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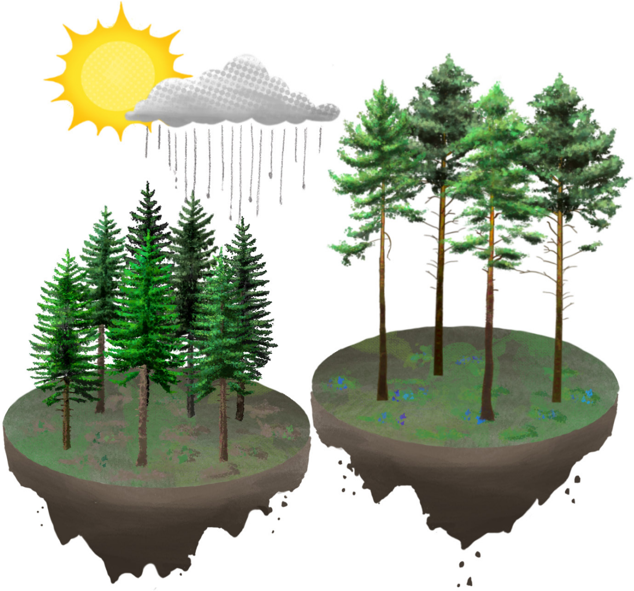
Hybrid growth models for Norway spruce and Scots pine

Using leaf area and light use efficiency for predicting stemwood production

MARTIN GOUDE



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Abstract

With a changing climate, it has become more challenging to make long-term sustainable forest management decisions because many models and planning systems have difficulties accounting for the effects of climate change. One way to improve these tools is to include ecophysiological variables that respond to changes in weather and climate. The aim of this thesis was to investigate the use and implementation of ecophysiological concepts around light interception and light use in models for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) forests in Sweden. Different methods for estimating leaf area were compared in eight established forest experiments and showed that tree- and stand-level leaf area could be estimated using stand and tree variables together with indirect optical canopy measurements (Paper I). The higher leaf area for Norway spruce showed the importance of species-specific models. When using leaf area models in practice, measures of stand heterogeneity improve accuracy (Paper II). New species-specific mensurational basal area models were developed using permanent sample plot data (Paper III). There were minor differences in precision between these new models and an existing stand basal area growth model. Climate-sensitive hybrid models were developed from the mensurational models by replacing time with potentially usable light sums modified by climate factors (Paper IV). The hybrid models did not improve prediction precision compared to the mensurational models. However, tests with different climate scenarios demonstrated the ability of the hybrid models to capture both positive and negative effect from changes in temperature and precipitation, with a sizeable local variation in growth response. This thesis shows that it is possible to include climate sensitivity in forest models through light interception and light use. These models allow for better predictions of forest development and better-informed decision making for sustainable forest management.

Keywords: leaf area index, basal area, forest modelling, growth and yield, climate change, light use efficiency, Norway spruce, Scots pine

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Hybridtillväxtmodeller för gran och tall

Sammanfattning

Med ett föränderligt klimat har det blivit svårare att fatta långsiktigt hållbara skogsskötselbeslut på grund av att många modeller och planeringssystem inte inkluderar klimatförändringseffekter. Ett sätt att förbättra dessa verktyg är att införa ekofysiologiska koncept som kan svara på klimatförändringar. Syftet med denna avhandling var att undersöka användning och implementering av ekofysiologiska koncept kopplade till skogens upptag och nyttjande av solljus i modeller för tall- (*Pinus sylvestris* L.) och granskog (*Picea abies* (L.) Karst.) i Sverige. Olika metoder för att mäta bladarea jämfördes i åtta etablerade fältförsök och visade att bladarea för träd och bestånd kunde uppskattas med hjälp av bestånd- och trädvariabler tillsammans med optiska indirekta mätningar av trädkronorna (Studie I). Den högre bladarean för gran visade också på vikten av trädslagsspecifika modeller. Vid användning av bladareamodellerna i praktiken ger ett mått på beståndets heterogenitet högre noggrannhet (Studie II). Med hjälp av data från permanenta provytor togs nya artspecifika empiriska modeller för grundyta fram (Studie III). Skillnaden i precision var liten mellan de nya modellerna och en befintlig tillväxtmodell. Från de empiriska modellerna utvecklades klimatkänsliga hybridmodeller genom att ersätta tid med potentiellt användbar ljussumma modifierad av klimatfaktorer (Studie IV). Hybridmodellerna förbättrade inte precisionen jämfört med de empiriska modellerna. Däremot visade tester av olika klimatscenarier på hybridmodellernas förmåga att fånga upp både positiva och negativa effekter efter förändringar i temperatur och nederbörd, med stor lokal variation i tillväxtrespons. Denna avhandling visar att det är möjligt att inkludera klimatkänslighet i skogliga modeller genom att använda ljusupptag och ljusanvändning. Dessa modeller möjliggör bättre förutsägelser om skogens utveckling och ett mer informerat beslutsfattande för ett hållbart skogsbruk.

Nyckelord: bladareaindex, grundyta, skoglig modellering, tillväxt, klimatförändringar, ljusanvändningseffektivitet, gran, tall

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Dedication

To Ida and Emil
In memory of my mother Kerstin (1958 - 2018)

Contents

List of publications 9

List of tables 11

List of figures 13

Abbreviations 15

1. Introduction 17
   - 1.1 Forests and climate change 17
   - 1.2 Solar radiation and forest growth 19
   - 1.3 Estimating leaf area 20
   - 1.4 Using light interception in forest growth predictions 20

2. Thesis aim 25

3. Materials and methods 27
   - 3.1 Leaf area measurement 27
   - 3.2 Swedish National Forest Inventory 28
   - 3.3 Swedish long term forest experiment data 29
   - 3.4 Stand and spectral heterogeneity 29
   - 3.5 Mensurational growth and yield modelling 30
   - 3.6 Hybrid growth and yield modelling 33

4. Results and discussion 35
   - 4.1 Leaf area correlations with stand and site measurements 35
   - 4.2 Basal area – LAI relationships can be improved with structural and spectral heterogeneity 38
   - 4.3 Growth and yield model comparisons 39
   - 4.4 Effect of climate change on hybrid model predictions 41
   - 4.5 Difficulties in using Swedish NFI data for growth and yield modelling 44
   - 4.6 Model limitations and future development and improvements 45

5. Conclusions 49

References.. 51

Populärvetenskaplig sammanfattning 59

Acknowledgements 63

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I. Goude, M.*, Nilsson, U. & Holmstrom, E. 2019. Comparing direct and indirect leaf area measurements for Scots pine and Norway spruce plantations in Sweden. *European Journal of Forest Research*, 138, 1033-1047.

- II. Mensah, A. A.*, Petersson, H., Saarela, S., Goude, M. & Holmstrom, E. 2020. Using heterogeneity indices to adjust basal area - Leaf area index relationship in managed coniferous stands. *Forest Ecology and Management*, 458.

- III. Goude, M.*, Nilsson, U., Mason, E. G., Vico, G. Comparing growth and yield models for Norway spruce and Scots pine monoculture stands. (Manuscript)

- IV. Goude, M.*, Nilsson, U., Mason, E. G., Vico, G. Effects of climate change on Norway spruce and Scots pine stands – Evaluation using hybrid physiological/mensurational models of basal area. (Manuscript)

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The contribution of Martin Goude to the papers included in this thesis was as follows:

I. Developed the research idea, was responsible for data collection, analysis and manuscript writing with support of the co-authors.

II. Supported in the analysis of hemispherical photos and leaf area measurements and participated in manuscript writing led by Mensah, A. A.

III. Developed the research idea, led the work in data analysis and manuscript writing with support of the co-authors.

IV. Developed the research idea, led the work in data analysis and manuscript writing with support of the co-authors.

List of tables

Table 1. Description of the Norway spruce (NS) and Scots pine (SP) data used for model fitting and model comparison in **Paper III**. The models are the basal area five-year growth models (Growth-S and Growth-P) and total basal area growth and yield models (GY-S and GY-P). Data sources were Swedish National Forest Inventory (NFI) and Swedish long term forest experiments (LFE). 31

List of figures

Figure 1. The difference between a time-based mensurational model and a PULSE hybrid model in their ability to respond to environmental changes through increased and decreased potentially usable light sums (PULS). a) climate adjusted PULS for the PULSE hybrid model and historical average PULS for the time-based mensurational model. b) basal area development over time for the time-based mensurational model and the PULSE hybrid model. 23

Figure 2. Two hemispherical photographs used in **Paper I** from the Främlingshem experimental site in central Sweden (60.5059˚ N, 16.9058˚ E). 28

Figure 3. Locations of plots used in the modelling process. (a) plots used in the growth and yield model (GY-P and GY-S) fitting (552 Norway spruce and 1288 Scots pine), (b) plots for GY-P and GY-S validation (284 Norway spruce and 634 Scots pine), (c) plots for growth model (Growth-P and Growth-S) fitting (1422 Norway spruce and 2059 Scots pine), and (d) plots for Growth-P and Growth-S validation (708 Norway spruce and 1029 Scots pine). 32

Figure 4. The potentially usable light sum (PULS) calculation. Monthly incoming light is multiplied by the minimum modifier value of temperature or frost and soil water or VPD to get monthly potentially usable light. PULS is obtained by summing all monthly potentially usable light since stand establishment. 34

Figure 5. Direct measurements of LAI (m^2 m^{-2}) against indirect measurements, LAIe (m^2 m^{-2}), for Scots pine and Norway spruce. LAIe in the

plots comes from (a) an LAI-2200C plant canopy analyzer, and hemispherical photos analysed with (b) Gap Light Analyzer (GLA) or (c) CAN-eye. The dashed red lines represent the conversion models from LAIe to LAI for Norway spruce, and the solid red lines the conversion models for Scots pine. The solid black line shows a 1 to 1 relationship (Goude et al., 2019).. 36

Figure 6. Individual tree half total leaf area (LA, m^2) plotted against diameter at breast height (DBH, mm) for Norway spruce and Scots pine. The site-specific regression models used to estimate LA are represented by the black (Norway spruce) and grey (Scots pine) lines. The thicker red lines represent the general site-independent models for LA, where dashed = Norway spruce and solid = Scots pine (Goude et al., 2019). 37

Figure 7. Residual plots of the model comparison against independent data from the GG experiment. Panels (a), (b) and (c) are Scots pine, and (d), (e) and (f) are Norway spruce. (a) (GY-P) and (d) (GY-S) show residuals for the growth and yield models. (b) (Growth-P) and (e) (Growth-S) show residuals for the growth models, while c and f show residuals for Elfving's model used on Scots pine and Norway spruce data, respectively. The thick red lines show the residual trend. 40

Figure 8. Relative change in basal area (%) from altered input climate data compared with current climate after 20-year simulations. The part of the scenario name ending with % refers to the relative precipitation increase, and the part ending in ˚C refers to the temperature increase; where one of these is absent, that variable was not changed. The simulations were conducted using the hybrid models for Scots pine and Norway spruce containing modifiers for temperature, frost, vapour pressure deficit, and soil water. .. 43

Figure 9. Relative change in basal area (%) from altered input climate data compared with current climate after 20-year simulations. The simulations were conducted using the hybrid model for Scots pine containing modifiers for temperature, frost, vapour pressure deficit, and soil water. Each dot represents a randomly selected permanent sample plot from the Swedish NFI. 44

Abbreviations

DBH	Diameter at Breast Height
GLA	Gap Light Analyzer
LA	Individual tree leaf area
LAI	Leaf Area Index
LAIe	Effective/ indirect leaf area index
LUE	Light Use Efficiency
NFI	National Forest Inventory
PULS	Potentially Usable Light Sum
PULSE	Potentially Usable Light Sum Equations
SLA	Specific Leaf Area
SMHI	Swedish Meteorological and Hydrological Institute
VPD	Vapour Pressure Deficit

1. Introduction

1.1 Forests and climate change

In Sweden, wood has been an essential product for mining, housing, shipbuilding, energy, and export for centuries. During the 19th and 20th centuries, more wood resources moved to the pulp and timber industries (Eliasson and Hamilton, 1999). However, the extensive use of forests in industrialisation led to overexploitation, with reduced forest area and volume. The overexploitation led to the implementation of new forest legislation and policies at the beginning of the 20th century, focusing on sustainable wood production (Fries et al., 1997). Because of forests' importance to the Swedish economy, silviculture has a long tradition. The first Swedish silviculture handbook was published in the 18th century (Rosensten, 1737), and forestry higher education was started at the Royal Forest Institute in 1829 (Kardell, 2004). Today, Sweden is a forest-rich county with 69% (27.9 million ha) of its land area covered by forest, and 58 % (23.5 million ha) by productive forests. There are two dominant species in Swedish forests, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), which make up 39.3% and 39.7% of the standing volume, respectively (SLU, 2021). Scots pine is a light-demanding pioneer species adapted to recurrent disturbances like fires, with a high stress tolerance which allows it to grow under a wide range of conditions (Engelmark and Hytteborn, 1999). Norway spruce is a highly competitive, shade tolerant, and late successional species adapted to more stable conditions without frequently-occurring disturbances (Engelmark and Hytteborn, 1999; Lundmark, 1988).

Lately, climate change has arisen as a challenge that puts new demands on forest management. In a future with changing growing conditions, it is more difficult to make sustainable forest management decisions that work both in a short- and long-term perspective. The expected climate changes are mainly increased temperatures and changed patterns of precipitation (IPCC, 2014). The temperature changes are expected to be larger further north, resulting in more significant changes in boreal forest regions (Jacob et al., 2014; Cattiaux et al., 2013). The effects on precipitation are less clear than temperature, with possible drier summers and wetter winters in boreal regions of northern Europe. However, substantial local variation is expected (Eklund et al., 2015; Ruosteenoja et al., 2018; SMHI, 2020).

These climate predictions contain many uncertainties, resulting in even greater uncertainty around climate change effects on forests. There are suggestions that warmer temperatures will lead to higher production in boreal forests because of current temperature limitations (Allen et al., 2010; Bergh et al., 1999). Positive effects on production have already been seen, where higher temperatures can partly explain increased height growth (Mensah et al., 2021). Other studies have also suggested that warmer temperatures will increase production, but combined with the adverse effects of increased evapotranspiration, the net effect could be negative (Belyazid and Zanchi, 2019; Ruiz-Pérez and Vico, 2020). Droughts caused by high temperatures and low rainfall, such as in the summer of 2018, reduce forest production and could be more common in the future (Ruosteenoja et al., 2018; Peters et al., 2020). Apart from these more direct effects of climate change, other more indirect aspects like insects and pathogens, mineralisation and nutrient availability, and forest fires will also affect future forest production (Ciais et al., 2014).

Making accurate estimates of the effects of climate change on forests and forest production is essential for sustainable forestry. An example illustrating the importance of this is the Swedish forest impact assessment (SKA; Claesson et al., 2015), where different forest management scenarios are projected to show the potential future wood supply and future forest conditions. These forecasts provide a basis for sustainable wood harvest and industry investment and show potential future forest landscapes depending on management strategy. If the climate effect on production is not accurately accounted for, these projections could give a misleading image of future forest conditions. Faults in the projections will increase the risk of poor choices about what management strategy will provide the best outcomes for the set objectives.

With the ongoing and predicted changes to climate in the boreal region, tools for management planning and predicting forest development need to be flexible and respond to these changes. One way to do this is to implement variables affecting tree growth into models and forest practice, for example, photosynthesis and how forests' use of solar radiation is affected by climate change.

1.2 Solar radiation and forest growth

Through photosynthesis, leaves transform solar radiation, together with carbon dioxide (CO_2) and water (H_2O), into carbohydrates that trees use to grow and stay alive. The efficiency of turning solar radiation into biomass is called light use efficiency (LUE) (Monteith, 1977). LUE varies depending on species and site properties like nutrient and water availability (Cannell, 1989). However, the relationship between absorbed radiation and total biomass produced is linear (Cannell, 1989; Waring et al., 2016). This simple relationship can be used to estimate crop production but requires quantification of incoming solar radiation absorbed by the canopy.

The most common way of estimating absorbed radiation is by using Beer's Law (Monsi and Saeki, 2005). The equation represents a logarithmic relationship between leaf area index (LAI) and light interception. For needle-like leaves, the definition of LAI is half the total green leaf area per unit ground surface area ($m^2 m^{-2}$) (Chen and Black, 1992). More simply, LAI is a measure of the foliage area that absorbs solar radiation. LAI is primarily a stand-level measurement. Beer's Law as used in forest stands is often an oversimplification of the relationship between LAI and light interception because few forests live up to its assumption of a closed canopy with randomly distributed foliage (Waring et al., 2016). Therefore, the actual relationship between LAI and light interception varies. The shape of the relationship depends on whether trees or stands are studied and their canopy structure (Binkley et al., 2013a).

1.3 Estimating leaf area

Methods for estimating LAI can be divided into two categories: direct measurement and indirect measurement. With direct measurement, biomass is collected, and leaves are directly measured to calculate LAI. However, to avoid measuring all leaves, a foliage sample is often used to obtain the relationship between leaf area and dry leaf biomass: specific leaf area (SLA, $cm^2\ g^{-1}$). Together with the collected biomass, SLA is used to upscale sample leaf area to the whole tree (LA, m^2) and stand level (LAI) (Gower et al., 1999; Jonckheere et al., 2004). The biomass collection is done by either destructive harvesting or by collecting litterfall. Direct methods are the most reliable way of estimating LAI. Therefore, they are often used to compute the actual leaf area of a stand against which less accurate methods are compared and validated (Barclay, 1998; Fassnacht et al., 1994; Sampson and Allen, 1995; Gower et al., 1999). For indirect measurements, LAI is estimated using optical instruments that either try to quantify canopy closure or utilise Beer's Law by measuring the differences in solar radiation underneath and above the canopy (Chen and Cihlar, 1996; Chen et al., 1997; Jonckheere et al., 2004). There are many advantages with the indirect methods, like requiring less time and labour. With remote sensing methods, large areas can be covered and estimated quickly. However, indirect methods tend to underestimate LAI compared to direct measurements (Gower and Norman, 1991; Gower et al., 1999). Because of this, the LAI estimations from indirect measurements must be corrected using models developed from the comparison between direct and indirect LAI (Breda, 2003; Chen, 1996; Kussner and Mosandl, 2000; Stenberg, 1996). These correction models often include measures of stand density, such as basal area ($m^2\ ha^{-1}$) or stem density (stems ha^{-1}), to capture the relationships between LAI and stand structure (Mason et al., 2012; Barclay and Trofymow, 2000).

1.4 Using light interception in forest growth predictions

Reliable measures of foliage and absorption of solar radiation are essential for many models predicting and explaining plant growth, water usage, and carbon balances (Chen et al., 1997; Landsberg and Waring, 1997). The underlying processes and physiological responses in trees need to be integrated into these models to take light absorption and its impact on growth into account. Trying to explain the underlying processes behind tree growth is often associated with process-based modelling. Such models can often become very complex and challenging to use because of data requirements and a required deep understanding of the ecophysiological system. However, with the right type of data and models, this is a powerful tool for understanding and predicting plant ecosystems (Taylor et al., 2009; Weiskittel et al., 2011).

In forestry, such detailed information is often not available, and the demand is towards models that are easy to use in practice. Therefore, mensurational models based on empirical statistical correlations from forest inventories are often used. These sometimes simple models are often very good at predicting stand and tree development when the conditions are the same as when the model was parameterised (Vanclay and Skovsgaard, 1997). However, issues arise when growth conditions differ from those on which the model was based. These changed conditions will affect forest growth, but a mensurational model cannot account for them (Landsberg, 2003; Kimmins et al., 2008).

Hybrid models can obviate this problem by taking advantage of the simplicity and accuracy of mensurational models and the process understanding and flexibility of process-based models. A hybrid model is built around statistical correlations from forest inventory data, integrated with physiological concepts (Henning and Burk, 2004). It is important to remember that the distinction between model types is not so clear in practice, as many models contain some form of hybridisation. Mensurational models are rarely created without including any biological processes. Prosses-based models are also sometimes based on statistical relationships found in inventory data.

With a changing climate, it is necessary to account for the ecophysiological response of trees to make reliable predictions of forest development. One way is the potentially usable light sum equations (PULSE) hybrid approach (Mason et al., 2007). It combines LUE and mensurational principles to make models more flexible and predictive of climate change impacts on forest production. In the PULSE approach, time is replaced by the cumulative potentially usable light sum (PULS) to better reflect the ecophysiological processes driving tree growth. By also including key weather and other environmental factors regulating the proportion of radiation usable by trees, PULSE models can adjust to local circumstances and account for short- and long-term climate variation.

The difference between a traditional time-based mensurational model and a PULSE hybrid model is the ability to respond to climate change, illustrated in a hypothetical example in Figure 1. Mensurational time-based models assume the same amount of available radiation each period (an historical average from the period on which that model was based). In contrast, PULSE models adjust to environmental changes reflected by PULS. As illustrated in Figure 1, when PULS is low (because of cold temperatures or drought), basal area growth is low, as in period 1 (between years 1 and 2). With more PULS available (because of warm and wet weather), the result is higher basal area growth, as in period 2 (between years 2 and 3). Across all nine periods, there was a positive trend of better growing conditions that the PULSE model could capture through increased PULS. The mensurational model could not adjust to these changes and under-predicted basal area in the later periods. This example illustrates the usefulness of PULSE hybrid models in a future with a changing climate. By taking short- and long-term changes into account, PULSE models can make more accurate predictions of future growth than traditional mensurational models.

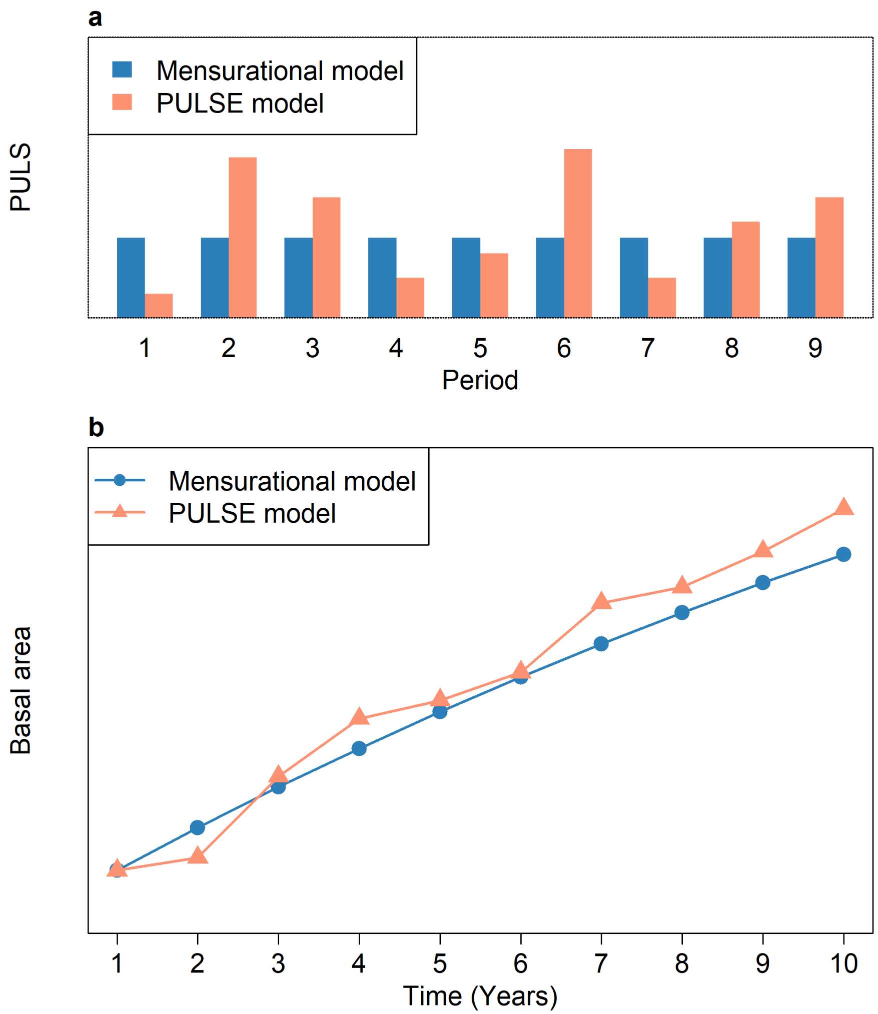

Figure 1. The difference between a time-based mensurational model and a PULSE hybrid model in their ability to respond to environmental changes through increased and decreased potentially usable light sums (PULS). a) climate adjusted PULS for the PULSE hybrid model and historical average PULS for the time-based mensurational model. b) basal area development over time for the time-based mensurational model and the PULSE hybrid model.

2. Thesis aim

This thesis investigates the use and implementation of ecophysiological concepts, specifically light interception and light use efficiency, into forest growth and yield models for Scots pine and Norway spruce in Sweden. The first part of the thesis focuses on individual tree leaf area (LA) and stand-level leaf area index (LAI). LA and LAI relationships with tree and stand measurements are explored, and different ways of measuring LAI in homogenous experimental plots are evaluated (**Paper I**). One of those methods was also tested in more heterogeneous managed forests. Here it was investigated whether measures of stand heterogeneity could explain variation in the relationship between basal area and LAI (**Paper II**).

In the second part of the thesis, new species-specific models for predicting basal area development were created using mensurational approaches (**Paper III**). The prediction precision of these new models was compared with an already existing basal area growth model.

Based on the mensurational models developed in **Paper III**, new hybrid models were developed to account for climate effects on basal area production (**Paper IV**). The hybrid models' response to climate changes was also illustrated by applying different scenarios of increased temperatures and precipitation.

The following research questions are addressed in this thesis:

I. Can leaf area be estimated using indirect measurements from optical instruments, tree size, and stand variables? Are there species differences in these leaf area relationships?

II. Will the increased structural heterogeneity in managed forests compared to experiments explain uncertainties in the relationship between basal area and LAI? Can this relationship be improved by including information on spectral heterogeneity?

III. Will growth and yield models give better long-term predictions than regression growth models? Will regression growth models based on data from the 2000s improve predictions compared to regression models from the 1980s?

IV. Will hybrid models have better precision compared to traditional time-based mensurational models? How do the hybrid models respond to changes in climate, and is the response different in different regions of Sweden?

3. Materials and methods

3.1 Leaf area measurement

Data for comparing leaf area measurements (**Paper I**) were collected at eight established forest experimental sites at latitudes between 55° and 64° N. The experimental sites consisted of even-aged monocultures of Norway spruce and Scots pine. The data collection was done outside of the growing season, in early spring, late autumn, and winter.

Indirect measurements were made in two ways; measuring diffuse sky radiation with an LAI-2200C plant canopy analyser and using a camera with a fisheye lens to take hemispherical photographs of the canopy. For the LAI-2200C, 60 measurements were taken in each plot and used to calculate an indirect leaf area index, called effective leaf area index (LAIe). The hemispherical photographs (Figure 2) were taken at five spots in each plot, and the LAIe values were based on the mean value of these five pictures. The pictures were analysed using two different software packages, Gap Light Analyzer (GLA) and CAN-eye.

Direct measurement of leaf area was conducted through destructive sampling. In total, 142 trees were sampled, 107 Norway spruce and 35 Scots pine. The selected trees were cut down, and the weight of all branches was measured. By measuring surface area of a needle sample and calculating the ratio of weight to surface area (specific leaf area, $cm^2\ g^{-1}$), leaf area was computed for the sampled trees. All trees in the plots were assigned a leaf area based on their diameter at breast height (DBH). Finally, the total plot leaf area was divided by plot size to get leaf area index (LAI).

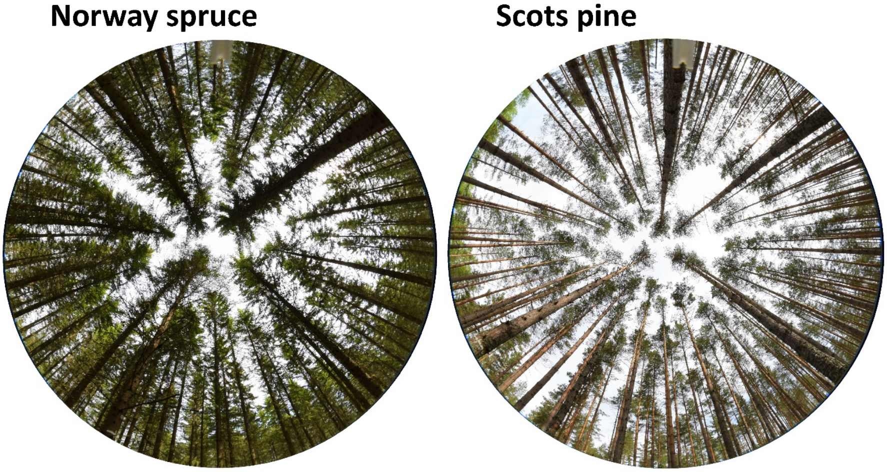

Figure 2. Two hemispherical photographs used in **Paper I** from the Främlingshem experimental site in central Sweden (60.5059˚ N, 16.9058˚ E).

3.2 Swedish National Forest Inventory

The Swedish National Forest Inventory (NFI) started its nationwide surveys using temporary sample plots in 1953. Permanent sample plot inventory, where the same plot is revisited, started in 1983. These permanent plots are re-measured once during each 5-year inventory cycle (with intervals up to 10 years during the 1990s). Each circular plot is divided into a large plot, with a radius of 10 m (7 m for temporary plots), and a small plot that has changed size over time (Fridman et al., 2014). In the large plot, the diameter at breast height (DBH) of all trees with a DBH ≥ 10 cm is measured with callipers. In the small plot, trees with a DBH ≥ 4 and < 10 cm are measured. Since trees are remeasured in the permanent plots, mortality can be captured. In addition, the cause of absence, damages and plot-level management are recorded. For the temporary plots, height and age are measured on a sample of the callipered trees and predicted for the rest based on those measurements. At permanent plots, age is measured outside the 10 m plot and predicted for the trees inside. Apart from individual tree measurements, data are recorded on site and stand properties like previous stand management, amount of deadwood, soil properties, and ground vegetation (Fridman et al., 2014). During 2016 and 2017, hemispherical photographs were also taken as part of both the temporary and permanent inventory sample plots.

In **Papers II**, **III**, and **IV**, only plots dominated by Norway spruce or Scots pine were used. If ≥ 70% of the plot basal area was either Norway spruce or Scots pine, it counted as belonging to that species. More specific information on NFI data used in **Papers II**, **III**, and **IV** is presented below.

3.3 Swedish long term forest experiment data

The Swedish long-term forest experiments data used in **Papers III** and **IV** were made up of even-aged monoculture stands of Norway spruce and Scots pine. These plots were spread across Sweden between latitudes of 55° to 67° N. The experiments were mainly focused on fertilisation, regeneration, spacing, and thinning. Most plots had a cultivated origin through planting, seeding, or natural regeneration (Elfving and Kiviste, 1997; Nilsson et al., 2010). The mean plot size was 0.06 ha (range 0.02–0.20 ha). Specific information on long-term forest experiment data used in **Papers III** and **IV** is presented below.

3.4 Stand and spectral heterogeneity

To investigate the relationship between measured basal area and corrected indirect LAI using models from **Paper I**, we used field inventory data measured in 2016 and 2017 from the Swedish NFI (**Paper II**). A total of 200 Norway spruce-dominated plots and 194 Scots pine-dominated plots were used. At each NFI plot centre, hemispherical photographs were taken. These photos were processed using the GLA software package to obtain LAIe. LAI correction functions (from **Paper I**) were then used to adjust underestimated LAIe closer to the actual canopy LAI.

From the field inventories, variables representing stand structure were calculated and used in the model exploring the relationship between basal area and LAI in managed forests. Simple plot variables like stem density, tree height, and stand age were taken from the NFI data. Also derived from the NFI data were variables quantifying stand heterogeneity and competition using species proportion, stand density, diameter distribution, and tree height to diameter relationships. Along with stand variables, site descriptors such as latitudinal gradient, temperature sum, and humidity were used to capture variation in the basal area-LAI relationship. Data for humidity and temperature sum were downloaded from a Swedish Meteorological and

Hydrological Institute database. In one set of the basal area-LAI models, satellite remote sensing data from Sentinel-2 was used to create variables for spectral heterogeneity. From different raster layers, a vegetation index and spectral variation index were derived.

3.5 Mensurational growth and yield modelling

In **Paper III**, four species-specific stand basal area models were developed: two total basal area (including mortality and thinnings) growth and yield models ($m^2\ ha^{-1}$) for Norway spruce (GY-S) and Scots pine (GY-P) and two five-year growth models for basal area of trees present at both the beginning and end of the growth period ($m^2\ ha^{-1}$ 5-years^{-1}) for Norway spruce (Growth-S) and Scots pine (Growth-P).

The growth and yield models were developed using a compatible growth and yield model approach (Clutter, 1963) by fitting a Schumacher difference equation (Schumacher, 1939) to the data, augmented by initial plot stem number before thinning (Equation 1).

$$G_2 = e^{log(G_1)\left(\frac{t_1}{t_2}\right)^{bST^c} + a\left(1-\left(\frac{t_1}{t_2}\right)^{bST^c}\right)} \quad (1)$$

where G_2 is total basal area ($m^2\ ha^{-1}$) at period end, G_1 is total basal area ($m^2 ha^{-1}$) at period start, t_1 (years) is age at period start, t_2 (years) is age at period end, ST is the initial plot stem number before thinning (stems ha^{-1}), and a, b and c are parameters to be estimated.

The growth models were developed using regression analysis and linear mixed effect models. Variables were chosen using a stepwise approach where significant variables were selected for the model, together with an evaluation of collinearity.

The four new models, together with the Elfving (2010) growth model currently used in the Swedish forest planning system Heureka (Wikström et al., 2011), were compared using independent data from the GG long-term thinning experiment (Nilsson et al., 2010). The models' ability to predict basal area was evaluated over a 30 to 40 year period.

The data used for model development and comparison in **Paper III** came from the Swedish NFI and long-term forest experiment permanent plots (Table 1). Before model fitting, the selected data for each model were randomly divided into two parts; two-thirds of the selected plots were used for model fitting and one-third was dedicated to validation (Figure 3).

Table 1. Description of the Norway spruce (NS) and Scots pine (SP) data used for model fitting and model comparison in **Paper III**. The models are the basal area five-year growth models (Growth-S and Growth-P) and total basal area growth and yield models (GY-S and GY-P). Data sources were Swedish National Forest Inventory (NFI) and Swedish long term forest experiments (LFE).

Data use	Period length (years)	Species	Number of plots	Number of periods	Measurement years (NFI/ LFE)
Growth-S	5	NS	2130	3286	2003-2017/ -
Growth-P	5	SP	3088	4961	2003-2017/ -
GY-S	1-36	NS	836	4623	1993-2017/ 1960-2017
GY-P	1-36	SP	1922	7798	1993-2017/ 1960-2017
Model comparison	3-11	NS	10	50	-/ 1966-2007
Model comparison	2-14	SP	10	50	-/ 1969-2015

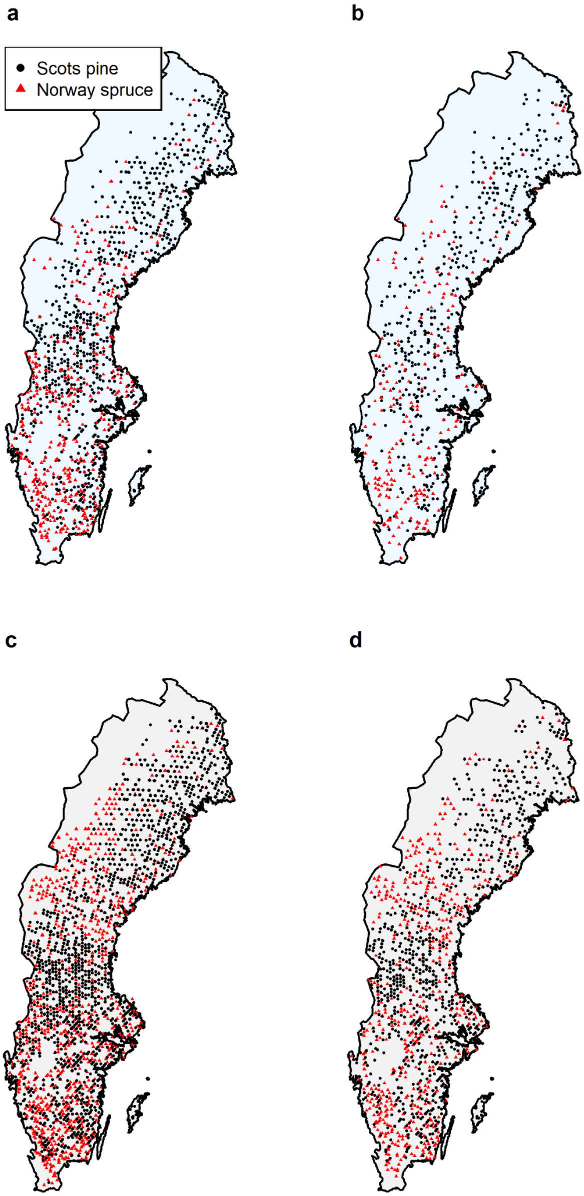

Figure 3. Locations of plots used in the modelling process. (a) plots used in the growth and yield model (GY-P and GY-S) fitting (552 Norway spruce and 1288 Scots pine), (b) plots for GY-P and GY-S validation (284 Norway spruce and 634 Scots pine), (c) plots for growth model (Growth-P and Growth-S) fitting (1422 Norway spruce and 2059 Scots pine), and (d) plots for Growth-P and Growth-S validation (708 Norway spruce and 1029 Scots pine).

3.6 Hybrid growth and yield modelling

In **Paper IV**, hybrid physiological/mensurational basal area models were developed. The hybrid model development was done using the potentially usable light sum equation (PULSE) hybrid approach (Mason et al., 2007), which combines the principles of light use efficiency (LUE) with mensurational time-based models. The mensurational models from **Paper III** (GY-P and GY-S) were refitted using the same plots, but time (age) was replaced with potentially usable light sum (PULS) since stand establishment. The form of the hybrid model equation was:

$$G_2 = e^{log(G_1)\left(\frac{PULS_1}{PULS_2}\right)^{bST^c} + a\left(1 - \left(\frac{PULS_1}{PULS_2}\right)^{bST^c}\right)} \quad (2)$$

where G_2 is basal area (m^2 ha^{-1}) at the period end, G_1 is basal area (m^2 ha^{-1}) at the period start, $PULS_1$ is the potentially usable light sum (MJ m^2) at the period start, $PULS_2$ is the potentially usable light sum (MJ m^2) at the period end, ST is the initial plot stem density before thinning (stems ha^{-1}), and a, b and c are parameters to be estimated.

To account for key climate and environmental factors regulating the proportion of radiation intercepted by leaves that stands could potentially use to grow, the incoming radiation is adjusted using modifiers from the 3-PG model (Landsberg and Waring, 1997). The modifiers used in this study adjusted for vapour pressure deficit (VPD), soil water availability, temperature, and frost. The modifiers are non-dimensional with a value from 0 to 1. A modifier value of 0 indicates that no available light could be used for growth because of this factor, and a value of 1 indicates that this factor did not hinder light use. The PULS calculation is illustrated in Figure 4. The calculation of modifiers and PULS was done using plot-specific monthly data on solar radiation and climate from 1958-2017 provided by the Swedish Meteorological and Hydrological Institute (SMHI).

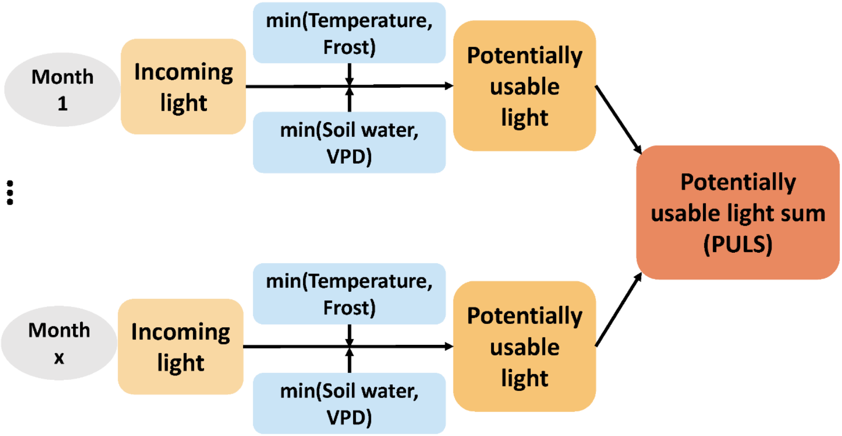

Figure 4. The potentially usable light sum (PULS) calculation. Monthly incoming light is multiplied by the minimum modifier value of temperature or frost and soil water or VPD to get monthly potentially usable light. PULS is obtained by summing all monthly potentially usable light since stand establishment.

The performance of the hybrid models was compared against the time-based mensurational models calculated on the same plots. For each model, precision and bias of predictions were compared. The climate sensitivity of the hybrid models and ability to respond to changes in climate input were also tested in **Paper IV**. A sensitivity analysis was conducted where 140 NFI plots got manipulated climate data. All plots had the same starting condition with an initial basal area of 20 m^2 ha^{-1} at 35 years, unchanged climate data for those 35 years, and an initial plot stem number before thinning of 1500 stems ha^{-1} for Scots pine and 2000 stems ha^{-1} for Norway spruce. The climate changes were increasing temperature by 2^o or 4^o C, and/or increasing precipitation by 10% or 20%. The hybrid basal area models were then run for 20 years. At the end of the simulated period, predicted basal area from the different scenarios was compared to basal area predictions from unmanipulated climate input.

4. Results and discussion

4.1 Leaf area correlations with stand and site measurements

In **Paper I**, the relationship between directly estimated LAI and indirectly estimated LAI (LAIe) was explored. For the three indirect methods used, there were significant correlations between LAI and LAIe. The comparison also showed an average underestimation of LAI by using the indirect methods (Figure 5). For the three indirect measurements, the LAI-2200C had the smallest underestimation at around 30%. Hemispherical photo analysis underestimated LAI by 70% for CAN-eye and 60% for GLA. This underestimation of LAI from indirect measurements agrees with previous studies where the same trend has been observed (Barclay and Trofymow, 2000; Mason et al., 2012; Sampson and Allen, 1995; Gower and Norman, 1991). The underestimation occurs because the indirect measurements use optical instruments to estimate LAI based on assumptions that the foliage is uniformly and randomly distributed (Gower et al., 1999; Demarez et al., 2008). However, conifer canopies have non-randomly distributed foliage aggregated around the branches (Chen and Cihlar, 1996; Lemeur and Blad, 1974; Nilson, 1999). The methods using hemispherical photographs (CAN-eye and GLA) illustrate this issue well. Here, there was a non-linear correlation between LAIe and LAI with increased underestimation with increasing LAIe for Norway spruce. This results in less accurate estimates in forests with higher LAI because of high foliage overlap (Sampson and Allen, 1995; Gower and Norman, 1991).

Spruce and pine showed different mismatch patterns between LAI and LAIe resulting in a need for species-specific conversion models for each measurement technique. Some of the models also included measures of stand density. Basal area was used as a covariate for Norway spruce models and stem number for the Scots pine LAI-2200C conversion model. The inclusion of stand density variables helped explain the variation in LAI caused by stand density and competition between trees (Barclay and Trofymow, 2000; Gonzalez-Benecke et al., 2012; Mason et al., 2012). The strong correlation with basal area also allowed for a simple model that could estimate LAI from only basal area measurements.

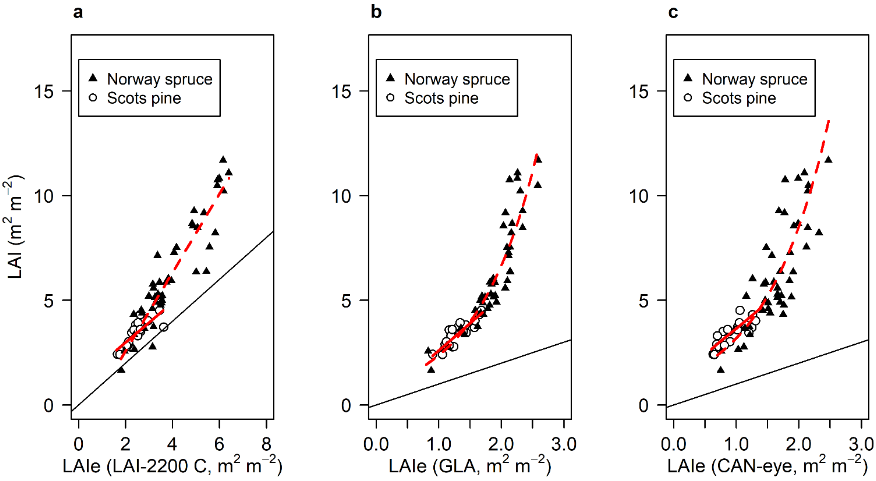

Figure 5. Direct measurements of LAI (m^2 m^{-2}) against indirect measurements, LAIe (m^2 m^{-2}), for Scots pine and Norway spruce. LAIe in the plots comes from (a) an LAI-2200C plant canopy analyzer, and hemispherical photos analysed with (b) Gap Light Analyzer (GLA) or (c) CAN-eye. The dashed red lines represent the conversion models from LAIe to LAI for Norway spruce, and the solid red lines the conversion models for Scots pine. The solid black line shows a 1 to 1 relationship (Goude et al., 2019).

In **Paper II**, the relationship between basal area and LAI (estimated with GLA and corrected using the models developed in **Paper I**) was further explored. Here, LAI was also highly correlated with stand basal area for both Scots spine and Norway spruce. The trend was non-linear, which was expected because of competition and self-shading (Gspaltl et al., 2013). With higher basal area, there is more competition for resources and more self-shading within the stand. With more competition and more shading, each additional unit of LAI has a reduced light interception compared to the previous. This means that at high LAI, each additional unit of LAI can produce and support proportionally less basal area (Binkley et al., 2013a; Binkley et al., 2013b). Competition could also be observed when looking at leaf area on an individual tree level (LA; **Paper I**). Here, stand basal area was negatively correlated to LA. The negative correlation is because higher basal area leads to more competition for growth resources, such as light and nutrients, resulting in a lower leaf area per tree.

In **Paper I**, the relationship between LAI and basal area was linear compared to the non-linear pattern in **Paper II**. An explanation for the difference could be the limited amount of data available in **Paper I**. If more data would have been available, especially for plots with higher and lower basal area, a non-linear trend between LAI and basal area could have been observed.

At tree level, LA was correlated with tree size measures like diameter at breast height (DBH) for both species (Figure 6) and tree height for Norway spruce. The correlation with tree size agreed with previous studies where LA could be estimated using these relationships (Gower et al., 1999; Mason et al., 2012; Xiao et al., 2006).

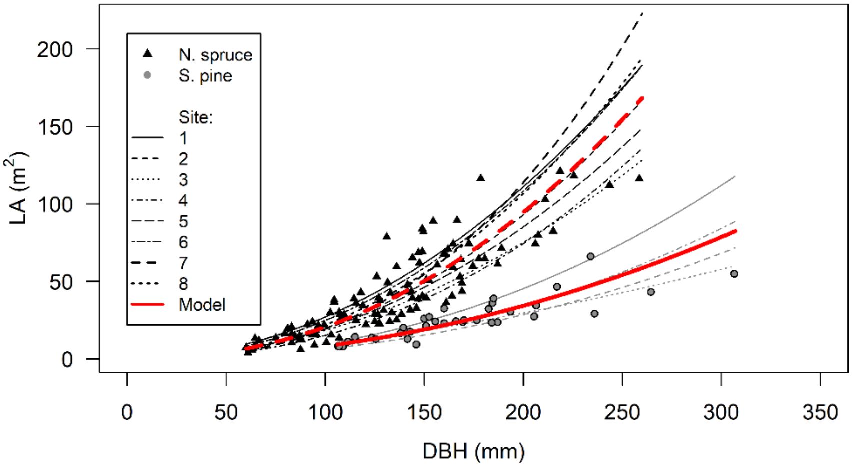

Figure 6. Individual tree half total leaf area (LA, m^2) plotted against diameter at breast height (DBH, mm) for Norway spruce and Scots pine. The site-specific regression models used to estimate LA are represented by the black (Norway spruce) and grey (Scots pine) lines. The thicker red lines represent the general site-independent models for LA, where dashed = Norway spruce and solid = Scots pine (Goude et al., 2019).

All measures and estimations of LA and LAI had a significant difference between the two species ($p < 0.05$). The explanation for why Norway spruce had more foliage could be needle longevity and canopy structure (Cannell, 1989). A shade-tolerant species like Norway spruce with needles that live for 7-15 years can build up large canopies. Such shade-tolerant species can have shaded branches, further down or into the crown, which photosynthesise despite low light levels. Also, the cone-shaped crown allows more light to reach the lower parts of the canopy. In contrast, Scots pine is light demanding with needles that live for 2-6 years (Albrektson et al., 2012). The short needle longevity and low shade tolerance mean that Scots pine cannot have needles far down or within the crown and cannot build up canopies as large as shade-tolerant species like Norway spruce. Scots pine also has a more rounded crown, resulting in less light reaching the lower parts of the canopy.

When comparing the different indirect methods used to estimate LAIe in this study, all had positive and negative features. A challenge was the lack of independent validation data. Had that been available, it would have been possible to compare the methods and the developed conversion models more rigorously. However, some conclusions can still be reached. The LAI-2200C had the smallest underestimation, and the conversion models for both species showed a good fit. In comparison, CAN-eye and GLA were less accurate, but with the correction models, LAI estimates for Norway spruce were as good as the LAI-2200C. In practice, all methods were easy to use in the field. However, the requirement of finding a large open area for LAI-2200C reference measurement made it quite time-consuming. Despite the higher risk of subjectivity when analysing hemispherical photos, these methods had many advantages, like more accessible equipment and faster field measurements. If the goal is to get more independent LAI measurements in the field, these hemispherical photo methods are a good alternative.

4.2 Basal area – LAI relationships can be improved with structural and spectral heterogeneity

To improve the explanation of the basal area-LAI relationship explored in **Paper II**, variables for stand and site structure were included. This resulted in a significant reduction of the model variance. These results indicate that structural heterogeneity should be considered when using models developed using data from experiments in regular managed forests. When stand structure heterogeneity was included, the variance was reduced by 55% for Norway spruce and 43% for Scots pine. The stand heterogeneity measures of species proportion and stand structure were captured by variables representing tree social status, height-diameter ratios, and tree diameter distribution. These variables were negatively correlated with basal area. This negative correlation supports previous studies where tree size inequality negatively affected production (Sun et al., 2018; Zeller et al., 2018). This decline in productivity can partly be explained by the difference in resource use efficiency between large and small trees. Smaller trees are less resource efficient and grow more slowly than larger, more dominant trees (Binkley et al., 2010). The negative effect of tree size inequality in monocultures has previously been explained by reductions in light interception and light use efficiency (Bourdier et al., 2016), where small trees have lower light interception and light use efficiency than their larger neighbours (Binkley et al., 2013a; Gspaltl et al., 2013; Pretzsch, 2009).

When spectral heterogeneity was included in the basal area-LAI models, it also reduced the variance by 25 % for Norway spruce and 13 % for Scots pine. These results indicate the usefulness of remote sensing data that can be used to quantify stand heterogeneity if forest measurements are not available (Kokaly et al., 2009; Zhu et al., 2017; Gitelson et al., 2006).

When using the LAI conversion function, some extrapolation was done. The functions were constructed for a latitude range of 55° to 64° N but used data from further north to test the functions for the entire range of the Swedish NFI data. The extrapolation resulted in a slight overestimation in stands from more than 64° N. This illustrated the risks associated with extrapolation and that using these functions outside their calibration range should be done cautiously.

4.3 Growth and yield model comparisons

The new basal area models for Scots pine and Norway spruce developed in **Paper III** showed a good and unbiased fit to their respective fitting data. Despite their differences in model structure, there were no substantial differences between them and the Elfving growth models when compared against each other using independent data (Figure 7). All models predicted basal area development with relatively similar precision and bias.

The only model that stood out for being slightly worse at predicting basal area over a long time was the Norway spruce growth model (Growth-S). This model's prediction showed a substantial increase in variation after 10-year predictions with a considerable overestimation for some unthinned plots (Figure 7e). The increased variation illustrated the risk of error accumulation when predictions built upon already biased estimations become even more biased (Holm, 1981; Kangas, 1997). The other models also demonstrated error accumulation, but to a much smaller degree.

The expected benefits for the growth and yield models (GY-S and GY-P) in more precise long-term projections (Clutter, 1963; Weiskittel et al., 2011) could not be shown for the tested plots and periods, regardless of plot treatment and location. These benefits might reveal themselves with a lengthier comparison than the 30 to 40 years used in this study. However, the growth and yield models still benefited from path invariance, varying period length, and only requiring basal area, age and initial stem number as input variables. These features made the GY-S and GY-P models flexible and easy to use, for example, in situations where stand data is limited, but stand age is known, and basal area and stem number are measured from remote sensing (Nilsson et al., 2017).

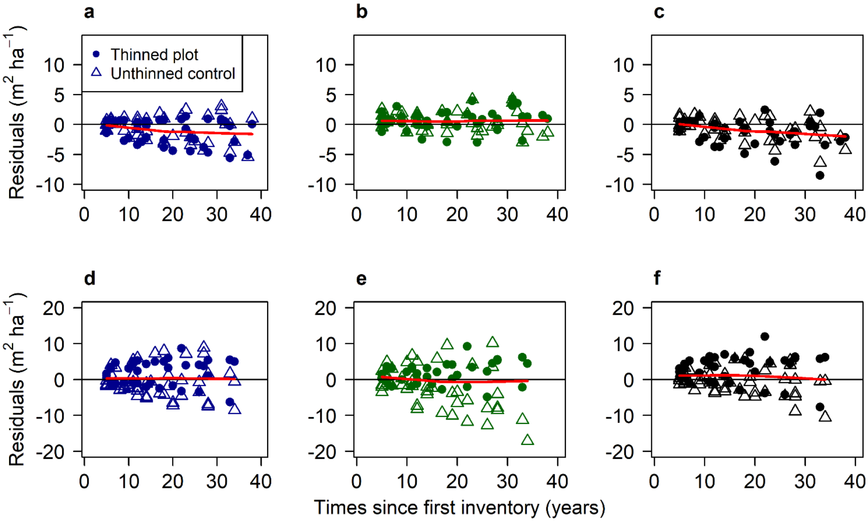

Figure 7. Residual plots of the model comparison against independent data from the GG experiment. Panels (a), (b) and (c) are Scots pine, and (d), (e) and (f) are Norway spruce. (a) (GY-P) and (d) (GY-S) show residuals for the growth and yield models. (b) (Growth-P) and (e) (Growth-S) show residuals for the growth models, while c and f show residuals

for Elfving's model used on Scots pine and Norway spruce data, respectively. The thick red lines show the residual trend.

The growth and yield models (GY-P and GY-S) from **Paper III** were used as a starting point for the hybrid model development in **Paper IV**. Like the time-based growth and yield models, the hybrid models showed a good and unbiased fit for both species. However, when the mensurational models and hybrid models were compared using the same validation data, there were no precision improvements for the hybrid models, regardless of species or included climate modifiers. However, the similar prediction precision of the hybrid and mensurational models shows that the hybrid models would probably also perform well in a model evaluation like the one in **Paper III**.

The lack of significant improvement was in contrast with other studies where the PULSE approach of hybridising basal area models resulted in substantial improvements (Mason et al., 2011; Rachid-Casnati et al., 2020). A reason for these differences could be the long rotations and slow growth of Scandinavian boreal forests. The previous studies that yielded significant improvements examined fast-growing forest plantations with rotations around 10 to 30 years. These forests respond more to short-term climate variation, which the hybrid models can capture. These short-term fluctuations tend to even out over time in slower-growing conditions and are more challenging to capture in hybrid models.

Even though precision did not improve, including climate-sensitive modifiers in the PULSE hybrid models allowed for better adjustment to site and climate variation and the ability to respond to climate changes. These are essential properties for a model to produce accurate long-term predictions.

4.4 Effect of climate change on hybrid model predictions

Different scenarios of increased temperature and precipitation were applied to test the hybrid models' sensitivity to climate change (**Paper IV**). The production responses were, on average, positive. However, there were sizable variations in response for each scenario (Figure 8). The scenarios where just temperature was increased (with no change in precipitation) showed the biggest variation. Some plots, primarily in north-western Sweden (Figure 9a), showed a large increase in basal area, up to around 25%, and others decreased by around 10 to 15%. The average positive effect of increased temperature was in line with previous studies where temperature was shown to be a limiting factor for growth in northern Europe (Bergh et al., 1999; Allen et al., 2010), and that observed increases in growth could be partly explained by increased temperatures (Mensah et al., 2021). The hybrid models capture the positive effect from warmer temperatures through more beneficial temperatures for photosynthesis and longer growing seasons because of higher temperatures in spring and autumn. These benefits result in more available PULS and higher growth.

The results from **Paper IV** also show the interaction between increased temperatures and water availability. In northern and western parts of Sweden, water availability is good, and the forest can take advantage of the higher temperatures to increase growth (Figure 9a). In the north, temperature was also a more limiting factor under the current climate, and a temperature increase relieves some of that limitation.

Under present-day climate, southern and eastern Sweden has drier soil and less limitation from low temperatures. Warmer temperatures in this region increase evapotranspiration and reduce available soil water to even lower levels, resulting in less light being available and decreased growth (Figure 9a). These different responses to temperature increases agree with other studies where increased temperature leads to reduced production due to less plant-available soil water (Ruiz-Pérez and Vico, 2020; Belyazid and Zanchi, 2019; Ruosteenoja et al., 2018).

The scenarios with increased precipitation and unaltered temperature showed an overall positive effect on production in the entire study area (Figure 9b). The resulting higher levels of available soil water led to less soil water limitation and more PULS. The largest response came in the south-eastern areas, where water was already a limiting factor under current climate.

When combining the effects of increased temperatures and precipitation, production increased all over Sweden since increased precipitation offset the adverse effects of increased temperatures. This positive effect held in all scenarios, except when temperature increased by 4^{o} C and precipitation increased by 10% (Figure 8). For some plots in south-eastern Sweden under this scenario, the increased precipitation could not buffer the increased evapotranspiration resulting from the temperature increase. The positive temperature effects on productivity were also greater in areas that were more limited by temperature. This resulted in a clear division in production responses between northern and southern Sweden when higher precipitation counteracted increased evapotranspiration due to warmer temperatures (Figure 9c). Similar differences in response to temperature increases between southern and northern Scandinavia has been seen in other studies (Ruiz-Pérez and Vico, 2020).

When interpreting the results from the scenario analysis, it is important to bear in mind that the plots were assigned a starting basal area, initial stem number and age to more easily compare the hybrid models' responses in different regions. However, with the same starting conditions, all plots were on the same yield curve. This meant that different site fertility effects that were otherwise captured by initial age and basal area were lost. Also, the climate input data was altered the same amount every month during the 20-year simulation. This was done to easily see how the models responded to warmer temperatures and wetter growing conditions. Therefore, future scenario analysis should be made using actual forest stand data and long-term predictions of future climate to estimate the effects on forests more accurately.

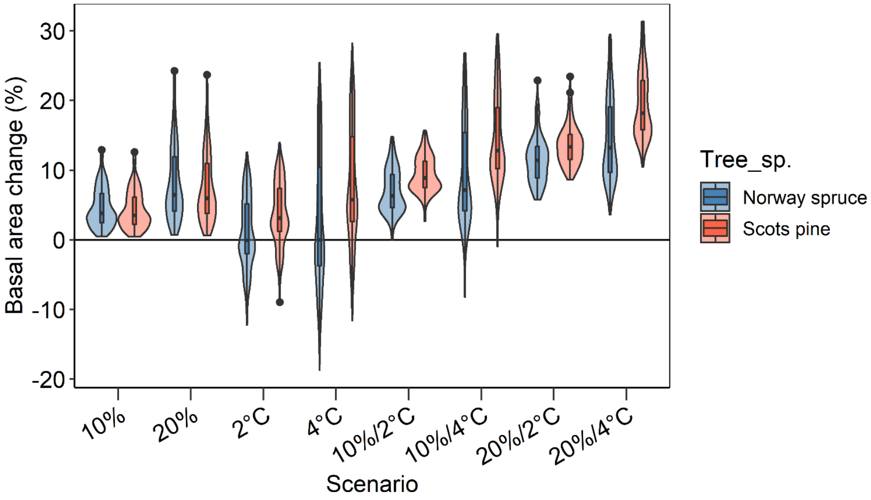

Figure 8. Relative change in basal area (%) from altered input climate data compared with current climate after 20-year simulations. The part of the scenario name ending with % refers to the relative precipitation increase, and the part ending in ˚C refers to the temperature increase; where one of these is absent, that variable was not changed. The simulations were conducted using the hybrid models for Scots pine and Norway spruce containing modifiers for temperature, frost, vapour pressure deficit, and soil water.

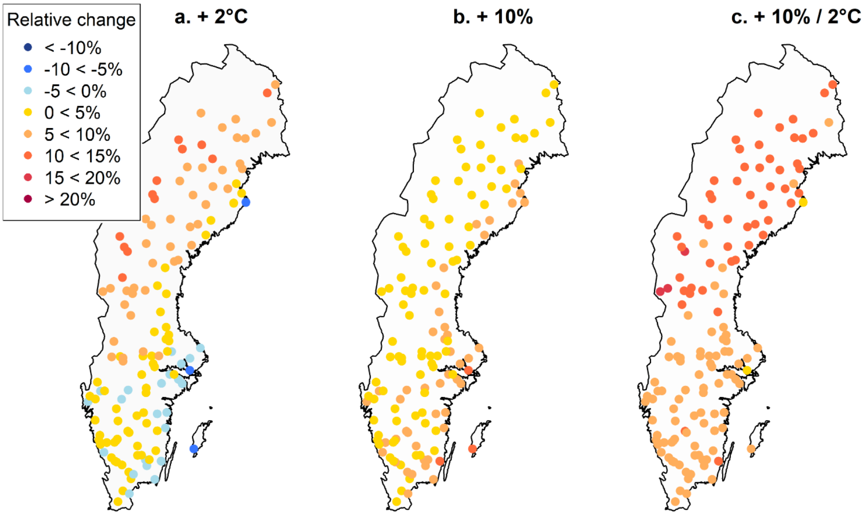

Figure 9. Relative change in basal area (%) from altered input climate data compared with current climate after 20-year simulations. The simulations were conducted using the hybrid model for Scots pine containing modifiers for temperature, frost, vapour pressure deficit, and soil water. Each dot represents a randomly selected permanent sample plot from the Swedish NFI.

4.5 Difficulties in using Swedish NFI data for growth and yield modelling

The Swedish NFI data provided an extensive set of temporary and permanent sample plots covering all of Sweden's forests. This vast dataset made it possible to conduct the studies in this thesis. However, several issues became apparent concerning NFI data and inventory inconsistencies after using it for growth and yield modelling.

Because the NFI is a survey of the Swedish forests where stand history is unknown, and trees inside the permanent plots are not cored, tree and stand age are difficult variables to estimate. This created difficulties in age determination and inconsistencies in the database where the age increase was different from the time between measurements. The uncertainty in age was also carried over to the hybrid models (**Paper IV**), where PULS was based on plot age. The same problems did not occur with the long-term experiment where year of establishment was known. The fact that age is a problem with the Swedish NFI data has been noted in previous studies (Fahlvik et al., 2014;

Elfving, 2010). However, age is a critical variable that explains a significant amount of the variation in growth and yield models. Lacking age, some other variable needs to be included to capture what growth curve the stand is on and where on that curve the stand is at a particular moment.

Plot sizes were also inconsistent among measurements. Until 2003, the small plot area (where trees with a DBH < 10 cm were measured) changed with every new inventory (Fridman et al., 2014). These inconsistencies created problems when analysing the development of individual plots. The biggest problems were artificial increases or decreases in growth between measurements just due to different plot sizes. However, even with consistent plot sizes over time, the problem with ingrowth would still exist. The underlying issue was that trees with a DBH ≥ 10 cm and < 10 cm were measured in different-sized plots. This design reduced the time spent measuring small trees. Ideally, if the trees with DBH < 10 cm in the small plot were representative of the larger plot, the issue with different-sized plots between tree size classes would not have created such problems. Unfortunately, that was not the case, and ingrowth, where trees with a DBH ≥ 10 cm suddenly appear, created significant problems before it was addressed.

The issues with the Swedish NFI data in this thesis are specific to analysing development of individual plots. The Swedish NFI focuses on providing national and regional statistics on forest status and development. In that context, even with changing plot layouts and incomplete coverage of small trees, NFI plots still provide the aggregate data needed for forest policy and planning. However, these issues create significant problems when individual plots are followed over time.

4.6 Model limitations and future development and improvements

The focus of this study has been on Scots pine- and Norway spruce-dominated stands since they are the most common forests in Sweden (SLU, 2021). However, this means that there is still a need for similar studies focused on stand structure, age, and composition of mixed forests and other species. Mixed forests will pose new challenges in accounting for heterogeneity in both leaf area and growth and yield models. The results from

Paper II highlight stand and spectral heterogeneity variables as a possible solution.

The results from **Paper II** also illustrate the limitations of using models developed from experiments on managed forests. Experiments are often better managed and more homogeneous than typical managed forests, resulting in the need to correct and adapt the models from experiments.

The models in this study were not developed for older forests. In particular, the leaf area models (**Paper I**) are only applicable to young or middle-aged stands and trees (25 to 60 years). For this study, older stands were not available. Restrictions put on the data limited the number of available plots in old stands for the growth and yield models' development and validation (**Paper III** and **VI**). For example, restrictions on height at first measurement were used to more confidently account for total production in the growth and yield models and hybrid models. These restrictions resulted in a final dataset with few plots older than 100 years. The lack of plots in old forests limits the models' application; if the models are to be extrapolated to older forests, it needs to be done with great caution.

Apart from data better representing stand ages and heterogeneity, there are other possibilities to improve the hybrid models developed in this thesis (**Paper IV**), particularly their responses to climate change and usability. One aspect that should be considered is the starting points of the models. They use initial basal area and PULS to decide what yield curve the plot should be placed on. The models are also limited to stands that are at least 10 years old and 5 meters high. When starting data is not available, for example, during multiple rotation simulations, another method is needed to choose model starting values. In that situation, the starting basal area needs to be simulated using regeneration models and growth and yield models for young forests. The same also applies to the other growth and yield models from this study that also require good starting values, especially when making long-term predictions.

Another possibility is including the effect of nutrient availability on the growth response and how nutrient availability is affected by climate change in the PULSE hybrid models. In the models' current state, site productivity and nutrient availability are accounted for by the curve a stand grows on, which is fixed by the initial basal area and PULS. The shape of the curve accounts for growth responses at different ages, leaf area, light use efficiency and allocation at different fertilities. If a plot has a high basal area at a certain age, the plot is assumed to be on a more fertile site that can produce more basal area with the same amount of light than plots on less fertile sites. At a fertile site, production is higher because that stand absorbs more light with its higher leaf area, the trees' higher light use efficiency can transform more of that light into biomass, and a difference in resource allocation provides more growth resources above ground (Waring et al., 2016; Cannell, 1989). However, since increased temperatures and water availability are expected to increase mineralisation and nutrient availability (Ciais et al., 2014), a fertility index that accounts for changes in light absorption, light use efficiency and resource allocation could be included in the hybrid models. Such a climate-sensitive fertility index should also account for the expected drier conditions in southern Sweden (Eklund et al., 2015; Ruosteenoja et al., 2018; SMHI, 2020), leading to less mineralisation.

To improve the hybrid models' usability, there is also a need to simplify the user experience and lower the required knowledge about climate data and modifier calculations. A simple way to do this is to provide an application where climate data and modifiers have already been analysed and calculated. In such an application, the user provides forest coordinates, basal area, age and initial stem number before thinning. If initial stem number is unknown, default values of 1500 stems ha^{-1} for Scots pine and 2000 stems ha^{-1} for Norway spruce could be used, based on the model parameterisation data (**Paper IV**). The application would automatically select climate modifiers and calculate PULS. It could then provide several climate scenario-specific projections. A system like this could also be combined with remote sensing data to get large-scale updated data to predict forest development at both local and regional scales.

5. Conclusions

This thesis has shown that leaf area can be reliably estimated for Scots pine and Norway spruce stands (**Paper I**). At a stand level, LAI can be estimated using optical instruments, together with stand variables. For individual trees, LA can be estimated using measurements of height and diameter. The correlations between leaf area and inventory stand and tree variables show the potential of estimating leaf area without any indirect optical measurements. Still, in many cases, independent leaf area measures are required, and direct or indirect methods need to be used. Hopefully, these results can lead to leaf area being more widely measured and available for growth and climate modelling.

The measures of leaf area also showed a clear species difference (**Paper I**), indicating the need for species-specific models and future studies that focus on species other than Scots pine and Norway spruce and the effect of species mixtures on LA and LAI.

Some of the LAI models were successfully applied to managed Scots pine and Norway spruce stands (**Paper II**). However, when the estimated LAI was used to model basal area, the models needed to be corrected for stand structural heterogeneity, illustrating the problems using models based on well-managed forest experiments on typical managed forests. Using spectral heterogeneity derived from Sentinel-2 satellite imagery to account for stand heterogeneity was also successful in improving the basal area-LAI relationship. The model improvements from spectral heterogeneity show the usefulness of this technology in modelling forest growth and canopy dynamics.

There was no apparent difference in prediction precision for the newly-developed mensurational basal area models (**Paper III**). The growth and yield models (also used to develop the PULSE hybrid models) did not show the expected advantages from path invariance or variable period lengths. However, despite the simple inputs, the growth and yield models were as precise as the regression growth models, illustrating the power of compatible growth and yield models. Features such as path invariance, low number of input variables, and adjustable period length also made the models easier to use. These features could also be useful in situations with limited on-the-ground data availability, but some stand variables are known from remote sensing.

Model developments to improve long-term predictions under climate change were sought in **Paper IV**. Climate-sensitive hybrid basal area models were developed for Scots pine and Norway spruce stands with the PULSE hybrid approach. These hybrid models did not improve prediction precision compared to the mensurational models. However, the major improvement was the increased flexibility and sensitivity to changes in temperature and precipitation. The ability to respond to climate changes makes the hybrid models useful for estimating long-term development of forests, testing different climate scenarios, and evaluating possible effects on forest production.

When different climate scenarios were tested using the hybrid models developed in **Paper IV**, results showed a significant response with considerable local variation, which agrees with expectations for the different regions. The results from the climate scenarios showed the importance of including the interaction between temperature and water availability. Without that interaction, the possible adverse effects of increased temperature on water availability, through increased evapotranspiration, would not have been captured. Climate affected growth response is the type of information that is vital for management decision making, like species choice and timing of silvicultural treatments. These results also show the importance of having prediction tools that can account for both positive and negative effects of climate change on a local level.

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Populärvetenskaplig sammanfattning

Den svenska skogen har varit betydelsefull för Sveriges utveckling och välstånd. Länge behandlades den som en oändlig resurs, men med tiden har det blivit allt tydligare att skogen måste brukas på ett hållbart sätt för att den ska räcka till och vara till nytta även för framtida generationer. Ett viktigt verktyg för att kunna bruka skogen på ett hållbart sätt är tillväxtmodeller. Dessa används för att förutspå skogens utveckling och framtida tillstånd. Därigenom blir det lättare att planera skogsskötseln utefter den skog man vill ha i framtiden. Men att planera långsiktigt har blivit svårare i och med klimatförändringarna. De tillväxtmodeller som används i skogsbruket idag kan inte räkna med effekterna av klimatförändringar eftersom de är fast i det klimat som de skogar modellerna är baserade på växte i. Detta gör långsiktiga prognoser osäkrare än vanligt. Ett sätt att förbättra dessa verktyg är att inkludera egenskaper som kan ta hänsyn till klimatförändringens effekter på skogen. Exempel på sådana egenskaper är skogens förmåga att ta upp och använda solljus. I detta arbete undersöktes därför hur man kan använda egenskaper kopplade till skogens upptag och nyttjande av solljus i modeller för tall- och granskog i Sverige.

För att veta hur mycket solljus en skog kan fånga upp behöver man känna till skogens så kallade bladareaindex, vilket är ett mått på hur stor yta av blad eller barr som kan ta upp solljus. Man kan säga att bladreaindex beskriver hur stor solfångare skogen har som tar upp solljus. Solljus som träden använder för att växa genom fotosyntes. Detta kan mätas både direkt genom att plocka, räkna och mäta barr eller indirekt genom att med optiska instrument mäta trädkronornas täthet. I **studie I** mättes bladareaindex för tall och gran med både direkta och indirekta metoder vid åtta skogliga försök spridda över Sverige. Resultatet visade att det går att, på ett säkert sätt, uppskatta bladarea för svenska gran- och tallskogar. Dock behöver de indirekta mätningarna korrigeras för att ge ett mer korrekt bladareavärde. Denna korrigering kan utföras med formler från denna studie. Den betydligt högre bladarean för gran jämfört med tall visade också på vikten av att ta hänsyn till trädslag när man mäter och använder bladarea.

Eftersom resultaten från **studie I** var framtagna på försöksytor fokuserade **studie II** på hur dessa mätmetoder och matematiska modeller fungerade i praktiken i brukade skogar. Under 2016 och 2017 togs foton på trädkronor ovanför ett antal provytor spridda över stora delar av Sverige. Med hjälp av dessa foton skattades ytornas bladareaindex. Den skattade bladarean användes sedan för att ta fram modeller för att räkna ut grundyta, vilket är ett mått på skogens täthet. Resultaten visade på ett starkt samband mellan grundyta och bladareaindex och att sambandet förbättrades om man också tog hänsyn till skogens heterogenitet så som blandningen av olika trädslag och trädstorlekar. Även heterogenitet uppmätt från satellitbilder förbättrade sambandet mellan grundyta och bladareaindex, vilket visade på möjligheterna att använda billiga och lättillgängliga satellitdata.

Eftersom tillväxtmodeller är ett viktigt verktyg för att kunna planera och förutsäga skogens utveckling fokuserade nästa del av arbetet på att utveckla nya tillväxtmodeller. Genom att använda data från permanenta provytor från riksskogstaxeringen, en nationell inventering av skog utförd av SLU, och skogliga långtidsförsök, utvecklades nya tillväxtmodeller för gran och tall i **studie III**. Dessa nya modeller togs fram med nya skogsdata och med hjälp av nya metoder jämfört med redan etablerade tillväxtmodeller. Efter att ha jämfört de nya modellerna med en befintlig tillväxtmodell visade resultateten att, förutom skillnad mellan trädslagen, var det ingen märkbar skillnad mellan modellernas förmåga att förutspå skogens utveckling. Därför kan alla de framtagna modellerna användas i praktiken.

Det som resultaten från **studie III** dock visade var att en av de nya modellerna var lika bra på att förutsäga skogens utveckling som de andra, trots att den krävde mindre information om skogens utgångsläge. Detta pekade på att denna typ av modell kan ge bra resultat även då det enbart finns mått på skogens ålder och täthet. Eftersom denna typ av tillväxtmodell även har andra fördelar såsom möjligheten att variera tidslängden för en projektion och att resultatet blir detsamma oavsett om man modellerar utvecklingen i flera små steg eller ett långt var den ett bra modellalternativ.

Modellerna från **studie III** visade på en god förmåga att förutsäga tillväxten vid dagens klimat, men saknar förmågan att anpassa sig till förändrade tillväxtförhållanden. I **studie IV** vidareutvecklades därför tillväxtmodeller för gran och tall till så kallade hybridmodeller som kan räkna med klimatförändringar. Hybridmodellerna utvecklades med samma skogsdata från permanenta provytor, men använder potentiellt användbart ljus i stället för tid. Det potentiellt användbara ljuset reflekterar på ett bättre sätt det som faktiskt driver skogens tillväxt. Det är inte tiden, utan hur mycket solljus som träden kan använda under den tiden, som styr skogens tillväxt. Hybridmodellerna möjliggör att effekter av till exempel höjda temperaturer och mindre vattentillgång kan fångas upp. Blir tillväxtförutsättningarna bättre kommer träden kunna använda mer av det tillgängliga ljuset och får då en högre tillväxt under samma tid. Blir tillväxtförutsättningarna sämre kommer träden kunna använda mindre tillgängligt ljus och får då en lägre tillväxt under samma tid. Resultaten visade att hybridmodellerna för både tall och gran hade samma precision som traditionella tidsbaserade modeller. Dessutom kunde hybridmodellerna fånga upp både positiva och negativa effekter av höjd temperatur och nederbörd som testades i olika klimatscenarion. Effekterna av de olika scenarierna hade stor lokal variation och visade att klimatförändringar kan komma att slå väldigt olika på skogens tillväxt i olika delar av landet. Generellt var det en positiv effekt på tillväxten i stora delar av norra och mellersta Sverige medan klimateffekterna på tillväxten var negativ i vissa delar av södra och östra delarna av landet. De negativa effekterna på produktionen var framför allt ett resultat av minskad vattentillgång.

Sammantaget visar denna avhandling att det går att inkludera egenskaper kopplade till ljusupptag och ljusanvändning i skogliga modeller och att man då kan utveckla klimatkänsliga tillväxtmodeller. Bladareaindex kan uppskattas på ett säkert sätt, om skattningarna korrigeras. Blandningen av trädslag och trädens storlek bör tas hänsyn till om bladareaindex används för att beräkna skogens täthet i brukade skogar. Dagens tillväxtmodeller fungerar bra för dagens klimat, men hybridmodellerna möjliggör bättre förutsägelser av skogens utveckling och ett mer informerat beslutsfattande. Resultat från testen med olika klimatscenarier visade att hybridmodellerna kan fånga både positiva och negativa effekter som klimatförändringarna kan ha på skogens produktion och pekar på vikten av att analysera effekterna lokalt.

Framtida studier kan utveckla dessa resultat genom att studera hur ljustupptag och ljusanvändning förhåller sig hos andra trädslag än tall och gran och för skogar med blandade trädslag och variation i ålder och trädstorlek. Detta skulle ge möjlighet att utveckla klimatkänsliga modeller och få bättre förutsägelser om utvecklingen i fler typer av skogar, inte bara i produktionsskog av gran och tall.

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Many forest models and planning tools struggle to account for the effects of climate change, making long-term sustainable forest management difficult. This thesis shows that by including ecophysiological concepts around light interception and light use, models for Scots pine and Norway spruce can become more responsive to environmental changes and can better account for the effect of climate change on forest production. These models allow for better predictions of forest development and better-informed decision making.

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