Forest Ecology and Management 460 (2020) 117879

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning

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ARTICLE INFO

*Keywords:*
Norway spruce
Long-term experiments
Short-term thinning reactions
Allometric drift
Thinning response
Growth losses after thinning
Diameter growth acceleration

ABSTRACT

Many current stand management guidelines propose low initial stand densities and strong density reductions in order to lower the costs of stand establishment, to accelerate stand growth and promote the diameter growth of selected future crop trees. The long-term effects of density reductions on growth and yield, however, are often neglected; they remain open for debate due to a lack of empirical evidence.

Here we examine 22 thinning experiments in Norway spruce *(Picea abies* (L.) Karst.) located in Germany with 127 plots and 1209 full stand measurements to revisit the density-growth relationship. These experiments cover both short- and long-term growth reactions to thinning since their establishment in 1882.

First, we show the temporarily unimodal optimum relationship between periodical increment and stand density; and how it results in a saturation curve between stand yield and stand density in the long term. We particularly highlight how the effect of stand density reductions on growth reduces across stand development. Second, we show the dependency of total yield on the thinning (kind, severity and intensity of thinning) and site quality. Over time, unthinned stands achieve the highest total yield of stem wood. Thinning causes severe growth losses, especially on rich sites and through thinning from below; e.g. on top sites a continuous density reduction by thinning from below to 50% of the maximum density reduced the total yield by 26% or 670 $m^3$ $ha^{-1}$ till the age of 100 years.

Third, we demonstrate that the effect of thinning on the diameter of dominant trees is strongest on rich sites and similar when thinned from above or below. Over time, accelerating diameter growth incurs a high cost in terms of stand yield.

Finally, we examine the relevance of our results to population ecology and production economy. We discuss the superior yield after thinning from above, the tradeoff between tree diameter growth acceleration and yield, and the relevance of long-term experiments and their impact on silvicultural prescriptions.

## 1. Introduction

How forests react to stand density reduction and how to thin them appropriately are questions as old as systematic forest science (Hartig, 1795; Cotta, 1828; Reventlow, 1879) and controversially debated till present (Dobner et al., 2019; Gebhardt et al., 2014; Reventlow et al., 2018; Zeide, 2002). Currently, management guidelines vie with one another in density reduction to lower the cost of stand tending (Bataineh et al., 2013; Chase et al., 2016; Johann, 1987; Pollanschütz, 1974), to accelerate the diameter growth of a selected number of future crop trees (Bücking et al., 2007; Klädtke et al., 2012; Utschig et al., 2011), or to prepare stands for drought stress considering climate change (D'Amato et al., 2013; Navarro-Cerrillo et al., 2019; Sohn et al., 2013). However, only high stand densities allow the exploitation of the accelerated growth shown in many regions in the northern hemisphere (Kauppi et al., 2014; Pretzsch et al., 2014, 2018; Spiecker et al., 1996); and the effective sequestration of athmosperic carbon through forest growth (Eriksson, 2006; Finkral and Evans, 2008; Schwaiger et al., 2018, 2019). These currently diverging tendencies revive the old question of the right thinning option. Key to answering it is a sound knowledge of the long-term effects of stand density regulation on the growth and yield of forest stands (Zeide, 2001, 2002).

Stand density reduction can both anticipate and liqidate part of the final harvest and accelerate the growth and improve the quality of the remaining trees. This renders stand density regulation the most essential silvicultural measure between stand establishment and final harvest. Thus, it is important to understand the effects of thinning, i.e. whether “a lot helps a lot” or whether strong thinnings may cause

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https://doi.org/10.1016/j.foreco.2020.117879
Received 19 September 2019; Received in revised form 10 December 2019; Accepted 6 January 2020
Available online 21 January 2020

severe yield reductions. Zeide (2001) described in an unmatched way the circle from the initial belief that unthinned stands produce the most – as "nature does best" (Rousseau, 1762) – to the conviction that thinning significantly increases stand growth through eliminating inefficient trees and anticipating mortality (Hartig 1795, p. 17; Cotta, 1828, p. 103), to "a full turnaround" (Zeide, 2001, p. 21) to the initial view that thinning mostly decreases the total yield. This full circle is reflected by the initial assumption of a saturation curve for the density-growth relationship, i.e. the maximum productivity is attained when stand density is kept at maximum. This initial view was replaced by the assumption of a unimodal optimum curve, i.e. that maximum productivity can be achieved through moderate density reduction (Mar-Möller, 1945; Langsaeter, 1941). Finally, we consider a return to the initial assumption of a saturation curve for the density-growth relationship (Bose et al., 2018; Curtis et al., 1997).

The main reasons for the knowledge gap regarding the density-growth relationship are the lack of long-term observations, the substitution of long-term experiments through temporary plots, the institutional hurdles to pooling a large number of long-term experiments, and the considerable challenge to evaluate such large datasets.

Examining general relationships requires long-term experiments with recordings of the method of silvicultural interventions, removals and the remaining stand over long periods; if possible, at least over one whole rotation. Short-term observations may result in the overestimation of thinning effects. A prominent early example for an overestimation comes from Schwappach, one of the founding fathers of growth and yield science, in his yield table for oak (1905). Out of the 133 plots used for his yield table, 99 plots were measured just once and resulted in an overly optimistic assumption concerning the growth response to thinning. After repeated measurement of the plots, Schwappach (1920) had to compile a second version of his yield table for oak. This second version represented a less optimist assumption regarding the stands' ability to compensate for stand density reduction through thinning from above (Dittmar, 2001, pp. 160–164) and a much lower stand density.

Thus, records from short-term observations can be misleading regarding long-term thinning effects. In addition to the length of observation, a representative number of long-term experiments are essential to reveal any statistical relationships between stand growth and species identity, kind of thinning, site conditions and other factors. Such long-term experiments should include unmanaged plots as references and, among other factors, cover different thinning regimes and sites and as many replications as possible. Otherwise, evaluations of the density-growth relationship may have the character of case studies, i.e. they may not allow any generalization and perpetuate circular views and assumptions (Zeide, 2001).

The debate about whether human intervention through thinning has a positive or negative effect on productivity has a biological-philosophical dimension. If thinning increased stand productivity, yield could be increased by removing part of the capital stock; similar to a bank account where the capital increases through occasional withdrawals. Conversely, this suggests that nature maintains individuals although they grow inefficiently, i.e. that trees waste energy to undermine or kill neighbours. In anticipating such wasteful processes, foresters may avoid energy losses and allocate growth to the remaining trees instead.

This fundamental question of whether nature or humans "do better" is fascinating and challenging for theoretical ecology purposes. Practically, however, most forest stands are thinned anyway in order to mechanically stabilize them (Bryndum, 1987; Rottmann, 1986), increase mean tree diameter (Klädtke et al., 2012; Mäkinen and Isomäki, 2004), or maintain a balanced mixture of species (Pretzsch and Zenner, 2017; Schwaiger et al., 2019); exceptions may be bio-energy or pulp plantations (Eriksson, 2006; Zeide, 2001).

As most forests in Europe are thinned regularly, the practically more relevant questions are how stand growth reacts to different kinds of thinning (thinning from above, from below, systematic thinning), how the thinning response depends on the site conditions, and how the long-term effects and the short-term reaction compare. Although they are essential for the development of site- and species-specific thinning guidelines and yield prognosis general answers to these questions are scarcely available in practice and also missing in textbooks.

In this study we revisit the density-growth relationship and analyse how it changes based on the temporal scale; and how it is modulated by site conditions, thinning, and interactions between these factors. We examined this relationship in monocultures using the example of Norway spruce *(Picea abies (L.) Karst.)*, which is the economically most important tree species in Europe. To avoid a case study character and arrive at general results, we used 22 thinning experiments in Norway spruce with 127 plots and 1209 full stand measurement surveys. These cover both short- and long-term reactions to thinning since their establishment starting from 1882. We focused on the questions Q1–Q3:

Q1 How do stand density reductions modify the mean periodical increment in the period after the thinning and the total yield in the long term?
Q2 How does the total yield depend on the mean stand density, site quality, and kind of thinning?
Q3 How does the stem diameter of the dominant trees depend on the thinning characteristics and the site quality of the stand?

Finally, we discuss the implications of our results for population ecology and production economy as well as the relevance of the site-dependency of the thinning response for silvicultural guidelines.

## 2. Material and methods

### 2.1. Material

#### 2.1.1. Long-term experiments as data base

We base our evaluation on long-term experimental plots which foresighted researchers began to establish in the late 19th century to procure growth and yield data as a quantitative basis for sustainable forest management as described among others by von Ganghofer (1881). In the beginning, these focused on thinning experiments that analyzed different kinds, severities and intensities of thinning measures on the growth and yield of monocultures (Verein Deutscher Forstlicher Versuchsanstalten, 1873, 1902). The kind of thinning characterizes how the vertical stand structure is modified (e.g., thinning from above, from below, systematic thinning) by the intervention, the severity characterizes the degree of stand density reduction (e.g., slight, moderate, or heavy thinning), and the intensity addresses the frequency of thinning (e.g., intervention every 3, 5 or 10 years).

The appropriate thinning was crucial for sustainable management. Therefore, most of the early experiments comprised differently thinned plots, as well as unthinned reference plots. Many of the observational plots established since the 1880s have been re-measured approximately 20 times to date, provide the longest existing time series data on forest stand dynamics available (approximately 140 years), and still form an essential component of the forest observation network in Central Europe to the present day.

To analyse the effects of various silvicultural treatment options on stand structure and yield, the unthinned plots provide a valuable reference. In Europe's entirely managed forests, the unthinned plots represent an exceptional case of 140 years of unmanaged ecosystem development, where growth is not confounded by any silvicultural treatment effects. In the present study, the unthinned plots serve as a reference for assessing the relative density and productivity of thinned plots. For the purposes of this analysis, we exclusively selected mono-specific and even-aged stands of Norway spruce which originated from planting or seeding.

#### 2.1.2. Location and site characteristics of the selected stands

A total of 22 long-term thinning experiments in Norway spruce with 127 plots and 1209 complete stand surveys were included in this study (see Supplementary Table 1). The plots represent growth conditions in the plains and highlands of Central Germany. The locations occur from 510 to 843 m a.s.l. The experiments are mainly located in submontane and montane highlands, and in the pre-alpine mountain zone. The long-term mean temperature and annual precipitation exhibit a broad range of climate conditions (6.0–7.6 °C and 800–1255 mm $yr^{-1}$). The experimental distribution over 8 eco-regions and 7 geological zones is reflected in the broad spectrum of soil types. The poorest soils are podsols derived from sandstone and cretaceous material in the Frankonia Alb; the most fertile soils are parabrown soils from diluvial loess-loam in the pre-alpine highlands. Located mainly between Nuremberg, Regensburg, and Garmisch-Partenkirchen, the majority of the included stands are growing on sites of mediocre fertility in the Central German gradual layer area “Schichtstufenlandschaft” and on sites of rich fertility in the pre-alpine highlands.

### 2.2. Methods

Table 1 gives an overview of the abbreviations and definitions of the variables used in this study.

#### 2.2.1. Growth and yield variables

Repeated measurements of tree characteristics (e.g stem diameter, tree height, survival, crown dimensions) were performed in several year intervals. The range of the measurement return intervals was 3–12 years and the mean measurement return time was 7 years. Mean tree (e.g DO, DQ, HO, HQ) and stand characteristics (e.g. V, PIV, TYV) were evaluated following DESER-Norm (Johann, 1993). These repeated measurements generated the mean periodic volume increment (PIV) values, i.e. mean annual growth rates over longer time intervals. Between two surveys at times $t_1$ and $t_2$, given wood volumes $V_1$ and $V_2$ of the remaining stand at $t_1$ and $t_2$, and $V_{removed}$, the volume which was removed (or died) in-between the surveys, PIV is

$$PIV = (V_{2\,remain} - V_{1\,remain} + V_{removed})/(t_2 - t_1)$$

Older plots, which were periodically measured for approximately one hundred years delivered unique information regarding the total volume yield (TYV). The total volume yield TYV at a given time t is obtained by integration of PIV from the first observation $t_0$ up to t:

$$TYV_t = \int_{t_0}^{t} PIV\, dt$$

Standing volume V at time t is derived from

$$V_t = \int_{t_0}^{t} PIV\, dt - \int_{t_0}^{t} V_{removed}\, dt$$

All volume information given in this study refers to merchantable wood volume (log diameter >7 cm at the smaller end), including bark.

To compare the short term-effect of thinning with the long-term effect (Q1), we calculated the relative mean periodical volume increment, PRIV, for each survey period separately; as well as the relative total yield of volume, RTYV, for the whole survey time in total. PRIV, was calculated as the quotient of the absolute periodic stem volume increment, $PIV_{thinned}$, on a thinned plot in $m^3\ ha^{-1}\ yr^{-1}$ and the absolute periodic stem volume increment, $PIV_{unthinned}$, on neighbouring unthinned plots that represent the increment for maximum stand density at the same age and in the same time perid ($PRIV = PIV_{thinned}/PIV_{unthinned}$). For instance, PRIV = 1.20 means that the volume increment on the plot in question achieves 120% of the unthinned reference plot. As reference plots we used the A-grade plots of the respective experiments. According to Verein Deutscher Forstlicher Versuchsanstalten (1873, 1902) A-grade plots are unthinned reference plots from which only dead or dying trees are eliminated. Analogously to the thinned plots they are also periodically measured and reflect the stand development without silvicultural interventions (e.g., the site specific maximum stand density).

RTYV, is the absolute stem volume yield, $TYV_{thinned}$, of the last survey of a thinned plot devided by the total volume yield, $TYV_{unthinned}$, of a neighbouring unthinned reference plots $RTYV = TYV_{thinned}/TYV_{unthinned}$. This analysis derives an advantage from the standard equipment of the Bavarian network with A-grade plots (Pretzsch, 2017; Pretzsch and Utschig, 2000). For all plots with PRIV and RTYV values we also derived the relative stand densities PRSDI and MRSDI according to Section 2.2.2.

To analyze the dependency of the total yield and dominant tree diameter on the stand density, site quality, and thinning grade (Q2 and Q3), we used the total stem volume yield, TYV, and DO. TYV quantifies the sum of the standing stem volume, $V_{remain}$, and the accumulated intermediate yield, $V_{removed}$, till the end of the last survey period ($TYV = +V_{remain} + V_{removed}$). DO is the quadratic mean diameter of the 100 thickest trees per hectare.

To quantify the site quality of the experimental plots we used the site index system of the yield tables by Assmann and Franz (1963, 1965). For giving an overview of the present site quality of the stands (Table 2) we calculated the mean height of the 100 thickest trees per hectare for each experimental plot for the last survey. For analyzing the effect of stand density on the total volume yield we calculated the mean SI during the whole observation time, based on the SI at the end of each of the included measurement periods. The yield table by Assmann and Franz (1963, 1965) is based on Norway spruce stands in South Germany and represents their growing conditions quite well. For stands exceeding the site index frame of the table (SI 20–40 m) we used the extension of the yield table developed by Röhle (1994, 1997).

**Table 1**
Abbreviations and definitions of used variables.

| Abbreviation | Definition of variable |
|---|---|
| AGE | stand age |
| CTH | continuity of thinning; relative coefficient of variation of return times between thinnings |
| DO | quadratic mean diameter of the 100 tallest trees |
| DQ | quadratic mean diameter |
| DR | quadratic mean stem diameter of the trees remaining after a thinning |
| DT | quadratic mean stem diameter of the thinned trees |
| DTDR | kind of thinning; DTDR = DT/DR |
| FRTH | frequency of thinning; means return time between thinning |
| FTH | stand age when the stand was thinned for the first time |
| HO | height of the tree with DO |
| HQ | height of the tree with DQ |
| IRSDI | initial SDI at the beginning of the long-term survey of a plot, $IRSDI = SDI_{obs}/SDI_{max}$ |
| MRSDI | mean relative SDI; ratio between the observed SDIs on a plot and the maximum SDIs on a neighbouring unthinned plot in the course of stand development |
| PIV | periodic annual volume increment per hectare |
| PRSDI | periodic relative SDI; ratio between the observed SDI on a plot and the maximum SDI on a neighbouring unthinned plot |
| PRIV | relative periodic annual volume increment; ratio between the PIV of thinned and unthinned plots |
| RTYV | relative total yield; ratio between the TYV of thinned and unthinned plots |
| $SDI_{max}$ | maximum SDI on an unthinned plot at the beginning of a measurement period |
| $SDI_{obs}$ | observed SDI at the beginning of a measurement period |
| SI | site index |
| TTH | trend of the thinning strength |
| TYV | total yield of the stem volume per hectare |
| V | standing stem volume per hectare |
| $V_{remain}$ | standing volume after thinning |
| $V_{removed}$ | stem volume removed by thinning |

**Table 2**
Overview over selected stand characteristics for the last survey of the 22 long-term spacing and thinning experiments in Norway spruce with a combined total of 127 plots.

| | Site index m | SDI $ha^{-1}$ | Stand age years | DO cm | MAI $m^3\ ha^{-1}\ yr^{-1}$ | HQDQ $m\ cm^{-1}$ | HODO $m\ cm^{-1}$ | $V_{remain}$ $m^3\ ha^{-1}$ | $V_{removed}$ $m^3\ ha^{-1}$ | TYV stem vol $m^3\ ha^{-1}$ | rel. inter-med.yield $m^3\ ha^{-1}\ m^{-3}\ ha^1$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| mean | 39.6 | 687 | 69 | 36.6 | 15.9 | 0.84 | 0.87 | 687 | 429 | 1098 | 0.37 |
| std | 3.07 | 355 | 32 | 12.3 | 4.1 | 0.13 | 0.19 | 355 | 301 | 563 | 0.17 |
| min | 31.4 | 36 | 27 | 12.6 | 6.5 | 0.44 | 0.39 | 36 | 2 | 213 | 0.00 |
| max | 47.9 | 1637 | 143 | 78.3 | 24.1 | 1.20 | 1.36 | 1637 | 1928 | 2459 | 0.44 |

Site index based on dominant height at age 100; SDI stand density index; DO quadratic mean diameter of the 100 tallest tree per stand; MAI mean annual stem volume increment; HQDG slenderness ratio HQ/DG based on the height and diameter of the quadratic mean tree; HODO slenderness ratio HO/DO based on the height and diameter of the 100 tallest trees; $V_{remain}$ standing volume stem wood; $V_{removed}$ sum of removed stem volume; TYV total volume yield until the last survey; relative intermediate yield is the ratio $V_{removed}$/TYV.

*2.2.2. Variables for the characterisation of the initial stand density and of thinning interventions*

To examine Q1 we required variables to characterize the stand density both in a given survey period and across the entire time, from the first till the last survey. To analyze the effect of stand density on the mean periodical volume increment RPIV we calculated the relative stand density PRSDI at the beginning of each survey period. PRSDI is the quotient of the current $SDI_{obs}$ according to Reineke (1933) on a plot at the beginning of a measurement period and the maximum $SDI_{max}$ derived from the neighbouring unthinned reference plots ($PRSDI = SDI_{obs}/SDI_{max}$).

The unthinned plots (A-grade plots or reference plots) represent the site specific maximum stand density and were part of all long-term experiments that were established according to the recommendations of Verein Deutscher Forstlicher Versuchsanstalten (1902). We used the recorded tree numbers per hectare, N, and the quadratic mean diameters, $d_q$, as basis for parameterization of the model $\ln(N) = aa + b\times \ln(d_q)$ by 95% quantile regression (Pretzsch and del Río, 2019; Pinheiro et al., 2017). In this way we derived a site-specific maximum stand density line for each experimental plot. This site-specific maximum stand density line was used as reference for calculating the ratios PRSDI, MRSDI, and IRSDI, that are introduced and applied subsequently.

For quantifying the stand density effect on the relative total volume yield we used the mean relative stand density index, MRSDI. The latter was based on the SDI values observed at the beginning and the end of the 1… n survey periods ($SDI_{obs,1b}$, $SDI_{obs,\ 1e}$, …, $SDI_{obs,\ nb}$, $SDI_{obs,\ ne}$), the period lengths ($per_1$, $per_2$, …, $per_n$), and the maximum SDI values at the beginning and the end of each survey period ($SDI_{max,1b}$, $SDI_{max,\ 1e}$, …, $SDI_{max,\ nb}$, $SDI_{max,\ ne}$). For this purpose we first calculated the mean weighted SDI level across the entire survey time

$$MSDI_{obs} = \frac{\left(\frac{SDI_{obs,1b} + SDI_{obs,1e}}{2}\right) \times per_1 + \ldots + \left(\frac{SDI_{obs,nb} + SDI_{obs,ne}}{2}\right) \times per_n}{per_1 + per_2 + \ldots + per_n}$$

Subsequntly, we set this absolute observed $MSDI_{obs}$ in relation to the maximum SDI during stand life, calculated analogously based on the maximum SDI values at the beginning and end of each survey period $MSDI_{max}$. MRSDI results as the ratio $MRSDI = MSDI_{obs}/MSDI_{max}$. MRSDI represents the weighted mean relative stand density over a longer period; its concept is analogous to Assmann's periodical mean basal area level (Assmann, 1961, pp. 211–212), and this approach has proved to be a useful method for quantifying the mean stand density over longer periods when analysing (Assmann, 1961, pp. 243–256) and modelling (Assmann and Franz, 1963, 1965) density-growth relationships. MRSDI = 0.8, for instance, indicates that the stand was kept on average on 80% of the maximum stand density during the entire survey time.

To analyze the effect of stand density regulation on the total yield, TYV, and the dominant tree diameter, DO, we also used the MRSDI. Additionally, we calculated a set of 6 others variables that characterize the initial stand density (IRSDI), the age of the first thinning (FTH), the graduation of the strength or trend of the thinning strength (TTH), the kind of thinning (DTDR), mean return time between thinnings (FRTH), and the continuity of thinning (CTH). Given that only the initial stand density (IRSDI) and the kind of thinning (DTDR) displayed a significant effect on TYV or DO, we only introduce these two out of the six measures.

The initial stand density, IRSDI, was quantified by the ratio between the actual stand density index on the plot and the site-specific maximum stand density index ($IRSDI = SDI_{obs}/SDI_{max}$). IRSDI refers to the stand density that was measured when the experimental plots were established and measured for the first time (respective dates given in Supplementary Table 1). IRSDI = 0.50 indicates an initial stand density of 50% of the maximum stand density measured on the neighbouring unthinned plots of the experiment. To calculate the plot-specific IRSDI we derived the maximum $SDI_{max}$ based on the unthinned or only slightly thinned plots of the respective experiment. IRSDI results as the ratio between $SDI_{obs}$ for the first inventory of each thinned plot and the $SDI_{max}$ derived from the neighbouring unthinned plots.

DTDR indicates the kind of thinning. It is based on the quadratic mean diameter of the thinned trees, DT, and the quadratic mean stem diameter of the stand after thinning, i.e. the quadratic mean diameter of the remaining stand (DTDR = DT/DR). High values indicate removal of relatively tall trees and thinning from above, while small ratios indicate thinning from below.

CTH quantifes the continuity of thinning. The time intervals between the thinnings in terms of years were used to calculate the coefficient of variation. A perfectly periodical thinning intervention, e.g. every 5 or 7 years results in the lowest CTH value (CTH = 0). Irregular thinning interventions, e.g., seldom thinning interventions in young stands followed by frequent thinnings in older stands would yield high CTH values.

Our regression analyses showed that MRSDI has a very strong effect on all analyzed growth and yield characteristics. IRSDI showed much lower effects. However, IRSDI did not contribute significantly to the estimation of TYV and DO when MSDI was already included in the model. Thus, although IRSDI is introduced in this section, it will not be mentioned below.

On long-term experimental plots the standing stock and stand density is measured only at the beginning and at the end of each measurement period (Johann, 1993). Consequently, from the trees which died within a given measurement period the exact time of their dropout is unknown. Usually their dropout is ascribed to the end of the measurement period; in this way the stand density within the measurement period can be overestimated. The overestimation increases with the post-thinning mortality, i.e. the mortality between the two surveys. For the last couple of surveys of our plots we could differentiate between trees removed due to mortality and due to thinning. We found that the post-thinning mortality was between 0.5 and 1% per year. This means that the density characteristics IRSDI, PRSDI, and MRSDI slightly overestimate the real stand density within the period as a minor portion of the trees may already have dropped out. This means for a given stand density the growth rates would be slightly higher than than reflected by models 1–6; i.e., the growth resilience to density reductions is slightly underestimated by the models.

### 2.3. Statistical analysis and models

To analyse the relationship between stand regulation characteristics (e.g. initial density and mean density) and the stand reactions (e.g. total volume yield and volume growth), we applied linear mixed effect models with nested random effects on the experiment and plot level in order to account for autocorrelation effects. The fixed effect parameters are $a_0$– $a_7$. The random effects $b_i$ and $b_{ij}$ cover the levels experiment and plot, ε represents the uncorrelated remaining errors. The indexes i, j and k describe the up to three nesting levels to be considered when analysing the data. The experiment level was i, ij represented plot j in experiment i, and ijk was observation k on plot j in experiment i. Log-transformation of the variable removed any heteroscedasticity. The decision between the full random effect model and potentially simpler sub-forms was made based on the Akaike Information Criterion (Burnham and Anderson, 2004).

The following numbers of the models refer to the results in the text (models 1 and 2) and in Table 4 and 5 (models 3–6). We restricted the results to the fixed effects.

Model 1: $$\ln(\mathrm{PRIV}_{ik}) = a_1 \times \ln(\mathrm{PRSDI}_{ik}) + a_2 \times (\ln(\mathrm{PRSDI}_{ik}))^2 + b_i + \varepsilon_{ik}$$

This model addressed the dependency of the relative periodical volume increment, PRIV, on the relative stand density index, PRSDI, at the beginning of the respective survey period. Random effects $b_i$ related to the experiment level in order to account for dependencies between plots of the same experiment. For the statistical characteristics see section 3.2.

Model 2: $$\ln(\mathrm{PRIV}_{ik}) = a_0 + a_1 \times \ln(\mathrm{DQ}_{ik}) + b_i + \varepsilon_{ik}$$

This model described the dependency of the relative periodical volume increment, PRIV, on the quadratic mean stem diameter, DQ. Random effects $b_i$ were conducted at the plot level to consider the dependencies between the successive surveys. For the statistical characteristics see Section 3.2.

Model 3: $$\ln(\mathrm{PRIV}_{ijk}) = a_0 + a_1 \times \ln(\mathrm{DQ}_{ijk}) + a_2 \times \ln(\mathrm{PRSDI}_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk}$$

This model fitted the effect of the quadratic mean stem diameter, DQ, and of the relative periodical stand density, PRSDI, to the relative periodical volume increment, PRIV. Random effects bi and bij at the experiment and the plot level took into consideration any spatial (several plots per experiment) and temporal (several successive surveys) autocorrelations between the measurements. Results see Table 4.

Model 4: $$\ln(\mathrm{RTYV}_{ik}) = a_1 \times \ln(\mathrm{MRSDI}_{ik}) + a_2 \times (\ln(\mathrm{MRSDI}_{ik}))^2 + b_i + \varepsilon_{ik}$$

This model analyzed the relationship between the mean relative stand density, MRSDI, and the total volume yield of the plots, RTYV, at the last survey. We introduced random effects at the experiment level to consider dependencies between plots of the same experiment. For results see Table 4.

Model 5: $$\ln(\mathrm{TYV}_{ik}) = a_0 + a_1 \times \ln(\mathrm{MRSDI}_{ik}) + a_2 \times \mathrm{MRSDI}_{ik} + a_3 \times \ln(\mathrm{SI}_{ik}) + a_4 \times \ln(\mathrm{AGE}_{ik}) + a_5 \times \ln(\mathrm{DTDR}_{ik}) + a_6 \times \ln(\mathrm{MRSDI}_{ik}) \times \ln(\mathrm{SI}_{ik}) + a_7 \times \ln(\mathrm{MRSDI}_{ik}) \times \ln(\mathrm{DTDR}_{ik}) + b_i + \varepsilon_{ik}$$

This model described the dependency of the total volume yield, TYV, on the mean relative stand density, MRSDI, the site index, SI, the stand age, AGE, and the ratio between the quadratic mean diameter of the thinned and remaining trees, DTDR. We used random effects $b_i$ at the experiment level to consider spatial dependencies between plots of the same experiment. For results see Table 5.

Model 6: $$\ln(\mathrm{DO}_{ik}) = a_0 + a_1 \times \ln(\mathrm{MRSDI}_{ik}) + a_2 \times \ln(\mathrm{SI}_{ik}) + a_3 \times \ln(\mathrm{AGE}_{ik}) + a_4 \times \mathrm{MRSDI}_{ik} + a_5 \times \ln(\mathrm{SI}_{ik}) \times \mathrm{MRSDI}_{ik} + b_i + \varepsilon_{ik}$$

This model described the dependency of the dominant stem diameter, DO, on the mean relative stand density, MRSDI, the site index, SI, and the stand age, AGE. Random effects $b_i$ at the experiment level accounted for spatial dependencies between plots of the same experiment. For results see Table 5.

The statistical software R 3.4.1 was used for all calculations, in particular the function lme from the package nlme (Pinheiro et al., 2017).

## 3. Results

### 3.1. Overview over the species-specific stand growth and the stand density regulation

Table 2 reflects the data used in these analyses. The characteristics are derived from the last survey. The data set of Norway spruce comprised 22 experiments with 127 plots. The site index was 39.6 m on average but reached maximum values of 47.9 m in the prealpine area. Due to the various density regulations, the mean SDI is only 687 trees $ha^{-1}$; an interestingly high packing density indicates the maximum SDI of 1637 trees $ha^{-1}$. As the stand age varied between 27 and 143 years, the dominant diameter and MAI also varied strongly. The minimum and maximum values of the slenderness ratios HQDQ and HODO indicated high stability (0.30–0.44) in the case of low density stands and low stability (1.20–1.36) in the unthinned stands. The standing volume amounted to 1638 $m^3$ $ha^{-1}$, the removed volume to 1928 $m^3$ $ha^{-1}$, and the total stem volume yielded up to 2459 $m^3$ $ha^{-1}$ at age 143. Notice that, thanks to the continuous survey since 1882, we knew that in many cases 30–40% of the total yield had already been removed by thinning. On average, the relative intermediate yield amounted to 37%. Intermediate yield refers to that part of the total yield that has been harvested before the final cut; the relative intermediate yield is the ratio of the intermediate yield and the total yield. Without thinning interventions and before the start of self-thinning the relative intermediate yield is 0%. Afterwards the relative intermediate yield increases in extreme cases up to 44%, i.e. 44% percent of the total yield are harvested already before the final cut.

Table 3 summarizes the broad range of initial densities, IRSDI, on the plots of the included experiments. On average, IRSDI is approximately 0.52. However, the minimum and maximum values show that there were also variants with very low and high initial stand densities (IRSDI = 0.06–0.98). On average, the first thinning, FTH, occurred at age 33; but the minimum and maximum values indicate that stands with early (FTH = 15) and no thinning were included as well. The mean relative density, MRSDI, ranges from 23% (MRSDI = 0.23) of the maximum stand density up to 100% in the case of unthinned stands (MRSDI = 1). The trend of density regulation is positive on average, i.e. the density mostly increases with progression stand age (TTH > 0). Note that DTDR ratios above 0.70 indicate thinning from above, whereas values below 0.70 result from thinning from below. The plots cover a broad range of both kinds of thinning and average DTDR values of DTDR = 0.67–95. FRTH indicates that, on average, the plots were thinned every 8 years. In fast cycles the return time was 3 years; in other cases 27 years. The continuity of thinning was CTH = 0 in cases with very regular thinning, e.g, every 5 years. The maximum value of CTH = 3.97 indicates that there were also adaptations and changes in

**Table 3**
Overview of the various treatment characteristics on the 22 long-term spacing and thinning experiments in Norway spruce with altogether 127 plots.

| Abbreviations | IRSDI | FTH | MRSDI | TTH | DTDR | FRTH | CTH |
|---|---|---|---|---|---|---|---|
| Characteristic unit | Initial density rel dens. $m^2\ m^{-2}$ | First thinning age years | Mean density rel dens. $m^2\ m^{-2}$ | Trend of Thinning strength slope | ratio $d_{thinned}/d_{remain}$ cm $cm^{-1}$ | Interval Length bet. thin. ret.time years | Contin- uity of thinning coef var |
| mean | 0.52 | 33 | 0.65 | + 0.003 | 0.67 | 8 | 0.40 |
| std | 0.25 | 15 | 0.17 | + 0.009 | 0.11 | 4 | 0.41 |
| min | 0.06 | 16 | 0.23 | − 0.037 | 0.16 | 3 | 0.00 |
| max | 0.98 | 100 | 0.99 | + 0.023 | 0.95 | 27 | 3.97 |

IRSDI, relative stand density index in the stand establishment phase; IRSDI = 1.0 means fully stocked stand. FTH age of first thinning intervention. MRSDI, mean relative stand density; MRSDI = 0.5 means on average 50% below the maximum stand density during the whole stand development. TTH trend of thinning strength. Positive slopes mean first low, later high density. Negative slopes mean first high, later lower densities. DTDR, ratio between stem diameter of the thinned and remaining trees. Small ratios indicate thinning from below, high ratios thinning from above. FRTH, frequency of thinning, i.e. number of years between the thinnings. CTH variation coefficient of the time intervals between thinnings. Low values indicate constant rota, high values increasing period length between thinnings.

the return with progressing stand development.

### 3.2. Long-term versus short-term effects of stand density reduction

Fig. 1a shows that the mean periodical volume increment, PRIV, after thinning was often much higher than the respective volume growth on the neighbouring unthinned plots over the same period. The PRIV values represent the stem volume growth in the survey periods, the PRSDI refers to the relative stand density at the beginning of the respective periods. For the density range PRSDI 0.80–1.0 we scrutinized by the one group *t*-test any deviation of the mean PRIV from PRIV = 1.0. RRIV = 0 would indicate no significant growth response to the previous thinning. The mean (±standard error) for Norway spruce (1.042 ± 0.009) indicated a significant exceeding of the mean periodical volume increment of neighbouring unthinned plots (1.0-line).

In order to visualize the density-growth relationship, we fitted it using the function $\ln(PRIV) = a_1 \times \ln(PRSDI) + a_2 \times (\ln(PRSDI))^2$ (model 1). The results in Fig. 1b show that Norway spruce can react to density reductions of up to to 0.6–0.8 with a strong growth acceleration of PRIV = 1.0–1.5. Rather than reporting the statistical results of all 110 individual regressions shown in Fig. 1b, we summarize the fixed effect coefficients as follows: The minimum, mean and maximum values were −7.115, −0.704 and 1.003 (for $a_1$); and −55.106, −3.907 and −0.104 (for $a_2$).

To explore this further we selected the plots with successive measurements and fitted their growth trend using the model $\ln(PRIV) = a_1 + a_2 \times \ln(DQ)$ (model 2). The resulting trends (Fig. 1c) show that the PRIV values can be high at the beginning and then decrease. This suggests that density reductions may first increase growth above the 1.0 line, but subsequently decrease it below this line across stand development. Instead of reporting the coefficients of all regression lines visualized in Fig. 1c, we only list the number of trajectories, n, the mean intercept $a_1$ ± SE and mean slope $a_2$ ± SE of $(\ln(PRIV) = a_1 + a_2 \times \ln(DQ))$. The characteristics were n = 119, 0.127 ± 0.078, −0.080 ± 0.014 and indicate the average negative slope of the PRIV-DQ relationship.

We also substantiated the general trend using regression analysis across all plots through model 3 $\ln(PRIV) = a_1 + a_2 \times \ln(DQ) + a_3 \times \ln(PRSDI)$. Norway spruce showed a significant decrease of PRIV with progressing stand development, as indicated through the proxy DQ (Fig. 1d, Table 4). This suggests that Norway spruce can increase in volume growth beyond the level of unthinned stands (1.0-line) until a stand mean diameter of about 20 cm is reached. Subsequent density reductions cause a decrease of volume growth below the maximum. The curves are based on the regressions shown in Table 4 and assume mean relative stand densities of PRSDI = 0.4–0.8, respectively.

Fig. 1, e and f substantiate that there was no significant exceeding above the 1.0-line that represented the level of total yield of respective unthinned stands. The regression lines were based on model 4 $\ln(RTYV) = a + b \times \ln(MRSDI) + c \times (\ln(MRSDI))^2$ (see model 4 and characteristics in Table 4). To address the long-term effects of thinning we only included stands older than 50 years in this specific evaluation. Their total stem volume yield in relation to the respective unthinned plots integrates and reflects optimally the effect of stand density reduction in relation to unthinned conditions. Only 2% of the observations lay above the 1.0-line and indicated an overyielding above the level of unthinned stands. The 95% confidence bands around the mean curve in Fig. 1f showed no significant increase above the reference line. The coefficient a2 in model 4 were not significant, indicating that there was no significant quadratic effect in the RTYV-MRSDI relationship (see Table 4, model 4).

### 3.3. Stand volume yield based on stand density, site quality, and thinning grade

The dependence of the total stem volume yield, TYV, at a stand age of 100 years on stand and thinning characteristics according to model 5 is visualized in Fig. 2. The model covers well the observed TYV and MRSDI observations (Fig. 2a). TYV mostly increases with increasing mean relative stand density, MRSDI. The TYV level is the highest on rich sites and decreases from SI 25 to SI 50. The coefficient $a_6$ of the model 5 (Table 5) represent the interaction between MDSDI and SI. This indicates that the slope of the TYV-MRSDI relationship is highest on rich sites and decreases significantly with decreasing site quality.

Most of the included Norway spruce plots range from SI 25 to SI 45. Fig. 2b visualizes the TYV-MRSDI relationships for this range. Specifically, it shows a clear saturation curve for SI 45, but a unimodal curve with a slight optimum for SI 25. On rich sites (SI 45), density reductions cause yield losses, whereas on very poor sites (SI 25), they can result in slight yield gains.

Fig. 2c highlights the strong effect of the site index on the thinning reaction represented by the significant interaction coefficient $a_6$ in model 5 (Table 5). While there were no great differences in the effect of thinning on TYV on poor sites (SI 25–30), the effects of thinning on TYV losses on rich sites (SI 40–50) are relevant. For instance, the graph shows that, for SI 45, a TYV reduction by about 500 $m^3\ ha^{-1}$ is associated with a density reduction of 40% (MRSDI reduction from 1.0 to 0.6), whereas the same density reduction causes only minor losses on sites with SI 30.

High DTDR ratios between the quadratic mean diameter of the thinned and remaining trees indicate thinning from above and low ratios indicate thinning from below. Fig. 2d visualizes the negative effect of thinning from below on the TYV represented by the significant interaction coefficient $a_7$ between MRSDI and DTDR in model 5 (Table 5). As an example, this relationship is shown for stands of SI 40, but it applies to high and medium site qualities as well. The graph shows for instance that a stand density reduction by 40% (MRSDI = 0.6) causes only minor yield losses when performed through

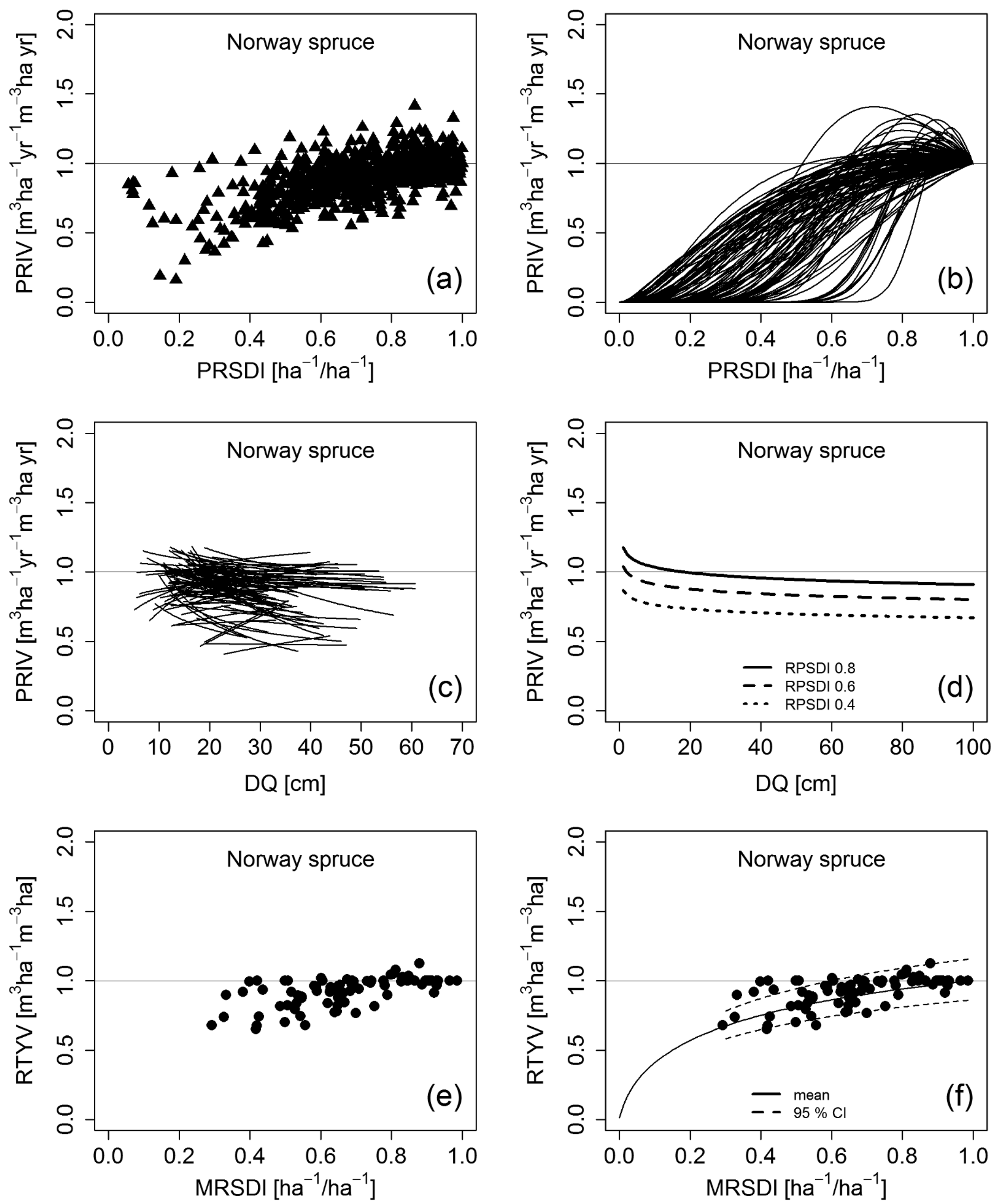


**Fig. 1.** Short- and long-term effect of stand density reduction on the volume growth and yield of Norway spruce. (a) Relative periodical volume increment plotted against relative stand density; both volume increment and stand density are shown in relation to the unthinned plots. (b) Relationship between the relative periodical volume increment and the relative stand density on the plots of thinnings experiments; each curves represents the PRIV-PRSDI relationship derived from neighbouring plots with different density levels in a given time period (see model 1). (c) Decrease of the PRIV on thinned plots with progressing stand development; each line represents the development of the PRIV traced over several successive survey periods (see model 2). (d) Mean PRIV-DQ relationship visualized for different levels of relative stand densities PRSDI (see model 3, Table 4). (e) Relative total yield, RTYV, of the last survey plotted against the mean relative stand density, MRSDI. (f) RTYV-MRSDI relationship with the shape of a saturation curve, i.e. a curve with maximum yield at maximum stand density. (see model 4, Table 4).

thinning from above (DTDR = 1.0); but much greater losses (by 250 $m^3$ $ha^{-1}$) when conducted through thinning from below (DTDR = 0.6) (Fig. 2d).

Fig. 2e shows how the previously introduced effect of the kind of thinning on TYV is modified by the site index. This relationship is reflected in a practically relevant MRSDI level of 0.5. On poor sites, the effect of the kind of thinning is small, but it increases slightly with increasing SI values.

If the stand density is slightly reduced (e.g. MRSDI = 0.8–1.0), the kind of thinning, indicated by DTDR on the abscissa, has only a minor effect on the yield (Fig. 2f, right). However, the stronger the stand density is reduced (e.g. MRSDI = 0.4–0.6), the more unfavourable the thinning from below (indicated by DTDR 0.6–0.8) becomes compared to the thinning from above (indicated by DTDR 1.0–1.4) (Fig. 2f, left).

### *3.4. Dominant tree diameter, DO, of Norway spruce depending on site quality, SI, and severity of thinning, MRSDI*

The dominant tree diameter, DO, depended mainly on the mean relative stand density, MRSDI, the site index, SI, the stand age, AGE, and the interaction between MRSDI and SI. Other variables such as the ratio DTDR for the kind of thinning and the initial relative stand

**Table 4**
Statistical characteristics of the model 3.
$\ln(PRIV_{ijk}) = a_0 + a_1 \times \ln(DQ_{ijk}) + a_2 \times \ln(PRSDI_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk}$ and model 4 $\ln(RTYV_{ij}) = a_1 \times \ln(MRSDI_{ij}) + a_2 \times (\ln(MRSDI_{ij}))^2 + b_i + \varepsilon_{ij}$.

| Model | Fixed Effect Variable | Fixed Effect Parameter | Estimate | Std. Error | p |
|---|---|---|---|---|---|
| 3 | ln(PRIV) | $a_0$ | 0.2609 | 0.0545 | 0.0000 |
| 3 | | $a_1$ | −0.0559 | 0.0124 | 0.0000 |
| 3 | | $a_2$ | 0.4398 | 0.0329 | 0.0000 |
| 3 | | **Random Effect** | **Std. Dev.** | | |
| 3 | | $b_i$ | 0.0786 | | |
| 3 | | $b_{ij}$ | 0.0320 | | |
| 3 | | **Residuals** | **Std.Dev.** | | |
| 3 | | $\varepsilon_{ijk}$ | 0.1252 | | |
| 4 | ln(RTYV) | $a_1$ | 0.1475 | 0.0711 | 0.0424 |
| 4 | | $a_2$ | −0.0886 | 0.0780 | 0.2607 |
| 4 | | **Random Effect** | **Std. Dev.** | | |
| 4 | | $b_i$ | 0.0603 | | |
| 4 | | **Residuals** | **Std.Dev.** | | |
| 4 | | $\varepsilon_{ij}$ | 0.0802 | | |

In the case of model 3 (n = 939), AIC comparisons recommended to retain random effects $b_i$ and $b_{ij}$ on $a_0$ at the experiment and plot level in the model. In case of model 4 (n = 81), AIC comparisons indicated to retain $b_i$ on $a_1$ at the experiment level in the model.

density, IRSDI, had no additional significant influence on the final DO on the thinning plots. Fig. 3a and the coefficients $a_1$, $a_4$ and $a_5$ in Table 5 show how DO increased with the reduction of stand density. On rich sites, the acceleration of the DO growth by stand density reduction was significantly stronger than on poor sites. For instance, a density reduction from MRSDI 1.0 to 0.5 increased the DO at age 100 by 56% (from 46.5 cm to 72.7 cm) on sites with SI 45, but by only 26% on sites with SI = 35 (from 37.4 cm to 47.3 cm).

This depencency of the DO reaction on the site index is visualized on Fig. 3b for different levels of mean relative stand density. Fig. 3b demonstrates that even small density reductions have strong effects on rich sites (SI 35–45) but few positive effects on poorer sites with SI 25–30.

The potential to accelerate the DO by thinning increases moderately with site fertility (broken line, Fig. 4a–c). While a density reduction from MRSDI 1.0 to 0.5 only has a small effect on DO on sites with SI = 30, the same MRSDI reduction can increase the DO by 10–20 cm on sites with SI = 35–40.

The total volume yield, in contrast, is very resilient to density reductions on poor sites, but decreases steeply when density is reduced on medium and rich sites (solid line, Fig. 4a–c). The scissors between the dominant diameter and the total yield curve represent the tradeoff between both variables.

## 4. Discussion

### 4.1. Short-term versus long-term effects of thinning on growth and yield

Using repeated measurements spanning up to 96 years (Supplementary Table 1), we showed that stand density reductions can temporarily raise the stem volume growth above the level of neighbouring unthinned plots (Fig. 1a and b). In the long term, however, the unthinned stands achieved the highest total stem volume yield (Fig. 1f). In the short term, the relationship between stand density and volume growth may follow an unimodal optimum curve, as found by Assmann (1970, pp. 227-235), Langsaeter (1941), Pretzsch (2005), discussed by Zeide (2001), and modelled in the yield table for Norway spruce by Assmann and Franz (1963, 1965). The authors hypothesize that the growth acceleration after thinning may result from the improved nutrient turnover in the soil and nutrient supply of the crown stimulated by the opening up of the stands (Assmann, 1961, p. 228). Another reason may be the elimination of dying trees with low water use efficiency in favour of the more efficient vital neighbours (Assmann, 1961, p. 227). Anticipation of self-thinning and mortality through active thinning may alleviate energy consumption for allelopathy and the struggle for survival and be beneficial for the growth of the remaining trees (Blanco, 2007; Hynynen, 1995; Tubbs, 1973; Zeide, 2001).

In contrast to the temporal volume growth, the long-term yield can only marginally rise above the level of unthinned plots (Fig. 2a and b); only on very poor sites we found an indication of a slight optimum relationship between density and yield (Fig. 2b). Like Assmann (1961, pp. 312-314), Bryndum (1987), Curtis et al. (1997), and Mäkinen and Isomäki (2004) we observed the highest yield on the unthinned plots and severe yield losses through density reductions. This is reflected in the prevailence of a saturation curve between the mean stand density and the total yield (Fig. 2a and b).

The contrast between the optimum density growth relationship in the short term and a saturation density yield relationship in the long term may be explained as follows: By reducing the number of remaining trees and increasing their diameter growth, thinning accelerates the aging of the remaining trees due to the allometric drift of growth with tree size (Assmann, 1961, p. 307). By allometric drift we mean according to Evans (1972) the general decrease of plant growth or plant growth per occupied space (growing space efficiency) with increasing plant size. Fig. 1c and d show that, on thinned plots, the growth may be higher than on unthinned ones in the juvenial state of the stand. However, with progressing stand development, their growth fell significantly below the unthinned stands. This suggests that the temporary advantages in volume growth were cancelled out later through the disadvantage of lower growth, which is caused by the lower number and advanced stem diameter of remaining trees. Both the lower number of trees and their decreasing growth due to the accelerated diameter growth and allometric drift contributed to a lower growth per unit area. This combined effect of the number of the trees and their growing space efficiency on stand growth has been analyzed in detail by (Pretzsch, 2004a, 2006).

The management for rapid growth “Schnellwuchsbetrieb” and short rotation (Cao et al., 2008; Knoche and Engel, 2012) may benefit from this acceleration and anticipation of growth in early stand phases at the expense of later losses of yield. However, across the usual length of a rotation, later growth losses cancel early benefits of thinning. Any rise beyond the level of neighbouring unthinned stands through density reduction occurs mainly in younger stands. In this period, the relative benefits (in terms of relative volume growth compared with unthinned plots) can be high (Fig. 1b). However, in this phase, the absolute stand volume growth remains relatively low, so that the effect on the final total yield is also marginal.

As the total yield integrates the growth over the whole rotation and represents optimally the long-term effect of density reductions, we based our further analyses on the relationship between the relative mean stand density and the total volume yield and dominant diameter in the last survey. This prevented a misinterpretation of the short-term effects of thinning and the wrongful assumption that they can continue across the entire rotation time.

Positive growth reactions after thinning can reverse to negative reactions with progressive stand development. This was shown in the long-term trend of the reactions of the relative volume growth for each plot of all included experiments. The regression lines in Fig. 1d reflected a significantly negative effect of DQ on the long term-trend of relative periodical growth. This may suggest a cancellation of early benefits through later losses. We showed the decrease of positive, transgressive growth reactions with progressing stand development and their transition to negative reactions with severe growth losses compared to the growth of respective fully stocked stands. This pattern contributed to our understanding of why thinning can show considerable benefits of periodical growth but little long-term increase of the total stand yield; it

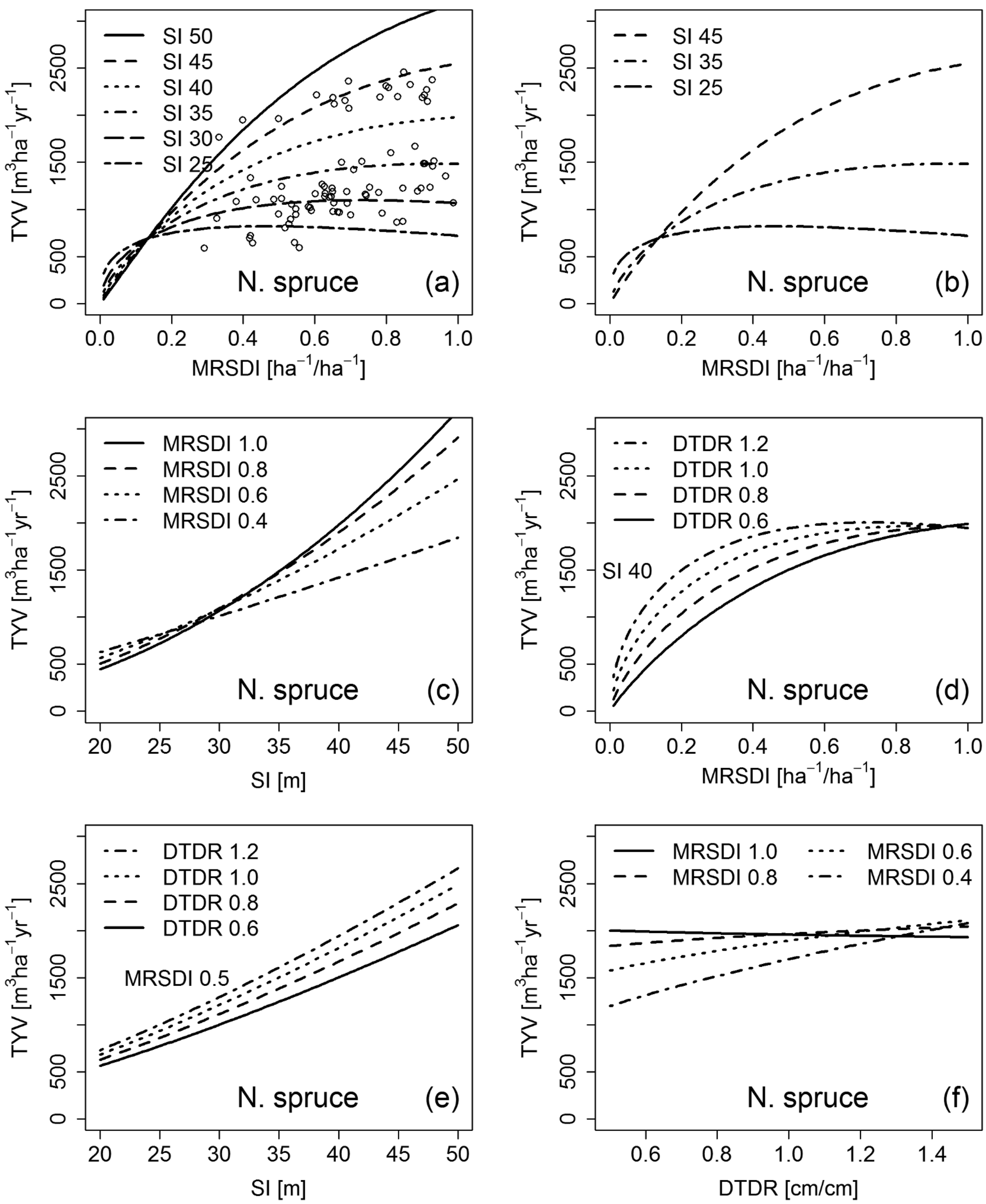


**Fig. 2.** Total stem volume yield TYV, at stand age 100 of Norway spruce depending on site quality, and kind and severity of thinning. (a) Observed and predicted total yield, TYV, at age 100, plotted against the mean relative stand density, MRSDI, depending on site index (SI 25–50 m dominant height at the age of 100 years) according to Assmann and Franz (1965). (b) TYV plotted against MRSDI for site index SI = 25, 35 and 45 m dominant height. (c) Yield losses by stand density reduction are more severe on high compared to low quality sites. (d) Thinning from below (indicated by low DTDR values) reduced yield more severely than thinning from above (indicated by high DTDR values). (e) TYV depending on SI and kind of thinning (shown using the example of a MRSDI level of 0.5). (f) Thinning from below reduced TYV more strongly than thinning from above. TYV, total yield stem volume; MRSDI, mean relative stand density; SI, site index; DTDR, ratio between quadratic mean stem diameter of thinned and remaining trees.

resolved the paradox and contrasting findings of short and long-term observations.

### *4.2. Modulation of thinning reactions through site quality and kind of thinning*

The TYV increased with site index (Fig. 2a and b). Interestingly, there was also a significant interaction effect of SI and MRSDI on the total yield (Fig. 2c, Table 5). This suggested that the same relative density reductions caused much stronger losses of TYV on rich compared to poor sites. The following values highlight the strong response in the total yield to reductions of the stand density, in particular on rich sites. They apply to stands at age 100 and assume DTDR = 0.7, which represents moderate thinning from below. In such stands, a density reduction from MRSDI = 1.0 to 0.5 reduced the TYV by 26% (by 670 $m^3\ ha^{-1}$ from 2549 to 1879 $m^3\ ha^{-1}$) on sites with SI = 45. The same relative density reduction reduced the TYV by only 12% (by 167 $m^3\ ha^{-1}$ from 1485 to 1318 $m^3\ ha^{-1}$) on sites with SI = 35. On very poor sites (≤SI 25), density reductions could even increase the total yield (lower curves on Fig. 2a and b). Note that a decrease of 670 $m^3\ ha^{-1}$ and 167 $m^3\ ha^{-1}$ over a timespan of 100 years corresponds to an average loss of 6.70 and 1.67 $m^3\ ha^{-1}\ yr^{-1}$, respectively.

**Table 5**
Statistical characteristics of model 5.
$\ln(TYV_{ij}) = a_0 + a_1 \times \ln(MRSDI_{ij}) + a_2 \times MRSDI_{ij} + a_3 \times \ln(SI_{ij}) + a_4 \times \ln(AGE_{ij}) + a_5 \times \ln(DTDR_{ij}) + a_6 \times \ln(MRSDI) \times \ln(SI_{ij}) + a_7 \times \ln(MRSDI) \times \ln(DTDR_{ij}) + b_i + \varepsilon_{ij}$ and model 6 $\ln(DO_{ij}) = a_0 + a_1 \times \ln(MRSDI_{ij}) + a_2 \times \ln(SI_{ij}) + a_3 \times \ln(AGE_{ij}) + a_4 \times MRSDI_{ij} + a_5 \times \ln(SI_{ij}) \times MRSDI_{ij} + b_i + \varepsilon_{ij}$.

| Model | Fixed Effect Variable | Fixed Effect Parameter | Estimate | Std. Error | p |
|---|---|---|---|---|---|
| 5 | ln(TYV) | $a_0$ | −5.10533 | 1.2882 | 0.0001 |
| 5 | | $a_1$ | −3.30924 | 1.3157 | 0.0135 |
| 5 | | $a_2$ | −0.71849 | 0.2535 | 0.0056 |
| 5 | | $a_3$ | 2.15014 | 0.2938 | 0.0000 |
| 5 | | $a_4$ | 1.18797 | 0.0747 | 0.0000 |
| 5 | | $a_5$ | −0.03264 | 0.0886 | 0.7133 |
| 5 | | $a_6$ | 1.06654 | 0.3488 | 0.0029 |
| 5 | | $a_7$ | −0.58191 | 0.2015 | 0.0048 |
| 5 | | **Random Effect** | **Std. Dev.** | | |
| 5 | | $b_i$ | 0.1967 | | |
| 5 | | **Residuals** | **Std.Dev.** | | |
| 5 | | $\varepsilon_{ij}$ | 0.0729 | | |
| 6 | ln(DO) | $a_0$ | −9.9584 | 2.1249 | 0.0000 |
| 6 | | $a_1$ | −0.4719 | 0.1973 | 0.0186 |
| 6 | | $a_2$ | 2.5603 | 0.5709 | 0.0000 |
| 6 | | $a_3$ | 0.9319 | 0.0547 | 0.0000 |
| 6 | | $a_4$ | 6.2154 | 3.0702 | 0.0456 |
| 6 | | $a_5$ | −1.6960 | 0.8501 | 0.0487 |
| 6 | | **Random Effect** | **Std. Dev.** | | |
| 6 | | $b_i$ | 0.0943 | | |
| 6 | | **Residuals** | **Std.Dev.** | | |
| 6 | | $\varepsilon_{ij}$ | 0.1111 | | |

In both models ($n = 127$), AIC comparisons suggested to retain random effects $b_i$ on $a_0$ at the experiment level in the model.

Strong thinning has become very common in forest practice. Therefore, fully stocked stands which reflect the site-specific maximum stocking density and growth of a species, and which might serve as a reference (1.0-benchmark) for density reductions, have become rare.

The general pattern of strong yield reductions on rich sites and lower reductions on poor sites after thinning is in line with findings by Assmann (1961, p. 292) based on experimental plots in Bavaria. Ample nutrient and water supply of the leaves enables a maximum light assimilation and photosynthetic production. Any removal of trees may cause gaps in the canopy, reduce the leaf area and light assimilation, and as a consequence may also reduce the stand growth below the maximum. On poor sites, even the canopies of unmanaged stands are less dense, as a lack of nutrients and water restrict the leaf area and growth (Long and Smith, 1988, 1990). By removing trees, the remaining ones may increase their efficiency of nutrient and water use. Consequently, the stand growth losses may be lower and the remaining stand may produce slightly more after thinning, especially on very poor sites (see curve for SI 25 in Fig. 2b and c).

In the long term, thinning from below reduced total yield more than thinning from above under ceteris paribus conditions. Hence, in particular on rich sites with strong thinning reactions, the yield losses after thinning from below can be significantly stronger than after thinning from above (Fig. 2d and e). We observed that all kinds of thinnings may boost the current increment in the short term. But in the long term, thinning from below reduced the number of the small trees that stabilize the growth when the taller trees reduce their growth following the allometric drift shown on Fig. 1c and d.

The removal of tall trees can induce a reduction of trees that are efficient now, but that will become inefficient in the long term, as trees with larger crowns become inefficient regarding their aea use compared

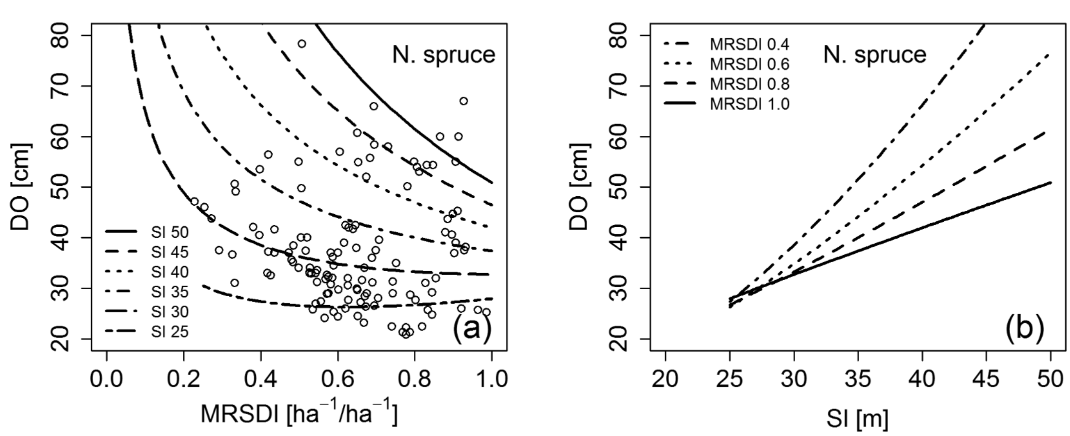


**Fig. 3.** Dominant tree diameter, DO, of Norway spruce based on site quality, SI, and severity of thinning MRSDI (see model 6, Table 5). (a) Observed and predicted DO at age 100 plotted over the mean relative stand density, MRSDI, visualized for different site index levels (SI = 25–50 m dominant height according to Assmann and Franz 1965). (b) The beneficial effect of stand density reduction on DO is much stronger on high quality sites (SI = 45–50 m) compared to poor sites (e.g. SI = 25–30 m). DO, dominant tree diameter; MRSDI, mean relative stand density; SI, site index.

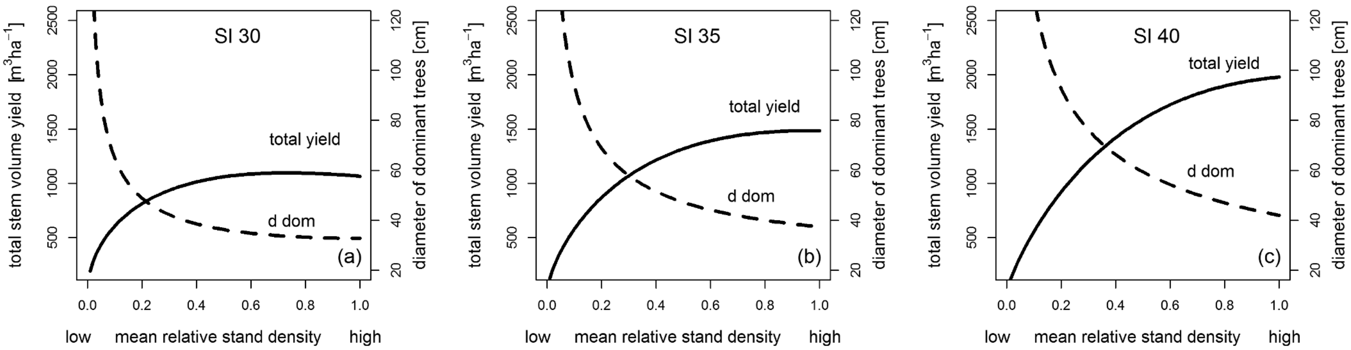


**Fig. 4.** Tradeoff between the effect of stand density reduction on stem diameter growth, DO, and yield, TYV, shown for site indexs levels of SI = 30, 40 and 50 (a–c). These relationships are based on models 5 and 6 (see Table 5), assume a stand age of AGE = 100, and a ratio between quandratic mean diameter of thinned and remaining tress of DTDR = 0.7 (for the underlying equations, please refer to model 5 and Table 5).

to the efficiency of smaller trees (Assmann, 1961; Sterba, 199, 2019). Based on a long-term thinning experiment in Norway spruce Pretzsch (2006) showed that the stand productivity can be increased by keeping small and medium sized trees in the stand; whereas keeping mainly large trees can significantly reduce the stand productivity. This may explain why the removal of many small trees caused stronger yield reductions than the removal of tall trees.

### *4.3. Relevance to silviculture and stand management*

If the management objectives are maximum volume yield or carbon sequestration, no active thinning and only the removal of dying or dead trees may be the best option. Thinning can severely reduce yield, and the current tendency towards strong thinnings may run the risk of causing significant yield losses.

The diameter growth acceleration of dominant trees through density reductions was most effective on high quality sites; but also caused the highest yield losses here. On sites with SI = 40, a DO increasd compared to unthinned stands of 25% (e.g. from 40 to 60 cm) costs yield losses of about 15% or 300 $m^3$ $ha^{-1}$ untill the age of 100 years. This is equivalent to an average loss of 3 $m^3$ $ha^{-1}$ $yr^{-1}$. On poor sites, the absolute yield level was lower, but so are the relative losses through density reductions. Here, the DO could hardly be accelerated through thinnings. On rich sites, the DO acceleration can be modulated by improving the light supply of a small number of released trees. On poor and water limited sites, however, the release effect was less punctual and the surplus water was distributed among a larger number of neighbouring trees (Pretzsch, 2010; Wichmann, 2001, 2002).

The growth increase resulting from thinning is commonly overestimated. Thinning can temporarily raise the growth above the level of neighbouring unthinned plots. But this benefit of thinning should not be expected to last over the entire lifetime of the stand. Rather, it abates, as thinning accelerates tree diameter growth, and this leads to faster physiological aging and ontogentic drift over time. Another reason for the overestimation of thinning effects is the growth acceleration and positive growth trend caused mainly by nitrogen desposition and climate warming (Pretzsch, 2004b). High growth levels, even after strong thinnings, partly result from this positive growth trend and should not be ascribed to thinning. Where available, unthinned stands nearby may also display enhanced growth due to environmental changes.

In the long term, thinning from above caused lower yield losses than thinning from below. The reason for this advantage may be the high growing area use efficiency of smaller trees and their slower decrease of growth with progressing stand development.

Thus far, we haave mainly considered the stem diameter as a quality measure of the produced wood. However, other wood quality aspects, such as wood density, tapering, crown size, branch number and diameter, as well as the regularity of the tree ring width pattern, need to be considered.

### *4.4. Long-term experiments as indispensable ultimate arbiters of thinning reactions*

Periodically remeasured long-term experiments provide substantial information on both the short-term and long-term effects of density reductions on stand growth and yield. In the short term, the volume growth can be accelerated, presumably by stimulating the nutrient cycling or by increasing the light supply after opening up. In the long term, this stand density reduction and short-term growth acceleration can have the opposite effect on tree and stand growth. The absence of the removed trees and the faster aging of the remaining ones may result in a decrease of the stand growth below the level of the neighbouring unthinned plots. Due to this difference between short- and long-term effects, short term surveys or those without unthinned reference plots may be misleading.

The overly short surveys and the lack of information about the natural maximum may have contributed to the contradictory findings regarding the relationship between density and growth reviewed by Zeide (2001). His literature review in particular states a "…full turnaround…" to the initial perception of thinning and growth after nearly a century of research; and warns against an endless cycle of revision and messing up of earlier results. Zeide claimed to tap the information potential of long-term thinning experiments as ultimate arbiters of thinning reactions on growth.

Note that the longest time series of experimental plots cover approximately 120 years of trials regularly thinned from below and only 100 years of trials thinned from above (Pretzsch, 2017). Here, we hypothesize that, due to the differences between short- and long-term effects of thinning, a century of observation time may be required to obtain more consistent results. At present, the oldest experiments cover the time span of a whole regular rotation of Norway spruce stands of 80–120 years. The availability of those ultimate arbiters suggested a revisiting and re-evaluation of the relationship between density and growth of forest stands.

Under changing growing conditions, the unthinned reference plots become increasingly relevant in order to avoid misinterpretation of thinning responses (Pretzsch, 2004b). The unthinned plots show general growth trends that are presently very obvious and positive in many Central European forest, because of eutrophication, temperature raise, and extension of the growing season (Pretzsch et al., 2014, 2018). The unthinned plots reflect that this is a general trend of increasing growth and stand density; hence, this should not be misinterpreted as particularly favourable thinning reactions. In forest practice, where unthinned plots are not available, modern rigorous density reduction might be promoted as practitioners do not realize that the growth after thinning simply represents a short-term effect and are so high partially because growing conditions are generally improving due to environmental changes. A-grade plots or unthinned plots may prevent the confusion of the effects of environmental changes with those stemming from thinning. In our analysis, we standardized the IV and TYV, and also the SDI of the thinned plots using the A-grade plots.

### 4.5. Critique and restrictions of the results

Our evaluations were based on merchantable stem volume yield. The form factors and volume equations for calculating the merchantable volume were derived (Franz, 1971) from stems and stem shapes from classical thinning experiments that do not sufficiently cover extremely sparsely or solitarily stocked stands with strongly tapering, conical stem shapes. Thinning usually decreases the form factor of the stem and increases the branchwood fraction of the tree. Consequently, the tree volumes and volume increments of low density stands may be overestimated by 5–10% (Forrester et al., 2017), and their density-growth relationship may be even less resilient than shown in Fig. 2a and b. Future measurements of stem shape and crown allometry may reveal how the density-growth relationship is modulated by thinning-dependent changes of the stem form. The density-growth relationship may be more resilient when including branchwood or even root volume in the total volume yield, as the crowns and roots are wider and longer in thinned compared to unthinned stands (Forrester et al., 2017; Pretzsch, 2019).

To a different result would probably come an analogous analysis based on the above ground or total tree biomass; given that conifers in particular can reduce their wood density by 5–10 % when growing more openly (Pretzsch et al., 2018). Measuring the wood density on the differently thinned plots would permit better upscaling from wood volume to biomass or biofuel production. As conifers, in contrast to broadleaved trees, tend to reduce the wood density with tree ring width (Knigge and Schulz, 1966, p. 138), their reduction of biomass growth caused by density reduction may be even higher than the losses calculated for wood volume. Future measurements in long-term experiments should cover such additional effects of initial density and thinning on the growth and yield of volume and biomass.

During the First and Second World War, unplanned stem removals occurred even on unthinned plots (e.g., Assmann, 1961, p. 251). This means that, especially in the years 1914–18 and 1939–1945, the maximum stand densities on the experimental plots may be slightly underestimated. This may result in an overestimation of the growth reduction by thinning and an underestimation of the growth resilience to thinning in this phase of the stands' development. However, these episodic interferences in the juvenile low-growth phase of the stands should be outweighed by the long observation periods from 1882 until the present day.

The stand dynamics on the unthinned reference plots reflect environmental changes and growth acceleration in the last decades (Kauppi et al., 2014; Spiecker et al., 1996). It is likely that part of the growth increase of the thinned plots is based not on the density reduction through thinning, but on the environmentally caused growth acceleration. However, to answer Q1, we standardized the growth of the thinned plots on the basis of the unthinned reference plots in the same period. Thus, we account for alterations in the absolute level of growth and focus on the relative changes due to thinning. For a statistical evaluation of Q 2 and 3, we pooled the final volume yield and dominant tree diameter of sets of unthinned and thinned stands, so that the relative effects of thinning was reflected well by the respective models; the change of the absolute growth level has been analyzed and published elsewhere (Pretzsch et al., 2014, 2018).

Our results apply to sites in the low mountain ranges with a mean temperature and annual precipitation of (6.0–7.6 °C and 800–1255 mm $yr^{-1}$). Similar analyses, including long-term experiments from boreal and Mediterranean regions with stronger limitation of temperature, water, or nutrients, may reveal different reaction patterns. Our results refer to Norway spruce and should not be applied to other tree species. Thinning reactions strongly depend on the species-specific light ecology and growth rate (Assmann, 1961), crown plasticity (Pretzsch et al., 2015; Purves et al., 2007), and mechanical limitations (Pretzsch, 2019). Among the primary tree species in Europe, Norway spruce may represent the thinning reactions of a medium shade-tolerant (Burschel and Huss, 1987, p. 266), medium plastic (Pretzsch, 2014), and primarily vertical oriented fast-growing conifer. Therefore, it may react similarly to thinning as silver fir (*Abies alba* Mill.) and Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco), more strongly than Scots pine (*Pinus sylvestris* L.), but less than European beech (*Fagus sylvatica* L.) or sessile/common oak (*Quercus petraea* (MATT.) LIEBL. and *Quercus robur* L.).

The informational content of long-term experimental plots is frequently unknown or underestimated by advocates of innovative "unprecedented" thinning methods. The founding fathers of systematic forestry were initially interested in growth and yield of fully stocked unthinned or only slightly thinned stands (Cotta, 1828; von Ganghofer, 1881; Hartig, 1795). They built normative yield tables "Normalertragstafel" (e.g., Grundner, 1913; Schwappach, 1890), which reflected this conservative approach to thinning. However, the experimental plots established since the end of the 19th century mostly comprise variants with very strong density reductions, as well as classical variants (Pretzsch, 2017). Table 3 shows that our dataset comprised plots with density reductions to IRSDI = 0.06 and MRSDI = 0.23, i.e. variants with densities far below the level of density recommend by the most rigorous modern silvicultural prescriptions. This means that, among others, these long-term experiments also cover such extreme variants and can offer insights into short- and long-term effects on stand growth and yield.

## 5. Conclusions

After about 100 years of long-term observation, the southern German thinning experiments in Norway spruce provide substantial insights into the relationship between stand density and yield. In times when forest stand management guidelines outbid each other in optimism regarding the positive effects of density reduction on saving cost for tending, accerelating tree and stand growth, and preparing stands for climate change-induced drought stress, our findings may be helpful. They show that short-term benefits in growth after thinning can turn into long-term losses in yield. Except on very poor sites, unthinned stands invariably overyield thinned stands. Especially on rich sites, thinning caused severe yield reductions. Under ceteris paribus conditions, thinning from above reduced the total stand yield less than thinning from below.

Long-term observations yielded a more realistic assessment of thinning reactions compared to short term measurements. A correct assessement of the long-term response of stand growth and yield on density regulation is inevitable for the development of resource efficient production systems. It is also essential for the assessment of many ecosystem services, as most of them are linked to forest structure and yield.

The fact that, over long term, thinning from above caused lower yield reductions than thinning from below highlights that small and medium sized trees strongly contribute to stand growth. This means that silvicultural interventions which create a stratified canopy can exceed the growth of monolayered stands that were thinned from below. This confirms findings of case studies by Sterba (1999, 2019), Vuokila (1977, 1980), and Reininger (1987), which revealed an underestimation of smaller and medium sized trees regarding their contribution to continuous stand yield in relation to tall trees. This finding may be interesting for current concepts of transitioning from homogeneous to more heterogeneous stands.

## CRediT authorship contribution statement

**Hans Pretzsch:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization.

## Declaration of Competing Interest

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

## Acknowledgements

The author thanks the Bayerischen Staatsforsten (BaySF) for supporting the establishment of the plots and the Bavarian State Ministry for Nutrition, Agriculture, and Forestry for permanent support of the project W 07 "Long-term experimental plots for forest growth and yield research" (# 7831-22209-2013). This publication has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 778322. Thanks are also due to Charlotte Pretzsch for the language revision and anonymous reviewers for their constructive criticism.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117879.

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