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Growth trends and site productivity in boreal forests under management and environmental change

Insights from long-term surveys and experiments in Sweden

Alex Appiah Mensah

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Cover: The old and the new forest – the pines at Bräntberg's car park, Umeå. In April 1987, the smaller pines were 40 years old and the bigger pines were 130 years old. In October 2019, after 33 years, the young pines (21 m) were 2 m taller than the old pines (19 m).

(photo: Professor emeritus Björn Elfving)

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Abstract

Under a changing climate, current tree and stand growth information is indispensable to the carbon sink strength of boreal forests. Important questions regarding tree growth are to what extent have management and environmental change influenced it, and how it might respond in the future. In this thesis, results from five studies (Papers I-V) covering growth trends, site productivity, heterogeneity in managed forests and potentials for carbon storage in forests and harvested wood products via differing management strategies are presented. The studies were based on observations from national forest inventories and long-term experiments in Sweden. The annual height growth of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) had increased, especially after the millennium shift, while the basal area growth remains stable during the last 40 years (Papers I-II). A positive response on height growth with increasing temperature was observed. The results generally imply a changing growing condition and stand composition. In Paper III, yield capacity of conifers was analysed and compared with existing functions. The results showed that there is a bias in site productivity estimates and the new functions give better prediction of the yield capacity in Sweden. In Paper IV, the variability in stand composition was modelled as indices of heterogeneity to calibrate the relationship between basal area and leaf area index in managed stands of Norway spruce and Scots pine. The results obtained show that the stand structural heterogeneity effects here are of such a magnitude that they cannot be neglected in the implementation of hybrid growth models, especially those based on light interception and light-use efficiency. In the long-term, the net climate benefits in Swedish forests may be maximized through active forest management with high harvest levels and efficient product utilization, compared to increasing carbon storage in standing forests through land set-asides for nature conservation (Paper V). In conclusion, this thesis offers support for the development of evidence-based policy recommendations for site-adapted and sustainable management of Swedish forests in a changing climate.

Keywords: long-term experiment, national forest inventory, growth trend, site productivity, heterogeneity, substitution, climate change mitigation, boreal forest

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Tillväxttrender och bördighet i boreala skogar givet skogsskötsel och ett förändrat klimat

Sammanfattning

I samband med klimatförändringar är kunskap om träd- och beståndstillväxt oumbärlig för att beakta kolsänkans roll i boreala skogar. Viktigt blir också att undersöka i vilken utsträckning skogsskötsel och miljöförändringar har påverkat skogens tillväxt och hur det kan komma att förändras i framtiden. Här presenterar jag resultaten från fem studier (Studie I-V) som avhandlar tillväxttrender och produktivitet i brukade skogar. Jag visar även på potentialen för kolbindning i skogar och träprodukter via olika förvaltningsstrategier. Studierna baserades på observationer från Riksskogstaxeringen och mätningar från fasta forskningsförsök i Sverige. Den årliga höjdtillväxten för tall (*Pinus sylvestris*) och gran (*Picea abies*) hade ökat mer än förväntat, särskilt efter millennieskiftet, medan grundytatillväxten varit stabil under de senaste 40 åren (Studie I-II). En positiv korrelation mellan höjdtillväxt och ökande temperatur observerades. Resultaten från studierna tyder på att skogens växtförhållanden och sammansättning förändrats över tid. I studie III identifierades systematiska fel i befintliga produktionsmodeller och de nya funktionerna som utvecklades gav bättre skattning av barrskogarnas produktionsförmåga i Sverige. I studie IV modellerades variationen i skogens sammansättning för att kalibrera förhållandet mellan grundyta och bladareaindex. De erhållna resultaten visar att beståndens struktur och trädslags-sammansättning kan utgöra viktiga förklarande komponenter för tillväxtmodeller, särskilt de som bygger på relationer mellan bladarea och grundyta. På lång sikt är det bättre för klimatet att aktivt bruka skogar för en varaktig hög tillväxt och ett effektivt produktutnyttjande, jämfört med att lagra biomassa i stående skogar genom avsättningar (studie V). Sammanfattningsvis ger denna avhandling underlag till evidensbaserade rekommendationer för en ståndortsanpassad och hållbar skötsel av svenska skogar i ett föränderligt klimat..

Nyckelord: fasta försök, Riksskogstaxeringen, tillväxttrend, bonitet, heterogenitet, substitution, begränsning av klimatförändringar, boreal skog

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Populärvetenskaplig sammanfattning

Det är en utmaning att med skogen möta samhällets ökande behov av skogens nyttor, i form av timmer, cellulosa, energikälla, rent vatten, biodiversitet, rekreation etc., särskilt nu under en pågående klimatförändring. Den norra hemisfärens boreala skogar är en av världens största biom, som levererar otaliga ekosystemtjänster, lokalt till globalt. Den pågående klimatförändringen är redan märkbar i de boreala skogarna där temperaturen ökar dubbelt så fort som medelvärdet globalt. Det kan ha motsatta effekter för skogsresurserna; en ökad tillväxt å ena sidan och å andra sidan en ökad frekvens av störningar i form av torka, stormar, brand, insekter och skadegörare. Det innebär att framtidsprognosen för de boreala skogarna är osäker. Under de senaste 40 åren i Sverige har medeltemperaturen ökat medans nederbörden har varit mer eller mindre oförändrad. Samtidigt har föreskrifterna för skogsbruk ändrats mot en balans mellan råvaruproduktion och biodiversitet. Men för en skogsskötsel med klimatanpassning och resiliens, behövs forskning på hur skogen har svarat på klimatförändringar nu och då.

Modeller för skogens tillväxt och produktion är en viktig del i verktygslådan för att bedöma boreala skogens resiliens under globala uppvärmningen. Tillväxt är här definierat som den positiva förändring i storlek (t.ex. diameter, höjd, grundyta, volym och biomassa) som en växt (ett träd) eller ett bestånd producerar under en viss tidsåtgång. Med produktion menas den ackumulerade (totala) storleken från etablering av beståndet. Eftersom träd är biologiska system så är tillväxten komplex. Det innebär att variation i produktionsförhållanden (som koldioxid, vatten, ljus, näring, temperatur och skötsel) förändrar tillväxten och påverkar den förväntade produktionen. I min avhandling har jag fokuserat på tillväxt och produktion ovanjord, som trädens höjd, grundyta och volym, för att utforska både den spatiala och temporala dynamiken i svenska skogar. Avhandlingen spänner över tre tematiska områden: (i) historisk och nutida förändringar i tillväxt över 40 år, (ii) förväntad total produktion skattat i volym samt beståndsstruktur för ett givet område och trädslag, samt (iii) framtida skogsbruksstrategier för ökad klimatnytta i svensk skog och skogssektor. Resultaten som beskrivs i studierna är baserade på skogliga långtidsförsök (urval med ogallrade bestånd) och riksskogstaxeringens data (den brukade skogen) i Sverige.

Under perioden 1983-2020 är träden (särskilt gran och tall) ungefär 2 meter högre än vad motsvarande träd var för 40 år sedan. Det här kan jag visa både i försök (Studie I) och i den brukade skogen (Studie II). En stor del av ökningen i höjdtillväxt observerades efter milleniumskiftet (efter år 2000) och sammanföll med en period med ökad temperatur i Sverige. Å andra sidan, grundytetillväxten förändras inte i samma tidsperod (Studie II). Det här visar på att träden nu är högre men smalare. Än så länge visar inte den ökade tillväxten på några omedelbara faror. Vi kan inte heller säga något om trenden med ökad höjdtillväxt stannar av eller inte. Det kommer också bero på störningar som skadegörare, torka, stormar och bränder. Till exempel förväntas avgångar efter extremtorka ha effekter under lång tid, som tex efter torråret 2018.

Generellt visar resultaten från Studie I och II att tillväxtförhållandena har förändrats för svensk skog. De här förändringarna kan ha betydelse på två sätt: volymproduktion och beståndsstruktur. Vid en konstant och stabil grundytetillväxt kan en ökad höjdtillväxt översättas till volymökninar. I Studie III utvecklade jag nya metoder för att bestämma potentiella volymproduktionen (boniteten) i svensk skog. Metodiken kan bli betydelsefull för praktiskt skogsbruk, till exempel för val av trädslag i föryngring, för optimering i beståndsbehandlingar och för att kvantifiera kolbindning och kolbudget i barrskog. I Studie IV visade jag att vetskapen om trädens variation kan öka precisionen i tillväxtmodeller i heterogena bestånd med tall och gran.

På lång sikt blir det en större klimatnytta i brukad skog jämfört med att inte avverka och lagra kol i stående skog (Studie V). Nyttan beror på en ökad tillväxt och substitutionseffekter, d.v.s. att avverkade skogen används istället för fossilbaserade material. Sammanfattningsvis, min avhandling kan användas som underlag för evidensbaserade rekommendationer för ett hållbar borealt skogsbruk.

Dedication

To my family, Mr and Mrs. Ankrah, Gabriel, Francis, Patrick, Yvonne and Alexandra

“The plant kingdom covers the entire earth, offering our senses great pleasure and the delights of summer”
~ Carl Linnaeus

Contents

List of publications

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

I. Mensah, A.A., Holmström, E., Petersson, H., Nyström, K., Mason, E.G. & Nilsson, U. (2021). The millennium shift: Investigating the relationship between environment and growth trends of Norway spruce and Scots pine in northern Europe. *Forest Ecology and Management*, 481, 118727.

II. Mensah, A.A., Petersson, H., Dahlgren, J. & Elfving, B. Increasing tree height but stable basal area growth according to data from the Swedish National Forest Inventory. (Manuscript)

III. Mensah, A.A., Holmström, E., Nyström, K. & Nilsson, U. (2022). Modelling potential yield capacity in conifers using Swedish long-term experiments. *Forest Ecology and Management,* 512, 120162.

IV. Mensah, A.A., Petersson, H., Saarela, S., Goude, M. & Holmström, E. (2020). Using heterogeneity indices to adjust basal area – Leaf area index relationship in managed coniferous stands. *Forest Ecology and Management*, 458, 117699.

V. Petersson, H., Ellison, D., Mensah, A.A., Berndes, G., Egnell, G., Lundblad, M., Lundmark, T., Lundström, A., Stendahl, J. & Wikberg, P-E. On the role of forests and the forest sector for climate change mitigation in Sweden. (*In press, GCB-Bioenergy*).

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The contribution of Alex Appiah Mensah to the papers included in this thesis was as follows:

I. Developed the research idea together with the co-authors. Performed the statistical analyses and wrote the manuscript with support from the co-authors.

II. Developed the research idea together with the co-authors. Performed the statistical analyses and wrote the manuscript with support from the co-authors.

III. Developed the research idea together with the co-authors. Performed the statistical analyses and wrote the manuscript with support from the co-authors.

IV. Developed the research idea together with the co-authors. Performed the statistical analyses and wrote the manuscript with support from the co-authors.

V. Supported the analysis and writing of the manuscript.

Abbreviations

ADA	Algebraic Difference Approach
ALS	Airborne Laser Scanning
CO_2	Carbon dioxide
DBH	Diameter at Breast Height
EC	European Commission
EPS	Expressed population signal
EU	European Union
FFS	Fossil-Free Sweden
GADA	Generalised Algebraic Difference Approach
IPCC	Intergovernmental Panel on Climate Change
LAI	Leaf Area Index
LiDAR	Light Detection and Ranging
LTE	Long-Term Experiment
MAI	Mean Annual Increment
NFI	National Forest Inventory
PAI	Plant Area Index
SIH	Site Index according to Height curves
SIS	Site Index according to Site factors
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

The levels of atmospheric greenhouse gases (e.g. carbon dioxide, CO_2) have increased during the last century, and now approaching the 410-ppm mark. Enormous commitments by national and international parties are being made to reverse the CO_2 emission trend and keep temperatures below 2 ^{o}C at the end of the century. Such global efforts to mitigate climate change are on one hand, urgently oriented towards the reduction of greenhouse gas emission into the atmosphere and on the other hand, to increase carbon removals from the atmosphere (IPCC 2014). Equally, the European Union (EU) aims to achieve zero net climate emissions by the year 2050 and the role of forests is increasingly discussed (EC 2020). Forests play an essential role as “natural climate solutions” as they sequester CO_2 through photosynthesis and store it as biogenic carbon in biomass and soils (Pilli et al. 2015). This offers the potential for increasing carbon sequestration in standing forests and in forest products or through harvested wood available for use as substitution of fossil-based materials (Lundmark et al. 2014; Leskinen et al. 2018; Eriksson & Klapwijk 2019; Grassi et al. 2021). Therefore, to achieve global targets on climate change mitigation and adaptation, information about forest growth and yield is essential. Important questions regarding tree growth are to what extent management and environmental change have influenced it, and how it might respond in the future. Furthermore, under changing growing conditions, new knowledge and tools for the inference of growth and yield compatible with long-term forest management systems are required.

Today, much more observations from long-term monitoring systems such as the Swedish National Forest Inventory (NFI) and permanent plots in the Long-Term Experimental sites (LTEs) have accumulated, enabling a detail spatio-temporal assessment of tree and stand growth to be made. This thesis assessed the impacts of changed forestry practice and environmental conditions on (*i*) forest growth, (*ii*) potential bias in forest site productivity estimates, and (*iii*) explicit modelling of long- and short-term future climate change mitigation potential of Swedish forests, utilizing dense time-series data from the NFI and LTEs.

1.1 Boreal forests under global change

The boreal forest represents ~30 % of the global forest area (*ca*. 1370 million hectares - Mha) and it stores a vast quantity of carbon in its vegetation and soils (Brandt et al. 2013; Xu et al. 2021). Located between latitudes 45 and 70 °N, the circumboreal belt stretches through Russia, Alaska, Canada and Fennoscandia (Soja et al. 2007). Despite the boreal forests containing the world's largest remaining intact forest ecosystem (largely unaffected by forestry and other human activities), nearly two-thirds of the forests are managed extensively (low input) in Canada and Russia and intensively in Fennoscandia (Gauthier et al. 2015). The boreal forests provide essential ecosystem services ranging from timber production to recreation (Gauthier et al. 2015). However, the boreal ecosystem is warming twice as the rest of the world (IPCC 2014) with prevalent outbreaks of disturbances (e.g. fire, insects, winds, etc.). This suggests that the forests' capacity to deliver future vital ecosystem services is largely uncertain (Boisvenue & Running 2006; Allen et al. 2010; Moen et al. 2014; Romeiro et al. 2022). In Europe, the boreal forests in Fennoscandia represent a significant proportion of the total forest area, and hence, constitute an integral part of the carbon stock balance of European forests. Assessment of the growth dynamics in northern Europe is equally important for attaining the EU's climate target by 2050 and beyond.

Sweden forms the southern edge of the circumboreal belt and it is characterized by a large north-south extent with considerable variations in growth, climate and soil conditions. About two-thirds of the forests are located in the boreal zones at the northern part and the remaining in a nemoral (temperate) climate at the southern part of the country. The forestland area is about 27.8 Mha (representing 70 % of the total land area); from which 23.4 Mha are productive (mean annual volume increment is greater than 1 m^3/ha/year), and 4.4 Mha are considered unproductive (Nilsson 2021). Main tree species (by contribution to the total growing stock on forestlands – excluding urban lands) are Norway spruce (*Picea abies*, 39.7 %), Scots pine (*Pinus sylvestris*, 39.3 %), Birch (*Betula pendula* and *Betula pubescens*, 12.9 %), followed by aspen (*Populus tremula*, 1.8 %), alder (*Alnus glutinosa and incana*, 1.7 %), oak (*Quercus robur*, 1.3 %) and beech (*Fagus sylvatica*, 0.7 %). Contorta (*Pinus contorta*, 1.3 %) is the most widespread exotic species planted on productive forestlands. Larch (*Larix decidua* – European Larch and *Larix sibirica* – Siberian Larch) also contribute 0.1 % to the total growing stock volume (Nilsson 2021).

The wealth of Sweden is highly dependent on the forests. The forestry sector accounts for about 2.2 % of the country's gross domestic products and 11 % of its total exports (SFA 2014). In the early 1920s, the total annual volume growth was around 50 million m^3. Today, the annual growth is about 120 million m^3 in Sweden and the growth has always exceeded the cut (Figure 1). In the same period, and on productive forestlands, the growing stock volume has also increased from about 1000 to 3100 million m^3 (Nilsson 2021). Important questions are to what extent changes in forest management and environmental conditions influenced the tree and stand-level growth dynamics in Swedish forests. This may provide significant pathways for identifying potential forest management strategies that are both robust to environmental changes and sustainable in the long-term.

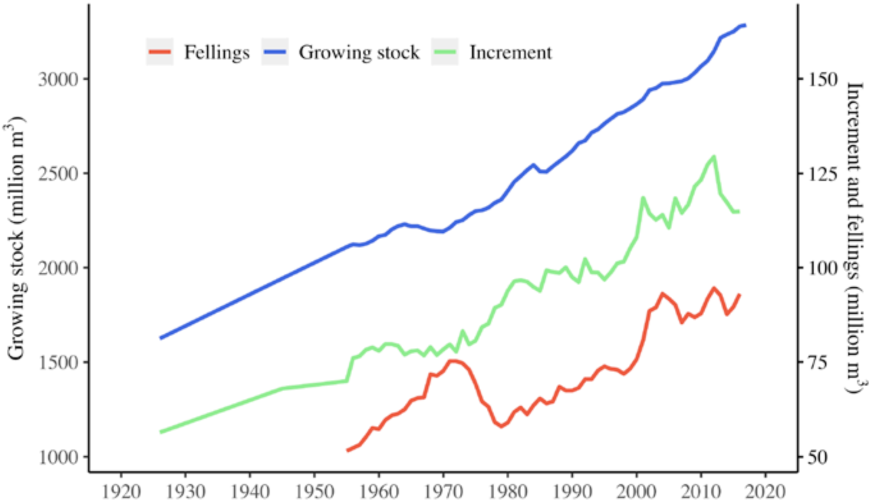

Figure 1. Development of total growing stock, growth (including increment of felled trees) and fellings in Swedish forests in the period 1920-2020 after Nilsson (2021). Note: estimates are five-year moving averages for all land-use classes excluding formally protected areas, alpine areas and urban lands.

1.2 Changes in environmental conditions

Tree and stand-level growth are influenced by (and also have influence on) the growing site. They are determined primarily by resource availability (e.g. radiation, CO_2, water, nutrients) and environmental conditions (e.g. temperature, soil acidity, air pollution etc.) (Nowak et al. 2004; Pretzsch 2009; Kint et al. 2012). Under global change, important variations in most of these factors and their impacts on terrestrial ecosystems have been assessed and reported over the past decades (Machta 1972; de Vries et al. 2014; Keenan et al. 2016; Collalti et al. 2020). Aside these known abiotic conditions, changes in forest growth rates have been attributed to emerging environmental factors such as diffuse fraction of light and galactic cosmic rays (Bontemps & Svensmark 2022).

The boreal forest is warming twice as fast as the other forest ecosystems, making it the biome with the greatest impact of global warming where observed changes are mainly increased temperature and altered patterns of precipitation (IPCC 2014). In Sweden, the annual mean temperature and precipitation have increased respectively, by +2 ^{o}C and 10 % relative to the normal climate in the period 1961-1990 (Figure 2). Depending on the Representative Concentration Scenario (RCP) used, the mean annual temperature and precipitation are projected to be 2-6 ^{o}C and 20-60 % more than for the period 1961-1990 by the end of the 21st century (SMHI 2018).

Largely, it is also expected that increases in nutrient availability, temperature and precipitation may lead to increased growth in the boreal forests (Myneni et al. 1997; Bergh et al. 1998; Boisvenue & Running 2006; Hyvönen et al. 2007; Kauppi et al. 2014). However, there has also been reports on negative effects associated with the increased warming during the last 50 years and which might even rise by the end of this century (Allen et al. 2010; Gauthier et al. 2015; Ruosteenoja et al. 2018). For example, longer dry spells (such as the 2018 summer drought) may override the beneficial effects of higher temperatures through decreased productivity and enhanced tree mortality (Girardin et al. 2014; Muukkonen et al. 2015; Belyazid & Giuliana 2019). Others such as increased frequency of fires (Rubtsov et al. 2011; Forzieri et al. 2021), insects and pests outbreak (Kurz et al. 2008) and storms (Blennow & Olofsson 2008; Senf & Seidl 2021) may affect the growth and productivity of the forests in northern Europe.

Boreal forest soils are mostly nitrogen (N) deficient (Tamm 1991; Högberg et al. 2021a), and large scale fertilization trials have shown N limitation to forest tree growth (Nilsen 2001; Nohrstedt 2001; Forsmark et al. 2020). During the period 1983-2013, the atmospheric deposition of nitrogen has decreased by 30 % in Sweden, with the largest decrease occurring in the south-western part of the country (Andersson et al. 2018). The mechanisms driving N limitations are mostly facilitated by both cold temperatures causing slower turnover rates of N in the soil and slow N delivery in the soil solution (Lim et al. 2015; Henriksson et al. 2021). Thus, increasing precipitation as well as air and soil temperature might increase N availability, which would enhance tree growth (Etzold et al. 2020).

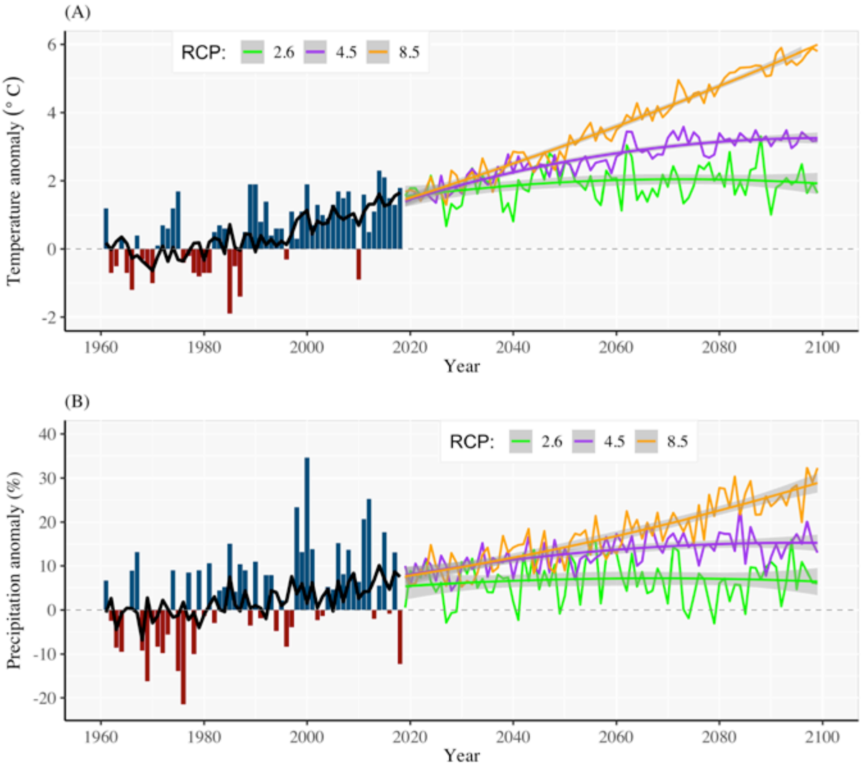

Figure 2. Changes in annual mean temperature (A) and precipitation (B) in Sweden during the period 1961-2100 compared with the normal period (mean 1961-1990), given a Representative Concentration Pathway (RCP). The black line shows ensemble mean of the historic trend. The bars show historic data from observations (blue and red bars indicate higher and lower than normal, respectively). Source: Swedish Meteorological and Hydrological Institute (SMHI 2018).

1.3 Changes in forest management

In Fennoscandia (Norway, Sweden, Finland), the boreal forests have been intensively managed under silvicultural practices and forest governance aimed at increasing forest productivity and minimizing rates of natural disturbances (Gauthier et al. 2015). Almost all productive forests in Sweden have been managed for timber production for a long period of time (Fries et al. 1997). The historical use of Swedish forests show large variations over the country, from the agricultural use of the forests in southern Sweden through to forest use for mining in the south-central Sweden and extensive logging by sawmill companies in the northern parts of the country (Roberge et al. 2020). Field based studies and practical observations across centuries have shown that forest management affects tree growth by changes in harvesting systems and precision silviculture (Örlander et al. 1990; Fries et al. 1997).

In the early 1800, rotational forestry with clearcutting as the main harvesting system was introduced in central Sweden and by 1900, the practice had been extended to the northern parts of the country (Lundmark 2020). As a general reaction against monocultures and uniform forests in continental Europe, the selection system was heavily popularised. From the 1900, both the clearcutting and selection systems were applied as silvicultural systems for forest management until the 1950, where the latter was abandoned completely in Sweden (Lundqvist 2017; Lundmark 2020).

As concerns of overexploitation of wood increased, new forest legislation and policies aimed at sustainable wood production in Swedish forests were instituted by the mid-20th century (Fries et al. 1997). Poorly stocked residual forests were from the 1950s cleared and reforested with Norway spruce and Scots pine, while broadleaves were cleared mechanically (cutting) and chemically (spraying with herbicides) since there was no large-scale industrial demand for these species (Roberge et al. 2020).

Since then, a large number of enhanced silvicultural practices have been implemented. Among these included: (*i*) soil preparation to reduce competition from field vegetation (Örlander et al. 1996), to increase the survival and early growth of seedlings (Nilsson et al. 2019) and to protect seedlings from damage by insects such as pine weevils (Wallertz et al. 2018); (*ii*) use of genetically improved materials (Egbäck et al. 2017) and (*iii*) drainage of peatlands and mineral soils (Hånell 1988; Sikström & Hökkä 2016) to increase forest growth.

To influence the stand structure, to increase diameter growth of individual trees and to enable higher economic return, thinning is mostly applied (Mäkinen & Isomäki 2004; Nilsson et al. 2010). Both pre-commercial (cleaning) and commercial thinning strategies became a standard silvicultural technique during the 1950s in Sweden and nearly 1 million ha of productive forestlands were thinned annually until the 1970s. Since then, about 400000 ha of forests are tended and commercially thinned annually (Nilsson 2021). Today, it is common with thinning grades (proportion of basal area removed) between 20-40 % in Swedish forests (Valinger et al. 2019). Large scale practical N fertilization (~ 150 kg N/ha in the form of calcium ammonium nitrate or urea) started in the mid-1960s, where 10 % (2 million ha) of productive forestlands were fertilized. During the late 1970s, about 200000 ha were fertilized annually. Nowadays, only about 30000 ha are fertilized annually (on a maximum of three occasions during a rotation period and mainly by forest companies) due to better fertilizer management and the fear of negative environmental effects (Nohrstedt 2001).

In the late 1980s, consideration of environmental values became increasingly relevant and in the new forest policy, environmental objectives were set to be of equal importance as those of timber production (Roberge et al. 2020). Examples of the large scale environmental considerations implemented were tree retention (preservation of old and dead trees) during harvest, the creation of high stumps, establishment of buffer zones along watercourses and the construction of retention patches of valuable habitats (Simonsson et al. 2015).

The changed forestry practices with increased demand of environmental considerations suggest young stands are more heterogeneous than they use to be in Sweden (Axelsson & Östlund 2001). Thus, there is an increased proportion of stands that are heterogeneous with respect to height, diameter, age and species composition compared to stands that were established in the period 1950-1980 (Nyström 2001). Consequently, assessment of tree growth under altered management and environmental conditions as well as growth and yield modelling in heterogeneous forests have become a topic of great interest.

1.4 Changes in forest site productivity

The productivity of forest sites is influenced by both management, natural factors inherent to the site, as well as climate change (Skovsgaard & Vanclay 2008; Bontemps & Bouriaud 2014). To many foresters, information on site productivity is used much for example, to select tree species during regeneration, to plan silvicultural treatments across the rotation, to forecast forest growth and to quantify potential wood biomass production at scales raging from local-to-regional and- national levels (Pretzsch et al. 2008). Additionally, estimates of site productivity can be valuable for the assessments of management and environmental impacts on the growth and carbon fluxes of forest ecosystems in the short- and long-term horizons (Boisvenue & Running 2006; Fontes et al. 2010). In Sweden, the site productivity is also the legislative boundary of the Forestry Act, and only forestlands where the mean annual wood production exceeds 1 m^3 ha^{-1} yr^{-1} are considered as productive forestland. On poorer sites, no harvest is allowed and Swedish national statistics are reported differently based on this boundary (Nilsson 2021). Accordingly, information on the site productivity may augment the evaluation of tree species' impact on wood biomass production, biodiversity and the provision of other ecosystem services (Felton et al. 2019).

In Sweden, most forest sites are regenerated with Norway spruce and Scots pine. While the two species have been used in forestry for over 100 years, there has also been considerable replacement of principal site species (Felton et al. 2019). In the southern part of the country, traditional productive forestlands of Scots pine are presently regenerated with Norway spruce (SFA 2022). On the other hand, older production stands that were once dominated by Norway spruce have predominantly been converted into Scots pine stands in the central-north of Sweden (Elfving & Nyström 1996). Reasons for such changes are typically centred on browsing effects (Wallgren et al. 2013), resistance to storm (Valinger & Fridman 2011) and competitive growth rates of the two species (Ekö et al. 2008).

However, another motivating reason could be that existing tools for site classification indicate lower productivity for the main site species (Hägglund & Lundmark 1982; Elfving & Nyström 1996; Ekö et al. 2008). The tools generally express site productivity (yield capacity, defined as maximum mean annual volume increment) through site index. Compared with the old site index models, current (operational) site index functions are indicating a change in the growth form (Elfving & Kiviste 1997). In addition, there is no existing functional relationship between the operational site index functions and yield capacity at the national scale. Thus, there is a potential bias if yield capacity is based on the older site index functions, especially in a changing climate and management regime (Mason et al. 2017). Therefore, valid data and new expressions for forest site productivity are needed in the growth models presently used in Sweden.

1.5 Growth and yield modelling

As a biological system, forests are dynamic entities affected by biotic and abiotic conditions. Hence, they often undergo changes in stand composition and structure over time. Growth is defined here as the change in size (e.g. diameter, height, basal area, volume, biomass, etc.) of a plant or a stand within a defined period. Yield refers to the accumulated (total) size from the time of stand establishment (Pretzsch 2009). Trees and stand growth over time are described by two main opposing factors: the biotic potential (i.e. the intrinsic tendency toward unlimited increase) and restraints imposed by environmental resistance and aging. The expansion phase is proportional to current size and prevails at the beginning of the tree's life, while growth decline occurs at the end. In this regard, most growth models are constructed to reflect these two components (Zeide 1993).

Growth and yield models can be classified into two broader groups: empirical (statistical) and mechanistic (process-based) models (Weiskittel et al. 2011). While process-based models describe explicitly the cause of growth, empirical models describe the growth without attempting to identify the causes and explain the phenomenon underpinning growth (Burkhart & Tomé 2012). Among the empirical models are stand-level and tree-level models. The stand-level models are usually simple and robust and require little information for parametrization (Yue et al. 2008). Tree-level models for instance, distance-dependent models require explicit tree spatial information and are computationally demanding than the distance-independent models (Yue et al. 2008). In the last years, hybrid models combining features of both empirical and process-based models have evolved; making them better suited for simulating growth under altered environment and management conditions (Antón-Fernández et al. 2016; Goude et al. 2022).

In Sweden, the planning package Heureka is a widely used simulator in both practical forestry and forest research. It is mainly an empirical growth simulator with sub-modules for simulating climate effects on growth etc. (Wikström et al. 2011). The Heureka system uses tree-level and stand-level models in tandem, where the former is used for modelling yield distribution and the latter for calibrating overall stand growth. Generally, the models within Heureka describe two stages in stand growth: the establishment period and the development of the established stand. While average stand height is the dependent variable during the establishment stage (7-8 m), basal area drives the models for established stands (Fahlvik et al. 2014).

In this thesis, the aboveground growth components, essentially height and basal area growth are investigated under altered management and environmental conditions, using extensive observational data from the LTEs and NFIs. The study is made either at the tree or at the stand (plot)-level, depending on the available growth data and the objective of the analysis.

1.5.1 National Forest Inventories

NFIs are one of the main data sources for forest resources assessment, planning and management from local-to-regional-to-national and – international scales (Tomppo et al. 2010). Generally, sample-based NFIs have probabilistic designs, cover large gradients of growth drivers and guarantee unbiased sample of tree populations and large-scale representative data. Many large-area forest inventories utilize permanent and temporary sampling units as a means to obtain accurate estimates of change in important variables, such as growing stock, biomass and carbon stocks (Tomppo et al. 2010). These data commonly provide a representative overview of the current growth behaviour as they include routinely managed stands with characteristics such as mean stand density and common silvicultural treatments (Pretzsch 2009). The data is characterized by short time series and often poor age records that may hardly provide the exact information about stand history (e.g. time of establishment, genetics) and accumulated yield (Pretzsch 2009), though, part of the above problems may be partly alleviated by the use of permanent plots over a longer time. Thus, data from NFIs generally indicate correlations in studies of growth-site assessment and they may be applied as initial values for simulation runs (Pretzsch 2009). Nevertheless, data from NFIs have the potential to identify site-specific drivers that may affect tree growth, and are suitable for the calibration of tree- and stand-level growth models along gradients of management and environmental conditions (Söderberg 1986; Hasenauer & Monserud 1997; Hynynen et al. 2002; Rohner et al. 2018; Trasobares et al. 2022).

In recent times, information about growth for individual years has become important, especially for greenhouse gas reporting where signatories to the Climate Convention are required to compile reports about annual greenhouse gas emissions (IPCC 2014). In order to normalize growth estimates from NFIs, growth indices for individual years are often used to adjust for non-normal weather conditions in the individual years (Jonsson 1969).

Periodic inventories (with permanent plots) normally are not designed to provide accurate estimates of annual growth, although some attempts to derive such information have been made (Heikkinen et al. 2012). However, many NFIs today derive growth series from tree ring measurements (Tomppo et al. 2010) in order to (1) assess tree growth response to the changes in weather conditions and the applied management from individual years (Biondi 1999; Ols et al. 2020) and (2) to improve the inference of annual growth at the national level (Svensson 1983; Suty et al. 2013). Since 1923, the development of Swedish forests has been monitored by the NFI through annual measurements on sample plots (Fridman et al. 2014). By examining comparable trees sampled annually over a longer period, it is possible to evaluate stand and climate-driven growth variations for individual years.

1.5.2 Long-term Experiments

Since their first establishments in Germany during the 19th century, long-term experiments (LTEs) have provided much of the scientific knowledge of tree and stand dynamics and the effects of silvicultural decisions in practical forestry (Pretzsch et al. 2019). Examples of such prominent knowledge derived from LTEs that have made significant contributions towards forest science and forest practice include the self-thinning rule (Reineke 1933; von Gadow 1986), the density-growth relationships (Zhao et al. 2020), yield tables (Assmann 1970) and the development of guidelines for spacing and thinning (Pattersson 1992; Pretzsch & Zenner 2017).

Despite the statistical constraints (e.g. no repetitions or only one replicate per site) of earlier experiments, the combination with later setups of similar experiments along productivity gradients are instrumental in disentangling the effects of other factors (e.g. dry deposition, acid rain or climate change) on tree growth for which they were not designed for (Spiecker et al. 1996). In contrast to NFIs, LTEs provide key stand information (such as history, age, provenance, etc.) with higher accuracy. By comparing treated and untreated units, LTEs can reveal to a larger extent the cause-effect relationships at the tree- and stand-level (Pretzsch 2009). The unthinned plots represent site-specific maximum density and may serve as a reference for evaluation of silvicultural treatments and natural mortality on a given site (Hynynen 1993; Elfving 2010a) or may be used for assessing temporal trends in species-specific carrying capacity in altered environments (Mäkinen et al. 2021). Additionally, by measuring the remaining as well as the removed stand, LTEs provide the total production at a given site since stand establishment, which is most relevant for examining the relationships among site conditions, stand density and productivity (Pretzsch et al. 2019).

In Sweden, several LTEs were established during the early 1900s throughout the country to examine effects of thinning and fertilization on growth and yield (Nilsson et al. 2010), wood quality (Pfister et al. 2007), biomass production (Eriksson 2006) and stand stability (Wallentin & Nilsson 2014) of many tree species including Norway spruce and Scots pine. Thus, the availability of plots spanning longer rotation periods and covering wider amplitudes in management and environmental conditions, have the potential to be used for the empirical examination of growth trend changes and site productivity in Swedish forests.

1.5.3 Modelling height growth trend by site index

Usually, the dominant height of a fully stocked even-aged stand describes the stand’s production capacity, because it is independent of density over a wide range of densities (Pienaar & Shiver 1984; Skovsgaard & Vanclay 2008), although, this invariance has been debated (MacFarlane et al. 2000). Hence, dominant (top) height at a given reference age is used as a measure of site productivity (Monserud 1984). Site index (expected height at a reference age) models are also examples of dominant height growth models and they are used to predict the maximum potential height growth and infer stand development in individual tree- and stand-level growth models (Elfving & Kiviste 1997; Sharma et al. 2011). Earlier dominant height growth and site index models were mostly constructed from guide-curve methods with static base-age curves that retain the same proportional relationship across all age classes (Clutter et al. 1983). Today, base-age invariant methods such as the algebraic (ADA) and the generalized algebraic (GADA) difference approaches have been used to develop dominant height growth models that make use of height-age data series exclusive of the base age. These models are also independent of the choice of the base age (Rivas et al. 2004; Nord-Larsen et al. 2009). The ADA allows one parameter to be site-specific and as such produces anamorphic curves or have single asymptote (Bailey & Clutter 1974). The GADA approach allows more than one parameter to be site-specific and therefore are polymorphic with multiple asymptotes (Cieszewski & Bailey 2000).

Site index and height growth models are often developed under the assumption of constant environmental conditions across the entire rotation period (Goelz & Burk 1992). As such, they generally show patterns of average height development expected at various ages for even-aged monoculture stands growing on different sites (Monserud 1984; García 2011). However, the relationship between dominant height and age can be used to investigate changes in temporal trends of height growth under altered environment and management conditions (Pretzsch 2009). This can be done by directly expressing the height growth model in terms of the growth site factors (Albert & Schmidt 2010; Sharma et al. 2012). Alternatively, the observed growth in an altered environment can be compared with the expected growth predicted from a reference model developed from the growth data prior to the change (Zeide 1993). Here, the reference model is valid if it suitably represents the site and stand conditions in the reference period (Spiecker et al. 1996).

The assumption of using height growth and site index models to detect growth trend change is exemplified for three hypothetical stands describing the cases of increased (positive), stable and slower (negative) trends in height growth (Figure 3). A growth trend change is defined here as a long-term change of tree growth rate from the expected, given stand, management and environmental conditions (Spiecker et al. 1996). In all cases, the actual height development is compared with the expected height from the site index curves at each age and measurement period. From this comparison, the relative bias in growth, which quantifies both the magnitude and the direction of the change in height growth pattern can be estimated as the difference between the observed and expected height increment according to the reference curves.

This approach is suitable for repeated growth data where dominant height, age and stand history can be reliably obtained. In Sweden, such growth data is readily available from the permanent plots in the LTEs. For instance, by using the untreated plot data (without intensive management or site quality intervention), it is possible to detect any eventual trend change in height growth and quantify potential growth response to altered climatic conditions.

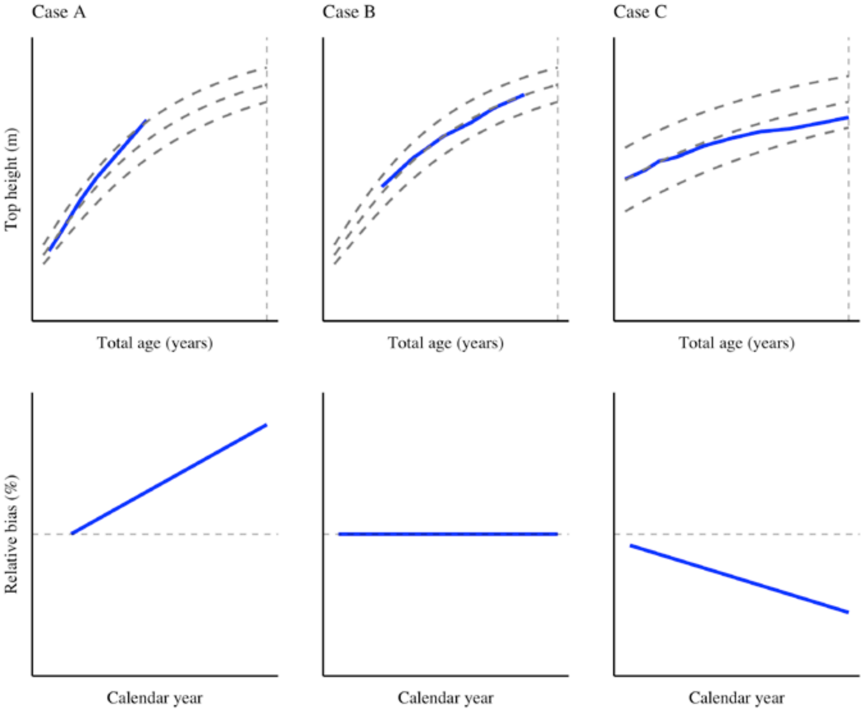

Figure 3. Illustration of changes in height growth trends of three hypothetical stands (denoted as cases). Upper panels show height development (solid lines) in relation to site index (dashed lines). Bottom panels show the magnitude (size and direction) of the growth trend change. The horizontal (broken) lines in bottom panels show equivalence in the observed and expected growth. Case A: increased (positive) growth than expected; Case B: stable growth; Case C: slower (negative) growth than expected.

1.5.4 Modelling growth variation using ring width

For many reasons, tree ring chronologies have become a valuable data material in most studies of environmental monitoring. Key reasons are: (1) environmental signals and management interventions can be linked to the year-to-year variations in the ring widths, and (2) it represents a non-destructive source of deriving information on the inter-annual to inter-decadal changes in tree growth (Lebourgeois et al. 2005; Henttonen et al. 2009).

The degree to which tree-ring widths capture inter-annual processes is dependent on the tree species and its surrounding environment (LeBlanc 1990). For a given species, the pattern of annual ring width variation may be similar for neighbouring trees (expressed population signal, EPS), even though the variations in different directions of the cross-sections of the stem can be quite large (Matérn 1961; Mäkinen & Vanninen 1999).

Despite increasing insights into growth processes and sharpness in measurement of weather parameters, it has still been difficult to explain largely, the variations in ring widths. Climatic factors mostly found to explain the variations include temperature and available water capacity during the growing season (Jonsson 1969; Mäkinen et al. 2002; Lebourgeois et al. 2005; Ols et al. 2020; Stern et al. 2021). Likewise, seasonal thermal conditions may influence the onset and cessation of radial increment of most tree species (Mäkinen et al. 2018). Others including fructification (Mund et al. 2010; Shestakova et al. 2021) and defoliation by pests and pathogens (Hoogesteger & Karlsson 1992) may also explain the variations in radial increment.

Stand-driven variations in ring width could be explained by the density and tree position within the stand. There are examples of trees grown in dense stands that increased their ring width by a factor of four over a period of 3-5 years after release by thinning, for example, pine and spruce in Sweden (Eklund 1952) and white pine (*Pinus strobus*) in Canada (Bevilacqua et al. 2005). This thinning response is independent of tree age and lasts 20-30 years for pine and spruce in Sweden (Jonsson 1995). As shown by Eklund (1952), the reactions of dominant and co-dominant trees to weather conditions are easier to detect than in dominated and suppressed trees. For this reason, studies of EPS are often based on cores from dominating trees, especially when the main objective is to disentangle the influence of environmental signals rather than density-induced competition trends (Stern et al. 2021).

Most past studies of inter-annual growth variation were based on ring width series. However, ring widths normally show a progressive decline along a cross-sectional radius due to the increase in stem size and tree age over time (Biondi & Qeadan 2008). The age-related trend may be removed by pre-whitening the series over year and those series may be expressed in the form of radial increments or may quantify the variation in relative terms (Jonsson 1969). Nevertheless, by relating the ring width to tree diameter enhances the formation of basal area growth series which could allow meaningful growth comparisons in quantitative terms for example, between tree species and geographical regions (Silva et al. 2010).

In Sweden, information from completed annual and cumulative (e.g. last 5 years) ring width of sample trees is available since the 1950. This growth dataset is obtained from annual sampling of temporary plots that consist of spatially independent observations but are statistically representative of the Swedish forest population over time (Fridman et al. 2014). By linking the basal area growth (from ring widths) with stand and environment conditions, it is possible to detect eventual trends and quantify the inter-annual growth variations over time.

1.5.5 Modelling forest site productivity

Forest site productivity is generally defined as the potential of a site to produce wood biomass (Hägglund 1981; McDill & Amateis 1992; Skovsgaard & Vanclay 2008). It is assessed largely by two approaches: geocentric and phytocentric methods. The geocentric methods are mostly based on site indicators of climate, topography and soil, whereas the phytocentric methods are vegetation related, made up of tree- or plant-based indicators (Skovsgaard & Vanclay 2008). The two methods have been widely applied in studies on forest site productivity assessment for several tree species across biomes (Hägglund & Lundmark 1977; Szwaluk & Strong 2003; Bueis et al. 2019).

The approach of determining site productivity is based on three main tenets (Figure 4): the site index hypothesis, the Eichhorn’s rule and Assmann’s yield level theory (Skovsgaard & Vanclay 2013). Since the twentieth century, the productivity of forest sites has been classified by site index (expected height at a reference age), especially in even-aged forests (Skovsgaard & Vanclay 2013). Site index based on height-age relations of the dominant trees is often desirable when estimating the potential of the growing site. This is due to the reasons that height growth correlates strongly with stand volume growth, and the height growth of the largest trees is relatively independent of stand density and thinning from below treatments (Skovsgaard & Vanclay 2008; Burkhart & Tomé 2012). However, expressing site index in terms of the potential average volume yield produced over the stand rotation is desired since timber volume is a key parameter in economic and ecological analyses of forest resources. Hence, for even-aged forest stands, the relation between site index and maximum mean annual volume increment (hereafter, referred to as yield capacity) can be directly used to describe the potential amount of wood volume that can be obtained per year on a site for a given species (Hägglund 1981).

Eichhorn’s rule (Eichhorn 1902) specifies that stands have the same total (accumulated) volume (including thinnings) when they reach the same dominant (top) height, independent of site and age. This was interpreted as the general or common yield level by Assmann (1970). On the other hand, Assmann (1966) for Bavaria as well as Bradley et al. (1966) for Britain showed that the potential volume yield might vary remarkably between stands of the same site index, for many tree species including Norway spruce and Scots pine. This may hold even within a specified growth region, and for a given well-defined silvicultural treatment (Skovsgaard & Vanclay 2013). Subsequently, yield level as an index of productivity has often been used to describe the variation in total volume production at a given site index (Assmann 1970). This implies that stands of different yield levels may have different trajectories for height-volume relations across the rotation period.

The local variation in yield levels at a given a site index has been attributed to many factors including site properties (e.g. soil type, available water supply, etc.), climate and genetics (Skovsgaard & Vanclay 2008). Nevertheless, for even-aged stands, potential density described as the different capacity of different sites within the same site index to support trees (Curtis 1972) is found to explain by a larger extent the variations in volume yield levels. As an index for this potential density, Assmann (1970) used maximum basal area, Sterba (1987) recommended using Reineke’s (1933) maximum stand density index and Hasenauer et al. (1994) successfully applied both the maximum basal area concept and stand density index to describe the variations in yield levels of loblolly pine plantations across the south-eastern United States.

In Sweden, the development of LTEs provides a unique insight into the evaluation of yield capacity using site index. This may provide information about potential bias in the existing tools for site classification and further enhance the meaningful comparison of productivity across species and regions (Skovsgaard & Vanclay 2008; Ekö et al. 2008).

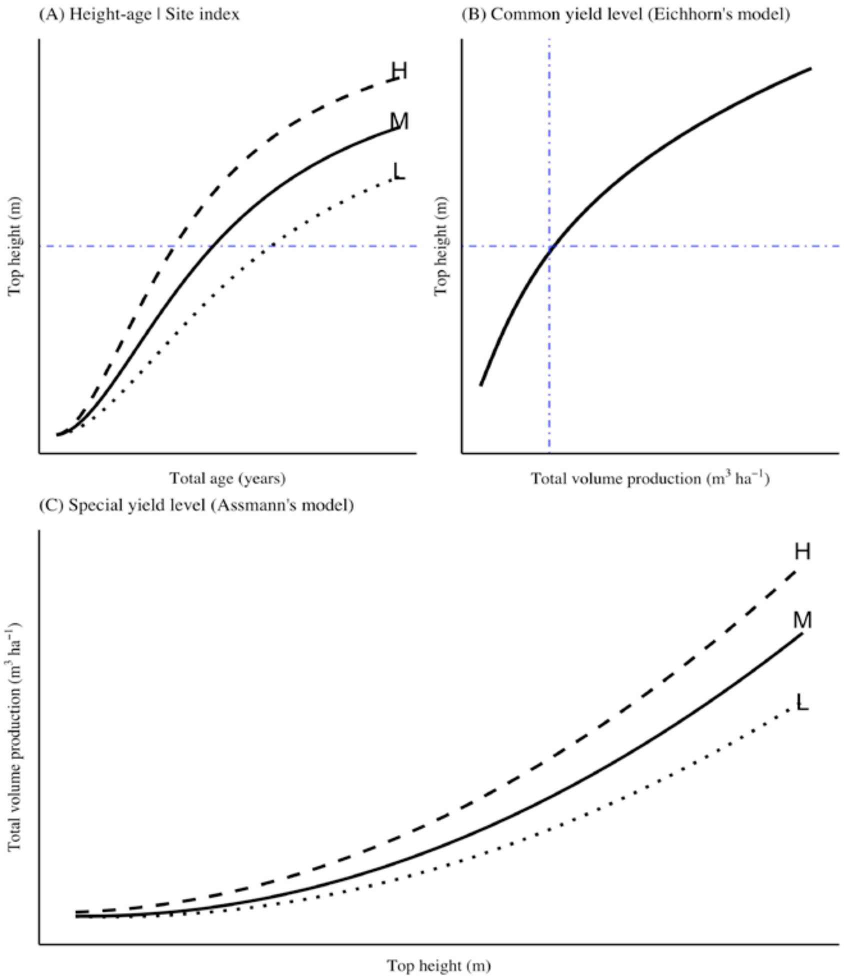

Figure 4. Illustration of the tenets of forest site productivity. (A) Height-age relationships (site index) can differentiate stands into productivity classes (H-high; M-medium and L-low). (B) Independent of site and age, stands may have the same total volume production when they reach the same dominant (top) height. (C) Stands of different yield levels may have different trajectories for height-volume relations.

1.5.6 Modelling growth in heterogeneous stands

Changes in forest management practices as well as environmental conditions have direct implications on the stand structure. This is becoming increasingly important as the young forests of today have a more heterogeneous composition compared to earlier stands established in the period 1950-1980 in Sweden (Nyström 2001; Fahlvik 2005). Heterogeneity defined as the variation in species composition, height and diameter distribution and spatial arrangement of the trees may subsequently induce uncertainty in the growth and yield modelling of managed stands, especially, for the emerging hybrid models based on physiological principles and statistical properties to infer forest growth and dynamics (Goude et al. 2022). As an example of hybrid growth models, those that incorporate potentially usable light sums better reflect the ecophysiological processes driving tree growth, flexibility to adjust to local circumstances and account for short- and long-term climate variation (Mason et al. 2007; Goude et al. 2022).

Leaf area index (LAI) is an important structural variable in these hybrid models because it represents the amount of foliage and the absorption capacity of solar radiation for plant growth (i.e. light interception and use efficiency) (Landsberg & Waring 1997; Binkley et al. 2013a). LAI is defined as half the total surface area of green leaves or needles per unit of ground horizontal surface area (Stenberg et al. 2004). This definition also applies to the plant area index (PAI, also referred to as effective LAI) when other light blocking tree elements (e.g. twigs, branches and stems) are considered. LAI or PAI is estimated either by direct biomass and litterfall sampling via destructive approaches (Jonckheere et al. 2004) or by indirect approaches using optical instruments that rely on Beer's law of radiation transfer and remote sensing techniques (Gower et al. 1999; Rautiainen et al. 2009). The indirect methods usually underestimate the LAI, therefore correction functions based on comparisons with the direct methods and stand parameters are recommended (Goude et al. 2019).

This far research studies about using LAI to model growth have focused on monocultures, while managed (mixed-species) forests have got less attention – this probably due to their complexity and the challenge to model LAI within heterogeneous ecosystems (Davi et al. 2008; Majasalmi et al. 2013). The spatial and temporal distribution of LAI is strongly influenced by stand characteristics (e.g. canopy architecture, tree size, tree species composition, density, etc.), site (e.g. temperature, radiation, topography, soil moisture) and management (Brusa & Bunker 2014; Bourdier et al. 2016). Additionally, forest management and disturbance influence the clumping of foliage within the canopy, which may violate the assumption of random distribution and potentially introduces a bias into estimates of absorbed photosynthetic active radiation (Chianucci & Cutini 2012). This implies that adjustments may be required when applying hybrid growth models on managed forests. Given the stronger relationship between canopy LAI and stem diameter (Kalliovirta & Tokola 2005) and with the two variables also related to productivity (Binkley et al. 2013b), the nature of the relationship between basal area and canopy LAI may give an indication of the magnitude of the uncertainties when modelling the production of heterogeneous forests.

1.6 Modelling future climate change mitigation potential

Forests and the forest sector are considered as one of the key pathways towards climate change mitigation (Pilli et al. 2015), including sequestering and storing carbon in standing forests and products (Eriksson & Klapwijk 2019; Grassi et al. 2021; Skytt et al. 2021) and use of harvested biomass in replacing fossil-intensive materials and fossil fuels (Lundmark et al. 2014; Nabuurs et al. 2017; Gustavsson et al. 2021). Sweden aims to become a fossil-free welfare nation with net zero greenhouse gas emissions by 2045 and negative emissions thereafter. In these roadmaps towards fossil-free future, biomass-based solutions are increasingly considered (FFS 2021). Essentially, forest management strategies aimed at reduction or increasing harvest intensities should be based on a system perspective approach of their short and long-term climate impacts (Cowie et al. 2021). Here, tree growth rate is an important component to determine the harvest potential and how much products can be used for substitution.

For even-aged forests, the optimal time for stand harvest is when the current and mean annual increments intersect (Assmann 1970). Thus, from a pure climate perspective, increasing growth (e.g. by fertilization) and harvesting intensity and establishment of new forests may provide large climate benefits (harvest and substitution potentials) at one hand (Nilsson et al. 2011; Baul et al. 2017; Gustavsson et al. 2021), but on the other hand, such approach may hamper biodiversity goals associated with older forests (Gao et al. 2015). In addition, substitution of fossil-intensive materials with long-lived products may increase both the carbon storage in wood products and emission reduction from the use of fossil-intensive materials (Baul et al. 2017). Nevertheless, alternative forest management scenarios may need to be studied together with alternative substitution factors used for wood-based products to obtain a reliable result on the future climate change mitigation potential of Swedish forests in the short and long-term horizons.

2. Thesis objectives

The main objective of this thesis was to investigate the spatio-temporal dynamics of growth under altered management and environmental conditions, using data from the national forest inventory (NFI) and the long-term experiments (LTE) in Sweden. The tree species focused in the thesis were Norway spruce, Scots pine, Lodgepole pine and Larch (European and Siberian larch). The thesis generally involved three aspects (Figure 5). The first part covered the examination of the changes in growth trends using methods of historical development and present state analyses (**Papers I and II**). The second part involved the assessment of variability in growing conditions and stand composition by modelling site productivity of conifer tree species (**Paper III**) and the uncertainty induced by forest structural heterogeneity in growth and yield modelling of managed stands (**Paper IV**). In the third part and by simulations, aspects on how future management strategies in Sweden may influence the forest carbon stock and wood harvest in the short and long-term horizons were examined (**Paper V**).

The specific objectives of the papers (I-V) were:

I. To investigate if the height growth of Scots pine and Norway spruce has changed during the last 40 years in Sweden, and to assess responses to altered temperature and precipitation.
II. To study the annual variation in the average height and basal area growth levels of individual trees of Scots pine and Norway spruce at comparable site and stand conditions in the period 1983-2020.
III. To evaluate the yield capacity of coniferous trees with data from LTEs in Sweden.
IV. To evaluate how structural heterogeneity indices can be used to describe the uncertainty in the relationship between basal area and LAI in managed stands of Scots pine and Norway spruce.
V. To investigate the impacts of alternative forest management strategies and substitution on climate change mitigation over different time scales in Sweden.

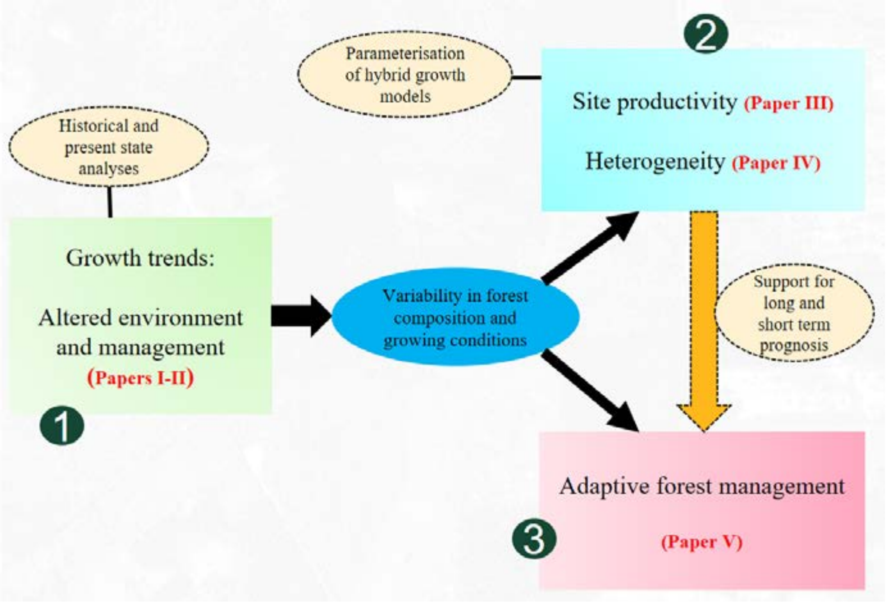

Figure 5. Overview of the structure of the thesis described by the individual papers (I-V). Using historical development investigation, present state analysis and correlative statistical approach, observations from long-term monitoring systems can facilitate the spatio-temporal assessment of growth trend changes under altered environment and management regimes (Papers I and II). A growth trend change may imply both an altered growing condition and variability in forest stand composition. For even-aged stands, height to volume relationships might change accordingly and that new expressions for forest site productivity are needed in contemporary growth models (Paper III). The variability in stand composition may induce large uncertainties in growth modelling, especially for those that are based on a process approach where LAI is a principal component. Thus, alternative ways to account for the local variation in modelling the growth and yield of regular (managed) forests is needed (Paper IV). To adapt the boreal forest to a changing climate, alternative forest management strategies are essential both in the short and long-term horizons (Paper V).

3. Materials and methods

3.1 Swedish long-term experimental data

In **Papers I** and **III**, data from the Swedish long-term experiments (LTEs) were used for the analyses. The experiments largely described thinning, spacing, regeneration and fertilization trials and comprised even-aged monocultural stands (Nilsson et al. 2010). The sites were distributed throughout the country from latitude 55 °N to 67 °N, and they had cultivated origins such as natural regeneration, planting or seeding using local seed sources. All selected LTEs were originally experiments in block designs where the total production (yield) was recorded, including mortality, harvest removals and standing volume. For each site, only the control and thinned-from-below plots with thinning grade (percent removed basal area) < 35 % and thinning ratio < 0.95 were used for the growth trend and yield analyses. Thinning ratio is expressed by the quotient between the basal area mean diameters of removed and remaining trees. Fertilized plots were also excluded from the dataset. These experiments have been measured extensively between 1920 and 2019 with irregular measurements, using permanent square or rectangular sample plots with net sizes of approximately 0.1 ha to collect tree, stand and site information. The time for remeasurements on a plot was on average 8 years and the frequency of remeasurements ranged from 2 to 14. For each plot and measurement occasion, the mean top height was estimated as the arithmetic mean of the 100 thickest (by diameter) trees ha^{-1}, after parameterization of the Näslund's height-diameter equation (Näslund 1947), using the observed height-diameter pairs of the sample trees. All calipered trees without measured heights were then assigned predicted heights based on the height-diameter function. Specific information on the LTE data used in **Papers I** and **III** is elaborated in *sections 3.3* and *3.5*, respectively.

3.2 Swedish national forest inventory data

Since 1923, nation-wide monitoring of Swedish forests has been conducted by the NFI through annual measurements on temporary and permanent sample plots. The Swedish NFI is a probability sample inventory with systematic cluster design, covering large gradients in management and climatic conditions. The clusters (also called tracts) consist of 4-12 circular sample plots located along the sides of a square, the side of which ranges between 400 and 1800 m depending on geographical location. In southern Sweden, the tracts are smaller and the sampling intensity is higher than in the northern part of the country. Between 1953 when the tracts were introduced and 1982, all tracts were temporary. Since 1983, the NFI has used an interpenetrating system where a set of both temporary and permanent plots (today about 6000 plots of which 3500 are permanent and 2500 are temporary) are measured annually. Since 2017, temporary plots have been established based on balanced sampling, where auxiliary information is used in the design stage (Grafström et al. 2017). The permanent plots have an inventory cycle of 5 years. The circular sample plots have an area of 314 m^2 (radius of 10 m) on permanent plots and 154 m^2 (radius of 7 m) on temporary plots. Larger plots (10 or 7 m radius plots) are used for sampling trees with diameter at breast height (DBH, 1.3 m from the ground) equal to or greater than 10 cm, while trees with DBH equal to 4 cm but less than 10 cm are measured on smaller plots (radius of 3.5 m). From the calipered trees, a set of sample trees is selected with probability proportional to their basal area at breast height. On all plots, a large number of observations concerning tree, stand and site variables are made. On temporary plots, an increment core at breast height to the pith is taken from each sample tree in the direction towards to the plot centre for later determination of tree age and annual ring width measurements using a modified Eklund instrument (Eklund 1949). Broken cores with suspected missing rings and with disturbances such as rot or branch wood are discarded. In cores missing the pith, the number of missing rings is estimated in order to register the total age at breast height. Only the last up to 60 full rings are measured. The specifics on the kind of data used in **Papers II**, **IV** and **V** are expanded in *sections 3.4*, *3.6* and *3.7*, respectively.

3.3 Temporal trends in dominant height growth

In **Paper I**, LTEs from different locations were used to evaluate temporal trends in the dominant height growth (hereafter, referred to as height growth) of Scots pine (226 locations) and Norway spruce (104 locations). For each plot, site index at an index age of 100 years was estimated using the mean top height and age information (Elfving & Kiviste 1997; Elfving 2003).

The data material were split into reference (Scots pine = 81 locations; Norway spruce = 31 locations) and validation (Scots pine = 145 locations; Norway spruce = 73 locations) datasets. The reference data were used for calibrating the reference (baseline) growth model, and consisted of repeated observations within the period 1950-1985. The validation data were used to assess the trend of height growth in the period 1986-2018. The two periods represented contrasting signals in climate (i.e. temperature and precipitation). The validation period represents a warmer climate (+2 ^{o}C) compared with the mean air temperature in the reference period (SMHI 2018). Thus, using untreated plots, the possible effects of climate on eventual trends of height growth could be assessed.

To calibrate the reference growth model, four dynamic growth functions with high flexibility were used. The GADA formulations of the following base equations were considered: (i) F01 (Korf 1939), (ii) F02 (Elfving & Kiviste 1997), (iii) F03 (Schumacher 1939), and (iv) F04 – von Bertalanffy-Richards (von Bertalanffy 1938; Richards 1959; Chapman 1961). The form of the functions was expressed generally as:

$$H = f(\, T_0, T,\ H_0, b_1,\ b_2, \dots, b_n) \qquad (1)$$

Where, H is the expected height at a future age (T), H_0 is current height at current age (T_0) and $b_1,\ b_2, \dots, b_n$ are global parameters. Equation 1 was fitted using generalized nonlinear least squares regression in the R statistical environment (R Core Team 2020). Possible autocorrelation was modelled as a first order error structure (Gregoire et al. 1995) and the residual error variance was modelled by a nonlinear power function following (Mehtätalo & Lappi 2020).

On the validation data, the best reference growth model (model with lowest prediction error and reliable trajectories on the observed data) was applied to compute the expected heights for the two species. The observed and expected annual height growth were compared and an estimator of relative height growth bias was calculated. A positive value of the growth bias suggested the annual height growth was higher than expected, while a negative value indicated otherwise.

To test for the possible impacts of climate on height growth, annual temperature sum and precipitation sum data for the period 1961-2018 were obtained from the Swedish Meteorological and Hydrological Institute (SMHI 2018). Temperature sum was defined as the product of the number of days with a mean temperature higher than +5 ^{o}C and the mean temperature during these days (Perttu & Morén 1994). Similarly, the climate data were also split into reference (1961-1985) and validation data (1986-2018). On the reference dataset, the average temperature- and precipitation-sums within the 24-year period was computed for each site. On the validation data, the observed climate values for each site in the growth period (i.e. time between measurements) were calculated as means over time one and two, corresponding to the years of top height measurements. An anomaly for climate was computed for each site to describe the magnitude of changes in climatic conditions within the validation period compared to the reference period.

Prior to modelling the relationship between height growth and climate, the Mann-Kendall’s non-parametric test was used to assess the significance of the trend in height growth over time (year). Then after, a multivariate regression using the generalized least squares method was fitted separately for Norway spruce and Scots pine. The predictors included climate anomaly (relative temperature sum bias and relative precipitation sum bias) and plot variables (total age, latitude, altitude) and the interaction among the predictors. Significance was tested at alpha levels of 1 % and 5 % and residuals were diagnosed for normality and homoscedasticity.

3.4 Average height and basal area growth

In Paper II, sample tree data from the Swedish NFI were used to assess trends of the average height and basal area growth of pine and spruce for the period 1983-2020. The data were selected from undivided temporary plots on productive forestlands, with basal area-weighted mean height above 7 m. In total, 44058 (21788 pines and 22270 spruces) dominant and co-dominant trees within the ages 20 to 60 years (at breast height) were studied. By using only the last full ring width of each increment core and the tree DBH under bark at the time of inventory, the basal area increment (BAI, cm^2) was calculated according to Elfving & Tegnhammar (1996). The annual ring for the inventory year was excluded since the inventory is normally performed during the growing season.

For the height study, a mean height growth curve was fitted. Total tree height as a function of age was modelled from two components: an asymptote and a shape over age describing how the asymptote is reached. The 3-parameter Bertalanffy-Richards' function (von Bertalanffy 1938; Richards 1959) was used to model the height growth (Eq. 2):

$$y = a\left(1 - e^{-bt}\right)^{c} + \varepsilon \qquad (2)$$

Where, y is the response variable, height (m) describing the change in size with time t (age, years); the parameter a is the asymptote, b is related to the growth rate, c is related to the location of the inflection point and ε is an error term. The total age was estimated by adding time to reach breast height according to Elfving (2010b). The asymptote, rate and shape parameters of the height-age model (Eq. 2) were modified further with variables describing the effects of stand density (stand closure estimated from basal area and mean height), site fertility (described by site index according to site factors, SIS), soil type (peat or moraine) and management (thinned or unthinned). Plots that have been thinned 6-25 years ago were used in order to capture tree growth response to changed density. The variance of the error term was modelled with a power function to handle residual homoscedasticity. To determine any potential trend in the height growth, the following steps were conducted. Firstly, the residual $(h - \hat{h})$ computed as the difference between the observed (h) and the predicted $(\hat{h})$ height was averaged for each sampling year. Secondly, the mean residuals (from step one) were expressed as a linear function of the year of sampling. The significance and direction of the coefficient for year gives an indication of any potential trend. Thirdly, to get a sharp estimate of the magnitude of the trend, the asymptote was modified with year of sampling. Thus, the coefficient for year directly expressed the amount by which trees have increased their maximum height during the observation period.

For the BAI study, the single tree growth model was expressed as a function of tree size (DBH), tree class (dominant or co-dominant), crown ratio (the ratio of crown length to tree height), site index, stand density, soil type and management. The dependent variable (BAI) was expressed in logarithmic form in order to satisfy normality assumptions. Appropriate transformations on the other numerical covariates were made to ensure residual homoscedasticity. The model parameters were estimated using the general linear regression and ordinary least squares method. To determine a trend in the annual basal area growth for the period 1983-2020, the residuals from the model were regressed on sampling year.

All the statistical analyses were made separately for pine and spruce using the R-statistical environment (R Core Team 2020). The significance of model parameters were tested at 1 % and 5 % alpha levels and non-significant variables ($p > 0.05$) were removed from the final models of both the height and basal area growth studies.

3.5 Forest site productivity

In **Paper III**, models for estimating the potential yield of stands were developed using yield data from the Swedish LTEs. The data material comprised 169 locations of Scots pine, 86 for Norway spruce, 34 for Lodgepole pine and 41 for Larch. The studied plots were fully stocked even-aged stands where more than 70 % of the total basal area consisted of the main tree species. On each plot and measurement occasion, total (accumulated) basal area and volume yields were recorded in addition to mean top height. Individual tree volumes were estimated using available species- and location-specific volume functions by (Brandel 1990). The initial stand densities (trees ha^{-1}) during installation of the plots as well as site information were also recorded.

The estimation of yield capacity was carried out in five main steps. Firstly, using the height development functions operational today in Sweden (Elfving & Kiviste 1997; Elfving 2003; Liziniewicz et al. 2016), the observed top heights and ages (including latest measurements) were used to estimate site index at the tree species-specific reference age (100 years for Norway spruce, Scots pine and Larch; and 50 years for Lodgepole pine). With a given site index, the expected mean top heights at ages corresponding to the observed measurement years (assuming the growth function passes through current height and age) were derived. Secondly, total basal area development functions were constructed from predictor variables of total age, initial stand density and site index, using difference equations and nonlinear mixed-effects time series models. Following Mehtätalo & Lappi (2020), the mixed-model was parameterized for both plot and site level random variances, and an autoregressive (first order) error structure to account for the within-plot serial correlations. The tested basal area functions were based on Pienaar et al. (1990), Hossfeld (Peschel 1938), Levakovic (1935), Bertalanffy-Richards (von Bertalanffy 1938; Richards 1959) and Schumacher (1939). Thirdly, the observed total volume production was related to the predicted mean top height and total basal area, assuming a constant form factor within the stand. The parameters were estimated using nonlinear mixed-effects modelling. The accuracy of the volume model was also compared with or without adjustments for total basal area production. Fourthly, the mean annual total volume increment (MAI) was derived from the ratio of predicted total volume and age. The MAI at the time of culmination or late culmination (maximum MAI) was used as a proxy for yield capacity, because it is related to the potential volume yield attainable on a specific site (Elfving & Nyström 1996). At the fifth stage, the yield capacity was related to site index using exponential and polynomial (second degree) functions.

Finally, the developed yield capacity functions were compared with existing functions (Hägglund and Lundmark, 1982) for Scots pine, Norway spruce and Lodgepole pine. For Norway spruce, additional comparisons were made with Elfving & Nyström (1996) in central-northern Sweden. The accuracy of the total basal area development and volume production models were evaluated using independent data (LTEs) from northern and southern Sweden. All statistical analyses were conducted in the R environment (R Core Team 2020).

3.6 Stand structure and spectral heterogeneity

To investigate the effect of heterogeneity on the relationship between basal area and canopy LAI in managed stands (**Paper IV**), temporary and permanent sample plot data from the Swedish NFI were used. During the inventory campaigns in 2016 and 2017, hemispherical photographs were collected from the plot centres in 200 Norway spruce-dominated and 194 Scots pine-dominated plots. These photos were analysed for effective LAI using the GapLightAnalyzer software (Frazer et al. 1999). The effective LAI was adjusted to "actual" LAI using available species-specific conversion functions (Goude et al. 2019).

From the inventory data, variables describing stand structure heterogeneity were computed. These included species proportion (expressed as an index of stem number or basal area), mean height, stand age, stand density, coefficient of diameter variation, tree social class (ratio of arithmetic mean diameter to the quadratic mean diameter), mean tree slenderness (ratio of arithmetic mean height to mean diameter). Site variables such as latitudinal gradient (an indicator of north and south Sweden), temperature sum and humidity (computed as the difference between precipitation and evapotranspiration in the growing season). The temperature sum and humidity data were downloaded from the SMHI database. In another dimension, remotely sensed heterogeneity variables were obtained from Sentinel-2 satellite data. These included metrics of spectral vegetation indices and Haralick's textural features (Haralick et al. 1973).

A two stage-modelling approach was used to test for the effects of heterogeneity on the basal area-LAI relationship in managed stands of Norway spruce and Scots pine: a base model (i.e. without heterogeneity metrics) and a final model with metrics of heterogeneity. The statistical analysis was done in the R statistical environment (R Core Team, 2020).

3.7 Scenarios for future forest management

To study the cumulative climate impacts of harvest and stocks in forest and products over time in Sweden (**Paper V**), national level scenarios given initial resources, biological limitations on growth and assumptions about forest management practices were simulated using the Heureka Regwise decision support system (Wikström et al. 2011). The initial state (e.g. living tree biomass, stem volume, deadwood) was set by measured data on the permanent sample plots of the Swedish NFI in 2010. In 2010, the total Managed Forest Land (MFL) area was estimated at 27.5 Mha, from which productive forests (23.4 Mha) consisted of about 19.8 Mha of forests used for wood supply and another 3.6 Mha of formally and voluntarily protected forests in which harvest was not permitted. Together, unproductive forests (4.0 Mha) and formally and voluntarily set aside lands constituted protected forests, representing 28 % (7.6 Mha) of the total MFL in Sweden. The MFL was defined as forestland remaining forest as well as land use conversions to forestland, and exclusion of forestland to other land use categories (National Inventory Report 2019).

Five scenarios were simulated. The scenario of *maximum potential harvest* was considered the baseline and it described contemporary conditions (land use classes and management practices) specified by the Forest Agency for the period 2000-2009 (Claesson et al. 2015). To study the consequences of setting aside additional MFL for nature conservation, the scenario of *increased nature conservation* was simulated by setting aside additional 3.6 Mha of mainly productive (and younger forests) MFL (representing a total of 11.4 Mha of protected forest area). The *increased fertilization* scenario accounted for the consequences of increased investments in forestry on net removals in carbon pools and substitution of fossil fuel-based alternatives. About 200000 hectares (1 % of productive MFL) were fertilized per year at a quantity of 150 kg N/ha of ammonium nitrate. Only matured forests were fertilized 10 years prior to final felling. To study the potential risks of negative effects on growth, the scenario *negative climate effects on growth* was simulated by doubling in natural mortality from the scenario of *maximum potential harvest*. Currently, mortality is estimated at around 11 % of the growth in Sweden (Nilsson, 2021). The potential positive effects of global warming on tree growth was simulated in the scenario *positive climate effects on growth*. The simulation involved a process-based adjustment of tree age, basal area, site index, vegetation index and temperature sum. The growth adjustments were based on the process-based model BIOMASS and the IPCC's RCP 4.5 pathway, which have been calibrated for Swedish conditions (Bergh et al. 1998).

The simulations covered all carbon pools (living biomass, deadwood, stumps, litter, soil and harvested wood products). Decomposition, changes in pools of deadwood, litter and soils were modelled using the Q-model (Ågren & Bosatta 1996). In all scenarios, 100 % of the growth on productive MFL used for wood supply minus self-mortality was harvested. Stumps and protected forests were not harvested. Different substitution levels of 0.5, 1 and 1.5 tonnes of avoided CO_2-emissions per 1 m^3 of wood (Lundmark et al. 2014; Leskinen et al. 2018) were simulated. By assuming the emergence of an equilibrium of stem volume (biomass) as well as a steady state on land set asides, the simulations were run for 200 years.

4. Results and discussion

4.1 Trends in tree height and basal area growth

In **Paper I**, trends in the stand height growth of Norway spruce and Scots pine were examined on the basis of LTE data. For both species, a significant upward trend in the height growth was observed in the period 1986-2014 (Figure 6). Over the period, the relative height growth was estimated as 3.94 %/year for Scots pine and 0.89 %/year for Norway spruce. However, the increased growth trend appeared more pronounced after the millennium shift (year 2000), where the magnitude of the annual height growth was 16.92 % and 9.54 % higher than expected respectively, for Scots pine and Norway spruce. The increased height growth correlated positively with the rising temperature but not precipitation during the observation period.

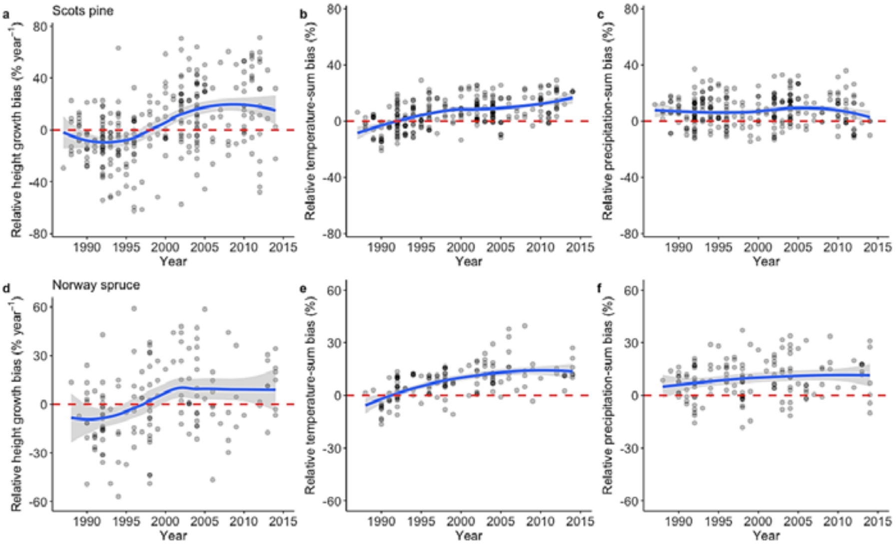

Figure 6. Trends in annual height growth, temperature and precipitation during the period (1986-2014) for Scots pine (upper panels) and Norway spruce (lower panels). The red lines show the equivalence of the expected and observed growth. Solid blue lines are LOESS smoothing. Shaded regions are 95 % confidence intervals.

Despite the increased growth on average in Sweden, substantial variations in the growth levels at the local (site) scale were observed. This was investigated further in **Paper II**, using extensive observations made on sample trees from the temporary plots of the Swedish NFI during the period 1983-2020. For height growth, a strong and significant positive (upward) trend was observed for both pine (R^2 = 88 %) and spruce (R^2 = 72 %), indicating that the average heights of the two species have increased during the observation period (Figure 7). The magnitude of the increased height in the 38-year period was 2.25 m for Scots pine and 2.12 m for Norway spruce. The trends were similar for the different regions in Sweden.

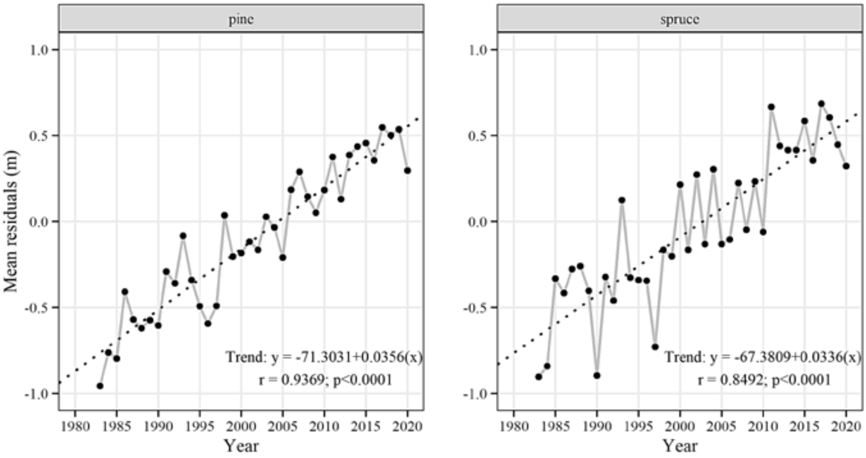

Figure 7. Trends (dotted lines) in average height growth of pine and spruce in the period 1983-2020.

However, the trend in basal area growth was stable for both species, despite an observed longer and shorter periods of higher and lower growth in the period (Figure 8).

The increased height growth but stable basal area growth means trees have become taller and slender. The slenderness defined as the ratio of height to diameter (H-D ratio) was examined for dominating and co-dominating trees. The variation in H-D ratio was studied as a linear function of total tree age, SIS and stand density. The trend of slenderness was studied by residual analysis over year. For a given height, trees in the period 1983-1987 were on average 1 cm thicker than trees in the last 5 years (2016-2020), and the trend shows an increasing slenderness during the 38-year period (Figure 9).

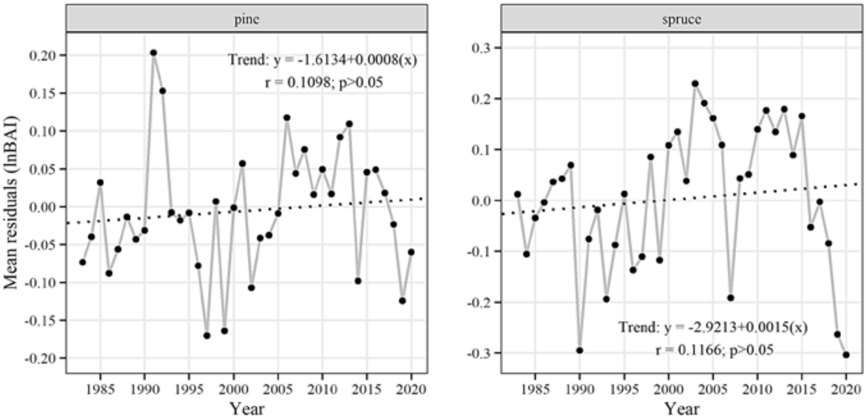

Figure 8. Trends (dotted lines) in annual basal area growth of pine and spruce in the period 1983-2020.

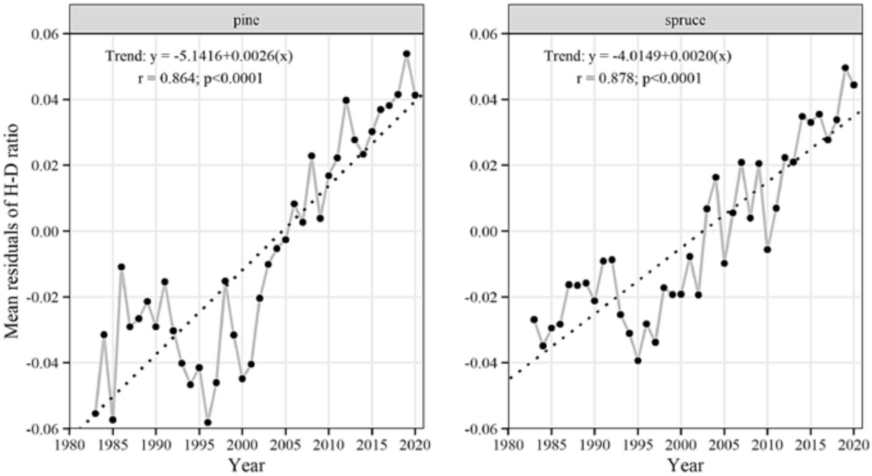

Figure 9. Increasing (positive trends) slenderness (H-D ratio) of pine and spruce in the period 1983-2020.

There are important limitations on the results presented here. Those of highest interest are related to a change of the method for sample tree selection and successive changes of instruments for height measurement. The selection of plots and stands influence trends in growth through the effects of age-bias in relation to site index. Generally, highly productive forest stands are managed under short rotation whereas those kept longer are mostly poor stands that require longer periods to produce certain amount of wood volume (Tegnhammar 1992). Despite the capabilities of LTEs in providing insights into the principles of forest production, their statistical requirements ("representativeness" especially for earlier LTEs) are usually questioned (Pretzsch et al. 2019). In **Paper I**, the similarities in the distribution of site indices for the reference and validation periods coupled with the wider ranges of site index suggested that a large portion of the fertility in Sweden were captured in the analyses. The age class distribution was quite different in both periods. This was attributable to the fewer number of sites for young stands in the validation period and they were located on fertile sites. Though these discrepancies could bias the parameters of the reference growth model, the wider range of top heights in the young stands presumes that the variability was captured in the growth trend analyses. The accelerated height growth was more or less consistent with the outcome in **Paper II**, which is based on the statistically representative sample of the Swedish NFI. Sample trees have always been selected in proportion to the trees' basal areas but in the period 1983-2002 without respect to their spatial distribution and in the period 2003-2020 with 1-3 trees per plot (Fridman et al. 2014). Before 2003, the probability for a plot to be represented increased with the density and sizes of the trees on the plot. The number of sample trees per plot varied from 0-9. This resulted in larger sample trees in the 1983-2002 data than in the 2003-2020 data (DBH 23.6 and 21.5 cm). There was also a larger difference in the distribution of trees on the classes of dominant and co-dominant trees, but the background to this difference is hard to explain. In the models (**Paper II**), site fertility was registered by site index (SIS). The SIS was on average 22.8 and 22.1 m respectively, for the 1983-2002 and 2003-2020 data. There is also a possible shift in the classification of sites according to most suitable tree species. For example, the proportion of plots that were classified as spruce sites was 54 % in the 1983-2002 data and 47 % in the 2003-2020 data.

Another possible source of variation may be changes of instruments for tree height measurements. Until 1970, the Tiréns device was used and in the period 1970-1995 the Suunto hypsometer. After that, the Haglöf-HEC electronic clinometer was used even though the Suunto was used to some extent on the sample plots from 2002 to 2007. Since 2008, the Haglöf-Vertex hypsometer has been used. The accuracy of the measured heights was higher for the Haglöf-Vertex hypsometer (upward bias by 2 cm) than for Haglöf-

HEC (upward bias by 20 cm) and the Suunto (downward bias by 12 cm), in a controlled examination by the Swedish NFI (Fridman et al. 2019).

Despite these limitations, the search for the existence of growth trends is nonetheless important for sustainable forest management (Spiecker et al. 1996; Kahle et al. 2008). As is the case with many survey data, it is difficult to isolate the causes of changes in forest growth trends. Here, the trends are discussed under changes in forest management and environmental conditions in Sweden. Forest management affects growth trends largely through silvilcutural practices (Högberg et al. 2021b), for example, changes in harvesting systems and precision silviculture with improved site preparation, nitrogen fertilization, density-regulation and planting with improved genetic materials (Kahle et al. 2008). In the period 1953-1992, an increase in both the annual height and basal area growth was observed in Swedish forests, and the major contributing factors were attributed to the shift from selective cutting and thinning from above to clear felling, cleaning and thinning from below (Elfving and Tegnhammar 1996). In **Papers I** and **II**, the results obtained indicate that the height growth increase has continued until now in Swedish forests and corroborates well with the reported increase in other forest regions (Sharma et al. 2012; Kauppi et al. 2014; Henttonen et al. 2017; Socha et al. 2021). However, the stable trend in basal area growth may imply that a peak growth was reached around 1992. It is difficult to attribute this effect to increasing stand density in the latter years, given that the mean basal area was about the same in the periods 1983-2002 and 2003-2020.

Variations in environmental conditions over time may strongly influence tree growth rates. The rising summer temperatures are mainly due to an increasing level of atmospheric CO_2. Temperature sum is also a very strong variable at the determination of SIS. However, the stable level for basal area growth is very surprising and posed the question if the increased CO_2 level itself has a direct impact on the height growth. The tallest trees are often found in humid climates. Givnish et al (2014) studied Eucalyptus in Australia over a humidity gradient and found that tree heights decreased from 60 to 10 meters from the humid to the dry sites. The water use efficiency means the balance between carbon intake and water loss through the leaf stomata and seems to have a strong impact on the height growth of trees. Increasing atmospheric CO_2 levels means that the stomata can take in required carbon faster with less loss of water (Keenan et al. 2013). Increased nitrogen deposition has probably contributed to an accelerated tree height growth

(Etzold et al. 2020), but the atmospheric nitrogen deposition in Sweden has decreased by 30 % in the period 1983-2013 (Andersson et al. 2018).

It remains unclear for how long the increases in maximum tree height growth will continue in Swedish forests. It is possible that drought-induced hydraulic limitations (e.g. the 2018 and 2019 heatwaves in Europe) and the frequency and intensity of forest disturbance agents such as storms, fires, pests and diseases may constrain the maximum tree height growth under a changing climate (Silva et al. 2010; Girardin et al. 2014; Belyazid and Giuliana 2019; Forzieri et al. 2021).

The changes in tree growth rates demonstrate a changing growing condition in Swedish forests. This implies potential variations in tree allometry such as height to volume relationships and stand composition, especially for even-aged (monocultural) stands. The use of top height as an indicator of site productivity may not be valid anymore, site curves must be revised and include a time factor that mirror the ongoing transition of the growing conditions. Thus, new expressions for forest site productivity in contemporary decision support systems are needed to enhance accurate predictions of tree growth and sustainable forest management in a changing climate.

4.2 Expressions for site productivity

The main objective of **Paper III** was to further develop methods for the expression of forest productivity through site index and to compare the new functions with earlier ones for coniferous trees in Sweden. The results were based on LTE data measured between 1920 and 2019, for Norway spruce, Scots pine, Lodgepole pine and Larch. By means of regression analyses, the estimation framework comprised the construction of component models describing basal area adjusted volume-height relationships.

For all species, predicting basal area yield at the end of the growth period from the basal area at the beginning of the period, total age, site index (predicted by height development curves) and initial stand density produced accurate estimates both for the calibration and test data (relative errors were within 1-13% of the average values). Inclusion of basal area in the volume-height models increased the precision and explained variation by a factor of 1.5 units compared to alternative volume models without basal area.

In addition, the volume yield levels (total volume at a given top height) increased with site index and were also consistent with the trajectories in basal area yield levels. This implies that basal area production describes a site's potential density at a given top height and it explains to a larger extent the productivity differences in site index (Assmann 1970; Sterba 1987; Hasenauer et al. 1994).

The adjusted coefficient of determination ranged from 80 – 96 % in the functions relating yield capacity (expressed as maximum mean annual volume increment) to site index. The relative model errors were largest for Scots pine (17 %) and lowest for Lodgepole pine (6 %). On average, predictions of yield capacity from the new functions (Figure 10) on lower site index classes were smaller (~20 %) than those given by Hägglund & Lundmark (1982). On higher site indices, current estimates were about 18 % higher than Hägglund & Lundmark (1982). The differences on lower site index classes were larger for Norway spruce than for Scots pine. However, for spruce, the predicted yield capacity was similar to the results by Elfving & Nyström (1996) in central-northern Sweden.

The differences between the functions were discussed under two main lines: (1) the type of data material used and (2) altered environmental conditions. In the earlier functions by Hägglund & Lundmark (1982), site index was estimated from stem analyses data collected in temporary plots during the 1940's (Hägglund 1974). However, the site index functions operationally used today in Sweden were based on repeated data from LTEs and they indicate a change in the growth form when compared to the older site index functions (Elfving & Kiviste 1997).

The differences in yield capacity could also be due to the variations in basal area at a given top height. In the central-northern Sweden, the estimated basal area for spruce were similar to that of Elfving & Nyström (1996), but those given by Hägglund (1981) was about 60 % higher for example, in stands with average top height of 11 m. Such higher initial levels of basal area could largely influence the trajectory of yield capacity with site (Elfving & Nyström 1996).

Altered site properties by changes in growing season temperature and precipitation, CO_2 fertilization and nitrogen deposition have already been seen, especially in the forests of northern Europe (Kauppi et al. 2014). This suggests height to volume relationships might have changed accordingly (Kuehne et al. 2022).

It was not possible to compare the tree species' productions in this study, given that the data material for each species was from different locations. Having the species on the same site or preferably at side-by-side may facilitated the comparisons. However, the functions can later support the selection and comparison of tree species' production in similar site and management regimes in Sweden.

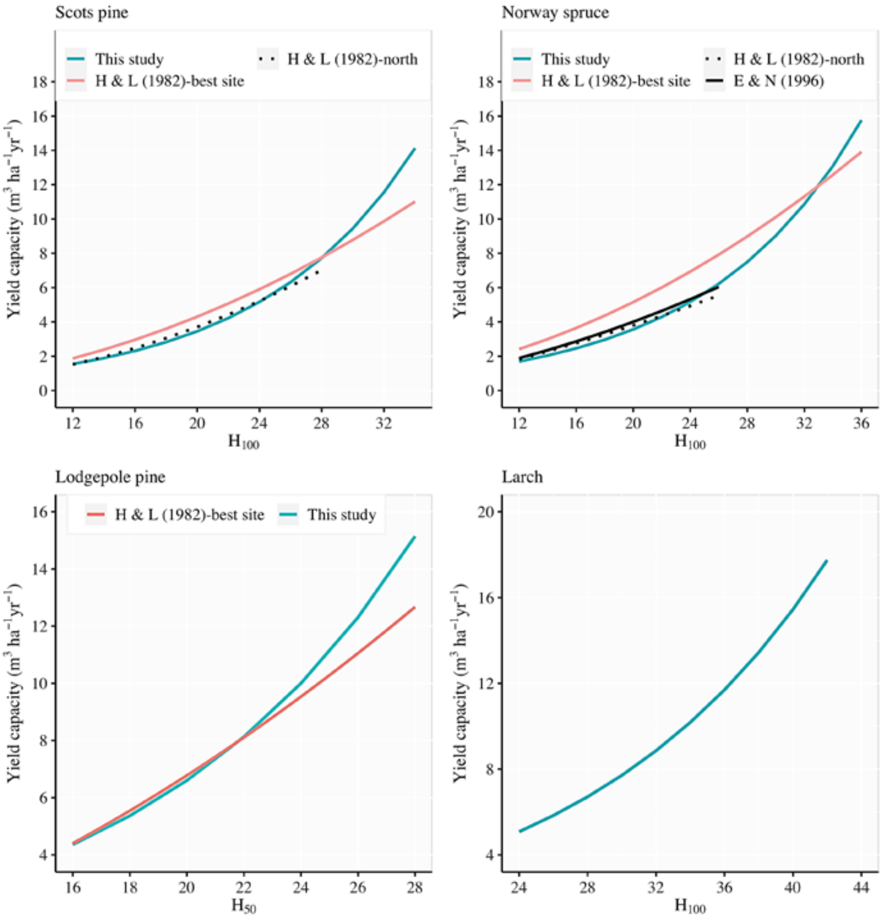

Figure 10. Predicted mean yield capacity from current (This study) and previous studies by Hägglund and Lundmark, 1982 [H&L (1982)] and Elfving and Nyström, 1996 [E&N (1996)]. H&L (1982)-best site refers to lingonberry and better sites for pine stands (below 200 m above sea level) and blueberry-sites for spruce over the whole country. H&L (1982)-north refers to pines (above 200 m above sea level) and spruces (poor sites) in northern Sweden. E&N (1996) refers to spruce sites in central-northern Sweden. Note that for Larch no previous model is available for comparison. Extrapolations are made beyond the observed site index range.

4.3 Accounting for heterogeneity

The objective of **Paper IV** was to relate stand basal area to canopy LAI and to describe how the average basal area changes with LAI via structural heterogeneity in managed stands of Norway spruce and Scots pine. Managed forests were represented by field data from the 2016 and 2017 Swedish NFI campaigns. Models with or without metrics of heterogeneity were compared by means of studying goodness-of-fit statistics (root mean squared errors) from the regression analyses.

By including heterogeneity metrics, the variance was reduced by 55 % for Norway spruce and 43 % for Scots pine, compared with the alternative models without heterogeneity (Figure 11). In addition to stand age, stem density and mean height, variations in tree diameter and slenderness were important in the models. For Scots pine, the addition of temperature sum was also significant.

Generally, the results demonstrate that the stand structural heterogeneity effects here are of such a magnitude that they cannot be neglected when applying theoretical growth functions to managed forests. This might be essential for the implementation of hybrid growth models, especially those based on light interception and use efficiency where LAI is a principal component (Goude et al. 2022).

Even in monocultures, the stand productivity has been shown to vary with variation in tree sizes (Sun et al. 2018). This variation is interpreted from the patterns of light interception and light-use efficiency. Dominant (larger) trees show greater light interception and light-use efficiency than do smaller trees in heterogeneous stands (Binkley et al. 2013a; Bourdier et al. 2016).

In another dimension, the addition of spectral heterogeneity metrics (normalised difference vegetation index, entropy and spectral variation index) from Sentinel 2 showed very little improvement for both pine (13 % reduction in the variance) and spruce (25 %), compared to those without heterogeneity. For these models, the field measured tree height was also included. However, the three-dimensional information derived from LiDAR (light detection and ranging) data may be suitable for improving the models. Already, the potential of using airborne LiDAR data to estimate tree size inequality and characterize forest structure has been demonstrated, at least in the boreal forest ecosystems in northern Europe (Valbuena et al. 2017).

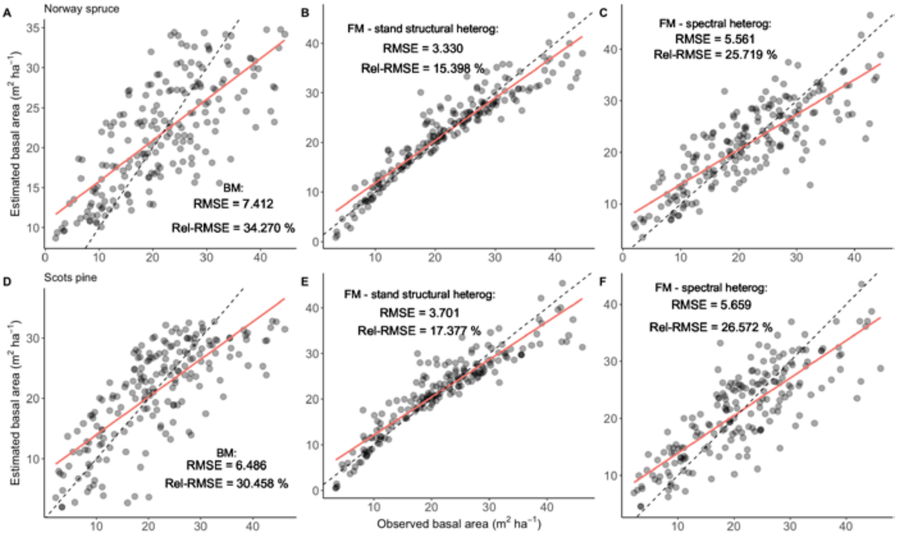

Figure 11. Observed and estimated basal area for Norway spruce (A-C) and Scots pine (D-F) based on models (solid red line) with (final models – FM) and without (base models – BM) heterogeneity metrics. The black dashed line is the 1:1 relationship.

4.4 Future forest management strategies

In **Paper V**, different forest management strategies were simulated to evaluate the total potential climate benefits of Swedish forests. The simulations were run for two forest rotation periods (200 years) and 100 % of the net growth was harvested in all scenarios. The harvest is used for substitution (as harvested wood products) and different substitution levels (0.5, 1 and 1.5 tonnes of avoided CO_2-emissions) were used to evaluate the annual net carbon sequestration potentials of the tested scenarios.

After 200 years, both stocks (storage) and growth were linear and reached a peak where cumulative harvest was greater than storage in all scenarios (Figure 12). After peaking, the constant annual sustainable harvest was estimated at 99 million m^3 for the scenario of *maximum potential harvest* and at 85 million m^3 for *increased nature conservation* scenario. Thus, the long-term loss in forest growth for setting an additional 3.7 Mha of productive forest land for nature conservation was estimated as 14 million m^3/ year. A larger share of the growth in the *increased nature conservation* scenario was lost to cumulative mortality. By increasing the fertilization to 1 % of the MFL available for wood supply (*increased fertilization* scenario), the annual harvest (112 million m^3) was about 13 % higher than the scenario of *maximum potential harvest* and about 32 % higher compared to the *increased nature conservation* scenario, after 200 years. The harvest level was highest for the scenario *positive climate effects on growth* (137 million m^3/ year) and lowest for the scenario *negative climate effects on growth* (57 million m^3/ year).

The total climate benefits (expressed as annual removals in mega-tonne (Mt) CO_2e/year) of the various scenarios (including changes in all carbon pools) were sensitive to the assumed substitution effect (0.5, 1 and 1.5 tonne CO_2e per 1 m^3 wood) (Figure 13). With a lower substitution effect, increasing the area of protected forests (*increased nature conservation* scenario) provided higher benefits compared to the scenario of *maximum potential harvest* in the short term. However, at an increasing substitution level, the long-term climate benefits associated with the scenario of *maximum potential harvest* was larger than the *increased nature conservation* scenario.

The large uncertainty regarding substitution makes it unclear which level of substitution rate is most appropriate for analysing the climate benefits of different forest management strategies (Sathre & O'Connor 2010). A review by Leskinen et al. (2018) provided estimates of substitution factors ranging from 0.53 to 3.83 tonnes CO_2e per m^3. In earlier analysis of the Swedish marketplace, Lundmark et al. (2014) estimated a substitution potential of 0.47-0.75 tonnes CO_2e per m^3 stem volume, in line with the lower level analysed for this study.

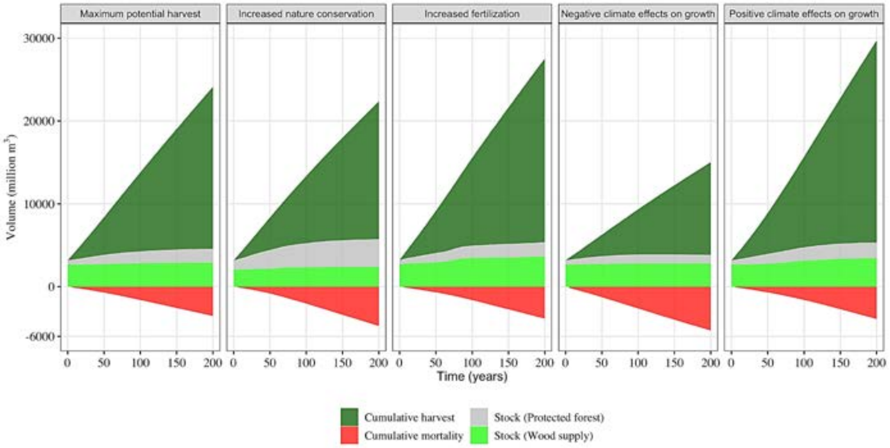

Figure 12. The simulated cumulative stem volume (million m^3) in MFL (lands available for wood supply and protected forests) over a period of 200 years, assuming that 100 % harvest of net growth in MFL is used for wood supply and no harvest in preserved forests.

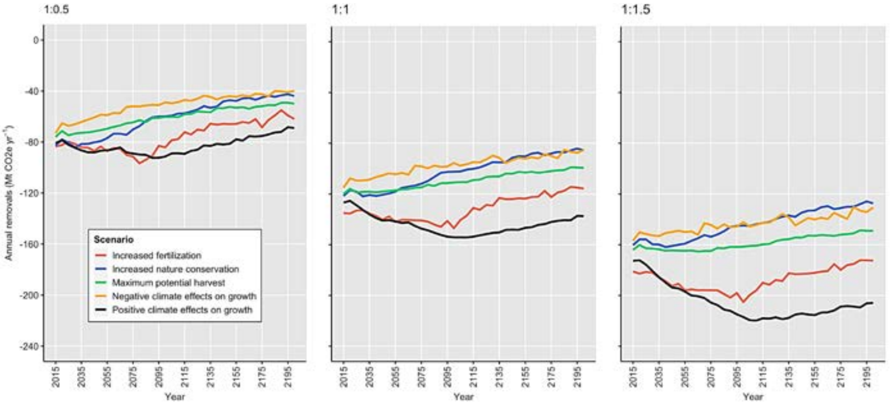

Figure 13. Total annual estimated net carbon sequestration (Mt CO_2e/year) of the different forest management scenarios in the period 2015-2195. The scenarios include changes in all carbon pools (living biomass, dead organic matter, soil and harvested wood products) and three different assumed substitution effects (0.5, 1 and 1.5 tonne CO_2e per 1 m^3 wood).

In an expanding bioeconomy harvested wood products offer opportunities for replacement of carbon-intensive non-wood products and fuels, however, the time dynamic climate impacts of such products needs to be carefully assessed along the value chains (Sathre & Gustavsson 2011). Thus, by shifting to longer-lived wood products, increasing the efficiency of wood resource and reuse via material recycling, the relative substitution effect will be larger (Gustavsson et al. 2017).

Despite the fact that some forest management strategies (e.g. the *increased fertilization* scenario) may provide rapid climate benefits in the short term of 10-30 years (Skytt et al. 2021; Grassi et al. 2021). Cowie et al. (2021) conclude that focusing on short term emissions reduction could affect the possibilities for achieving medium and long-term perspectives. In fact, many other studies have acknowledged that the integration of forest biomass in the ongoing bioeconomy can contribute to climate change mitigation in the medium to long-term horizons in the northern European forests (Lundmark et al. 2014; Gustavsson et al. 2021).

In a forested country like Sweden, active forest management with high forest levels and efficient forest product utilization will provide more climate benefits compared to reducing harvest and storing carbon in the forest (Gustavsson et al. 2017; Högberg et al. 2021b).

5. Conclusions

The main aim of this thesis was to investigate the spatio-temporal dynamics of aboveground tree growth under altered management regimes and environmental conditions. The results are presented for five studies (**Papers I-V**), regarding possible trends in tree growth, changes in forest site productivity, heterogeneity in stand compositions and potential management strategies that may provide larger climate benefits in Swedish forests and forestry sector. The findings were based on observations from permanent plots in the Swedish LTEs and temporary plots in the NFI.

Papers I and **II** have shown empirically that the maximum heights of Scots pine and Norway spruce have increased during the last 40 years in Swedish forests. A positive climate response with rising temperature on height growth increase was found for both species (**Paper I**). The increase in average height appears proportional in different parts of the country (**Paper II**). However, during the period 1983-2020, the basal area growth of the two species was stable (**Paper II**), suggesting that current stands are becoming taller but slender. The above results generally imply that the growing conditions have changed in Swedish forests. For even-aged forests, such changes in the growing conditions could potentially (*i*) affect allometric relationships for example, height to volume relations and (*ii*) induce high variability in stand composition.

Paper III demonstrated that there is a bias in existing tools for forest site productivity classification for coniferous forests in Sweden. If based on the earlier functions, an upward bias of the magnitude ~20 % in yield capacity was observed on lower site index classes. Whereas on higher site indices, a downward bias of ~18 % in the yield capacity was observed for the dominant coniferous tree species such as Scots pine, Norway spruce and Lodgepole pine. The new functions give better prediction of yield capacity. Hence, they could later be used for comparing tree species' production under similar site and management conditions.

The variation in a stand can be described with indices of heterogeneity. By studying the relationship between stand basal area and canopy LAI with or without heterogeneity indices, the results obtained suggest that the stand structural heterogeneity effects here are of such a magnitude that they cannot be neglected in the implementation of hybrid growth models that are based on LAI (light interception and light use efficiency) for managed stands of Norway spruce and Scots pine (**Paper IV**). Further, the results demonstrate that in growth models when extrapolating theoretical growth functions (i.e. functions developed from well-managed experimental forests) to regular managed forests, the local level variation needs to be accounted for. In general, stand structural heterogeneity offers accurate calibration, but the improvements from spectral heterogeneity shows greater potentials of using three-dimensional information from remote sensing (e.g. LiDAR).

Paper V focused on the potential management strategies that may be beneficial for attaining set climate targets in the Swedish forest sector. The results indicate that in the long-term, the net climate benefits in Swedish forests may be maximized through active forest management with high harvest levels and efficient product utilization, compared to increasing storage in standing forests through land set-asides for nature conservation.

Overall, the increased height growth at a stable basal area growth may still translate to increased volume production, if dominant height is considered as an indicator of productivity. However, for a sustained volume growth, enhancing the rate of basal area growth might be needed. This means that management strategies may probably be tailored towards reduction of stand density using more frequent and or intensive thinnings. Nonetheless, this may need to be done in consideration with the stability of the stands (e.g. with respect to storms). This thesis offers support for the development of evidence-based policy recommendations for site-adapted and sustainable management of Swedish forests in a changing climate.

5.1 Future research

In this thesis, the search for possible growth trends was of high scientific interest. In **Paper II**, I observed a stable basal area growth in the last 40 years. However, the trend was difficult to explain. Increasing stand density may be a factor, but this was difficult to detect in the dataset especially, given the changes in sample tree selection after 2002. Future work should probably focus on the calipered trees in the permanent plots of the NFI and LTEs to give a more thorough insight of the basal area growth trend.

In **Paper II**, site fertility was expressed in both the height and basal area growth functions as site index (expressed by site factors, SIS). Those SIS functions were from the late 1970s and the predictors included climate, site (latitude, altitude and distance from the coast) soil (texture and surface water flow frequency) and field vegetation (Hägglund & Lundmark 1977). The vegetation type is an indicator of soil nutrient regime, however, the field layer vegetation is by no means stable over the rotation period of a stand. It depends to some extent on the stand density, causing a shift of the vegetation association from young to old stands (Tegnhammar 1992). Conversely, the accelerated height growth (**Papers I** and **II**) implies a changing growing condition, and if dominant height is considered as an indicator of site productivity, then the volume production has probably increased in Swedish forests. But estimates may be biased if based on the existing SIS functions. Thus, new SIS functions are needed in Swedish forests. It is even more desirable that the two systems for site index estimation (SIS and SIH) in Sweden be comparable. Currently, the two methods differ in results considerably (~4 m), making it difficult to compare forest production (Elfving & Nyström 1996). Preferably, the new SIS functions should include a measure of the increased growth trends. By constructing an SIS model that links the differences in productivity on the basis of volume growth and changes in environmental conditions (temperature and precipitation sums), it is possible to capture for example, the change in photoperiodic regime when moving from south to north of Sweden and also enhance unbiased assessment of stand productivity over different areas and species.

In the future, forest data will to a greater extent be leveraged by remote sensing (point clouds from stereo-matched aerial images or LiDAR). This may primarily provide good data on the height distribution of the standing stock and the changes in it over time. Thus, new production models may be needed, preferably driven by height development. Using repeated airborne laser scanning data (ALS), it is possible to derive an age-independent ALS-assisted site index estimator driven by height and height growth. This has several advantages of representing current growing conditions, of not requiring tree age data and that it is a cost-effective method.

In an era of changing growing conditions, heterogeneous forests would be very common in Sweden. This may generate a lot of problems especially, when models based on well-managed forest experiments are applied on regular forests. It is therefore recommended that contemporary growth models be based on fused data from LTEs and NFIs in order to increase their accuracy and reliability in Swedish forests.

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The millennium shift: Investigating the relationship between environment and growth trends of Norway spruce and Scots pine in northern Europe

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ABSTRACT

For boreal forests in colder climates, changes in environmental conditions are hypothesised to substantially affect ecosystem processes. In this study, trends of top height growth of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) were analysed using permanent sample plot data from more than 300 long-term experimental sites distributed from temperate zones to the boreal forest conditions in Sweden. By regression analyses, the effects of temperature-sum and precipitation-sum on top height growth were assessed in the period 1986–2018. A significant upward temporal trend in height growth was observed for both species, with the trend more pronounced after the millennium shift. The magnitude of the annual relative height growth after the millennium was about 16.92% and 9.54% higher than expected, respectively for Scots pine and Norway spruce. A potential climate response on height growth was found for both species with temperature-sum positively correlated with top height growth. No significant effect of precipitation-sum on height growth was observed for either species. Our results suggest improved growing conditions and forest sites became more productive in response to increasing temperature in the northern temperate and boreal regions. The increasing growth trends may offer shorter rotation periods and increased forest value for Norway spruce and Scots pine, coupled with contributions of boreal forests to the emerging bio-economy and the regulation of global atmospheric carbon.

1. Introduction

In recent years, the growth of forests under changing environmental conditions has been a major concern across the globe. In Europe, changes in forest growth in temperate and boreal forests during the latter part of the 20th century were investigated and summarized in Spiecker et al. (1996). In central European temperate forests, increased tree and stand-level growth has been recorded (Spiecker et al., 1996; Pretzsch et al., 2014). In boreal forests of northern Europe, increases in the forest growth have also been reported (e.g. Elfving and Tegnhammar, 1996; Salminen and Jalkanen, 2005; Solberg et al., 2009; Kauppi et al., 2014; Henttonen et al., 2017). Several possible reasons for increased growth trends comprise the following: changes in forest management and improved silviculture (e.g. Elfving and Tegnhammar, 1996; Henttonen et al., 2017), genetics (e.g. King et al., 2013) and site amelioration by increased air temperature, precipitation and nitrogen deposition (e.g. Laubhann et al., 2009; Solberg et al., 2009; Kauppi et al., 2014; Rohner et al., 2018; Etzold et al., 2020). Although, several difficulties have been encountered in attempts to isolate and quantify the magnitudes of forest growth changes attributable to management and climate (Spiecker et al., 1996; Kahle et al., 2008), and few attempts have been successful. For example, in the Finnish forests from 1971 to 2010, Henttonen et al. (2017) found differences in forest management and changes in environmental conditions explained 67% and 37% respectively of the observed increase in annual volume growth (8.98 million m^3 $year^{-1}$).

Based on estimates from the National Forest Inventory (NFI) of Sweden, annual volume growth has increased from about 60 million m^3 in the 1920s to 126 million m^3 in 2018 (Skogsdata, 2019). Earlier studies by Elfving and Tegnhammar (1996) observed an increase in basal area and height growth trends of Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.) in Swedish forests between 1953 and 1992 using data from the temporary plots of the NFI. Reasons such as changes in silvicultural practice, i.e. from selective harvesting to clear felling,

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thinning from below, improved regeneration methods, nitrogen fertilization and ditching were largely proposed for the increased growth trends. In addition, increased dominant height growth of Norway spruce in southern Sweden due to a considerable higher atmospheric nitrogen deposition has been reported by Eriksson and Johansson (1993).

While effects of silviculture-induced growth trends have been assessed in the Swedish forests, growth trends due to changes in the ambient temperature and precipitation have less been investigated empirically on a national scale. By simulation, Claesson et al. (2015) estimated a positive climatic effect on growth, with the growth reaching about 56.8% more than expected after 100 years under Representative Concentration Pathways scenario analysis (RCP 8.5), using the Heureka Regwise model in Sweden. The report from the Swedish Commission on Climate and Vulnerability indicated a +2 °C increase in mean temperature during the periods 1961–1990 and 1991–2005, and thus, suggested a distinct warm period for the later decades in Sweden (Commission on Climate and Vulnerability, 2007). This provides a suitable window in which to investigate any environmentally related growth trends.

To detect a growth trend, repeated observations from long-term surveys or experiments are required (Spiecker et al., 1996; Pretzsch et al., 2019). A unique feature about long-term forest experiments is that they provide valid growth references relevant for estimating site quality and for detecting influences of site conditions on tree- and stand-level growth over time (Pretzsch et al., 2019). In Sweden, several long-term experiments were established during the 19th and 20th centuries throughout the country to examine effects of thinning and fertilization on growth and yield (e.g. Elfving and Kiviste, 1997; Valinger et al., 2000; Nilsson et al., 2010), wood quality (e.g. Pape, 1999; Pfister et al., 2007), biomass production (e.g. Eriksson, 2006) and stand stability (e.g. Valinger and Pettersson, 1996; Wallentin and Nilsson, 2014) of Norway spruce and Scots pine.

Assessment of forest site quality is vital for determining the productive capacity of forest sites and for providing a reference for silvicultural diagnoses and prescriptions (Burkhart and Tomé, 2012). Site index (SI), defined as the average height of the dominant trees of a given stand at a reference age is often used as a quantitative estimate to describe the realizable part of a site's potential to support tree growth (Skovsgaard and Vanclay, 2008). In Norway, an increased SI after 1940 has been reported (Sharma et al., 2012). In Sweden, new SI functions for Scots pine are steeper with higher growth curves (Elfving and Kiviste, 1997) compared to previous SI functions developed by Hägglund (1972; 1973; 1974). This necessitated further investigation of changed growth patterns in Scots pine stands of cultivated origin.

Using permanent plot data from long-term forest experiments, we focused on top height growth trends for the two most dominant tree species in Sweden: Norway spruce and Scots pine. This is because height growth is highly correlated with volume production, and top height is not greatly influenced by stand density and thinning treatments, assuming thinning from below for even-aged monocultures (Eichhorn, 1902; Skovsgaard and Vanclay, 2008; Burkhart and Tomé, 2012). We defined a growth change trend as long-term site-related deviations from the expected top height growth (Spiecker et al., 1996). The main hypothesis tested in the present study was that, for the two species, the top height growth was higher than expected due to temporal changes in environmental conditions during the last 30 years in Sweden.

2. Material and methods

In this study, for a forest stand and given fixed temperature-sum and precipitation-sum, we assumed that SI was constant and top height development followed SI curves over time. Using permanent sample plot data from long-term experiments measured at two different time periods, we developed a reference top height growth function using data from the period (1950–1985), and applied the function to the validation data (1986–2018) to compute the expected top heights. The biases, calculated as the difference between the observed and predicted top heights were used to assess the top height growth trends of Norway spruce and Scots pine. The relationships between height growth changes and changes in environmental (climate) conditions expressed as temperature-sum and precipitation-sum were investigated.

2.1. Data

Data for the study comprised 330 different locations (sites) of long-term experiments (Scots pine = 226 and Norway spruce = 104) of even-aged stands distributed throughout Sweden (Fig. 1). The experiments largely described thinning, spacing, regeneration and fertilization treatments of Norway spruce and Scots pine (Nilsson et al., 2010). The control (unfertilized and thinned from below) plots of these experiments were used for growth analyses, assuming that they were not influenced of management that would affect height development. The distribution of the data is summarized in Table 1. Most of the stands had cultivated origin (regenerated naturally, planted or seeded from local seed sources) (Elfving and Kiviste, 1997; Nilsson et al., 2010).

For the Scots pine dataset, 4940 observations were made in 77 permanent sample plots with a net plot area of 0.1 ha (range is 0.01–0.50 ha) between 1925 and 2018. The time between the remeasurement of a plot ranged from 1 to 41 years (mean = 8), and plots were re-inventoried at least twice and at maximum of 11 times (mean = 4).

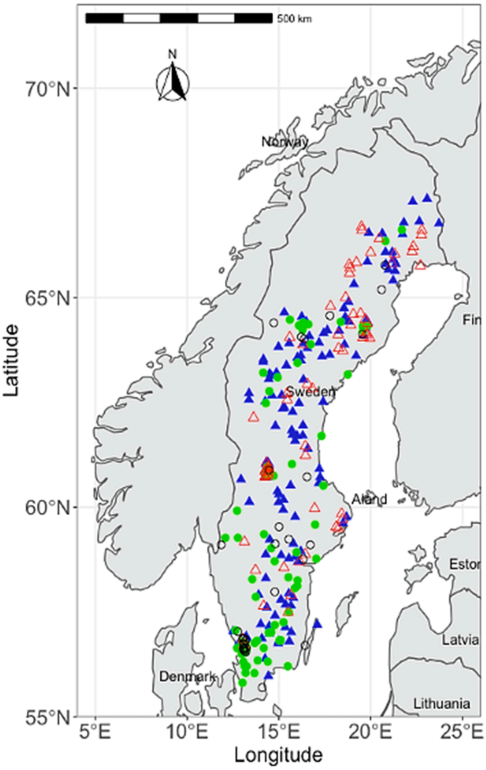

Fig. 1. Locations of the experimental sites in Sweden. Opened symbols denote reference sites, whereas validation sites are shown by filled symbols (triangles for Scots pine and circles for Norway spruce).

Table 1

Descriptive statistics of observed top height within age classes for Scots pine and Norway spruce in the experimental sites.

	Top height (m)[**]														
	Whole data (1925–2018)					Reference data (1950–1985)					Validation data (1986–2018)				
Age class (years)	N[a]	Mean	Min	Max	Sd	N[a]	Mean	Min	Max	Sd	N[a]	Mean	Min	Max	Sd
Scots pine (no. experimental sites)			**226**					**81**					**145**		
0–20	301	5.67	2.30	17.30	2.52	234	5.08	2.30	8.40	1.35	14	7.81	3.50	15.50	4.42
20–40	1611	10.73	3.70	19.80	2.92	837	10.03	3.70	17.00	2.81	321	11.91	6.20	19.80	2.94
40–60	1592	16.53	4.80	25.40	2.85	491	15.17	6.40	23.00	2.47	730	17.80	9.60	25.40	2.70
60–80	732	19.42	9.40	29.30	3.46	74	21.84	16.50	29.30	3.13	499	20.19	13.20	28.30	2.81
80–100	329	19.63	11.60	31.80	3.68	100	18.81	12.70	26.20	3.62	99	22.39	17.00	31.80	2.28
100–120	228	19.35	13.60	29.80	3.08	154	18.99	13.80	29.80	2.95	12	22.93	17.90	27.30	3.73
120–140	85	21.76	14.60	30.90	3.48	57	21.54	14.60	27.30	3.27	4	25.60	24.10	28.60	2.03
140–160	30	22.14	16.20	26.60	3.38	6	19.88	16.20	25.80	4.19	7	24.84	23.60	26.60	1.02
160–180	10	22.13	17.60	27.50	3.77	4	22.05	18.90	26.30	3.53	2	26.90	26.30	27.50	0.85
180–200	14	21.61	18.50	27.40	2.94	6	21.60	18.50	26.90	3.22					
200–220	4	23.95	20.60	28.40	3.84										
220–240	4	25.23	21.20	28.50	3.71										
Norway spruce (no. experimental sites)				**104**				**31**						**73**	
0–20	170	5.69	1.90	12.90	2.33	116	5.04	1.90	8.80	1.91	35	6.80	2.20	12.90	2.95
20–40	979	13.03	2.10	23.20	4.59	419	12.70	2.10	19.50	3.89	263	13.90	4.40	23.20	5.28
40–60	768	20.16	6.00	29.00	4.12	199	19.26	6.20	29.00	4.67	417	20.86	8.70	28.60	3.86
60–80	217	24.46	8.70	31.00	5.35	48	24.09	9.70	29.50	5.09	125	24.45	8.70	31.00	5.58
80–100	61	26.41	11.90	33.40	6.79	39	30.38	23.10	33.40	1.96	2	29.20	28.20	30.20	1.41
100–120	28	26.06	15.20	34.10	7.78	14	24.09	15.70	33.90	7.58	5	30.58	18.70	34.10	6.65
120–140	26	17.73	8.30	36.10	9.81	5	22.28	17.80	33.20	6.19	4	35.20	34.00	36.10	0.88
140–160	25	15.56	9.90	24.70	4.96	10	12.93	10.90	14.50	1.21	8	22.39	19.90	24.70	1.44
160–180	8	15.50	14.30	16.90	0.88	4	14.90	14.30	15.70	0.58					

[a] Number of observations (measurements) in the age class.

[**] Mean (Mean), minimum (Min), maximum (Max) and standard deviation (Sd) of observed top heights in the age class.

For the Norway spruce dataset, about 2282 observations were conducted from 1927 to 2018 in 44 sample plots with a net plot area of 0.1 ha (range is 0.01–0.25 ha). The time interval for plot remeasurement ranged from 1 to 27 years (mean = 7). The remeasurement of sample plots was done at least once and at maximum of 14 times (mean = 4).

The tree height observations between 1940s and 1990s were made using Suunto hypsometers. From the 1990s to 2018, the Haglöf Vertex hypsometer was used for height measurements. Such changes in instruments could introduce errors in the measurements, however, in this study, the errors in tree height measurements were assumed negligible.

2.1.1. *Top height estimation*

At each plot remeasurement, *H* was measured for sample trees while calipered trees without measured heights were assigned predicted heights from Näslund's curve function (Eq. (1), Näslund, 1947). The

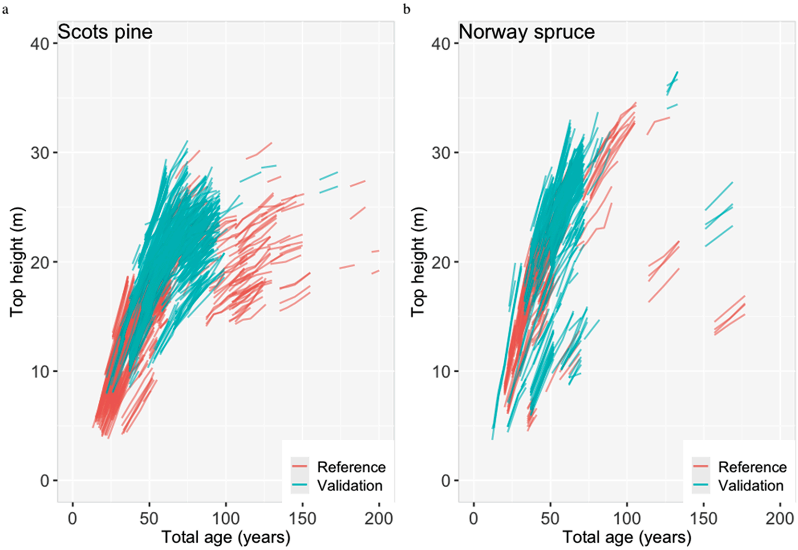

Fig. 2. Observed top height development for (a) Scots pine and (b) Norway spruce in experimental sites measured between 1925 and 2018 (whole dataset).

Table 2
Base and dynamic (GADA) equations considered for the reference growth modelling.

Function	Base equation	Dynamic equation
F01 (Korf)	$H = a_1 \left[exp^{\left(\frac{-a_2}{T^{a_3}} \right)} \right]$	$H = b_1 . \left(\frac{H_0}{b_1} \right)^{\left(\frac{T_0}{T} \right)^{b_2}}$
F02 (Elfving and Kiviste)	$H = \frac{a_1}{\lfloor 1 + (a_2/T^{a_3}) \rfloor}$	$H = \frac{H_0 + d + r}{\left\lfloor 2 + \frac{(4b_1/T^{b_2})}{(H_0 - d + r)} \right\rfloor}$ Where $d = \frac{b_1}{Asi^{b_2}}, \quad r = \sqrt{(H_0 - d)^2 + 4b_1 H_0 {T_0}^{-b_2}}$
F03 (Schumacher)	$H = a_1 \left[exp^{(-a_2/T)} \right]$	$H = H_0 \left[\frac{exp^{(-b_1/T)}}{exp^{(-b_1/T_0)}} \right]$
F04 (Chapman-Richards)	$H = a_1 \left[1 - exp^{(-a_2 T)} \right]^{a_3}$	$H = H_0 \left[\frac{1 - exp^{(-b_2 T)}}{1 - exp^{(-b_2 T_0)}} \right]^{b_3}$

function was modelled using paired *DBH* and *H* measurements of sample trees in the plot.

$$H = \frac{DBH^c}{(a + b.DBH)^c} + 1.3 \qquad (1)$$

where *H* is the tree height (m), *DBH* is the calipered tree diameter at breast height (cm), *a*, *b* and *c* are parameters to be estimated. Mean top heights, defined as the arithmetic mean height of the 100 thickest (by diameter) trees ha^{-1} were computed for each sample plot (Elfving and Kiviste, 1997; Liziniewicz et al., 2016). The distribution and development of the measured top heights for the two species are shown in Table 1 and Fig. 2.

2.2. Reference top height growth model

To estimate changes in growth trends, a reliable and efficient reference growth model is required. A reference growth model is considered valid when it suitably represents the site and stand conditions of the investigated forests during the reference period (Spiecker et al., 1996). To satisfy this condition, the data material were split into reference (Scots pine = 81 sites; Norway spruce = 31 sites) and validation (Scots pine = 145 sites; Norway spruce = 73 sites) dataset (Table 1). The reference data were used for calibrating the reference (baseline) growth model and consisted of repeated observations within the growth period 1950–1985. The validation data were used to analyse top height growth trends for the two species during the last three decades (1986–2018). The two datasets represented different time periods, but similar regeneration methods (local seed sources and soil preparation) and management. For both species, the distributions of SIs (estimated based on Elfving and Kiviste, 1997 at the latest remeasurement) were similar in the two periods, though the SIs were slightly higher (Scots pine: $t = 11.2$, $p < 0.0001$, $d.f. = 3514$; Norway spruce, $t = 2.9$, $p = 0.0042$, $d.f. = 1690$) in the validation period (Scots pine: mean = 26.1 m, range = 16.0–34.6 m; Norway spruce: mean = 31.5 m, range = 14.1–39.2 m) than in the reference period (Scots pine: mean = 24.8 m, range = 11.1–33.9 m; Norway spruce: mean = 30.8 m, range = 10.0–37.7 m) (Figure A.1, supplementary file). The wider ranges of SI in the two periods for the two species indicate that sites covered a large portion of the range of fertility in Sweden. Earlier reports suggested stable temperatures during the reference period in Sweden (Commission on Climate and Vulnerability, 2007). Additionally, using observations during the reference period to construct the reference growth models coincides with earlier studies (Hägglund, 1972, 1973, 1974; Elfving and Kiviste, 1997) utilizing observations in this window to develop SI functions for Norway spruce and Scots pine in Sweden. We assumed that the reference growth model depicted the climatic conditions within this reference period.

Modelling the relationship between top height and age can be used to investigate changes in tree growth patterns (Elfving and Kiviste, 1997; Cieszewski and Bailey, 2000; Pretzsch, 2009; Burkhart and Tomé, 2012). Dynamic growth functions formulated using algebraic and generalised-algebraic difference approaches (ADA and GADA) (Cieszewski and Bailey, 2000) are widely preferred to the static and fixed-base-age equations for assessing site quality, because they are parsimonious, robust and provide base-age invariant results (Cieszewski, 2001; Liziniewicz et al., 2016). The GADA functions theoretically transform basic growth functions into a dynamic form by replacing one or two parameters with site-specific coefficients, generating SI curves with polymorphic asymptotes (Cieszewski and Bailey, 2000; Burkhart and Tomé, 2012; Liziniewicz et al., 2016).

For this study, four dynamic growth functions (F01-F04) with high flexibility were used to develop the reference growth models (Table 2). These functions have yielded satisfactory outcomes for SI estimation in other studies (e.g. Rivas et al., 2004; Nord-Larsen et al., 2009; Johansson, 2012; Kahriman et al., 2018). The GADA formulations of the following base equations: (i) F01 (Korf, 1939), (ii) F02 (Elfving and Kiviste, 1997), (iii) F03 (Schumacher, 1939), and (iv) F04 – von Bertalanffy-Richards (henceforth called Chapman-Richards) (von Bertalanffy, 1938; Richards, 1959; Chapman, 1961) were considered. The F02 equation is a special dynamic formulation of the Hossfeld II base equation (Peschel, 1938) and has been widely used in Sweden for SI estimation. In the considered reference functions, $a_1, a_2, \cdots, a_n$ and H, T are parameters of the base equations, while b_1,$b_2, \cdots, b_n$ and T_0, T, H_0, H represent parameters in the GADA equations. Together with the global parameters$(b_1, b_2, \cdots, b_n)$ and by assuming the growth function passes through the current height (H_0) at current age (T_0), then the expected top height (H) at a future age (T) of a plot was expressed implicitly as: $H = f(T_0, T, H_0, b_1, b_2, \cdots, b_n)$. In all the tested functions, H_0 was considered as a site-specific parameter and was estimated locally for each plot. For the F02 function, initial starting values used were $b_1 = 7395.60$, $b_2 = 1.78, Asi = 25$ for Scots pine, and $b_1 = 1495.30, b_2 = 1.59, Asi = 10$ for Norway spruce. These values were obtained from (Elfving and Kiviste, 1997). The *Asi* parameter denotes the age corresponding to maximum growth and which minimizes the model residuals (Elfving and Kiviste, 1997). The starting values for other GADA functions were iterated using the "*selfStart*" function in the "*nlme*" package in R (R Core Team, 2018).

2.3. Calibration of reference growth functions and autoregressive modelling

On the reference dataset, the reference GADA functions (Table 2) were fitted via the generalised nonlinear least squares regression function ("*gnls*") with the restricted maximum likelihood (*REML*) method in R (R Core Team, 2018). The parameters of the growth functions were estimated through autoregressive modelling and by accounting for within-plot and site variance. The presence of autocorrelation and heteroscedasticity may bias the model parameters and violate hypothesis testing procedures in standard regression analysis (e.g. Monserud, 1984; Rivas et al., 2004). The possible autocorrelation was modelled as a first order error structure, due to many plots having just two observations (Gregoire et al., 1995; Liziniewicz et al., 2016). The expanded error (Eqs. (2)–(3)) was structured as:

$$H_{ij} = f\left(H_j, t_i, t_j, \beta\right) + e_{ij} \tag{2}$$

$$e_{ij} = \rho e_{i-1,j} + \gamma e_{ij-1} + \varepsilon_{ij} \tag{3}$$

where H_{ij} is the height i prediction using height j (H_j), age i (t_i) and age j (t_j) as predictor variables together with the global parameters ($\beta : b_1, b_2, \cdots, b_n$) and age $j \neq$ age i; ρ is the parameter accounting for the autocorrelation between the current residual and the residual from estimating H_{i-1} using H_j as a predictor within each plot; γ denotes the parameter accounting for the autocorrelation between the current residual and the residual from estimating H_i using H_{j-1} as a predictor within each plot; and ε_{ij} is the independent and identically distributed errors with an expectation, $\mathrm{E}(\varepsilon) = 0$ and a constant variance, $\mathrm{Var}(\varepsilon) = \sigma^2$.

The within-plot and -site variations were modelled as power weighted variance of total age to improve upon the precision of SI curves in the young (less than 20 years) and the old stands (more than 150 years) (Rivas et al., 2004; Liziniewicz et al., 2016).

2.3.1. Comparison of reference growth functions

Performances of the reference growth functions after model fitting were compared using the following four statistical criteria (Eqs. (4)–(7)); Akaike information criterion (*AIC*), root mean square error (*RMSE*, to quantify the average difference between the observed and estimated top heights, lower value indicates a better model), relative RMSE (*relRMSE*, to assess the magnitude of the top height estimation error rate, lower value indicates a better model), and the adjusted coefficient of determination ($R^2{}_{adj}$, to measure the strength of the agreement between observed and estimated top heights, larger value indicates a better model):

$$AIC = nlog\left(\frac{\sum_{i=1}^{n}(\widehat{y}_i - y_i)^2}{n}\right) + 2p \tag{4}$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(\widehat{y}_i - y_i\right)^2}{n-p}} \tag{5}$$

$$relRMSE = 100\%\mathrm{x}\frac{RMSE}{\overline{y}} \tag{6}$$

$$R^2{}_{adj} = 1 - \frac{(n-1)\sum_{i=1}^{n}(\widehat{y}_i - y_i)^2}{(n-p)\sum_{i=1}^{n}(y_i - \overline{y}_i)^2} \tag{7}$$

where $\widehat{y}_i$, y_i and $\overline{y}_i$ are the predicted, measured and average values of the dependent variable, respectively; n represents the total number of observations used for fitting the model and p denotes the number of model parameters.

The residuals of the fitted growth functions were investigated for potential heteroscedasticity and autocorrelation by using both graphical and numerical analyses. The Durbin-Watson test statistic (d) was used to detect autocorrelation in lag residuals after modelling. Values of $d = 2$ indicate absence of autocorrelation, smaller values ($0 \leq d \leq 1$) indicate positively correlated successive error terms and larger values ($d > 2$) suggest negative correlation of successive error terms (Durbin and Watson, 1971). The test statistic d was expressed as:

$$d = \frac{\sum_{i=1}^{n}(e_i - e_{i-1})^2}{\sum_{i=1}^{n}e_i{}^2} \tag{8}$$

where e_i is the error value for the i^{th} data and n is the number of observations.

The reliabilities of all reference growth functions were explored by the trajectories of the SI curves (passing through the top heights (m): 36, 32, 28, 24, 20, 16 and 12 at 100 years) on the profiles of the observed top height development. This was considered as an important step for final evaluation, as even though the models could have significant parameters, yet they might not adequately describe the data used to construct them (Dieguez-Aranda et al., 2005; Liziniewicz et al., 2016). The iteration of SI was done by setting the index age to 100 years for both species, as this age is closer on the average to actual rotations in Sweden.

2.3.2. Estimation of the observed and expected top height growth

After model evaluation, the best reference growth model was applied to the validation dataset to compute the expected top heights for the two species. The expected top heights ($\widehat{h}_2$) at time (age) two (t_2) were predicted from the SI model using information on observed top heights (h_1) at time one (t_1) and time two (t_2). The observed and expected top height growths were estimated as follows:

$$ih = h_2 - h_1 \tag{9}$$

$$\widehat{ih} = \widehat{h}_2 - h_1 \tag{10}$$

where ih and $\widehat{ih}$ are the observed and expected top height growth respectively.

The ih and $\widehat{ih}$ values were compared and the absolute bias (Δih, growth difference, cm), normalised bias (Δih_n, annual growth difference, cm/year) and relative bias (Δih_{rel}, %/year) in top height growth were computed as:

$$\Delta ih = ih - \widehat{ih} \tag{11}$$

$$\Delta ih_n = \frac{\Delta ih}{t_2 - t_1} \tag{12}$$

$$\Delta ih_{rel} = 100\mathrm{x}\frac{\Delta ih_n}{\widehat{ih}_n} \tag{13}$$

where $\widehat{ih}_n$ denotes the expected annual top height growth $\left(\frac{\widehat{ih}}{t_2 - t_1}\right)$ in cm/year.

The relative height growth bias estimator, Δih_{rel} was considered in this study, as the response variable to quantify the magnitude (i.e. proportion) of the observed annual height growth in relation to the expected annual height growth. This was intended to capture site-specific growth response. A positive value of Δih_{rel} suggests the annual top height growth was higher than expected, while negative value indicates the observed growth was less than expected.

2.4. Weather data

Annual temperature and precipitation data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI). The SMHI produced monthly annual weather data, based on the European FP7 project on the re-analysis of meteorological observations (http://www.uerra.eu). Weather variables were delivered in a 55 × 55 km resolution raster covering the study area. The annual temperatures were expressed as temperature-sums (in degree days), defined as the summation of day-mean degree Celsius (°C) when the air temperatures exceed +5 °C during the vegetation period (Perttu and Morén, 1994; Bergh et al., 2005). Precipitation was also expressed as annual precipitation-sums during the vegetation period. The temporal resolution of the climate data provided was from 1961 to 2018, and thus covered a significant portion of our top height measurements.

Similar to the measured top height dataset, the climate data were also split into reference (1961–1985) and validation data (1986–2018). On the reference dataset, we computed for each site, the average temperature- and precipitation-sums within the 24-year period (Eq. (14)).

On the validation data, the observed climate values for each site in the growth period were calculated (Eq. (15)) as means over time one and two, corresponding to the years of top height measurements. Finally, we computed the relative bias (ΔY_{rel}) in the climate value (Eq. (16)) for each site to describe the magnitude of changes in climatic conditions within the validation period compared to the reference period. Positive values of ΔY_{rel} suggested the climate value was higher in the validation period than in the reference period, while negative values suggested otherwise. The ΔY_{rel} values were used as regressors to assess the height growth response of Norway spruce and Scots pine to changes in climatic conditions.

$$\overline{Y}_{refk} = \frac{1}{n_i}\sum_{i=1}^{k} y_i \tag{14}$$

$$\overline{Y}_{pk} = \frac{y_{t_1} + y_{t_2}}{2} \tag{15}$$

$$\Delta Y_{rel} = 100\mathrm{x}\frac{\overline{Y}_{pk} - \overline{Y}_{refk}}{\overline{Y}_{refk}} \tag{16}$$

where $\overline{Y}_{refk}$ represents the observed mean climate variable (as either temperature-sum or precipitation-sum) for site k in the reference period, n_i is the number of annual observations for each site within the reference period, y_i is the observed annual climate values for site k in the reference period, $\overline{Y}_{pk}$ is the mean climate variable in the growth period (p) corresponding to the top height measurements at time one (y_{t_1}) and time two (y_{t_2}) for site k in the validation period, and ΔY_{rel} (%/year) denotes the relative temperature-sum or precipitation-sum bias.

2.5. Modelling top height growth and weather relationship

Preliminary analysis involved testing the significance of the relative height growth bias (Δih_{rel}) and the climate bias (ΔY_{rel}, i.e. relative temperature-sum bias and relative precipitation-sum bias) trends over years, in the validation period. The year was set as the mid-point of two consecutive measurements. We used the Mann-Kendall's (MK) non-parametric tau coefficient as an estimate (δ) to determine the temporal (annual) height growth and climate trends for the two species. Presence of a statistical trend is recorded when δ differs significantly from zero ($p < 0.05$), positive δ indicates an upward temporal trend, while negative δ is indicative of a decreasing trend. The MK test was fitted using the "*MannKendall*" function in R (R Core Team, 2018). Prior to fitting the MK test, we investigated whether the values of relative height growth, temperature-sum and precipitation-sum biases were serially correlated using the "*acf*" function in R. We observed the presence of partial temporal autocorrelations (Figure A.2). Therefore, the MK test was applied in conjunction with block bootstrapping using five fixed block lengths as lag intervals and over 1000 repetitions. Summary of the results on the growth and climate trends were reported for δ and two-sided p-values at 95% confidence interval.

To investigate the relationship between changes in the top height growth and climate within the validation period, multivariate regression analysis using the generalised least squares method was fitted separately for Norway spruce and Scots pine. The model was fitted to account for the growth-site heterogeneity and temporal autocorrelations (Zuur et al., 2009). The heterogeneity was modelled as power weighted variance proportional to the response variable, and the autocorrelation was modelled as the first order autocorrelation adapted to the site and year of measurement. The predictors included climate (relative temperature-sum bias and relative precipitation-sum bias) and plot variables (total age, latitude, altitude) and the interaction between these predictors. Non-significant variables were excluded from the final regression models. Statistical and graphical analyses were done to assess the normality and heteroscedastic patterns of the model residuals. The normality of residuals was tested by the Shapiro-Wilk test (W) and the heteroscedastic patterns were assessed by the distribution of residuals over year of measurement, latitude and total stand age.

3. Results

3.1. Performance of reference growth models

The autoregressive modelling procedures for reference growth functions converged successfully for both Scots pine and Norway spruce. The model parameters and fitting statistics produced for the two species are summarized in Table 3. In all functions for both species, the model parameters were statistically significant from zero ($p < 0.0001$). The fitting statistics were similar for all models and indicated more than 95% of the total explained variance (based on R^2_{adj}) in the fitting phase. However, those of Korf (F01) and Elfving and Kiviste (F02) were much more superior to the Schumacher (F03) and Chapman-Richards (F04) functions. Compared to the other functions, the Schumacher (F03) function exhibited the poorest performance based on the residual error variance (RMSE = 0.64 m for Scots pine and 1.07 m for Norway spruce).

Graphical analysis of the fitted SI curves for both Norway spruce and Scots pine showed realistic height-age patterns for the models based on F01 and F02 (Fig. 3). The growth curves of F01 and F02 followed the trajectories of the observed top height development compared to the functions F03 and F04, which displayed strong intersections with the underlying top height profiles. Hence, models F03 and F04 were excluded from further analyses.

For Scots pine, function F02 exhibited higher accuracy than F01 (Table 3). For Norway spruce, the F01 model marginally out-performed the F02 counterpart. However, the smoothness and flexibility of the F01 curves indicated higher site indices at both younger and older ages compared to the F02 function (Fig. 3e and f). Thus, the Elfving and Kiviste function (F02) was finally considered as the reference growth model for the subsequent top height growth analysis of the two species. The parameters of the F02 model reflect the range of boreal site conditions and the model is widely used for SI estimation in Sweden.

The residual plots of F02 (Figure A.3) showed no apparent trends of heteroscedasticity across the range of observed top heights and stand age for the two species. Both graphical and numerical analyses of the model residuals indicated absence of autocorrelation for Norway spruce ($d = 1.66$, $p < 0.0001$) and Scots pine ($d = 1.42$, $p < 0.0001$). The observed and predicted top heights also showed a good agreement for the two species.

3.2. Temporal trends in height growth, temperature-sum and precipitation-sum

The temporal (annual) trends (δ) in relative height growth bias and temperature-sum bias were positive and differed significantly from zero ($p < 0.05$), suggesting the presence of statistically upward trends for both species in the validation period, except for the relative precipitation-sum bias which was non-significant for either species (Table 4). The trends appeared more pronounced after the millennium (year 2000) as shown in Fig. 4. The mean top height growth over the whole validation period was estimated as 3.94% year^{-1} for Scots pine and 0.89% year^{-1} for Norway spruce. However, after the millennium shift, the magnitude of the top height growth was 16.92% year^{-1} and 9.54% year^{-1} higher than expected respectively, for Scots pine and Norway spruce.

3.3. Height growth and climate relationship

Pearson's correlation (R) was used to explore the initial relationship

Table 3
Parameter estimates and goodness-of-fit statistics for the four tested GADA models for Scots pine and Norway spruce. “Par” is the parameter and “SE” is the standard error. “ρ” is the first-order autocorrelation parameter.

				Confidence interval			Fit statistics			
Model	Par.	Estimate	SE	2.5%	97.5%	P-value	*AIC*	*RMSE*(m)	*relRMSE*(%)	R^2_{adj}
Scots pine										
F01	b_1	55.23	2.12	51.08	59.38	< 0.0001	1068.63	0.57	3.93	0.99
	b_2	0.72	0.02	0.68	0.76	< 0.0001				
	ρ	0.06								
F02	b_1	6435.04	306.83	5833.67	7036.41	< 0.0001	1235.09	0.55	3.79	0.99
	b_2	1.71	0.02	1.67	1.75	< 0.0001				
	ρ	0.14								
F03	b_1	35.37	0.28	34.83	35.91	< 0.0001	1922.26	1.05	7.24	0.97
	ρ	0.47								
F04	b_1	0.02	0.001	0.016	0.019	< 0.0001	1656.02	0.64	4.41	0.98
	b_2	1.48	0.03	1.42	1.54	< 0.0001				
	ρ	0.36								
Norway spruce										
F01	b_1	68.46	4.67	59.31	77.61	< 0.0001	1038.57	0.81	4.68	0.99
	b_2	0.71	0.03	0.64	0.78	< 0.0001				
	ρ	0.08								
F02	b_1	1981.88	124.12	1738.61	2225.15	< 0.0001	1081.97	0.86	4.97	0.99
	b_2	1.69	0.04	1.62	1.77	< 0.0001				
	ρ	0.06								
F03	b_1	35.61	0.41	34.79	36.41	< 0.0001	1232.79	1.25	7.22	0.98
	ρ	0.05								
F04	b_1	0.02	0.002	0.018	0.024	< 0.0001	1214.12	1.07	6.18	0.98
	b_2	1.52	0.05	1.41	1.62	< 0.0001				
	ρ	0.05								

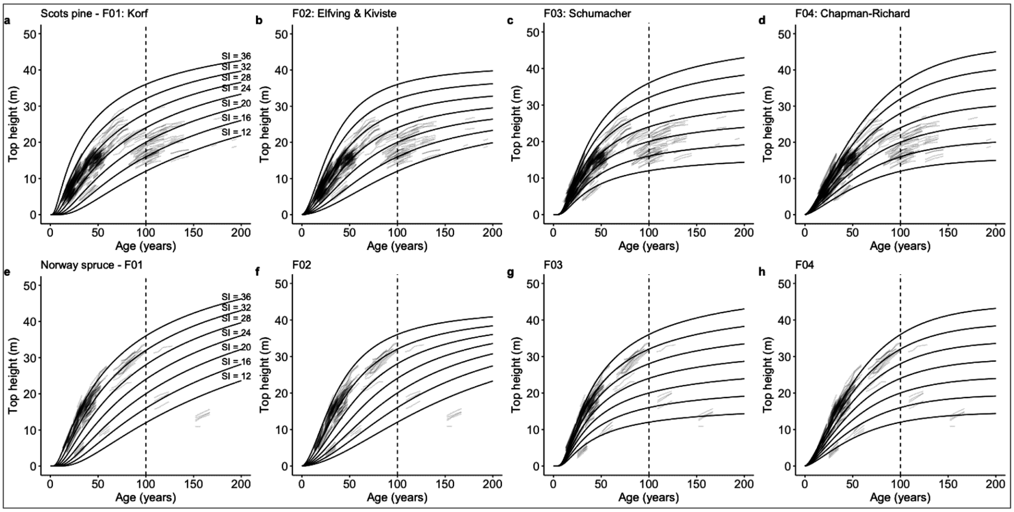

Fig. 3. Fitted SI curves of the reference growth functions using the reference data (1950–1985) for Scots pine (a-d) and Norway spruce (e-h). The curves represent the top heights at base age of 100 years (vertical dashed lines) and overlaid on the observed top height-age profiles.

between relative top height growth and the climate variables. For both species, Scots pine ($R = 0.19, p = 0.0017$) and Norway spruce ($R = 0.24, p = 0.003$), the growth correlations with temperature-sum was significant and positive, whereas no significant correlation with precipitation-sum was found for either species (Figure A.4). The full regression analyses involved modelling the relative height growth bias as a function of climate and plot characteristics for each species (Table A.1). The effects of precipitation-sum, total stand age and altitude were not significant, hence removed from the final regression models.

The final regression results for the two species are summarized in

Table 4
Mann-Kendall estimates for temporal trends in height growth, temperature-sum and precipitation-sum bias of Norway spruce and Scots pine.

	Scots pine		Norway spruce	
	δ	P-value	δ	P-value
Relative height growth bias	0.30	< 0.0001	0.20	< 0.001
Relative temperature-sum bias	0.36	< 0.0001	0.41	< 0.0001
Relative precipitation-sum bias	0.03	0.432	0.09	0.108

Table 5. The model residuals of both species were normally distributed (Scots pine: $W = 0.991$, $p = 0.099$; Norway spruce: $W = 0.992$, $p = 0.589$) and exhibited no patterns of heteroscedasticity over measurement year, latitude and total age (Figure A.5). In both species' models, the estimated autocorrelation levels (ρ) were smaller (Scots pine: $\rho = 0.054$ and Norway spruce:$\rho = 0.071$). The effects of temperature-sum on the height growth were significant and positive for both species, suggesting positive height growth response to climatic changes. The effect of temperature-sum was larger for Norway spruce than for Scots pine.

4. Discussion

4.1. Data and models

To detect growth trends, a reference growth model (or value) is required (Spiecker et al., 1996). Permanent plot observations from long-term forest experiments are essential for developing reference growth models, and for quantifying site-related growth deviations (Pretzsch et al., 2019). In this study, control plots in long-term experiments with observations dating back from the early 20th century, facilitated the investigation of growth trend changes in Swedish forests. Particularly, splitting the data material into reference (1950–1985) and validation (1986–2018) periods enhanced smooth comparison of the observed and expected top height growth trends (Table 1). The similarities in the distribution of site indices (SIs) for the two periods, coupled with the wider ranges of SIs suggested our growth assessment captured a large portion of the fertility gradient in Sweden (Figure A.1). In Table 1, the age class distribution was quite different in the two datasets for both species and this was due to fewer number experiments for young stands, especially in the validation dataset. Those young stands analysed in the validation dataset were mostly located in fertile sites (Figure A.6) in contrast to the distribution of young stands in the reference dataset. Such discrepancies could have significant effects on the parameters of the SI models; however, the wider range of top heights in young stands presumes that the variability was captured in the growth trend analyses.

The performances of the tested top height growth functions (Table 2) were highly accurate at the fitting phase for both Norway spruce and Scots pine (Table 3). The functions exhibited realistic growth characteristics (Fig. 3) as they (i) represented a parsimonious and dynamic site equations, (ii) polymorphic with variable asymptotes allowing them to adapt to different site conditions, (iii) had a zero-point and (iv) were increasing (Elfving and Kiviste 1997; Cieszewski and Bailey, 2000; Burkhart and Tomé, 2012; Liziniewicz et al., 2016). The Elfving and Kiviste growth function (F02) which is a special formulation of the Hossfeld II growth equation, best described the data and exhibited no trends of residuals' heteroscedasticity and autocorrelation (Table 3; Fig. 3; Figure A.3). This function has been widely used for SI modelling in Sweden, and its flexibility and reliability in this study, indicates the reflection of changing growth patterns in Swedish boreal forests (Elfving and Kiviste, 1997). Additionally, the models' adaptation to age class discrepancies ensured satisfactory residual distribution and reliability of SI curves (Fig. 3; Figure A.3).

The temporal and spatial resolution of the climate data aided the analysis of changes in environmental conditions over time. The annual time series of temperature- and precipitation- sums showed on the average stable climate conditions in the reference period (1961–1985) and increasing trends in the validation period (1985–2018) for both species (Figure A.7). More importantly, pairing measured climate values in the calibration and validation periods enhanced the characterization of height growth response to changes in climatic conditions for the two species (Table 5).

The absence of heteroscedasticity in the final regression models linking the relative height growth bias as a linear function of climate variables, showed a well-adapted model structure and satisfactory outcomes of the height growth response to climatic conditions for Scots pine and Norway spruce (Table 5; Figure A.5).

4.2. Interpretation of the growth trends

Our study has revealed increased top height growth trends during the 30-year period, with the trend more discernible after the millennium shift for Norway spruce and Scots pine in Sweden. Likewise, we found significant temporal upward trends in temperature-sum for both species. Neither species showed significant precipitation-sum trends over time (Table 4; Fig. 4; Figure A.4). After the millennium shift, we observed that the magnitude of the relative increases in height growth were about 16.92% year^{-1} and 9.54% year^{-1} higher than expected, respectively for Norway spruce and Scots pine. On the local (site) levels, there were substantial variations in the magnitudes of top height growth, with the relative annual height growth varying considerably from -70% (less) to $+70\%$ (more) than expected. This highlights the site specific signals of climate effects on forest growth (Cook and Peters, 1997). The trends of top height growth were similar for both species as the growth declined (growing less than expected) in the early-to-mid 1990′s in Sweden. This observed growth decline is similar to the growth patterns observed for Norway spruce and Scots pine stands using ring-width indices in the Kronoberg and Kalmar counties (Tufvesson and Holmström, 2018). The authors found the radial growth decline to be highly correlated with the hot and dry summers of 1992–1997, and that could partly explain our observed growth decline within this period. We also speculate that the larger variations in growth may be due to factors such as disturbances, management, pests and pathogens.

The presence of significant positive correlation between the height growth and temperature-sum (Figure A.5; Table 5) suggests climate changes that occurred within the studied periods are at least related to the height growth trend increase in Sweden. This supports our main hypothesis. The correlation was moderately stronger for temperature-sum for both species. In both species, precipitation had not changed over time (Fig. 4). This probably suggests that boreal forest ecosystems in northern Europe might show greater responses to changes in air temperature than to precipitation. The results are in agreement with other growth studies done in the northern European forests (e.g. Salminen and Jalkanen, 2005; Kauppi et al., 2014; Henttonen et al., 2017). Using the Finnish NFI data, Kauppi et al. (2014) and Henttonen et al. (2017) observed positive correlations between the growing season temperature-sum and tree growth in Finnish's forests. In stands located at the latitudinal transects from the Arctic Circle up to the northern timberline in Finland, a significant effect of the mean July temperature of the previous year on the height growth of Scots pine was found (Salminen and Jalkanen, 2005). Other studies from the temperate forests in central Europe found tree growth to be positively correlated with temperature (Kahle et al., 2008; Pretzsch et al., 2014; Rohner et al., 2018).

Though not evaluated in this study, increased height growth might also be ascribed to the increasing atmospheric CO_2 and nitrogen deposition (which is about 2 kg N ha^{-1} year^{-1} in the north, 5 in the southeast and 10 in the southwest) in Sweden. Temperate and boreal forest soils are mostly deficient in soil nitrogen and hence, tree growth and productivity are limited. Therefore, an increase in nitrogen deposition would potentially enhance tree growth (e.g. Eriksson and Johansson, 1993; Kahle et al., 2008; Solberg et al., 2009; Laubhann et al., 2009;

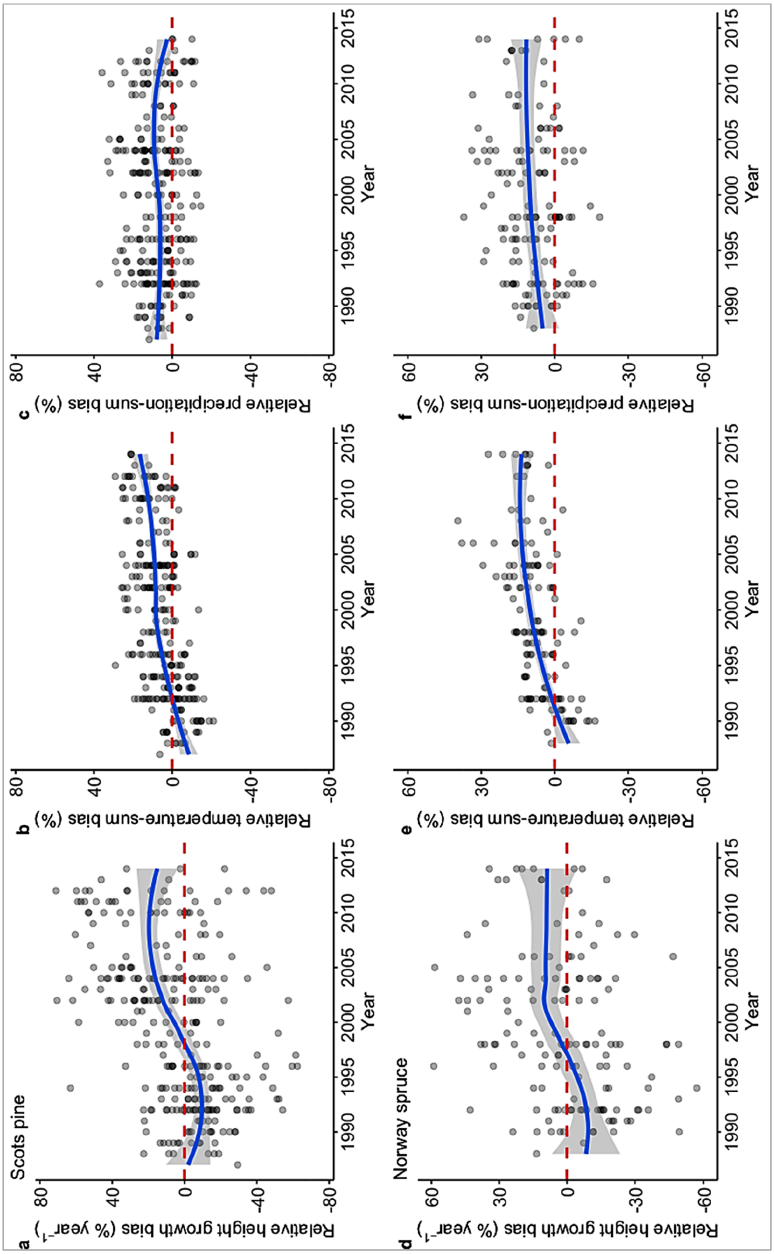

Fig. 4. Trends of annual top height growth, temperature-sum and precipitation-sum of the experimental sites over period of measurements (1986–2014) for Scots pine (a-c) and Norway spruce (d-f) after Eqs. (13) and (16). The horizontal red dashed-lines highlight where the equivalence of the observed and expected top value. Shaded regions are 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5

Relationship between height growth [$\Delta ih_{rel}, \%/year$] and climatic changes for Scots pine and Norway spruce. “SE” denotes standard error.

Species		Coefficient	SE	t-value	P-value
Scots pine	Intercept	1.155	1.842	0.627	0.531
	Temperature-sum bias	0.497	0.153	3.251	0.0013
Norway spruce	Intercept	−3.732	2.547	−1.465	0.145
	Temperature-sum bias	0.601	0.193	3.121	0.0022

Kauppi et al., 2014; Etzold et al., 2020).

It has often been difficult to separate the factors responsible for forest growth or decline, especially in the context of management and climate. In Sweden, earlier studies by Elfving and Tegnhammar (1996) found an increase (of the magnitude 0.5–0.8%) in annual basal area and mean height growth of Norway spruce and Scots pine in the 1953–1992 time period. A number of reasons were cited as possible factors behind the increased growth trends, for example, the extensive shift from selective harvesting, target diameter cutting and thinning from above to clear felling, thinning from below and improved regeneration methods in the 1950s have contributed greatly to the growth increase in the Swedish forests. We acknowledge that, improved silviculture, genetics and management may also have brought about the observed changes in top height growth during the two studied periods.

A key issue to highlight here is the effect of measurement errors on height growth trajectories. Measuring heights of standing trees has considerable uncertainties (often overestimation), especially for taller trees with bigger crowns, and this gives higher site indices (Elfving and Tegnhammar, 1996; Elfving and Kiviste 1997). A change in tree height measurement device can also be a source of measurement errors (Elfving and Tegnhammar, 1996; Henttonen et al., 2017). For instance, in the early 1990s of the Swedish NFI, Suunto hypsometers were replaced with the Haglöf Vertex hypsometer, which had a relatively higher precision compared to the former. From 2002 to 2007, the Suunto was used to measure tree heights only on a small portion of the sample plots in combination with the Haglöf Vertex hypsometer. The outcome was the presence of a systematic bias of 30 cm lower with the Suunto hypsometer. Hence, the Haglöf Vertex was recommended for measuring tree heights in all sample plots of subsequent NFIs. Height estimation via controlled inventory showed the measurement error was less than 3% in the Swedish NFI (Fridman et al., 2019). Therefore, in this study, we cannot rule out the effect of measurement errors in the observed top height growth trends.

Since top height growth is positively correlated with volume production (Eichhorn, 1902; Skovsgaard and Vanclay, 2008), the increase in annual top height growth may suggest increased volume production, forest value, site productivity, biomass production, and carbon sequestration within the studied period. This provides a suitable window to compare the growth rate and productivity of tree species in varying site conditions. Additionally, the results indicate future rotation periods can be shorter now than before as the length of the growing season becomes longer in northern Europe. This offers significant inputs into the development of new silvicultural methods and the overall contribution to sustainable boreal forest management.

5. Conclusion

This study has shown that top height growth of Norway spruce and Scots pine increased during the last 30 years in the Swedish forests. The increase in growth was more pronounced after the millennium. Temperature showed positive correlation with the increased growth. We acknowledge that other factors such as atmospheric nitrogen deposition, increased atmospheric CO_2, improved genotypes from tree breeding and improved silvicultural systems may have contributed to the observed growth changes in Sweden, but that climate changes that occurred between the two periods studied are at least possible contributors. The higher growth patterns may result in reductions in the rotation periods for both species in the future. Significant correlations between changes in climate and growth increases suggests that climate-sensitive growth models are required for characterising boreal forest growth under warming climates in the higher latitudes. In the future, we anticipate climatic conditions may influence the height growth either positively or negatively, depending on the severity and frequency of extreme biotic and abiotic conditions.

CRediT authorship contribution statement

Alex Appiah Mensah: Conceptualization, Methodology, Formal analysis. **Emma Holmström:** Conceptualization, Methodology. **Hans Petersson:** Methodology, Funding acquisition. **Kenneth Nyström:** . **Euan G. Mason:** Conceptualization, Methodology. **Urban Nilsson:** Conceptualization, Methodology.

Declaration of Competing Interest

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

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Declaration of Competing Interest statement

The authors declare no competing interest.

Data availability statement

The data material used in this study is available upon request from the authors.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118727.

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The millennium shift: Investigating the relationship between environment and growth trends of Norway spruce and Scots pine in northern Europe

Alex Appiah Mensah, Emma Holmström, Hans Petersson, Kenneth Nyström, Euan G. Mason, Urban Nilsson

Appendix A: Supplementary material

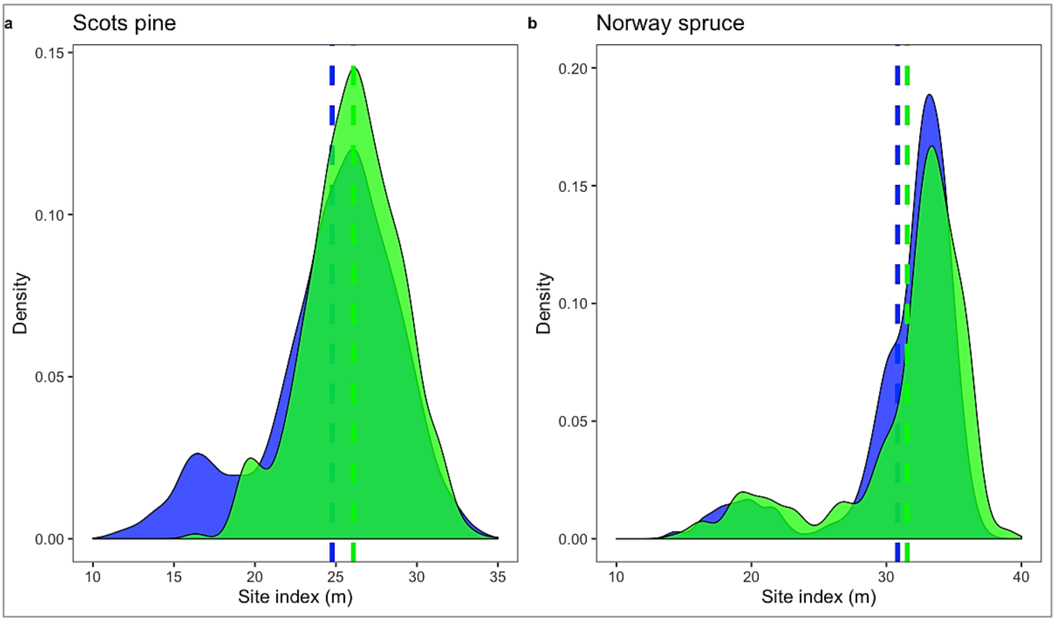

Fig. A.1. Distribution of SIs in the reference (blue) and validation (green) periods for (a) Scots pine and (b) Norway spruce. The vertical dashed-lines indicate the means.

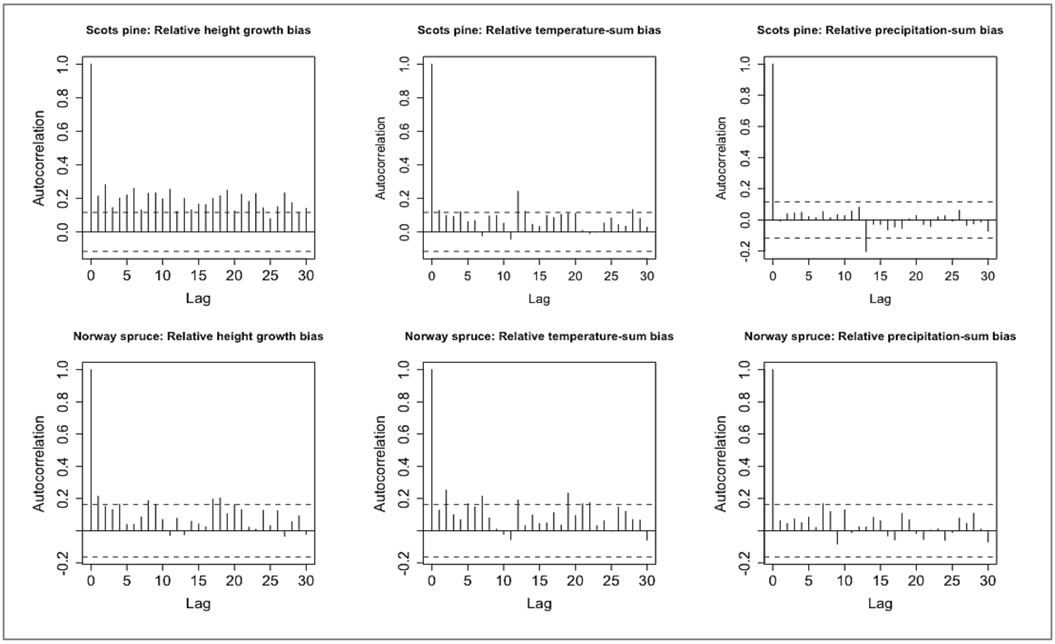

Fig. A.2. Autocorrelation detection in the time series of relative height growth bias, temperature-sum bias and precipitation-sum bias for Scots pine (upper panel) and Norway spruce (lower panel).

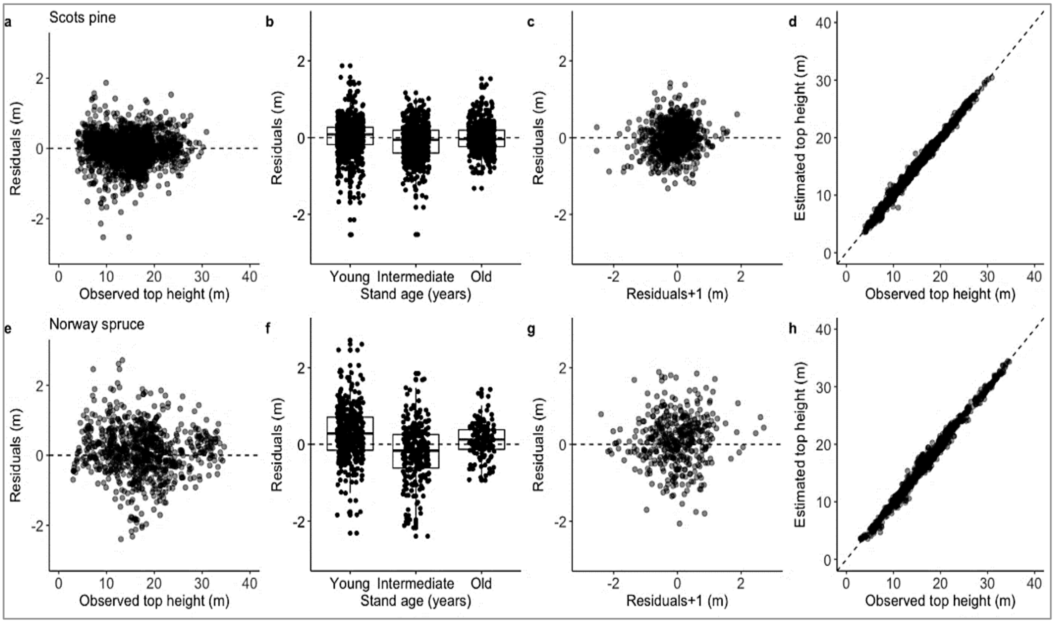

Figure A.3. Residual diagnostic plots for the Elfving and Kiviste (F02) GADA-site index model for Scots pine (a-d) and Norway spruce (e-h). Young forests (< 41 years), intermediate forests (41-80 years) and old forests (> 80 years).

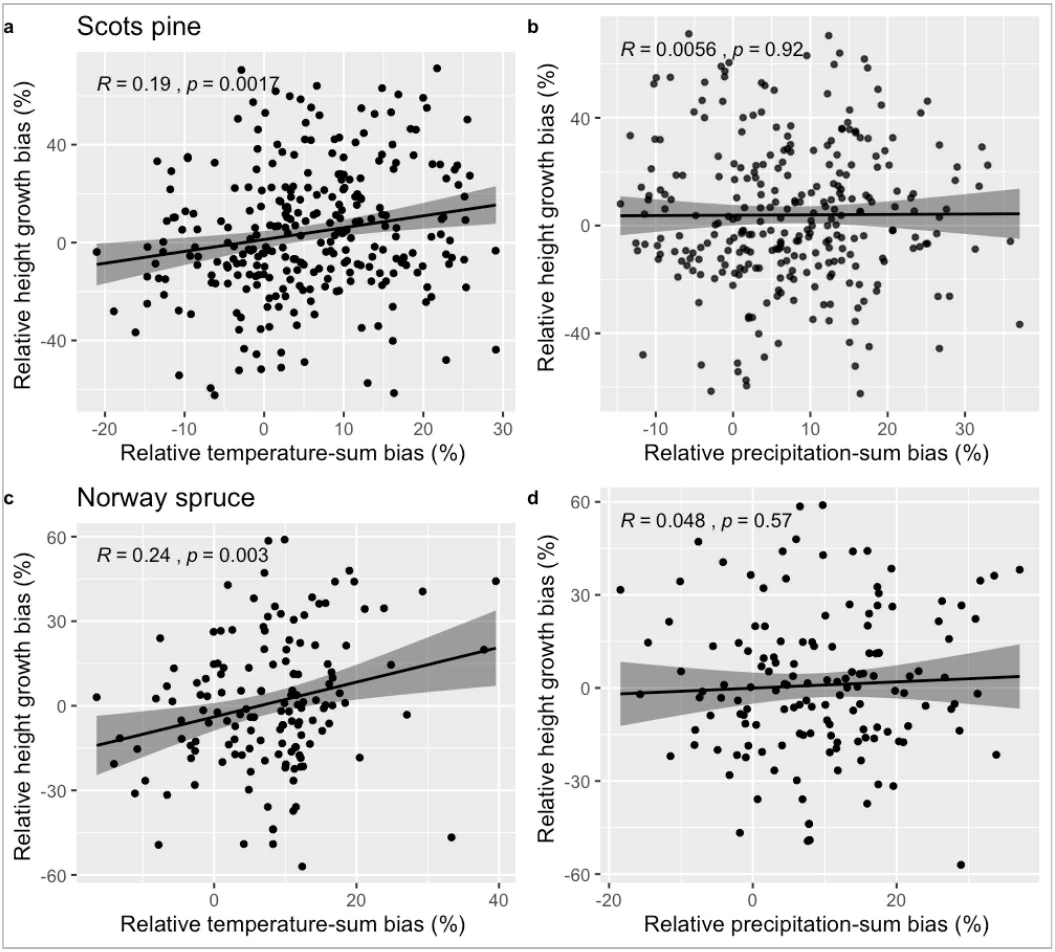

Fig. A.4. Pearson correlation (R) between relative height growth bias and the climate variables (relative temperature-sum and precipitation-sum biases) for Scots pine (upper panel) and Norway spruce (lower panel).

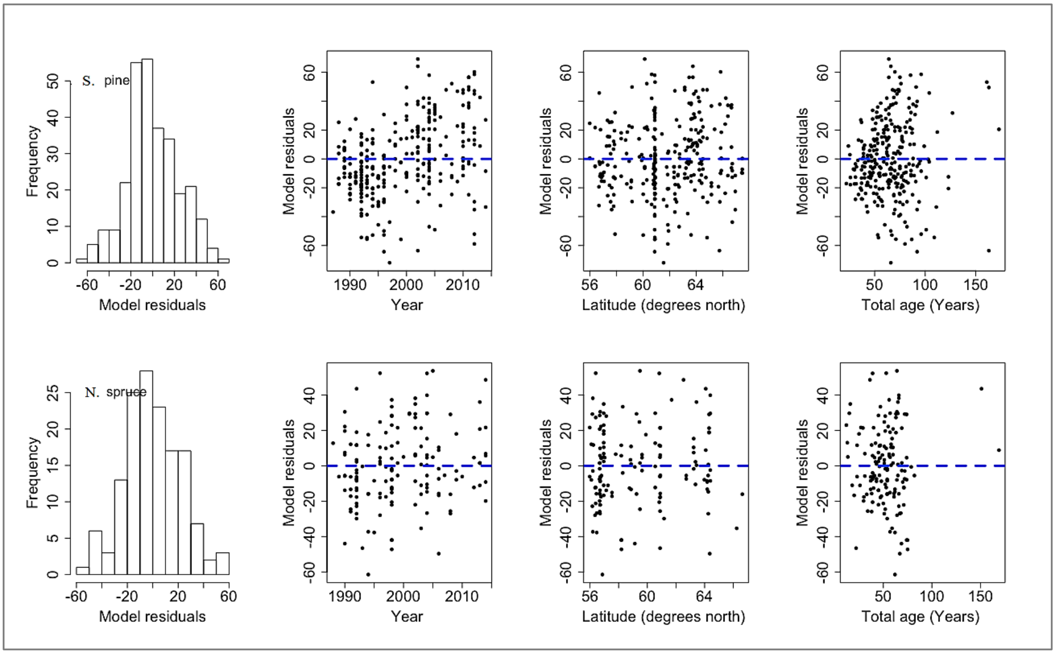

Fig. A.5. Residual distribution and heteroscedasticity test of the final regression models linking relative height growth bias as a function of relative temperature-sum bias for Scots pine (S. pine, upper panel) and Norway spruce (N. spruce, lower panel).

Table A.1. Full regression functions of relative height growth changes (% yr^{-1}) and climate and site variables.

	Scots pine				Norway spruce			
	Estimate	SE	t-value	p-value	Estimate	SE	t-value	p-value
Intercept	-9.65	0.32	-1.52	0.128	-0.24	6.19	-0.04	0.969
Temperature-sum bias	0.58	0.18	3.31	**0.001**	0.69	0.21	3.21	**0.003**
Precipitation-sum bias	0.22	0.17	1.34	0.181	0.17	0.17	0.96	0.340
Total age	0.069	0.076	0.91	0.366	-0.026	0.10	-0.25	0.799
Altitude	0.018	0.015	1.23	0.218	-0.022	0.017	-1.34	0.183

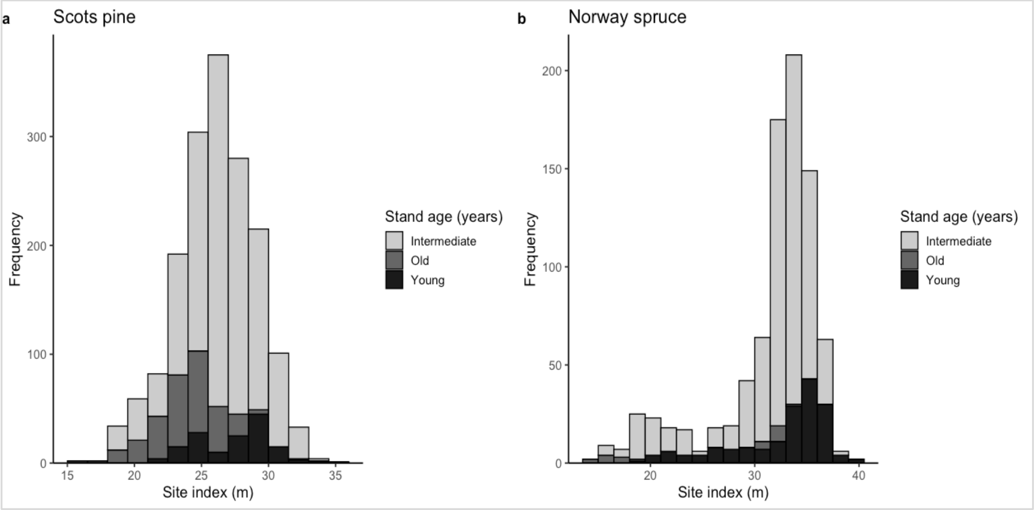

Fig. A.6. Site index distribution by age class for (a) Scots pine and (b) Norway spruce long-term forest experiments in the validation dataset. Age class thresholds: young forests (< 41 years), intermediate forests (41-80 years) and old forests (> 80 years)

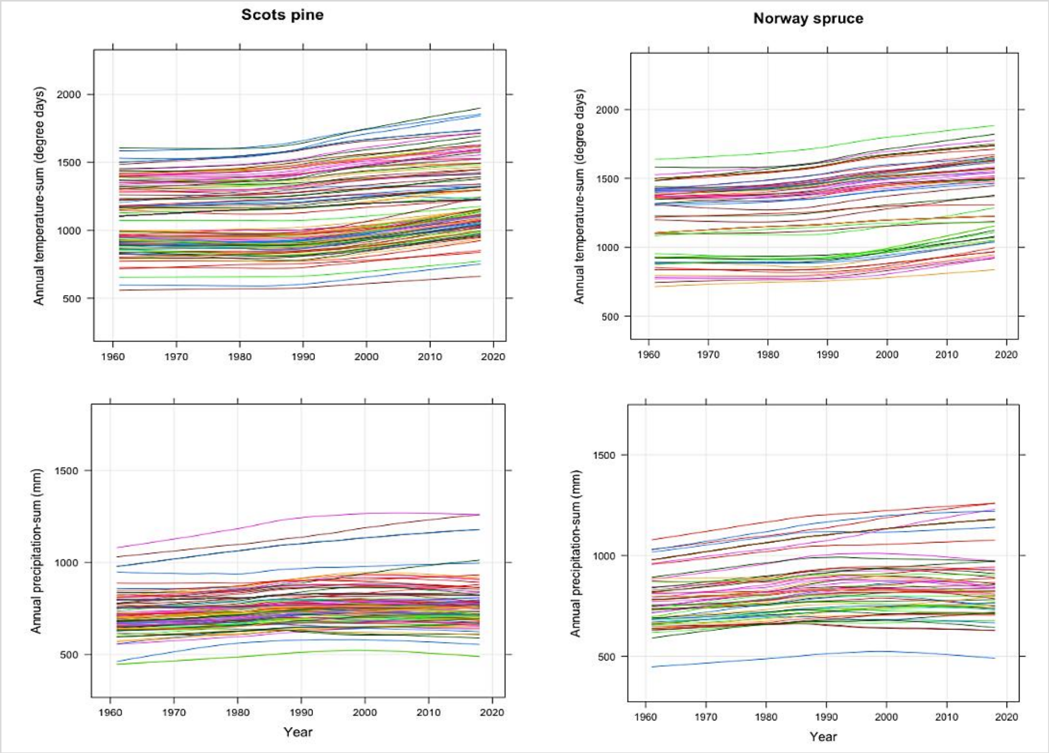

Fig. A.7. Annual time series (1961-2018) of precipitation-sums and temperature-sums for Scots pine and Norway spruce sites in the validation dataset. Each line represents an experiment. The climate conditions were on the average stable in the reference periods (1961-1985) in contrast to the validation periods (1986-2018), especially for the temperature-sums of both species.

III

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Modelling potential yield capacity in conifers using Swedish long-term experiments

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ABSTRACT

Information on forest site productivity is a key component to assess the carbon sequestration potential of boreal forests. While site index (SI) is commonly used to indicate forest site productivity, expressions of SI in the form of yield capacity (potential maximum mean annual volume increment) is desirable since volume yield is central to the economic and ecological analyses of a given species and site. This paper assessed the functional relationship between SI and yield capacity on the basis of yield plot data from long-term experiments measured over several decades for Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Lodgepole pine (*Pinus contorta*) and Larch (*Larix decidua* and *Larix sibirica*) in Sweden. Component models of total basal area and volume yield were also developed. SI was determined by existing height development functions using top height and age, whereas functions for stand-level (m^2 ha^{-1}) basal area development were constructed based on age, SI and initial stand density using difference equations and nonlinear mixed-effects models. The relation between volume yield (m^3 ha^{-1}) and top height was adjusted with total basal area production through nonlinear mixed-effects models. Species-specific parametric regression models were used to construct functional relationships between SI and yield capacity. The root mean square errors of the species-specific models ranged from 2 to 6% and 10–18% of the average values for the basal area and volume equations, respectively. For the yield capacity functions, the explained variations (R^2) were within 80–96%. We compared our yield capacity functions to earlier functions of the species and significant differences were observed in both lower and higher SI classes, especially, for Scots pine and Norway spruce. The new functions give better prediction of yield capacity in current growing conditions; hence, they could later be used for comparing tree species' production under similar site and management regimes in Sweden.

1. Introduction

The rate of forest growth is an important component of the boreal forest carbon stocks' balance. Recent reports have shown forest management- and environment- induced growth increase, for example, in the boreal forests of northern Europe (e.g. Sharma et al., 2012; Kauppi et al., 2014; Henttonen et al., 2017; Appiah Mensah et al., 2021; Mäkinen et al., 2021). Thus, the boreal forest is a critical component of the global carbon cycle and its health (growth and productivity) is of primary concern (Gauthier et al., 2015). Valid data and new expressions for forest site productivity in growth models are needed for unbiased assessments of management and environmental impacts on the growth and carbon fluxes of boreal forests in the short- and long-term horizons (Boisvenue and Running, 2006; Skovsgaard and Vanclay, 2008; Fontes et al., 2010; Bontemps and Bouriaud, 2014).

Information on site productivity is also needed by foresters in many ways, for example, to plan silvicultural treatments across the rotation period, to forecast forest growth and to quantify wood biomass production potential from local-to-regional and- national scales (Pretzsch et al., 2008). Site productivity may also be important when to assess biodiversity and other ecosystem services in relation to forest management (e.g. Felton et al., 2017, 2019). In Sweden, the site productivity is also the legislative boundary of the Forestry Act, and only forestlands where the average annual potential wood production exceeds 1 m^3 ha^{-1} yr^{-1} are considered as productive forest land. On poorer sites, no harvest is allowed and Swedish national statistics are reported differently based

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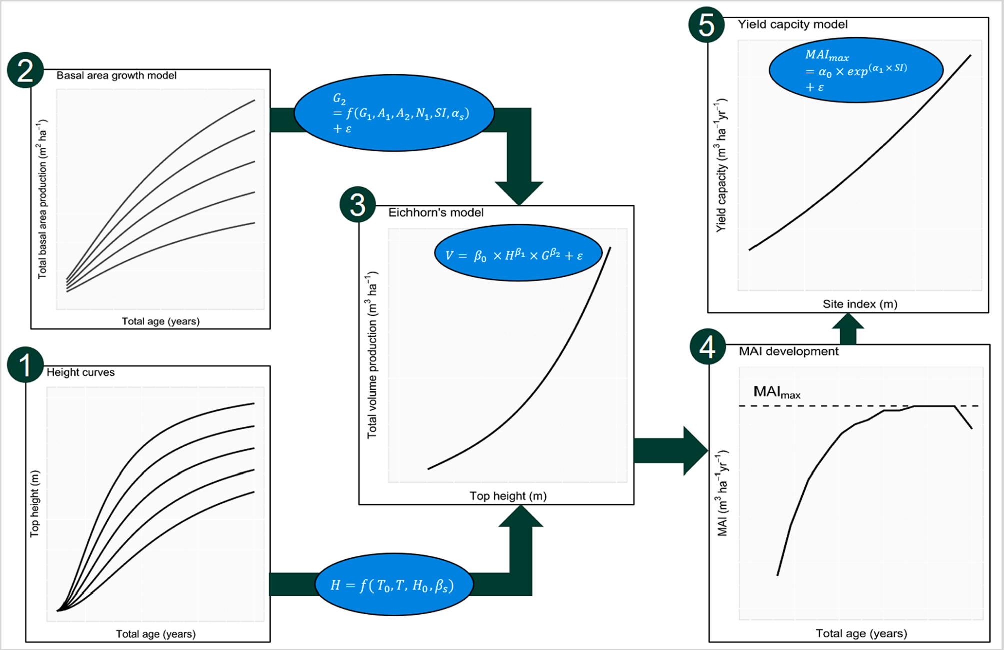


Fig. 1. Stepwise estimation of yield capacity in this study. The elongated circles denote the models applied at each step.

on this boundary (Nilsson, 2020).

Forest site productivity is generally defined as the potential of a site to produce wood biomass or tree volume (Skovsgaard and Vanclay, 2008). It is assessed by several methods that can be broadly grouped into two: geocentric and phytocentric. The geocentric methods are mostly based on site indicators of climate, topography and soil, whereas the phytocentric methods are vegetation related, made up of tree- or plant-based indicators (Hägglund, 1981; Skovsgaard and Vanclay, 2008). The two methods have been widely applied in studies on forest site productivity assessment for several tree species across biomes (e.g. Hägglund and Lundmark, 1977; Szwaluk and Strong, 2003; Mason et al., 2017; Bueis et al., 2019; Eckhart et al., 2019; Liu et al., 2021).

Site index (SI), defined as the height attained at a reference age is the most commonly used indicator of forest site productivity. In Sweden, SI is generally estimated in three ways: (1) by height development curves, (2) by site factors (combination of climate, soil, field and bottom vegetation) and (3) by intercept method. Method 1 is used for matured stands (above 20 years), while method 3 is applied mainly in young stands (below 20 years). Method 2 can be applied on all forestlands and is used by the National Forest Inventory to estimate SI (Hägglund and Lundmark, 1977; Elfving and Kiviste, 1997; Nilsson, 2020). For even-aged monoculture stands, SI based on height development curves (height-age relations) of the dominant trees is often desirable when estimating the potential of the growing site. This is because height growth is strongly related to volume production, and the height growth of the largest trees is relatively independent of stand density and thinning from below treatments (Eichhorn, 1902; Skovsgaard and Vanclay, 2008; Burkhart and Tomé, 2012). However, expressing SI in terms of the potential average volume yield produced over the stand rotation is desired since timber volume is a key parameter in economic and ecological analyses of forest resources. Hence, for even-aged forest stands, the relation between SI and maximum mean annual volume increment (hereafter, referred to as yield capacity) can directly be used to describe the potential amount of wood volume that can be obtained per year on a site for a given species (Hägglund, 1981; Hägglund and Lundmark, 1982; Elfving and Nyström, 1996) and for further classification of forest lands as productive and unproductive units.

Nevertheless, the relation between SI and yield capacity is not always straightforward, especially when the methods used rely on the general Eichhorn's law (Eichhorn, 1902). The law stipulates that stands have the same total volume yield when they reach the same dominant height, independent of age and SI (Eichhorn, 1902). However, under comparable management regimes, the total volume yield over the rotation has been shown to vary within the same SI for several species including Norway spruce (*Picea abies*) by Assmann (1955), Scots pine (*Pinus sylvestris*) by Schmidt (1973) and loblolly pine (*Pinus taeda*) by Hasenauer et al. (1994). Therefore, for a given species and management regime, significant site-dependent variations may occur in the yield levels (total volume production at a given height), suggesting that stands of different yield levels may have different trajectories for height-volume relations across the rotation period (Assmann, 1970; Hasenauer et al., 1994; Skovsgaard, 1997). Including variables that capture the variations in yield levels can therefore improve estimates of yield capacity and enhance meaningful comparisons across species, sites and regions (Skovsgaard and Vanclay, 2008; Ekö et al., 2008). Differences in yield levels are attributable to many factors such as climate, soil, seed provenance, silviculture, stand density, basal area production and form factors (Skovsgaard and Vanclay, 2008). Basal area production as a measure of potential density has been found to explain larger variations in the volume yield levels and thus, provide satisfactory outcomes of site productivity assessment (Assmann, 1966; Sterba, 1987; Ung and Ouellet, 1991; Hasenauer et al., 1994; Sterba and Monserud, 1995; Hall et al., 2019; Allen et al., 2020).

The maturation of long-term yield experiments (LTEs) of tree species

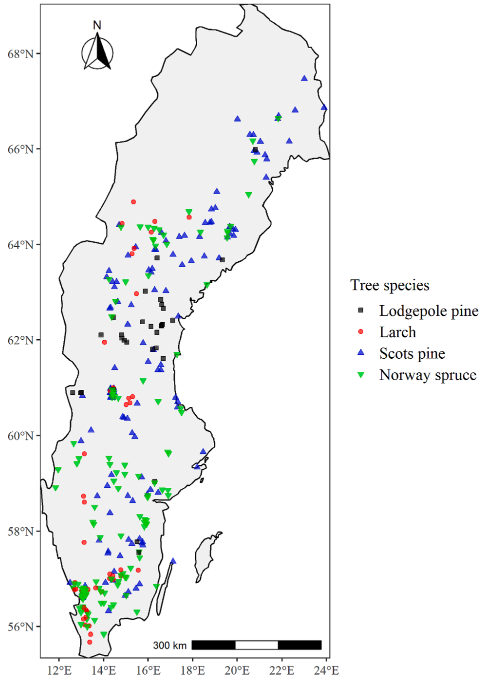


Fig. 2. Locations of LTE sites for the different tree species in Sweden.

where height development, carrying capacity (described by total basal area production) and total stem volume produced over time could be easily and reliably estimated provides a unique insight into the evaluation of yield capacity by using SI (Pretzsch et al., 2019). In Sweden, LTEs were established throughout the country in the 20th century to provide quantitative results for forest management planning (e.g. Elfving, 2010a; Nilsson et al., 2010). Now, tree growth data in the LTEs have accumulated and this paper presents an investigation of site productivity for the major tree species under Swedish conditions.

The general objective of the study was to improve the estimates of yield capacities for major forest tree species in Sweden. The specific objectives were two fold; (i) to develop functional relationships between yield capacity and SI predicted by height curves using data from LTEs, and (ii) to compare the estimated yield capacities with those predicted by earlier functions from Hägglund and Lundmark (1982) for forest tree species in Sweden.

The study was limited to the tree species where we had measured data series from unthinned and thinned (from below) stands and with measurements of total volume production including mortality, harvest removals and standing volume, which resulted in four species being selected: Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Lodgepole pine (*Pinus contorta*) and Larch (*Larix decidua* – European Larch and *Larix sibirica* – Siberian Larch). Together, these species contribute more than 80% to the total growing stock volume on forest lands in Sweden (Nilsson, 2020).

2. Material and methods

The study approach was generally centred on the principles of forest yield production (Fig. 1). The stepwise approach was carried out in five main steps: based on height development (1) and corresponding basal area development (2), total volume production was estimated (3). Yield capacity was then derived from volume yield and age (4), and functional relationships between yield capacity and site index were established (5). The constructed yield capacity functions in the present study were compared to earlier functions and the observed differences were discussed in relation to methodological approaches and changes in environmental conditions. The five modelling steps are expanded in the following sub-sections.

2.1. *Data*

The data material comprised LTEs from 330 locations in Sweden (Scots pine = 169, Norway spruce = 86, Lodgepole pine = 34, Larch = 41). All selected LTEs were originally experiments in block designs where the total production (yield) was recorded, including mortality, harvest removals and standing volume. The sites covered a wide range of fertility, latitudinal and altitudinal gradients in Sweden (Fig. 2; Table 1). For each site, only the control and thinned-from-below plots with

Table 1
Summary of stand and site data for included plots.

Tree species		Age (years)	Top height (m)	Basal area (m^2 ha^{-1})	Volume (m^3 ha^{-1})	Stand density (trees ha^{-1})	Site index (m)	Thinning ratio	Measurement year	Latitude (°N)	Altitude (m a.s.l)	No. LTEs (plots)	*N*
Scots pine	min	10	2	0.7	0.7	300	13	0	First: 1927	56	0		
	mean	46	14	29	207	2116	24	0.09	–	–	207	169	4498
	max	119	31	105	1169	15,867	32	0.95	Latest: 2018	67	560	(981)	
Norway spruce	min	12	2	0.8	0.2	433	16	0	First: 1928	55	3		
	mean	42	16	35	327	2615	29	0.04	–	–	136	86	2022
	max	133	37	140	1608	13,106	36	0.95	Latest: 2018	66	610	(427)	
Lodgepole pine	min	15	4	4	2	333	16	0	First: 1953	56	0		
	mean	33	14	29	211	2028	22	0.03	–	–	291	34	742
	max	83	26	72	700	9062	30	0.95	Latest: 2019	69	480	(273)	
Larch spp.	min	6	3	0.1	0.9	355	24	0	First: 1949	55	20		
	mean	32	19	36	311	1923	36	0.23	–	–	160	41	462
	max	104	35	94	1043	11,687	42	0.95	Latest: 2019	64	435	(108)	

min: minimum; max: maximum; thinning form describes unthinned plots (0) and thinned from below plots (1)≤; N is the total number of measurements.

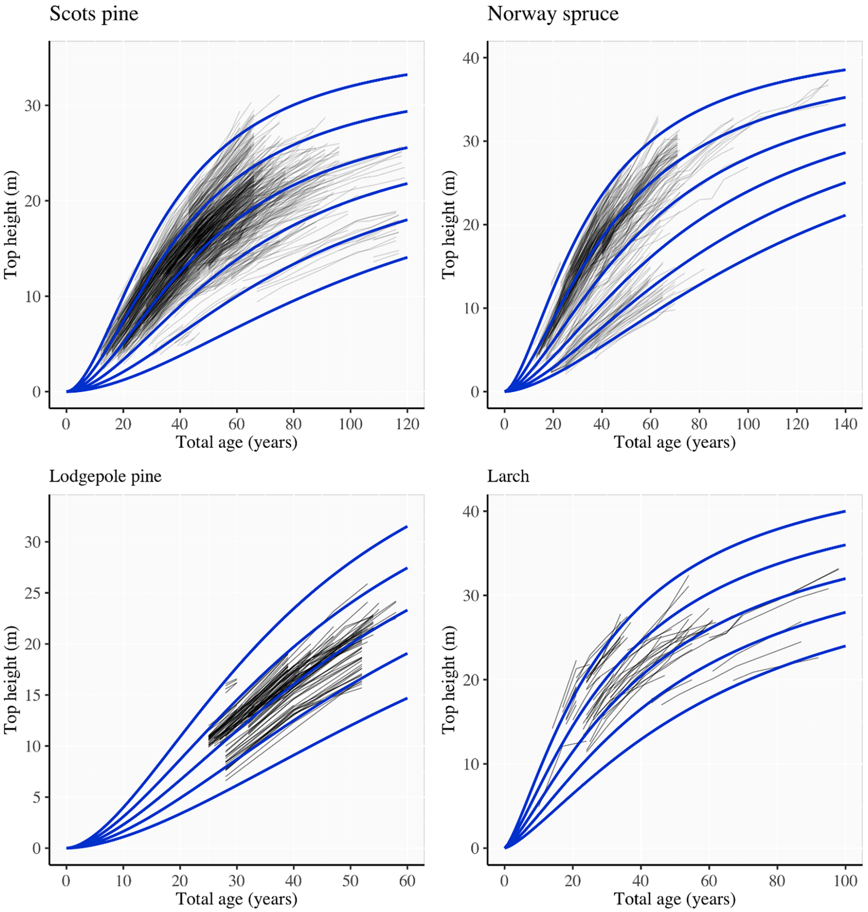


Fig. 3. Observed height development (black lines) in relation to site index curves (blue lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

thinning grade (percent removed basal area) $< 35\%$ and thinning ratio < 0.95 were used for the yield analyses. Thinning ratio is expressed by the quotient between the basal area mean diameters of removed and remaining trees. Fertilised plots were excluded from the dataset. The studied plots were fully stocked even-aged stands where more than 70% of the total basal area consisted of the main tree species. For most sites, plot measurements had been conducted between 1920 and 2019, with irregular measurement intervals. The remeasurement interval was on average 8 years and the frequency of remeasurements on a plot ranged from 2 to 14 times. Permanent square or rectangular sample plots with net sizes of approximately 0.1 ha were used to collect the tree information. Total age, tree species and damages were recorded in addition to perpendicularly calipered tree diameters at breast height (1.3 m from the ground). Trees were numbered at first measurement to ensure that remeasurements in subsequent years could be linked to the same individual trees.

Among the trees recorded on the plot, a sub-sample was taken for total height measurement using the Tiréns device before 1970, Suunto hypsometer 1970–1995 and the Haglöf Vertex hypsometer afterwards. Sample trees were followed over time for total height, except for cases of damages by storm, snow, diseases, etc., in which they were replaced by equally good candidates. The observations of height-diameter pairs were used to estimate coefficients of the height-diameter equation (Eq. (1)) presented by Näslund (1947), where coefficients were estimated for each plot and measurement occasion, and all calipered trees without heights were assigned predicted heights. Based on the predicted heights, the thickest trees on every plot were selected as the top (dominant) height trees. Top height was defined as the arithmetic mean height of the 100 thickest (by diameter) trees ha^{-1}. The initial stand densities (trees ha^{-1}) during installation of the plots as well as site information were recorded. Other variables such as basal area and stem volume were computed for every calipered tree and aggregated to the plot level in per hectare units. The tree volume was estimated for living, thinned and dead trees using the species-specific volume functions by Brandel (1990). Summary of the plot and site variables are given in Table 1.

$$H = \frac{DBH^{\gamma}}{(\alpha + \beta \times DBH)^{\gamma}} + 1.3 \qquad (1)$$

Table 2
Tested total basal area development functions.

No.	Equation
F01	$G_{ijk} = exp^{\left[ln(G_{ijl})+\mu+\alpha_0\left(\frac{1}{A_{ijk}}-\frac{1}{A_{ijl}}\right)+\mu+\alpha_1(N_1)+\mu+\alpha_2(SI)\right]} + \varepsilon_{ijk}$
F02	$G_{ijk} = \frac{1}{\left[\left(\frac{1}{G_{ijl}}\right)\left(\frac{A_{ijl}}{A_{ijk}}\right)^{\alpha_0+\mu}+\mu+c_0\left(1-\left(\frac{A_{ijl}}{A_{ijk}}\right)^{a_0+\mu}\right)+\mu+\alpha_1(N_1)+\mu+\alpha_2(SI)\right]} + \varepsilon_{ijk}$
F03	$G_{ijk} = \left[\left((G_{ijl})^{\mu+c_0\left(\frac{A_{ijl}}{A_{ijk}}\right)^2}+\mu+\alpha_0\left(1-\left(\frac{A_{ijl}}{A_{ijk}}\right)^2\right)\right)^{\frac{1}{c_0+\mu}}+\mu+\alpha_1(N_1)+\mu+\alpha_2(SI)\right] + \varepsilon_{ijk}$
F04	$G_{ijk} = \left[G_{ijl}\left(\frac{1-exp^{\mu-\alpha_0(A_{ijk})}}{1-exp^{\mu-\alpha_0(A_{ijl})}}\right)^{\mu+c_0+\mu+\alpha_1(N_1)+\mu+\alpha_2(SI)}\right] + \varepsilon_{ijk}$
F05	$G_{ijk} = \left[exp^{\left(\ln(G_{ijl})\left(\frac{A_{ijl}}{A_{ijk}}\right)^{\mu+\alpha_0++\mu+\alpha_1(N_1)}+\mu+\alpha_2(SI)+\mu+c_0\left(1-\left(\frac{A_{ijl}}{A_{ijk}}\right)^{\mu+\alpha_0+\mu+\alpha_1(N_1)}\right)\right)}\right] + \varepsilon_{ijk}$

Table 3
Summary of fit-statistics for the tested basal area functions. Relative RMSEs and MDs are given in parenthesis. The selected model for each species is highlighted in bold.

		Scots pine	Norway spruce	Lodgepole pine	Larch
F01	RMSE (%)	1.09 (3.39)	0.97 (2.14)	1.31 (3.35)	3.40 (7.04)
	MD (%)	−0.15 (−0.47)	−0.10 (−0.22)	−0.12 (−0.33)	−0.65 (1.36)
F02	RMSE (%)	2.68 (8.32)	2.73 (6.04)	1.57 (4.23)	6.37 (13.2)
	MD (%)	−0.06 (−0.19)	−1.33 (−2.95)	−0.60 (1.61)	−5.25 (10.87)
F03	RMSE (%)	3.42 (10.63)	1.90 (4.21)	3.10 (8.34)	10.56 (18.31)
	MD (%)	1.66 (5.15)	0.14 (0.31)	2.37 (6.38)	−8.33 (−24.75)
F04	RMSE (%)	2.53 (7.86)	1.82 (4.03)	1.22 (3.29)	2.79 (5.78)
	MD (%)	0.26 (0.82)	−0.09 (−0.20)	−0.01 (−0.03)	−0.29 (−0.59)
F05	RMSE (%)	3.29 (10.22)	1.96 (4.32)	1.94 (5.21)	3.68 (7.58)
	MD (%)	0.04 (0.12)	−0.11 (−0.55)	1.00 (2.69)	0.05 (0.11)

where, H is the tree height (m), DBH is the calipered tree diameter at breast height (cm), α, β are parameters to be estimated and γ was 3 for Norway spruce and 2 for other tree species (to minimize the sum of squared residuals).

2.2. Site index estimation from height development curves

The SI functions operationally used today in Sweden were used to estimate SI from the observed top heights on each plot and thereafter, averaged to provide the SI for each site (experiment location). More information concerning the form and parameter estimates of the SI functions can be found in Elfving and Kiviste (1997), Elfving (2009) and Liziniewicz et al. (2016). SI was defined as the mean top height at the tree species-specific reference age (100 years: H_{100}, for Norway spruce, Scots pine and Larch; and 50 years: H_{50}, for Lodgepole pine). Preliminary assessment showed that the SI curves adequately described the patterns in the observed top height development for all species (Fig. 3). With a given plot SI, we derived the expected mean top heights at ages corresponding to the observed measurement years, assuming the growth function passes through current height and age. The expected top heights were used to simulate the expected plot-level total volume productions (see Fig. 1 and Section 2.4).

2.3. Functions for total basal area development

Basal area is often used to describe stands' potential density (carrying capacity) and due to its strong relationship with stem volume and woody biomass production, it is of central significance to modelling forest stand development (Burkhart and Tomé, 2012). To determine the carrying capacity of forest stands, projections of basal area growth require repeated observations from plots covering gradients in stand and environmental conditions (Gadow and Hui, 1999).

Studies from long-term spacing trials shown the significant influence of initial spacing on stand productivity (Pettersson, 1992; Samuelson et al., 2010), and as such the basal area growth increases asymptotically with age and the asymptote is largely dependent on site quality and initial stand density (Pienaar and Shiver, 1986; Elfving, 2010a; Hall et al., 2019). Hence, the following growth functions (Table 2) were used to examine the development of total basal area production (including surviving, removed and dead trees) for the different tree species. Model one (F01) is identical to Pienaar et al. (1990), F02 is based on Hossfeld (Peschel, 1938), F03 is based on Levakovic (Levakovic, 1935), F04 is based on Bertalanffy-Richards (von Bertalanffy, 1938; Richards, 1959) and F05 is derived from Schumacher's growth function (Schumacher, 1939).

Under a model-based framework, the yield function relates the response variable (total basal area, m^2 ha^{-1}) to a set of independent variables and was expressed generally as

$$y_i = f(X_i; B) + \varepsilon_i \tag{2.1}$$

where i indexes the population units; y_i is the observation of the response variable on the ith unit; X_i is a vector of predictor variables comprising total age (years), site index (m) and initial stand density (trees ha^{-1}); B is a vector of parameters to be estimated from the sample data; $f(X_i; B)$ expresses the nonlinear relationship between predictor variables and the parameters; and ε_i is a normally distributed random residual term $\left[\varepsilon_i \sim N(0, \sigma^2)\right]$ to account for the unexplained variation in the observed values of y_i. Given repeated plot measurements, difference equations are more suitable for modelling the dynamics of yield within an observed growth period and as such, produce robust base-age invariant results compared to static base-age equations (Cieszewski and Bailey, 2000). Therefore, Eq. (2.1) was expressed in an algebraic difference form (Eq. (2.2)) where the basal area at time two (G_2) was modelled from the basal area at time one (G_1), total age at times one (A_1) and two (A_2), site index (SI) and initial stand density (N_1).

$$G_2 = f(G_1, A_1, A_2, N_1, SI, \alpha_s) + \varepsilon_i \tag{2.2}$$

where N_1 was transformed as: $N_1 = \sqrt{\frac{10000}{N}}$ and the α_s are model parameters.

The tested functions (F01-F05) have polymorphic asymptotes and their difference forms are presented in Table 2. We used all measurements within the observed growth period to model the basal area growth. The growth period was defined as the time interval between consecutive measurements. The sample data for model fitting were hierarchical in structure, i.e., several plots nested within a site. The plots had many revisions, which suggest observations within a plot might exhibit temporal dependencies. Similarly, the distance between sample plots within each site is small (about 20–500 m apart) and this may induce a spatial autocorrelation among observations from a site. The lack of independency among observations may violate standard regression analysis through biased model parameter estimates and subsequently, lead to erroneous inferences. Hence, the tested basal area growth equations were expressed as nonlinear mixed-effects time series models to account for both plot and site random variances (Gregoire and

Table 4
Parameter estimates of species-specific basal area ($m^2\ ha^{-1}$) functions. Values in parenthesis are estimated standard errors.

		Scots pine	Norway spruce	Lodgepole pine	Larch
Class	Parameter	Estimates			
Fixed effects	$\widehat{\alpha}_0$	−52.8873 (1.5744)	−55.1743 (4.2183)	0.0507 (0.0027)	0.0287 (0.0151)
	$\widehat{\alpha}_1$	0.0064 (0.0023)	0.0273 (0.0066)	1.0931 (0.2019)	0.7837 (0.2485)
	$\widehat{\alpha}_2$	−0.0007 (0.0003)	−0.0012 (0.0006)	−0.1089 (0.0281)	0.5909 (0.4267)
	$\widehat{c}_0$			2.6904 (0.1896)	0.0887 (0.0302)
Plot-level random effects					
(μ_p)	$\widehat{var}(\widehat{\alpha}_0)$	61.856	22.242		1.37×10^{-18}
	$\widehat{var}(\widehat{\alpha}_1)$	5.89×10^{-6}	4.39×10^{-5}		
	$\widehat{var}(\widehat{\alpha}_2)$	1.84×10^{-19}	4.11×10^{-7}	0.0028	
	$\widehat{cov}(\widehat{\alpha}_0,\widehat{\alpha}_1)$	0.0164	−0.0291		
	$\widehat{cov}(\widehat{\alpha}_0,\widehat{\alpha}_2)$	0	0.0029		
	$\widehat{cov}(\widehat{\alpha}_1,\widehat{\alpha}_2)$	0	-4.23×10^{-6}		
Site-level random effects					
(μ_s)	$\widehat{var}(\widehat{\alpha}_0)$	285.958	1068.321		3.77×10^{-5}
	$\widehat{var}(\widehat{\alpha}_1)$	9.817×10^{-6}	0.0013		
	$\widehat{var}(\widehat{\alpha}_2)$	6.371×10^{-6}	1.31×10^{-5}	0.1254	
	$\widehat{cov}(\widehat{\alpha}_0,\widehat{\alpha}_1)$	0.0269	0.2797		
	$\widehat{cov}(\widehat{\alpha}_0,\widehat{\alpha}_2)$	0.0281	0.0936		
	$\widehat{cov}(\widehat{\alpha}_1,\widehat{\alpha}_2)$	7.77×10^{-6}	5.33×10^{-6}		
Residual Variance					
$V(\varepsilon_{ijk})$	$\widehat{\omega}^2$	4.6439	2.7276	837.5821	$5.75\text{x}10^5$
	$\widehat{\delta}_1$	−0.1747	−0.0979	−1.4996	−1.5454
	$\widehat{\delta}_0$			0.0382	1.14×10^{-10}
Autocorrelation	$\widehat{\rho}$	0.042	0.215	0.146	0.294
n		3447	984	237	78

Schabenberger, 1996; Mehtätalo and Lappi, 2020).

In Table 2, G_{ijk} is the plot basal area (at the end of the growth period) at age A_{ijk} (k th observations at plot/series j and site i), G_{ijl} is the plot basal area (at the beginning of the growth period) at age A_{ijl} at the same plot/series and site (l th observations at plot/series j and site i and $l \neq k$), the μ denotes between group variances of the two level groups denoted as plot-level (μ_p) and site-level (μ_s) random effects, which are independent and normally distributed $\left[\mu_p\ N(0,D^*)\text{and}\mu_s\ N(0,D^*)\right]$ with between group variance–covariance matrix (D^*) identical for all plots and sites. G_{ijl} was considered as a fixed-effect parameter and was locally estimated for each plot and site. The within group variance specified by the individual random model errors (ε_{ijk}) is normally distributed $[\varepsilon_{ijk}\ N(0,\sigma^2)]$ and independent among observations and μ_p and μ_s. The random-effects parameters were added sequentially to the fixed-effects parameters until convergence was achieved. The model parameters were estimated by approximations of the likelihood function of the Lindstrom-Bates algorithm implemented in the "nlme" package of R statistical environment (Pinheiro et al., 2020; R Core Team, 2020).

Due to unequal variances (heteroscedasticity) arising from measurements at differing stand ages and sites, the within-group random error variance $[V(\varepsilon_{ijk})]$ associated with every predicted plot-level basal area ($\widehat{G}_{ijk}$) were modelled by nonlinear power models (Eqs. (3.1) and (3.2)) with either two parameters (scale and shape, denoted as ω^2 and δ_1 respectively) or three parameters (ω^2 and δ_1 plus a constant,δ_0). Negative ($\delta_1 < 0$), or positive ($\delta_1 > 0$) values of δ_1, suggests the error variance may be decreasing or increasing linearly with $\widehat{G}_{ijk}$ (Mehtätalo and Lappi, 2020). Given that our basal area measurements were unevenly spaced over time and only one single pair of basal area-age measurement were used for basal area projection, the first order autoregressive [AR(1)] error structure (Eq. (3.3)) was chosen to account for the within-plot serial correlation.

$$V(\varepsilon_{ijk}) = \omega^2 \left|\widehat{G}_{ijk}\right|^{2\delta_1} \tag{3.1}$$

$$V(\varepsilon_{ijk}) = \omega^2 \left(\delta_0 + \left|\widehat{G}_{ijk}\right|^{\delta_1}\right)^2 \tag{3.2}$$

$$\rho^z = cor(\varepsilon_{ijk} + \varepsilon_{ijk+z}) \tag{3.3}$$

where ρ the correlation between successive observations is a parameter to be estimated and z is a time lag in terms of measurement intervals between successive observations in the same plot. The accuracy of the tested basal area models were compared using the following estimators (Eqs. (4.1)–(4.4)): root mean square error $\left(RMSE,\ m^2\ ha^{-1}\right)$, relative root mean square error ($RMSE_{rel}$, %); mean deviation $\left(MD,\ m^2\ ha^{-1}\right)$; and relative mean deviation (MD_{rel}, %).

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(\widehat{y}_i - y_i)^2}{n}} \tag{4.1}$$

$$RMSE_{rel} = 100\text{x}\frac{RMSE}{\overline{y}} \tag{4.2}$$

$$MD = \frac{1}{n}\sum_{i=1}^{n}(\widehat{y}_i - y_i) \tag{4.3}$$

$$MD_{rel} = 100\text{x}\frac{MD}{\overline{y}} \tag{4.4}$$

where $\widehat{y}_i$, y_i and $\overline{y}_i$ are the predicted, measured and mean values of total basal area, respectively and n is the number of observations used for model calibration. Models with good statistical precision and low prediction error were considered for further analysis of volume yield. The quality of the final basal area projection model was studied graphically

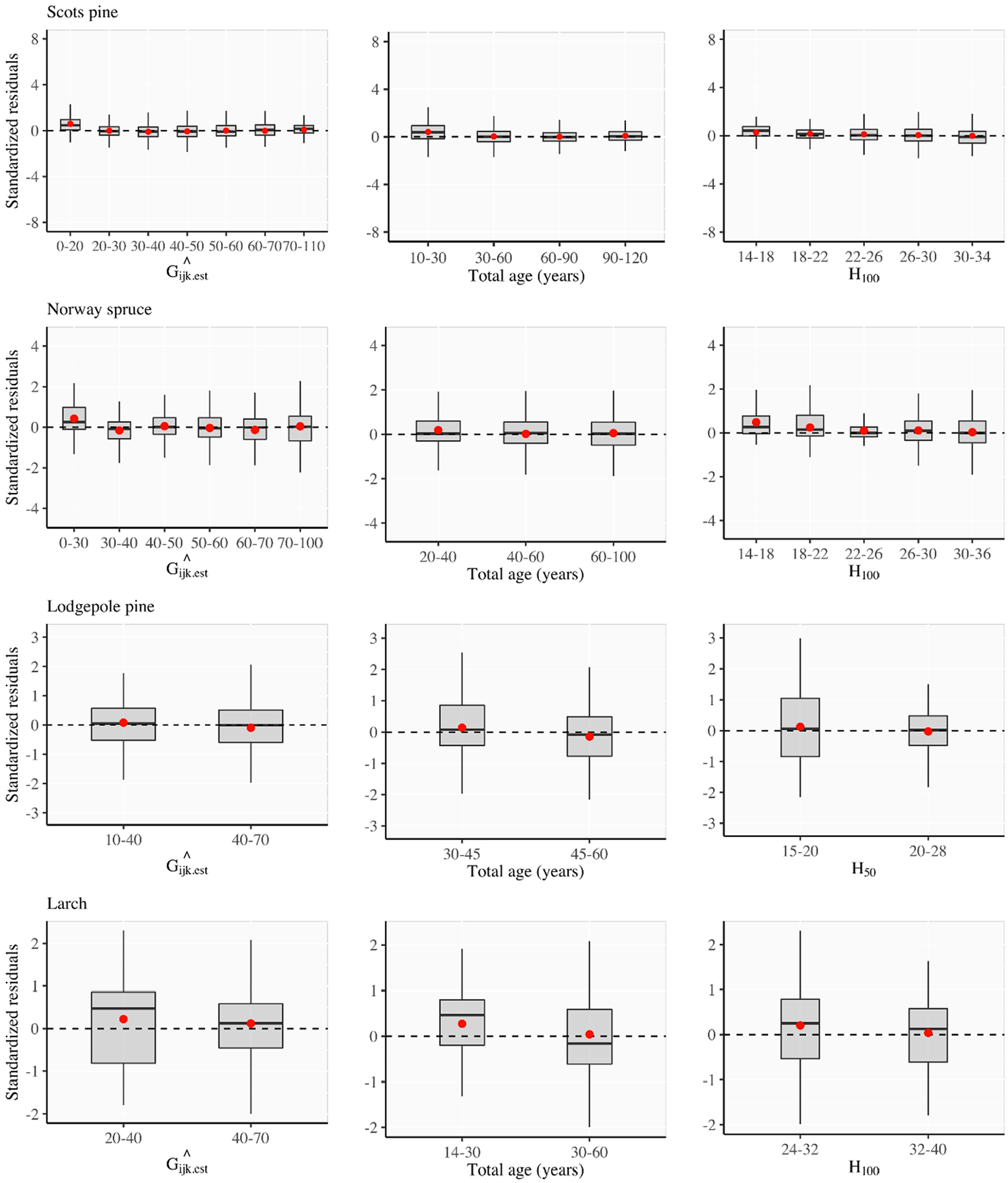


Fig. 4. Standardized (Pearson) residuals versus predicted basal area ($\widehat{G}_{ijk}$, m^2 ha^{-1}), age and site index (m). Site index is expressed as height at 100 years (H_{100}) for Scots pine, Norway spruce and Larch, and at 50 years (H_{50}) for Lodgepole pine. The red dots are calculated residual means, and horizontal dashed lines denote the expected mean residual ([E(ε) = 0]). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by (1) the distribution of model residuals over plot-level basal area predictions ($\widehat{G}_{ijk}$), stand age and SI; and (2) the trajectories of the $\widehat{G}_{ijk}$ curves on the profiles of observed G_{ijk} for different SI, assuming the growth function passes through current basal area (G_{ijl}) at initial measurement age (A_{ijl}). Using the fixed-part of the selected model, the expected total basal area productions at ages corresponding to the observed measurement years for each plot were derived. These predictions of basal area were used as predictors to simulate the expected plot-level total volume yield.

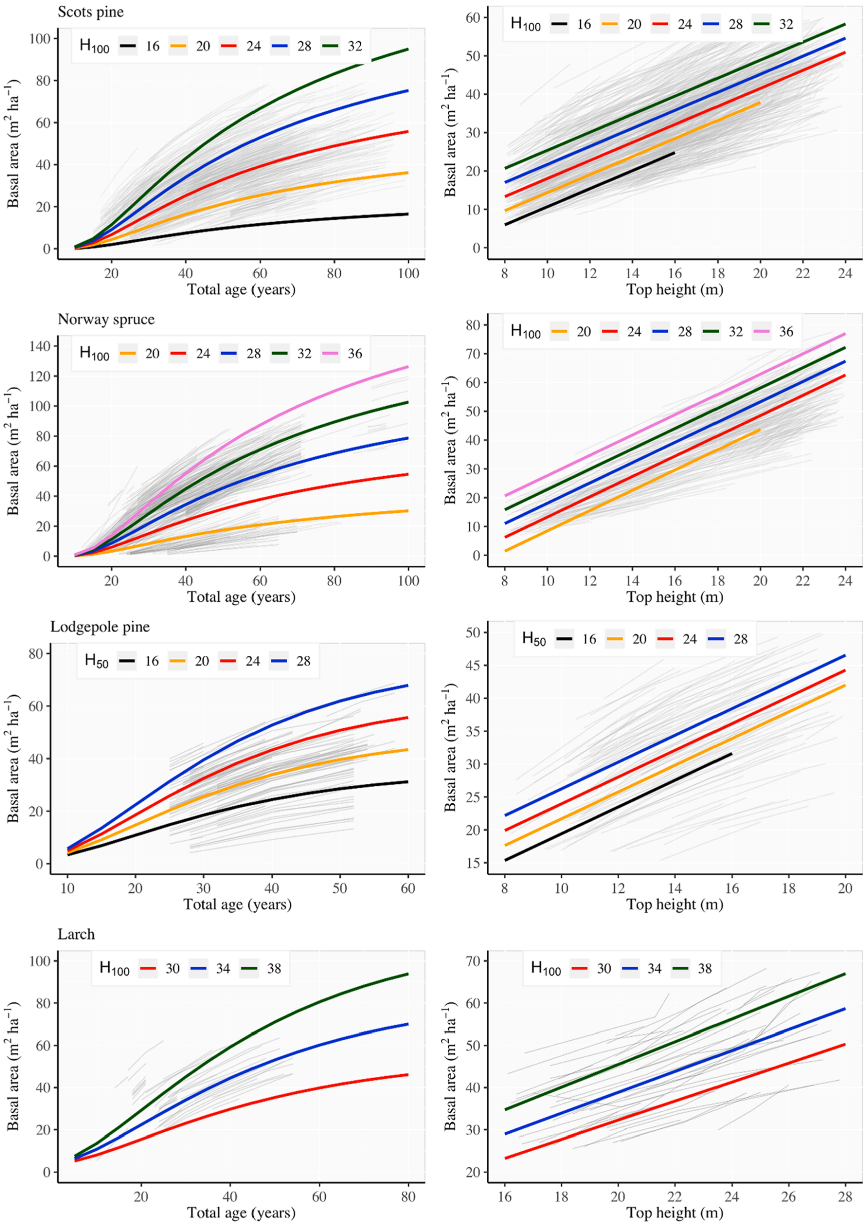


Fig. 5. Left panel: mean predicted basal area over age according to site index; Right panel: Basal area-mean top height relationships. Observed data are shown as solid grey lines.

2.4. Modelling the variations in total volume-top height relationship

To show potential differences in total volume yield (including volumes of removed and dead trees) between sites, the observed volume yield (V) was expressed as an allometric function of mean top height (H). However, the volume-height relationship (Eq. (5)) was adjusted with information from total basal area production (G), assuming a constant form factor as

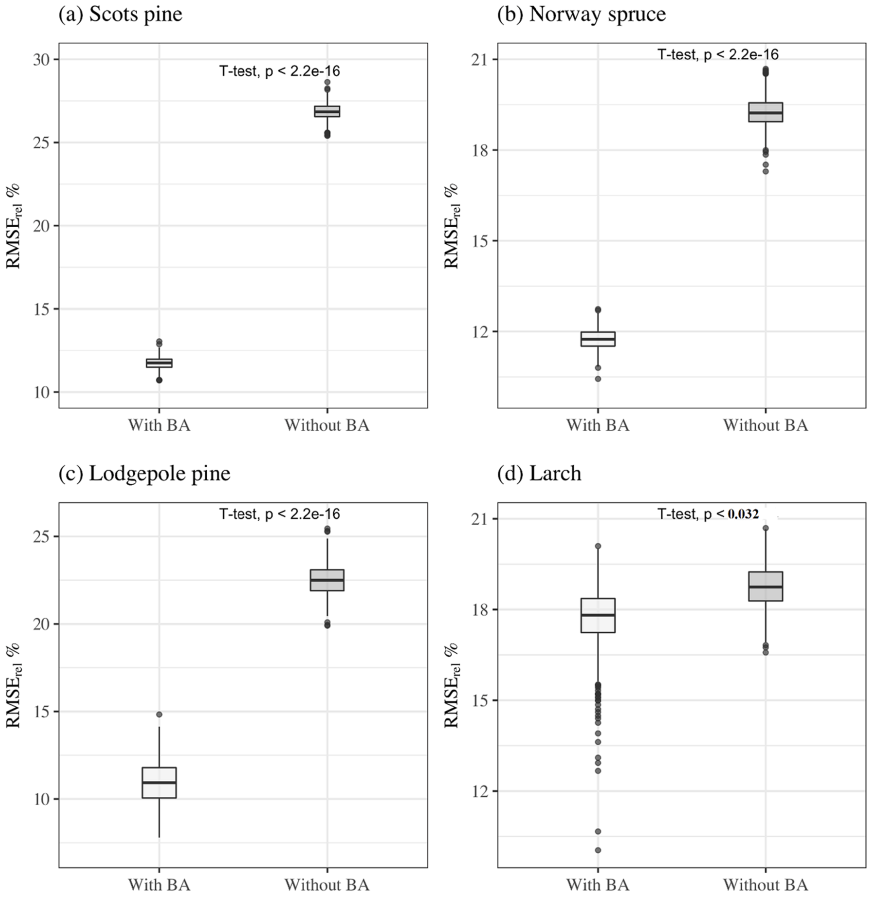


Fig. 6. Accuracy (relative *RMSE, %*) of species-specific volume yield equations with or without basal area as a covariate to top height (Eq. (5)). Note the different scales on the y-axis.

$$V = \alpha_0 \times H^{\alpha_1} \times G^{\alpha_2} + \varepsilon \tag{5}$$

where ε is randomly distributed errors with a zero mean [E $(\varepsilon) = 0$] and with an unknown constant variance [$\mathrm{Var}(\varepsilon) = \sigma^2$], and α s are parameters to be estimated.

Variables (H) and (G) were derived from the height and basal area development functions (see Sections 2.2 and 2.3). Due to the hierarchical structure of the data, Eq. (5) was expressed as a nonlinear mixed-effects time series model to account for both plot and site random variances as:

$$V_{ijk} = \gamma_i + c_{ij} + \alpha_0 \times H_{ijk}{}^{\alpha_1+\gamma_i+c_{ij}} \times G_{ijk}{}^{\alpha_2+\gamma_i+c_{ij}} + \varepsilon_{ijk} \tag{5.1}$$

where V_{ijk} is the total volume for plot j of site i in year k, γ_i and c_{ij} are the random effects of for site i and for plot j of site i, respectively. Both γ_i and c_{ij} are independent of ε_{ijk} and are normally distributed with mean zero and variances $\sigma^2{}_s$ and $\sigma^2{}_p$, respectively [i.e.,γ_i $N(0, \sigma^2{}_s)$ and c_{ij} $N(0,\sigma^2{}_p)$].

The random-effects parameters were added sequentially to the fixed-effects parameters until convergence was achieved. The volume-height relationship typically exhibits a curvilinear form with heteroscedastic variance of the individual model errors (ε_{ijk}) (Haworth and Vincent, 1982; McRoberts and Westfall, 2016). Therefore, the mean of the response variable was modelled with a nonlinear power variance function with three parameters as:

$$V(\varepsilon_{ijk}) = \omega^2\left(\delta_0 + \left|\widehat{\mathrm{V}}_{ijk}\right|^{\delta_1}\right)^2 \tag{5.2}$$

The temporal and spatial dependencies among the observations were also modelled using a first order autoregressive covariance structure (see estimator 3.3). The use of predicted values of top height and basal area as explanatory variables in the volume models (Eqs. (5) and (5.1)) has the tendency of propagation of error which could inflate the variances of the estimated model parameters (McRoberts and Westfall, 2016). To check this, non-parametric bootstrap resampling (with replacement) was used to examine the uncertainty associated with the estimated model parameters (Eq. (5.1)). We drew 1000 bootstrapped samples from a population made up of the original sample data. For each bootstrapped replicate, the model parameters were determined and the means of each parameter for the 1000 samples were estimated. The sampling distribution of the estimated model parameters were

Table 5
Parameter estimates of species-specific volume ($m^3\ ha^{-1}$) yield functions (Eq. (5.1)). Values in parenthesis are estimated standard errors.

		Scots pine	Norway spruce	Lodgepole pine	Larch
Class	Parameter	Estimates			
Fixed effects	$\widehat{\alpha}_0$	0.8013 (0.0117)	0.7498 (0.0196)	0.8783 (0.0379)	1.4005 (0.0749)
	$\widehat{\alpha}_1$	1.0208 (0.0116)	1.1781 (0.0215)	0.9251 (0.0243)	1.6359 (0.0309)
	$\widehat{\alpha}_2$	0.8062 (0.0083)	0.7169 (0.0149)	0.8839 (0.018)	0.1558 (0.0127)
Plot-level random effects (c_{ij})	$\widehat{var}(\widehat{\alpha}_0)$	0.0012		1.02×10^{-07}	8.28×10^{-10}
	$\widehat{var}(\widehat{\alpha}_1)$				
	$\widehat{var}(\widehat{\alpha}_2)$		8.17×10^{-05}		
Site-level random effects (γ_i)	$\widehat{var}(\widehat{\alpha}_0)$	0.0023		0.002	0.0172
	$\widehat{var}(\widehat{\alpha}_1)$				
	$\widehat{var}(\widehat{\alpha}_2)$		5.52×10^{-04}		
Residual Variance $V(\varepsilon_{ijk})$	$\widehat{\omega}^2$	1.1546	17.795	2.232	1.883
	$\widehat{\delta}_1$	0.4784	0.2951	0.4749	4.0237
	$\widehat{\delta}_0$		1.59×10^{-07}	1.34×10^{-04}	1.86×10^{-11}
Autocorrelation	$\widehat{\rho}$	0.104	0.009	0.002	0.2807
	$RMSE$	24.27	36.98	22.44	54.18
Fit statistics	$RMSE_{rel}$, %	11.74	11.75	10.96	17.72
	MD	−0.1584	−0.1629	−0.1283	1.1717
	MD_{rel}, %	−0.0765	−0.0517	−0.0626	0.3834
n		4405	1789	725	453

visualized graphically using histograms, and the confidence interval (the lower and upper limits of the bootstrapped statistic using the percentile method and 95% confidence level) was considered as an approximate variance in the estimated model parameters. The quality of the volume yield model was assessed graphically by the distribution of residuals over plot-level total volume predictions ($\widehat{V}_{ijk}$), total age and SI, and numerically by using the accuracy estimators in Eqs. (4.1)–(4.4) (by changing the response variable from basal area to volume). The accuracy of Eq. (5.1) was also compared with alternative models where basal area was excluded as a covariate of top height.

2.5. Relationship between yield capacity and site index

To compute the plot-level mean annual total volume increments (MAI) at each measurement occasion, the predicted volume yields were divided by their corresponding total ages. On each plot and site, the MAI at the time of culmination (or late culmination) was considered as the maximum MAI (MAI_{max}), and the plot-level MAI_{max} values were averaged to estimate the site-level MAI_{max}. The MAI_{max} was then used as a proxy for yield capacity because it is related to the potential volume yield attainable on a specific site (Elfving and Nyström, 1996). To determine the functional relationship between SI (H_{100} or H_{50}) and MAI_{max}, two models with MAI_{max} as the response variable and SI as a predictor were fitted and compared. Model one (Eq. (6.1)) is an exponential function fitted in R statistical environment through the generalised nonlinear least squares ("gnls") function.

$$MAI_{max} = \alpha_0 \times exp^{(\alpha_1 \times SI)} + \varepsilon \tag{6.1}$$

For model two (Eq. (6.2)), the relation between MAI_{max} and SI was fitted by a second-degree polynomial function. This model was identical to the earlier yield capacity functions developed by Hägglund and Lundmark (1982):

$$MAI_{max} = \alpha_0 + \alpha_1 \times SI + \alpha_2 \times SI^2 + \varepsilon \tag{6.2}$$

The accuracy and precision of the fitted yield capacity functions were evaluated using the estimators (Eqs. (4.1) and (4.2)), by changing the response variable from basal area to MAI_{max}. For each species, the yield capacity estimates from the best model in this study was compared to the earlier estimates from Hägglund and Lundmark (1982). For spruce, additional comparisons were made with Elfving and Nyström (1996) in central-northern Sweden.

3. Results

3.1. Regression functions for basal area growth prediction

Predicting basal area yield at the end of the growth period as a function of current basal area, initial stand density, site index and total age through nonlinear mixed-effects time series models produced acceptable estimates for the studied tree species. All tested functions converged and model accuracies are presented in Table 3. The largest deviations in relative terms were found for F03 (Levakovic) models, especially for Larch where the error was about 18% of the observed mean. The function F01 (Pienaar et al., 1990) was most suitable for Scots pine and Norway spruce, whereas those of Lodgepole pine and Larch were adequately modelled by the Bertalanffy-Richards function (F04). For these functions (F01 and F04), the relative errors around basal growth predictions were within 2–6%, though they all underestimated the average basal area growth. Nevertheless, in absolute terms, the underestimation of the models was <1% for all species.

For Scots pine, Norway spruce and Lodgepole pine, the estimated fixed-effects parameters were statistically significant at 1% error margin. However, the parameters of age $(\widehat{\alpha}_0)$ and site index $(\widehat{\alpha}_2)$ for Larch were not significant ($p > 0.05$) as the estimated standard errors had similar values as the coefficients (Table 4).

As expected, the mixed modelling approach produced variance estimates that were larger between sites than between plots within sites. For Norway and Scots pine, the random slopes of age, site index and initial density enhanced efficient model calibration. For Larch, random age was relevant, whereas site index improved the calibration of random variances of Lodgepole pine. The within-group residual error variances were adequately modelled by the two-parameter power function for Norway spruce and Scots pine, while the three-parameter was suitable for Lodgepole pine and Larch. The estimated first order temporal autocorrelations were also small (0–0.294) for all species (Table 4). The model residuals exhibited constant variance that suggests unbiased predictions of basal area over total age and site index (Fig. 4).

The development of total basal area production according to SI was visualized in Fig. 5. The forms of the curves were statistically and practically acceptable on the observed data for all species. As expected, higher site indices reached larger basal area values quicker than lower site indices for all tree species. To explore the between-site variations in basal area yield levels, an increasing relation was observed between total basal area production and mean top height (Fig. 5).

$\widehat{\rho}$ is the estimated first order temporal autocorrelation; n is the number of observations used for model fitting; $\widehat{var}$ is the estimated variance; $\widehat{cov}$ is the estimated covariance of parameters.

3.2. Regression functions for total volume-top height relationships

To characterize total volume yield and the variations across sites, allometric expressions of volume yield and mean top height were adjusted with information on total basal area production. Addition of basal area improved the volume-height relationships where the relative

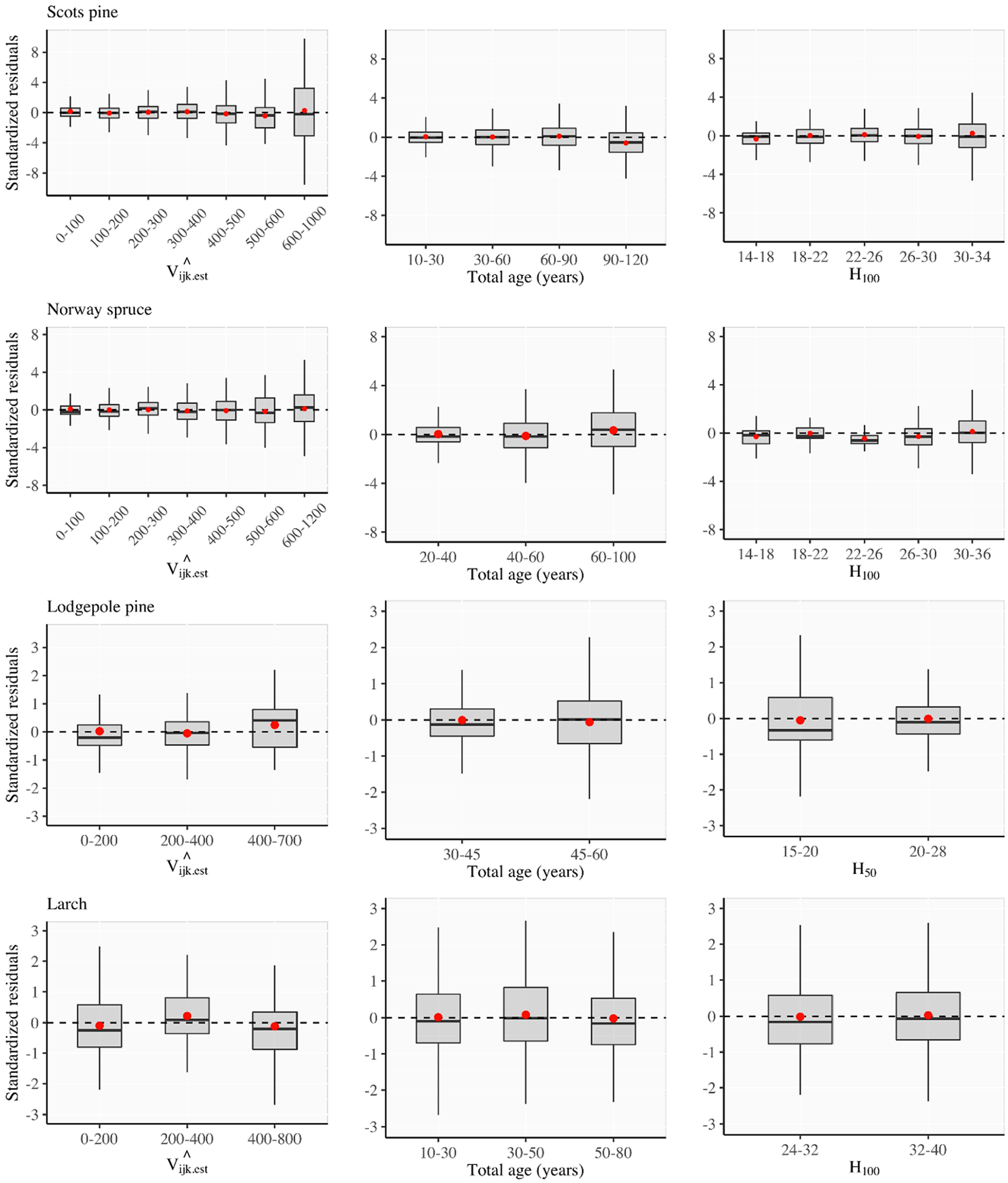


Fig. 7. Standardized (Pearson) residuals versus predicted total volume ($\widehat{V}_{ijk}$, m^3 ha^{-1}), age and site index (m). Site index is expressed as height at 100 years (H_{100}) for Scots pine, Norway spruce and Larch, and at 50 years (H_{50}) for Lodgepole pine. The red dots are calculated residual means, and horizontal dashed lines denote the expected mean residual ([E(ε) = 0]). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

model errors were reduced on the average by a factor of 1.5 for all species (Fig. 6).

Table 5 presents the regression summary of the species-specific volume yield equations. The relative errors (RMSE$_{rel,}$ %) of the species-specific volume yield models were within 10–18% of the mean values for all species (Table 5). For Larch, the model overestimated the volume yield by 0.4%, whereas those Scots pine, Norway spruce and Lodgepole pine were underestimated on the average by 0.2%. The calibration of plot- and site-level random components adequately captured the variances in volume yields, and the within-group error

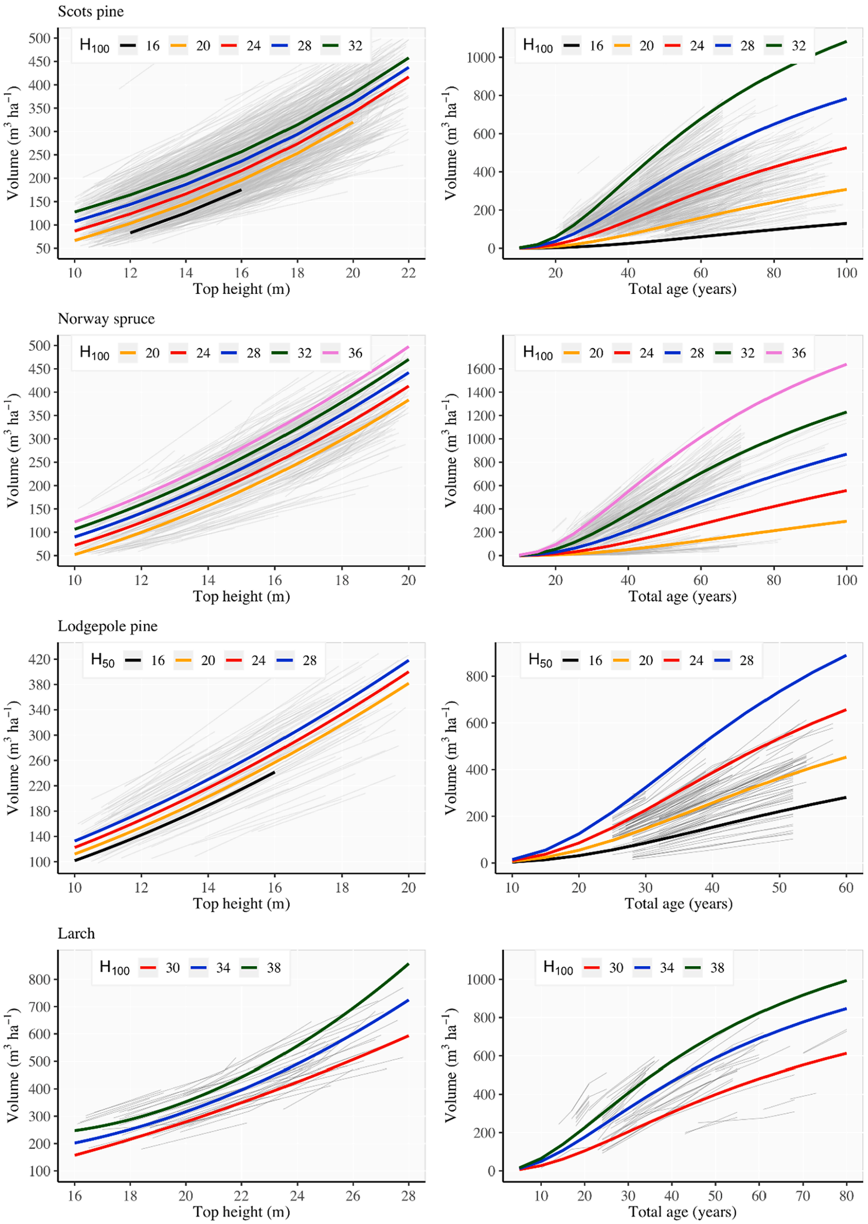


Fig. 8. Left panel: total volume yield levels (volume-height relationship); Right panel: examples of the development of total volume production over age with a given site index.

variances were efficiently modelled by the power functions. Evaluation of the models' residuals showed variance homogeneity over predicted volume yields, total age and site index (Fig. 7).

$\hat{\rho}$ is the estimated first order temporal autocorrelation; n is the number of observations used for model fitting; $\widehat{var}$ is the estimated variance.

In the volume models, predicted mean top height and basal area were used as predictors, and there is a tendency of error propagation. Un-

Table 6
Parameter estimates and fit-statistics of functions relating yield capacity to site index for different tree species. "SE" is estimated standard error.

Species	Parameter	Estimate	SE	p-value	*RMSE (rel, %)*	R^2
Scots pine	$\widehat{\alpha}_0$	0.4613	0.0511	<0.0001	0.9757	0.809
	$\widehat{\alpha}_1$	0.1006	0.0041	<0.0001	(16.73)	
Norway spruce	$\widehat{\alpha}_0$	0.5558	0.0889	0.0037	1.047	0.904
	$\widehat{\alpha}_1$	0.0929	0.0049	<0.0001	(11.14)	
Lodgepole pine	$\widehat{\alpha}_0$	0.8291	0.0729	<0.0001	0.436	0.956
	$\widehat{\alpha}_1$	0.1038	0.0039	<0.0001	(5.52)	
Larch	$\widehat{\alpha}_0$	0.9583	0.1547	<0.0001	1.164	0.876
	$\widehat{\alpha}_1$	0.0695	0.0044	<0.0001	(10.82)	

certainty analyses of the parameter estimates were conducted by bootstrap resampling. The estimated model parameters occurred within the interval from the 2.5th to the 97.5th confidence limits, indicating no apparent systematic effects of error propagation in all species, except for Larch, which showed large uncertainty in the estimated model parameters ($\widehat{\alpha}_1$ and $\widehat{\alpha}_2$) (Fig. A.1, appendix). This might be due to the combined dataset for the two Larch species for modelling since we had very few observations for either species. However, the two species have different growth rates (Siberian Larch has slower growth rate than European Larch) which could introduce additional uncertainty. Despite this limitation, a larger part of the sampling distribution of estimated parameters were within the acceptable error bounds (Fig. A.1, appendix).

The volume production at a given top height is shown in Fig. 8. As expected, the volume yield levels showed increasing relationships, suggesting site-dependent variations in volume-height trajectories (Fig. 8, left panel). Thus, larger volume yields are attained at higher SIs (Fig. 8) and the culmination in mean and current annual volume increments is earlier than for lower SIs (Fig. A.2, appendix). The observed volume-height trajectories follow the same order as the basal area yield levels (Fig. 5) for all species. This offers support to the assertion that given the same mean top height, the volume yield levels would be different between sites if the basal area production levels are also different.

3.3. *Functional relationship between site index and yield capacity*

The relationship between yield capacity and SI was best fitted by the exponential regression function (Eq. (6.1)) for the studied tree species. Information on model parameter estimates and goodness-of-fit statistics are given in Table 6. Generally, SI was significant in predicting yield capacity and the form of the curves described by the models was statistically and practically acceptable (Fig. 9). The explained variation (adjusted R^2) ranged from 80 to 96% and the relative model errors ranged from 6 to 17%, with Scots pine and Norway spruce showing the largest variations around the observed mean.

In Fig. 10, the yield capacities predicted from the present study were compared to earlier estimates from Hägglund and Lundmark (1982). For Scots and Norway spruce, significant differences were observed at both lower and higher SIs. At lower SIs, the estimated yield capacities from the current study were smaller than the predictions by Hägglund and Lundmark (1982) and vice versa at higher SIs. For Norway spruce, predicted yield capacity was similar to Elfving and Nyström (1996) in central-northern Sweden. For Lodgepole pine, the estimates were similar at lower SI, but differed markedly at higher SI classes between the functions.

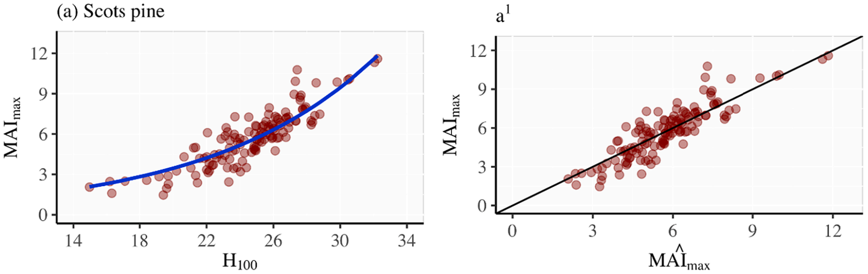
4. Discussion

The purpose of this study was to develop functional relationships between yield capacity and site index (SI) for the major tree species in Swedish boreal forests. The newly developed yield capacity functions were also compared with earlier functions made for the studied species. This was approached by utilizing measured tree growth data from long-term experiments (LTEs). The observations covered almost the entire rotation periods and a wide range of site fertility gradients that represent managed forests in Sweden. Thus, in this study, the LTE data were assumed as valid growth references for yield capacity estimation.

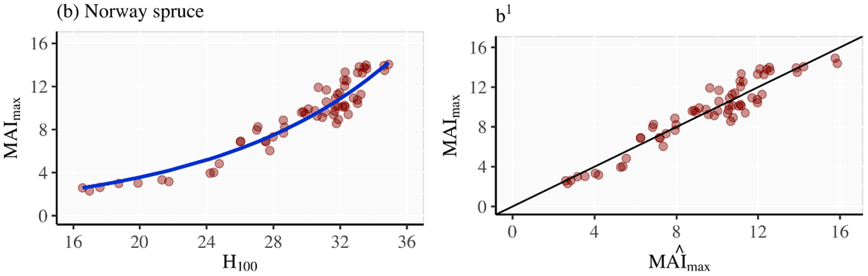
Height and basal area are key variables in the empirical growth models used in Sweden, for example in the Heureka planning system. While height is the dependent variable during the establishment stage (mean height<7 m), basal area drives the growth models for established stands (Elfving, 2010b; Wikström et al., 2011). As such, their estimations are crucial for evaluation of forest yield capacity (Elfving and Nyström, 1996; Burkhart and Tomé, 2012). Height growth models were not developed in the current study, but instead, the observed top heights were used for SI estimation with existing height development functions, which when combined with initial stand density, produced accurate and reliable estimates of basal area production over time (Table 4, Fig. 4). This follows earlier reports on the influence of initial spacing and site quality on the asymptotic basal area growth of even-aged stands (Pienaar and Shiver, 1986; Pettersson, 1992; Elfving, 2010a; Hall et al., 2019). Expressions for basal area often include mean top height and or mean height (Elfving and Nyström, 1996; Hall et al., 2019) but such expressions were avoided in our basal area development functions because top height was later used as a predictor in the total volume estimations. The basal area functions developed in this study show lower residual variations than the current stand-level basal area growth models for Scots pine and Norway spruce in the Heureka system (*RMSE* m^2 ha^{-1}: 1.03 vs. 2.32) but, the conditions for the estimations differ. In the Heureka case, basal area growth is estimated at 5-year periods (Elfving, 2010b; Fahlvik et al., 2014), whereas in our study, the development of total basal area production (yield) is modelled.

The observed increasing relation between total basal area production and mean top height describe the concept of carrying capacity in forest stands (Fig. 5). Usually, "natural basal area" is used to describe the maximum basal area production for un-thinned stands (e.g. Assmann, 1961; Hasenauer et al., 1994), however, we modelled the total basal area production (including dead, ingrowth trees etc.) for each site and the observations spanned across plots with many measurements before and after first thinnings. In addition, the thinning interventions were mainly of thinning-from-below. Thus, our basal area estimates can potentially describe the productivity differences in relation to site index. This was supported by Eq. (5) and Figs. 6 and 8. Errors in the volume-height relations were significantly reduced by a factor of 1.5 units when including basal area (Fig. 6) and the yield level trajectory was higher for high site index (Fig. 8). A similar study by Ung and Ouellet (1991) found an improved estimation of total volume (11–12% error) from both top height and basal area per hectare for black spruce (*Picea mariana* (Mill.)) stands in the Boreal Forest Region of Lebel-sur-

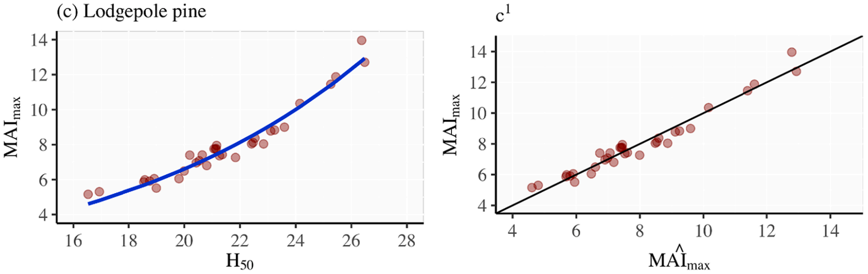
(a) Scots pine



(b) Norway spruce



(c) Lodgepole pine



(d) Larch

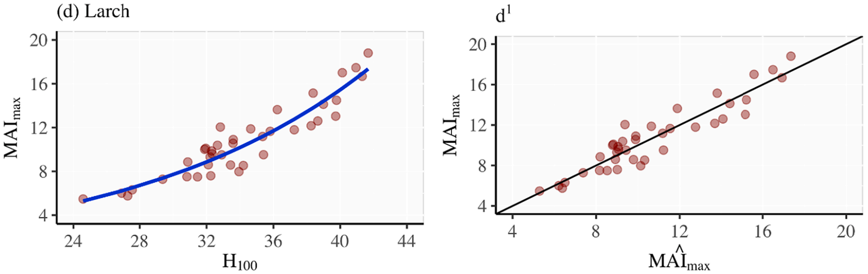


Fig. 9. Relationship between yield capacity (MAI_{max}, $m^3\ ha^{-1}\ yr^{-1}$) and site index (expressed as height (m) at 100 years (H_{100}) for Scots pine, Norway spruce and Larch, and at 50 years (H_{50}) for Lodgepole pine). Right panels show 1:1 relationship between the observed (obtained from measured total volume yield and age) and predicted yield capacity.

Quévillon, Canada. In other studies of growth-density relationships, Allen et al. (2020) also found that gross volume increment increased with increasing basal area for Norway spruce plantations in Norway. Our results follow closely Assmann's yield level investigation of Norway spruce, where differences in stands' common yield levels (total yield at a certain top height) and special yield levels (reaching this certain top height in a particular age) were attributed to differences in basal area levels given the same initial spacing and treatment (Assmann 1955). Schmidt (1973) also found that yield level variations in Scots pine is not only site index dependent, but it is also dependent on the basal area development for a given age and top height. Generally, basal area differences at a given top height and age result from the variations of number of stems per hectare and the quadratic mean diameter at breast height (QMD). At the same QMD but differing stand density, different

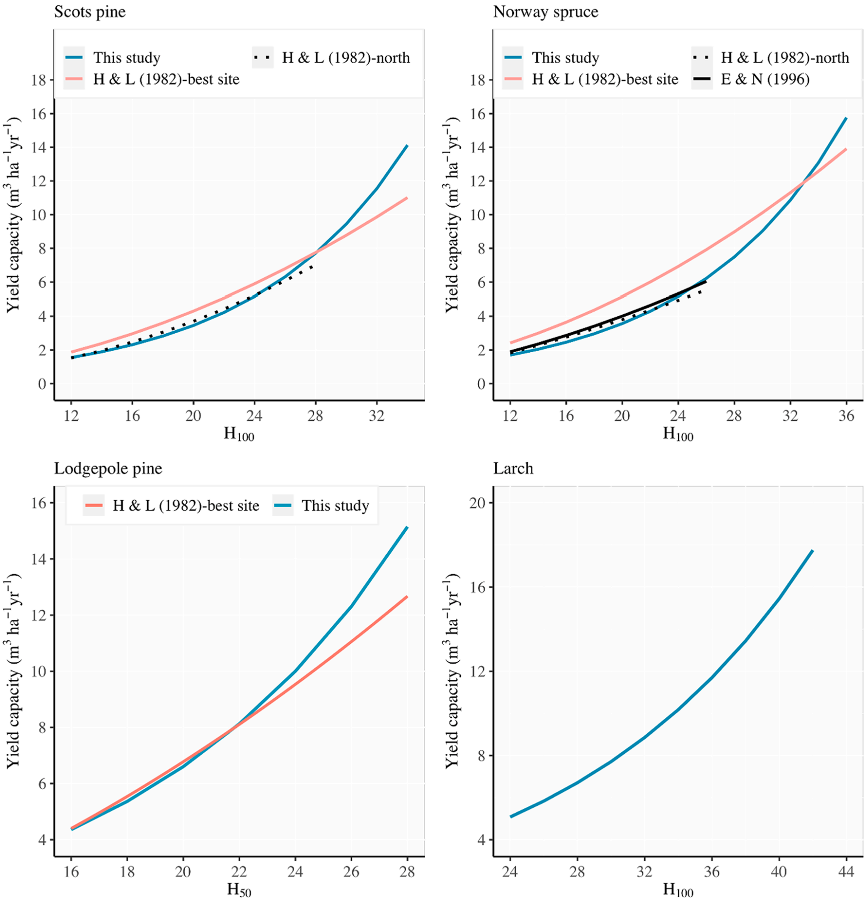


Fig. 10. Predicted mean yield capacity from current (denoted as "This study") and previous studies (Hägglund and Lundmark (1982) denoted as [H&L (1982); Elfving and Nyström (1996) denoted as E&N (1996)]. H&L (1982)-best site refers to lingonberry-sites for pine stands (below 200 m above sea level) and blueberry-sites for spruce over the whole country. H&L (1982)-north refers to pines (above 200 m above sea level) and spruces (poor sites) in northern Sweden. E&N (1996) refers to spruce sites in central-northern Sweden. Note that for Larch no previous model is available for comparison. Extrapolations are made beyond the observed SI ranges (see Table 1).

yield levels are observed using the relative space system. Different QMDs at the same stem number also allude to differences in taper and yield levels. For example, Hasenauer et al, (1994) found that differences in volume yield levels of Loblolly pine across the physiographic regions in southern United States were largely explained by differences in maximum basal area development, which was in turn supported by the sites' potential number of stems per unit area at a given top height. This suggests that, the Eichhorn's law is exclusively rapid for total volume estimation, but augmenting the volume-top height relationship with basal area guarantees high accuracy in yield level estimation (Bontemps and Bouriaud, 2014). Other reasons such as changes in stem form may have effects on the volume growth, but this was assumed to have very little influence in the present study.

Yield capacity was positively correlated with SI for all studied tree species and the exponential model adequately described the functional forms of the relationship (Fig. 9 and Table 6). The developed yield capacity functions from the current study were compared to earlier functions by Hägglund and Lundmark (1982) and significant differences were observed (Fig. 10). Two possible explanations pertaining to (1) the data origin and method of estimation and (2) environmental changes could be given for the observed differences.

The material (data) used for constructing SI functions differed in this study and that of Hägglund and Lundmark (1982). In the latter, the calibration data were from felled-sectioned trees (in temporary plots) growing in the 1940′s with an average age at breast height of about 70 years. Thus, the data mostly represented tree development conditions at the first half of the 20th century. The site indices were estimated by functions constructed from static- and fixed-base age equation of Chapman-Richard (Hägglund, 1972, 1973, 1974). However, in the current study, the SI functions (Elfving and Kiviste, 1997; Elfving, 2009; Liziniewicz et al., 2016) used were derived from difference equations that were parameterised with repeated sample plot data from homogeneous stands (even-aged monocultures) in the LTEs, and the data mainly reflected growth in the second half of the 20th century up to 1990. The difference equations have shown better performance in SI estimation for several studies than their static counterparts (e.g. Cieszewski and Bailey, 2000; Nord-Larsen et al., 2009). Currently, the new SI functions demonstrate a change in the growth form and they adequately describe the growing conditions of Swedish forests. For example, in Scots pine stands; the new SI functions are indicating about 2 m increase in the height growth compared to older SI functions (Elfving and Kiviste, 1997). Thus, there is a potential bias if yield capacity is based on older SI functions. In a similar study, Elfving and Nyström (1996) observed that the yield capacity for new generation of Norway spruce plantations in northern Sweden is underestimated (by ~35%) if the site quality estimation is based on height and age in old-growth stands.

On the methods of yield capacity estimation, existing growth functions were used to simulate the yield capacities from NFI data collected using temporary sample plots in the early 1980s (Hägglund, 1981; Hägglund and Lundmark, 1982; Ekö, 1985). The Swedish NFI is a statistically distributed sample and so therefore covers a wider amplitude of stand variation (Fridman et al., 2014). Thus, there is the tendency of including stands that are more heterogeneous as well as sites that naturally do not represent the species' distribution. This could potentially affect the growth trajectories during simulation. In addition, with data from the NFI, information on stand history such as provenances is generally unknown and silvicultural treatments (e.g. fertilisation) are mostly uncertain. For instance, in older stands that are naturally regenerated, the site-specific maximum height is mostly affected by early suppression and it would be a misrepresentation when top height is used as an indicator for site quality assessment in such stands (Elfving and Nyström, 1996; Elfving and Kiviste, 1997). Thus, it is not clear whether the NFI data adequately described the growth trajectories in Hägglund and Lundmark (1982). In contrast, this study made use of data from the LTEs where the total volume yield has accumulated and tree growth trajectories can be reliably estimated. It is important to note that Hägglund and Lundmark (1982) stratified their yield capacity functions based on latitude, altitude and forest type described by vegetation classes. However, comparisons were made with the functions that represent the whole country as well as those that describe higher site quality. For Norway spruce and Scots pine, the larger difference (Fig. 10) in the estimated yield capacities is difficult to explain. For Norway spruce, the difference might be due to overestimation of basal area at a given top height (Table S1, appendix). For spruce plantations in central-northern Sweden (62–65°N), for example, at 10 m top height, our function gives on the average the same basal area levels as that of Elfving and Nyström (1996), but the estimates according to (Hägglund, 1981) was about 60% higher than observed. Such higher initial levels of basal area could largely influence the relation between yield capacity and SI as shown by Elfving and Nyström (1996). Other reasons may be attributable to selection effects and low stocking. For instance, there were fewer observations (LTEs) in the lower SIs of Norway spruce at northern Sweden. In addition, these plot had lower levels of stocking, suggesting many small trees in the diameter distribution, which eventually leads to a lower stem-wood volume production (e.g. Nilsson et al., 2012). Nevertheless, our yield capacity estimates for spruce in northern Sweden was on the average similar to Hägglund and Lundmark (1982), when comparisons are made with the northern-specific function. For Lodgepole pine, the estimated yield capacities were similar on lower SIs, but differed markedly on higher SIs (Fig. 10).

Other reasons such as altered site properties by changes in environmental conditions may have also contributed to the observed deviations in the two yield capacity functions. For boreal forests of northern Europe, recent years' growing season temperature and precipitation, atmospheric CO_2 fertilization and nitrogen deposition have improved tree growth and current stands seem to sustain higher stand densities (e.g. Sharma et al., 2012; Kauppi et al., 2014; Henttonen et al., 2017; Appiah Mensah et al., 2021; Mäkinen et al., 2021). Similarly, effects from improved silviculture and changes in forest management have also contributed to the increased tree growth (Elfving and Tegnhammar, 1996).

Another important comment to highlight is the validity of the total basal area development, stem volume production and yield capacity functions developed in the current study. We used all tree growth observations during the model fitting to provide robust and confident parameter estimation. To validate the models, independent dataset from LTEs in northern and southern Sweden were used. Higher accuracies similar to levels obtained during model calibration (Tables 3 and 5) were observed for the test data (Fig. A.3, appendix).

5. Conclusion

This study highlights the unique contribution of LTEs for evaluating forest site productivity of major forest tree species in boreal Sweden. These observational plots have the capacity to support studies on the health and climate change mitigation potential of boreal forests in northern Europe. The developed functions for total basal area development and total volume production indicated statistical and practical acceptability on both calibration and validation datasets. The total basal area production as a proxy for stands' carrying capacity explained largely the site variations in total volume yield levels. The developed yield capacity functions adequately described stand productivities. Compared with Hägglund and Lundmark (1982), we found differences in the estimated yield capacities on both lower and higher site indices, particularly for the two dominant coniferous species, Scots pine and Norway spruce. For Lodgepole pine, the old functions generally underestimated the yield capacities on higher site indices, but fairly agreed with our estimates on lower site indices. The yield capacity functions from this study describe well the site productivity in the current climate, and are suitable for growth and yield assessment of even-aged (monocultures) Swedish forests. It was not possible to compare the tree species' productions in this study given that the data material for each species was from different locations. However, the functions can later be used for selection and comparison of tree species' production in similar site and management regimes in Sweden.

CRediT authorship contribution statement

Alex Appiah Mensah: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Emma Holmström:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Kenneth Nyström:** Methodology, Writing – review & editing. **Urban Nilsson:** Conceptualization, Methodology, Data curation, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

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Appendix

Uncertainty in estimated volume model parameters

The uncertainty around the volume parameter estimates using predicted mean top height and basal area as explanatory variables was investigated by bootstrap resampling. We drew 1000 bootstrapped samples from a population made up of the original sample data. For each bootstrapped replicate, the model parameters were determined and the means of each parameter for the 1000 samples were estimated. Sampling distribution of the estimated model parameters were visualized graphically using histograms, and the confidence interval (2.5th and 97.5th limits of the bootstrapped statistic using the percentile method) was considered as approximate variance in the estimated model parameters. No systematic propagation of errors was observed (Fig. A.1).

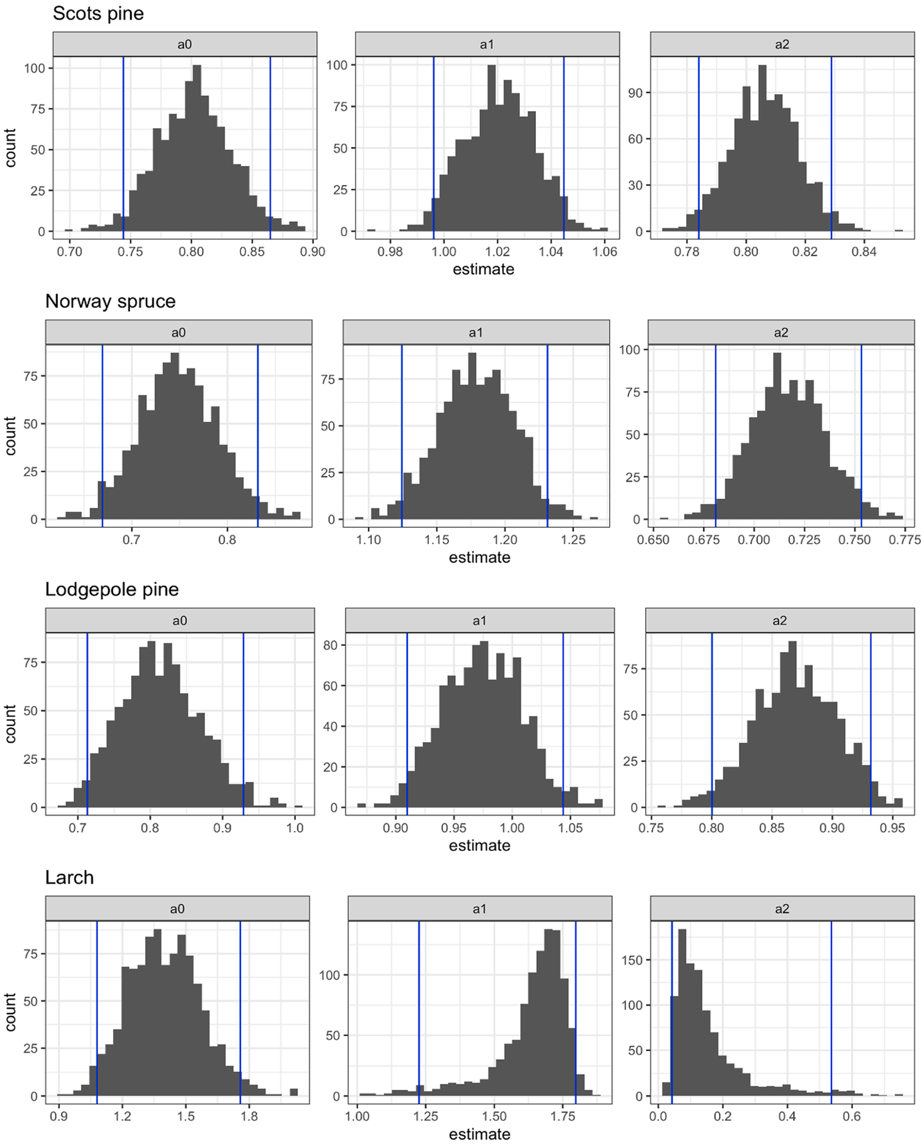

Fig. A.1. Sampling distribution of estimated volume parameters from 1000 bootstrap resamples. The vertical lines show the 2.5th and 97.5th intervals around the bootstrap estimate at 95% confidence level. See Eq. (5) for the definition of model parameters.

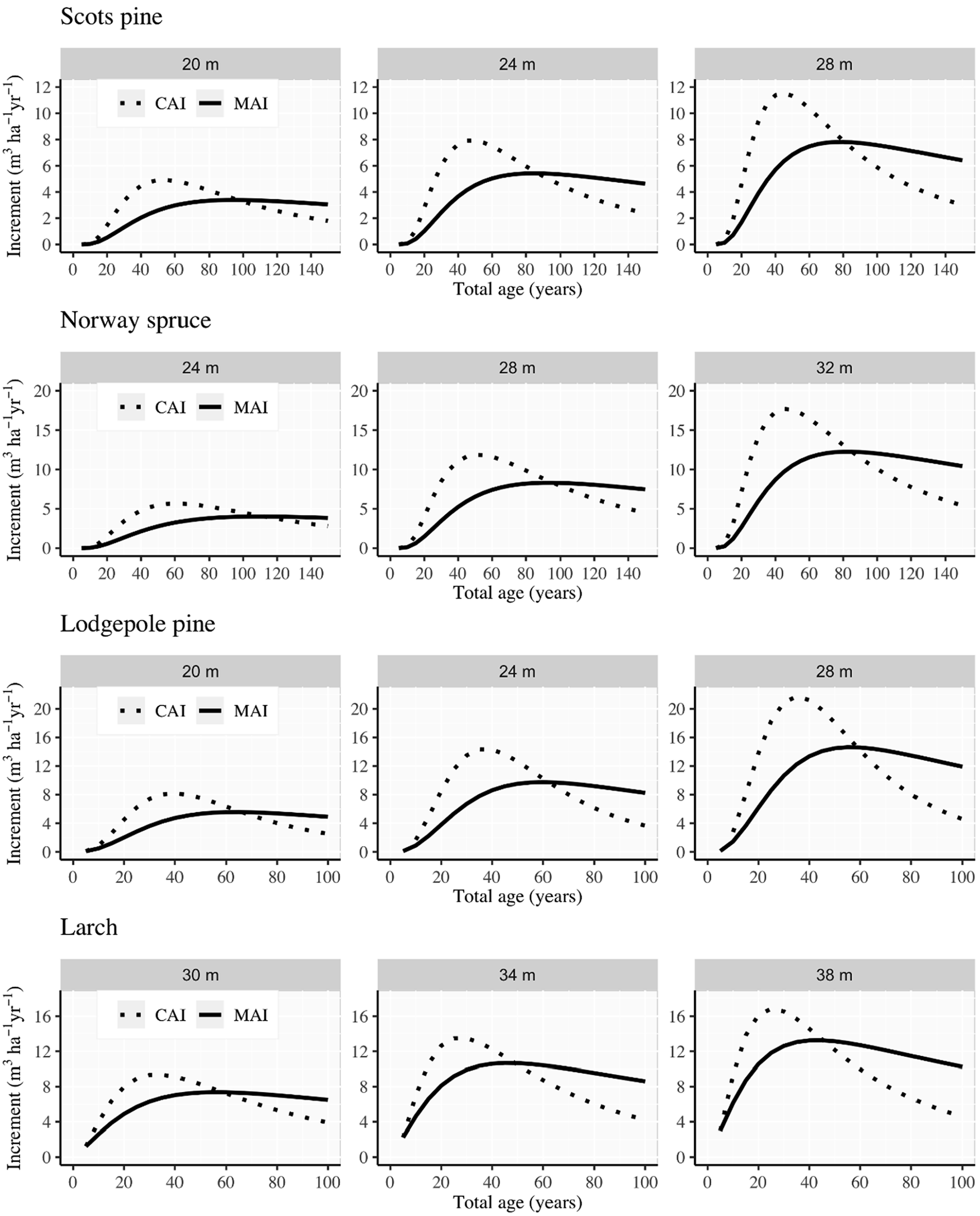

Fig. A.2. Predicted mean (MAI) and current (CAI) annual volume increments for different site indices and species according to the basal area and volume functions developed in this study.

Table S1

Observed and predicted mean basal area ($m^2\ ha^{-1}$) in different classes of top height. Comparison with earlier studies for Norway spruce at central-northern Sweden (62–65°N).

	Top height (m)					
Data/function	≤8.4 Mean (SD)	8.5–9.4 Mean (SD)	9.5–10.4 Mean (SD)	10.5–11.4 Mean (SD)	≥11.5 Mean (SD)	Total Mean (SD)
G_{ijk}	4.5 (2.9)	10.9 (3.2)	15.8 (6.8)	18.9 (3.5)	39.2 (23.9)	22.6 (10.1)
$\hat{G}_{ijk}$	3.6 (3.0)	10.5 (3.4)	14.4 (7.3)	18.6 (7.3)	39.1 (26.4)	22.1 (11.3)
EN96	10.9 (3.5)	12.9 (4.8)	12.6 (3.5)	15.3 (6.9)	17.9 (10.7)	14.2 (6.7)
H81	14.5 (0.8)	16.5 (1.0)	19.4 (0.9)	22.6 (1.0)	26.8 (2.7)	20.5 (3.9)
n	25	3	6	6	35	75

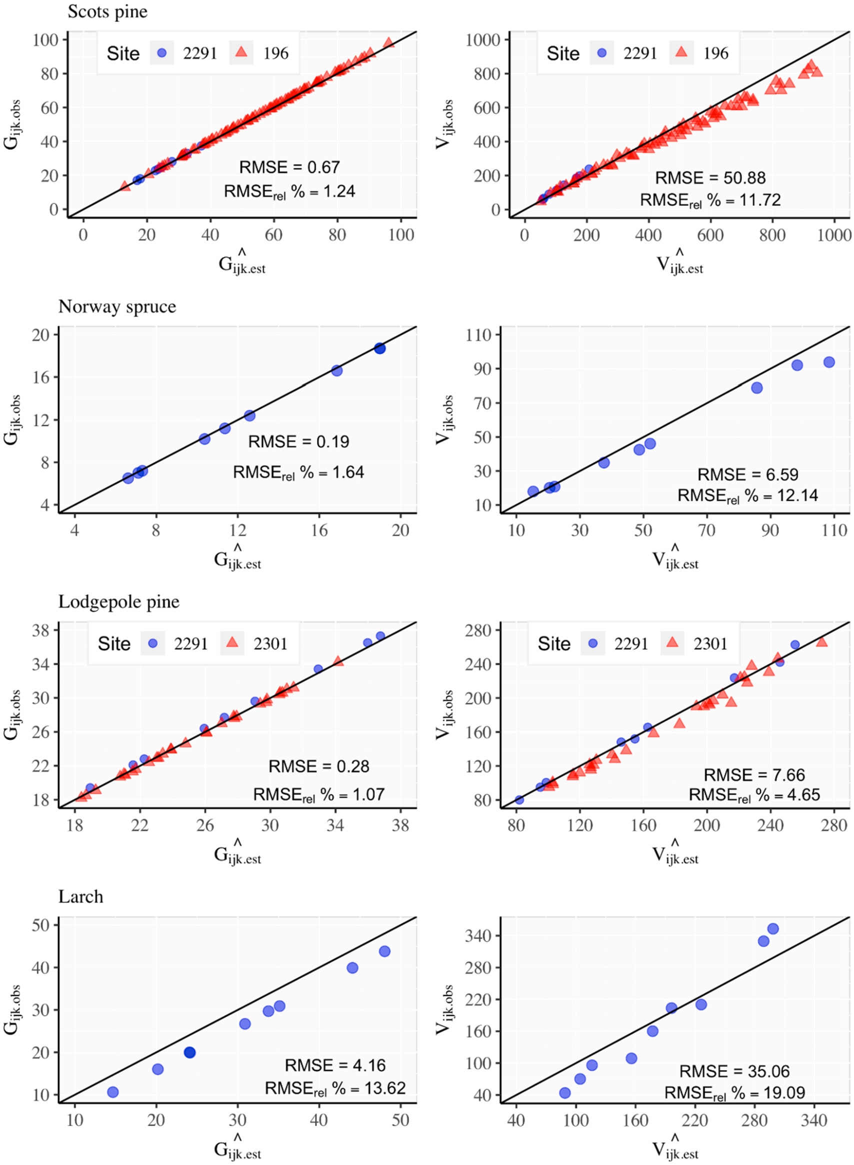

Fig. A.3. Validation of the species-specific basal area and volume (m^3 ha^{-1}) functions (Tables 4 and 5) on independent data from three sites in Sweden (northern Sweden- latitude 64°N, southern Sweden- latitude 58°N). $G_{ijk.obs}$ is observed total basal area (m^2 ha^{-1}); $\widehat{G}_{ijk.est}$ is predicted total basal area (m^2 ha^{-1}); $V_{ijk.obs}$ is observed total volume (m^3 ha^{-1}); $\widehat{V}_{ijk.est}$ is predicted total volume (m^3 ha^{-1}).

G_{ijk} is observed basal area; $\widehat{G}_{ijk}$ is basal area according to functions (F01 and F04) in the present study (Tables 2 and 4); H81 is basal area according to Hägglund (1981); EN96 is basal area according to Elfving and Nyström (1996); ***n*** is number of observations; SD is standard deviation. Note that the conditions for basal area estimations differed among the functions.

Model validation on independent data

The basal area and volume functions developed in the present study (Tables 2, 4 and 5) were validated using independent dataset from LTE sites in northern and southern Sweden. The northern sites were located at latitude 64°N and an altitudinal range of 250–300 m above sea level (a.s.l). Site 2291 is a tree species trial established in 1992 involving spruce, pine, Lodgepole pine, larch and other exotic species. So far, three inventories have been conducted at 5-year intervals: 2009 (at total age of 19 years), 2014 (at total age of 23 years) and 2019 (at total age of 29 years). The SIs for the tree species were: spruce, 30 m at 100 years; scots pine, 29 m at 100 years; Lodgepole pine, 26 m at 50 years and larch, 33 m at 100 years. Site 2301 is a spacing trial of Lodgepole pine established in the year 1982. First measurement was done in 2011 at 31 years old and the last measurement was in the year 2020 at a total age of 40 years. The SI at latest remeasurement is 20 m at 50 years. The southern site (196) is a Scots pine thinning and yield experiment located at latitude 58°N and an altitude of 120 m (a.s.l). The experiments were established at 1931 and first measurements conducted within the same year when the stands were 26 years old. The measurement period is on average 5 years interval and the last measurement was done in 2008 at 102 years. The SI is 28 m at 100 years.

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IV

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Using heterogeneity indices to adjust basal area – Leaf area index relationship in managed coniferous stands

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ABSTRACT

The structure of contemporary managed forests is complex and deviates from experimental forests which are usually even-aged monocultures and single-storied. To apply theoretical growth and yield functions on managed forests, adjustments are required, especially for leaf area index (LAI) which is a key biophysical variable in process-based growth models. To asses this, the performance of canopy LAI in modelling the basal area (BA) of managed boreal forests dominated by Norway spruce (*Picea abies* (L). Karst) and Scots pine (*Pinus sylvestris* L.) was investigated by heterogeneity analysis. The study was based on the assumption that canopy LAI and BA are strongly related and are vital for estimating stand productivity and growth. Managed forests were represented by field data from the 2016 and 2017 Swedish National Forest Inventory (NFI) campaigns. Species-specific LAI conversion parameters were applied on the general plant area index (PAI) values from hemispheric fish-eye photos taken from the permanent and temporary NFI sample plots. The heterogeneity analysis was studied in two parts by: (a) ground-based stand structural heterogeneity (SSH) described by species composition, coefficient of tree diameter variation, tree social status and height-diameter ratio, and (b) spectral heterogeneity (SPH) by vegetation and textural indices developed from Sentinel-2. Species-specific final (with heterogeneity metrics) and base (without heterogeneity metrics) models were fitted for BA-LAI and BA-PAI relationships by nonlinear least squares and generalised additive regression functions, respectively. The performance of models was assessed by the root-mean-squared error (RMSE, $m^2\ ha^{-1}$) and the relative root-mean-squared error (RelRMSE, %) metrics. For both species, BA-LAI final models (FMs) accounting for heterogeneity resulted in larger explained variance than the base models (BMs). Compared with the BMs, FMs with SSH reduced the variance by 55% in Norway spruce (RMSE = 3.33, RelRMSE = 15.39) and 43% in Scots pine (RMSE = 3.70, RelRMSE = 17.38). The fit between BA-LAI with SPH also showed an improvement for Norway spruce (RMSE = 5.56) and Scots pine (RMSE = 5.66) over the BMs, suggesting the potential use of Sentinel-2 in future growth models. The results of the study suggest that in growth models when extrapolating theoretical growth functions to managed forests, there is a need to calibrate the models with the forest structural heterogeneity. This is important for drawing realistic conclusions from growth and yield modelling of managed stands of Norway spruce and Scots pine.

1. Introduction

The photosynthetic capacity of trees is correlated to leaf area index (LAI). To monitor growth and leaf phenology at various scales and to understand physiological processes behind growth, knowledge about and how to model LAI are essential (Landsberg and Waring, 1997; Stenberg et al., 2004; Mason et al., 2012; Binkley et al., 2013a). In their investigations of tree growth and resource-use relationships, Landsberg and Waring (1997) and Binkley et al. (2013a) found stem growth per unit of absorbed light to be positively related to per unit growth of tree canopy LAI. Thus, LAI represents an essential structural variable in many process-based growth and ecosystem models (Chen et al., 1997; Johnson and Thornley, 2006; Propastin and Erasmi, 2010). In this study, we use the widely accepted definition of LAI as half the total surface area of green leaves or needles per unit of ground horizontal surface area (Stenberg et al., 2004). This definition also applies to the plant area index (PAI) when other light blocking tree elements (e.g. twigs, branches and stems) are considered. In a recent study, Goude et al. (2019) have developed LAI-conversion functions from direct and optical LAI estimation methods in pure (even-aged monocultures) Norway spruce (*Picea abies* (L). Karst) and Scots pine (*Pinus sylvestris* L.) forests in Sweden. These functions provide a piece of dependable

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information about the true LAI and have the potential to be used for rapid estimation of forest variables such as stand-level basal area (BA) and the modelling of growth.

These far research studies about using LAI to model growth have focused on monocultures, while managed (mixed-species) forests have got less attention – this probably due to their complexity and the challenge to model LAI within heterogeneous ecosystems. In recent years, mixed-species forests have been recognised and a number of studies relating mixture effects on productivity (Pretzsch et al., 2015; Pretzsch and Schuetze, 2016), provision of multiple ecosystem services (Gamfeldt et al., 2013; Forrester and Pretzsch, 2015; Felton et al., 2016) and as an adaptation strategy to cope with climate change (Bolte et al., 2009; Kolstrom et al., 2011) have been published.

The lack of growth models for mixed forests have resulted in the use of theoretical growth functions (e.g. in the Physiological Process for Predicting Growth – 3PG model) which are built on data from experimental forests, mostly even-aged monocultures and single-storied. However, the estimates of growth are largely uncertain as contemporary managed forests do deviate from the above characteristics of experimental forests (Landsberg and Waring, 1997; Forrester and Tang, 2016). For example, in mixed forests, the stand structural heterogeneity described by species composition, density, horizontal and vertical tree size distribution patterns, climate and management activities (or disturbances) regulate resource availability and use, and thus, affecting the total LAI spatially and temporary (Garber and Maguire, 2004; Forrester, 2014; del Rio et al., 2016). Hence, the accuracy of productivity estimation in mixed forests could be affected by varying levels of heterogeneity in the canopy LAI. Therefore, adjustments are required when applying the LAI-conversion functions on managed forests. Given the stronger relationship between canopy LAI and stem diameter (Kalliovirta and Tokola, 2005) and with the two variables also related to productivity (Landsberg and Waring, 1997; Binkley et al., 2013a), investigating the relationship between the BA and LAI can provide information about the uncertainties in the productivity estimation of heterogenous forests. In this study, we test the hypothesis (**H1**) that the uncertainties in the relationship between BA and canopy LAI will increase with increasing structural heterogeneity of managed forests. This information is crucial for the optimal planning and modelling of growth and yield of managed forests.

On the other hand, the use of remote sensing can also be suitable for adjusting the BA-LAI relationship in heterogenous forests. Recent advancements in space and airborne-satellites (e.g. Sentinel, Landsat, etc.) have triggered the use of remote sensing techniques in estimating forest canopy variables (e.g. Rautiainen et al., 2009) and the monitoring of forest health over larger land areas (e.g. Franklin et al., 1997; Baret and Buis, 2008). The reflectance spectra of different species, for example, the high within-shoot scattering (Rautiainen et al., 2005) and absorption by conifers in the near-infrared spectrum (Williams, 1991; Roberts et al., 2004) account for the distinct reflectance properties of coniferous and broadleaved forests. This provides a possibility for measuring the spectral heterogeneity of forest canopies. We test the second hypothesis (**H2**) that differences in the reflectance properties of tree species can provide spectral heterogeneity information that would improve the relationships between BA and LAI in managed forests. This information can provide an alternative cost-effective approach to using the stand structural heterogeneity metrics derived from laborious field inventories and appraise the prospects of Sentinel's inclusion in future growth and yield models.

Recently, hemispherical photos have been taken from sample plots in the Swedish National Forestry Inventory (NFI) to estimate LAI. The new approach with this study is to model BA from the LAI and to describe how the BA-LAI relationship is moderated by the heterogeneity in stand structure for complex managed coniferous forests. The specific aims are (1) to explore the relationship between the stand BA and canopy LAI and (2) to determine the influence of heterogeneity in (*a*) stand structure and site (reflected by: the species composition and dominance, tree height, stand age, tree size variation, stand density, temperature sum, humidity, latitude gradient) and (*b*) spectral and textural indices derived from remote sensing on the BA-LAI relationship in managed stands of Norway spruce and Scots pine.

2. Materials and methods

The true canopy LAI is assumed strongly related to BA (measured at breast height for trees on a sample plot) in a monoculture but for a heterogeneous stand, this relation may not hold. We applied species-specific conversion functions (Goude et al., 2019) on PAI from hemispheric photos captured in heterogeneous stands to predict LAI. Then the relationship between measured BA and modelled LAI was studied by forest structural attributes inventoried by the Swedish NFI (SLU, 2018) and remotely-sensed variables derived from Sentinel-2. The forest structural attributes were scaled and the population consisted of the Swedish boreal forests.

2.1. The population of Swedish boreal forests

Sweden's forest covers about 28 million hectares representing 69% of the total land area of the country and it is characterized by a north–south gradient (from 55° N to 69° N) with temperate to boreal vegetation zones, respectively (Skogsdata, 2018). Productive forestland covers about 23.5 million hectares with coniferous species largely dominant (*Pinus sylvestris* L., 39% and *Picea abies* (L). Karst, 27%). Birch species (*Betula pendula* and *Betula pubescens*) also accounts for 12% of the total productive forest area. On the other hand, the share of the area by mixed-species forests have also increased with 14% and 8% of mixed conifers and mixed conifer/broadleaves on productive forest lands, respectively (Fridman and Westerlund, 2016). Additionally, there is a pronounced variation in climate and soil conditions which are more favourable for tree growth in the southernmost part of Sweden (11.0 m^3 ha^{-1} $year^{-1}$) and decreases considerably in the northern and north-western directions. The average site productivity for the entire country is 5.3 m^3 ha^{-1} $year^{-1}$ (Fridman and Westerlund, 2016).

2.2. Field sample inventory design for assessing structural variables

We used the sample plot (stand) data (2016 and 2017) from the Swedish NFI. The design of the NFI is a systematic sample grid (with a random position of the grid) with square and rectangular cluster subplots (depending on region 4–12 subplots) representing the prevailing local conditions at different parts of the country (Fridman et al., 2014). The country is divided into five regions and due to autocorrelation, the sample intensity is higher in the South (fewer clusters and longer distances between plots within clusters in the North). The NFI uses a five-year inventory cycle (with five different cycles) for the permanent plots and one-fifth of the total plots are measured each year. The NFI also inventories temporary plots that are only visited once. All trees per species are calipered for diameter measurements at breast height (1.3 m above the ground; dbh) $\geq$ 10 cm on a 7 m radius for temporary plots and 10 m radius for permanent plots. A sample of the calipered trees is measured for height and age (age at breast height and only for temporary plots). Each calipered tree obtained a predicted height based on the sampled trees measured for height (Fridman et al., 2014). Different tree species, site and stand variables are also registered (SLU, 2018). The sampling of hemispheric photos was done in a total of 577 NFI-sample plots and 8,568 number of trees were inventoried. With the intention to exclude shrubs and understorey vegetation, plots with a mean tree height $<$ 4 m were excluded. The LAI-conversion functions (Goude et al., 2019) were developed for stand ages up to 100 years, and therefore at the application on the NFI data, stands with age above 100 years were excluded. Given the two restrictions, 504 sample plots remained.

Table 1
Summary of stand and site characteristics of Norway spruce and Scots pine from the sample plots of the NFI (2016 – 2017).

Variables	**Norway spruce (n = 200)**				**Scots pine (n = 194)**			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Basal area (m^2 ha^{-1})	1.93	44.50	21.63	9.91	2.20	46.11	21.30	9.86
Tree height (m)	5.62	28.02	14.56	4.32	5.62	28.02	14.07	4.20
Stand age (years)	15	100	58	25	15	100	62	24
Stem density (trees ha^{-1})	190.99	2078.73	758.23	377.40	127.32	2078.73	728.59	367.37
Arithmetic mean diameter, $\bar{d}$ (cm)	6	37.07	18.46	5.84	7.64	37.07	18.64	5.43
Quadratic diameter, Dq (cm)	6.93	39.40	19.78	6.10	8.26	39.40	19.96	5.83
CVD	0.10	0.92	0.38	0.15	0.09	0.89	0.38	0.17
Species proportion (% of basal area)	0.69	100	45.06	31.56	0.98	100	65.43	30.85
Species proportion (% of stem number)	2	100	46.66	28.92	3	100	55.91	32.11
Tree social status, $\bar{d}/Dq$	0.44	0.99	0.93	0.06	0.77	0.99	0.94	0.05
H-D ratio, $\bar{h}/\bar{d}$	48.23	146.35	80.02	12.35	38.87	107.06	76.19	12.30
Latitude	56.37	67.70	60	3.20	56.37	67.70	60.54	3.40
Temperature sum (degree days)	490	1540	1236.58	273.23	490	1540	1196.04	289.52
Humidity (mm)	– 49	200	30.16	66.94	– 49	196	32.45	65.63

*The estimation procedures of the variables: temperature sum and humidity are described in section 2.6. Min is minimum, Max is maximum and SD is the standard deviation.

2.3. Scaling stand structural variables to be used to explain the relationship between measured BA and modelled LAI

To study the relationship between measured BA and modelled LAI by stand structural variables in heterogeneous forest stands (**H1**), a set of forest structural variables were selected and scaled. The selected variables assumed influencing on this relationship were: the species composition and dominance, tree size heterogeneity, stem density, tree height, stand age and a set of variables describing site characteristics (latitudinal gradient, temperature sum and humidity). The variables are defined below and were calculated for each sample plot. The summaries of the variables are presented in Table 1.

2.3.1. Species composition and dominance:

The definition of dominance has been a subject of discussion in classifying stands as a monoculture or mixed forest typologies. However, measures that consider the maximum densities and growing space ratios of species are appropriate for characterizing species dominance (Reineke, 1933; Hein and Dhote, 2006; del Rio and Sterba, 2009; Woodall et al., 2011; del Rio et al., 2016). To capture the dominance of a particular species on the plot, tree sizes and stem density proportions were computed (Eqs. 1–3). The species composition was defined as the arithmetic proportion of the number of calipered trees for a specific species to all calipered trees on a sample plot and the relative stem density proportion of each species in the plot was then estimated (Eq. (1)). The species dominance was expressed by Eqs. 2–3. The two equations were calculated based on the total BA on a plot. These approaches were considered appropriate as species-specific sizes and crown allometry of dominant (larger) trees show greater light use and light use efficiency than for smaller trees in heterogenous stands (Pretzsch, 2009; Binkley et al., 2013b).

$$SPI_{SD} = \frac{\sum_{i=1}^{n} N_{is}}{\sum_{i=1}^{n} N_i}x100 \tag{1}$$

$$BA = \sum_{i=1}^{n} \frac{\pi d_i^2}{4}xEF \tag{2}$$

$$SPI_{BA} = \frac{BA_s}{BA}x100 \tag{3}$$

Where in Eqs. (1), (2) and (3), SPI_{SD} is the relative stem density proportion of species, N_{is} is one if the ith calipered tree on the sample unit is of species s, otherwise zero. N_i is one for each calipered tree on the sample unit, BA is the total basal area per plot area in [m^2 ha^{-1}], d_i is the diameter of the ith tree measured at breast height in [m], EF is the plot expansion factor that converts to per hectare units [ha^{-1}].SPI_{BA} is the relative basal area proportion of each species and BA_s is the basal area of species s on the plot per hectare.

Tree species dominance in the NFI is set by a threshold of greater than 65% in terms of the proportion of stems or BA per hectare (Fridman and Westerlund, 2016). A similar approach was used in this study to classify the sample plot as either (1) a Norway spruce stand or (2) a Scots pine stand based on the species with the largest proportion (greater than 70%) of the BA. Due to the absence of LAI-conversion parameters for broadleaves, plots dominated by broadleaves were removed. Mixed coniferous forests (mixing Norway spruce and Scots pine), were included based on the relative stem density proportion and relative BA proportion of species.

2.3.2. Tree size heterogeneity:

To estimate tree size heterogeneity for each plot, we computed the minimum and maximum tree diameter, quadratic diameter (Dq) that relates the BA to the number of trees for a plot, the coefficient of tree diameter variation (CVD), which measures the degree of diameter dispersion (standard deviation, sd) from the arithmetic mean tree diameter ($\bar{d}$) (Zeller et al., 2018), the tree social status relating the arithmetic mean tree diameter to the quadratic mean diameter ($\bar{d}/Dq$) and the H-D ratio, relating the arithmetic mean tree height to the arithmetic mean tree diameter ($\bar{h}/\bar{d}$).

The Dq was calculated as:

$$Dq = 100x\sqrt{\frac{4xBA}{\pi xn}} \tag{4}$$

Where Dq is the quadratic diameter in cm, BA is the basal area in [m^2 ha^{-1}] and n is the number of trees (higher than 1.3 m) per ha.

The CVD (values are scaled from 0, homogenous to 1, heterogenous tree sizes) and was computed as:

$$CVD = \frac{sd}{\bar{d}} \tag{5}$$

Where:

$$\bar{d} = \frac{1}{n_i}\sum_{i=1}^{n} d_i \tag{5a}$$

$$sd = \sqrt{\frac{\sum_{i=1}^{n} (d_i - \bar{d})^2}{(n_i - 1)}} \tag{5b}$$

$$\bar{h} = \frac{1}{n_i}\sum_{i=1}^{n} h_i \tag{6}$$

Eqs. (5), 5a and 5b include the diameter (d_i) of the i^{th} measured tree at breast height in cm and the number of trees (n_i) per inventory plot. In Eq. (6), h_i is the height of the i^{th} measured tree in meters [m].

2.4. Sampling of hemispheric photographs and estimation of leaf and plant area indices

To estimate LAI and PAI, circular (180° field of view) digital hemispheric fish-eye photos (DHP) were taken from the sample plot centres of both permanent and temporary NFI plots using Nikon D5300 camera with 16 mm lens. The DHP-photos were taken simultaneously with the inventory corresponding with the growing season (from April to September in both 2016 and 2017) and to the leaf-on periods. To avoid the influence of direct sunlight, photos (e.g. Fig. A.1 in Appendix A, supplementary material) were acquired under diffused light conditions in the early mornings or late afternoons as recommended in the literature (Chianucci and Cutini, 2012). Images were taken with the camera mounted on a tripod at 1.3 m above the ground to avoid the interference of ground vegetation (González et al., 2011) and magnetic north-alignment towards the plot centre using a compass (Beaudet and Messier, 2002). During image acquisition, vegetation within 1 m of the lens was moved out of the frame's view.

The processing and retrieval of LAI from the DHPs were done in ImajeJ (version 1.52a: Rasband, 2014) and in the GapLightAnalyzer software (GLA, version 2.0: Forest Renewal BC) (Frazer et al., 1999). The detailed procedures are presented in the Appendix A (A.3, supplementary material). The GLA computes PAI as effective LAI (LAIe) due to lack of differentiation between woody materials and leaves using four to five zenith rings. However, due to the strong influence of multiple scattering occurring at larger zenith angles, the fourth ring has been found to provide accurate estimates of the LAIe. Similarly, Goude et al. (2019) used the LAIe from the fourth ring to develop the relationships between LAI from direct and optical methods. Hence, we considered the LAIe values at the fourth ring for subsequent analysis in this study. We estimated LAI from the LAIe values using species-specific LAI-conversion functions developed by Goude et al. (2019).

2.5. Sentinel-2 data acquisition, processing and feature extraction

Sentinel-2 Level-1C tiles (100x100 km^2, *ortho*-images in UTM/WGS 84 projection) with minimum cloud cover ($<$ 10%) and covering the spatial extent of Sweden were acquired from the Google Earth Engine platform (Google Earth Engine, 2018). The tiles covered the growing season periods as in the field inventory of 2016 and 2017. The Multi-Spectral Instrument (MS1) of Sentinel-2 provides multi-spectral images in 13 spectral bands (Table A1: Appendix A in supplementary material) from the visible, near and shortwave infrared at different spatial resolutions ranging from 10 m to 60 m on the ground (Drusch et al., 2012).

Pre-processing of the image tiles involved atmospheric correction by dark object subtraction and conversion of pixel values from digital numbers to surface (bottom-of-the-atmosphere) reflectance values. To mask out opaque and cirrus clouds, the "QA60" band provided in the Level-1C product was applied. Tiles were mosaicked and the overlapping areas blended with the mean function for efficient processing (Pope and Treitz, 2013). Image pre-processing and mosaicking were done in the Google Earth Engine platform (Earth Engine Data Catalog, 2018).

A unique feature about the Sentinel-2 sensor is the vegetation red-edge bands which lie between the visible red and near-infrared (NIR) portions of the electromagnetic spectrum (Table A.1). Reports have shown that vegetation indices (VIs) derived from red-edge bands are suitable for retrieving leaf chlorophyll and nitrogen content and estimating canopy LAI (Dash and Curran, 2004; Gitelson et al., 2005; Delegido et al., 2011; Asam et al., 2013; Sibanda et al., 2016; Korhonen et al., 2017; Forkuor et al., 2018). Making use of these red-edge bands (resampled to 10 m spatial resolution), we built specific VIs such as the normalized difference vegetation index (NDVI)-red-edge and chlorophyll-red-edge. Other developed VIs (Table A.2) included the chlorophyll-green ($\mathrm{Cl_{green}}$), simple ratio (SR), NDVI-green ($\mathrm{NDVI_{green}}$), NDVI and the soil adjusted vegetation index (SAVI) to correct for soil variability due to perturbing factors of solar elevation and canopy structure (Baret and Guyot, 1991).

Additional information derived from the mosaicked Sentinel-2 spectral bands were the textural features. By a moving window, texture features can be used to quantify the spatial heterogeneity of pixels and complement the spectral information in assessing and mapping the distribution of vegetation (e.g. Wulder et al., 1998; Colombo et al., 2003; Gallardo-Cruz et al., 2012; Beckschäfer et al., 2013). Thus, texture describes the nature of canopy cover by assessing the patterns of shadows, greenness and openness/closeness of tree crowns (Oldeland et al., 2017). We calculated five Gray Level Co-occurrence Matrix (GLCM) based textural measures describing spectral (pixel) heterogeneity such as the mean, variance, contrast, entropy and correlation (Table A.2) on the NIR band using a probabilistic quantizer on 32 grey levels, 2 moving windows of sizes 3 × 3 and 7 × 7 and an offset distance of 1 pixel over all directions (0°, 45°, 90° and 135°) (Haralick et al., 1973; Lu and Batistella, 2005; Pratt, 2007). A single spatially-invariant texture value was computed for each inventory plot as an average of the texture measurements of each direction (Gallardo-Cruz et al., 2012).

In total, 8 spectral VIs and 10 textural features were developed. Image spectra data were extracted as area-weighted mean values of pixels found within the field sample plot area of 10 m radius. To determine the variability of neighbouring stands to the sample plot characteristics (as the hemispheric photographs covered an area larger than our sample plot area), we also tested for the effect of increasing the data extraction radius to 20 m on the NIR spectral band. We computed the spectral variation index as the ratio of the NIR reflectance at 10 m to the 20 m radii. This was intended to capture the variation within (inside plot) and between pixel (outside plot). All spectral analyses were done using the "*raster*" and "*glcm*" packages in the R statistical environment (R Core Team, 2018).

2.6. Site heterogeneity (latitude gradient, temperature sum, humidity)

To capture the effect of site heterogeneity on BA, we created an indicator variable, latitudinal gradient of northern and southern gradients, where northern comprised plots or stands above latitude 64 °N and southern gradients comprised latitudes below 64 °N. In addition, we used temperature sum defined as the summation of average daily temperatures exceeding 5 °C during the vegetation period (Perttu and Morén, 1994; Gamfeldt et al., 2013). Humidity was defined as the difference between precipitation (addition of water) and loss of water by transpiration and evapotranspiration during the growing season period where the temperature exceeds 5 °C (Gamfeldt et al., 2013). The temperature sum and humidity were downloaded from the database of the Swedish Meteorological and Hydrological Institute (SMHI, 2018) and incorporated as covariables during model fitting.

2.7. Statistical data analysis

Descriptive statistics was used to estimate the LAI for Norway spruce and Scots pine in managed stands. Additionally, we compared the LAI variations at the northern and southern gradients and at different stand ages: young (15–30 years), intermediate (31–60 years) and mature (60–100 years). Bivariate scatter plots were also used to explore the relationship between LAI and tree height.

The modelling procedures were made in two steps: first, by fitting base models (BMs) and second, by fitting final models (FMs). The BMs were constructed to determine the relationships between BA and LAI whereas, the FMs were to test for the effect of heterogeneity on the BA-LAI relations. Both BMs and FMs were fitted separately for Norway spruce and Scots pine.

To compare the relationship between BA and LAI with that of stand BA-PAI, scatter plots (not shown here) were initially used to visualize the patterns for the two relations: BA-LAI and BA-PAI. For the BA-LAI base model, we fitted a non-linear least squares regression model (Eq. (7)) identical to the Michaelis-Menten equation of kinetics of enzyme reactions (Michaelis and Menten, 1913) using the "*nls*" function in R. In forest production ecology, the classical Michaelis-Menten equation has been used to describe patterns of resource-use efficiency where production increases with increasing resource use, but the rate of increase is slowed by the limitations of other resources (Binkley et al., 2004). A similar concept was considered here with the BA used as a surrogate for production or growth variable and LAI as the proxy defining resource capturing and use.

$$BA = \frac{a(LAI)}{c + LAI} + \varepsilon \tag{7}$$

Where $a$is the maximum basal area at LAI saturation and c is the LAI value at which the BA is half of$a$, ε is the random error which is normally distributed and has constant variance. The best starting values iterated using the self-starting 'SSmicmen' function in "*nlme*" package to estimate the parameters a and c at model convergence were respectively 35 and 0.16 for Norway spruce and 38 and 0.10 for Scots pine.

For the BA-PAI base model, we set up a generalised additive model (GAM: Crawley, 2007) using the "*mgcv*" package in R. GAM models are flexible which allow for the fitting of smoothers to capture the non-linear relations among predictors and have yielded satisfactory results in recent forest ecosystem studies (Zeller et al., 2018). The GAM specified the BA-PAI model by the relation below:

$$BA = b + f(PAI) + \varepsilon \tag{8}$$

Where b is intercept and f denotes the non-linear smoother to be fitted.

The fitting of the final models (FM) was done by adding other covariables to the base models above. To test for **H1**, explanatory variables describing general stand structure (stand age, tree height, Dq, stem density and species proportion indices) and tree size heterogeneity (CVD, minimum and maximum diameter, tree social status and H-D ratio) and site characteristics (temperature sum, humidity, latitudinal gradient) were used. Similarly, to test for **H2**, FMs were fitted with heterogeneity variables described by the vegetation and textural indices.

Before adding the covariables, we checked for collinearity among the predictors using the variance inflation factor (VIF) method (e.g. Imdadullah et al., 2016). Lower values of VIF implies less collinearity. The threshold of acceptable VIFs have been varying among researchers as some recommend VIFs < 10 (Dormann et al., 2013), < 5 (Hair et al., 2011) and < 3 (Hair et al., 2018). In this study, we compared and excluded all variables with VIFs greater than 5 and also on the basis of the ecological significance of the variable.

The FM with stand structure heterogeneity variables describing the BA-LAI relationship **(H1)** for both Norway spruce and Scots pine was explicitly specified as:

$$BA = \frac{a(LAI)}{c + LAI} + f(stand\ structure\ heterogeneity) + f(site) + \varepsilon \tag{9}$$

Similarly, the FM with spectral heterogeneity variables **(H2)** for each species was also specified explicitly as:

$$BA = \frac{a(LAI)}{c + LAI} + f(Stand\ age,\ tree\ height) + f(VIs + texture) + f(site) + \varepsilon \tag{10}$$

To obtain best fitting models, non-significant variables (that is, variables which did not improve the explained variation in the model) were excluded. The residuals of the FMs were investigated for potential heteroscedasticity on the latitudinal gradient, stand age and tree height. Model performances were assessed by the root-mean-squared error (RMSE) and the relative root-mean-squared error (RelRMSE) as:

$$RMSE = \sqrt{\frac{\sum (\widehat{y}_i - y_i)^2}{n}} \tag{11}$$

$$RelRMSE = 100\%\text{x}\frac{RMSE}{\bar{y}} \tag{12}$$

Where, $\widehat{y}_i$ is the estimated BA of the ith observation (plot), y_i is ith measured BA, n is the number of plots and $\bar{y}$ is mean of the measured BA ($\bar{y} = \sum_{i=1}^{n} y_i/n$).

In Eq. (9), the contribution of each variable in the model was computed by means of permutations using the loss-root-mean square function (defined as the square root of averaged square differences between the measured and estimated BA) in the "*DALEX*" package in R (Biecek, 2018). All the statistical data analyses and modelling were done using the R statistical software (R Core Team, 2018).

3. Results

3.1. Leaf area index estimation

Descriptive statistics of the LAI for Norway spruce and Scots pine is presented in Table 2. The average LAI (± SD) for Norway spruce was 3.26 ± 1.74 and 3.01 ± 1.79 for Scots pine. For both species, the average LAIs were significantly higher ($p < 0.05$) in the southern than in the northern gradients. The LAIs were also higher in matured and intermediate stands compared to young stands and showed an increasing trend with increasing tree height (Fig. 1).

3.2. Base models of stand basal area and leaf or plant area index relationship

Using LAI-conversion functions, a nonlinear relationship between the BA and LAI was found for both Norway spruce (Fig. 2A) and Scots pine (Fig. 2C). However, with the general PAI, a linear relationship was observed (Fig. 2B and 2D). The above trends were also similar in both northern and southern gradients.

The base models (BM) fitted with LAI as the sole predictor yielded RMSE ($m^2\ ha^{-1}$) values of 7.41 and 6.49 in Norway spruce and Scots pine, respectively. Similarly, the BMs with PAI yielded corresponding increase (relative to the BMs with LAI) in the RMSEs by about 4% in Norway spruce and by 5% in Scots pine. The absolute residuals were slightly larger in the BA-PAI models than in the BA-LAI models for both Norway spruce and Scots pine (Fig. A.2, shown in supplementary file).

3.3. Basal area – Leaf area index model with stand structural heterogeneity indices

By including the general stand structural attributes and heterogeneity (SSH) variables, the final models (FM) of LAI were significant ($p < 0.05$) with lower (compared to the BMs) RMSE ($m^2\ ha^{-1}$) for

Table 2
LAI ($m^2\ m^{-2}$) statistics for Norway spruce and Scots pine plots.

	Norway spruce (n = 200)	**Scots pine(n = 194)**
Mean	3.26	3.01
Standard deviation (SD)	1.74	1.79
Minimum	0.83	0.14
Maximum	7.69	6.93

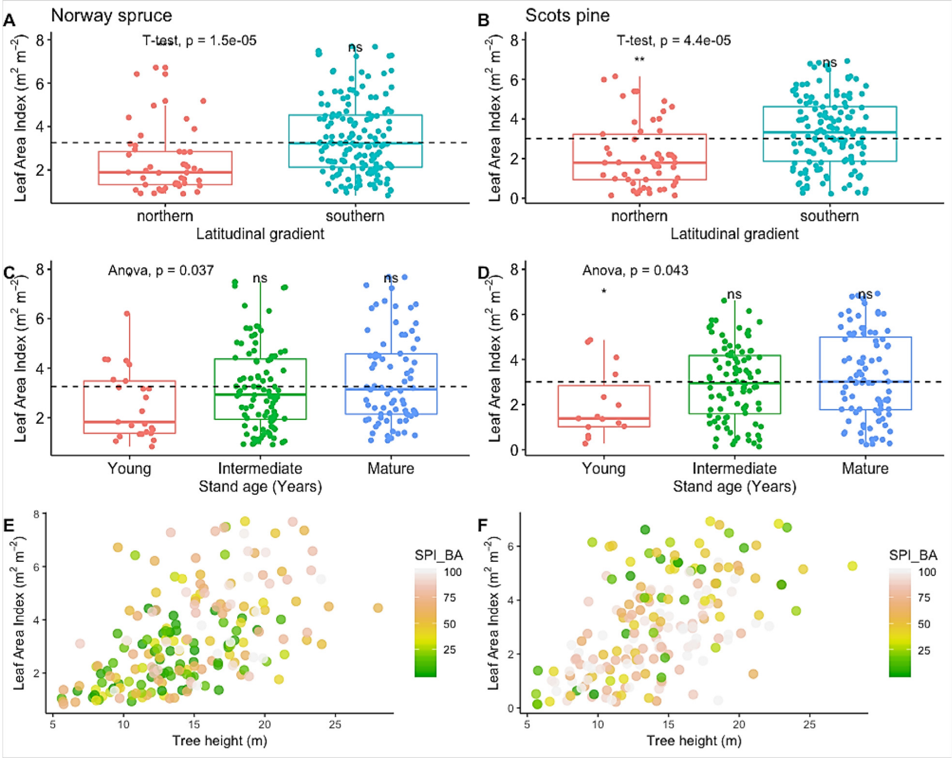

Fig. 1. LAI variation across the latitudinal gradient, stand age and tree height in Norway spruce (left panel) and Scots pine (right panel) stands. The solid horizontal dashed lines represent the grand mean LAI. The 'ns' indicated a non-significance when compared to the grand mean LAI.

both Norway spruce (3.33) and Scots pine (3.70), after pre-selection of competing explanatory variables. The residual diagnosis of the final models did not show any apparent signs of heteroscedasticity over latitude, stand age and tree height (Fig. A.3).

Table 3 shows the estimated parameters of the significant variables in the BA-LAI final models fitted for Norway spruce and Scots pine with heterogeneity variables. For both species, general stand structural variables such as tree height, stand age, stem density and heterogeneity variables by CVD, tree social status and H-D ratio were the most significant variables in the final models. For Scots pine, the addition of temperature sum was also significant to the final model.

The top 5 contributive variables (Fig. 3A) to the performance of BA-LAI final model of Norway spruce were tree height (10.429), stand density (7.35), H-D ratio (3.21), tree social status (2.17) and CVD (0.31). The corresponding top 5 variables influencing the performance of BA-LAI final model of Scots pine (Fig. 3B) were in the order: tree height (10.05), stem density (8.07), H-D ratio (3.81), CVD (0.62) and stand age (0.14).

3.4. Basal area – Leaf area index model with spectral heterogeneity indices

Final models with spectral heterogeneity (SPH) variables yielded significant regression parameters ($p < 0.05$) and lower RMSEs (m^2 ha^{-1}) compared to the base models for Norway spruce (5.56) and Scots pine (5.66). For both species, the significant heterogeneity variables were NDVI-rededge1 and entropy derived from the 3x3 spatial window. The spectral variation index was also significant for the FM of Norway spruce (Table 4). The visualization of residuals showed the absence of heteroscedasticity (Fig. A.4).

3.5. Comparison of base and final models with the stand structural and spectral heterogeneity

Generally, by accounting for heterogeneity in the stands, higher accuracies were observed for both Norway spruce and Scots pine (Fig. 4). Relative to the BMs, FMs accounting for stand structural heterogeneity (SSH) reduced the variance (RMSE) by 55% and 43% in Norway spruce and Scots pine, respectively. Additionally, by substituting the SSH with spectral heterogeneity from Sentinel-2, the variance was reduced respectively by 25% and 13% in Norway spruce and Scots pine, compared to the BMs.

4. Discussion

4.1. Relationship between basal area and canopy leaf area

The primary objective of this modelling was to explore the applicability of experimentally developed LAI conversion functions on managed stands by investigating the relationships between stand BA and canopy LAI. The relationship between stem-wood production and canopy LAI has thoroughly been investigated in the literature (Cannell, 1989; Binkley et al., 2010; Binkley et al., 2013a; del Rio et al., 2016).

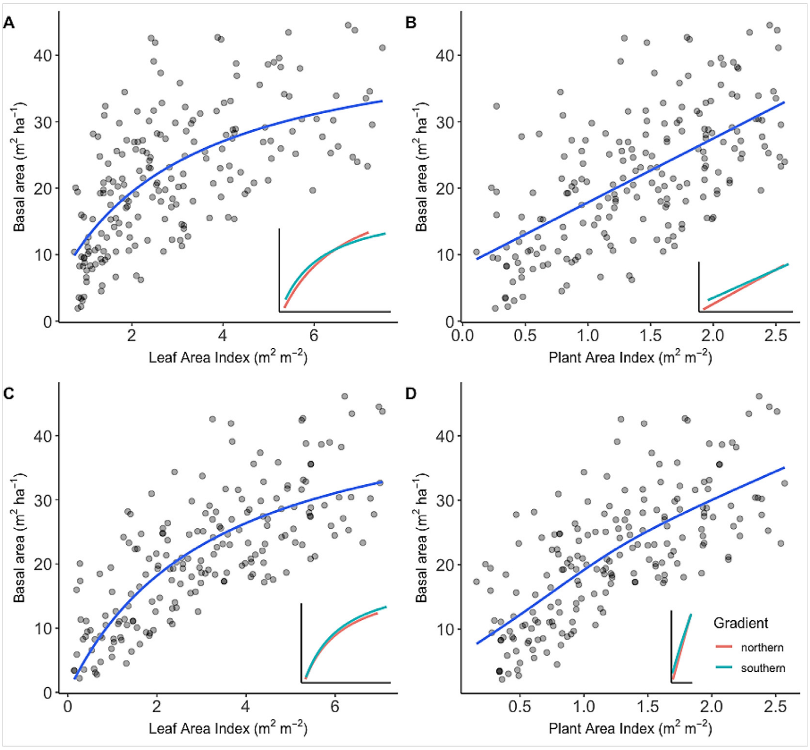

Fig. 2. Relationship between stand BA and LAI or PAI for Norway spruce (A-B) and Scots pine (C-D) stands. The solid blue lines were fitted using the parameters of the base models (Eqs. (7) and (8)). Insets represent the latitudinal trends described by northern and southern gradients of Sweden. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Such relationships have been demonstrated in this study as the BA-LAI models were all significant ($p < 0.05$) for both Norway spruce and Scots pine (Tables 3 and 4). When using LAI as the only predictor, a positive nonlinear relationship was found whereas using the PAI exhibited positive linear trends for both Norway spruce and Scots pine (Fig. 2).

The significance of LAI shows the physiologic and allometric roles played by forest canopies in the processes of resource acquisition, production and distribution of photosynthates to the plants' organs and tissues (Binkley et al., 2004). Binkley et al. (2004) found higher volume production in stands with higher LAI. Light interception has been found to be a function of the amount of leaves within the tree crowns and this function is nonlinear at higher LAI values (Binkley et al., 2013a; Binkley et al., 2013b). This nonlinear trend can be attributed to the effects of tree competition, needle longevity and self-shading as a unit of LAI could receive different amounts of light (Gspaltl et al., 2013). Tree crown and stem allometry patterns illustrate that an increase in LAI leads to higher sapwood formation in trees, increasing the sapwood content, which in turn increases the tree stem diameter (West, 2014). In predicting tree stem diameter and volume, the addition of LAI as a

Table 3

Parameter estimates of significant variables in the BA-LAI final models fitted with the stand structural heterogeneity metrics for Norway spruce and Scots pine. Values in parenthesis are the standard errors. Predictors are significant at $p < 0.0001$ (***), $p < 0.001$ (**) and $p < 0.05$ (*) probability levels and n is the number of sample plots.

	Norway spruce (n = 200)		**Scots pine** (n = 194)	
	Estimate	p-value	Estimate	p-value
LAI ($m^2 m^{-2}$)	0.07 (0.04)	0.042*	0.01 (0.07)	0.045*
Stem density (trees ha^{-1})	0.02 (0.001)	< 0.001***	0.02 (0.001)	< 0.001***
Tree height (m)	2.15 (0.10)	< 0.001***	2.21 (0.11)	< 0.001***
Stand age (years)	0.10 (0.004)	0.007**	0.01 (0.003)	< 0.001 ***
CVD	−2.35 (0.32)	< 0.001**	−2.52 (0.21)	< 0.001 ***
Tree social status	−51.90 (7.31)	< 0.001***		
H-D ratio	−0.34 (0.03)	< 0.001***	−0.38 (0.03)	< 0.001***
Temperature sum (degree days)			0.002 (0.001)	0.048*

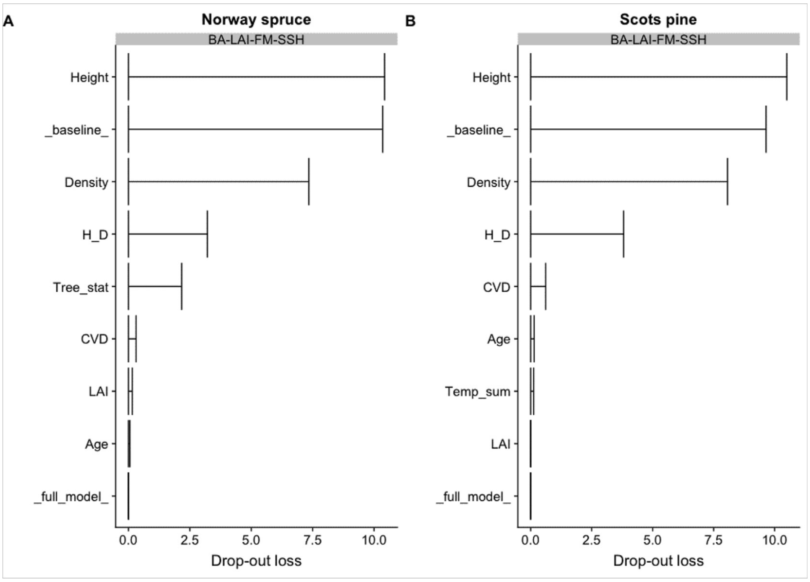

Fig. 3. Variable contribution to final BA-LAI models of Norway spruce (A) and Scots pine (B). The importance of the predictors in each model was computed by permutations (drop-out loss) using the loss-root-mean-square function. The baseline represented the worst-case-loss when variables were compared randomly in the model. The full model showed model performance when variables were not resampled.

Table 4
Parameter estimates of significant variables in the BA-LAI final models fitted with spectral heterogeneity metrics for Norway spruce and Scots pine. Values in parenthesis are the standard errors. Predictors are significant at $p < 0.0001$ (***), $p < 0.001$ (**) and $p < 0.05$ (*) probability levels and n is the number of sample plots.

	Norway spruce (n = 200)		**Scots pine** (n = 194)	
	Estimate	p-value	Estimate	p-value
LAI (m^2 m^{-2})	1.65 (0.67)	0.015*	8.83 (3.49)	0.012*
Tree height (m)	0.11 (0.006)	< 0.001***	0.10 (0.009)	< 0.001***
Stand age (years)	0.02 (0.002)	0.007**	0.02 (0.002)	< 0.001***
NDVI-rededge1	0.41 (0.22)	< 0.001**	1.01 (0.42)	0.017*
Entropy	0.79 (0.18)	< 0.001***	0.65 (0.23)	0.005**
Spectral variation index	−16.12 (6.38)	0.012*		

covariable to tree height largely increased model performance of longleaf pine (*Pinus palustris*) plantations in the Western Gulf Coastal Plains, U.S. (Gonzalez-Benecke et al., 2014). Similar results demonstrating strong positive relationships between LAI and stem diameter have also been reported for *Pinus sylvestris*, *Picea abies* and *Betula pendula* in Finland (Kalliovirta and Tokola, 2005).

4.2. Accounting for stand structure heterogeneity in the basal area – Canopy leaf area index relationship

Despite the significance of LAI in the models, the RMSEs were extremely high in the base models without accounting for the stand structural heterogeneity (Fig. 4A and 4D). The variations were reduced significantly when stand and site structural attributes were incorporated into the final models (Fig. 4B and 4E). The absence of heteroscedasticity in the residuals demonstrated that the nonlinear structure of the models was adequately adapted to the data (Fig. A.3). Traditional stand variables such as tree height, stand age, stem density and the structural heterogeneity variables defined by tree social status, CVD and H-D ratio greatly improved the performance of the final models (Table 3, Fig. 3). This evidently supports the first hypothesis (H1) that stand structure heterogeneity largely modulates the relationships between BA and LAI in managed forests.

The interactions of stand age, tree height, stem density and LAI have been well documented and widely used to explain forest stand growth (DeAngelis et al., 1981; Ryan et al., 1997; Gonzalez-Benecke et al., 2014). The LAI and stand age are positively correlated during the early stages of stand development (Ryan et al., 1997; Gonzalez-Benecke et al., 2014). But in older stands, the correlation is relatively weaker, a reason probably ascribed to management operations such as thinning. Thinning reduces the BA (Nilsson et al., 2010) and the LAI of the residual stands (Boczon et al., 2016) and subsequent reduction in the photosynthetic power as the number of trees is reduced (Gershenson et al., 2009; Hogberg, 2010).

The introduction of tree height as a covariate largely improved the final models (Figs. 3 and 4). Taller trees have larger stem-wood which provides mechanical strength (West, 2014). Ecologically, tall tree height plays a supportive role in holding leaves high up in the air for the tree to receive much sunlight, supports the total tree weight, provides strong resistance to stresses of wind and serves as conducting channels for water and food transport (West, 2014). Therefore, the larger must be the stem diameter to hold it upright and hence, the subsequent increase in tree BA with increasing tree height.

Recent surveys from the Swedish NFI reports that about 20% of the productive forest-land is a mixture of Scots pine and Norway spruce (Fridman et al., 2014; Holmström et al., 2018). Similarly, multi-layered Scots pine stands with understory layer of Norway spruce and birch created by mass regeneration and size stratification have been observed in central and northern Sweden (Lundqvist et al., 2019). These reports reinforce that the current structural outlook of managed Scots pine stands is heterogeneous in tree species and size (Fig. 5). The

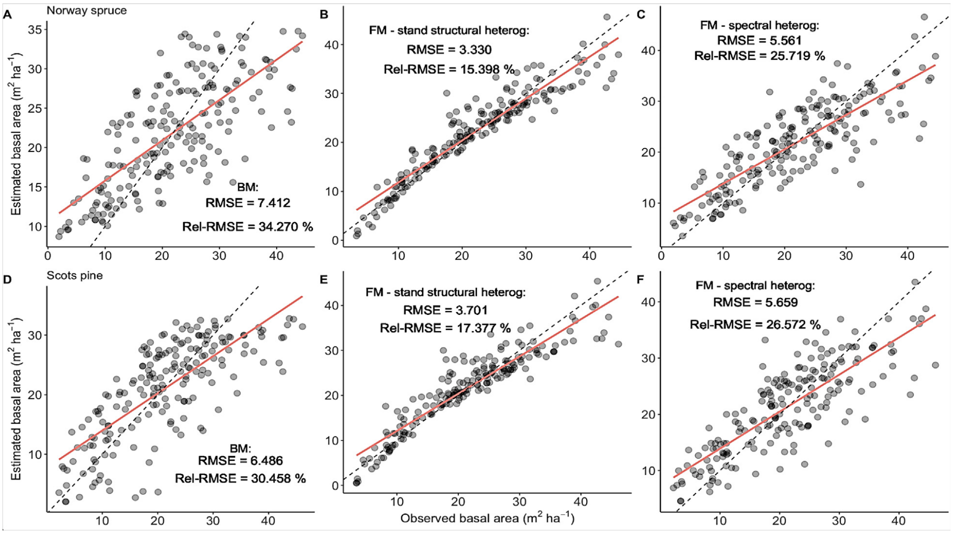

Fig. 4. Observed and estimated BA for Norway spruce (A-C) and Scots pine (D-F). The black dashed line is the 1:1 relationship. The solid red lines show the relationship between the observed and estimated BA from the base models (BM) and the final models (FM) fitted using stand structural and spectral heterogeneity indices. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

performance of the final models was sensitive to the species proportion of the total BA (Fig. A.3). The sensitivity was largely controlled by the variations in LAI and tree height (Figs. 1 and 3). For Norway spruce, the LAI was higher in the monocultures (100% of the total BA) than in the mixtures because of the lower tree heights observed in the mixtures (Fig. 1E). This highlights the sub-dominant feature (thus secondary species and self-shading) of Norway spruce in mixtures (Goude et al., 2019). Scots pine on the other hand, had LAI values within the reported range for the species in monocultures (LAI of 1 to 4) (Chen et al., 1997; Goude et al., 2019; Holmström et al., 2018). However, LAIs larger than 4 were also observed in stands with lower proportion of Scots pine (Fig. 1F). This might be due to the larger tree heights of Scots pine in the mixtures (Fig. 1F). Scots pine is a shade intolerant species and therefore, exhibits dominance in mixtures (Goude et al., 2019). Norway spruce was the most frequent ingrowth species in the Scots pine stands. Characteristically, the final model of Scots pine was more stable with decreasing proportion of Norway spruce in the plot (Fig. A.3). The ground-based heterogeneity (species proportion and tree size) was captured in the final models by the inclusion of tree social status, H-D ratio and coefficient of variation of tree diameter as independent variables (Table 3, Figs. 3 and 4). All the size heterogeneity variables had negative coefficients (Table 3) and this supports earlier reports of

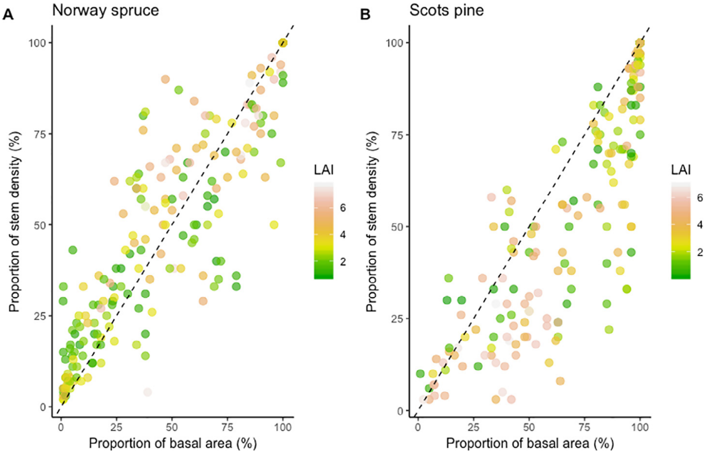

Fig. 5. Relationship between species proportion of plot total BA and stem density for (A) Norway spruce and (B) Scots pine stands in Sweden. The short dash lines represent a 1:1 relationship.

the negative correlation between tree size inequality and stand productivity (Zeller et al., 2018; Sun et al., 2018). The influence of stand structure heterogeneity can be understood from patterns of light interception and light-use efficiency (Duursma and Makela, 2007; Binkley et al., 2010; Bourdier et al., 2016). Species-specific sizes and crown allometry of dominant (larger) trees show greater light interception and light-use efficiency than for smaller trees in heterogenous stands (Pretzsch, 2009; Gspaltl et al., 2013; Binkley et al., 2013a).

4.3. Significance of heterogeneity variables from Sentinel-2

Given the role of LAI in estimating the production potential of forests and monitoring of forest health (Gitelson et al., 2006), the use of remote sensing to monitor forest canopies and retrieve leaf traits has gained wider attention (Kokaly et al., 2009; Zhu et al., 2017). In this study, the incorporation of spectral heterogeneity variables reflected by NDVI, entropy and spectral variation index were significant in the final models of both Norway spruce and Scots pine (Table 4). The final models with these spectral heterogeneity variables showed an improvement over the base models for both Norway spruce and Scots pine (Fig. 4C and 4F). The model residuals showed no apparent signs of heteroscedasticity (Fig. A.4). The finding supports our second hypothesis (H2). The models' structure included stand age and tree height as covariables (Table 4) but we speculate that the increasing availability of LiDAR (light detection and ranging) data could provide canopy height metrics that would improve upon the detection of spectral heterogeneity. The significance of the vegetation indices and texture measures demonstrate the sensitivity and usefulness of the multispectral Sentinel-2 satellite, particularly its red-edge bands in vegetation assessment. In a recent study of mapping the leaf chlorophyll content of Norway spruce stands in the Bavarian Forest National Park in Germany, a higher fit between measured and retrieved leaf chlorophyll was found using Sentinel-2 red-edge bands ($R^2 = 0.45$) than RapidEye data ($R^2 = 0.39$) (Darvishzadeh et al., 2019). Similarly, the use of Sentinel-2 narrowly performed better than Landsat-8 in estimating forest canopy cover and LAI in Norway spruce, Scots pine and birch dominant stands in central Finland (Korhonen et al., 2017). The slightly larger residuals in the spectral heterogeneity models of our study (Figs. 4 and A.4) presumably suggest the multiple within-shoot-scattering of radiations in boreal coniferous forests (Rautiainen et al., 2005), the heterogenous crown surface (Schull et al., 2011) and the understory vegetation composition (Eriksson et al., 2006; Rautiainen et al., 2007; Rautiainen et al., 2011; Pisek et al., 2012). By using a dataset of managed forests (NFI data), it represents that these stands are subjected to several forms of management such as thinning. Thinning opens the canopy and largely contributes to leaf clumping and thereby affecting the reflectance properties of forest canopies (Rautiainen et al., 2007).

4.4. Characterizing the influence of site variables/ conditions

To quantify the regulatory effects of site conditions on the canopy LAI, the addition of temperature sum and humidity in the models provided satisfactory results. These variables represented the latitudinal gradient of Sweden. For both Scots pine and Norway spruce, the humidity was not statistically significant and hence removed from the final models. Temperature sum was statistically significant only in the final models of Scots pine (Table 3) and it contributed marginally to the overall model performance (Fig. 3B). Generally, temperature influences stomatal conductance and efficiency of the conversion of radiation into chemical energy (Landsberg and Waring, 1997) hence, its usefulness in the final model. The limitation here is that the climate grid used in this study was modelled at the scale of the tracts (a cluster of sample plots in the Swedish NFI) and such estimates can be affected by large uncertainties (Laubhann et al., 2009). We recommend a grid with finer resolution so as to fully comprehend the interaction of forest canopies with local (on-site) conditions.

4.5. Limitations of the study

The fitted BA-LAI final models showed slight overestimation (Fig. 4) for both Norway spruce and Scots pine stands from northern Sweden (above latitude 64 °N). This probably might be due to extrapolation of the LAI conversions functions which represented the latitude range 55 °N to 64 °N (Goude et al., 2019). We suggest that any extrapolation of these LAI conversion functions should be made with great caution. In this current study, the effects of genetics, fertilization and management on LAI were not separated and quantified (due to their unavailability in the dataset). Knowledge about these variables and their correlation to LAI may be useful for improving future models.

5. Conclusion

This study highlights that stand BA and canopy LAI are highly related. Experimentally developed LAI-conversion functions can satisfactorily be applied on managed stands of Norway spruce and Scots pine particularly when stand structural heterogeneity is accounted for, though extrapolation of these functions should be treated with caution. The explanatory variables included in the species-specific models have ecophysiological significance suggesting their usefulness in hybrid (process-based and empirical) forest growth and yield models. The significance of spectral heterogeneity variables (vegetation and texture indices) indicates the potential use of the multispectral Sentinel-2 satellite imagery in modelling tree growth and forest canopy dynamics. Also, these spectral variables provide a cost-effective approach as they illustrate potential substitution for the structural heterogeneity variables which are derived from laborious field inventories.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117699.

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ORIGINAL RESEARCH

On the role of forests and the forest sector for climate change mitigation in Sweden

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Abstract

We analyse the short- and long-term consequences for atmospheric greenhouse gas (GHG) concentrations of forest management strategies and forest product uses in Sweden by comparing the modelled consequences of forest resource use vs. increased conservation at different levels of GHG savings from carbon sequestration and product substitution with bioenergy and other forest products. Increased forest set-asides for conservation resulted in larger GHG reductions only in the short term and only when substitution effects were low. In all other cases, forest use was more beneficial. In all scenarios, annual carbon dioxide (CO_2) sequestration rates declined in conservation forests as they mature, eventually approaching a steady state. Forest set-asides are thus associated with increasing opportunity costs corresponding to foregone wood production and associated mitigation losses. Substitution and sequestration rates under all other forest management strategies rise, providing support for sustained harvest and cumulative mitigation gains. The impact of increased fertilization was everywhere beneficial to the climate and surpassed the mitigation potential of the other scenarios. Climate change can have large—positive or negative—influence on outcomes. Despite uncertainties, the results indicate potentially large benefits from forest use for wood production. These benefits, however, are not clearly linked with forestry in UNFCCC *reporting*, and the European Union's Land Use, Land-Use Change and Forestry *carbon accounting*, framework may even prevent their full realization. These reporting and accounting frameworks may further have the consequence of encouraging land set-asides and reduced forest use at the expense of future biomass production. Further, carbon leakage and resulting biodiversity impacts due to increased use of more GHG-intensive products, including imported products associated with deforestation and land degradation, are inadequately assessed. Considerable opportunity to better mobilize the climate change mitigation potential of Swedish forests therefore remains.

KEYWORDS

adaptation, conservation, forest, land set-asides, LULUCF, mitigation, substitution

1 | INTRODUCTION

Forests and the forest sector influence atmospheric carbon dioxide (CO_2) concentrations through removing CO_2 from the atmosphere and storing carbon in forests and forest products (Pilli et al., 2015). Greenhouse gas (GHG) savings arise when forest products substitute fossil fuels and other GHG-intensive products, such as cement and steel (Gustavsson et al., 2017, 2021; Leskinen et al., 2018; Lundmark et al., 2014; Sathre & O'Connor, 2010). Sweden aims to become a fossil-free society with net zero GHG emissions by 2045 and negative emissions thereafter. Biomass is currently the largest energy source in Sweden, and a nation-wide initiative to develop roadmaps towards a fossil-free future (Fossilfritt Sverige, n.d.) highlights that biomass-based solutions are increasingly considered. Most of this biomass is expected to come from forests, which are expected to support mitigation also through enhanced forest carbon storage, wood supply for industries producing construction wood and other bio-based products. The European Union's (EU's) LULUCF (Land Use, Land-Use Change and Forestry) policy, on the other hand, may in effect discourage further increases in forest biomass use (Ellison et al., 2014, 2021; Grassi et al., 2019; Matthews, 2020; Nabuurs et al., 2017).

Potential trade-offs exist between the objectives of storing carbon in the forest, on the one hand, and harvesting wood, on the other. How best to balance forest carbon storage and wood production with respect to the climate has long been a subject of debate and scientific inquiry (Cintas, Berndes, Cowie, et al., 2017; Cintas, Berndes, Hansson, et al., 2017; Cowie et al., 2021; Eriksson & Klapwijk, 2019; Klapwijk et al., 2018). Forest owners tend to favour the harvesting of wood to produce forest products, while environmental groups tend to favour conservation, highlighting short-term carbon storage effects in standing forests and improvements in biodiversity (Eriksson & Klapwijk, 2019). Continued debate surrounds the share of set-aside forests required to ensure the protection of wildlife habitats and associated wild species (Dinerstein et al., 2019; Ellis, 2019; Roberts et al., 2020) with some studies identifying important weaknesses in arguments favouring set-asides (Schulze, 2018; Schulze et al., 2022). Disagreements may also arise due to opposing views concerning short- vs. long-term climate objectives, expectations regarding society's future dependence on carbon-based energy and materials, and whether these needs can be met in climate-friendly ways without using biomass (Berndes & Cowie, 2021; Cowie et al., 2021; Rodrigues et al., 2022).

In principle and with respect to the climate, forestry is considered an acceptable practice because wood supply is ideally and traditionally harvested when annual growth rates slow and mean annual carbon accumulation rates begin to plateau (Eriksson, 1976). When conducted under the conditions of sustainable harvest to growth ratios, forestry allows for harvest without comparable C stock declines. Moreover, because younger forests sequester more carbon and net rates of carbon sequestration decline as forests get older (Gao et al., 2018; Holdaway et al., 2017; Repo et al., 2021), it is preferable from a mitigation perspective to harvest growth and produce forest products that provide mitigation through product substitution and carbon storage in harvested wood products (HWPs). In line with existing regulations, forests are immediately and actively regenerated after harvest in Sweden, and carbon sequestration in young forests increases rapidly turning forests into net carbon sinks in 5–20 years (Misson et al., 2005; Rebane et al., 2019). Growth rates and timber production can further be improved by increased regeneration efforts, the use of improved plant material, fertilization, forest thinning and planting density modifications (Högberg et al., 2017; Nilsson et al., 2011; Kauppi et al., 2022).

Forest set-asides are proposed both as a means for providing biodiversity protection as well as for increasing climate change mitigation potential through carbon sequestration in forests. Immediate biodiversity goals are best achieved with older forests (Gao et al., 2015; Martikainen et al., 2000) and the common practice in Sweden is to set aside remote, little-used forests and older high biodiversity potential forests (much like the primary forests highlighted in the *EU Biodiversity Strategy for 2030*). However, such older forests can weaken the potential short- to medium-term climate change mitigation benefits many anticipate due to the likely trade-offs with biodiversity-driven set-aside goals.

UNFCCC *reporting* and EU LULUCF *accounting* rules favour and even encourage net removals in standing forest and land set-asides. By constraining harvest levels (Forest Reference Level, FRL), disincentivizing benefits for promoting additional forest growth (cap) and not linking mitigation benefits from wood use with the forest sector, both UNFCCC *reporting* and EU-level carbon *accounting* create disincentives to additional climate change mitigation (Ellison et al., 2014, 2020; Nabuurs et al., 2017). UNFCCC *reporting* outcomes, however, are reputational in character and do not weigh heavily on individual Parties. EU *accounting* outcomes, on the other hand, can result in penalties (i.e. debits). Parties (or EU Member states) who fall short of their commitments are expected to purchase surplus carbon credits from other Parties/countries.

By displacing fossil fuels, the use of forest biomass for energy helps countries meet their UNFCCC targets and provides real, positive contributions to mitigation. However, UNFCCC reporting focuses only on the net change in forest carbon pools and does not assess effects beyond the impact on carbon pools. All biomass used for bioenergy and HWPs which substitute other products are considered 'oxidized' and fully accounted as 'harvest'. Since harvest is already accounted as a decline in living biomass (i.e. an emission), to avoid double-counting emissions, the combustion of tree biomass is accounted as zero in the energy sector. Although the biomass use for energy results in 'avoided emissions', these are not attributed to the LULUCF sector.

EU LULUCF carbon accounting similarly does not credit the LULUCF sector for avoided emissions, via substitution of fossil fuels, cement, etc. in other sectors. Furthermore, the EU LULUCF regulation (2018/841) creates a separate LULUCF pillar which limits the role of climate-promoting incentives by making it possible to regulate 'flexibility' (the trading/offsetting of credits/debits) across sectors. By limiting the impact of LULUCF on other sectors of the climate policy framework, setting limits on forest resource use with the FRL, and placing a crediting cap on managed forest land (MFL), the EU policy framework represents one of the most restrictive LULUCF frameworks in the world. For another, debits are imposed for harvesting beyond (i.e. for failing to achieve) the FRL. These strategies explicitly discount and set strict limits on the offsetting potential of the forest and forest resource-based sector. Likewise, not achieving the FRL (no-debit rule) is perceived as a policy failure (Solberg et al., 2019). The EU LULUCF regulation does, on the other hand, promote long-lived HWP-based carbon sequestration. The remaining components of the carbon accounting framework, however, fail to incentivize the climate benefits of forest growth and substitution (Ellison et al., 2013, 2014, 2020; Nabuurs et al., 2017).

In the current study, we assess how different forest management strategies in Sweden influence the forest carbon stock and wood harvest over time. Forest management strategies are discussed in relation to their climate change mitigation potential, while possible climate change impacts on forests are also considered. More specifically, the study aims to analyse:

- the role of forests and forestry by comparing how atmospheric CO_2 concentrations are affected over different timescales by carbon storage in forests and HWPs, and by substitution (given a fixed management system)
- forest protection, nature conservation and their long-term impacts on forest-based climate change mitigation
- the potential for increased fertilization to sustainably increase net CO_2 substitution and removals
- the potential benefits and/or increased risks associated with a changing climate on mitigation (we simulate both positive and negative effects on growth due to a rise in global temperatures and potential nutrient deprivation)
- the differences between the *real* effect of forests and forestry on atmospheric CO_2 concentrations and the *reported* and *accounted* climate reporting estimates implied by different accounting frameworks

2 | MATERIALS AND METHODS

2.1 | Scenarios at National Scale: Modelling of biomass, carbon flows and pools

To study the cumulative climate impacts of harvest and stocks in standing forest over time in Sweden, national-level scenarios were generated using the empirical Heureka RegWise decision support system to simulate the future given initial natural resources, biological limitations on growth and assumptions about forest management practices (Wikström et al., 2011). Modelled growth is conditioned by measured site fertility and the initial stand at the beginning of the simulation. These two factors are set by the measured data on sample plots inventoried by the Swedish National Forest Inventory (NFI). The Swedish NFI compiles detailed, robust and constantly updated information about the state of the forest. Multiple types of data are recorded at tree, site and stand level and data quality is checked in several steps after the inventory. The models for basal area growth, mortality and ingrowth (with varying growth equations for young stands, productive forests, unproductive stands [growth less than 1 m^3/ha/year] and natural mortality) are empirical in character and build primarily upon data from NFI permanent plots.

For all scenarios, the initial state is set by adopting the existing measured data on the permanent sample plots of the Swedish National Forest Inventory (NFI) in 2010 (Fridman et al., 2014). The Swedish NFI employs area-based sampling on 30,000 permanent sample plots and each sample plot measures 10 m in radius. All plots together represent the total land and freshwater area of Sweden. The NFI is an annual, systematic cluster-sample inventory organized as a systematic grid of sample clusters. The square-shaped clusters are distributed in a denser pattern in the southern than in the northern part of the country. Each cluster consists of four to eight sampling plots. Each sample plot is occasionally delineated into more than one land-use category. A variety of tree, stand and site variables are registered on the plots. On each plot, all trees with DBH $\geq$ 4 cm are calipered, height is measured and sample tree damage recorded. Dead wood with diameter $\geq$ 10 cm is calipered and stumps are measured (Marklund, 1987; Näslund, 1947; Petersson & Ståhl, 2006). Land use is assessed in the field with the help of site and stand variables and the existing vegetation cover.

The NFI data used to simulate these scenarios consist of many parameters. Stem volume and living tree biomass starting in 2010 are estimated with the help of allometric equations (Marklund, 1987; Näslund, 1947; Petersson & Ståhl, 2006; Wikström et al., 2011). The dead wood state is measured on the plots (Lundblad et al., 2021; Sandström et al., 2007). Changes in carbon pools (living biomass, dead wood, stumps, litter, soil and HWP) are estimated using the stock difference method (IPCC, 2006). Inflows to the HWP pool are estimated based on simulated harvest. All stem wood is harvested, and a proportion (equivalent to approximately 10 TWh) of tops and branches are also harvested for bioenergy. Stumps are not extracted. Since substitution factors are uncertain, we model the scenarios with three levels of substitution, where 1 m^3 harvested stem wood is assumed to result in 0.5, 1 and 1.5 tonnes of *avoided CO_2 emissions* (Leskinen et al., 2018; Lundmark et al., 2014). We return to the debate on substitution factors in the Discussion. Other emissions (Tables 2 and 3; IPCC 2006) are generally minor under Swedish conditions and were assessed as a constant emission of 0.096 $MtCO_2e$/year for all years and scenarios.

Heureka consists of several underlying models (e.g. stand growth, mortality and decomposition models). Decomposition and changes in pools for dead wood, litter and soils are modelled using the Q-model (Ågren et al., 1996). The Q-model is a process-based model that uses empirical data. The inflow of organic material is assumed to originate from dead organic matter after harvest, natural mortality and non-tree vegetation. Model parameterization settings for the four main Swedish climatic regions (see Figure S1) have been applied. For model initiation, carbon stock estimates from the Swedish Forest Soil Inventory were used as the starting point for a 20-year spin-up period preceding the actual simulation starting point. Inflow/turnover rates were modelled for branches, needles and root fractions, and constants assessed for grasses, herbs, shrubs, mosses and lichens. Inflows from harvest residues were estimated per fraction of needles, branches, stems, tops, stumps, roots and excluded stem wood. In Sweden, roundwood is harvested. But a small share of the stems is left on harvest sites. Natural mortality is empirically modelled. Stumps and harvest residues left in the forest are assumed to decompose at an annual rate of 4.6% (Melin et al., 2009) and 15% (Lundblad et al., 2021) respectively. The Q-model is only applied to mineral soils, and emissions from drained organic soils are estimated using activity data (area) multiplied by emission factors. Different emission factors are used per nutrient status and climate region (Lundblad et al., 2021).

Fahlvik et al. (2014) demonstrate that the growth and mortality modelling in Heureka generates reliable results. The specification of forest management between two consecutive points in time may include, for example, fertilization, harvest type and intensity, regeneration type and areas set aside for nature conservation. An algorithm (based on forest owner behaviour identified on NFI sample plots) was used to select stands for harvest. Given regular harvests and no natural disturbances, we assume that no unknown variable would change the principal findings. As with all empirical models, precision diminishes if the aim is to simulate the development under circumstances that deviate from the prevailing circumstances at data collection. The positive climate effects from assuming the IPCC scenario RCP 4.5, for example, rely on process-based assumptions. The future climate impact on tree vitality and growth, however, is uncertain.

2.2 | Scenarios for future forest management—Scenario model specification

To study the cumulative climate impacts of harvest and standing forest-based stocks over time in Sweden, future developments are simulated using five different scenarios. The total Managed Forest Land (MFL) area was estimated at 27.5 Million hectares (Mha) in 2010. MFL was further subdivided into productive (average growth >1 m^3/ha/year; around 23.4 Mha) and unproductive MFL (average growth <1 m^3/ha/year, around 4.0 M ha). Productive forests consisted of approximately 19.8 Mha of forests used for wood supply and another 3.6 Mha of formally and voluntarily protected forests in which harvest was and is not permitted. Low productive forests were also considered 'protected'. In total, 7.6 Mha have been protected and excluded from harvest, representing approximately 28% of total MFL.

We focus on MFL defined as forest land remaining forest land (e.g. Lundblad et al., 2021), that is, we include land-use conversions to forest land and exclude forest land converted to other land-use categories. Land transitions from and to MFL are simulated based on the average conversion rate over the period 1990–2017 (Lundblad et al., 2021; afforestation rates are approximately 15 kha/year and deforestation rates 11 kha/year). Land actively converted to forested land is first classified as Afforested Land for 20 years and thereafter included under MFL. Land actively converted from MFL is immediately considered and reported as Deforested Land for 20 years and thereafter reported in the land category it was converted to.

In all scenarios, we assume 100% of the growth on productive MFL used for wood supply, minus self-mortality, is harvested. We assume zero harvest in protected forests. We further assume an equilibrium stem volume (biomass)

TABLE 1 Scenarios and objectives

Scenarios	Assumptions
Maximum Potential Harvest	Base scenario
Increased Nature Conservation	Study effects of increasing forest land set-asides (3.7 Mha)
Increased Fertilization	Fertilization (restricted by law)
Negative Climate Effects on Growth	Double mortality
Positive Climate Effects on Growth	Growth based on IPCC RCP 4.5 scenario

will emerge, as well as a steady state on land set-asides after approximately 200 years. Table 1 provides an overview of the five scenarios and their objectives.

In the *maximum potential harvest* scenario, areas of different land-use classes as well as management practices (excluding harvest intensity) are assumed to simulate the conditions specified by the Forest Agency for the period 2000–2009 (Claesson et al., 2015; Forest Agency, 2008, 2015). This scenario is closely modelled on a previous scenario analysis of Swedish Forest Reference Level (FRL) options (Lundblad, 2018) and is described in more detail in a companion document (Petersson et al., 2022). To study the consequences of setting aside additional MFL for nature conservation, we assume an additional 3.7 Mha of mainly productive MFL is set aside for nature conservation in the simulation. This amount is equivalent to approximately 18.5% of currently available, productive MFL, bringing the total protected forest area to 11 Mha. In the *increased nature conservation* scenario, except for the area set aside for nature conservation, all parameters remain the same as in the *maximum potential harvest* scenario. In the increased conservation scenario, we assume comparatively younger forest set-asides.

To study the consequences of increased investments in forestry on net removals in carbon pools and substitution of fossil fuel-based alternatives, we simulate the *increased fertilization* scenario. This model specification represents a moderate fertilization scenario approximating established fertilization practices on a larger area, but within the legal fertilization guidelines. Established fertilization mainly targets, older, middle-aged Scots pine stands after thinning, around 10 years before final felling (Högberg et al., 2014; Jacobson & Pettersson, 2010). The simulated fertilized area is thus about 200 kha per year or approximately 1% of productive MFL, roughly seven times more fertilization than assumed in the other scenarios. The simulated fertilization thus considers the effect of a one-time addition of 150 kg N/ha (ammonium nitrate). Apart from fertilization, all other parameter settings are identical with the *maximum potential harvest* scenario.

To study the potential risks of negative climate effects on growth, net removals in carbon pools and assumed substitution of fossil fuel-based alternatives, we modify the *maximum potential harvest* scenario by assuming a doubling in natural mortality. For the *negative climate effects on growth* scenario, all other parameter settings remained identical (currently mortality is estimated at around 11% of the growth in Sweden; Forest Statistics, 2021). To estimate the potential consequences of positive climate effects on tree growth, we use the corresponding IPCC RCP 4.5 pathway (IPCC, 2013) to simulate the *positive climate effects on growth* scenario. Using the process-based model BIOMASS (McMurtrie et al., 1990), the IPCC RCP 4.5 pathway has been calibrated for Swedish conditions (Bergh et al., 1998, 2003). The principal components for the process-based growth adjustment comprise age, basal area, site index, vegetation index and temperature sum. In both the negative and positive climate effects scenarios, all other parameter settings remain identical.

3 | RESULTS

In the *maximum potential harvest* scenario (Figure 1), after around 200 years both stocks (storage) and growth become linear. This equilibrium finding occurs because we assume 100% harvest of the net growth on MFL and 0% harvest in protected forests. After peaking, the constant annual sustainable harvest is estimated at 99 Mm^3/year. After 200 years, approximately two forest rotation periods, the cumulative harvest is 4.3 times greater than stocks (we assume mortality is emitted to the atmosphere through decomposition). Total gross growth is estimated at 119 Mm^3/year, similar to current gross growth in Sweden (Forest Statistics, 2021). Assuming forests remain viable over the very long term, this relationship is expected to continue in a linear fashion over time.

In the *increased nature conservation* scenario (Figure 1), on the other hand, after peaking, the constant annual sustainable harvest (growth) is estimated at 85 Mm^3/year. The long-term loss in forest growth from setting aside an additional 3.7 Mha of productive forest land for nature conservation compared to the *maximum potential harvest* scenario is 14 Mm^3/year, from peak to perpetuity (a loss of 3.8 m^3/ha/year of additional forest growth per year over the entire scenario period). Since the two scenarios generate similar total amounts of forest growth, after 200 years, estimated stocks + cumulative mortality + cumulative harvests were not significantly different. An important share of the growth in the *increased nature conservation* scenario, however, is lost to cumulative mortality and eventually becomes an emission. In the *maximum potential harvest* scenario, on the other hand, less growth is

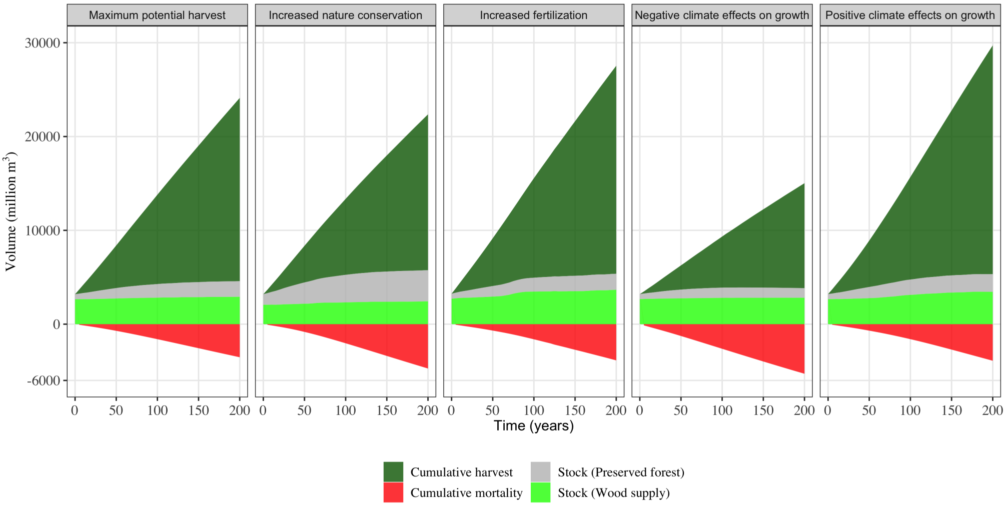

FIGURE 1 The simulated cumulative stem volume [Mm^3] stored in MFL forests, cumulative harvest and (decomposed) cumulative mortality over a period of 200 years, assuming that 100% harvest of net growth in MFL is used for wood supply and no harvest in preserved forests. In all scenarios, after 200 years, cumulative harvest is greater than storage. From a pure climate perspective, if harvest is used for substitution or storage (where no decomposition occurs), harvesting mature trees and using *maximum potential harvest* provides greater climate benefits than storing carbon in standing forests. This is explained by the higher mortality in the *increased nature conservation* scenario (compared with the *maximum potential harvest* scenario). The *increased fertilization* scenario simulates the possibility that intensive forest management may increase the climate benefits associated with forest use. Finally, the *negative* and *positive climate effects on growth* scenarios simulate outcomes depending on whether climate change is negative or positive for tree growth. Since 100% of the net growth is harvested, after peaking at 200 years, the yearly additional growth for harvest remains linearly constant

lost and mortality is substantially lower. In the *increased nature conservation* scenario, more volume is also stored in the forest and harvest is smaller than in the *maximum potential harvest* scenario.

In the *increased fertilization* scenario (Figure 1), after 200 years, the long-term harvest increases to approximately 112 Mm^3/year (Figure 1), or approximately 13 Mm^3/year more than in the *maximum potential harvest* scenario (and about 27 Mm^3/year greater than in the *increased nature conservation* scenario). As noted above, however, since significant restrictions on the use of fertilization apply, fertilization is only simulated on approximately 1% of available MFL.

The *negative climate effects on growth* (Figure 1) and the *positive climate effects on growth* (Figure 1) scenarios both suggest powerful impacts on forest-based mitigation potential. After 200 years, total sustainable harvest growth was significantly lower under the *negative climate effects on growth* scenario (57 Mm^3/year) and emissions from mortality were higher. On the other hand, the *positive climate effects on growth* scenario, primarily because this scenario affects all MFL equally, resulted in the highest sustainable harvest levels and the largest cumulative impact (137 Mm^3/year).

Table 2 provides more detailed information on the direct climate impact/benefit of change across all carbon pools in the *increased nature conservation* and *maximum potential harvest* scenarios over the same 200-year period, expressed in terms of their climate impact in carbon equivalents (MtCO$_2$e/year). In the short term (i.e. by 2025), the climate benefits are similar in both scenarios. However, in the long term, i.e., after the carbon pools peak within a period of approximately 200 years, significant differences arise between the two scenarios. In this case, the climate benefit in the *maximum potential harvest* scenario is 16% greater per year (−99.5 MtCO$_2$e/year) than in the *increased nature conservation* scenario (−85.6 MtCO$_2$e/year). The climate benefit from the *maximum potential harvest* scenario is −99.5 MtCO$_2$e/year from peak to perpetuity, an amount greater than the benefit from *increased nature conservation* by −14 MtCO$_2$e/year. Setting aside an additional 3.7 Mha MFL for nature conservation thus reduces the growth/harvest cycle in the circular bioeconomy, thereby impacting future mitigation opportunities.

The results in Table 2 are further sensitive to the assumed substitution effect (here 1 m^3 to 1 tonne CO$_2$e). Depending on the assumed rate of substitution, projected outcomes for the total annual net forest-related impact on

TABLE 2 Total climate benefit across carbon pools for the increased nature conservation and maximum potential harvest scenarios, given a '1 to 1' substitution effect (the shaded year corresponds to the 2021–2025 reporting period under EU/2018/841)

	Increased nature conservation (maximum potential harvest) [M tonne CO_2/year]								
Year	Living biomass	Soil litter	Other emissions	(stumps) Dead wood	(Lying/Standing) Dead wood	Long-lived HWP	Short-lived HWP	'1 m^3 to 1 tonne CO_2' substitution harvest	Sum
10	−26.8 (−11.6)	−5.41 (−4.47)	0.10 (0.10)	−1.14 (−3.23)	−2.97 (−2.47)	−2.79 (−4.65)	0.05 (−0.52)	−77.9 (−89.0)	−117 (−116)
15	−33.3 (−16.9)	−5.32 (−5.44)	0.10 (0.10)	−0.02 (−2.25)	−2.63 (−2.07)	−1.96 (−3.88)	0.27 (−0.25)	−75.3 (−88.1)	−118 (−119)
30	−31.3 (−17.1)	−3.40 (−1.87)	0.10 (0.10)	−1.50 (−2.24)	−2.47 (−1.52)	−2.29 (−3.30)	−0.43 (−0.44)	−80.3 (−92.3)	−122 (−119)
50	−22.9 (−13.8)	−3.74 (−0.97)	0.10 (0.10)	−1.47 (−1.97)	−2.28 (−1.21)	−0.83 (−1.45)	−0.54 (−0.56)	−83.5 (−96.5)	−115 (−116)
70	−18.3 (−9.38)	−2.34 (0.20)	0.10 (0.10)	−1.27 (−1.33)	−2.07 (−1.06)	−1.11 (−1.29)	−0.37 (−0.17)	−84.4 (−99.7)	−110 (−113)
90	−14.2 (−7.78)	−0.87 (0.86)	0.10 (0.10)	−0.49 (−0.92)	−1.36 (−0.73)	−0.66 (−1.26)	−0.04 (−0.14)	−84.9 (−101)	−102 (−111)
110	−10.5 (−5.58)	−0.81 (0.39)	0.10 (0.10)	−0.40 (−0.48)	−0.81 (−0.51)	−0.64 (−1.17)	0.03 (−0.07)	−86.0 (−101)	−99.0 (−109)
130	−7.33 (−2.79)	−1.00 (0.69)	0.10 (0.10)	−0.29 (−0.30)	−0.48 (−0.25)	−0.19 (−0.44)	−0.01 (−0.03)	−85.8 (−101)	−95.0 (−104)
150	−3.36 (−3.46)	−0.38 (0.35)	0.10 (0.10)	0.26 (0.22)	−0.10 (−0.06)	0.02 (−0.14)	0.07 (0.07)	−84.7 (−99.6)	−88.1 (−103)
170	−0.26 (−0.97)	0.36 (0.76)	0.10 (0.10)	−0.40 (−0.23)	0.13 (0.06)	−0.20 (−0.29)	−0.12 (−0.07)	−86.5 (−101)	−86.8 (−101)
190	−3.34 (−1.62)	−0.02 (0.86)	0.10 (0.10)	0.49 (0.26)	0.24 (0.15)	0.19 (−0.19)	0.16 (0.10)	−83.4 (−99.1)	−85.6 (−99.5)

climate change mitigation vary dramatically (see Figure 2). In most cases, however, the short-term impact of setting aside an additional 3.7 Mha of land for nature conservation is relatively minor compared to the long-term impact of forest use, carbon sequestration in long-lived products and substitution. Only in the most conservative case (1 to 0.5) is the additional carbon sequestration in standing forests simulated by the *increased nature conservation* scenario greater in the short term than the sequestration/substitution impact of *maximum potential harvest*. The difference in impact is measured as the space between the *increased nature conservation* impact (blue line) and the *maximum potential harvest* impact (green line). As the estimated sequestration/substitution impact increases in size, however, the respective substitution benefits of *maximum potential harvest* increase relative to the *increased nature conservation* scenario. In the Discussion section, we further elaborate the logic behind different estimated substitution impacts.

The *positive climate effects on growth* and *increased fertilization* scenarios likewise have very large, continuous impacts on the total net annual sequestration/substitution potential. While the *positive climate effects on growth* are larger, due to legal restrictions in Sweden, we assume fertilization only on a total of 1% of the available MFL in the *increased fertilization* scenario. The *positive climate effects on growth* scenario, however, is not similarly restricted in extent. We cannot really say, however, what might happen if fertilization were permitted on an additional 10% or more of the Swedish MFL (see, however, the example of Gustavsson et al., 2021).

4 | *REPORTING* AND *ACCOUNTING* RULES IMPACT ON MITIGATION INCENTIVES

Table 3 highlights the UNFCCC and EU level *reporting* and *accounting* consequences of the respective LULUCF frameworks based on each of the five simulated scenarios for the period 2021–2025. Ideally, the optimal choice is the scenario that both sequesters the most carbon over both the short and the long term and has the greatest potential climate impact. Based on the scenario results, the short-term benefits of increased nature conservation are marginal, while the potential long-term gains from the maximum potential harvest scenario are significantly greater. However, as noted in the Introduction both the UNFCCC *reporting* and the EU *accounting* frameworks ignore the LULUCF role in the climate effects that arise from the avoided emissions associated with HWP carbon sequestration, product substitution and bioenergy use. Considering this factor, it may make more sense to pursue long-term strategies.

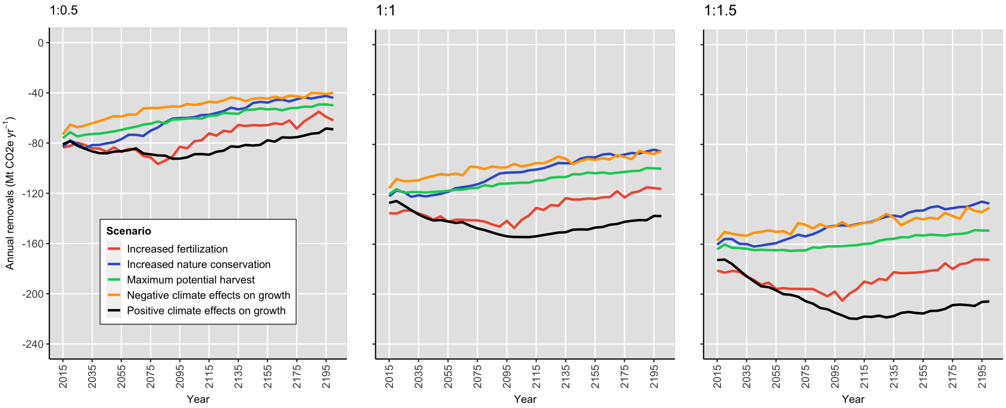

FIGURE 2 Total annual estimated net carbon sequestration and substitution, selected scenarios (2015–2195). The scenarios include changes in all carbon pools (see Table 2) and substitution for three different assumed substitution effects (0.5, 1 and 1.5 tonne CO_2e per m^3 stem wood)

Both UNFCCC reporting and EU accounting, however, encourage short-term impacts. As highlighted in Table 3, both for the UNFCCC *reporting* framework and the EU *accounting* framework, the scenario yielding the largest benefits is *increased nature conservation*: this strategy provides −42.9 $MtCO_2$e/year in UNFCCC reporting benefits and −1.1 $MtCO_2$e/year in EU accounting benefits. The principal difference between the UNFCCC and EU outcomes derives from the decision to harvest 100% of the annual net increment. Since the EU accounting framework penalizes harvesting above the FRL, this framework yields an emission in all the scenarios except increased nature conservation. Harvesting less to fulfil the FRL would improve accounted removals in all cases but would not alter the linear relationships between the different scenarios and would not change the substitution-related benefits from harvesting the full amount. Moreover, this would only serve to further raise lost net potential harvest to a point further below the increased nature conservation scenario over the longer term (since this amount is greater than the set-aside amount of forest). Harvesting less (this is the direct FRL impact) is essentially 'equivalent' to increasing the relative share of protected forest and would yield mitigation outcomes comparable to those predicted by this scenario, with a comparable reduction in the substitution effect. Apart from the *negative climate effects on growth* scenario, both reporting and accounting frameworks (UNFCCC and EU) encourage LULUCF sector strategies that will, in the long term, provide smaller total climate benefits relative to the alternatives.

Depending on future substitution effects, the long-term mitigation loss from adopting an *increased nature conservation* scenario may become significant. Given constant climate conditions, compared to the *maximum potential harvest* scenario and based on 1 to 1 substitution, the *increased nature conservation* scenario provides climate benefits of approximately −85.6 $MtCO_2$e/year, while the *maximum potential harvest* scenario provides −99.5 $MtCO_2$e/year from peak to perpetuity. If we consider the potential climate effects across variation in the substitution effect, the opportunity costs of failing to choose either the *maximum potential harvest* or the *increased fertilization* scenarios may be substantially greater.

5 | DISCUSSION

Forest management in Sweden involves harvesting (final felling) about 1% of total MFL per year and legally requires immediate, active regeneration after harvest (Forest Agency, 2020a, 2020b). Tree species composition has not been significantly altered over the course of the 20th century (Forest Statistics, 2021), but there is concern about a gradual decline in old growth forests (Jonsson et al., 2019). Furthermore, the targeting of biologically young stands for harvest may limit the delivery of several ecosystem services, resulting in less multifunctional forest (Jonsson et al., 2020). In parallel with increasing wood harvesting levels, forest management has resulted in significant increases in forest carbon stocks. Following a historic period of declining forest resources, forests in Sweden have continuously accumulated carbon since the early 1920s, resulting in more than a doubling of carbon stocks over the past century (Forest Statistics, 2021; see also Kauppi et al., 2022). The focus on forest policies and management strategies has, over time, integrated

TABLE 3 UNFCCC *reported* and EU *accounted* LULUCF impacts relative to their pure climate change mitigation effects, 2021–2025

UNFCCC Reporting	**NET change in pools [M tonne CO_2/year]**						**REPORTED**
Sweden: MFL 2021–2025							
Scenario	**Living biomass**	**Soil litter**	**Other emissions**	**Dead wood**	**Long-lived HWP**	**Short-lived HWP**	**Total**
Maximum Potential Harvest	−16.9	−5.4	0.1	−4.3	−3.9	−0.2	−30.7
Increased Nature Conservation	−33.3	−5.3	0.1	−2.7	−2.0	0.3	−42.9
Increased Fertilization	−9.3	−4.7	0.1	−7.7	−6.1	−1.2	−28.9
Negative Climate Effects on Growth	−10.6	−5.7	0.1	−5.6	−3.3	−0.1	−25.2
Positive Climate Effects on Growth	−19.1	−5.8	0.1	−5.6	−4.4	−0.5	−35.3

EU Accounting	**NET change in pools relative to the required Reference Level [M tonne CO_2/year]**						**ACCOUNTED**
Sweden: MFL 2021–2025							
Scenario	**Living biomass**	**Soil litter**	**Other emissions**	**Dead wood**	**Long-lived HWP**	**Short-lived HWP**	**Total**
Maximum Potential Harvest	13.4	−4.0	0.0	−1.6	−0.6	0.8	8.1
Increased Nature Conservation	−3.1	−3.8	0.0	0.1	1.3	1.4	−1.1
Increased Fertilization	20.9	−3.2	0.0	−5.0	−2.8	−0.1	9.9
Negative Climate Effects on Growth	19.6	−4.2	0.0	−2.8	0.0	1.0	13.5
Positive Climate Effects on Growth	11.1	−4.3	0.0	−2.9	−1.1	0.6	3.4
Reference Levels (effective caps)	−30.2	−1.5	0.1	−2.7	−3.3	−1.1	−38.7
	(cap)	(cap)	(cap)	(no cap)	(no cap)	(cap)	(Total FRL)

1 m^3 to 0.5 tonne CO_2		**1 m^3 to 1.0 tonne CO_2**		**1 m^3 to 1.5 tonne CO_2**	
Harvest	**Total climate effect**	**Harvest**	**Total climate effect**	**Harvest**	**Total climate effect**
−44.0	−75	−88.1	−119	−132.1	−163
−37.6	−81	−75.3	−118	−112.9	−156
−50.8	−80	−101.7	−131	−152.5	−181
−42.1	−67	−84.2	−109	−126.4	−152
−46.8	−82	−93.6	−129	−140.4	−176

Changes in carbon pools are reported to the UNFCCC. For MFL, changes in carbon pools, living biomass, soil + litter, other emissions and short-lived HWP are accounted with a cap compared to the FRL, while dead wood and long-lived HWP are accounted without a cap compared to the FMRL (under CP2). For Sweden, the cap, which limits credits from MFL, is −2.5 M tonnes CO_2e/year. The total climate effect is calculated as the reported net change in carbon pools, plus the substitution effect. Three alternative substitution effects have been used.

securing wood supply for the forest industry with other objectives, such as climate change mitigation and adaptation, biodiversity conservation, social aspects and water resource management (Eriksson et al., 2018).

As highlighted in Figure 3, forest stands are traditionally harvested when annual growth rates decline and mean annual carbon accumulation rates begin to plateau (Eriksson, 1976). For a given site in Sweden, the optimal harvest should occur after the year annual growth culminates. The optimal rotation period is the period which maximizes growth (or carbon uptake) in trees. On average, this occurs after approximately 100 years of growth and carbon sequestration (Figure 3), later in the North and earlier in the South. After this peak, each additional year of forest growth sequesters less additional carbon. Harvesting at later than optimal time points is thus assumed to yield declining amounts of additional biomass and slowing rates of carbon uptake. In the long term and moving from an approximately even-aged stand distribution to the landscape scale, carbon uptake will eventually become equal to decomposition rates, yielding a steady state, net zero rate of carbon sequestration. Over time, older forests therefore provide no significant additional mitigation benefit via carbon sequestration.

From a climate perspective, the impact of forestry is typically considered acceptable because, given an even-aged stand distribution, constant fertility over the forest landscape and maximum harvest at the optimal rotation period for all stands, net marginal tree growth will eventually stop increasing (saturation point). This point defines a steady-state equilibrium where tree growth and harvest removals are essentially balanced and equal at the landscape scale. The *maximum potential harvest* scenario (Figure 1) illustrates that after around 200 years both stocks (storage) and growth become linear, reflecting this equilibrium prediction. Harvesting after the saturation point ultimately means the loss of additional net growth potential in replanted forest. Although equilibria can be affected by 'natural disturbances' such as insect attacks, wildfires and storms (Forzieri et al., 2021; Senf et al., 2020; Senf & Seidl, 2021a, 2021b), the concept of a more or less stable, long-term equilibrium potentially remains relevant (Eliasson et al., 2013). However, as discussed below, there are many uncertainties.

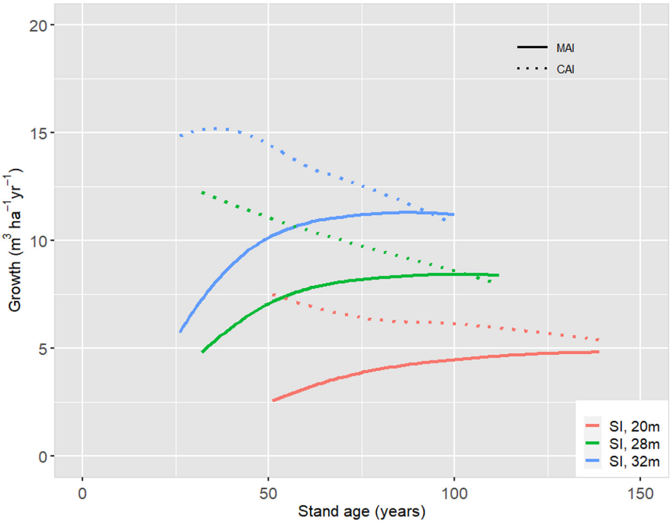

FIGURE 3 Measured development of mean annual and current annual increment in three common Norway spruce stands. SI = "site index" and refers to tree height at 100 years (considering total tree biomass, 1 m^3 stem wood roughly corresponds to 1.4 tonnes CO$_2$e). *Notes*: After stand establishment, a tree stand first grows slowly, then more rapidly, then peaks, and after this point the growth rate begins to decline. The optimal rotation period which maximizes growth occurs when the MAI line crosses the CAI line. Growth will be lost if harvest occurs before or after this optimization point. Current annual increment (CAI) is the total annual growth in any given year. Mean annual increment (MAI) is the average annual growth a stand exhibits at a given age and is calculated as the cumulative growth divided by the stand age. The figure is based on measured data and supports the theory of growth in tree stands (Eriksson, 1976)

5.1 | Growth in older forests

One possible objection to this analysis arises from the literature on old growth forests. Suggestions that old-growth forests arrive at a steady state with stable C stocks have been challenged with evidence that old-growth forests continue to act as C sinks (Hadden & Grelle, 2016; Luyssaert et al., 2008; Seedre et al., 2015). Measurements over entire landscapes or long-term stand measurements may, however, provide more robust determinations about old growth forests (Gundersen et al., 2021; Luyssaert et al., 2021). Based on data from 874 forest plots, Holdaway et al. (2017) estimated biomass growth and identified drivers for biomass change in old-growth forests and secondary managed forests in New Zealand. Over the period 2002–2014, a significant biomass increase was detected in the secondary forest, whereas no significant change was detected in the old-growth forest. The drivers for biomass growth in the secondary forest were growing stock (biomass) and past disturbance, while growth in old-growth forests was determined by recent disturbance (mortality among large trees). This pattern is confirmed by Derderian et al. (2016) who resampled a 700-year chronosequence in Colorado (US) and discovered that C stocks, due to high spruce tree mortality caused by a bark beetle attack, had declined compared to 30 years earlier, despite the fact that net C uptake was recorded at both sampling occasions.

A recent study conducted by a team of 25 scientists appointed by the International Boreal Forest Research Association (IBFRA) (Högberg et al., 2021) found substantially increased C stocks in living tree biomass from 1990 onwards in the more intensively managed, higher harvest Nordic countries, as compared to the boreal forests in Canada, Russia and Alaska, where C stocks have remained stable or even declined (Alaska). A partial explanation was C losses due to forest fires in the less intensively managed boreal forests, together with fire protection measures in the Nordic countries, which maintained annual burned area well below natural conditions. Sharma et al. (2013) demonstrate that national parks in Canada with large shares of old-growth forests have large C stocks and low annual CO_2 uptake, whereas parks with large shares of younger forests, due to natural disturbances, have reduced but still large C stocks and comparatively high annual CO_2 uptake. Thus, while C stocks can be preserved in national parks, large C stocks have limited mitigation potential.

In another recent study, based on data from the Norwegian NFI, the rapid drop in current annual increment (CAI) at a certain age (cf. Figure 3) was challenged (Stokland, 2021a). The methodology behind that study has been questioned (Brunner, 2021), but Stokland defends his findings and suggests more studies looking into the fate of CAI after the point where CAI crosses MAI are needed (Stokland, 2021b). A more stable CAI over several decades would, from a climate mitigation perspective, speak for extended rotation periods in managed forests. However, with the exception of very poor sites that illustrate flatter CAI development with age, another recent study based on the Finnish NFI confirms the rapid drop in CAI and hence in MAI (Repo et al., 2021).

One might consider the old forest sink issue a ‘red herring’ in the sense that the question whether forests eventually reach a steady state or continue to sequester more carbon each year distracts from the more relevant questions: (1) How much mitigation per hectare can old forest landscapes generate?; and (2) is the mitigation per hectare large or small compared to the mitigation from an average hectare of forest managed to maintain net forest growth at high levels under sustained harvest practices?

5.2 | Can increased fertilization provide additional climate benefits?

Although the *increased fertilization* scenario increased growth from about 99 (*maximum potential harvest* scenario) to about 112 Mt CO_2e/year, fertilization was only applied on 1% of the forest area per year. This raises interesting questions about the possible outcome of greatly increasing MFL fertilization rates. Due to legal restrictions in Sweden, we have only simulated small changes in older forests fertilized about 10 years before final felling. Gustavsson et al. (2021), however, have investigated a more intensive fertilization scenario in which growth increased by 40% after 100 years. Presumably there is great potential to increase growth with the help of fertilization. In the same study, Gustavsson et al. (2021) ran a scenario where as much as 50% of the forest land area was protected. Fertilization may thus provide an opportunity to preserve larger areas for biodiversity while simultaneously managing other forest areas more intensively, thereby maintaining total growth.

5.3 | Consequences of a changing climate

Despite the perceived benefits of climate change for forest growth, considerable uncertainty surrounds the possible positive and negative climate effects on future growth. For the Nordic boreal forests, the prevailing assumption is that gradual climate change will be positive for growth due to higher temperature, precipitation, atmospheric nitrogen deposition and extended growing seasons (Appiah Mensah et al., 2021; Etzold et al., 2020; Henttonen et al., 2017; Kauppi et al., 2014; Keenan, 2015; Kellomäki et al., 2008; Koca et al., 2006; Tamm, 1991). Compared to current levels in Sweden, climate effects suggest positive future productivity increases of about +300% and +100% in the northern and southern regions, respectively, resulting in shorter rotation periods (Bergh et al., 2005). Forested northern regions are expected to expand further northward and into higher elevations, yielding larger areas of forest cover and increasing forest density (Claesson et al., 2015). However, we have not modelled these expanding growth patterns with the Heureka model.

Climate-related factors can, however, challenge the positive effects of CO_2 fertilization and longer growing seasons (Hanewinkel et al., 2013; Reyer et al., 2017). Both negative and positive growth responses have been measured across the Canadian forest landscape (Girardin et al., 2014; Taylor et al., 2017). Changes in water availability provided one possible explanation for these divergent responses. Water availability could further level out or reverse positive effects on growth in boreal tree species (Reich et al., 2018). Likewise, nutrient availability has also been singled out as a potential explanation for not benefitting from these increased concentrations (Hyvönen et al., 2007; Norby et al., 2010; Sigurdsson et al., 2013).

Extreme and frequent changes in abiotic conditions could have damaging effects on trees, thereby affecting growth capacity in succeeding years (Keenan, 2015). Tree growth rates in Sweden, for example, were found to be about 20% lower than expected in 2018 due to summertime hot and dry conditions (personal communication, Swedish NFI). While temperature effects on tree growth can be severe, precipitation effects may be minimal during the growing season due to the recharge of the ground water table from melted winter snow (Bergh et al., 2005). Increases in evapotranspiration may result in more persistent drought during the growing season, potentially counteracting growth (Koca et al., 2006). Higher groundwater levels and shorter winter soil frost seasons may increase the risk of storm damages and soil damages from off-road timber transport (Oni et al., 2017). On the other hand, events such as storms, frosts and droughts can trigger wildfires, pest and disease outbreaks (e.g. root rot and bark beetles) that may reduce forest growth and productivity (Björkman et al., 2011; Blennow & Olofsson, 2008; Subramanian et al., 2015). For example, Pinto et al. (2020) found that both climate and vegetation correlate with fire size, whereas human-related landscape features shape ignition patterns.

Increasing disturbances from wind, bark beetle and wildfires at European level (Seidl et al., 2014), may become greater concerns in Sweden. From a Swedish perspective bark beetle attacks by the spruce bark beetle (*Ips typographus* [L]) are an identified threat—not least in the climate change context (Eidmann, 1992; Jönsson et al., 2009; Kärvemo et al., 2016). Incident rates and magnitude of forest damage by spruce bark beetle are higher in older stands (Martikainen et al., 1999). Under specific climatic conditions, forest growth could exhibit varied risks depending on stand age, development stage and management practice (Blennow, 2012).

Hence, both the boreal forest growth response and carbon cycle feedback to climate change remain uncertain. Adaptive forest management practices could be essential for mitigating negative effects, while maximizing forest growth and production (e.g. Bolte et al., 2009; Keenan, 2015). For instance, reducing the intensity of forest thinnings and rotation lengths has been suggested as the best practice to enhance stem volume production and the profitability of Norway spruce in southern Sweden due to reduced storm risk, root and butt rot (Subramanian et al., 2015).

5.4 | Substitution effects

The relative magnitude of substitution effects is key to the understanding of the mitigation effects of forest use and different forest products. At 'low' levels of substitution (1 m^3 to 0.5 tonne CO_2e), the *increased nature conservation* scenario performs better than the *maximum potential harvest* scenario up until approximately 2085. However, in later years and especially with larger substitution effects, the *maximum potential harvest* scenario quickly becomes the better short- *and* long-term scenario. Moreover, even under the more conservative low substitution estimate, the long-term differences are substantial. Vis-à-vis the climate, only the *positive climate effects* and the *increased fertilization* scenarios perform better than the maximum forest use scenario. The magnitude of the substitution effect thus strongly impacts outcomes.

Hudiburg et al. (2019) suggests that, at least in places like the United States, large shares of HWP simply end up in landfills and are never used for substitution. While such outcomes indicate important 'missed opportunities', the substitution that occurs earlier in the HWP life cycle still remains. HWPs can substitute for a range of carbon-intensive products (cement, steel, plastics, glass). And long-lived HWPs sequester carbon over extended periods, while newly planted forests simultaneously sequester additional carbon. The circular bioeconomy clearly falters when end-of-life-cycle wood resources are squandered. Prior substitution effects, however, are not thereby eliminated: only opportunities for additional substitution lost. Moreover, even if HWP resources end up in landfills, this is by no means a justification for reducing forest use. Such shortcomings instead signal failed policy intervention and inefficient resource use, requiring corrections of a different kind.

Several factors related to circular economy principles can influence the magnitude of substitution effects. The *quality* of the circular bioeconomy can be measured in the relative efficiency of wood resource use, the number of times forest products are used and reused for different purposes, and the way recycling multiplies the substitution effect (Lundmark et al., 2014; Stegmann et al., 2020; Ubando et al., 2020). The relative share of wood ending up in long-lived vs. short-lived HWPs further influences the mitigation effect. The carbon in short-lived HWPs can, however, remain in the HWP pool via material recycling. When substitution arises several times, this increases GHG savings per unit of wood harvested. When wood waste is used as a bioenergy feedstock, high conversion efficiency is also an important objective. Deployment of carbon capture, utilization and storage (CCUS) can further enhance the circular bioeconomy by recycling biogenic carbon into new products or by storing carbon in geological reservoirs (Shahbaz et al., 2021; Tcvetkov et al., 2019).

The substitution effect is thus a compound component of the following elements: the HWP energy content, the HWP carbon pool content and the substitution content, which in turn is a compound effect made up of multiple substitutions along the entire product pathway. Improving the efficiency and effectiveness of the circular bioeconomy presumably requires public policy intervention, i.e., policy frameworks that promote or require circular behaviours and material flows (e.g. fines on disposing wood resources in landfills, legal requirements on paper and used wood resource recycling, value added and other related tax reductions/benefits to encourage HWP use instead of GHG-intensive products). Policy interventions can further support research on the quality of the circular bioeconomy.

The calculation of multiple substitution rates begs the question of which substitution rates are most appropriate? There is, however, no easy answer to this question. In an analysis of the Swedish marketplace, others estimated a substitution potential of 0.47–0.75 tonnes CO_2e/m^3 stem volume (Lundmark et al., 2014), in line with our lower conservative estimate. Since Lundmark et al.'s study was conducted, the resource and energy efficiency of the forest industry has improved, and the product portfolio expanded, suggesting the substitution factor is now likely higher. Leskinen et al. (2018) provide a review of some 51 studies which provide estimates of different substitution factors ranging from −0.7 to 5.1 kg C/kg C (approximately −0.53 to 3.83 tonnes $CO_2e/1\ m^3$), with an average of 0.9 tonnes $CO_2e/1\ m^3$ and 90% of estimates on the positive side of this range. To the extent substitution effects can be compounded by shifting to longer lived HWPs, increasing the efficiency of wood resource use and reuse via material recycling and ensuring that incineration plants effectively use the energy content of wood waste, the relative substitution effect will be larger.

Additional concerns regard declining substitution potential due to the decreasing GHG intensity of economies (Brunet-Navarro et al., 2021; Harmon, 2019). However, carbon-based fuels and materials are expected to remain important because they are essential in energy, transport and industrial infrastructures which change slowly. In a scenario where variable electricity generation based on solar and wind increases, biomass will remain an important alternative to fossil fuels providing the balancing power needed to maintain power stability and quality (Tafarte et al., 2020). Similarly, electrification of the transport sector is a relatively slow process due to long turnover times of the vehicle stock. Biofuels will therefore remain an alternative to petrol and diesel in the coming decades (Bacovsky, 2020). Moreover, biofuels will remain an alternative to fossil fuels for longer times in sectors where the substitution of carbon-based fuels is difficult, such as long-distance aviation and marine transportation (Skea et al., 2022).

Carbon dioxide removal (CDR) from the atmosphere will likely be required to meet the Paris Agreement goal of keeping the increase in the global average temperature well below +2°C above pre-industrial levels (Rogelj et al., 2019). Carbon sequestration and storage via forests and forest product-based net removals, including construction wood in buildings and CCUS, are among the options for providing CDR (Burns & Nicholson, 2017; Churkina et al., 2020). Thus, while both future substitution effects of forest products and the relative importance of forest/biomass-based CDR are difficult to project, the scientific literature suggests they will be important in the longer term for reaching climate goals (IPCC, 2019).

For another, as long as forests are sustainably managed and the net annual exchange of biomass use and net annual biomass growth is zero (i.e. harvest does not exceed gross growth), HWPs should remain a core component of a carbon neutral circular bioeconomy, even as GHG savings from substitution become less relevant. By the same token, squandering biomass resources and forest residues by failing to use them represents an absolute loss to the system. A key circular economy issue is how best to source 'renewable' resources and *avoid*, or *reduce*, the use of scarce, *non-renewable* resources. The availability of renewable, replenishable resources is of great significance, especially under the more general conditions of limited resources, peak resource production and declining resource availability. Precisely because wood resources can continue to meet demand due to their *circular* benefits, more emphasis should ideally be placed on better understanding the limits of sustainable forest resource use, in conjunction with the relevant biodiversity requirements.

5.5 | LULUCF in the EU climate policy framework

The FRL strategy potentially discourages some Member states from fully using available forest resources for wood production (Ellison et al., 2014, 2020, 2021; Nabuurs et al., 2017). Although the FRL is theoretically set to protect annual net removals (sinks) and limit the increasing intensity of forest use (Grassi et al., 2021; Matthews, 2020), it ignores the substitution-related benefits of the HWP and bioenergy-based *avoided emissions* accounted outside the LULUCF sector. Since gains (*avoided emissions*) are not weighed directly against harvest-related emissions, the FRL approach may conflict with the bioeconomy interests of many Member states. Thus, to the extent that substitution represents an efficient and effective mitigation strategy, existing policy frameworks fail to represent this appropriately and can thus discourage effective forest use.

Clearly, part of the answer to this question lies both in the magnitude of the real substitution effect, as well as in the shape of public policy intervention. Although the FRL strategy may limit forest use intensity, there is little evidence this will either promote additional forest protections and conservation, or that it will promote climate change mitigation at comparable rates. In fact, our results suggest the opposite. To the extent the FRL has the potential effect of reducing forest use, it is likely to increase mortality and thus reduce the production of usable forest biomass and its related substitution effects. We have highlighted the significant losses in terms of the future biomass resource.

The FRL strategy further sets limits on countries that have regularly been harvesting comparatively low shares of the available net increment across the 2000–2009 period. The EU LULUCF ruling essentially locks in behaviour and suggests countries should continue to harvest *at the same rate*: that is, 'harvest intensity should not increase'. The Netherlands, for example, harvested approximately 55% of the annual net increment over the period 2003–2013 (Arets & Schelhaas, 2019), while Sweden has historically harvested a significantly large share of its overall net increment (on average, approximately 82% over the period 2000–2009, excluding commercial thinnings) (Swedish Ministry of the Environment, 2019). This approach thus discourages countries that use smaller shares of their forest resource from increasing production and promoting increased substitution.

Equally important but frequently neglected (see e.g., Gustavsson et al., 2022; Skytt et al., 2021) are the leakage effects potentially driven by the FRL and/or increasing forest set-asides, thereby reducing the amount of European forest available for harvest. Leakage can take on at least two different forms. On the one hand, it can result in the increased use of carbon-intensive materials like cement and steel (Churkina et al., 2020; Elhacham et al., 2020; Holmgren, 2021). On the other, leakage can lead to increased forest use in other locations around the world (Grassi et al., 2018; Kallio et al., 2018; Solberg et al., 2019). Increased consumer demand pressures on international trade may drive carbon and biodiversity loss in parts of the world that still host the principal share of global primary forests and some of the richest carbon stores (Santoro et al., 2021).

By excluding a share of the forest resource from harvest, the FRL further has the effect of increasing uncertainty regarding future forest resource use, thereby weakening investment incentives. While the potential to gain carbon credits from afforesting unmanaged forest lands may make up for this in some cases, the EU LULUCF regulation requires afforested lands outside forest management be integrated into MFL after a period of 20 years (EU, 2018/841). Because new forest growth can only be accounted for the first 20 years but then presumably becomes subject to the MFL-based FRL and cap strategies, both public and private sector investment incentives may be diminished. Investors interested only in the long-term set-aside effects on biodiversity, for example, may lose interest due to the threat of eventual privatization, while profit-seeking investment is weakened through the FRL and the cap.

On the other hand, to the extent land set-asides and increased forest protections do not affect the practice of forestry, they will likely influence overall mitigation potential only to the extent they involve the regeneration of degraded forest lands. In Sweden, for example, newly proposed land set-asides do not include intensively managed lands. Similarly, the plan to set aside some of the remaining primary forests in Europe does not address degraded lands and is not likely to significantly affect mitigation potential. This could, however, have important impacts on European biodiversity (Sabatini et al., 2018, 2020).

To optimize the mitigation effects of forestry, it is preferable to consider substitution effects and remove inflexibilities in trade across sectors (Ellison et al., 2021). Understanding what is best for the climate requires studying all land and atmosphere fluxes over extended periods of time. Current consideration of the next version of the EU LULUCF policy framework (COM(2021) 554 final) provides opportunities to address these concerns.

6 | CONCLUSIONS

Although storing carbon in standing forests can clearly contribute to climate change mitigation, this strategy has definable limits and potentially unrecognized opportunity costs. To achieve long-term reductions of atmospheric CO_2, it may be better to view the forestry enterprise—the circular forest-based bioeconomy—as the principal mechanism by which climate change mitigation can be progressively maximized, that is, by simultaneously increasing the magnitude of total annual forest growth alongside carbon sequestration and substitution effects. As our scenarios suggest, the reduction in atmospheric GHG concentration is maximized when forest growth and the potential annual substitution effect are maximized.

Given constant climate conditions and compared to the *maximum potential harvest* scenario, the net effect of increasing forest set-asides on a relatively modest share of productive forest land (18.5%) is estimated at −13.9 $MtCO_2e$/year from peak to perpetuity. The total net carbon sequestration impact of Swedish LULUCF during the second commitment period is approximately −49 $MtCO_2e$/year. Based on this total, future mitigation losses from increased forest set-asides amount to approximately 28% per year from peak to perpetuity. If we consider the potential magnitude of substitution effects, as well as the benefits of improved policy intervention, this amount could be greater.

Pursuing forest management as a strategy for maintaining and strengthening the forest role as a 'regulator' of atmospheric GHG concentrations thus makes good sense. Policy interventions that could meaningfully mobilize the climate benefits of forest use are, however, currently hamstrung by a preference for carbon sequestration and storage in forests and a perceived need to harness forest use intensity. As the above scenarios suggest, more refined policy interventions could go a long way toward better mobilizing forest use in favour of the climate. The key policy and research innovations that could further help mobilize forests in favour of the climate are as follows: support for technology and market development in circular bioeconomy solutions; achieving greater flexibility in the trading of carbon credits across the multiple sectors (pillars) of the climate policy framework; eliminating the 'no-debit rule', the FRL and the cap; and improving the accounting of, knowledge about, and policies surrounding substitution effects.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

HP conceptualized and designed the study; DE designed the study within the FORCLIMIT project. DE, HP, GB, GE, JS, ML, TL and AAM drafted and revised the manuscript. PW, JS, AL and AAM were involved in data acquisition, analysis and interpretation.

DATA AVAILABILITY STATEMENT

The article data has been made available at: https://zenodo.org/record/6390892.

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Under a changing climate, this thesis examines growth trends in Swedish forests during the last 40 years and in the future, using survey data from long-term forest experiments and the national forest inventory. The results obtained indicate a stable basal area growth rate but an accelerated height growth, especially after the millennium shift. In the future, active forest management with high harvest levels and efficient product utilization may give higher net climate benefits in the Swedish forestry sector.

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