Competition-based mortality and tree losses. An essential component of net primary productivity

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ABSTRACT

Even-aged stands can regenerate with many thousand seedlings per hectare before the density declines to just a few hundred trees per hectare 100 years later; management practices can lead to even lower tree numbers due to quality selection and thinning. In other words, during the development of unmanaged stands, the majority of individuals die naturally due to competition. Despite the far-reaching consequences for structural and genetic diversity, dead wood and fuel wood accumulation, we have only limited quantitative knowledge about the continuous mortality of trees and the wood volume loss over longer timespans.

For this study, we used a unique set of 476 unmanaged, monospecific experimental plots of Norway spruce (*Picea abies* (L.) H. Karst.), silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.), European larch (Larix decidua Mill.), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)), European beech (*Fagus sylvatica* L.), and oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) throughout Europe to analyze the competition-based mortality of trees and its dependency on age and site conditions.

First, we show that the total stem volume production, standing stock, and mortality were continuously increasing until an age of 100–150 years. The accumulated competition-caused stem volume loss at that age amounted to 500–1000 m^3 ha^{-1}.

Second, the net growth of the stands (share of the growth that is accumulated in the standing stock) strongly decreased with increasing age even when the gross growth was still high. The proportion of the net growth versus gross growth continuously decreased with increasing age regardless of site quality.

Third, we show a degressive decrease of the annual relative tree number mortality rates from 0.05 to 0.20 in young down to 0.01–0.02 in mature stands. For some species, we found these rates to be site dependent with different directions of the site effect. The interplay of decreasing mortality rates and increasing average volume of the dead trees resulted in unimodal mortality curves over time of the annual mortality, peaking at 3–12 m^3 ha^{-1} yr^{-1} at ages of about 75–150 years.

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Over the whole rotation, the average annual biomass loss from mortality ranged between 0.8 and 2.1 t ha^{-1} yr^{-1} with a carbon content of 0.4–1.1 t C ha^{-1} yr^{-1}. We discuss the relevance of the results for measuring, understanding, modelling, and managing forest stands. Our results reveal that the withdrawal of forest management and setting aside (previously managed) forests over a rotation time of 100–150 years means that about one third of the total production in monospecific stands would flow to the debris pool rather than being exploited for carbon sequestration and related emission savings in harvested wood products. The mortality related loss fractions of above ground biomass we quantified in this study indicate the trade-off between wood production and setting aside forest to allow deadwood accumulation and associate changes in biodiversity.

1. Introduction

In high density forest stands, inter-individual competition for space and resources causes competition-based mortality. The process of increasing mean tree size, decreasing availability of resources per individual tree, and the resulting loss of trees is studied since long (Assmann, 1970; Hutchings and Budd, 1981; del Río et al., 2017) and commonly called natural thinning (Myers and Van Deusen, 1960; Zeide, 2001, 2005). In forest stands with lower density, mortality is mainly driven by competition-independent abiotic or biotic disturbances and stress such as storm, ice breakage, drought or herbivore browsing, insects, and fungi. Both competition-driven and competition-independent mortality may co-occur and can be difficult to distinguish. However, with increasing stand density the relevance of competition-based mortality increases. This study into even-aged, unthinned, monospecific stands deals with competition-driven mortality; in even-aged stands, this kind of natural thinning is referred to as self-thinning (Harper, 1977. p. 171, Reineke, 1933). For an explanation of technical terms see Box 1.

Even-aged plantations and natural stands mostly start with low competition and therefore low competition-based mortality until the canopy closes. Canopy closure marks the beginning of a process of tree elimination by self-thinning. In the absence of active thinning, self-thinning reduces the tree density from many thousands per hectare at the juvenile stage to a few hundred trees in the mature phase at the age of 100–150 years (Schober, 1975). The size growth of the trees in a stand and their increasing individual demand for resources causes competition and, as a result, mortality and growth in size occur simultaneously. The regular tree elimination by mortality means that the standing stock, e.g. at age 100 years, represents only a part of the total stand production up to that point in time. Other trees will have already died and fully or in part been decomposed, providing nutrients for the survivors. Net primary productivity is important for forest ecosystem functioning (Haberl, 1997; McNaughton et al., 1989; Zhou et al., 2015), directly related to tree growth and carbon sequestration, as well to other ecosystem services (Alcamo et al., 2003). In forestry, NPP is often estimated by total stem volume growth or gross growth (Pretzsch, 2009), as stem volume is the fraction of tree biomass usually measured in forest inventories. Part of the stem volume growth is lost by natural mortality, thus, to know this amount is essential to have a good picture of NPP development with age.

The quantification of the competition-based mortality and consequent volume loss caused by self-thinning requires long-term surveys of unmanaged stands with continuous surveys of both standing stock and mortality (Assmann, 1970). Many studies addressed the self-thinning line, an important related principle (Bravo-Oviedo et al., 2018; Pretzsch, 2006; Zeide, 1987), the resulting maximum stand density (Skovsgaard and Vanclay, 2008; Zeide, 1991), and the dependency of both on site conditions (Morris, 2002). However, few studies have focused on the volume loss by self-thinning, although all are related (Zhang et al., 2005) and depend on site fertility (Nilsson and Allen, 2003).

The knowledge about the volume loss due to self-thinning and its dependency on site conditions is limited as it requires time-consuming remeasurements of unthinned long-term experiments. Alternatively, the total production can be estimated provisionally based on age-series of temporary plots (Gatzojannis, 1999; Magin, 1964; Pretzsch and Grote,

2023). However, non-recurring inventories or temporary plots can provide only a part of the required information. For instance, information about the mortality in the past of such stands is usually missing and there is rarely concise knowledge about whether the stands were thinned and may therefore not represent maximum stand density and the related self-thinning. Thus, many models and yield tables in Europe and the anglo-american region, where long-term experiments, especially with unthinned plots, are not available, only include the standing stock and not the total yield (see Boudoux, 1978; Bravo et al., 2011; Palahí et al., 2002; Plonski, 1971) although the total yield may be 30–40 % higher than the current standing stock. This omission may have been acceptable for wood-centered forest management based on managed stands where thinnings are regularly applied and a focus is on larger logs (Pretzsch et al., 2008; Yaffee, 1999). However, modern forest ecosystem management is also interested in the quantity and quality of the dead trees and their volume or mass, which provide essential knowledge for carbon storage, wood production, nutrient cycling, deadwood, habitat provision, and other forest functions and services (Biber et al., 2015; Dieler et al., 2017).

The first systematic long-term thinning experiments, which also included unthinned plots, were established at the end of the 19th century throughout Europe (Pretzsch et al., 2019). In such experiments, the so-called A-grade plots, which are not actively thinned but inventoried regularly to record the remaining stand and losses, serve as references. Plots of this kind were used in this study. Assmann (1970, p. 227–228), who assessed the volume losses due to self-thinning on some of such experiments, found that self-thinning accounted for >50 % of the total production at medium stand ages. The data available for this study, however, allowed us to scrutinize natural mortality and its relation to total production on a large number of plots throughout Europe which were continuously surveyed for about 100–150 years.

Box 1. Overview of the most important technical terms used in this paper.

Technical term	Explanation
natural thinning	process of tree elimination in a stand by competition for resources
self thinning	natural thinning in even-aged forest stands
total volume production (TVP)	accumulated stem volume growth of a stand up to a given time, comprising surviving and mortal trees
standing volume (VST)	standing volume of a stand at a given time, i.e. including only the living trees at that time
cumulative volume loss	the volume lost due to mortality up to a given time, i.e. the difference of TVP and VST
total volume increment	annual stem volume growth of a stand or gross growth, an indicator of NPP
standing volume increment	the share of the total volume increment that is accumulated in the standing volume or net growth
accumulation fraction of the total volume increment	relative share of the total volume increment that is accumulated to the standing volume
loss fraction of the total volume increment	relative share of the total volume increment that is lost due to mortality

(continued)

Technical term	Explanation
annual mortality rate	number of trees in a stand that died during a given year divided by the number of living trees at the beginning of the year

From the rather unique set of 476 even-aged long-term A-grade plots throughout Europe we used 154 stands of Norway spruce (*Picea abies* (L.) H. Karst.), 11 stands of silver fir (*Abies alba* Mill.), 137 stands of Scots pine (*Pinus sylvestris* L.), 14 of European larch (*Larix decidua* Mill.), 16 of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), 67 of European beech (*Fagus sylvatica* L.) and 77 stands of oak; in the latter case we pooled common oak (*Quercus robur* L.), and sessile oak (*Quercus petraea* (Matt.) Liebl.). The taxonomic status of both taxa has been subject to repeated reassessment (Aas, 1991). They have long been described as two distinct species, *Q. robur* L. and *Q. petraea* (Matt.) Liebl., while they are currently placed as two subspecies *Q. r. robur* and *Q. r. petraea* within the species *Quercus robur* L. (Roloff et al., 2008, pp. 506–507).

In detail, our questions were:

Q1: How much stand volume is lost to competition related mortality within a rotation, both in absolute terms and as a proportion of the total production? How does the volume loss vary between the seven tree species and depend on site conditions indicated by the site index?

Q2: How does the annual volume loss and the relationship between total volume increment and standing volume increment develop within the life of a stand?

Q3: How do tree mortality patterns change over time and between sites? How do the numbers and dimensions of trees lost to mortality vary with age and site index?

Our study concerns temperate even-aged forests planted at close spacing, and may be less applicable for close-to-nature silviculture, or for short-rotation plantations. We studied the above ground biomass; further research into the below ground biomass is required to make the full carbon balance.

We discuss how the standing volume growth, which makes up the final standing stock, results from the interplay between total volume growth and competition related mortality. We emphasize the relevance of our results for ecological indication of forest stands, for their measurement, understanding, modelling, and sustainable management.

2. Material and methods

2.1. Data

We used a dataset of 476 long-term experimental plots that were fully stocked, completely untreated or only lightly thinned according to the available records. They all belong to the international network of long-term growth and yield experiments and are located in Austria, Denmark, the United Kingdom, France, Germany, Poland, Spain, Sweden, and Switzerland (Pretzsch et al., 2019). The establishment and survey of most of these long-term experiments started in Central Europe with the foundation of the Association of German Forest research stations in 1872 (von Ganghofer, 1881), and was extended to the pan-European and later worldwide scale by the International Union of Forest Research Organization founded in 1892 (IUFRO, 1993; Pretzsch et al., 2019). Most of the long-term experiments included in this study were established, surveyed, silviculturally steered, and evaluated as set out by the abovementioned organizations (Hummel, 1953; Johann, 1993).

The raw data of each survey comprised the stand age, plot size, the stem diameter of all trees at 1.3 m height, information on the status (living or dead) of the tree, information about whether the tree was removed or remained in the stand, and the tree heights measured on all trees or on a sample of 30–50 trees covering the whole stem diameter range. The inventories were repeated every 3–12 years and up to 31 times. Typical plot sizes are between 2,000 and 5,000 m^2.

All included long-term plots are fully stocked, completely untreated or only lightly thinned, as most of them serve as control plots (reference) of thinning experiments. In this way we excluded, e.g. plots with tree losses due to hazard-caused mortality e.g. by bark beetles or storms. Thus, these plots reflect the competition-based mortality, and associated volume loss over periods of up to 150 years. The light thinning on control plots removes only dying and dead trees as well as any bent trees that mechanically jeopardize neighbors (IUFRO, 1993; Verein Deutscher Forstlicher Versuchsanstalten, 1902). This light thinning was designed to just anticipate mortality, and to allow for other removals, if any, exclusively for special scientific purposes (Assmann, 1970, p. 212; Pretzsch, 2009, pp. 157–158).

In order to be sure that all included plots were fully stocked throughout the whole survey period and thus represent competition-based mortality, we excluded stands which might have undergone un-known human disturbances (e.g. unplanned thinnings during World War I or II) or natural disturbances (e.g. insect damages, snow-breakage) in the past. For this purpose, we calculated and visualized the relationship between the stem number (N) and quadratic mean tree diameter (dq) for all of the potentially suitable plots (see Section 2.2 and Supplementary Fig. 1). Then we identified plots with unsuitable N-dq trajectories in two steps. First, we eliminated (by visual assessment) all plots with partly positive slopes of the N-dq trajectories caused by ingrowth of trees (e.g. by natural regeneration) and those with N-dq trajectories showing abrupt slumps caused by hazard-related mortality (e.g. due to wind-throw or snow breakage). Second, we excluded the 25 % of plots with the lowest minimum stand density in terms of Reineke's (1933) stand density index, SDI, within the long-term survey period. For this purpose, we calculated plotwise SDI values for each survey and identified the lowest SDI within each of the time series. Then we eliminated the plots in the lower quartile. With this procedure, we wanted to be sure that plots with un-recorded thinnings or disturbances in the past (e.g. wood theft during World War I and II) were not used in our study.

This resulted in n = 476 experimental plots from which we used the trajectories in the statistical analyses; the dataset comprised Norway spruce (n = 154), silver fir (n = 11), Scots pine (n = 137), European larch (n = 14), Douglas-fir (n = 16), European beech (n = 67), and common & sessile oak (n = 77) (Supplementary Table 1, Fig. 1). Supplementary Fig. 1 shows the N-dq trajectories for all seven tree species and for the 476 plots that were included in the study (red) and the plots that were excluded (black).

These plots comprise a broad variety of site conditions. For providing an overview of the climate conditions covered, we used the data obtained from the JRC MARS Meteorological Database, which was available at a 25 km spatial resolution and daily temporal resolution from 1975 to 2017 (Toreti, 2014). The extremes were annual precipitation sums of 409–2952 mm, and −0.1–16.1 °C mean annual temperature (see Supplementary Table 1). The plots represent Mediterranean, Atlantic, continental, as well as boreal ecoregions in Europe. The aridity index by Martonne de (1926) ranged from 19.4 to 222.0 mm yr^{-1}/°C (Supplementary Table 1).

2.2. Data evaluation

The stand level characteristics used in this study (Box 1) were derived from the successive inventories of the tree diameters, tree heights, and records of the dropout trees. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (in German "Deutscher Verband Forstlicher Forschungsanstalten") (Biber, 2013; Johann, 1993). The stem volume was calculated with functions that were provided by the research institutions involved in the study and included regional-specific stem form equations and coefficients. The results of the standard evaluation encompassed the quadratic mean tree diameter, stand
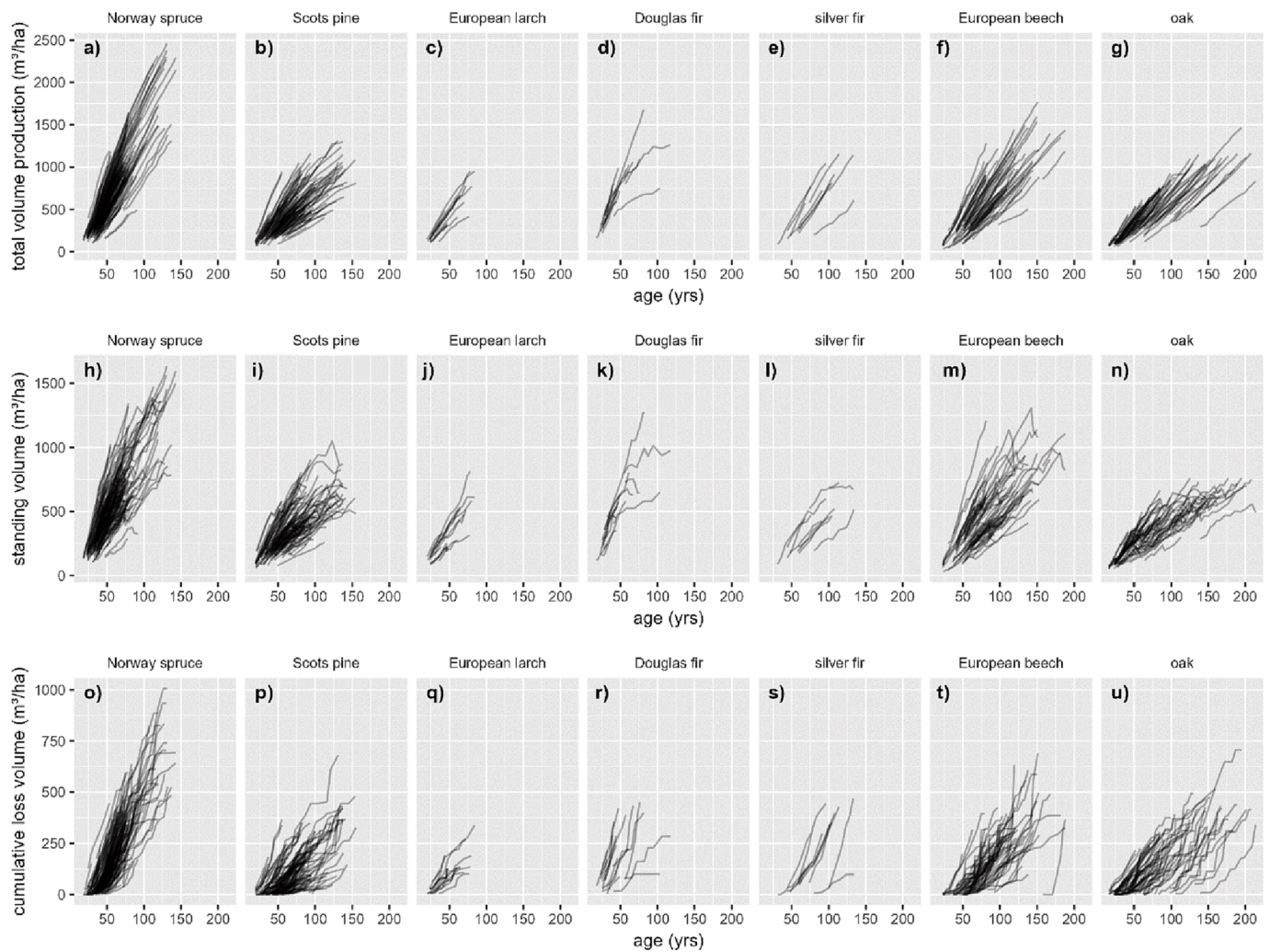
Fig. 1. Development of the total stem volume production (a–g), standing stock of stem volume (h–n), and stem volume loss (o–u) over age for all 476 experimental plots of Norway spruce, silver fir, Scots pine, Douglas-fir, European beech, and oak.

volume, and volume growth.

As an integrated measure for site quality, we determined plot- and survey-wise the site index based on the yield tables for Norway spruce by Wiedemann (1936/42), for silver fir by Hausser (1956), Scots pine by Wiedemann (1943a), European larch by Schober (1975), Douglas-fir by Bergel (1985), European beech by Schober (1975), and oak by Jüttner (1955). The site indexes we report in this text are always to be understood as expected stand heights at an age of 100 years. We selected the abovementioned Central-European yield tables for site indexing, as they cover the range of sites between the extremes of boreal and Mediterranean conditions. We are aware that the height growth patterns can differ across regions, however, in order to simplify and easily interpret and compare the site indices, we used only one yield table per species.

For estimating stem biomass and carbon content based on the calculated stem volume, we used species-specific wood density values for Norway spruce ($0.38\,\mathrm{t\,m^{-3}}$), silver fir ($0.38\,\mathrm{t\,m^{-3}}$), Scots pine ($0.43\,\mathrm{t\,m^{-3}}$), European larch ($0.49\,\mathrm{t\,m^{-3}}$), Douglas-fir ($0.41\,\mathrm{t\,m^{-3}}$), European beech ($0.55\,\mathrm{t\,m^{-3}}$), and common & sessile oak ($0.56\,\mathrm{t\,m^{-3}}$) as given by Knigge and Schulz (1966) and assumed an average carbon content of biomass of 0.5 tC per t biomass following Körner (2002, p. 945).

2.3. Statistical models, secondary variables

For modelling the total stem volume production and the standing stock of stem volume we fitted non-linear mixed effect models of the following form for each species separately:

$$y_{ij} = (a + b_i) \bullet \mathrm{SI}_{ij}{}^{m} \bullet \left(1 - \mathrm{e}^{-k \bullet t_{ij}}\right)^{p} + \varepsilon_{ij} \qquad (1)$$

On the left side, y symbolizes either total volume production or standing volume with the indexes i and j referring to the jth survey on the ith plot. The right side, in essence, is a Chapman-Richards growth function (Zeide, 1993) of stand age t, with the site index, SI, affecting the asymptote. The fixed effect parameters are a, m, k, and p. Correlation between the surveys on one plot is covered with the random effect b_i $N(0, \tau^2)$, and ε_{ij} $N(0, \sigma^2)$ are i.i.d. errors. We used the fitted functions with b_i and ε_{ij} set to 0 for calculating the expected values of the total volume production and the standing volume at a given age t and site index SI.

To answer Q1 and Q2, we derived several secondary variables from these estimates, most importantly the expected cumulative volume loss up to a given age at a given site index. This variable was calculated as the difference between the expectations for total volume production and and standing volume at the same age and site index. The time sequence of the expected values from Eq. (1) was used for calculating the expected total and standing annual volume increments as

$$\Delta y_t = \widehat{y}_{t+1} - \widehat{y}_t \qquad (2)$$

where $\widehat{y}_{t+1}$ and $\widehat{y}_t$ are the estimates of total volume production or standing volume at subsequent ages. While the first derivative of Eq. (1)

with respect to time is obvious, we preferred to calculate the increments as annual differences (in contrast to the time-continuous perception, which is associated with a derivative), because this is in line with the usual definition of increments in forest mensuration. Subtracting the annual standing volume increment from its corresponding total volume increment yields the annual stem volume loss for a given age and site index. In order to estimate the accumulation fraction of the total volume increment, we divided the annual standing volume increment at a given age and site index by the corresponding total volume increment. The resulting number represents the share of the total increment which is not lost due to mortality.

In order to relate the annual stem number loss per hectare, ΔN, to stand age and site index (Q3), we fitted species specific mixed linear models of the following form:

$$\log(\Delta N_{ij}) = a_0 + a_1 \bullet \log(t_{ij}) + a_2 \bullet \text{SI}_{ij} + a_3 \bullet \log(t_{ij}) \bullet \text{SI}_{ij} + b_i + \varepsilon_{ij} \quad (3)$$

Here, $a_0, \cdots, a_3$ are the fixed effect parameters to be estimated; all other symbols have the same meaning as in Eq. (1). When the interaction of $\log(t_{ij})$ and SI_{ij} did not turn out significant, we eliminated it from the model and re-fitted the simplified model again. In case the interaction was significant, we kept the contributing main effects, even if they were not significant themselves.

Another variable of interest was the average volume of lost trees, vmloss, at a given age and site index. While this value could have been estimated from the volume loss divided by the corresponding stem number loss from Eq. (3), we preferred to fit a separate statistical model to avoid as much bias as possible, because the vmloss values were directly accessible in our data. While the data indicated a clear dependency of vmloss from age, we observed an even more pronounced allometric connection between vmloss and the stem number loss, ΔN. Hereby, obviously, vmloss is low at high ΔN and vice versa. The time relation is implicit insofar, as ΔN is high at young stand ages and continually decreases thereafter. In order to make use of this allometric relationship we formulated it as a log–log mixed linear model additionally allowing for an effect of the site index:

$$\log(\text{vmloss}_{ij}) = a_0 + a_1 \bullet \log(\Delta N_{ij}) + a_2 \bullet \text{SI}_{ij} + a_3 \bullet \log(\Delta N_{ij})$$
$$\bullet \text{SI}_{ij} + b_i + \varepsilon_{ij} \quad (4)$$

Again, all symbols have the same meaning as in all other equations above. When the interaction of $\log(\Delta N_{ij})$ and SI_{ij} turned out non-significant, we removed it and re-fitted the model. Our procedure of removing non-significant effects from the model was the same as described above for Eq. (3). When the interaction had been already omitted, non-significant main effects were also omitted, followed by a re-fit of the simplified model. In order to demonstrate the age-dependency of vmloss, we estimated ΔN for the stand ages and site index values of interest with Eq. (3) and inserted the obtained estimates in the fitted models after Eq. (4).

The dependency of the annual mortality rates, mr, from age and site index was investigated species-wise with a logistic mixed regression model:

$$\log\left(\frac{\text{mr}_{ij}}{1 - \text{mr}_{ij}}\right) = a_0 + a_1 \bullet t_{ij} + a_2 \bullet \text{SI}_{ij} + b_i + \varepsilon_{ij} \quad (5)$$

The left side of the equation is the logit-transformed mortality rate, mr; all other variables and symbols have exactly the same meaning as in the equations above. An interaction of age, t, and site index, SI, was not taken into account, as this always produced implausible model fit results. If one of the predictors did not turn out significant, it was removed from the model which was then refitted.

For all evaluations we used the statistical software R 4.2.2 (R Core Team, 2022), especially the packages lme4 for linear mixed-effects regression models (Bates et al., 2015), and MASS (Venables and Ripley, 2002) and ggplot2 (Wickham, 2016) for graphics.

3. Results

3.1. Stand characteristics of the underlying long-term experiments

Knowledge about the mortality of permanently unthinned stands is rare but highly relevant as a reference for managed stands, for modelling, and carbon balance calculations. Therefore, we also report the respective volume records for tree species with small sample sizes, such as silver fir, European larch, and Douglas-fir.

For a first descriptive overview and comparison of the stand characteristics of the different tree species we selected out of the total number of 476 plots 157 plots with similar lengths of the observation time span. This subset comprised 24 growth trajectories for Norway spruce, 11 for silver fir, 36 for Scots pine, 9 for European larch, 7 for Douglas-fir, 40 for European beech, and 30 for oak (Supplementary Table 2). Mean values over all plots would have made the species less comparable as the data include many young and medium aged plots for Norway spruce and Scots pine and old plots in case of European beech and oak. Characteristics such as total production, standing stock, or cumulative volume loss are only comparable if they are related to similar stand ages.

The mean cumulative volume loss ranged between 170 and 641 m^3ha^{-1} and on average 25–38 % of the total volume production was lost to mortality at stand ages of 100–150 years. The maximum shares of the cumulative volume loss relative to the total volume production ranged from 35 % in case of European larch to 48 % in case of oak. For Norway spruce, Scots pine, European beech, and oak that were observed over at least 100 years, the biomass loss amounted to 105–244 t ha^{-1} with a carbon content of 53–122 t C ha^{-1}. For silver fir, European larch, and Douglas-fir that were observed at least until an age of 50 years, the biomass loss was 83–122 t ha^{-1} with a carbon content of 42–61 t C ha^{-1}. We found a mean annual stem volume loss, calculated for time spans up to 131 years of 4.21 m^3 ha^{-1} yr^{-1} for Norway spruce, 1.85 m^3 ha^{-1} yr^{-1} for Scots pine, 3.00 m^3 ha^{-1} yr^{-1} for silver fir, 2.44 m^3 ha^{-1} yr^{-1} for European larch, 5.02 m^3 ha^{-1} yr^{-1} for Douglas-fir, 2.54 m^3 ha^{-1} yr^{-1} for European beech, and 2.40 m^3 ha^{-1} yr^{-1} for oak.

When comparing the different species, it is important to consider that the represented maximum stand ages were different; Norway spruce, Scots pine, European beech and oak were older than 100 years, silver fir, European larch, and Douglas-fir were older than 50 years. For those plots that were established at medium ages (see start of trajectories > 25 years in Fig. 1) losses before were unkown. Thus, the total production may be slightly underestimated.

We visualized the total production, standing stock, and volume loss with increasing stand age for all 476 experimental plots that were included in this study for answering the questions 1–3 (Fig. 1). The total volume production (Fig. 1, a–g) showed, in general, sigmoid, almost linear growth over the covered age span. Norway spruce and European beech reached values of 1500–2500 m^3 ha^{-1} at age 100–150 years; Scots pine and common & sessile oak 1000–1500 m^3 ha^{-1}; silver fir and Douglas-fir grew similar as Norway spruce, European larch similar to Scots pine. The standing volume (Fig. 1, h–n) increased and showed some losses beginning around age 100 years. The absolute levels were 1000–1500 m^3 ha^{-1} in mature stands of Norway spruce and European beech and 500–1000 m^3 ha^{-1} in stands of Scots pine or common & sessile oak. The cumulative volume loss (Fig. 1, o–u) increased until mature stand ages; the losses at age 100–150 years totalled 500–1000 m^3 ha^{-1}.

3.2. Total production versus standing stock (Q1)

In Fig. 2, we plotted the total volume production (a-d), the standing volume (e-h), and the resulting cumulative volume loss (i-l) as resulting from the fitted models based on Eq. (1) (Table 1). As the total volume production increases more strongly than the standing volume, the cumulative volume loss (i.e. the difference between the two curves)
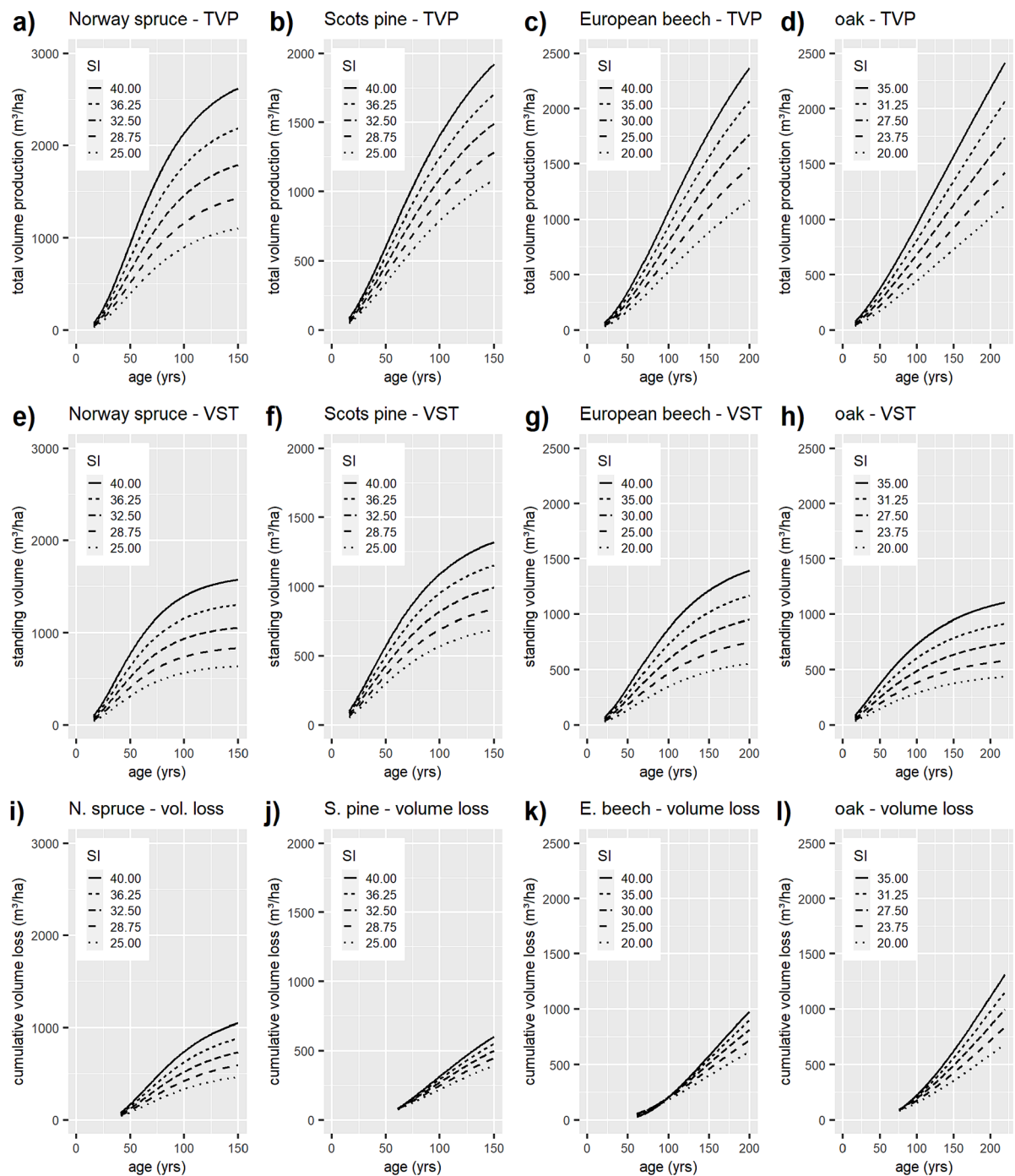
Fig. 2. Development of total stem volume production (a–d), standing stock of stem volume (e–h), and cumulative stem volume loss (i–l) over age for the species Norway spruce, Scots pine, European beech, and oak resulting from the fitted models for total volume production and standing volume after Eq. (1). The displayed ranges of site indexes represent the species specfic occurences in our data. See Table 1 and Supplementary 3 for the statistical characteristics of the fitted models. Note that, for the sake of readability, the diagram axes are identically scaled on species level only (i.e. same scaling in each column), but not across the species (i.e. different scaling along each row).

increases up to 500–1000 m^3 ha^{-1} at ages of 100–150 years. The species-specific cumulative loss was higher on rich than on poor sites, higher for faster growing tree species than for slower, and the difference between the loss on different sites increases considerably with increasing stand age (Fig. 2, i–l).

The model curves in Fig. 2, a–d are based on Eq. (1) fitted with the total volume production data (see Table 1 for the statistical results). The curves e–f result from Eq. (1) fitted to the standing volume data (see Supplementary Table 3). As we had only a low number of trajectories for

silver fir (11), European larch (14), and Douglas-fir (16) in some part of the result section, like in Fig. 2, we will focus on Norway spruce, Scots pine, European beech, and oak. Information about the other tree species is given in the Supplementary Material.

3.3. Standing versus total volume increment and accumulation fraction (Q2)

The modelled growth trajectories showed that in the first phase of

Table 1
Fit result of the model for total stem volume production depending on stand age and site index (Eq. (1)).

Fixed effect coefficients		Norway spruce n = 1292	Scots pine n = 1051	silver fir n = 71	European larch n = 100	Douglas fir n = 91	European beech n = 812	oak n = 839
a	estimate	**3.2122**	**27.4729**	93.6716	**51.3599**	**2.6243**	**84.4424**	**55.8161**
	std. error	0.3338	2.7241	51.8103	22.9392	1.0049	12.4894	9.0941
	p	0.0000	0.0000	0.0706	0.0252	0.0090	0.0000	0.0000
m	estimate	**1.8392**	**1.2217**	**1.0693**	**0.9175**	**1.8664**	**1.0201**	**1.3717**
	std. error	0.0286	0.0292	0.1645	0.1324	0.1120	0.0392	0.0312
	p	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
k	estimate	**0.0245**	**0.0144**	**0.0117**	**0.0230**	**0.0215**	**0.0088**	**0.0029**
	std. error	0.0004	0.0004	0.0020	0.0023	0.0015	0.0003	0.0003
	p	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
p	estimate	**3.1791**	**2.1258**	**3.1156**	**2.4909**	**2.7504**	**2.2718**	**1.4849**
	std. error	0.0446	0.0319	0.2956	0.1688	0.1243	0.0391	0.0218
	p	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Random effect		τ^2	τ^2	τ^2	τ^2	τ^2	τ^2	τ^2
b_i		0.3236	45.57	283.7	78.10	0.2048	748.9	519.1
Residuals		σ^2	σ^2	σ^2	σ^2	σ^2	σ^2	σ^2
ε_{ij}		1011	421.6	1070	421.4	736.7	676.2	671.5

the stand development, total and standing volume increment were rather identical for the four main tree species (Fig. 3, a–d), i. e. most of the annual growth contributes to increase the standing stock. However, at medium stand ages, large proportions of the total volume increment were lost due to competition-related mortality. Thus, the standing volume increment decreased considerably with increasing age even if the total volume increment was still at a high level.

The increasing loss due to mortality becomes obvious by the decrease of the accumulation fraction of total volume increment with stand age (Fig. 3, e–h). This proportion continuously decreases with progressing age and was similar for stands of all site indexes covered by our data.

3.4. Mortality and quality of the stem volume loss (Q3)

The annual stem volume loss caused by competition-based mortality showed a unimodal development over age with a maximum at age 75–150 years except for oak, which peaked later (Fig. 4, a–d). At this age, the annual loss amounted to 3–12 m^3 ha^{-1} yr^{-1}. For all species the loss was higher on rich compared with poor sites.

For the purposes of forest management and utilization, as well as for quantifying turnover and decomposition, it is of major interest how the lost volume is composed in terms of both tree number and mean tree volume.

The loss of trees due to competition-induced mortality decreases exponentially with progressing stand age (Fig. 4, e–h, Supplementary Table 4), from several hundreds or thousands in the juvenile phase to only a very few trees per year in stands approaching maturity. In contrast, the mean stem volume of the lost trees increases progressively with stand age (Fig. 4, i–l, Supplementary Table 5). These patterns result in the unimodal course of the total annual volume loss (Fig. 4, a–d) with the total annual volume loss expressing the product of dropout tree number × mean stem volume loss.

Tree mortality rate decreased degressively with age. It was higher on poor compared with rich sites for European beech and oak, lower for Scots pine, whereas the site index was non-significant for Norway spruce and the other species (Fig. 5, Supplementary Table 6). In younger stands, the annual mortality rate was 0.05–0.20 yr^{-1}; meaning that 10–20 % of the trees died per year mainly due to competition.

4. Discussion

4.1. Competition-based tree losses as essential component of net primary productivity

Net primary production (NPP) is the basis of all ecosystem services (Alcamo et al., 2003) and a comprehensive ecological indicator (Haberl, 1997; McNaughton et al., 1989; Zhou et al., 2015). In forests NPP can be assessed indirectly by field measurements (Clark et al., 2001) and modelled (Ruimy et al., 1999; Running et al., 2000; Cramer et al., 1999) but needs further improvement (Gu et al., 2022; Chaubey et al., 2022). Chambers et al. (2001) showed that the loss of tree mass over time can lead to underestimates in above-ground net primary productivity of forests if not quantified properly. Here, we address the loss of trees from competition-based mortality as another frequently neglected component of NPP. We show that the competition-based mortality can account for 30–40 % of the net stem volume production in forest stands during a rotation period of 100–150 years. Thus it is a highly relevant part of the NPP and, if decomposing, a source of carbon emission in only slightly thinned or unmanaged stands (Ruiz-Peinado et al., 2016).

4.2. Mortality and stem volume loss as a result of gross growth and maximum density

Whenever the growing stands exceed the site-specific maximum carrying capacity (density) the living stands suffer volume losses. Then, only parts of the stem volume growth can be accumulated, and the additional stem volume exceeding the maximum density is lost from the living stand due to mortality. If young stands are below the maximum density, a major part of the annual volume growth can be accumulated and increase the standing stock. Even if the stands reach and follow the self-thinning line (determined by the site-specific maximum LAI), the stand volume still increases, as tree volume or mass increase over-proportionally to the tree leaf area, $m \propto la^{4/3}$, according to the allometric scaling theory (West et al., 1997). Thus, even when the LAI stays constant and the stand follows the self-thinning line, the volume or mass can increase (Pretzsch and Mette, 2008; Enquist et al., 1998).

Total volume production increased linearly for a long time before reaching higher stand ages and showing an asymptotic growth pattern. As the maximum standing stock ranges on a lower level than the total production (Fig. 2), competition-based natural thinning driven by
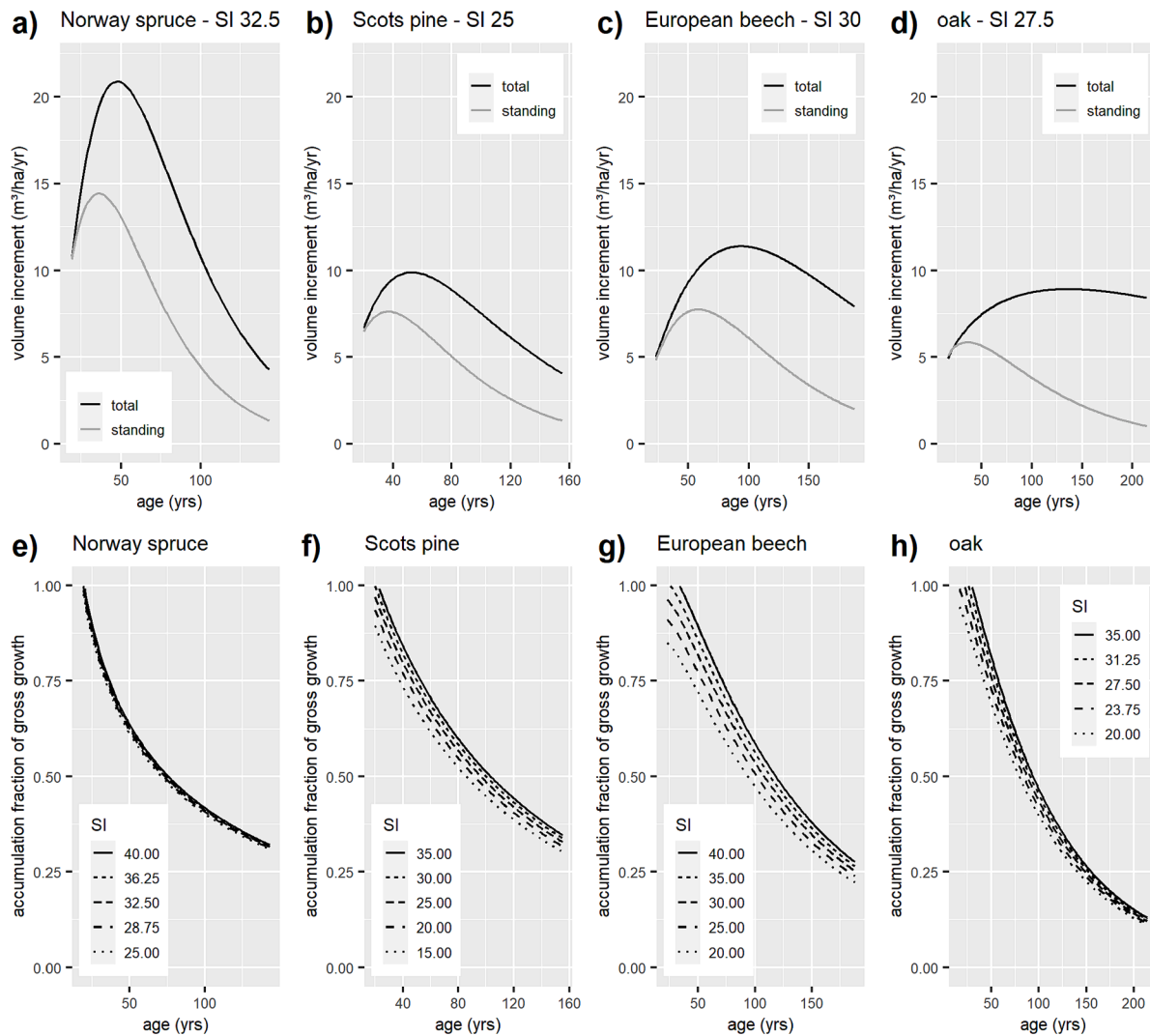
Fig. 3. Development of total and standing stem volume increment over age (a-d) for Norway spruce, Scots pine, European beech, and oak stands over age as calculated from the fitted models for total volume production and standing volume (Eq. (1) using Eq. (2)) for a site index SI (32.5, 25, 30, 27.5) which represents the middle of the species-specific range covered by our data. The diagrams e-h show the accumulation fractions of gross growth deduced from dividing the standing volume increment by the total volume increment for each species over stand age and the whole species-specific range represented by our data. See Table 1 and Supplementary Table 3 for the statistical characteristics of the fitted models.

density is inevitable. With increasing stand age, the annual gross growth developed unimodally (Fig. 3, a–d) with continuously smaller contributions being accumulated to the standing stock (Fig. 3, e–h) until the maximum standing stock was reached and the net growth became zero, i.e. the volume loss was equivalent to the gross growth. The asymptotic decrease of the net to gross growth ratio towards 0 (Fig. 3, e–h), indicates that in old, fully stocked stands an equilibrium between annual growth and loss may be achieved in accordance with Odum's hypothesis (Odum, 1969), i.e., over longer time spans the standing stock remains constant as the loss is similar to the growth. In managed stands of advanced development state (selection forests, mountain forests), the equivalent of the annual growth may continuously be exported by harvest. In both unmanaged and managed stands the standing stock may remain in a steady state close to the maximum (Nord-Larsen et al., 2019). The proportion of volume lost from gross growth was found to be almost independent of site conditions (Fig. 3, e–h).

4.3. From the evidence to the relevance of the loss portion of the total yield

The result of the interaction between continuous growth and

maximum density level is a competition-caused stem volume loss that can accumulate to 500–1000 m^3 ha^{-1} up to an age of 100–150 years which is 30–40 % of the total volume production. The annual volume loss peaked at 5–15 m^3 ha^{-1} yr^{-1} at ages about 75–100 years. Over the whole rotation, this equates to an annual biomass loss of 0.80–2.06 t ha^{-1} yr^{-1}. The corresponding carbon mass amounts to 0.40–1.03 t C ha^{-1} yr^{-1} with the ranking Douglas-fir > Norway spruce > European beech > common & sessile oak > silver fir > European larch > Scots pine.

Certainly, the lost material consisted mainly of smaller suppressed trees, whereas the growth was mostly accumulated to the taller trees that cause the loss of the smaller neighbors. Thus, at advanced ages stem volume growth and loss are similar in quantity but not identical in characteristics. Without management in stands of advanced ages the equivalent of the annual growth will pass to the debris pool. The composition of the stem volume loss changes from many small logs in younger stands, which may decompose more quickly, to lower numbers of less rapidly decomposing bigger logs in older stands (Cornwell et al., 2009; Tuomi et al., 2011).

We focussed the analyses on the interaction between growth and mortality until the age of 100–150 years, which covers the typical
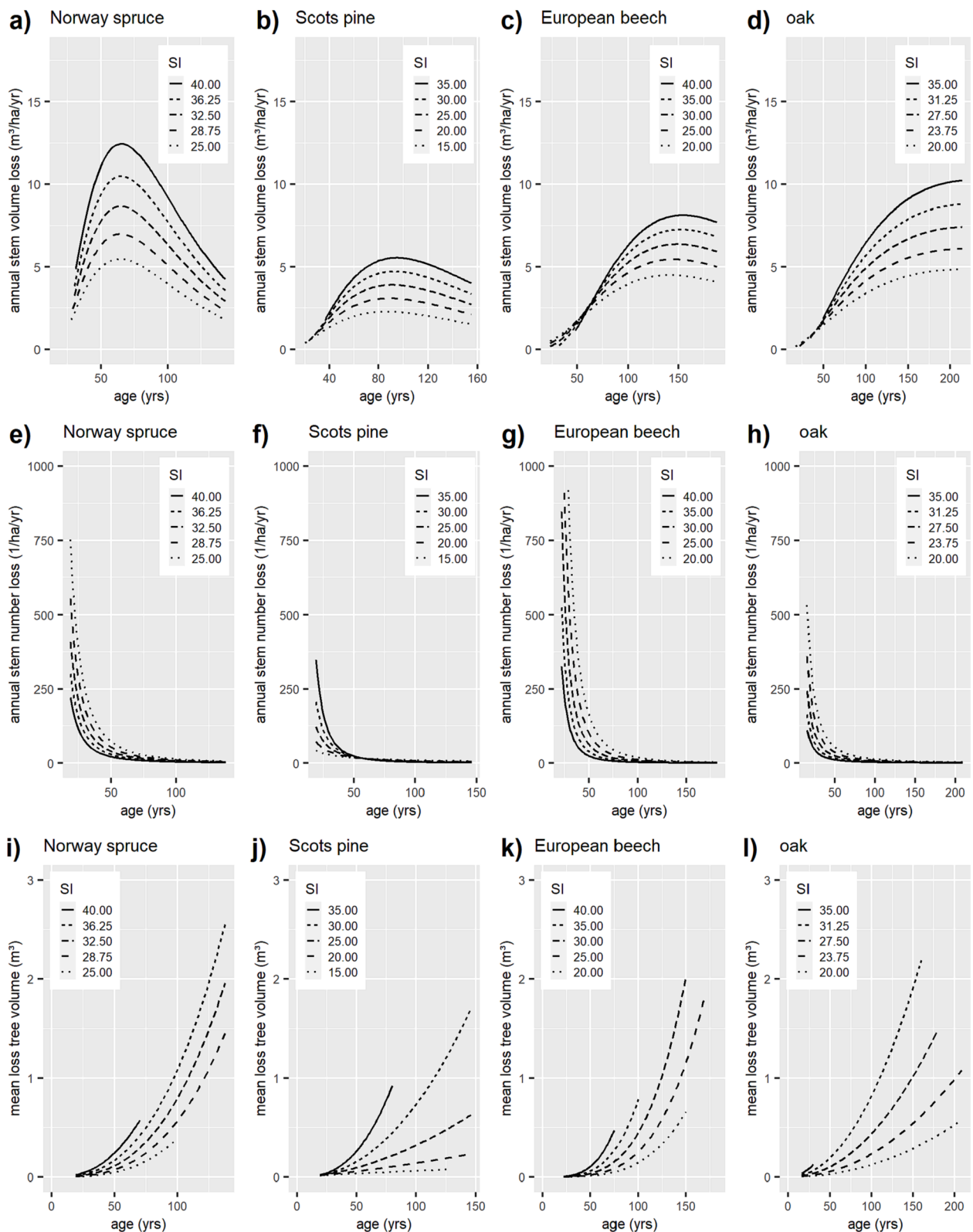
Fig. 4. Development of the annual stem volume loss (a–d), tree number reduction (e–h), and mean stem volume of the lost trees (i–l) depending on age and site index, shown for Norway spruce, Scots pine, European beech, and oak over the whole species-specific range of site indexes covered by our data. The diagrams a-d were derived from the fitted models after Eq. (1) (using Eq. (2), e–h from the fitted models after Eq. (3). The diagrams i-l were obtained by inserting the estimated stem number losses over age from the diagrams e-h into the fitted models after Eq. (4). The relationships between age and mean loss tree volume were extremely sensitive to extrapolation. Therefore, we closely restricted the displayed lines to the data coverage. See Table 1 and Supplementary Tables 3–5 for the statistical characteristics of the fitted models.
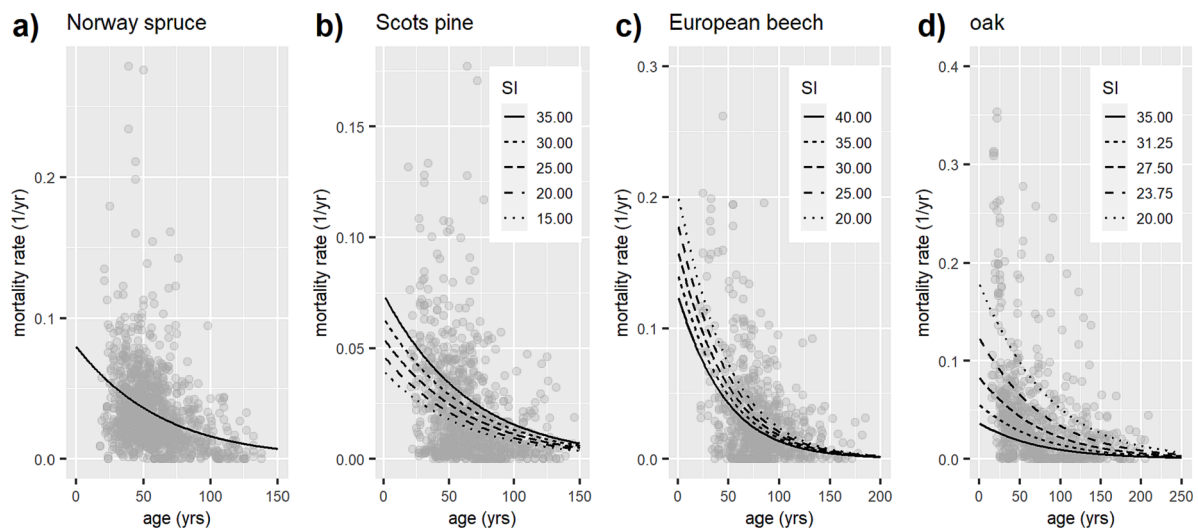
Fig. 5. Annual tree mortality rate depending on age and site index, shown for Norway spruce, Scots pine, European beech, and oak (Eq. (5); for statistical characteristics of the underlying models see Supplementary Table 6).

rotation length for the respective species. In very young or old stands there may be deviations from our findings. During the very early stand development phase, tree numbers and stand density may be so low, and still well under the self-thinning line, that mortality is less competition driven. In old stands, beyond the rotation length, the tree number may decrease below the self-thinning line due to a disturbance-based mortality that may strike in principle trees of all sizes or even target the larger trees as for example with storm damage (Holzwarth et al., 2013; Schmidt et al., 2010).

The species-specific mortality rates may be useful for growth models (Salas-Eljatib and Weiskittel, 2020) as they reflect the tree elimination without thinning. Most North American yield tables (normal yield tables) were developed from one-time measurements of unmanaged stands and thus they reflect the maximum stand density but do not include total production (Plonski, 1971; Weiskittel et al., 2011) because long-term measurements of both standing stock and previous losses were not available. European yield tables based on long-term thinning experiments are based on repeated measurements but rarely include information about unthinned or lightly thinned stands (Assmann, 1970; Schober, 1975). This study provides unique information about both the remaining and lost stand volume of unthinned stands within a whole rotation.

Knowledge of the natural loss is of special interest for models that address the development of the structural and genetic diversity with increasing age (Davies et al., 2016; Ratnam et al., 2014). Knowledge of the natural reduction in tree numbers is also useful for experimental design; it can be used to develop a conception of adequate plot sizes and/or minimum numbers of remaining sample trees at advanced development stages. Furthermore, any silvicultural prescriptions aiming to anticipate "natural" mortality through thinnings may use the mortality rates for scheduling the species-specific decrease of thinning intervals and intensity with progressing stand development.

4.4. Consequences for forest management

Our study concerns temperate even-aged, monospecific forests, planted at close spacing, and may be less applicable for close-to-nature silviculture, or for short-rotation plantations. We studied the above ground biomass; further research into the below ground biomass is required to make the full carbon balance. Further research should also consider that a large portion of the below ground biomass does not come from litter, but from below ground processes such as exudates and mycorrhiza. So the effects of different silvicultural interventions are not

limited to wood that is removed, but they also affect the biomass that is linked to the soil (Adamczyk, 2021).

With increasing stand age, the above ground standing volume stock in even-aged, monospecific forests is sigmoidally increasing (Fig. 2, e–h) and approaching a site dependent maximum of 500–1000 $m^3 \, ha^{-1}$ at ages of 100–150 years. During early stand phases, when the growing stock is still far from this maximum, losses tend to be low (Fig. 2, i–l) as high proportions of the annual gross growth are accumulated to the growing stock (Fig. 3, e–h). Until middle stand ages, growing stock and, likewise, gross growth increase considerably. However, continuously decreasing proportions of the gross growth are added to the standing stock, and, consequently, increasing proportions are lost (Fig. 3, e–h).

Without question, there are many good arguments in favour of keeping stands of advanced development stages in the forest portfolio (habitats, biodiversity, recreation, landscape aesthetics, seed provision for regeneration). However, the contribution of such mature stands to continuous carbon sequestration decreases continuously with age (Fig. 3, a–d). At middle stand ages, the gross growth decreases but the net growth decreases even faster, so that e.g. at age 100 years the gross growth may be 10 $m^3 \, ha^{-1} \, yr^{-1}$ but less than 50 % of this is added to the standing stock because the rest adds to the debris pools. In comparison, younger stands contribute considerably more to carbon accumulation than older stands (Fig. 3).

Knowledge of gross growth, density-driven mortality, and net growth is essential for sustainable management and derivation of an adequate annual thinning yield. Losses from the living stand in terms of basal area, volume, or mass provide cumulative information regarding turnover. If the natural dropout in unmanaged stands remains unexploited it is transferred from the pool of the living trees to the debris pool. Typically, a large proportion of the wood produced during a rotation in traditional forest management is used for relatively long-lived products like sawn wood or wood-based products with half live times of > 30 or > 20 years, respectively (Schwaiger et al., 2019). Even if we account for thin logs being used as fuel wood, the average lifetime of a unit of harvested wood should typically exceed the lifetime of a unit deadwood as e.g. reported by Přívětivý et al. (2016). We wish to point out, that this does not necessarily mean that the accelerated deadwood production through natural thinning is completely lost in decomposition. Actually, it might increase humus content, nutrition status, and water storage capacity of the soil, which depends, however, on nutrient status and temperature (Lal, 2005).

In order to exploit a higher fraction of gross growth for carbon sequestration, adapted thinning guidelines and felling budgets would

thus be required (Marland and Schlamadinger, 1997; Nunes et al., 2020; Ruiz-Peinado et al., 2013). As outlined above, simply accumulating deadwood may not provide the most effective carbon sink in the long term for European forests. It could be much more effective to apply adapted thinning guidelines and felling budgets in order to pre-empt the increased mortality and to transfer the harvested wood into uses/ products facilitating carbon sequestration or C-emission substitution rather than losing sequestered carbon from a forest's debris pool with its considerably faster turnover (Nielsen et al., 2021). Our study may contribute to revelation of the environmentally-optimal tradeoff between deadwood for the environment and carbon sequestered in wood products. Our results indicate the leeway for management decisions between wood utilization (and related carbon storage and emission savings) and deadwood accumulation for facilitating biodiversity. The mortality related losses and loss fractions we quantified in this study might serve as indicators for the leeway in decisions between active forest management and shutting down silvicultural activities.

CRediT authorship contribution statement

Hans Pretzsch: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Miren del Río:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Catia Arcangeli:** Writing – review & editing. **Kamil Bielak:** Writing – review & editing. **Malgorzata Dudzinska:** Writing – review & editing. **David Ian Forrester:** Writing – review & editing. **Ulrich Kohnle:** Writing – review & editing. **Thomas Ledermann:** Writing – review & editing. **Robert Matthews:** Writing – review & editing. **Ralf Nagel:** Writing – review & editing. **François Ningre:** Writing – review & editing. **Thomas Nord-Larsen:** Writing – review & editing. **Henryk Szeligowski:** Writing – review & editing. **Peter Biber:** Conceptualization, Formal analysis, Methodology, Writing – original draft, 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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121204.

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