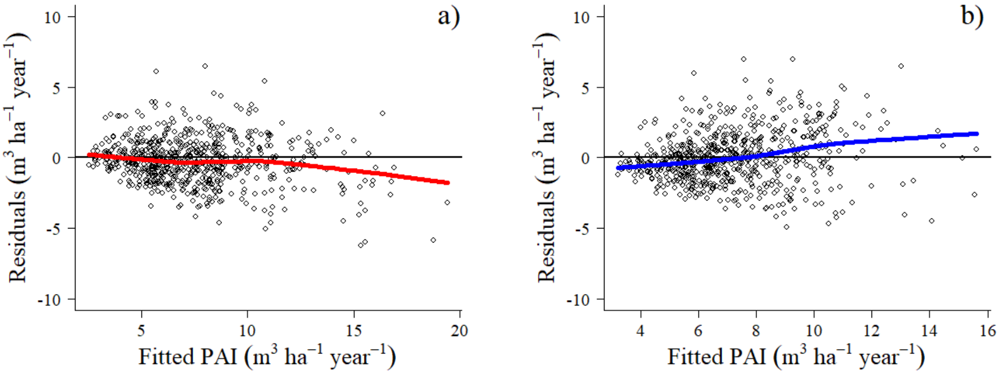

Figure 5. Residuals of the fitted PAI model based on averaged variables (M_1) ***(a)*** *and model based on variables from the beginning of the measurement periods (M_2)* ***(b)****. Coloured lines indicate the trend of the residuals. Note: The values shown in the graphs are back-transformed.*

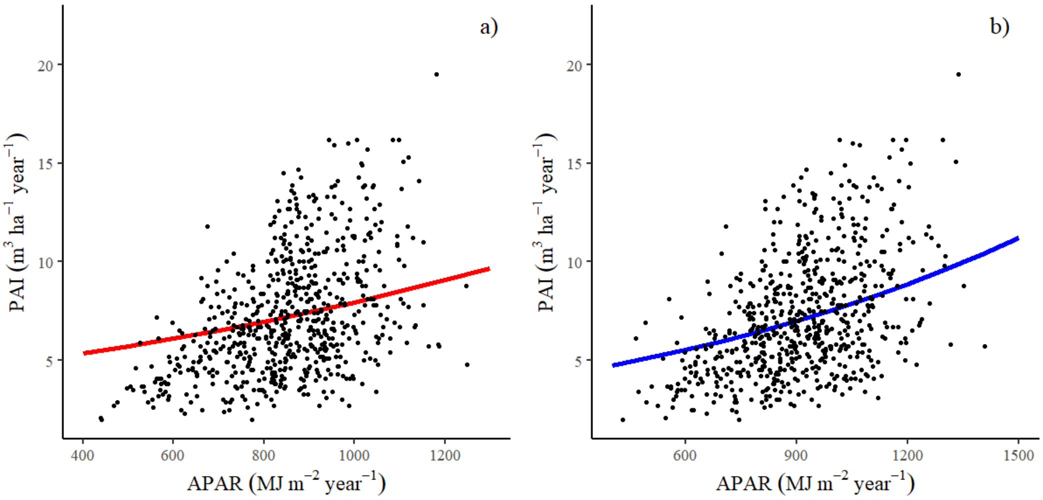

Figure 6. Absorbed photosynthetically active radiation (MJ m^{-2} $year^{-1}$) plotted against periodic annual volume increment (m^3 ha^{-1} $year^{-1}$). The lines represent the marginal effect of APAR on PAI in Model 1 ***(a)*** *and Model 2* ***(b)****.*

The inclusion of climate and stand variables in the models significantly improved their accuracy. The age of the stand was the most influential additional parameter, increasing the explained variance from 28 to 51 % for M_1 and from 26 to 41 % for M_2. The site index enhanced the model fit by another 14 % (M_1) and 7 % (M_2), while the stand density and the annual rainfall sum together accounted for a further 7 % and 8 % of the explained variance for M_1 and M_2, respectively. The additional parameters also reduced the RMSE from 37.6 to 21.9 % (M_1) and from 37.5 to 25.7 % (M_2).

3.2 Model validation

The validation of the models showed a similar performance in respect of the prediction error to that indicated by the analysis of the fit. The validation RMSE of M_1 and M_2 were 21.0 and 21.6 %, respectively. Likewise, the fitted and predicted values of M_2 explained a similar share of variability in the datasets. However, R^2 of M_1 dropped from 0.72 to 0.62 (Table 3). Therefore, despite differences in the fit of the models, their predictive power appeared to be similar.

Taking into account the smaller range of PAI values included in the validation dataset, the trend of the residuals from validation and fitting of M_1 was essentially the same. M_1 overestimated predictions for the most productive stands and slightly underestimated the mid-range PAI values (Fig. 7a). In contrast, the values fitted and predicted by M_2 showed different residual patterns for PAI > 8 m^3 ha^{-1} $year^{-1}$. In the validation, M_2 overestimated the stem volume increment for both the fastest and slowest-growing stands (Fig. 7c). Large discrepancies occurred when the models were validated against incompatible datasets (e.g., Model 2 with a validation data set based on averaged variables). It showed growing overestimation (M_1) or underestimation (M_2) with increasing PAI (Fig. 7b, d).

Table 3. Model validation results against data sets processed according to the methods used in Model 1 and Model 2. The validation data set M_1 consisted of averaged variables, and M_2 contained variables from the beginning of the measurement periods.

Models	Validation data set M_1		Validation data set M_2	
	RMSE (RMSE%)	R^2	RMSE (RMSE%)	R^2
Model 1	1.40 (21.0 %)	0.62	1.68 (23.4 %)	0.45
Model 2	1.50 (24.1 %)	0.56	1.47 (21.6 %)	0.58

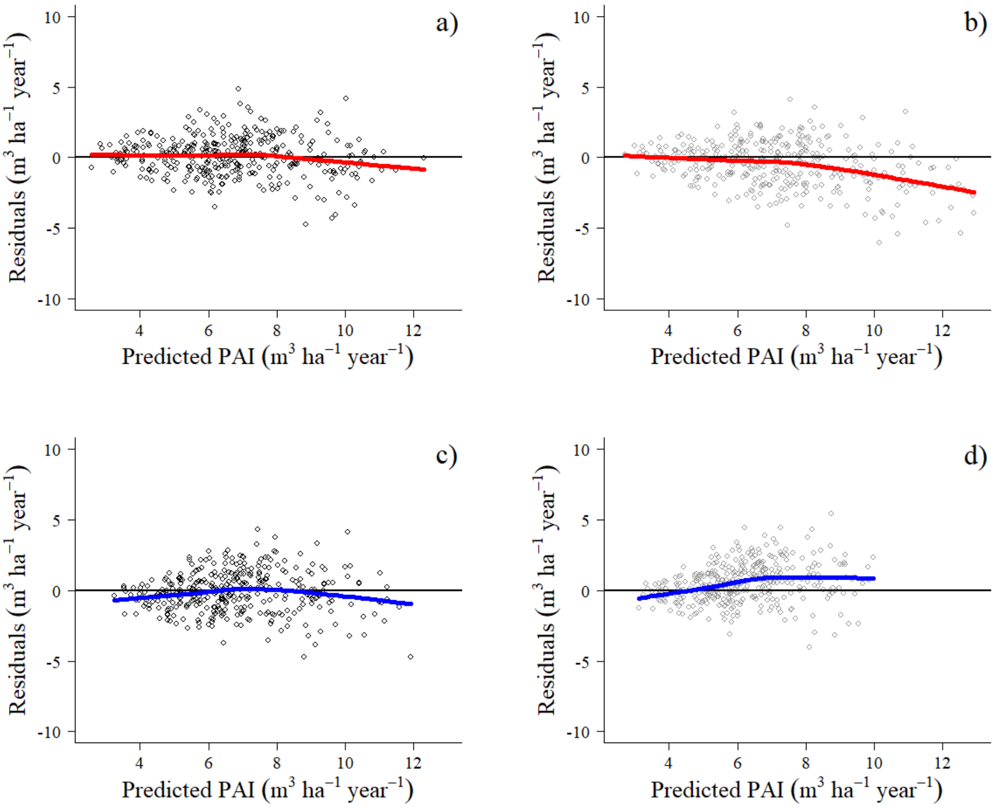

Figure 7. Residuals from the validation of the model based on averaged variables (M_1) ***(a,b)*** *and model based on variables from the beginning of the measurement periods (M_2)* ***(c,d)****. The plots* ***a*** *and* ***c*** *show the validations against the compatible data sets (method of data processing), while the plots* ***b*** *and* ***d*** *against the incompatible data sets. Coloured lines indicate the trend of the residuals.*

4. Discussion

The models developed in this study display a reasonable fit with the data. Moreover, the models showed a moderately large error, over 20%, which was additionally confirmed by the validation results. As expected, Model 1 offered a better fit as the use of averaged values smoothed out the year-to-year variability of the climate variables. However, the validation against the separate data sets indicated that both models explained a similar share of variance. This may suggest that although the year-to-year variation was reduced using averages, the variability between sites remained large and resulted from factors not considered in the models. The worse fit of models for high-production stands was caused by the asymmetric distribution of the PAI values in the data set, resulting in fewer plots with annual volume increment above 9 m^3 ha^{-1} $year^{-1}$. In addition, M_2 showed inconsistent residual patterns between model fitting and validation. This can be attributed to the larger marginal effect of APAR in M_2 compared to M_1, which relationship with PAI was highly variable for large APAR values (Fig. 6). The validation indicated that the unbiased predictions can only be obtained for part of the volume increment range, which implies that these models should be used with caution for the fastest and slowest-growing stands. Neither can these models be used interchangeably without producing negatively or positively biased predictions. M_2 tends to underestimate PAI over the one-year prediction period and M_1 produces the overestimated longer-term predictions.

Compared to the Heureka empirical model commonly used in Sweden, both models displayed significantly inferior performance. Fahlvik et al. (2014) showed that the volume increment predictions generated by Heureka deviated on average by less than 0.5 % from the observed values. This likely indicates that the benefits of including climatic variables that allow adjustment to changing conditions are outweighed by the lower accuracy of the models developed in this thesis.

One of the reasons for the inferior performance could be the replacement of the above-ground or total biomass production with the stem volume increment. Growth conditions affect not only the rate of biomass production but also the partitioning of assimilated carbon between foliage, branches, stem, and roots (Cannell 1989). Focusing only on the main harvestable part of the tree, while practical, could disrupt the linear relationship between absorbed radiation and biomass production. In studies in which gross primary productivity estimated from measurements on the eddy covariance flux towers was used, the R^2 coefficients of the LUE relationship ranged from 0.45 to 0.64 (Turner et al. 2003; Garbulsky et al. 2010), which largely exceeds the share of the explained variance by M_1 ($R^2=0.28$) and M_2 ($R^2=0.26$), when only APAR was included.

The lower precision could also result from the lack of accurate and frequent measurements of the absorbed radiation or LAI. APAR estimates were derived indirectly from the basal area using two Equations (2 & 3), possibly resulting in accumulation of inherent uncertainties. Rarely do forest canopies meet the requirements of the Beer's Law, and the accuracy of the estimates is influenced by the crown's structure and the properties of the leaves (Binkley et al. 2013; Waring et al. 2016). Uncertainties related to the calculation of LAI could stem from the model itself and from disregarding possible temporary changes in leaf area caused, e.g., by water stress or defoliation caused by pests. In addition, possible errors in the interpolation of climate variables could also have some impact on the precision of the PAR data, which resulted in lower accuracy of the APAR estimates. Direct measurements of absorbed radiation and dry biomass produced are expensive and labour-intensive. Still, they can accurately estimate the light use efficiency, as exemplified by the well-fitted LUE models developed for willow by Cannell et al. (1987) with R^2 exceeding 0.9.

The inclusion of climate and stand variables in the models developed in this thesis substantially improved their accuracy. The significant parameters retained correspond to all the major factors influencing LUE, such as age, soil fertility and water availability. The influence of temperature was included by the modifier of useable PAR, which allowed to exclude the sum of radiation intercepted in the winter months when the photosynthesis process ceases.

The age was negatively correlated with PAI, which corresponds with the findings of Saldarriaga and Luxmoore (1991) and Martin and Jokela (2004) on the steady decline of LUE with the development of the stand after exceeding a certain age. The significant positive effect of the site index in the models satisfactorily reflected the impact of site fertility on the stand growth, as the photosynthesis rate and the allocation of carbon to aboveground biomass, and thus the stem volume increment, increase alongside the soil nutrient content (Cannell 1989; Landsberg & Sands 2011; Waring et al. 2016). The effect of stand density can be attributed to the impact of tree spacing on biomass partitioning between stem and branches (Cannell 1989). In addition, higher density may also result in faster and greater development of the leaf area, which allows for more efficient canopy expansion if gaps are formed. The annual precipitation was poorly positively correlated with the stem volume increment. This was in line with the observed effects of water availability on LUE (Stape et al. 2008; Waring et al. 2016). However, the poor correlation contradicts the findings of Garbulsky et al. (2010) indicating that annual rainfall is the main factor controlling growth across terrestrial biomes and best explains the spatial variability of LUE. This may suggest that water scarcity rarely limits forest growth in Sweden, which is in line with other studies that found water to be a significant limiting factor only in certain regions (Bergh et al. 1999; Belyazid & Zanchi 2019). Furthermore, Scots pine is characterized by high resistance to drought and low soil moisture requirements (Houston Durrant et al. 2016).

On the other hand, the poor correlation could also result from omission of the influence of temperature, water holding capacity of soil and runoff on the overall water balance (Landsberg & Sands 2011), which may also explain the negative relationship between precipitation in summer months and the PAI obtained in the initial models. Due to its incompatibility with plant physiology, this parameter was removed. Another variable not retained in the final models was latitude, which showed a positive correlation with PAI. This was in clear contradiction to the global patterns of changes in productivity which diminishes with growing distance from the equator (Gillman et al. 2015).

The results of the validation suggest that replacing the complex equations expressing physiological processes with the linear relationship of climate, site and stand variables against the volume increment failed to reflect adequately the influence on stand growth, which deteriorated prediction accuracy of the models. Probably, the lack of sufficient representation of factors influencing the water balance, for example, by disregarding equations of air vapor pressure deficit and soil water content, was of great importance, as they describe in more detail the impact of water availability and temperature on the stomatal conductance, and thus on the photosynthesis rate (Landsberg & Sands 2011). Hybrid models with a greater proportion of mechanistic elements showed a better performance. For instance, the popular 3-GP model tested against independent data from southern Sweden produced stand volume estimates that explained 97% of the variation (Landsberg et al. 2003), over 1.5 times more than in the case of M_1 (R^2=0.62) and M_2 (R^2=0.58).

While the models developed in this study proved less accurate than the more complex hybrid models, their undoubted advantage is the ease of application. They require only readily available climatic variables collected by meteorological stations and basic stand and site parameters measured in forest inventories, as well as necessitate no complex calculations. Considering their simplicity combined with climate sensitivity, this simplified hybrid modelling approach appear worthy of further exploration.

Possible improvements may include, in particular, the use of better-quality APAR data, which is a key variable for LUE-based models. While thorough and frequent measurements of the absorbed radiation may prove unattainable, especially when applied on a large scale, the rapidly developing remote sensing might offer new, promising opportunities. Research has shown that contemporary fAPAR products are close to meeting the 10% accuracy requirement set by the UN Global Climate Observing System (Liang & Wang 2020). Although their spatial resolution stays predominantly within the range of 1 km, some may already provide information at the level of a single stand (Putzenlechner et al. 2019). However, instrument limitations and high costs make it impossible to achieve both high spatial and temporal resolutions simultaneously. In the future, this could be overcome by using a constellation of relatively inexpensive microsatellites that enable detailed and frequent data acquisition (Dash & Ogutu 2016), which could not only improve the accuracy of the models but also greatly facilitate their practical application.

5. Conclusions

1. The simplified hybrid models based on the LUE concept were able to predict stem volume growth in boreal Scots pine stands whereas the inclusion of climate and stand variables significantly improved their prediction accuracy. However, the greater simplicity of use was attained at the expense of precision of the estimates with both models underperforming compared to the popular hybrid and empirical models.
2. Possible reasons for the inferior performance were the replacement of aboveground or total biomass production with stem volume increment, the accumulation of uncertainties related to the APAR estimation method, and insufficient representation of the effect of individual factors on the stand growth.
3. Using better quality APAR data could possibly improve the prediction accuracy and rapidly developing remote sensing may soon enable the acquisition of more accurate data with high temporal resolution. This would allow for a relatively inexpensive and low labour-intensive method of constructing models built upon the LUE concept. Moreover, the easy availability of the data would greatly facilitate their practical application.

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