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Variable associations of annual biomass increment with age, latitude and germination year in four tree species in Sweden



Anders Forsman^{a,*}, Jonatan Isaksson^a, Markus Franzén^{a,b}, Johannes Edvardsson^c

^a Department of Biology and Environmental Science, Linnaeus University, SE-391 82 Kalmar, Sweden

^b Department of Physics, Chemistry and Biology (IFM), Linköping University, SE-581 83 Linköping, Sweden

^c Laboratory for Wood Anatomy and Dendrochronology, Department of Geology, Lund University, Lund, Sweden

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ABSTRACT

Forests are pivotal for biodiversity, food webs, and human economies, and as carbon sinks their climate change mitigation potential is undisputed. However, whether trees continue to efficiently accumulate biomass at an increasing rate with age, how growth trajectories respond to climate change, and vary with latitude at species range margins is under debate. Here, we combine tree-ring data with biometric equation modeling to analyze how annual biomass increment varies according to tree age, species, latitude, and germination year. We generated 26,225 estimates of annual biomass increments for 136 individual trees, representing two evergreen gymnosperm conifer species (*Picea abies* (L.) H.Karst., and *Pinus sylvestris* L.) and two deciduous angiosperm species (*Quercus* spp. L. and *Fagus sylvatica* L.). Our dataset includes some old trees (range 150 - 405 years), and samples from locations spanning >10° latitude (55.0 - 66.3 °N) in Sweden. Annual biomass increment remained positive throughout the lifespan across trees, species, and latitudes. Age-specific biomass increment was higher in the deciduous than in the evergreen species and declined with increasing latitude within species. For spruce and beech, biomass increment increased significantly with germination year, possibly reflecting faster growth in recent times in response to a warmer climate. The findings have implications for forestry practices aimed at productivity, biodiversity conservation, and climate change mitigation.

1. Introduction

Forests support associated biodiversity and socio-economic interests (Norman et al., 2010; Aerts and Honnay 2011; Götmark 2013; Löf et al. 2016; Piovesan et al. 2022; Kozák et al. 2023; Forsman et al. 2024), and are key components in global policy-making to mitigate climate change, as a complement to reducing anthropogenic carbon emissions (Vieira et al. 2005; Stephenson et al. 2014; Friedlingstein et al. 2022; Peng et al. 2023; Roebroek et al. 2023). Old forests are considered pinnacles of biodiversity, as larger and older trees provide structural complexity, accumulate more niches, and tend to support a greater diversity of species (Piovesan et al. 2022; Kozák et al. 2023; Storch et al. 2023; Zeller et al. 2023). In principle, large trees should have the potential to contribute disproportionately to biomass increment, due to the allometric scaling that amplifies linear growth in stem diameter to a volume increase (e.g., Stephenson et al. 2014, Pretzsch 2020, Zhou et al. 2021). However, recent evidence from a global analysis point to a pervasive

fecundity reduction in large trees, consistent with a physiological decline with old age in 80 % of the 597 species included in the analyses, thus suggesting an important role of tree senescence (Qiu et al. 2021). If the deterioration of physiological performance at old age has a negative effect also on tree growth, then the annual biomass increase of trees might gradually level off in an asymptotic manner or show a unimodal pattern with a decline at older ages (Pretzsch 2020). Knowledge of spatiotemporal patterns and sources of variation in growth trajectories of trees is hampered by that examples of long-term analysis of mass growth of individual trees are relatively rare (Pretzsch 2020).

Previous investigations into the association of growth and tree size or age have arrived at mixed results and conclusions. For example, Stephenson et al. (2014) report on a global analysis of 403 tropical and temperate tree species, and show that for most species the rates of absolute tree mass growth increases continuously with tree size, consistent with metabolic scaling theory. By contrast, Anderson-Teixeira et al. (2022) state that biomass increments consistently reached maxima at

* Corresponding author. E-mail address: Anders.Forsman@lnu.se (A. Forsman).

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intermediate size (diameter at breast height, DBH) throughout globally distributed forests. Muller-Landau et al. (2006) report that there are no universal scaling relationships of growth or mortality with size among trees in tropical forests.

These variable findings probably reflect a combination of different methods, sampling designs, assumptions, and analytical approaches, together with a true context dependence of results related to, for example, study species (e.g., deciduous versus evergreen), and the location of study areas (e.g., tropical versus temperate or boreal). Variation among geographic regions is to be expected because the ontogeny of tree growth is influenced by a complex interplay of environmental constraints imposed by seasonality, light, temperature conditions, water availability, and the community species richness and composition associated with latitude (plus longitude and altitude) that together define phenology, duration of the growth period, and the nature and intensity of competition (Gamache and Payette 2004; Vieira et al. 2005; Way and Oren 2010; Hulshof et al. 2015; Pretzsch 2020; Anderson-Teixeira et al. 2022; Gazol et al. 2024). Geographic variation and latitudinal gradients in the intraspecific growth trajectories may thus reflect a combination of microevolutionary adaptations and developmentally plastic responses (Forsman 2015). The potential for tree growth is further modified by forestry management and harvesting (Harmon et al. 1990; Klein et al. 2013; Peng et al. 2023; Roebroek et al. 2023).

Studies of size-related growth can inform about patterns of importance for understanding life-history evolution as well as forest ecosystem processes and services. However, systematic evaluations of how growth trajectories of trees change with age, whether their annual biomass increase follows an S-shaped curve, continues indefinitely, or declines at old age due to senescence, whether the relationship between growth and age varies among different types of tree species, and how growth trajectories change and vary according to latitude within species requires an approach based on longitudinal time-series analysis of annual growth rings, i.e., dendrochronology (Johnson and Abrams 2009; Brienen et al. 2020; Pretzsch 2020; Anderson-Teixeira et al. 2022). While sampling old trees is necessary to detect signatures of senescence, it also comes with a potential caveat because trees growing fast early in life may suffer increased mortality and reduced lifespan, in line with the 'live fast die young' hypothesis (Johnson and Abrams 2009; Brienen et al. 2020; Begović et al. 2023). This may induce a systematic bias (spurious negative correlation) manifesting as reduced growth in old compared to young trees. Conversely, evidence is accumulating that age-specific growth rate was lower in historical times than presently, due to a plastic performance response to warmer temperatures, lessened climatic constraints, decreased density of trees with age, and increased CO2 levels in the atmosphere (McMahon et al. 2010; Pretzsch et al. 2014; Brienen et al. 2020; Pretzsch 2020; Walker et al. 2021; Begović et al. 2023), although decreasing growth trends have also been reported (e.g., Nock et al. 2011, Martinez del Castillo et al. 2022). The former may manifest as enhanced growth in old trees, particularly at high latitudes towards the poles where climate tends to shift the most (Way and Oren 2010; IPCC 2023).

Despite an accelerating use of tree-ring data, generalizations and comparisons of findings between studies are complicated by that commonly applied sampling designs (how and which trees are investigated) can impart biases of varying magnitude, independent of the total number of samples considered, with quantifications of forest growth and productivity being particularly susceptible to biases (Nehrbass-Ahles et al. 2014). Comparisons of findings are also complicated by spatial variation in the coverage of data. For example, while tree-ring data have been frequently deployed to analyze growth trajectories of trees in central Europe (e.g., Pretzsch 2020), investigations of tree growth in more northern latitudes, where many species have their range boundaries remain relatively rare. Yet, average annual temperatures, precipitation, and seasonality all show strong latitudinal patterns, with climate change induced temperature increments being faster towards the poles (IPCC 2023; Sunde et al. 2023). This emphasizes the need to investigate temporal and intraspecific latitudinal trends in tree growth trajectories at more northern latitudes.

Evaluating hypotheses and answering the key questions about growth patterns in trees is of paramount interest from physiological, ecological, evolutionary and conservation perspectives. The results also have applied value as they can inform forest management aimed at improved productivity, assisted migration for the purpose of reforestation, afforestation and range expansions, as well as biodiversity values and climate change mitigation (Sillett et al. 2010; Forster et al. 2021; Twardek et al. 2023).

In this study, we combine tree-ring data obtained using dendrochronology with biometric equation modeling to estimate and compare how annual biomass increment (dry mass) change with age in two evergreen conifer species (Picea abies (L.) H.Karst., and Pinus sylvestris L.) and two angiosperm deciduous species (Quercus spp. and Fagus sylvatica L.), including some very old individuals (average maximum age = 261years, range 150 - 405 years), sampled at 14 locations that span $> 10^{\circ}$ latitude towards the northern range distribution limits of some of these species in Sweden. The main objectives were fourfold: *i*) to quantify the relationship between age and current annual biomass increment of trees (henceforth CABI); ii) to investigate whether CABI increases with germination year as expected if trees grow faster in recent times; iii) to assess whether and how CABI is modified by latitude within species; and iv) to contrast growth trajectory trends among the four species. As such, this study contributes to further the knowledge and understanding of spatiotemporal patterns and sources of variation in growth trajectories of trees. A visual summary of the study area, study species, methodology, and key findings is provided in Fig. 1.

2. Material and methods

2.1. Study species

Our data set included two evergreen coniferous species and two angiosperm deciduous species.

Spruce trees are evergreen conifers known for their pyramidal shape and whorled branches. They are predominantly found in temperate and boreal regions of the Northern Hemisphere. Spruces are ecologically significant, forming extensive forests and serving as critical carbon sinks. They are essential for wildlife habitats and vital to timber production. The Norway spruce (*Picea abies*) is particularly noteworthy, a critical species in European forestry (Burns and Honkala 1990; Tjoelker et al. 2007).

Pines are coniferous trees comprising over 120 species globally. They are characterized by their long-lived nature and evergreen foliage, with needles often grouped in fascicles. Pine species occupy various habitats, from arctic and subarctic to tropical regions, exhibiting remarkable adaptability. Ecologically, pines play a significant role in forest ecosystems, contributing to biodiversity and serving as crucial habitats for wildlife. They are also economically important and widely used in timber and paper industries. Notable species include the Scots pine (*Pinus sylvestris*), a dominant tree in European forests and included in the present study, and the ponderosa pine (*P. ponderosa* P.Lawson & C. Lawson) in North America (Richardson 2000; Farjon 2021).

Oaks comprise approximately 500 species and are widespread across the Northern Hemisphere. Oaks exhibit significant ecological diversity, with species adapted to various habitats, from dense forests to arid savannas. They are deciduous or evergreen, characterized by their distinctive lobed leaves and acorns. Oaks are ecologically crucial, supporting a wide range of wildlife and playing a vital role in ecosystem services. They are also of economic importance, valued for their hardwood. The pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) are dominant in European forests (Rennenberg et al. 2006; Gil-Pelegrín et al. 2017).

European beech is the most common beech species and is



Fig. 1. Overview of study. Visualization of study design, including study area, the four study species, methods, and key findings.

predominantly found in Europe. It is a deciduous tree, notable for its smooth, grey bark and elliptical leaves. Beeches prefer well-drained, fertile soils and are common in mixed forests. They are ecologically significant, contributing to forest structure and biodiversity. European beech (*Fagus sylvatica* L.) forests are critical for carbon sequestration and are home to various fauna and flora. The species is also valued for its wood, used in furniture and flooring (Packham et al. 2012; Leuschner and Ellenberg 2017).

2.2. Sampling locations

Dendrochronology data was collected from 14 locations (spruce n = 4, pine n = 4, oak n = 4, beech n = 2 locations) that span > 10° latitude (55.0 - 66.3 °N) towards the northern range distribution limits of the respective species in Sweden (Table 1 and Fig. 2).

2.3. Dendrochronological methods

We use tree-ring data obtained by dendrochronology sampling to determine tree age, and to estimate how CABI of trees varies according to species, study site, and latitude. Dendrochronological samples were collected using a 5.15 mm increment borer at breast height (1.3 m above ground level) from each selected tree. Depending on stand-specific conditions and restrictions, one or two cores were extracted per tree. When two cores were taken, they were sampled from opposite sides of the trunk. Care was exercised to ensure that each core included as many tree rings as possible from the bark to the pith to enable age determination as well as annual and radial growth rate analysis. Sampling sites on the trunks were carefully chosen to avoid areas affected by injuries or branches. For trees on sloped terrain, cores were taken in a manner that minimized the impact of the slope gradient on tree-ring structure.

Table 1

Location of study sites. Geographic distribution (location and elevation) of the 14 study sites, the four study species, and the number and age (mean and maximum) of trees sampled for dendrochronology at each site. m a s l = meters above sea level.

Study sites	Coordinates (WGS84)	m a s l	Species	Samples (no. trees)	Mean age	Max age
Arjeplog*	66.07°N	600	Spruce	12	191	303
	17.98°E					
Nyteboda*	56.15°N	90	Spruce	9	128	162
	14.07°E					
Transtrand 1	61.07°N	530	Spruce	12	185	312
	13.16°E					
Transtrand 2	61.09°N	610	Spruce	11	165	207
	13.24°E					
Hovfjället	60.28°N	450	Pine	12	179	275
	12.98°E					
Sunnet	61.53°N	650	Pine	8	290	355
	13.97°E					
Skallbergsmyra	63.91°N	370	Pine	10	153	168
	18.04°E					
Arjeplog*	66.33°N	460	Pine	12	393	422
	18.45°E					
Testeboån	60.77°N	50	Oak	8	126	190
	16.98°E					
Västervik	57.67°N	10	Oak	10	165	180
0 0 0	16.35°E					
Vårgårda	57.95°N	110	Oak	10	145	154
	12.83°E					
Fulltofta	55.88°N	60	Oak	6	228	405
	13.61°E			_		
Odensjön	56.00°N	70	Beech	8	124	177
	13.27°E					
Møns klint	54.96°N	120	Beech	8	151	288
	12.55°E					

* From the International Tree-Ring Data Bank (ITRDB) at NOAA's National Center for Environmental Information (NCEI) database (available at https://www.ncei. noaa.gov/products/paleoclimatology/tree-ring).



Fig. 2. Geographic distribution of the 14 study sites across Sweden and Denmark. Each site is marked with a unique black symbol representing one of the four study species (Pine = cross, Spruce = square, Oak = triangle, and Beech = dot).

The surface of the increment samples was prepared with industrial razor blades and, when necessary, talcum powder was used to increase the contrasts and make the boundaries between the annual rings visible. The increment samples were analyzed and data processed following standard dendrochronological procedures (Fritts 1976; Bräker 2002).

Tree-ring widths (TRW) were measured to the nearest 0.01 mm using a digital LINTAB positioning table connected to an Olympus stereomicroscope and TSAPWin Scientific software (Rinn 2003). Prior to further estimates based on the TRW data, all data series were cross dated for missing rings and dating errors using COFECHA (Holmes 1983; Cook and Holmes 1984). Each observation in the dataset represents an annual ring size measurement from individual trees, a certain species, and located at specific sites.

The estimations of diameter at breast height (DBH) are based on the TRW data of trees from which it is possible to estimate radial growth (radii, r) and thereby the diameter (2r) at a given point in time. Radial increment refers to the increase in tree diameter as measured from the center of the tree stem and outwards.

Basal area increment (BAI) is a crucial metric for quantifying tree growth, typically articulated in square meters per annum. The computation of BAI necessitates specific data, primarily the tree's diameter at breast height (DBH) at the commencement and conclusion of a designated time interval. This study employed tree ring width (TRW) data to estimate DBH values. where DBH_end denotes the tree's DBH at the end of the period, DBH_start represents the tree's DBH at the beginning of the period, and π (pi) is the mathematical constant (appr. 3.14159). The number of years corresponds to the duration of the period. In this analysis, BAI has been estimated annually; hence, the duration was set to one year. This approach to BAI calculation has been validated and utilized in various dendrochronological and forest ecology studies (e.g. Piovesan et al. 2005), providing reliable estimates of annual tree growth.

2.3.1. Estimating current annual biomass increment (CABI, kg/year)

Biomass functions explicitly developed for spruce (*P. abies*) and pine (*P. sylvestris*) in Sweden were obtained from Marklund (1988). This work aimed to estimate the aboveground biomass, including stems, branches, and needles. The methodology involved destructive sampling across various diameter classes. The primary independent variable was diameter at breast height (DBH).

Spruce Biomass Function (Marklund 1988): Gd = exp(-2.2471+11.4873*d/(d + 14))

Pine Biomass Function (Marklund 1988): Td = exp(-2.2184+11.4219*d/(d + 14))

In the above equations, the dependent variables (Td and Gd) are expressed in mass units, and 'd' stands for the diameter at the tree's breast height (DBH), measured in centimeters.

Cienciala et al. (2008) presented biomass functions for oak species (*Q. robur* and *Q. petraea*) under Central-European forestry conditions. These functions estimated total aboveground biomass and its components, using DBH as a single independent variable or combined with tree height (H). In this study, the version of the Cienciala et al. (2008) function in which H = f(DBH) is based on empirical data has been employed. The study also identified the optimal variable combinations for each biomass component, including DBH, H, crown length, crown width, and crown ratio. This research provides a comparative analysis with other available oak biomass references.

Oak Biomass Functions (Cienciala et al. 2008):

$$H = \exp(-12.669/d) * 35.294 + 1.3$$

 $E_d = 0.999^* exp(-3.371 + 1.933^* ln(d) + 1.036^* ln(H))$

In the first equation, H represents the estimated height of the tree, in centimeters. In the second equation, Ed is the estimated biomass of the oak tree. 'd' denotes the diameter at breast height (DBH) in centimeters.

Cienciala et al. (2005)) detailed the parameterization of allometric functions for estimating biomass in European beech (*F. sylvatica*). The study used field data from mature trees with varying DBHs, focusing on aboveground biomass, including stem and branch biomass (for details see Cienciala et al. 2005).

Beech Biomass Function (Cienciala et al. 2005): B_d = 0.494*dbh^{2.070} where 'Bd' represents the estimated biomass of a beech tree, and 'dbh' denotes the diameter at breast height, in centimetres.

The estimates of CABI (kg/year) for each tree and year obtained using the approach described above were subsequently used as the dependent observations in the statistical analyses.

2.4. Statistical analyses

2.4.1. Comparing CABI between age categories To provide an overall coarse description of the relationship between

BAIIscalculatedutilizingtheformula : BAI = $((DBH_end^2 - DBH_start^2) / (4^*\pi)) / numberofyears$

CABI and tree age, all observations were classified in six age intervals (0–60, 61–110, 111–160, 161–210, and > 210 years). Next, average CABI was calculated for each age interval using a nonparametric bootstrap with 1000 replications in the "boot" package in R v4.3.0 (RCoreTeam 2023, v.1.3–28), see also (Davison and Hinkley 1997). Bootstrap percentile intervals were calculated for each mean using the same package. To help evaluate whether the growth pattern was general or species specific, these calculations were done both for the pooled data across all four species, and separately for each species.

2.4.2. Evaluating whether relationships with age and latitude are general or species-specific

To formally evaluate whether the relationship linking CABI to tree age was similar in all four species and independent of latitude, or whether the association with age varied according to latitude in different ways in different species, we analyzed the pooled data for all four species. For this, a general linear mixed model was used with calendar year of tree birth, tree age, and latitude included as fixed continuous numeric predictors, and species as a fixed categorical explanatory variable. To evaluate whether the association of CABI with age was differently modulated by latitude in different species, the threeway interaction between species, tree age and latitude was included, together with all the two-way interactions. The model also included a random effect allowing the intercept to vary between trees nested under site, acknowledging the non-independence of repeated observations within sites and individual trees.

CABI = species + latitude + species * latitude + age + species * age

- + age * latitude
- + species * age * latitude(Random = SiteID / treeID)

The statistical significance of the three-way interaction was evaluated using a Type III Wald Chi-square test. Because the results showed that the interaction was significant (see Results Section 3.1), we proceeded with separate analyses of data for each species. This was done to avoid potential problems associated with model overparameterization and to facilitate interpretation of results.

2.4.3. Comparing the fit of linear versus curvilinear models

Previous studies indicate that the shape of the relationship linking tree growth to age may vary between species and geographic regions (see Introduction). We therefore evaluated the relationship between CABI and tree age using three different models: one linear, one curvilinear (including both the linear and quadratic terms), and one with only the quadratic term. This was done separately for each species and latitude, with a random intercept term to account for repeated observations of each tree. Models were compared based on their Goodness of fit (conditional R² and AIC). To aid convergence, variables were standardized and centered prior to analyses. The results of these comparisons suggested that the model assuming a linear relationship provided a better fit to the data on average than the model assuming a quadratic relationship in 13 of the 14 cases (average conditional $R^2 = 0.56$ versus 0.50, paired *t*-test, t = -4.99, p = 0.0002, see Results Section 3.1, Appendix A, Table A1). Models assuming a curvilinear relationship provided a marginally, but not statistically significantly better fit compared with models assuming a linear relationship (average $R^2 = 0.59$ versus 0.56, t = 2.0, p = 0.067). In the remaining statistical analyses used to evaluate sources of variation in CABI, the association of CABI with age was therefore modeled assuming a linear relationship. This avoided the uncertainty that is associated with including an additional term, avoided problems associated with low predictive power of results indicated by wide 95 % confidence intervals of the parameter estimates for the curvilinear model, and also avoided problems of model overparameterization in the remaining statistical analyses performed to evaluate associations with tree age, latitude and germination year,

described below.

2.4.4. Evaluating associations of CABI with age, latitude, and germination year

General linear mixed models were used to evaluate associations of CABI (kg/year) with germination year, tree age, and latitude included as continuous numeric predictors. To evaluate whether the effect of age differed depending on latitude, an interaction between tree age and latitude was also included, together with a random effect allowing the intercept to vary between trees nested under site. Germination year was included for two reasons, to evaluate effects and to ensure that the estimated effects of age and latitude on CABI were not compromised by any differences in and associations with year of birth. To enable comparisons of slope estimates among the predictors, all predictor variables were centered and standardised with the 'scale' function in base R. Data for each species was analyzed separately.

CABI = latitude + age + yearofbirth + age * latitude (Random = SiteID / treeID)

Statistical significance of model terms was assessed using Likelihood Ratio tests (type III) in the 'Anova' function as implemented in the 'car' package (v3.1–2 Fox and Weisberg 2018). The alpha level was set to 0.05, and P-values < 0.05 were considered significant.

3. Results

Using dendrochronology, we generated 26,225 estimates of CABI (kg/year) for 136 individual trees representing *Picea abies, Pinus sylvestris, Quercus* spp. and *Fagus sylvatica*. The samples were collected from 14 locations that span $> 10^{\circ}$ latitude (55.0 - 66.3 °N) (Table 1). Our data set includes old individuals (average maximum age per was 261 years, range 150 - 405 years) (Table 1).

The estimated CABI remained positive throughout the lifespans of every tree, in all four species, and throughout the entire latitudinal range covered in our dataset (Table 2). Comparisons between age classes showed that when considering the pooled estimates for all four species, average CABI peaked at intermediate ages (i.e., in the 111–160 years age class), but this pattern was not consistent in all species, with pine and oak instead reaching the highest values in the oldest age class (i.e., > 210 years) (Table 2).

Table 2

Average current annual biomass increment (CABI, in kg/year, \pm 95 % confidence intervals) in five different age classes of trees. The estimates shown are based on pooled data for all species and also based on separate analyses of data for spruce, pine, oak and beech. The rightmost column shows the number of tree individuals that contributed with data for estimation of the means, which decreased with increasing age as the dataset contained trees of varying ages. Estimates are based on pooled data for all stands within each species. Information on sampling locations and the number of trees in each sample is available in Table 1.

Age intervals (years)	All species	Spruce	Pine	Oak	Beech	Number of trees included
0 - 60	1.84	1.30	0.58	2.73	4.80	136, 43,
	± 0.078	± 0.078	± 0.035	± 0.186	± 0.404	43, 34, 16
61 - 110	4.69	3.16	1.43	8.48	9.82	136, 43,
	± 0.151	± 0.126	± 0.055	± 0.379	± 0.674	43, 34, 16
111 - 160	6.61	3.51	1.97	15.58	12.94	126, 38,
	± 0.277	± 0.149	± 0.067	± 0.773	± 1.485	43, 32, 13
161 - 210	5.92	2.88	2.23	26.22	13.94	80, 22,
	± 0.419	± 0.169	± 0.090	± 2.283	± 1.298	38, 15, 5
> 210	4.79	2.35	2.40	39.37	7.79	37, 9, 23,
	± 0.323	± 0.243	± 0.045	± 2.215	± 0.770	3, 2



Fig. 3. Relationships between annual growth rate and age in four different tree species (spruce, pine, oak and beech) and according to latitude of sampling location. Figures show growth trajectories for individual trees based on raw data (gray curves). Blue lines indicate predicted linear regression lines estimated from random intercept models. Red lines indicate 95 % confidence intervals. The scale of the vertical axis for spruce and pine (0–25 kg/year) is different from that for oak and beech (0–100 kg/year). Lines of best fit were modeled using linear mixed models (separately for each species and latitude) with random intercepts for repeated measures.

3.1. On the shape of the relationship linking CABI and age

The results of the analysis of pooled data for all four species showed that the relationship linking CABI to tree age varied according to latitude in different ways in the different species (effect of the three-way interaction between age, latitude, and species: Chi-square = 610.61, *d*. *f*. = 3, p < 0.0001).

Visual inspection of the relationships linking CABI to tree age revealed that there were pronounced yearly fluctuations and variation in growth trajectories among trees within species and stands (Fig. 3). As can be seen in Fig. 3, CABI seemed to peak at an intermediate age in some stands (primarily spruce), tended to approach an asymptote with increasing age in some stands (primarily pine), and tended to increase at a disproportionately faster rate with increasing age in some stands (Fig. 3). However, the model assuming a linear relationship with age provided a better fit to the data (according to comparisons of measures of Goodness of fit) than the model assuming a solely quadratic (nonlinear) relationship in 13 of the 14 cases, the single exception being oak in the Vårgårda population (paired *t*-test, t = -4.99, p = 0.0002, **Table A1**, Fig. 3).

3.2. Associations of CABI with age, latitude, and germination year

The results from the species-specific general linear mixed models showed that there was a statistically significant effect on CABI of the interaction between latitude and age in all four species (all p < 0.0001). The association of CABI with age was positive in all species and populations (all p < 0.0001) and tended to be less steep in more northern populations (Table 3 and Fig. 3). These results show that the rate of annual biomass increment becomes progressively faster in older trees.

Age-specific annual growth rate increased with germination year in spruce and beech (indicating that trees of these species grow faster today compared with how fast conspecific trees of similar age grew in historical times, p < 0.05) (Table 3). No such effect of germination year on

Table 3

Associations of current annual biomass increment in four different species of trees with age and environmental factors. Results from generalized linear mixed models for associations of annual growth rate (kg/year) with calendar germination year, tree age, and latitude, as well as the interaction between tree age and latitude. Estimates are slope estimates. Estimates in bold are statistically significant (p < 0.05) according to the Wald Chi-square test. Data for each species was analyzed separately. Information on sampling locations and the number of tree individuals in each sample is available in Table 1.

Species/ Source of variation	Wald Chisq	Estimate	s.e.	Z	р
Spruce					
Intercept		0.26	0.121	2.11	0.0345
scale	9.94	0.42	0.135	3.15	0.0016
(germinationYear)					
scale(age)	1980.49	0.57	0.013	44.50	<
					0.0001
scale(lat)	7.62	-0.29	0.106	-0.76	0.0058
scale(age):scale(lat)	380.15	-0.21	0.011	-20.26	<
					0.0001
Pine					
Intercept		0.04	0.096	0.39	0.6939
scale	0.40	0.08	0.119	0.63	0.5269
(germinationYear)					
scale(age)	3476.65	0.50	0.008	58.96	<
					0.0001
scale(lat)	0.85	0.11	0.123	0.92	0.3566
scale(age):scale(lat)	157.79	-0.10	0.008	-12.56	<
					0.0001
Oak					
Intercept		-0.01	0.156	-0.08	0.9327
scale	0.24	0.08	0.164	0.49	0.6253
(germinationYear)					
scale(age)	2832.88	0.51	0.010	53.22	<
					0.0001
scale(lat)	2.07	-0.24	0.169	-1.44	0.1498
scale(age):scale(lat)	191.72	-0.12	0.009	-13.85	<
					0.0001
Beech					
Intercept		-0.07	0.102	-0.64	0.5194
scale	5.32	0.31	0.133	2.31	0.0210
(germinationYear)					
scale(age)	834.09	0.44	0.015	28.88	<
					0.0001
scale(lat)	1.42	0.15	0.123	1.19	0.2335
scale(age):scale(lat)	90.88	0.16	0.016	9.53	<
					0.0001

CABI was evident in pine and oak (p > 0.5) (Table 3).

4. Discussion

The current study combined tree-ring data obtained using dendrochronology with biometric equation modeling to investigate how CABI varies according to species, tree age, latitude, and germination year using data for two evergreen coniferous species (*Picea abies* and *Pinus sylvestris*) and two deciduous species (*Quercus* spp. and *Fagus sylvatica*) in Sweden. A major finding was that trees overall continue to accumulate biomass at a progressively faster rate with increasing age, also at high latitudes and despite being several hundred years old. This persistence of individual growth of old trees conforms with some earlier reports (Sillett et al. 2010; Sillett et al. 2015a; Sillett et al. 2015b; Pretzsch 2020).

Besides extensive variation in growth trajectories among tree individuals within stands, the slope of the linear relationship linking CABI to tree age varied according to latitude and species, with higher growth rates in old trees at lower latitudes and in deciduous species compared to evergreen species. The reduced growth with increasing latitude might reflect constraints imposed by low temperatures and shorter growth seasons, while the faster growth in deciduous than evergreen species may be due to differences in total leaf areas, leaf turnover rates, and root carbohydrate storage strategies (Antúnez et al. 2001; Way and Oren 2010; Tomlinson et al. 2014). However, the higher estimated CABI in oak and beech compared with spruce and pine should be interpreted with some caution, as the species-specific biometric models used may have introduced some systematic bias between these deciduous and evergreen coniferous species (Antúnez et al. 2001; Way and Oren 2010; Tomlinson et al. 2014).

Contrary to expectations, our species-and-latitude-specific models suggested that, in general, the relationship between CABI and tree age was linear, rather than peaking at an intermediate age or gradually reaching an asymptote in line with the law of diminishing returns, and that most trees in all age classes, stands, and species exhibited a progressive increase in CABI throughout their lives. This is contrary to the expected and previously reported unimodal relationship with a decline in growth performance at old age due to physiological limitations and senescence (Qiu et al. 2021), and may in part reflect that our samples did not include very old trees (Pretzsch 2020).

Germination year was identified as a determinant of growth trajectories in two of the investigated species, with CABI increasing with germination year in spruce and beech (but not in pine and oak), meaning that age-specific biomass growth was higher in recent than in historical times. This corroborates the findings of some previous studies and suggests a positive effect of a warmer climate, protracted growing seasons, and CO₂ enrichment on growth in some species (McMahon et al. 2010; Way and Oren 2010; Pretzsch 2020). As such, this result supports the potential for some tree species and forest ecosystems to adjust and adapt to changing climatic conditions. That both the effect of germination year and how age-specific growth responds to latitude vary according to species requires careful recognition in forest management strategies aimed at improved productivity, reforestation, afforestation and range expansions (Sillett et al. 2010; Forster et al. 2021; Twardek et al. 2023).

An important caveat to consider is that the trees in the present study were unevenly distributed among the different species and study locations, which limits inference space regarding differential responses and the generalizability of the results (Nehrbass-Ahles et al. 2014; Voelkl et al. 2020). For example, results based on modelling of annual basal area increment (BAI) of beech indicate growth declines of trees in recent decades due to modified temperature and precipitation, especially towards the southern margin of the distribution (Martinez del Castillo et al. 2022). However, there are also conflicting results from long-term experiments, stem analyses, and increment cores from European beech in Germany showing that size growth has increased over time (Pretzsch 2020), in agreement with our findings. That our results for beech were different from those of Martinez del Castillo et al. (2022) may partly reflect that our samples represent the northern part of the distribution, and that the present study modelled CABI rather than BAI.

As carbon sinks, the climate change mitigation potential of forests is undisputed. However, the relative importance of old tree individuals and forests for carbon sequestration is under debate (Brienen et al. 2020; Pretzsch 2020; Gundersen et al. 2021). Besides showing that all four investigated species accumulate biomass at an accelerating rate with increasing age, this study also suggested that the average annual biomass increase of a single 200-year-old tree can corresponds to the pooled growth of about 5 to 25 younger trees, depending on species and stand (see also Stephenson et al. 2014). Admittedly, our estimations of CABI rely on biomass functions derived from previous studies (Marklund 1988; Cienciala et al. 2005; Cienciala et al. 2008) that may not accurately reflect the biomass of the specific trees in the current study. It is also possible that more sophisticated analytical approaches, such as the use of dynamic allometric scaling relationships of tree biomass and size (e.g., Zhou et al. 2021), provide more reliable estimates compared with power-law allometric equations. The biometric models used here concern the above ground biomass, but do not take into consideration below ground processes and growth of the root system (see also previous studies, e.g., Stephenson et al. 2014, Qiu et al. 2021, Martinez del Castillo et al. 2022). Yet, we can see no reason as to why these issues would qualitatively change the main conclusion regarding accelerated biomass

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increment of older trees. Although old trees may gain more biomass than sometimes assumed and the carbon sequestration potential of forests depends to some extent on the continued fast growth of individual trees, stand-level productivity - and carbon sequestration - per unit land area is also determined by age related reductions in population density and increases in the release of CO_2 due to faster decomposition (Pretzsch 2020).

The benefits of old and large trees extend beyond any positive effects that their continued high capacity for biomass accumulation may have for carbon sequestration. From an ecological perspective, old forests support a greater number and diversity of associated species (Piovesan et al. 2022; Kozák et al. 2023; Storch et al. 2023; Zeller et al. 2023). Mixed-species forests also come with ecological advantages over monocultures in terms of productivity and resistance to environmental stressors (e.g., Zhang et al. 2012, Pretzsch et al. 2013, Tilman et al. 2014). Further, a mixture of species, ages, sizes and genotypes brings with it variance reducing portfolio effects that buffer against variable conditions (Wennersten and Forsman 2012; Pretzsch et al. 2013; Forsman 2014; Schindler et al. 2015; Forsman and Wennersten 2016; Hui et al. 2017), and offers more complex habitats that support both biodiversity and recreational values (Piovesan et al. 2022; Kozák et al. 2023; Storch et al. 2023; Zeller et al. 2023).

4.1. Conclusions and future directions

The present study based on analyses of dendrochronology data for spruce, pine, oak and beech across ecosystems in Sweden supports that trees continue to accumulate biomass at a progressively faster rate with increasing age, also at high latitudes and despite being several hundred years old. A noteworthy observation was that germination year had a significant positive effect on growth trajectories in two of the species (spruce and beech). This faster age-specific growth in recent than in historical times conforms with some previous studies (e.g., Pretzsch et al. 2014; Pretzsch 2020; Begović et al. 2023) and can inform the use of assisted latitudinal migration as a climate change adaptation strategy, and to promote growth (Twardek et al. 2023). Our finding that the relationship linking growth to age is differently modified by latitude in the four species emphasizes the need to explore the physiological and molecular mechanisms that underlie the variable growth responses of old trees to climate change. Zooming out, future comparisons of growth patterns and climate sensitivities of old trees and forests across different regions, biomes, and continents can help identify the drivers and consequences of the observed variations (e.g., Way and Oren 2010, Anderson-Teixeira et al. 2022). This includes investigating the context dependence of whether and how germination year impacts subsequent growth.

Data deposition

Data and statistical code is available as Supplementary materials.

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CRediT authorship contribution statement

Anders Forsman: Conceptualization, Methodology, Formal analysis, Investigation, Validation, Writing – original draft, Visualization, Supervision, Funding acquisition. Jonatan Isaksson: Methodology, Software, Formal analysis, Data curation, Writing – review & editing, Visualization. **Markus Franzén:** Methodology, Software, Investigation, Data curation, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Johannes Edvardsson:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing.

Declaration of competing interest

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

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Supplementary materials

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