

Fertilization modifies forest stand growth but not stand density: consequences for modelling stand dynamics in a changing climate

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Received 9 November 2020

Knowledge of the maximum forest stand density and the self-thinning process is important for understanding, modelling and scheduling thinnings in silviculture. The upper trajectories of stem number, N , vs mean diameter, d_q or mean tree volume vs stem number are often used for quantifying maximum stand density. The long debate about how site conditions modify these relationships is presently revived due to global change. A crucial question is whether environmental conditions alter the trajectories themselves or just the velocity at which stands move along them. Our contribution is based on fully stocked plots from long-term Scots pine (*Pinus sylvestris* L.) fertilization experiments along an ecological gradient in South Germany. This allows us to compare the self-thinning trajectories of fertilized and unfertilized plots under different environmental conditions. We can show that repeated fertilization with nitrogen did not change the $N \sim d_q$ trajectories. Assuming that fertilization affects forests in a similar way as an ongoing atmospheric N -deposition, this means that presently growth, mortality, and volume accumulation in forest stands proceed faster in time but still follow the same $N \sim d_q$ allometric trajectories. Furthermore, we found that the level of the self-thinning line generally increases with the annual precipitation. The allometric self-thinning exponent, however, did not respond to environmental conditions. Finally, we quantitatively demonstrate and discuss the implications and consequences of the results regarding understanding and modelling forest stand dynamics, carbon sequestration and the development and adaptation of silvicultural guidelines in view of climate change.

Introduction

For better understanding the effects of atmospheric nitrogen deposition on forest stand dynamics and stand density in particular, this study harnessed long-term fertilization experiments established in the period 1950–1979. Forest tree growth and stand dynamics are strongly modulated by changes of the environmental conditions. Depending on the initial site conditions, the growth reaction patterns range from thriving to regressing tree and stand growth. In some cases, accelerating growth is interrupted by slumps due to drought events. In temperate and boreal forest areas growth rates can strongly increase due to, among others, extension of the growing season, higher temperature and nitrogen deposition (Spiecker *et al.*, 2012; Pretzsch *et al.*, 2014; Charru *et al.*, 2017). So far, studies were mainly focused on growth rates (Kahle, 2008; Hilmers *et al.*, 2019) with much less attention given to changes in maximum stand density and mortality rates. A possible reason for this lack of knowledge is the requirement for unthinned or only slightly thinned stands for studying such effects. Such data, as has been pointed out, are comparably rare (Pretzsch and Biber, 2005).

However, the question remains highly relevant, whether environmental conditions just cause forest stands to move faster

along the same invariant self-thinning line, or whether they even increase the level of potential stand density. An ongoing increase of maximum stand density would mean a temporary additional C-storage, potentially a decrease of mortality and a need for adapting thinning guidelines.

In forest science, the self-thinning condition is usually expressed as the relation of the quadratic mean tree diameter, d_q and the corresponding number of trees, N , per unit area (Puettmann *et al.*, 1993; Bégin *et al.*, 2001; Zeide, 2005; Gadow and Kotze, 2014; Gadow *et al.*, 2015). Logarithmically scaled, this relationship is linear: $\ln(N) = a + b \cdot \ln(d_q)$ with the intercept, a , and the slope, b (Reineke, 1933).

As previous studies indicate, different soil conditions and fertilization seem, *ceteris paribus*, to move the $N \sim d_q$ points only slower or faster along the same invariant, stationary self-thinning line (Sukatschew, 1928; Weiskittel *et al.*, 2009). Differences in light intensity, in contrast, altered the self-thinning line itself (Harper, 1977, p. 189–194, Lonsdale and Watkinson, 1982).

So far, these relationships were studied mainly for young plants and only for short periods in time (Harper, 1977; Van der Werf *et al.*, 1995; Weiskittel *et al.*, 2009). For the study described here, we used the data of long-term fertilization experiments in Scots pine (*Pinus sylvestris* L.), which were established in the

period 1950–1979, when forest fertilization was considered a standard silvicultural practice compared with the present position in Central Europe. Today, with considerable permanent N depositions, e.g. annual average of 20 kg ha⁻¹ and a maximum of almost 40 kg ha⁻¹ in Southern German forest ecosystems according to Umweltbundesamt (2017), these plots have gained special value for studying the effect of nitrogen input on the long-term stand dynamics, in particular with regard to stand density and mortality. Scots pine was of special interest for the study because of its vigorous early growth, which it was hoped might show revealing dynamics at young ages. In addition, it is a typical species occurring on poor sites where fertilization has in the past been a traditional silvicultural practice (Foerster, 1990; Prietzel *et al.*, 2008; Prietzel *et al.*, 2020).

While forest fertilization has widely lost its former importance, atmospheric N-deposition remains one of the main drivers of the accelerated of forest stand growth in many regions of Europe (Etzold *et al.*, 2020). The N-deposition increased rapidly until the 1990s (Kreutzer, 1972; Hofmann *et al.*, 1990; Binkley and Högberg, 2016, 1997). Subsequently, it was reduced by technical advances in agriculture, combustion engine design, exhaust gas treatment and industrial processes (Erisman *et al.*, 2003; Jonard *et al.*, 2012; UNECE, 2020), but it is still at a rather high level of ~10–50 kg ha⁻¹ yr⁻¹ in many regions of Europe (Umweltbundesamt, 2017; Etzold *et al.*, 2020). In other parts of the world with similar technological and societal conditions, e.g. in the US (Thomas *et al.*, 2010) or Japan (Fang *et al.*, 2014) similar tendencies are observed. In areas where forest growth is mainly limited by light and nitrogen, the effects on stand growth are positive, forest stands grow faster (Spiecker *et al.*, 2012; Pretzsch *et al.*, 2014; Charru *et al.*, 2017). Insofar, the atmospheric deposition of Nitrogen is an important reason for revisiting fertilization plots instead of considering them outdated.

In detail, we asked (1) if and how N-fertilization modifies the $N \sim d_q$ relationship of fertilized Scots pine (*Pinus sylvestris* L.) stands compared with control plots and (2) if there are interactions between the effects of fertilization and the respective prevailing site conditions of the stands? Finally, we quantitatively demonstrate and discuss the consequences of a dependency of $N \sim d_q$ on environmental conditions for forest monitoring, understanding and modelling stand dynamics, C-sequestration and silvicultural stand management.

Material and methods

Material

For scrutinizing both research questions, we screened the 16 long-term Scots pine fertilization experiments maintained by the first author and his group at the Chair of Forest Growth and Yield Science at the Technical University of Munich. Scots pine was chosen for this analysis as it is a rather fast growing species that might show interesting behaviour of the course of growth at relatively young ages. Another reason was that it frequently occurs on poor sites and therefore was the focus of fertilization measures in the 1950–1970s. The experiments comprise 95 fertilized and 64 unfertilized plots under the same site conditions (Foerster, 1990) and are, insofar, ideal material for the purpose of this study. See

Supplementary Table S1 for the geographic locations and site conditions of the experiments, and Supplementary Table S2 for stand characteristics. The fertilized plots were repeatedly treated with, among others, N (max. 1200 kg ha⁻¹ in up to five applications) or NPKCaMg (max. 1900 kg ha⁻¹ in up to five applications). Both, fertilized and unfertilized plots underwent different degrees of stand density reduction (unthinned, density reduction to mostly 80 or 50 per cent of the unthinned plots in terms of stand basal area). For details regarding the fertilization and thinning measures on the experimental plots see Supplementary Table S3.

For the purpose of our study, only fully stocked, at most moderately thinned plots were taken into account. Thus, we selected only the 10 per cent densest plots and surveys (stand density measured by means of the stand density index (SDI), see Equation (1)) independently from both groups, fertilized and unfertilized. This procedure yielded 11 trials with 41 fertilized plots and 18 unfertilized plots, and in total 148 surveys between 1961 and 2018. Their stand characteristics at the last survey are summarized in Table 1 (see Supplementary Table S4 for a summary across all surveys). At the last survey, all plots had an age of ~100 years. Remarkably, the site index (mean height at age 100 years) of the fertilized plots is on average not substantially higher compared with the unfertilized ones. And, while the experiments are generally located on soils with mostly low water capacity and nutrient supply (Supplementary Table S1), their mean site index of 25.4 m (unfertilized) and 25.8 m (fertilized) indicates conditions between the best and the second best yield class after Wiedemann (1943/48). While, on average, the standing volumes of unfertilized and fertilized plots are about the same (357/365 m³ ha⁻¹), their volume increments differ substantially (7.4/8.1 m³ ha⁻¹ yr⁻¹). But even the lower value is considerably above the increment predicted by the Wiedemann (1943/48) yield table for a 100-year old stand in the best yield class (6.4 m³ ha⁻¹ yr⁻¹).

Indicator variables for stand density and site conditions

As an indicator of stand density, we used the SDI after Reineke (1933), which is calculated as

$$SDI = N \cdot \left(\frac{25}{d_q} \right)^b \quad (1)$$

with the number of trees per ha, N , the stand's quadratic mean diameter, d_q (cm) and an exponent, b . While the SDI is usually calculated with the general assumption of $b = -1.605$, we used the specific value for Scots pine, $b = -1.593$ published by Pretzsch and Biber (2005). We calculated the SDI for each plot and each survey. If a plot was thinned at a survey, we used N and d_q before thinning as the input variables to the calculation of SDI. All N and d_q values mentioned in this study are to be understood in this way.

As an integrative site variable, we calculated the site index of each plot at each survey by the yield table for Scots pine, moderate thinning, by Wiedemann (1943/1948). This method takes the quadratic mean height, h_q , attained at a given stand

Table 1 Overview of the main stand characteristics of all non-fertilized and fertilized Scots pine plots used for statistical evaluation in this study (11 trials, 59 plots altogether).

Variable	Unit	Un-fertilized plots all				Fertilized plots all			
		Mean	Standard deviation	Min	Max	Mean	Standard deviation	Min	Max
Stand age	yr	99	12	82	119	99	12	82	127
SI (h_q age 100)	m	25.4	2.6	23.3	30.5	25.8	2.5	23.1	30.8
N	ha ⁻¹	465	110	292	722	470	167	247	925
h_q	m	25.2	2.0	22.6	29.2	25.5	2.1	22.1	29.9
d_q	cm	29.4	2.4	25.9	32.7	30.0	3.4	22.6	36.3
ho	m	26.4	2.0	23.8	29.9	26.9	2.0	23.4	31.8
do	cm	35.9	2.4	32.2	39.9	36.8	3.0	30.7	43.3
SDI	ha ⁻¹	591	107	424	779	599	118	403	867
V	m ³ ha ⁻¹	357	81	237	495	365	69	239	508
id_q	mm yr ⁻¹	2.8	0.8	1.8	4.4	3.1	1.1	0.9	6.3
iV	m ³ ha ⁻¹ yr ⁻¹	7.4	1.4	4.4	9.7	8.1	2.3	4.8	13.6

The table reflects the stand characteristics at the last survey. The full set of plots taken into account is shown in [Supplementary Tables S1 and S2](#). Abbreviations: SI = Site index (mean height at age 100, based on the yield table by [Wiedemann \(1943/48\)](#) for Scots pine, moderate thinning); N = Number of trees per hectare remaining after mortality/thinning recorded at last survey; h_q = Quadratic mean height, remaining trees after mortality/thinning recorded at last survey; d_q = Quadratic mean diameter, remaining trees after mortality/thinning recorded at last survey; ho = Stand top height (h_q of the 100 thickest stems per ha); do = Stand top diameter (d_q of the 100 thickest stems per ha); SDI = stand density index ([Reineke, 1933](#)), species-specific version by [Pretzsch and Biber \(2005\)](#), see subsection 'Indicator variables for stand density and site conditions'; V = Standing wood volume per ha after last thinning; id_q = Periodic annual increment of d_q between the penultimate and the last survey; iV = Periodic annual volume increment between the penultimate and the last survey.

age as an indicator for overall site quality. While the Wiedemann site index is usually written in roman numerals (I, II, III, . . . , from good to poor site conditions), we expressed it as the stand height (h_q), which is expected at a stand age of 100 years according to the yield table.

To obtain site-climate characteristics we used the Europe-wide available agro-meteorological data provided by the [European Commission's Joint Research Centre \(2020\)](#). This source comprises interpolated weather station data, most prominently temperature (T) and precipitation (P), on a 25 x 25 km grid on a daily basis since 1975. For each of our plots, we extracted all grid points which were no more than 25 km away (2–4 grid points per plot). On each of these gridpoints, we aggregated the daily to monthly values. After that, the monthly T and P-values of the grid points attributed to a plot were averaged to plot-level values. In order to obtain the long-term characteristics for each plot, several indicator variables were first calculated as per-year values and after that averaged for the years from 1975 to 2000 (inclusive). These indicator variables included the aridity index by [Martonne de \(1926\)](#) for the whole year as well as for the vegetation period (defined as the months from May to September), which has been widely used in recent studies ([Rötzer et al., 2012](#); [Pretzsch et al., 2013](#); [Quan et al., 2013](#)). We also calculated the climate vegetation productivity index (CVP) of [Paterson \(1956\)](#) and one of its components, the latitude-dependent radiation ratio. In addition, we also provided the geographical latitude of each plot as a variable of interest for our analysis. Due to the close vicinity of the plots belonging to one trial, there was virtually no intra-trial variation of the climate variables. This means that the data are not confounded with different climate characteristics of the fertilized and unfertilized plots at the trial level.

Statistical models

The fundamental model used in this study is the logarithmic form of the self-thinning line:

$$\ln(N) = a + b \cdot \ln\left(\frac{d_q}{25}\right) \quad (2)$$

where N is a stand's number of trees per hectare and d_q is the corresponding quadratic mean diameter in cm. Note that d_q is divided by 25 in this equation. This is convenient, because it makes $\exp(a)$ express the number of trees for $d_q = 25$ cm, which is the individual SDI of the stand in question. This modification does not change the self-thinning line itself, but it improves the interpretability of the parameter a .

We approached our first research question (does fertilization have an effect on the self-thinning-relationship?) with the following mixed linear regression model:

$$\ln(N_{ijk}) = a_0 + a_1 \cdot \text{fert}_{ij} + \ln\left(\frac{d_{qijk}}{25}\right) \cdot (b_0 + b_1 \cdot \text{fert}_{ij}) + c_i + c_{ij} + c_{m(ijk)} + \varepsilon_{ijk} \quad (3)$$

In addition to the variables and symbols explained with Equation (2), fert is a dummy variable, which is 0 for an unfertilized plot and 1 for a fertilized one. The indexes i , j and k represent the nested data levels trial, plot and survey. The fixed effect parameters a_0 and a_1 together represent the intercept of the self-thinning line, and in the sense as shown with Equation (2), the

plot's individual SDI. If a_1 turns out significant this means that fertilizing altered the SDI. Very similarly, b_0 and b_1 represent the slope of the self-thinning line. If b_1 is significant we can conclude that fertilizing alters the slope.

The parameters c are random effects, all assumed to be normally distributed with different variances but all with expectancy 0. Here, c_i and c_{ij} are nested random effects on trial and plot-in-trial level; these were implemented in order to cover correlation on both levels, including autocorrelation of the surveys on plot level. An additional random effect is $c_{m(ijk)}$; the index $m(ijk)$ indicates the year in which the k th survey of plot j in trial i was conducted. This random effect is intended to cover for overarching climate influences that might have influenced the status of self-thinning observed at a given year of survey. For all regression models presented in this study, including this random effect was strongly supported by Akaike Information Criterion (AIC) comparison. Finally, ε_{ijk} represents identically and independently distributed errors with the assumption of normal distribution and expectation 0.

For the second research question, preliminary systematic model comparison and selection procedures (Barton, 2020) showed only the mean annual temperature, T ($^{\circ}\text{C}$), and the annual precipitation sum, P (mm), both calculated as described in the subsection 'Indicator variables for stand density and site conditions', to have considerable statistical connection with the self-thinning line. While Condés et al. (2017) use the Martonne de (1926) aridity index for their investigations on Scots pine self-thinning, this transformation of temperature and precipitation did not turn out superior to using these variables as such in the study at hand. Brunet-Navarro et al. (2016) find an influence of temperature on the self-thinning line of Scots pine, which is directly in line with our preliminary findings. Based on this insight, we formulated the following mixed linear regression model:

$$\begin{aligned} \ln(N_{ijk}) = & a_0 + a_1 \cdot \text{fert}_{ij} + a_2 \cdot T_{ij} + a_3 \cdot P_{ij} + \text{fert}_{ij} \\ & \cdot (a_4 \cdot T_{ij} + a_5 \cdot P_{ij}) + \ln\left(\frac{d_{qijk}}{25}\right) \\ & \cdot (b_0 + b_1 \cdot \text{fert}_{ij} + b_2 \cdot T_{ij} + b_3 \cdot P_{ij} + \text{fert}_{ij} \\ & \cdot (b_4 \cdot T_{ij} + b_5 \cdot P_{ij})) + c_i + c_{ij} + c_{m(ijk)} + \varepsilon_{ijk} \quad (4) \end{aligned}$$

This global model includes potential effects of fertilization, temperature and precipitation on both, the intercept (i.e. the SDI) and the slope of the self-thinning line. It also includes all possible two-way interactions of fertilization with temperature and precipitation. The statistical power of the data, however, was not strong enough for also including an interaction between temperature and precipitation. Note that for precipitation, P , the usual value given in mm was divided by 100 in order to avoid very unequal scaling of the model's predictor variables. Note, that T and P were derived individually for each plot (see sub-section *Indicator variables for stand density and site conditions* above) which is indicated by the subscript ij (i.e. 'plot in trial') used with both variables. With an automated procedure (Barton, 2020), this model and, with regard to the fixed effects, all simpler models nested in it were fitted and ranked by their AIC afterwards. The best model identified by this procedure was chosen and interpreted (see Results section).

Auxiliary relationships for the demonstrating the long-term effects of N addition on stand dynamics

The connection of the self-thinning line to fertilization, as investigated with the statistical models shown above, has important consequences for the dynamics of fertilised vs unfertilised stands (or stands undergoing environmental influences which have a fertilising effect). This, in turn, is important for silvicultural practice. Therefore, we use the second and the third subsection of the Discussion section to demonstrate and interpret these consequential dynamics. In order to do so, we wanted for a few auxiliary relationships. In detail, we required the typical acceleration of stand diameter growth resulting from fertilization and a typical self-thinning line, both representative for our research plots. To this end, we calculated the quadratic mean tree diameter of the trees before and after the period of fertilization on both the fertilized and control plots and for each plot separately. This enabled us to estimate the average fertilization-induced relative diameter growth acceleration and its range. In order to obtain an appropriate $\ln(N)$ vs $\ln(d_q)$ relationship, we simply used the intercept and the slope resulting from the fitted model after Equation (4) for typical site conditions. For calculating the mean tree volume of a stand, we finally derived an auxiliary allometric relationship between the quadratic mean stem diameter and mean tree volume. These representative relationships result from the 11 trials with 59 plots, and we used them to demonstrate how the development of the stands along the self-thinning line, the mortality, the accumulation of total stand volume and the intermediate volume yield are modified by N-addition (see subsection 'Auxiliary relationships for demonstration purposes' in the Results section for the outcomes).

Results

Effect of N-fertilization on the $N \sim d_q$ relationship

The results of fitting Equation (3) to the data of the fertilization trials are presented in Table 2 and Figure 1. Evidently, fertilization had no influence on the intercept (SDI) and the slope of the self-thinning line. Note that removing the interaction of mean diameter and fertilization (Parameter b_1) and re-fitting the model did not indicate any possible significant main effect of fertilization.

Interactions between the effects of fertilization and the respective prevailing site conditions on the $N \sim d_q$ relationship

The model selection procedure with Equation (4) as the global model (see Material and methods section) revealed a very simple submodel as optimal:

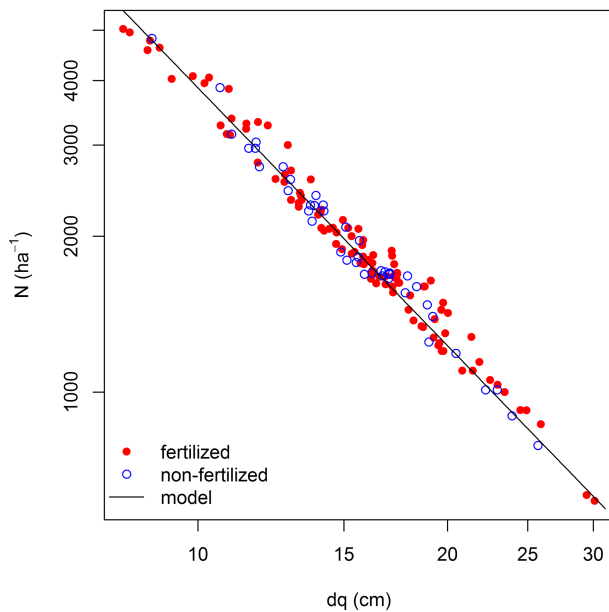
$$\ln(N_{ijk}) = a_0 + a_3 \cdot P_{ij} + b_0 \cdot \ln\left(\frac{d_{qijk}}{25}\right) + c_i + c_{ij} + c_{m(ijk)} + \varepsilon_{ijk} \quad (5)$$

Evidently, this model does not indicate any significant interaction of fertilization with precipitation or temperature. In line with the results obtained from fitting Equation (3), this model does

Table 2 Results of fitting Equation (3) to the data of the fertilization trials.

Fixed effects	Parameter	Estimate	Standard error	<i>P</i>
Intercept	a_0	6.7458	0.0294	0.000 ***
fert	a_1	-0.0085	0.0279	0.761
$\ln(d_q/25)$	b_0	-1.6539	0.0502	0.000 ***
$\ln(d_q/25) \cdot \text{fert}$	b_1	-0.0255	0.0478	0.594
Random effects	Parameter	Standard deviation.		
Trial level	c_i	0.0212		
Plot-in-trial level	c_{ij}	0.0353		
Year-of-survey level	$c_{m(ijk)}$	0.0485		

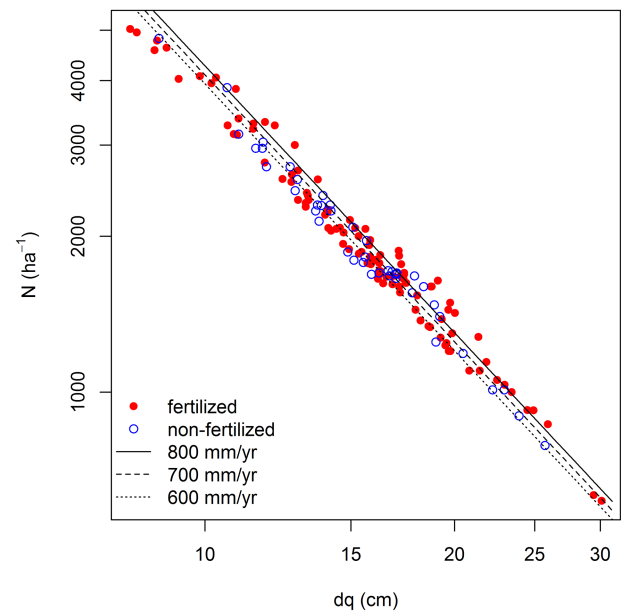
Significant parameter estimates are printed in bold; significance codes ‘*’, ‘**’ and ‘***’ indicate $P < 0.05$, 0.01 and 0.001, respectively. The residual standard deviation, ε_{ijk} , amounted to 0.0388.

**Figure 1** Plot data and fitted model after Equation (3) (only with the significant parameters a_0 and b_0).

not contain fertilization as a predictor variable, due to its non-significance. The annual precipitation, however, has a significant influence being positively correlated with the self-thinning line's intercept (the SDI). Table 3 shows the fitting results of Equation (5); Figure 2 shows the model together with the data.

Auxiliary relationships for quantitatively demonstrating the consequences of our findings

We found that on average the mean tree diameter growth was by 31 per cent (min 14 per cent, max 41 per cent) ahead on fertilized compared with non-fertilized plots. Figure 3 illustrates that the mean diameter growth was 2.26 mm yr^{-1} (standard deviation 0.62 mm yr^{-1}) on the non-fertilized and 2.95 mm yr^{-1} (standard deviation 0.59 mm yr^{-1}) on the fertilized plots at the survey after the period of fertilization. In order to be on the cautious side, we assumed a 20 per cent diameter increment acceleration caused

**Figure 2** Plot data and fitted model after Equation (5) with annual precipitation values of 600, 700 and 800 mm yr^{-1} .

by fertilization for our exemplary demonstration in the subsections ‘Accelerated growth, mortality, and carbon sequestration. Explanation and interpretation of the results’ and ‘Relevance of our findings for key variables of stand dynamics’ of the Discussion section.

For the auxiliary relationship between quadratic mean diameter, d_q , and the corresponding merchantable mean stem volume, v_q , we found

$$\ln(v_q) = -9.9093 + 2.8988 \cdot \ln(d_q) \quad (6)$$

by linear regression (see also Figure 4). It allowed us to calculate the mean stem volume in m^3 depending on the quadratic mean tree diameter in cm. The estimates of both coefficients were highly significant ($P < 0.001$) with the intercept = -9.9093 ± 0.043 and the slope = 2.8988 ± 0.016 and also a highly significant overall regression result with $R^2 = 0.996$ and

Table 3 Results of fitting Equation (5) to the data of the fertilization trials.

Fixed effects	Parameter	Estimate	Standard error	P
Intercept	a_0	6.4696	0.1084	0.000 ***
P	a_3	0.0401	0.0156	0.023 *
$\ln(d_q/25)$	b_0	-1.7116	0.0331	0.000 ***
Random effects	Parameter	Standard deviation.		
Trial level	c_i	0.0072		
Plot-in-trial level	c_{ij}	0.0337		
Year-of-survey level	$c_{m(ijk)}$	0.0492		

Note that P, the variable for annual precipitation is the actual precipitation in mm divided by 100. Significant parameter estimates are printed in bold; significance codes **, *** and **** indicate $P < 0.05$, 0.01 and 0.001, respectively. The residual standard deviation, ε_{ijk} , amounted to 0.0384.

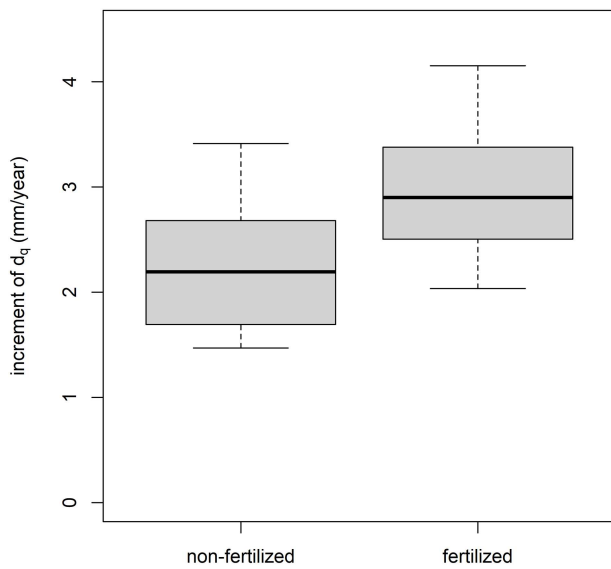


Figure 3 Mean stem diameter growth of non-fertilized trees (mean 2.26 mm yr^{-1} , standard deviation 0.62 mm yr^{-1}) and fertilized trees (mean 2.95 mm yr^{-1} , standard deviation 0.59 mm yr^{-1}) from the first to the last survey within the period of fertilization.

$P < 0.001$. We could not detect any fertilization effect on this relationship.

The required representative $\ln(N)$ vs $\ln(d_q)$ relationship was easily obtained from the parameters of Equation (5) (see Table 3), which turned out the best submodel of Equation (4) during the model selection process as mentioned in the subsection ‘Statistical Models’ in the Material and methods. As there was neither a fertilization nor a temperature effect, only an influence of precipitation, P , on the intercept, Equation (5) with inserted parameter values (and precipitation given in mm/yr) reads as:

$$\ln(N) = 6.4696 + 0.0401 \cdot \frac{P}{100} - 1.7116 \cdot \ln\left(\frac{d_q}{25}\right) \quad (7)$$

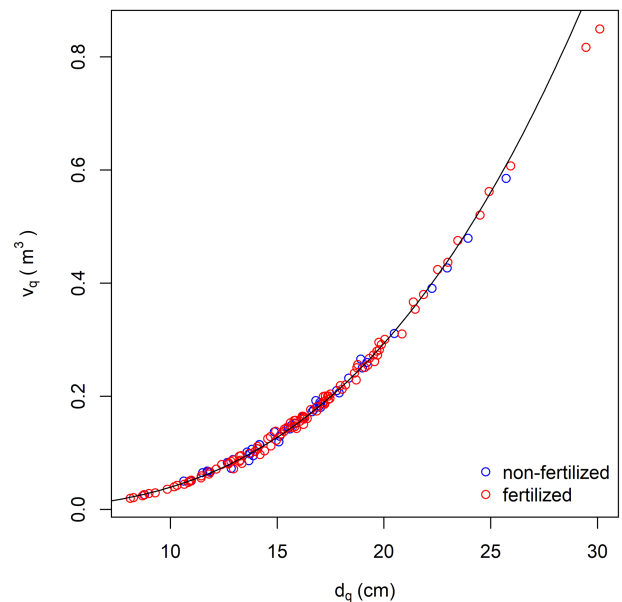


Figure 4 Allometric relationship $\log(v_q) = -9.9093 + 2.8988 \cdot \log(d_q)$ between quadratic mean stem diameter, d_q and the corresponding merchantable stem volume v_q (merchantable wood defined as having a diameter $> 7 \text{ cm}$ at the smaller end). The relationship was derived from the survey data of the non-fertilized and fertilized plots included in this study.

Using a typical precipitation of 700 mm yr^{-1} (cf. Supplementary Table S1), this reduces to:

$$\ln(N) = 6.7501 - 1.7116 \cdot \ln\left(\frac{d_q}{25}\right) \quad (8)$$

as the desired self-thinning line. Together with the assumed 20 per cent diameter increment acceleration, Equations (6) and (8) are the backbone of our exemplary demonstrations in the Discussion section (second and third subsection).

Discussion

Modulation of the self-thinning line by site conditions

Evidence for the modulation of maximum density of forest stands by site conditions is mainly based on the evaluation of inventory data from different sites. The resulting statistical correlations may suggest causalities but can also be spurious relationships. Our dataset, in contrast, allows *ceteris paribus* scrutinizing the effect of nutrient import on the maximum stand density. The slight increase of the maximum stand density line with increasing water supply is in line with Aguirre *et al.* (2018) and Kimsey Jr. *et al.* (2019). Aguirre *et al.* (2018) found for Iberian pine forests a strong increase in density of *Pinus pinea*, *Pinus halepensis* and *Pinus pinaster* stands and a moderate increase for *Pinus sylvestris* and *Pinus nigra*. In the case of *P. sylvestris*, the water supply raised the slope of the self-thinning line but not the intercept. In the Inland Northwest of the US, Kimsey Jr. *et al.* (2019) found a similar increase of the maximum stand density with increasing water supply for *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies grandis*. The revealed invariance of the maximum density regarding nutrient supply is also in line with the analyses by Kimsey Jr. *et al.* (2019). They revealed geographic, topographic and climatic variables as significant predictors of the maximum stand density. However, soil characteristics only made a slight difference to their model fits; the main predictors being geographic, topographic and climatic variables. They found a positive effect of volcanic ash on the intercept of the maximum stand density line. They explained this effect, however, by the up to twofold water holding capacity of volcanic ash rather than by its high nutrient content. Condés *et al.* (2017) came to similar results when analysing and modelling the maximum size-density relationship of Scots pine and European beech depending on climate variables throughout Europe. Their resulting models showed that both parameters of the species boundary lines, the slope and the intercept, were climate-dependent, but that the pattern of variation differed between species.

Accelerated growth, mortality and carbon sequestration. Explanation and interpretation of the results

In order to demonstrate schematically the consequences of our findings' meaning for the temporal dynamics of fertilized and unfertilized stands, we use the auxiliary relationships as explained and developed in the Material and methods and the Results section. In short, this implies the stationary self-thinning line described with Equation (8), the mean diameter—mean volume relation from Equation (6), and the assumption of a 20 per cent diameter increment acceleration due to fertilization. Moreover, we assumed a linear development of the mean stand diameter over age. This assumption of linearity seems justified, especially for a schematic representation and age spans relevant for forest management, as our data and many other studies showed an approximately linear mean and single tree diameter development over age up to stand ages of 100 years (Assmann and Franz, 1965, Pretzsch, 2001, p. 111). This simple representation of diameter development is visualized in Figure 5e. When discussing stand dynamics in the following sections, we often relate to the stand age, because age is a key

variable for silvicultural management in practice, while it is less appropriate for studying stand density.

Based on these conditions, Figure 5a,b illustrate that non-fertilized and fertilized stands follow the same allometric trajectory. Importantly, however, the allometric trajectory does not imply any conclusions for the development in time. Indeed, Figure 5a,b also show that the accelerated diameter growth of the fertilized stands moves them considerably faster along the same self-thinning line. Consequently, this leads to different age-stem number relationships as visualized in Figure 5c. Figure 5d shows the stand-level standing volume, V , plotted against d_q . This is a time-invariant relationship, and from the stationary (i.e. not responding to fertilization) $N \sim d_q$ allometry follows that it is stationary as well (assuming that fertilization does not fundamentally alter stem shapes and height diameter allometries). Figure 5d also demonstrates that the temporal development of fertilized and unfertilized stands is different along the same $V \sim d_q$ relationship. The faster growth of the fertilized stands results in a higher d_q and V at the same age compared with the controls (Figure 5e,f).

Supposing that the effect of nitrogen-deposition on forest growth is similar to the effect of fertilization (see subsection 'N-deposition and fertilization effect' below), the findings bundled in Figure 3 would mean that presently size growth proceeds faster and causes a faster self-thinning process along unchanged $N \sim d_q$ trajectories. This means that the $N \sim d_q$ relationship is still similar, the stands have the same structural appearance as in the past, however, they simply arrive at a defined structural phase much earlier than in the past. This, and not an increased level of the $N \sim d_q$ allometry, is the reason why at the same age V and d_q are much higher at present than in the past as reported by Pretzsch *et al.* (2014) for a large set of long-term plots in Central Europe.

Relevance of our findings for key variables of stand dynamics

Expanding from the insights by the statistical analyses, we quantitatively demonstrate the relevance of our findings for selected key variables of stand dynamics such as mortality, total yield, standing and removal volume depending on age (Figure 6).

In combination with a stationary self-thinning line an accelerated diameter growth due to fertilization or N-deposition means an increase of tree mortality under self-thinning conditions. If neither the self-thinning line's intercept increases nor its slope flattens due to fertilization, there is no additional carrying capacity for tree biomass per unit area that would be filled while mortality is temporarily reduced during such an extension process (assuming no trend in precipitation). A constant self-thinning slope of, as assumed, $b = -1.71$ means that tree number is reduced due to mortality by 1.71 per cent if the mean stand diameter increases by 1 per cent. Suppose that fertilization or N-deposition would accelerate the diameter growth by 20 per cent, this would also accelerate mortality by 20 per cent from 1.71 to 2.05 per cent. Figure 6a–c show the effects of this increased mortality, caused by a diameter growth acceleration by 20 per cent, on the mortality rate, the absolute number of dying trees and the absolute number of dying trees on the fertilized minus the number of dying trees on the non-fertilized plots. In detail, Figure 6a reveals that the relative mortality rate in fully stocked, fertilized

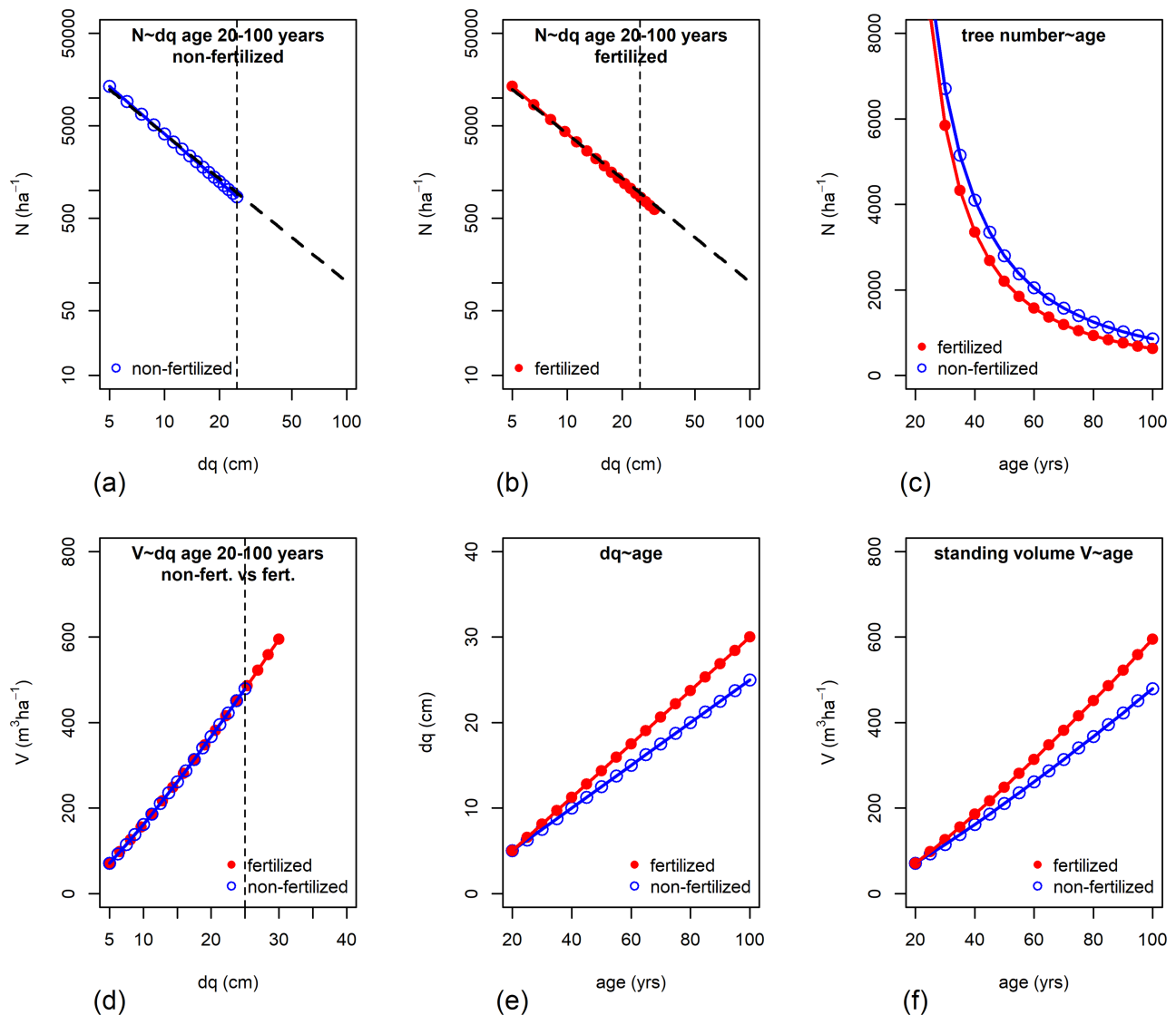


Figure 5 Effect of fertilization on the development of the stand density, the quadratic mean diameter and the standing volume for fully stocked stands in 5-year steps. Fertilized stands are assumed to have an accelerated diameter growth by 20 per cent. Tree number per ha over quadratic mean diameter for (a) non-fertilized, (b) fertilized stands, (c) tree number plotted over stand age, (d) standing volume over quadratic mean diameter, (e) quadratic mean diameter over stand age and (f) standing volume over stand age. The broken lines in (a) and (b) represent self-thinning lines with a slope of -1.605 as assumed by Reineke (1933).

stands is continuously higher than in non-fertilized stands, due to the accelerated size growth by fertilization. Therefore, in younger stands with high tree numbers the absolute number of dying trees due to self-thinning is higher in fertilized compared with non-fertilized stands (Figure 6b,c). Because of the accelerated self-thinning and tree number reduction the absolute number of dying trees may become lower in fertilized stands at a moderate age; due to the accelerated self-thinning, these are ahead in tree number reduction compared with the reference stands.

Total volume yield and standing volume are considerably higher at age 100 in fertilized compared with non-fertilized stands (Figure 6d). The surplus of total volume growth amounts to $250 \text{ m}^3 \text{ ha}^{-1}$ at age 100, the surplus of removal volume and

the standing volume to $\sim 135 \text{ m}^3 \text{ ha}^{-1}$ and $115 \text{ m}^3 \text{ ha}^{-1}$ at age 100, respectively (Figure 6e). This means that about half of the surplus of volume growth contributes to a higher turnover if not anticipated by thinning measures. The intermediate yield accumulates to almost 50 per cent in non-fertilized stands but to more than 60 per cent in their fertilized counterparts (Figure 6f).

Note an interrelation that might seem at the first glance a paradox: although the number of trees decreases faster as a result of fertilization, stand volume accumulates faster (Figure 6d,e). The reason for this is the interplay of allometries: the self-thinning slope is with $b \approx -1.71$ shallower than -2.0 which would mean a full compensation of the increasing mean

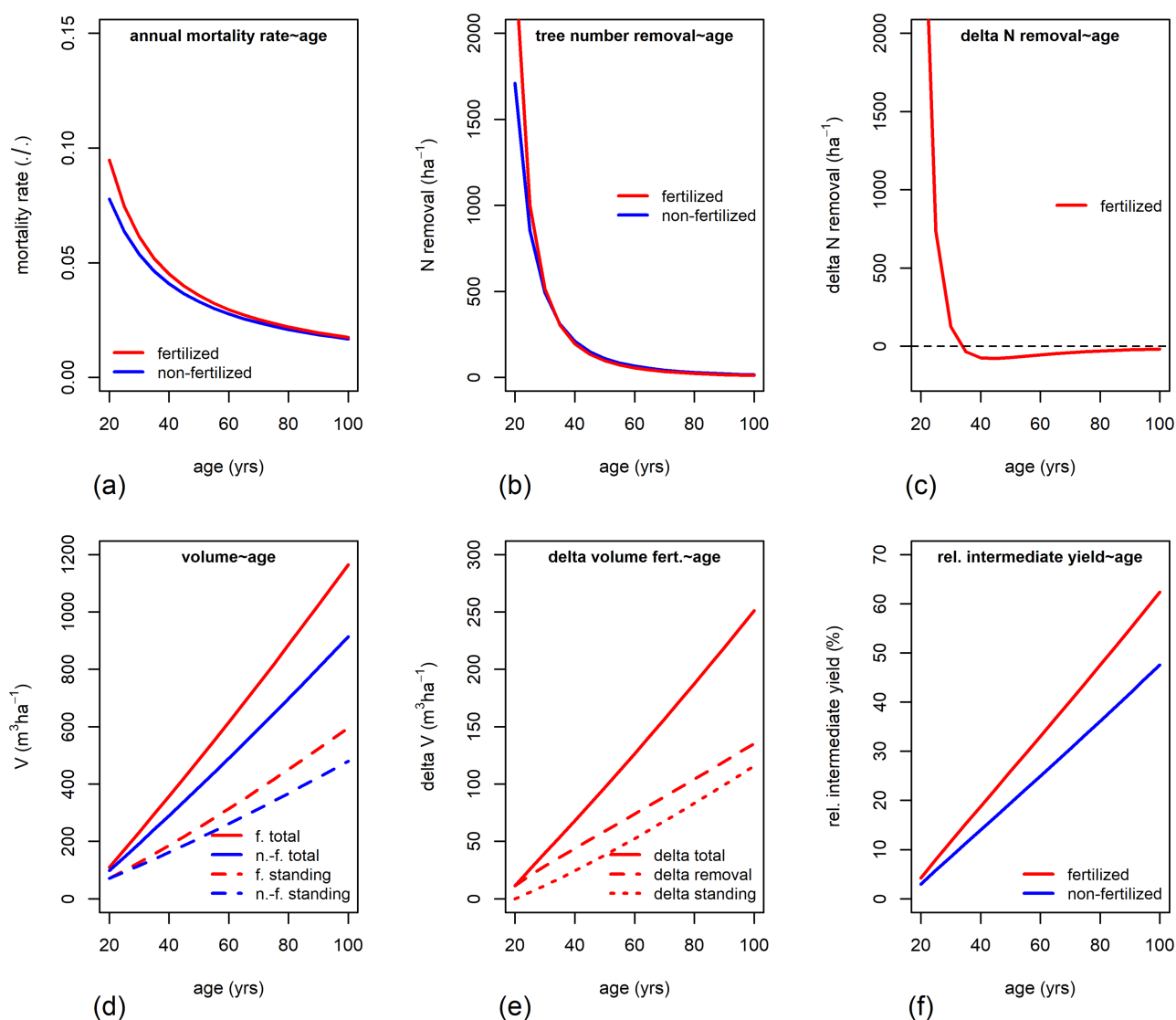


Figure 6 Effect of nitrogen fertilization on the mortality and volume growth of fully stocked unthinned Scots pine stands in schematic representation. Change of (a) annual mortality rate, (b) number of trees dying due to self-thinning and (c) surplus of dying trees in fertilized compared with non-fertilized stands. Development of (d) total volume yield and standing volume of fertilized compared with non-fertilized stands; (e) surplus of total yield, removal and remaining volume of fertilized compared with non-fertilized stands and (f) percentages of intermediate yield in fertilized vs non-fertilized stands.

tree size by the decreasing number of trees. In this case, the standing volume would remain constant over time. However, as in reality the tree number reduction proceeds allometrically slower than the increase of mean tree size, stand basal area and standing volume are accumulating as tree size increases. The background is that the leaf area of the whole stand is more or less constant. With increasing size, the remaining trees certainly build up more leaf area and require more growing space in the stand. However, the leaf area increase is under-proportional to their size increment. Thus, the stand's standing stem volume can increase although the leaf area remains constant. Our results provide empirical evidence for the conceptual models of forest stand property-density relationships by Long and Vacchiano (2014) and

Long et al. (2004). We can show that neither water supply nor nitrogen availability modifies the slope of the self-thinning line. Only the intercept of the self-thinning line is slightly raised when water availability increases. The main effect of fertilization is a faster development along the self-thinning line as hypothesized by Long et al. (2004), see Figure 5. As our stands were unthinned or only lightly thinned and fully stocked both non-fertilized and fertilized were near the self-thinning line since their first surveys. The fertilization, however, accelerated the growth of the trees and their forward movement along the self-thinning line. So, the fertilized trees are ahead of the non-fertilized ones but run along the same trajectory. Obviously, the fertilization did not increase the maximum leaf area due to water limitation. Water is limiting

the effect of N-fertilization in a way that trees grow faster but the maximum leaf area and related carrying capacity of the number of trees per unit area and the SDI do not change.

Given the framework of modelling approaches for the self-thinning line provided by Hann (2015) our study strives to identify the density-size relationship on population level and tests whether it is influenced by fertilization, precipitation and temperature. The data we are using are pooled time-series data from multiple measurements on multiple plots inside multiple installations. The time series do definitely not include surveys from before the stands were not fully stocked. We can therefore exclude any bias due to the use of premature surveys. Each installation comprises fertilized and unfertilized plots which have the same history except for the fertilization. Our plots do also not suffer from the potential problem that plot sizes correlate with initial stand densities. By selecting the 10 per cent densest plots and surveys we may have introduced what Hann (2015) would call a 'subjective element'. However, by doing so independently for both groups, the fertilized and the unfertilized plots, the selection is balanced among both treatments. Furthermore, this selection can be justified as it brings us safely into the group of the densest stands, our goal being not an ultimate quantification of the self-thinning line but testing for influences of fertilization, precipitation and temperature on stand density. Instead of non-linear regression, our model uses the widespread linear log(density) vs log(size) concept. In theory, this requires a correction of the estimated densities when applying the model, i.e. multiplication with $e^{\frac{\sigma^2}{2}}$ with σ^2 being the total variance which is not explained by the model's fixed effects (i.e. random effects' and residual variance). For both models we show in this study, however, this factor is smaller than 1.003 and thus negligible for our purposes.

N-deposition and fertilization effect

We showed that forest stands whose growth is accelerated due to increased nitrogen supply do not exceed their previous maximum stand density level (maximum $N \sim d_q$ relationship), but still follow the same self-thinning trajectories. The fact, that higher volumes are observed at the same age must not be mistaken as an indicator for an increased level of stand density. This is important to know in order to appropriately interpret the current mortality rates and C-sequestration and to adapt modelling and silvicultural management of forest stands.

Evaluations of long-term fertilization responses by Högborg *et al.* (2006) showed that dose rates of application were more important than the total amount of N added. Repeated low fertilizer dose rates (20–50 kg N ha⁻¹ yr⁻¹) caused greater growth acceleration per kg N than higher rates less frequently applied. Our plots were fertilized over 30–40 years up to five times with a repeated application of 1200 kg N ha⁻¹ and 1900 NPKCaMg ha⁻¹ and cumulative totals of 1000–2000 kg N ha⁻¹. This means that the total sums may be similar, however, the effects on growth may be stronger by the regular and long-lasting input by deposition of 10–50 kg ha⁻¹ yr⁻¹. This suggests that the permanent deposition might affect the growth even stronger than fertilizer applications such as on our plots.

When the fertilization of Scots pine stands in northeast Bavaria was initiated in the period 1950–69, nitrogen was the main limiting factor for growth (Preuhsler and Rehfuess, 1982) as many stands were degraded due to long-term litter raking, forest pasture and overexploitation (Schmidt, 1971; Kreutzer, 1972; Pretzsch, 1985). To avoid limitation by other nutrients multi-element fertilizers such as NPKCaMg, NPK or CaCO₃ and NPK were used on most plots (see Supplementary Table S3). From that angle of view, N deposition may remedy the nitrogen limitation but cause new limitations (Prietzl *et al.* 2009) or even toxic conditions in the soils in N saturated soils (Skeffington and Wilson, 1988). During the most recent 40 years, the N nutrition of the unfertilized control plots improved considerably, whereas the foliar P, K and Ca concentrations decreased. The comprehensive evaluation of soil, foliage and growth data by Prietzl *et al.* (2020) revealed a key relevance of the N and P nutrition of the stands for their growth, and a change from initial N limitation to a limitation by other growth factors (P, Mg, Ca and water). Although a P and S scarcity has to be expected in the foreseeable future, the tree and stand growth is still accelerated by the on-site nitrogen deposition in the northeast of Bavaria (Prietzl *et al.*, 2008, 2020) and also on many sites in Europe (Pretzsch *et al.*, 2014; From *et al.*, 2015, 2016).

The effects of N-deposition are regionally specific (Schmitz *et al.*, 2019), as growth limitation by water (Bolte *et al.*, 2010), phosphorus (Prietzl *et al.*, 2008, 2020; Braun *et al.*, 2010) or effects of ozone (Matyssek and Sandermann, 2003) may limit the growth acceleration. Of further interest is any effect of the water supply on the maximum $N \sim d_q$ relationship. While we did not find any interaction between fertilization and water supply that might have indicated an increase of stand density by fertilization on dry sites compared with wet sites, we can show a slight increase of the self-thinning line's level with increasing precipitation. Independent from fertilizing or nitrogen deposition, this suggests higher mortality rates and forest carbon stock losses under future drier climates and deserves further investigation with data from a wider climate gradient.

Modelling tree and stand dynamics

Mortality models, as part of modern dynamic forest simulation models, often use the self-thinning relationship as a stand-level constraint for density (Yang and Titus, 2002; Monserud *et al.*, 2004), as a control mechanism for logistic models or other probability models for survival or mortality at the single tree level (Eid and Tuhus, 2001; Yao *et al.*, 2001; Palahí *et al.*, 2003) or a combination of both (Pretzsch *et al.*, 2002; Monserud *et al.*, 2004). Our finding that fertilization does not change the self-thinning line and the assumption that this applies also for atmospheric nitrogen deposition, suggests that models relying on self-thinning lines as the backbone of estimating mortality may work unflawed even under changing nitrogen deposition regimes. Notwithstanding, while this applies to stand level predictions, breaking these down to the level of single trees may definitely require adaptations to changing environmental conditions.

Depending on the site conditions and respective limiting resource for tree growth both one-sided (asymmetric) or two-sided (symmetric) competition may cause mortality (Schwinning and Weiner, 1998; Wichmann, 2001); the former mode of

competition prevails when light is the limiting factor, the latter indicates limitation by water or nutrients. Many studies suggest that in light-limited systems mortality at high stand densities strongly concentrates on the smaller trees, whereas in water or nutrient limited systems taller trees have less advantage from pre-empting light and smaller trees may even benefit from their understorey status that implies lower exposition to radiation (Schwinning and Weiner, 1998; Wichmann, 2001; Pretzsch and Biber, 2010).

The individual tree mortality model by Monserud and Sterba (1999) also showed that the basal area of larger trees strongly determines the mortality of Scots pine in Austria. This indicates the light limitation as the main cause of mortality and an inverse-J shaped mortality distribution over stem diameter under temperate climate conditions. Bravo-Oviedo *et al.* (2006) found that even in the Mediterranean environment asymmetric competition process indicates the importance of light and size inequality on the mortality and stand dynamics in case of Scots pine in Spain. Thus both mortality models by Bravo-Oviedo *et al.* (2006) and Monserud and Sterba (1999) showed for even-aged Scots pine stands that the smaller the trees the higher their probability of death.

Thus, self-thinning lines may be constant but the survival probability of single trees may change on the expense of tall trees and stand structure may slightly change by changes in resource supply. Clearly, in order to estimate correct mortality rates, correct self-thinning lines, and, in case of single tree models, correct tree-level mortality models must be complemented with adequate stand or tree growth models. If the latter do underestimate the actual growth, the actual production of stands can be considerably underestimated, even though the self-thinning line guarantees realistic predictions of stand density, basal area and volume.

When using self-thinning lines in modelling, the question is often, which allometric exponent (i.e. which slope) to choose. While Reineke (1933) suggested to use of -1.605 as a generic value, this has triggered considerable debate, and Pretzsch and Biber (2005) could show species specific differences with a large data set of unthinned long-term research plots. For Scots pine, they suggest a value of -1.593 , which seems to contradict the values reported in the study at hand (-1.6539 , Equation (3), Table 2; -1.7116 , Equation (5), Table 3). Note, however, that the 95 per cent confidence interval ($\sim \pm 2 \times$ standard error) of our slope for Equation (3) certainly includes -1.593 . While the 95 per cent-confidence interval reported by Pretzsch and Biber (2005) and the confidence interval of the slope value in Equation (5) overlap, -1.593 is not included in the latter. However, it must be taken into account that the inclusion of another additional fixed effect in Equation (5) (compared with Equation (3)) is a considerable change in the model's structure. For modelling purposes we suggest to use the value reported by Pretzsch and Biber (2005) as the time series behind that study were longer, and the plots were strictly unthinned since their establishment.

Implications for silvicultural stand management

It seems plausible that the common atmospheric nitrogen deposition would modify stand dynamics similar to fertilization.

In this case, size growth would be faster and stands (passing faster through the previous $N \sim d_q$ trajectories) would reach defined development phases by 10–20 years earlier than in the past. An increase of the growth rates by 10–30 per cent as revealed among others by Pretzsch (2020), Silva *et al.* (2016), Spiecker (1999, 2012) would mean that target diameters that trees arrived at an age of 100 years in the past would presently be reached earlier. The faster size growth leads to accelerated competition effects and tree number reduction by mortality, and also to a faster stand volume accumulation in the remaining stand. It follows that there are numerous implications for stand management, and here we stress the most important ones.

In order to anticipate the accelerated self-thinning and dying of trees, the thinning frequency and intensity may be adapted. As suggested by Pretzsch and del Rio (2020) thinning guidelines should be based on achieved stand height or diameter instead of stand age. Whereas the allometric and dendrometric relationships between, e.g. mean tree height and tree number or mean tree diameter and stand volume are still valid, the development of dendrometric stand characteristics over stand age have has accelerated.

Stationary self-thinning lines in co-occurrence with accelerated tree growth have two interesting implications when considering forest biodiversity and carbon sequestration. In the ongoing discussion about forest biodiversity, the requirement of having more deadwood per unit area is regularly pointed out (Müller and Bütler, 2010; Dieler *et al.*, 2017). Our findings suggest that more deadwood will automatically accumulate in stands that are selected as set aside areas and taken out of regular management. This was not true only if the accelerated growth is counteracted by an accelerated deadwood decomposition. We see here an interesting point for empirical studies on untreated long-term plots. If carbon sequestration is a major management goal, it seems evident that an increase of the forest bound C-stocks cannot be expected as a result of increasing area-related carrying capacities for tree biomass. Accumulating deadwood will not be a C sink in the long run. In line with what has been said before, this would take adapted thinning guidelines and felling budgets in order to pre-empt the increased mortality and to put the harvested wood into uses where the carbon sequestration or C-emission substitution is as high as possible (Marland and Schlamadinger, 1997). Clearly, the accelerated growth would lead to higher standing volumes at rotation age, and thus to more carbon stored in the forest at the estate level. But possibly, lowering rotation ages would, under current conditions, also increase the mean annual increment. Optimizing these relations requires careful consideration.

Conclusions

Long-term nitrogen fertilization experiments that were established in the 1970s for improving Scots pine stand growth still provide valuable information for improved insights into the impact of atmospheric nitrogen deposition on forest ecosystems. This is the more important in the context of global environmental change. Insofar, in addition to its specific results, this study also

demonstrated the multipurpose value of long-term experiments in forest stands.

Nitrogen input accelerates growth velocity without changing the allometric relationship that governs self-thinning; thus, defined stand structures and development stages for Scots pine growing on good sites in southern Germany are presently reached one or two decades earlier than in the past. The dependency of stand characteristics on age changed, but not their dependency on mean tree size.

This means faster self-thinning and accelerated mortality in unthinned stands and suggests higher thinning frequencies, higher removal volumes and shorter rotation in managed even-aged stands in order to utilize their faster growth. We conclude that silvicultural prescriptions depending on mean tree size are more consistent than age-dependent guidelines. More deadwood accumulating in set aside or weakly thinned stands would be an evident consequence as well, and desirable from the standpoint of biodiversity-oriented management.

Carbon sequestration and storage are increased due to the faster growth and higher standing stocks compared with the past. As the level of the self-thinning line was fertilization-invariant we found no additional storage capacity beyond this acceleration effect.

The maximum density correlated positively with the water supply; from this, we conclude that the acceleration due to nitrogen input may turn into decreasing growth rates and storage capacities on sites or in times where the water supply is limiting stand growth.

Supplementary data

Supplementary data are available at *Forestry* online.

Acknowledgements

The authors would like to thank two anonymous reviewers for their constructive criticism.

Data availability statement

The data underlying this article will be shared on reasonable request to the authors.

Conflict of interest statement

None declared.

Funding

The authors would like to thank for networking support by the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions—CA15226), financially supported by the EU Framework Programme for Research and Innovation HORIZON 2020. The publication is also part of the CARE4C project that has received funding from

the European Union's HORIZON 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 778322. Thanks go also to the Bayerische Staatsforsten for supporting the establishment and maintenance of the underlying long-term experiments and to the Bavarian State Ministry for Nutrition, Agriculture and Forestry for permanent support of the project W07, entitled 'Long-term experimental plots for forest growth and yield research' (# 7831-22209-2013).

Author contributions

Hans Pretzsch initiated and conceptualized the study, Peter Biber and Hans Pretzsch evaluated the data, wrote and revised the manuscript.

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