

Stand density biases the estimation of the site index especially on dry sites

Astor Toraño Caicoya and Hans Pretzsch

Abstract: The site index (SI) has been widely used in forest management and silviculture. It relies on the assumption that the height of dominant trees in a stand is independent from the local density. However, research on climate change suggests that under certain moisture stress conditions, this may not hold. Here, based on 29 plots from five long-term research experiments, we tested the effect of local stand density on the SI of Norway spruce (*Picea abies* (L.) H. Karst.). With generalized additive models (GAMM), we analyzed the effect of stand structure and climate predictors on SI. The two evaluated models revealed that local stand density and age had a significant effect on SI ($p \leq 0.001$), showing a clear negative trend especially significant on sites with poor and dry soils, which may reduce the SI by a maximum of approximately 4 m for an increase in density of between 400 and 600 trees/ha. We stress that the physiological characteristics of Norway spruce, flat-rooting system and xeromorphism, especially when growing in pure stands, may explain these effects. Thus, density control and growth in mixtures may help to reduce the water stress and losses in height growth under future climate conditions.

Key words: Norway spruce, climate change, silviculture, monocultures, mixture, long-term experiments.

Résumé : L'indice de qualité de station (IQS) a été largement utilisé en aménagement forestier et en sylviculture. Il s'appuie sur l'hypothèse que la hauteur des arbres dominants dans un peuplement est indépendante de la densité locale. Cependant, la recherche sur les changements climatiques indique que cette hypothèse pourrait ne pas tenir dans certaines conditions de stress hydrique. Dans cette étude, sur la base de 29 places-échantillons faisant partie de cinq projets de recherche expérimentale de longue durée, nous avons testé l'effet de la densité locale sur l'IQS de l'épicéa commun (*Picea abies* (L.) H. Karst.). Avec des modèles additifs généralisés (GAMM), nous avons analysé l'effet de la structure du peuplement et des variables descriptives du climat sur l'IQS. Les deux modèles qui ont été évalués révèlent que l'âge et la densité locale du peuplement ont un effet significatif sur l'IQS ($p < 0,001$) et montrent une nette tendance négative particulièrement importante dans les stations avec des sols pauvres et secs, ce qui peut réduire l'IQS d'une valeur pouvant atteindre jusqu'à environ quatre mètres pour une augmentation de la densité locale de 400 à 600 tiges/ha. Nous soulignons le fait que les caractéristiques physiologiques, le système racinaire traçant et la xéromorphose de l'épicéa commun, particulièrement lorsqu'il croît en peuplements purs, pourraient expliquer ces effets. Par conséquent, le contrôle de la densité et la croissance en peuplements mixtes pourraient contribuer à réduire le stress hydrique et les pertes de croissance en hauteur dans les conditions climatiques futures. [Traduit par la Rédaction]

Mots-clés : épicéa commun, changement climatique, sylviculture, monocultures, peuplement mixte, essai de longue durée.

Introduction

Measuring the quality of a site has been a major concern of forestry science since its beginning. The height of dominant trees at a defined reference age, in even-aged stands, known as the site index (SI), has been widely used as a measure of site quality (MacFarlane et al. 2000). First experiences in forest science have assumed that the SI equations, the dominant height versus age relationship, remain unchanged by stand density (Huang and Titus 1993). In the 1960s, Vincent (1961) recognized in his comprehensive review that the use of total height over age as an index of site quality is not as simple as some textbooks on forest mensuration might lead one to believe. Besides, many things may happen to a tree that can alter the height–age relationship so as to obscure any differences ascribed to site quality (Puhlick et al. 2013; Vincent 1961).

While it is recognized that stand density affects average stand height, the evidence on the dominant height is yet unclear (Burkhardt and Tomé 2012). Many authors have discussed the influence of stand density on the height of the dominant trees, finding both no effects and negative effects, depending on the experiment and species carried out in the respective studies. Studies such as those of MacFarlane et al. (2000) or Antón-Fernández et al. (2011) maintain that assessments of site index are confounded by the influence of population density on height growth, even when only the tallest trees in the stand are used to obtain the index.

Due to the general lack of long-term studies with a broad density variation in most regions, Nelder plots (Nelder 1962) have been commonly used to study tree growth under different densities. However, studies are frequently based on the very early

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growth stages. For example, Kuehne et al. (2013) observed that the total tree height in Nelder plots from oak is lower at higher densities, especially due to the presence of smaller suppressed trees. Woodruff et al. (2002), in a plantation density experiment of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), observed how high initial planting density has a positive effect on height growth. However, Newton (2015) observed a negative relationship between density and height in Nelder plots of Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.), tending to be asymptotic in nature. This means that the differences in height growth declined with age, and initial density has a different impact on growth than does density at later development phases. In an experiment on a Nelder plot in Scots pine (*Pinus sylvestris* L.), which was first reported in Dippel (1982) and then repeated in Spellmann and Nagel (1992), it was observed that in advanced stages of development, the heights in the middle of the plot, where the density is the highest, were lower than in the less dense parts. This indicated a possible effect of higher density and showed the effects on a later stage of development, compared with other studies.

In Nelder studies, during the earliest measurement periods, the relationship of height increment to tree density may be a result of the extremely high densities in the plots (Hummel 2000). Thus, the impact of high densities on height growth in young trees is demonstrated through such experiments (Woodruff et al. 2002). Also, studies focused on the dominant height, for example, MacFarlane et al. (2000), which was extended by Antón-Fernández (2011), questioned the density-independence assumption of the dominant height in even-aged stands of loblolly pine (*Pinus taeda* L.), stating that high densities may have a negative impact on dominant height. Antón-Fernández (2011) even stated that forest managers should adapt the site index for different planting densities, especially if high densities are involved. The general consensus states that these effects are compensated during stand development (microsite occupation, best individuals grow faster, the others die). However, it remains in question whether stress factors on poor sites that affect the rooting system, such as drought, may have an impact on growth at high densities.

Density can be controlled through initial escapement and thinning operations. In studies of stress by drought, it can be observed how thinning mitigates growth reduction, i.e., increases resistance, during a drought year, and enhances recovery of stem growth during following years (Sohn et al. 2016). It has also been proved by Sohn et al. (2013), D'Amato et al. (2013), and Gebhardt et al. (2014) that a reduction in density can enhance the capacity of spruce stands to cope with lack of water availability. However, this mitigating effect depends on the time span between thinning and drought; the extra water availability decreases as trees grow and increase their leaf area and fine root biomass. Another indicator that points out towards impacts of density on the height-age relationship is the hydraulic limits to the height growth (Ryan and Yoder 1997), which may play an even more relevant role under conditions of water stress.

An indication that the reduction of height growth with higher competition for water in denser stands may be especially relevant on poor sites is explained as follows. As trees compete mainly for belowground resources, and density especially increases competition for them, height growth may be reduced. This means, a prioritization of the height growth does not bring any competitive advantage and, thus, both diameter and height growth may decrease monotonically (Pretzsch 2019). This can be especially relevant in monocultures of Norway spruce (*Picea abies* (L.) H. Karst), whose physiological characteristics (flat rooting system and isohydric) make this species particularly sensitive to water stress conditions (Lyr et al. 1992; Puhe 2003).

With increasing drought stress, such negative effects of stand density and water limitation on height growth (Briffa et al. 2009; Spiecker 2003) and bias in the estimation of the site index are

prone to increase. Moreover, in addition to stand density and ageing, climatic factors are reported to affect growth partitioning, with species-specific differences (Trouvé et al. 2017). Thus, it can be expected that especially on sites under water stress, the effects of stand density on height growth may introduce substantial variances on the estimation of the site index, also motivated from different allocation strategies (Uhl et al. 2015).

To assess these effects, in this study, we used statistical modelling based on the long-term Bavarian experimental plots. Inventory data from over 40 years for Norway spruce stands, distributed along the southern region of Bavaria, will offer new insights to address the following specific questions:

Q1-Is the estimation of the site index biased by a reduction of height growth due to local density?

Q2-Does water availability or drought modulate the effect of the local density on the estimation of the site index?

Materials and methods

Data

In this study, we used data from the long-term forest experimental plots network from Bavaria. For this purpose, we chose monocultures of Norway spruce spread throughout the state. These correspond to a diverse range of thinning and planting experiments (see Appendix Table B1). For each research experiment, different kinds of thinning (from above, below, and selective) and strength of thinning (unthinned, slight, moderate to strong density reduction) have been tested in independent plots, which lie in close vicinity. For this reason, a wide range of densities was available, from sparse densities, where trees are growing under low competition, to dense unthinned plots. In the following, research experiment will denote the specific experiment per site, and research plot the individual thinning or plantation density plots within the experiment.

The inventories were repeated every 10 years. Some of the plots have been measured since 1880. However, as the climatic data are only available since 1975, we have used inventory data only since this year. The spatial position of all the trees within the plot is known, together with the diameter at breast height (dbh), which is measured for every tree. Stand age was calculated based on the time passed since the establishment of the experiment. Since all experiments are based on even-aged stands, stand age can be assumed equal for all trees in each plot.

During the standard inventory of the research experiments, tree height was only measured for a subset of trees. Such measurements are designed to cover a representative spectrum of heights and diameters. To have height estimates for all trees, we fitted a log-function $H = a + b \ln(\text{dbh})$ (where H denotes the tree height, dbh the diameter at breast height, and a and b are empirical parameters) to the measured height-diameter relationship for each year, and applied it to the rest of the individuals. This was performed at the research (thinning) plot level, to have enough measured individuals to ensure a representative curve for each experiment and silviculture regime. A summary of the main characteristics of the stands and sites is provided in Tables 1–3, and detailed information regarding the number of plots and subplots (Table B2) and the specific structure characteristics depending on the thinning experiment (Table B1) are included in Appendix B.

We have then grouped the experiments in two classes of water availability; we used the information provided by the forest administration data, according to the type of substratum, depth of the soil, and overall water availability. We named these groups “moist” and “dry”. The dry group comprises the research experiments of Vohenstrauß 622 and Weißenburg 613, and the moist group comprises the rest of the available plots, as spruce monocultures in Bavaria have been generally established on good sites. These are Denklingen 05 and 606; Sachsenried 602, 607, 67, and 68;

Table 1. Climate characteristics for each research experiment.

Research experiment	Number of plots (P×SP)	Coordinates	TotPrepVP (mm)	MeanTempVP (°C)	TotPrep (mm)	MeanTemp (°C)	Vegetation period (days)
Denklingen 05	3×63	10°50'32"E, 47°52'15"N	648	14.5	1114	6.8	140
Denklingen 606	6×25	10°49'26"E, 47°51'36"N	648	14.5	1114	6.8	140
Eurach 605	7×13	11°20'20"E, 47°46'48"N	700	13.3	1200	6.2	133
Sachsenried 602	4×9	10°45'37"E, 47°51'06"N	700	13.3	1200	6.2	133
Sachsenried 607	12×21	47°52'1"E, 10°49'23"N	648	14.5	1114	6.8	140
Sachsenried 67	3×63	10°45'13"E, 47°50'03"N	701	13.3	1204	6.2	133
Sachsenried 68	3×49	10°45'18"E, 47°50'03"N	701	13.3	1204	6.2	133
Schongau 623	7×1	10°45'54"E, 47°51'58"N	700	13.3	1200	6.2	133
Vohenstrauß 622	9×15	12°26'26"E, 49°40'59"N	375	12.5	904	6.0	124
Weißenburg 613	7×21	11°02'16"E, 49°00'11"N	470	14.5	800	7	—
Zusmarshausen 603	6×15	48°23'49"E, 10°28'46"N	538	15.2	800	7.5	150
Zusmarshausen 604	4×9	48°23'56"E, 10°28'59"N	525	15.4	800	7.5	150

Note: P, thinning plots within a research experiment; SP, circular subplots within a research experiment. TopPrepVP, total precipitation during the vegetation period; MeanTempVP, mean temperature during the vegetation period; and TopPrep and MeanTemp, total precipitation and mean annual temperature, respectively.

Table 2. Soil characteristics for each research experiment.

Research experiment	Soil type	Substrate	Texture	Depth	Water availability
Denklingen 05	Pseudogley, brown earth	Old moraine	Lime	Deep	Very high
Denklingen 606	Pseudogley, brown earth	Old moraine	Lime	Deep	Very high
Eurach 605	—	Old moraine	—	—	High*
Sachsenried 602	(Para-)/brown earth	Ripped old moraine	Lime, rocky	Very deep	High
Sachsenried 607	—	—	—	—	—
Sachsenried 67	(Para-)/brown earth	Old moraine	Lime, slightly rocky	Very deep	High
Sachsenried 68	(Para-)/brown earth	Old moraine	Lime, slightly rocky	Very deep	High
Schongau 623	Pseudogley, brown earth	Old moraine	Lime	Deep	Very high
Vohenstrauß 622	Podsol/brown earth	Biotite-rich gneiss	sandy to mica-lime	Deep	Low
Weißenburg 613	Pseudo-vergley Para-brown earth over terra fusca	White Jura	Lime	Very shallow	Low
Zusmarshausen 603	Brown earth	Upper fresh water molasses + quaternary crushed stone + colluvial	Sandy to lime	Deep	High
Zusmarshausen 604	Brown earth	Upper fresh water molasses + quaternary crushed stone + colluvial	Sandy to lime	Deep	High

*Water availability was assumed based on experience records from the manager of the experiment.

Table 3. Structural characteristics for each research experiment calculated from the 10-m-radius subplots.

Research experiment	Stand density (tree/ha)			SDI (adm)			Age (years)			D_q (cm)			Acquisition year	
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	First	Last
Denklingen 05	191	415	767	713	1269	2026	132	137	143	40	51	67	1980	1991
Denklingen 606	64	1017	1974	91	972	1744	45	54	62	19	26	45	1998	2015
Eurach 605	32	782	1623	61	918	1686	39	48	55	20	30	42	1992	2007
Sachsenried 602	668	1247	1973	941	1223	1796	41	49	51	21	26	32	2003	2013
Sachsenried 607	127	781	1973	227	854	1737	43	52	60	18	27	39	1996	2013
Sachsenried 67	32	335	605	91	1057	1593	119	122	126	41	52	70	1978	1985
Sachsenried 68	159	381	700	560	1123	1667	118	122	125	41	51	64	1978	1985
Schongau 623	1210	1443	1878	1146	1245	1372	43	43	43	20	23	25	2015	2015
Vohenstrauß 622	222	510	828	330	596	963	39	42	44	23	28	37	2013	2018
Weißenburg 613	127	799	1974	280	922	1465	55	78	100	17	30	51	1982	2016
Zusmarshausen 603	255	1096	1974	554	1031	1716	32	45	54	16	27	44	1995	2017
Zusmarshausen 604	350	960	1941	376	821	1349	37	48	54	19	23	29	2000	2017

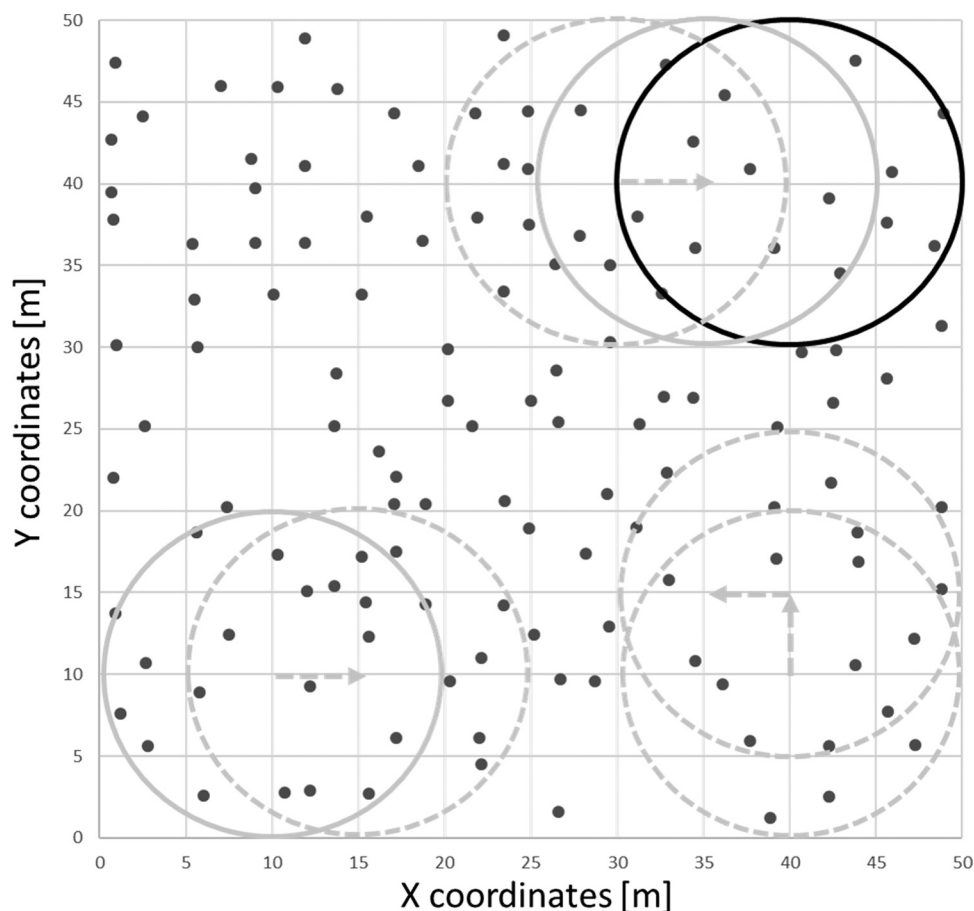
Note: SDI, stand density index; and D_q , quadratic mean diameter.

Eurach 605; Schongau 623; and Zusmarshausen 603 and 604 (Table 2). The dry group is characterized by low water availability, low precipitation, and especially by low-quality soils. Vohenstrauß 622 presents only 375 mm of precipitation during the vegetation period, and it is additionally located on sandy soils. Weißenburg 613 has a better substratum but also not optimum soil, being very shallow and with a low water availability. The rest of the sites present

optimum soil conditions, over moraines and with high precipitation, indicating optimum growth conditions for Norway spruce. A special case was Eurach 605. This site is a desiccated swamp over moraines. The exact soil site is unknown, but records of the forest enterprise suggest good water availability.

To track differences in local density, and thanks to the known location of each tree, we virtually extracted subplots with 10 m

Fig. 1. Sketch of the experimental design. A circle of 10 m radius is used as a moving window, which is displaced in 5 m steps, east and north bounds until the entire surface is covered by the research (thinning) plot.



radii, overlaid on the actual research (thinning) plot (Fig. 1). First, we decided the radius to be constant instead of height dependent, to have the same probability of having a dominant tree in each circle and across the research plots. Second, we considered that a 10 m radius results in enough replications per research plot, which typically have dimensions between 500 and 1000 m². Thus, as a kind of moving window, we moved the circle in 5 m steps in the x and the y directions to cover the entire research plot. Within the mentioned circle, we calculated at every step the following (local) stand structural variables: age (years), number of trees per hectare (N) in tree/ha, quadratic mean diameter (D_q) in cm, dominant height (H_{100}) in m, calculated as the mean height of 100 thickest trees/ha, and the stand density index (SDI), which was calculated according to Reineke (1933), but using the allometric exponent (-1.664) estimated for Norway spruce by Pretzsch and Biber (2005).

$$(1) \quad \text{SDI} = N \times \left(\frac{25}{D_q}\right)^{-1.664}$$

Finally, the site index (SI) by Assmann and Franz was calculated based on the dominant height at age 100 according to yield tables for spruce in Bavaria (Assmann and Franz 1972). The SI was calculated dynamically for each year, so it reflects changes in site quality with time. The suitability of this SI can be observed in Fig. 2, in which we have plotted the development of the dominant height (H_{100}) for the research experiments under study, compared with the SI curves by Assmann and Franz (1972). These SI curves were fitted with data that go back to the 1880s, being the most appropriate curves to track forest development before the climate change effects became substantial.

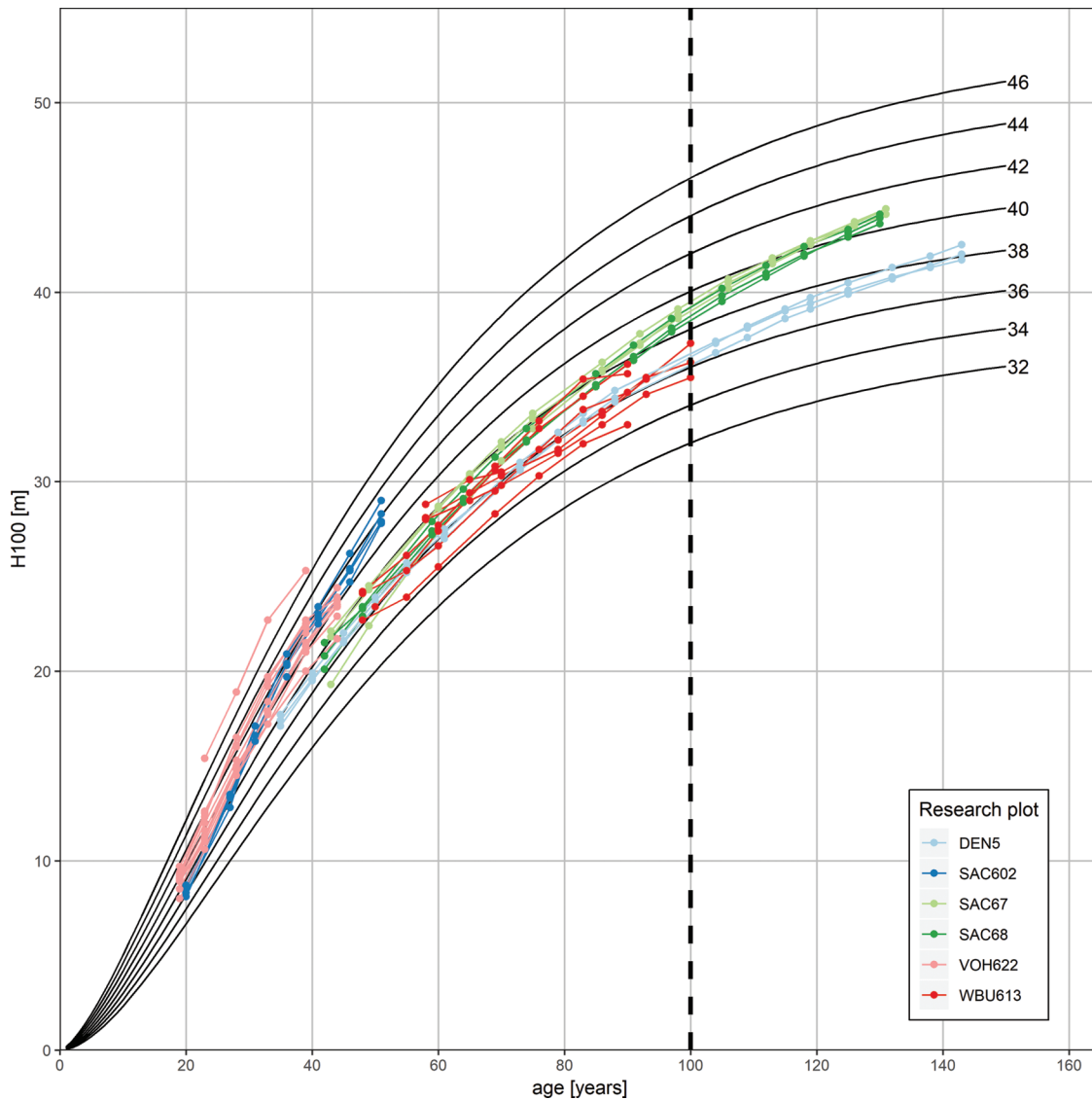
Due to the size of the circular subplots, only three trees per subplot are selected for the estimation of the dominant height, which can lead to underestimations of the H_{100} and as consequence in the SI (García 1998). Even if for the rather homogeneous vertical structure of the research experiments studied here such biases could be negligible ($H_{100} \cong \bar{H}$), the effect must be taken into account when discussing the results.

Two climatic variables were additionally estimated: mean precipitation of the vegetation period (TotPrepVP) in mm and the mean temperature of the vegetation period (MeanTempVP) in °C. The vegetation period was defined as the months with a mean temperature above 10 °C. These data were estimated using the Gridded Agro-Meteorological Data from the European Commission, Joint Research Center with 25 km × 25 km resolution grid (CGMS 2014) and assigned to each experimental plot based on their geographical coordinates. The data were available from 1975 until the present time.

Statistical analysis

We have chosen generalized additive mixed models (GAMMs) (mgcv package) (Wood 2017; R Core Team 2018) as our main statistical tool to examine the impact of stand density on the SI. GAMMs offer a convenient way to incorporate nonlinear effects (Biber et al. 2013). Due to spatial and temporal correlation effects between the observation units, we adopted a nonlinear mixed-effects model with random effects potentially at each of the hierarchical plot units (moving subplot, plot, and research experiment) and (or) the year. To scrutinize which levels are optimum, we carried out an Akaike information criterion (AIC) (Akaike 1974) analysis for all levels of nesting, showing that including

Fig. 2. Yield curves from Assmann and Franz (1972) and development of the dominant height (H_{100}) for a subset of the research experiments used in this study. DEN, Denklingen; SAC, Sachsenried; VOH, Vohenstrauß; and WBU, Weißenburg.



the research (thinning) plots and the “moving window circle” subplots would not improve the estimation. Therefore, we accounted for the autocorrelation effect by introducing a random effect only at the research experiment level (RE) and the year. The approach is logical given that the data from the research experiments, included in this study, have been collected for over 40 years, so main random effects are assumed to be reflective of the different measuring teams and climate effects. The random effect at the research experiment can additionally account for potential site effects and different population clusters.

The predictor function η for a GAMM has the following form:

$$\eta(X_{1ij}, \dots, X_{qij}, Y_{1ij}, \dots, Y_{qij}) = \beta_0 + \beta_1 X_{1ij} + \dots + \beta_q X_{qij} + f_1(K_{1ij}) + \dots + f_n(K_{nij}) + b_i + b_{ij} + \varepsilon; \quad (2)$$

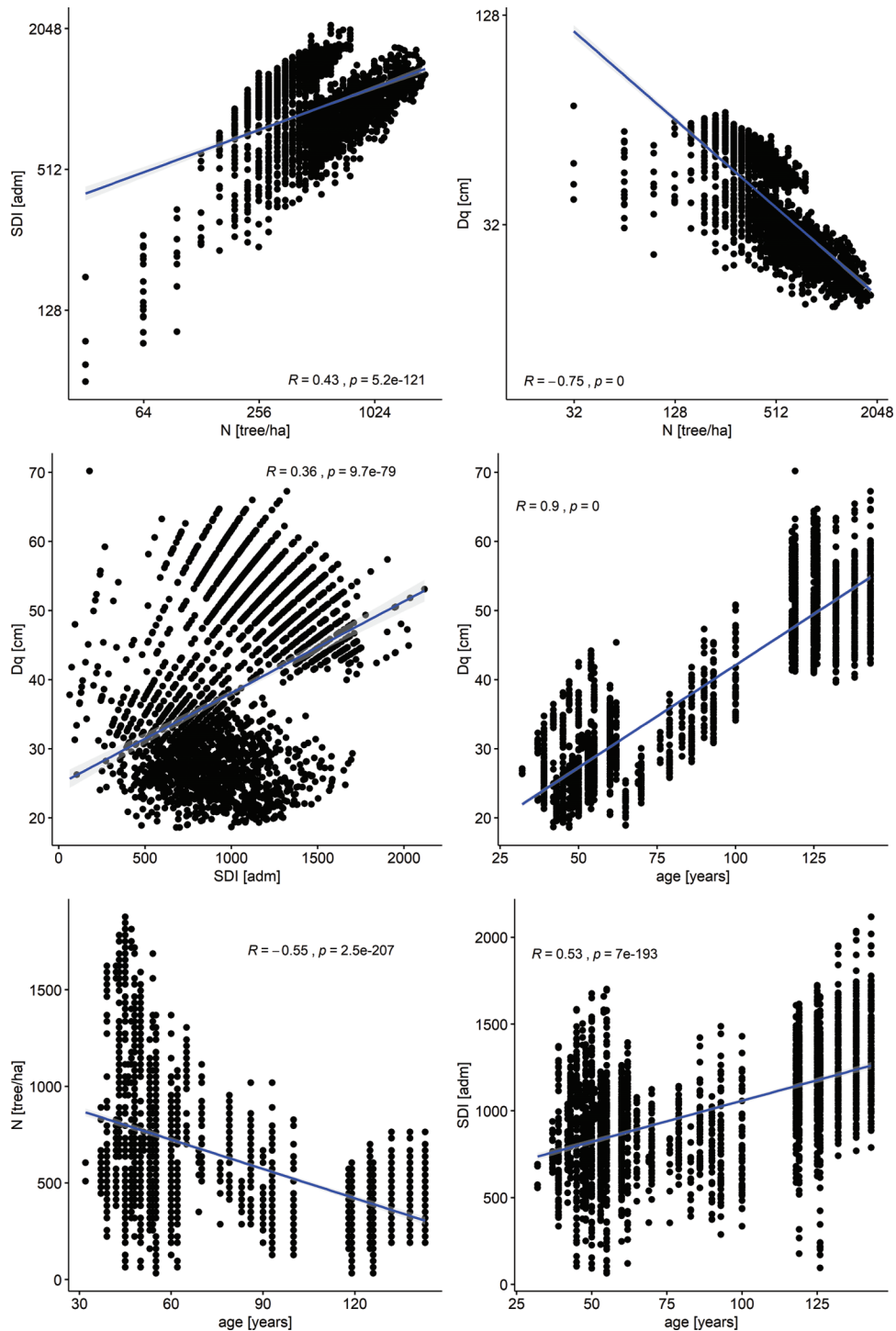
$$b_i, b_{ij}, \text{ and } \varepsilon \in \sim N(0, \sigma_{1-3}^2)$$

where $X_1 \dots X_q$ is a set of q explanatory variables, $K_1 \dots K_n$ is a set of n explanatory variables, $f_1 \dots f_n$ is a set of nonparametric smoother functions, β_q are regression parameters, b is the research

experiment and year specific random effect ($i = \text{year}, j = \text{RE}$), and ε is the error term. The indices i and j denote the i th observation year on the j th research experiment. In this work, the dependent variable will be SI, and the explanatory variables are the structural and climatic variables we have introduced above, and their potential interactions. These are N , age, SDI, D_q , TotPrepVP, MeanTempVP, and the type of soil as a categorical variable. As N , SDI, and D_q are variables explaining local stand density they may be codependent. Thus, we analyzed possible collinearity effects calculating the correlation between each pair. For pairs with a correlation coefficient, $|r|$, of > 0.7 , one of the predictors was excluded from the model (Dormann et al. 2013).

Only significant variables ($p < 0.05$) were included in the final model specification as predictors; nonsignificant variables were excluded during the model runs. Yet, GAMMs are best interpreted by visual examination instead of the statistical significances, as these are less expressive in GAMMs than in other model types (Biber et al. 2013). Variable importance was assessed based on the relative proportion of variance explained by each predictor. To quantify the explained variance for some relevant variables, we

Fig. 3. Correlation plots for the structural predictors tested in the model selection. SDI, local stand density index; N , local stand density; and D_q , local quadratic mean diameter. [Colour online.]



ran AIC tests between models, which were identical, except for including or not the target variable.

Results

Test of collinearity and variable selection

After the collinearity test among the density predictors, we observed potential nonlinear effects between N and SDI and between N and D_q , so we decided to estimate the correlation between the log-

transformed pairs. The correlation coefficients among N , SDI, and D_q and their transformations were lower than $|r| = 0.7$, $p < 0.05$, except for $\ln(N)$ and $\ln(D_q)$ ($|r| = 0.75$, $p = 0.00$). Moreover, as we decided to include the interaction between N and age, we also tested the correlation between the density variables and tree age. In this case, a correlation coefficient of $|r| = 0.90$ ($p = 0.00$) between D_q and age was observed. For this reason, we decided to exclude D_q during model selection. Correlations plots with the correlation coefficients and p values for the mentioned pairs can be seen in Fig. 3.

Table 4. Parameter estimates and significances for the model estimating the site index (SI) as shown in eq. 3.

Variable	Trend	Parameter	Estimate	Std. error	Significance
	—	β_0	31.1140	0.4677	***
SDI	↑	β_1	0.0059	0.0002	***
$f_1(N_{\text{moist}}, \text{age}_{\text{moist}})$	↘		Nonparametric smoother		***
$f_2(N_{\text{dry}}, \text{age}_{\text{dry}})$	↘		Nonparametric smoother		***
$f_3(\text{TotPrepVP}_{\text{moist}})$	→		Nonparametric smoother		**
$f_4(\text{TotPrepVP}_{\text{dry}})$	↗		Nonparametric smoother		**
$f_5(\text{MeanTempVP}_{\text{moist}})$	↘		Nonparametric smoother		**
$f_6(\text{MeanTempVP}_{\text{dry}})$	→		Nonparametric smoother		**

Note: Significance levels: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. The variance of the random effects in eq. 3 are 3.9×10^{-13} for b_{year} and 4.341 for $b_{\text{year,RE}}$. Trend: qualitative illustration of linear predictor variables' significant influences. ↑ and ↓ denote SI increases and decreases, respectively, with increasing values of the respective predictor. ↘, ↗, and → denote, for the nonparametric smoothers, whether the effect on SI has a decreasing, increasing, and null trend, respectively. The predictors used in this model are the stand density index (SDI), local stand density (N), local stand age (age), the total precipitation during the vegetation period (TotPrepVP), and mean temperature during the vegetation period (MeanTempVP).

Preliminary model selection was based on biological plausibility including the structure variables with the climatic variables TotPrepVP and MeanTempVP and differentiating between the effects that may be a consequence of the soil water availability. These were models that included the density indicators, linearly or as smoother terms, and the interactions between pairs. Specifically, we compared the relative importance of SDI and the interaction (N, age). First, the AIC value for a model with a linear SDI predictor (eq. A1) was 8814.354, and when including only the interaction (N, age) (eq. A2) resulted in a value of 8450.864. This showed that the interaction (N, age) could explain a higher proportion of the variance than the SDI could. Moreover, a model with linear SDI and the interaction (N, age) (eq. 3) resulted in an AIC value of 7521.481, so the model combining the two predictors

resulted in the lowest AIC, thus, explaining the highest proportion of the variance. The specific models described above can be found in Appendix A, and below we describe the selected model.

Thus, we decided to select a model with the combination of N with age for each soil type. While N depends on age and is very sensitive to silvicultural treatments, SDI tends to remain constant over time and represents effects connected to the site quality and the competition constellation. In summary, the first selected model (model 1) included (eq. 3) SDI as a linear predictor and the interaction of age and local stand density (N), and the total precipitation (TotPrepVP) and mean temperature (MeanTempVP) of the vegetation period as nonlinear predictors, expressed as smoother factors:

$$(3) \quad \text{SI}_{\text{year,RP}} = \beta_0 + \beta_1 \text{SDI}_{\text{year,RE}} + f_1(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{moist}} + f_2(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{dry}} + f_3(\text{MeanTempVP}_{\text{year,RE}})_{\text{moist}} + f_4(\text{MeanTempVP}_{\text{year,RE}})_{\text{dry}} + f_5(\text{TotPrepVP}_{\text{year,RE}})_{\text{moist}} + f_6(\text{TotPrepVP}_{\text{year,RE}})_{\text{dry}} + b_{\text{year}} + b_{\text{year,RE}} + \varepsilon;$$

$$b_{\text{year}} \sim N(0, \sigma_1^2), \quad b_{\text{year,RE}} \sim N(0, \sigma_2^2), \quad \text{and} \quad \varepsilon \sim N(0, \sigma_3^2)$$

In model 1, all predictors included as smoother terms were grouped by type of soil (dry or moist). The coefficient of determination for this model resulted in an R^2 of 0.31 and the abovementioned AIC was 7521.481. The parameter estimates (eq. 3) are summarized in Table 4. With a closer look into Fig. 4, we can observe with higher detail the nonlinear predictors.

In Fig. 3, we observed that the correlation coefficient between $\ln(\text{SDI})$ and $\ln(N)$ was low ($|r| = 0.43$) but reflected a nonlinear effect due to collinearity, and it showed some clustering effect that can be caused by the site effects. A GAM model can account for these nonlinear effects; however, we decided to test a second model that includes a smoother term with the interaction between SDI and N resulting in model 2 (eq. 4). Model 2 had higher coefficient of determination ($R^2 = 0.46$) and also a lower AIC (6901.675).

$$(4) \quad \text{SI}_{\text{year,RP}} = \beta_0 + f_1(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{moist}} + f_2(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{dry}} + f_3(\text{SDI}_{\text{year,RE}}, N_{\text{year,RE}})_{\text{moist}} + f_4(\text{SDI}_{\text{year,RE}}, N_{\text{year,RE}})_{\text{dry}} + f_5(\text{MeanTempVP}_{\text{year,RE}})_{\text{moist}} + f_6(\text{MeanTempVP}_{\text{year,RE}})_{\text{dry}} + f_7(\text{TotPrepVP}_{\text{year,RE}})_{\text{moist}} + f_8(\text{TotPrepVP}_{\text{year,RE}})_{\text{dry}} + b_{\text{year}} + b_{\text{year,RE}} + \varepsilon;$$

$$b_{\text{year}} \sim N(0, \sigma_1^2), \quad b_{\text{year,RE}} \sim N(0, \sigma_2^2), \quad \text{and} \quad \varepsilon \sim N(0, \sigma_3^2)$$

Is the estimation of the site index biased by a reduction of height growth due to local density? (Q1)

The reduction of height growth was evaluated looking especially at the effect that the interaction between age and N had on the site index. In model 1, we first observed a negative effect in the interaction between age and N, indicating that density decreases the value of SI for a constant age.

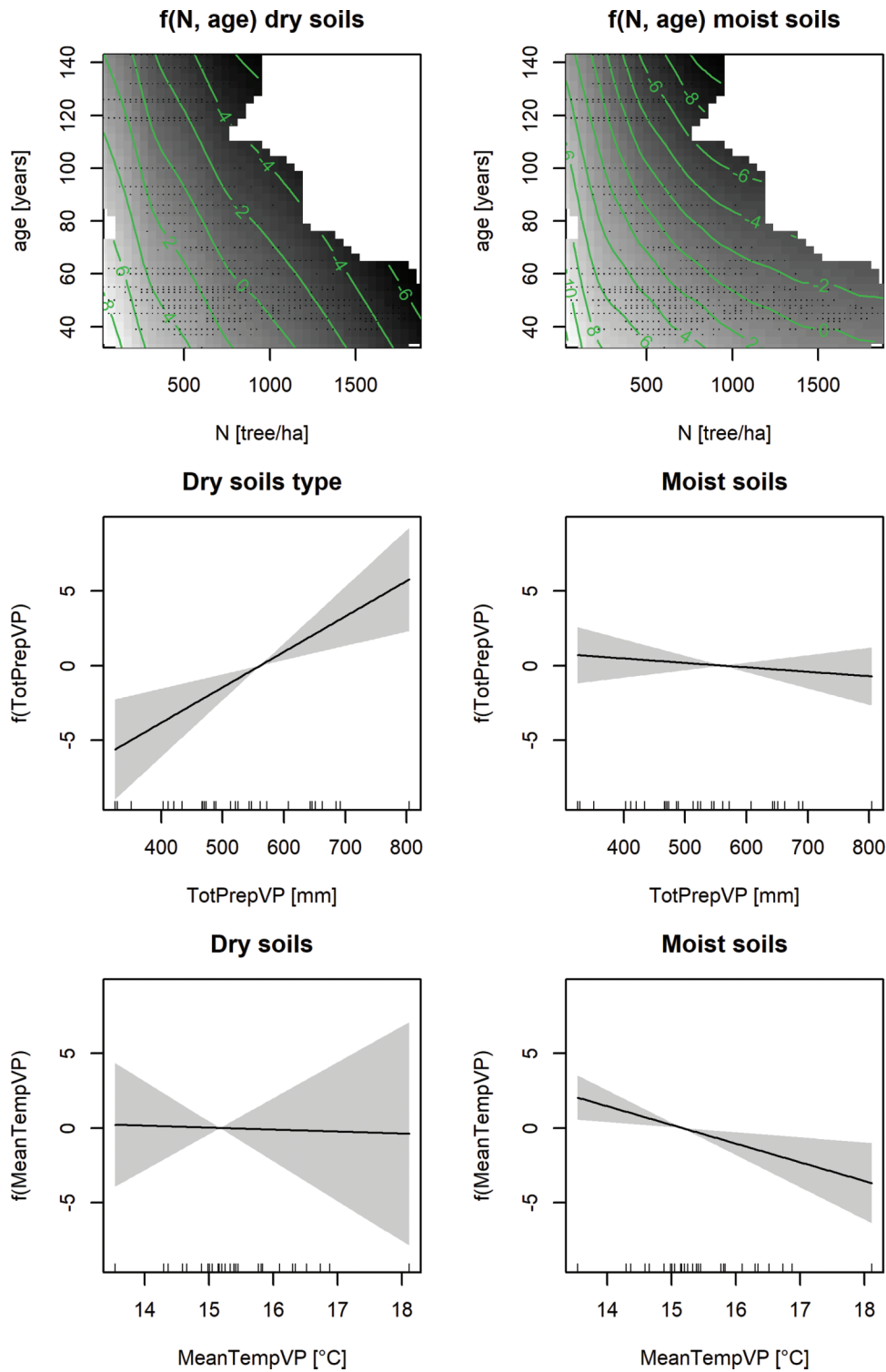
Model 2 showed a higher biological plausibility that is worth discussing. Most importantly, the slope in the interaction between age and N, which also showed a negative effect, decreased (see Fig. 5,

top panel), but only for the moist soil types, showing higher slopes for lower values of N. Moreover, in this model this tendency showed a strong attenuation with increasing N, which was not as visible in model 1.

Does water availability or drought modulate the effect of the local density on the estimation of the site index? (Q2)

Even if the effects of both TotPrepVP and MeanTempVP showed a linear effect, we decided to keep them in the models as smoother terms to assess the differences observed between the soil moisture

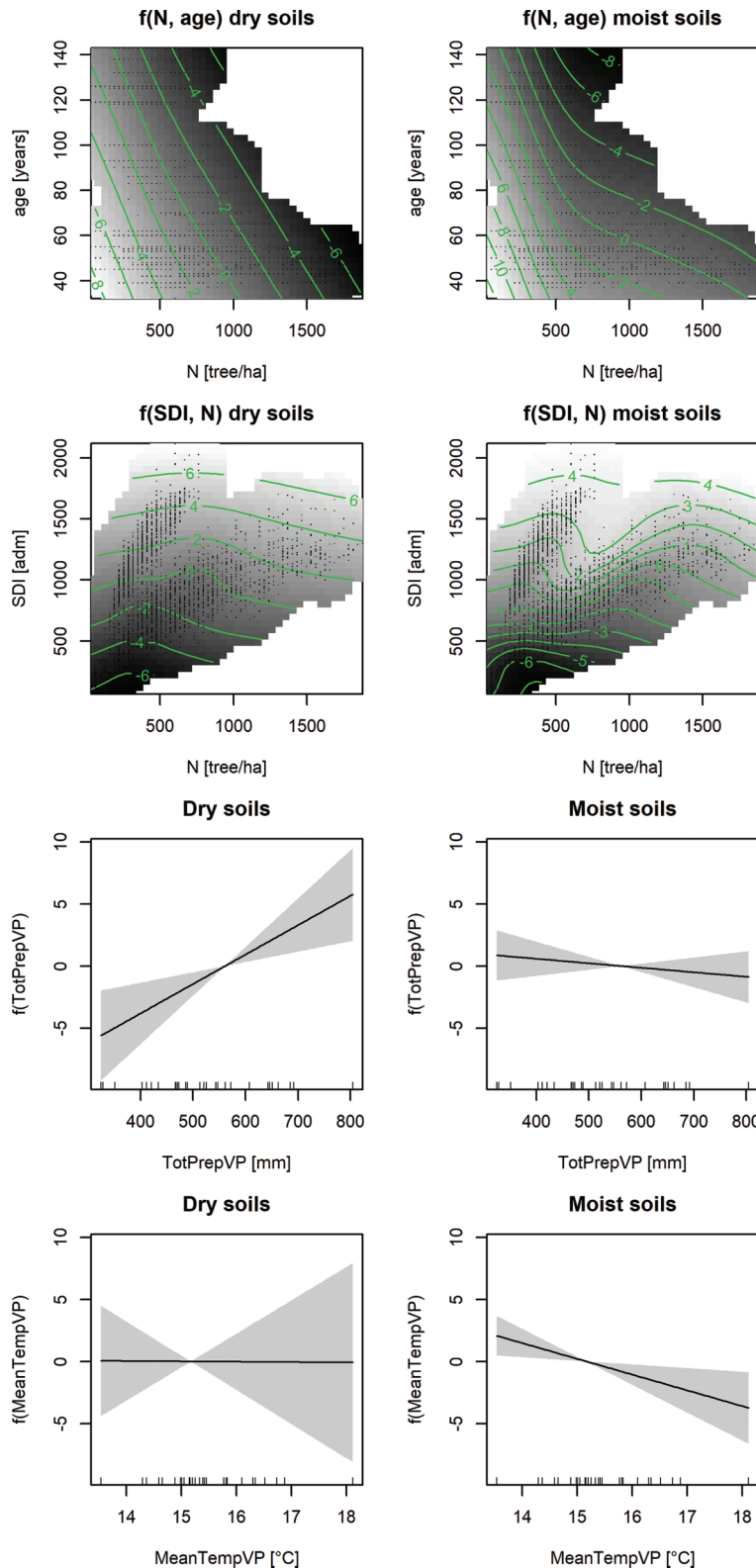
Fig. 4. Nonlinear effects of the interaction between local stand density (N) and local stand age (age) and the interaction between the total precipitation during the vegetation period ($TotPrepVP$) and mean temperature during the vegetation period ($MeanTempVP$) (see eq. 3). In the two-dimensional plots (N -age and N -SDI), white indicates a positive effect on site index, while black indicates a negative effect. The green contour lines show where the function has a constant value. Shaded: 95% confidence area.



types (the distinction by type with the R *mgcv* package is only possible when the predictors are included as smoother terms; Wood 2017). Tested in model 1, if both terms were considered linear and independent from the soil type. $TotPrepVP$ and $MeanTempVP$, with a negative and positive slope, appeared to be nonsignificant

($p = 0.1946$) and highly significant ($p = 0.0101$), respectively. However, when we included both terms depending on the soil moisture type, we then observed that $MeanTempVP$ appeared significant ($p = 0.0053$) but only for the moist soil type, while $TotPrepVP$ was significant ($p = 0.0015$), but only for the dry soil type,

Fig. 5. Nonlinear effects of the interaction between local stand density (N) and local stand age (age), the interaction between the local stand density (N) and the stand density index (SDI), and the interaction between total precipitation during the vegetation period (TopPrepVP) and mean temperature during the vegetation period (MeanTempVP) (see eq. 4). In the two-dimensional plots (N -age and N -SDI), white indicates a positive effect on site index, while black indicates a negative effect. The green contour lines show where the function has a constant value. Shaded: 95% confidence area.



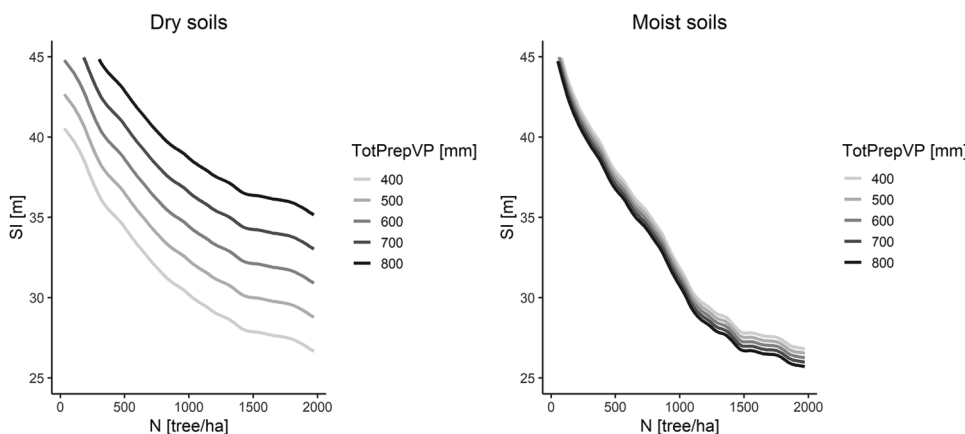
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Table 5. Parameter estimates and significances for the model estimating the site index (SI) as shown in eq. 4.

Variable	Trend	Parameter	Estimate	Std. error	Significance
	—	β_0	37.0575	0.428	***
$f_1(N_{\text{moist}}, \text{age}_{\text{moist}})$	↘	Nonparametric smoother			***
$f_2(N_{\text{dry}}, \text{age}_{\text{dry}})$	↘→	Nonparametric smoother			***
$f_3(\text{SDI}_{\text{dry}}, N_{\text{dry}})$	↗	Nonparametric smoother			***
$f_4(\text{SDI}_{\text{moist}}, N_{\text{moist}})$	↗	Nonparametric smoother			***
$f_5(\text{TotPrepVP}_{\text{moist}})$	→	Nonparametric smoother			***
$f_6(\text{TotPrepVP}_{\text{dry}})$	↗	Nonparametric smoother			**
$f_7(\text{MeanTempVP}_{\text{moist}})$	→	Nonparametric smoother			**
$f_8(\text{MeanTempVP}_{\text{dry}})$	↘	Nonparametric smoother			

Note: Significance levels: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. The variance of the random effects in eq. 4 are 3.5×10^{-7} for b_{year} and 4.275 for $b_{\text{year,RE}}$. Trend: qualitative illustration of linear predictor variables' significant influences. ↑ and ↓ denote SI increases and decreases, respectively, with increasing values of the respective predictor. ↘, ↗, and → denote, for the nonparametric smoothers, whether the effect on SI has a decreasing, increasing, or null trend, respectively. The predictors used in this model are the stand density index (SDI), local stand density (N), local stand age (age), the total precipitation during the vegetation period (TotPrepVP), and mean temperature during the vegetation period (MeanTempVP).

Fig. 6. Prediction results from model 1 (eq. 3). Local site index (SI) is displayed against the local stand density (N) for mean SDI ($\overline{\text{SDI}} = 993$) and age ($\overline{\text{age}} = 81$). On the left side the predicted results are displayed for the soil type “dry” and on the right side for the type “moist” for intervals of total precipitation during the vegetation period (TopPrepVP) of 100 mm.



indicating that only when water is limiting in the soil, lower precipitation reduces SI. For the dry sites, the effect has been negative below 560 mm and positive above this level. Accordingly, the opposite effect was observed for MeanTempVP on the moist sites: above 15 °C, higher temperatures have a negative effect on the SI while the effect is linearly positive below this level. In model 2, the effects of the weather variables (MeanTempVP and TotPrepVP) remained unchanged with similar levels of statistical significance (Table 5).

With the selected models we performed model predictions, using constant values for SDI and age to evaluate how strong the impact of density on the estimation of the site index can be under ceteris paribus conditions (e.g., constant SDI and age for different levels of TotPrepVP). The magnitude of such effect can be observed in the model predictions (Figs. 6, 7) performed for the mean SDI ($\overline{\text{SDI}} = 993$) and age ($\overline{\text{age}} = 81$) and different levels of precipitation from 400 to 800 mm in 100 mm steps. The range of data for this combination is broad (Fig. 3). Thus, we have chosen to display levels of precipitation from very dry to very moist years, to show the potential effects of future extreme climates. For moist soils (plots on the right in Figs. 6, 7), it is important to note that the effect of TotPrepVP was not significant, thus all lines appear very close to each other. Here, the effects of the interaction (N, age) could be clearly observed. On the dry sites, SI decreases rapidly for an increase of N, especially for a low total precipitation. This effect declines with increasing precipitation.

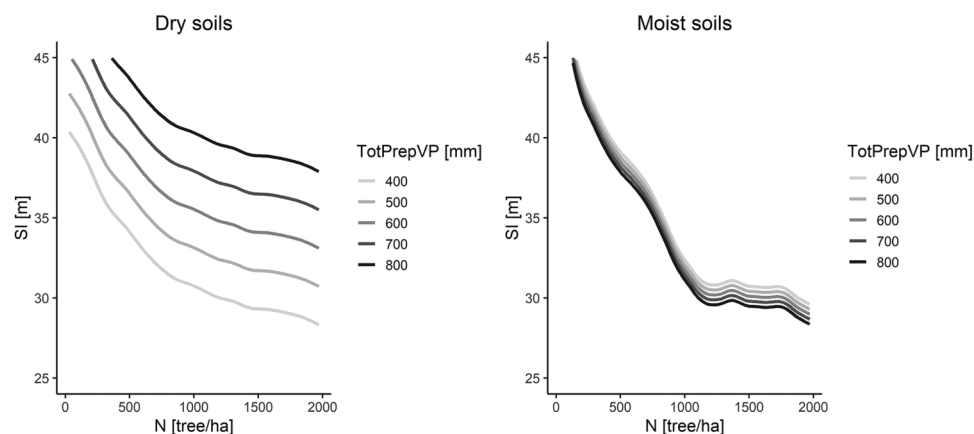
Discussion

Explanation of the findings

Site index and growth can be misjudged when using common SI systems when not acknowledging the potential effect of stand density. In this study, the effect of local stand density in the estimation of SI was found significant for spruce monocultures in Bavaria, southern Germany (Q1). In line with other studies that analyzed the effect of density, in terms of initial planting density, on growth patterns (MacFarlane et al. 2000; Antón-Fernández et al. 2011), wider spacing results in higher top heights, which by inference suggests that higher densities can limit height growth, and as consequence, affect the estimation of the site index. Particularly, in this work, we have observed the different effects that density, depending on water availability and soil quality, can have on SI, using continuous data that covers density effects during the evolution of the stand until mature ages (Q2).

According to Assmann and Davis (2014), sites with the same SI can have different maximum densities. This is explained in the theory of yield levels and can be expressed using SDI (Franz 1967; Bergel 1989). Thus, here, we hypothesized that sites with higher availability of water are able to support a higher number of individuals. For this reason, such effect can be potentially explained by the SDI, included in the models. Moreover, thanks to mixed models, the codependence and thus nonlinear effects between the interaction terms (N, age) and (N, SDI) were accounted for,

Fig. 7. Prediction results from model 2 (eq. 4). Local site index (SI) is displayed against the local stand density (N) for mean SDI ($\overline{\text{SDI}} = 993$) and age ($\overline{\text{age}} = 81$). On the left side the predicted results are displayed for the soil type “dry” and on the right side for the type “moist” for intervals of total precipitation during the vegetation period (TopPrepVP) of 100 mm.



and thus, are able to answer our first research question (Q1). This manifested the different effects that N has on SI (and as a conclusion on height growth), but also showed that N is dependent on the climate and water availability in the soil (Q2).

Specifically, the models we tested provided consistent results that supported the assumptions made prior to this study. First, the interaction between N and age have remained robust independently from the predictors chosen in the model. Particularly interesting was the difference in the effects of this interaction between groups of sites with a lower and higher water availability in the soil between the two models. When looking at model 2 (Fig. 5) we could observe that SI decreases almost linearly when increasing N . Such attenuation effect is much stronger for the moist soils than for the dry ones. In this case, in moist soils after a density $N \sim 1000$, SI is almost not affected for an increase in N for the same age. In model 2, this attenuation is even stronger, indicating a higher biological plausibility (supported by a low AIC) and more clearly distinguishing the hypothesized differences in the SI response to density between moist and dry soils (Q2).

With the model predictions in Figs. 6 and 7, the dominant influence of the interaction between N and age could be clearly observed, as expected from the variance importance assessment. Such predictions manifested the differences between the potential effects of local density depending on the quality of the site, in terms of water availability, and this depending on the precipitation. On sites with poorer water supply, the effect increased up to a maximum reduction in the order of ~ 4 m dominant height for an increase of ~ 300 trees/ha. As abovementioned, we could observe, in both models, how such maximum potential density biases in the estimation of SI would occur at the lower densities, that is, stands with a greater number of large trees. The observed linear and negative relationship between TopPrepVP and SI (in sites with lower water availability) may also indicate that under future trends of reductions in precipitation (especially during the vegetation period) and drought events, reductions of height growth are expected to be stronger. At the same time, under climate change conditions, the reduction of precipitation can be strong enough to limit water availability even on sites where currently the water supply in the soil is not limiting tree growth.

As pointed out by García (1998) and later by Ritchie et al. (2012), the smaller plot size (respect to the plot size used for development of the SI curves) here selected may incur an underestimation of the top height (H_{100}) and therefore the SI. However, this effect would not affect the conclusions we derived here. Especially in the case of few large trees, an overall underestimation of the dominant height would mean that the impact that density

has on the underestimation of SI could even be larger than estimated. On the one hand, and as abovementioned, this bias is expected to be low in homogeneous pure stands, and as such, it is systematic over all plots. On the other hand, the differentiation in height growth we found between sites with high and low soil water availability must therefore stand. Antón-Fernández et al. (2011) also pointed out that the definition of the dominant height and the estimation of SI are sensitive to initial planting density. Here, we decided to use the dominant height (H_{100}) and site index curves by Assmann and Davis (2014) as they are the most common ones applied in Bavaria. Those are especially well suited for spruce monocultures (see Fig. 2), as they have been originally derived from the research experiments used in this study.

Our finding, that dominant trees reduce height growth especially on poor sites, is also substantiated by findings of Carl et al. (2018), Ding et al. (2019), or Pretzsch and Biber (2010). Under water stress, the growth partitioning of the trees in forest stands becomes more size symmetric. The dominant trees get drought stressed, make less use of their privileged access to light, and may reduce growth (Pretzsch et al. 2018).

Ecological implications

These results also manifest the specific physiological characteristics of Norway spruce. Norway spruce is very sensitive to competition effects (Klimo 2000). The shallow rooting system (Puhe 2003) enhances the competition for water and mineral nutrients in the soil, which is particularly relevant in monocultures (Schmid and Kazda 2002). Especially when repeatedly cultivated on the same sites, as it is common in many European forests, the shallow root system can contribute to soil compaction and acidification that may further reduce the access to the storage of water (Wiedemann 1923). This results in a strong height zonation and root concentration in the soil, therefore, reducing the portion of soil for water absorption. Thus, the described effect of stand density on growth on dry sites may be less than for other deeper rooting species such as European beech or Scots pine (Gale and Grigal 1987).

Xeromorphism of needles may be a feature to preserve water in the tree once the stomata have closed. However, spruce has proven to be more drought-susceptible than, for example, beech (Kölling et al. 2007), despite xeromorphic foliage. Under nonlimiting water supply, the lower leaf-level transpiration rate of spruce is counteracted by higher leaf biomass and leaf area index at the stand level relative to most other tree species in Europe (Ellenberg et al. 1986; Lyr et al. 1992). Moreover, Norway spruce is an isohydric species, which reduces stomatal conductance at early stages of soil drought to prevent cavitation and temporary loss of the water conducting

system. Leaf stomata in trees with higher resistance (taller trees) close earlier in the day or earlier in a drought cycle (Ryan and Yoder 1997). Early stomata closure under drought means reduction of carbon uptake and growth. In addition, xeromorph needles contribute to preserve water better in the tree under water stress. Both early stomata closure and xeromorph needles may increase the revealed height growth reduction under water limitation, especially under high competition for water due to high stand density. This means that periods with a reduction in height growth, due to stomata closure, will be longer for higher densities with increasing water stress, and thus stronger competition for it. In summary, we could observe how especially sensitive Norway spruce is to stand density, decreasing height growth when the limiting resources are in the soil, but not so much when water availability is sufficiently high so it still can allocate more resources to compete for the light.

Consequences for forest management

An underestimation of the site index by ~4 m for density changes in the range of 200–300 trees/ha on moist limiting sites may underestimate the prognosis of future productivity (>2 SI-classes) and increase impression in annual cut estimates and, therefore, leading to an inadequate forest management decision-making. Norway spruce is still the main productive tree species in southern Germany, so such consequences may translate to important deviations in the estimation of productivity, which will potentially increase as climate becomes dryer.

The effects observed on higher densities, above ~1000 trees/ha, are particularly affected by the soil conditions and precipitation (especially according to model 2). This range of densities, which corresponds mostly with a lower age range (25–30 years), may indicate the effect of an increasing spacing on height development as shown for loblolly pine (*Pinus taeda* L.) by MacFarlane et al. (2000) and Antón-Fernández et al. (2011). According to this study, this will be relevant to control density in new plantations of spruce under growing dry conditions, especially in poorer sites, while it would not have a big impact on well-supplied sites.

Our results may also explain the sit-and-wait phenomenon already reported for lodgepole pine on dry sites and high density (Cole 1975; Cole and Koch 1995). Due to extreme water competition under such circumstances, height growth nearly stops. A density reduction may finally improve the water supply of the remaining individuals and cancel the standoff condition (Sohn et al. 2013). In our stands, the water stress of Norway spruce was not so extreme to completely stop height growth, but it substantially reduced it. For this reason, the reduction of local density in spruce stands under drought periods could then reduce the stress caused by the lack of water. This, at the same time, would improve height growth, especially on sites where the availability of water in the soil is generally low. Moreover, these results suggest that maintaining stands at medium density level (reducing rotation length and minimize risk of exposure to extreme climatic events) may serve as a potential effective measure to reduce water stress (Trouvé et al. 2017).

In the natural range mountain regions with high precipitation, the previously discussed processes of water stress, height growth reduction, reduced competitiveness due to drought stress, and shallow root system may be irrelevant. However, on moisture-limiting sites and particularly during dry years, those ecological traits and limitations become critical in the lowlands. Moreover, intraspecific neighbourhood can mean niche similarity, niche restriction, limited resource uptake, and reduction of overall competitive ability.

Main conclusions

Especially under dramatic climatic change, well-established forestry rules like the independence of the site index estimation from the local stand density must be questioned and revised. In this work, we carried out a study to tackle this issue, using the

long-term experimental plots from Bavaria, and we chose thinning experiments of Norway spruce monocultures, one of the most economically important but also sensitive tree species. Here, we saw that especially on poor sites with shallow soils, local density must be considered in the estimation of SI. Such effects may result in a misleading SI when it is used as a criterion for reference plot selection, as site effects may be mixed with density effects, especially on such sites.

The special physiological characteristics of Norway spruce makes it especially sensitive to drought conditions when growing in monocultures. For example, unmanaged unthinned plots of thinning experiments may develop lower a site index with progressing stand development, which may suggest site differences between the plots, even though the sites are similar. Moreover, especially on dry sites, instead of using traditional SI models to predict growth, spatial explicit growth models may be more suitable given that they account for the effects of local density, and therefore, biases in the estimation of the dominant height can be corrected as indicated in this study.

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Appendix A

Model 1A (eq. A1) and model 1B (eq. A2) were rejected during the model selection process.

Model 1A:

$$\begin{aligned}
 \text{SI}_{\text{year,RP}} = & \beta_0 + \beta_1 \text{SDI}_{\text{year,RE}} + f_1(\text{MeanTempVP}_{\text{year,RE}})_{\text{moist}} + f_2(\text{MeanTempVP}_{\text{year,RE}})_{\text{dry}} + f_3(\text{TotPrepVP}_{\text{year,RE}})_{\text{moist}} \\
 & + f_4(\text{TotPrepVP}_{\text{year,RE}})_{\text{dry}} + b_{\text{year}} + b_{\text{year,RE}} + \varepsilon; \\
 & b_{\text{year}} \sim N(0, \sigma_1^2), \quad b_{\text{year,RE}} \sim N(0, \sigma_2^2), \quad \text{and} \quad \varepsilon \sim N(0, \sigma_3^2)
 \end{aligned}
 \tag{A1}$$

Model 1B:

$$\begin{aligned}
 \text{SI}_{\text{year,RP}} = & \beta_0 + f_1(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{moist}} + f_2(N_{\text{year,RE}}, \text{age}_{\text{year,RE}})_{\text{dry}} + f_3(\text{MeanTempVP}_{\text{year,RE}})_{\text{moist}} + f_4(\text{MeanTempVP}_{\text{year,RE}})_{\text{dry}} \\
 & + f_5(\text{TotPrepVP}_{\text{year,RE}})_{\text{moist}} + f_6(\text{TotPrepVP}_{\text{year,RE}})_{\text{dry}} + b_{\text{year}} + b_{\text{year,RE}} + \varepsilon; \\
 & b_{\text{year}} \sim N(0, \sigma_1^2), \quad b_{\text{year,RE}} \sim N(0, \sigma_2^2), \quad \text{and} \quad \varepsilon \sim N(0, \sigma_3^2)
 \end{aligned}
 \tag{A2}$$

Appendix B

Table B1. Stand structure characteristics per research experiment and plot.

Research experiment	Plot	Thinning regime	Stand density (tree/ha)			SDI (ND)			Age (years)			D _q (cm)			
			Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	
Denklingen 05	1	Below light	382	568	764	1055	1484	2026	132	138	143	39.6	45.6	53.1	
	2	Below mod.	255	381	509	713	1256	1812	132	138	143	47.1	52.5	58.9	
	3	Below int.	191	291	382	774	1055	1411	132	138	143	47.2	56.0	67.3	
Denklingen 606	1	70% of G	605	1148	1687	859	1122	1369	45	53	62	19.4	25.3	33.5	
	2	50% of G	64	427	1050	91	507	947	45	53	62	21.3	29.3	45.4	
	3	Below light	1655	1789	1942	1563	1643	1699	55	61	62	22.3	23.7	24.8	
	4	Below light	1719	1812	1974	1449	1587	1744	55	59	62	21.4	23.0	24.6	
	5	50% of G	509	903	1305	739	884	1029	50	56	62	20.7	25.3	31.8	
	6	70% of G	446	1148	1878	478	1041	1380	45	53	62	19.3	24.2	30.5	
Eurach 605	1	Below strong	637	647	668	722	756	782	39	39	39	27.0	27.5	28.0	
	2	Below strong	32	217	796	62	355	804	39	49	55	25.2	36.2	42.5	
	3	Below strong	350	528	732	553	718	844	39	49	55	26.1	30.7	37.0	
	4	Below strong	446	608	1050	739	900	1006	39	48	55	24.2	32.8	38.6	
	5	Below mod., 1×2	605	881	1241	694	785	903	45	50	55	20.5	24.0	27.2	
	6	Below mod., 1×2	509	923	1369	644	807	948	45	50	55	19.9	24.2	28.9	
	7	Below light	987	1347	1592	1163	1348	1568	39	48	55	21.3	25.2	28.3	
	8	Below light, 5×1	891	1298	1623	1120	1401	1686	39	47	55	22.5	26.3	30.2	
Sachsenried 602	1	Below light	1783	1869	1974	1671	1707	1796	51	51	51	23.0	23.6	24.1	
	2	Above light	668	1122	1814	941	1111	1316	41	46	51	20.5	26.0	32.0	
	3	Above strong	1114	1441	1878	1150	1297	1470	46	49	51	21.0	23.7	26.3	
	4	Above mod.	987	1343	1878	1008	1162	1320	41	46	51	18.8	23.4	27.6	
Sachsenried 607	1	Selective, 50% of G	286	582	955	417	714	911	48	54	60	24.0	29.1	35.8	
	2	Rows, 50% of G	127	435	796	227	577	877	48	54	60	24.6	30.7	39.2	
	3	Below light	1146	1648	1974	1125	1405	1737	48	57	60	18.7	22.7	25.4	
	4	Selective, 60% of G	318	718	1655	571	831	1304	43	53	60	21.2	28.7	36.3	
	5	Below, 60% of G	350	779	1623	491	847	1256	43	51	60	20.6	28.5	36.3	
	6	Rows, 50% of G	318	579	891	531	737	935	48	54	60	24.8	29.5	36.0	
	7	Rows, 80% of G	477	843	1432	633	959	1283	48	54	60	23.0	27.4	33.3	
	8	Below, 80% of G	477	876	1401	658	1013	1337	48	54	60	23.0	28.0	32.2	
	9	Selective, 80% of G	668	1151	1783	752	1035	1393	43	51	60	19.5	24.1	30.7	
	10	Below light	573	1106	1974	632	950	1286	48	55	60	18.2	23.4	29.1	
	11	Rows, 70% of G	350	734	1273	524	837	1041	43	51	60	22.1	28.0	35.8	
	12	Selective, 80% of G	382	685	1050	612	840	1050	43	52	60	23.0	28.9	35.9	
Sachsenried 67	1	Below light	286	580	1019	369	723	1074	48	54	60	22.6	29.1	34.8	
	2	Below mod.	32	361	605	91	1013	1594	119	122	126	41.2	49.3	70.2	
	3	Below int.	191	372	573	748	1147	1557	119	123	126	41.4	50.9	60.3	
Sachsenried 68	1	Below light	127	263	350	494	986	1350	119	123	126	51.8	57.1	64.7	
	2	Below mod.	509	590	700	1134	1448	1668	125	125	125	41.0	43.8	46.5	
	3	Below int.	255	425	573	726	1189	1547	118	122	125	41.3	47.7	53.1	
Schongau 623	1	5000/ha, 1.41×1.42	159	237	318	560	896	1316	118	122	125	51.6	57.4	64.4	
	2	2500/ha, 3.0×1.33	1878	1878	1878	1373	1373	1373	43	43	43	20.6	20.6	20.6	
	3	5000/ha, 2.5×0.8	1241	1241	1241	1146	1146	1146	43	43	43	23.8	23.8	23.8	
	4	2500/ha, 2.0×2.0	1751	1751	1751	1298	1298	1298	43	43	43	20.8	20.8	20.8	
	5	2500/ha, 4.0×1.0	1241	1241	1241	1306	1306	1306	43	43	43	25.8	25.8	25.8	
	6	5000/ha, 2.0×1.0	1210	1210	1210	1161	1161	1161	43	43	43	24.4	24.4	24.4	
	7	2500/ha, 5.0×0.8	1337	1337	1337	1191	1191	1191	43	43	43	23.3	23.3	23.3	
Vohenstrauß 622	1	—	350	537	700	532	663	811	39	39	39	27.0	28.7	32.4	
	4	—	223	271	318	378	414	474	39	39	39	30.6	32.7	34.7	
	5	—	223	223	223	330	330	330	39	39	39	32.0	32.0	32.0	
	6	—	414	446	509	438	492	567	39	39	39	25.9	26.6	27.1	
	7	—	350	582	764	440	693	872	39	39	39	26.8	27.9	29.2	
	8	—	414	548	668	453	578	654	39	39	39	24.1	25.9	27.3	
	9	—	446	605	700	444	567	645	39	39	39	23.0	24.1	24.9	
	10	—	509	509	509	490	490	490	39	39	39	24.4	24.4	24.4	
	11	—	541	605	668	595	656	717	39	39	39	26.1	26.3	26.5	
	Weißenburg 613	1	Selective light	127	610	1401	280	764	1163	65	82	100	20.3	31.5	47.9
		2	Below light	286	865	1687	487	1016	1468	65	82	100	18.9	29.1	41.8
3		Selective strong	159	506	1210	467	747	1044	65	82	100	21.4	35.6	50.8	

Table B1 (concluded).

Research experiment	Plot	Thinning regime	Stand density (tree/ha)			SDI (ND)			Age (years)			D_q (cm)		
			Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
Zusmarshausen 603	4	Below light	605	1053	1974	891	1074	1431	60	76	90	18.1	26.4	34.3
	5	Above strong	286	873	1942	627	982	1207	55	72	90	17.5	30.9	47.3
	6	Above mod.	191	831	1974	352	862	1264	55	72	90	17.3	28.3	40.9
	7	Below light	573	1151	1846	1073	1262	1412	60	76	90	19.9	27.8	37.0
	1	Below light, 5000/ha	1751	1866	1974	1215	1343	1492	47	51	54	18.5	20.4	21.8
	2	Below light, 10 000/ha	1719	1827	1878	1207	1304	1390	47	51	54	19.0	20.3	21.4
	3	Below light, 2500/ha	1305	1686	1942	1017	1431	1716	42	50	54	18.7	22.5	25.2
Zusmarshausen 604	4	Durchforstung, 10 000/ha	1082	1551	1942	738	1109	1403	37	46	54	16.1	20.4	24.7
	5	Durchforstung, 5000/ha	573	955	1369	699	987	1367	32	43	54	19.5	26.1	33.9
	6	Durchforstung, 2500/ha	255	447	668	554	762	960	32	44	54	26.3	35.5	44.2
	1	Selective, 2×1	1432	1544	1655	1269	1300	1331	47	51	54	21.2	22.5	23.9
	2	Thinning in rows: 1.4×1.4	350	732	1305	377	709	952	37	47	54	20.0	25.1	29.7
	3	Selective, 2×1	573	1215	1942	454	895	1349	47	51	54	18.6	20.8	23.0
	4	Thinning in rows: 2×1	859	1122	1464	970	1028	1082	37	45	54	19.5	24.2	28.7

Note: SDI, stand density index; D_q , quadratic mean diameter; G, basal area; ND, nondimensional. "Below" denotes a thinning from below, "Above" a thinning from above, and "Selective" a selective thinning; the numbers after thinning regimes denote the spacing of the thinning in lines.

Table B2. Number of thinning experiments (plots) and subplots per acquisition year and research experiment.

Research experiment	Year	Thinning experiments	No. of subplots
Denklingen 05	1980	3	63
Denklingen 05	1985	3	63
Denklingen 05	1991	3	63
Denklingen 606	1998	3	23
Denklingen 606	2003	4	25
Denklingen 606	2008	6	25
Denklingen 606	2015	6	25
Eurach 605	1992	6	9
Eurach 605	1997	7	13
Eurach 605	2002	7	13
Eurach 605	2007	7	13
Sachsenried 602	2003	2	9
Sachsenried 602	2008	3	9
Sachsenried 602	2013	4	9
Sachsenried 607	1996	5	15
Sachsenried 607	2001	13	21
Sachsenried 607	2006	13	21
Sachsenried 607	2013	13	21
Sachsenried 67	1978	3	63
Sachsenried 67	1985	3	63
Sachsenried 68	1978	2	49
Sachsenried 68	1985	3	49
Schongau 623	2015	6	1
Vohenstrauß 622	2013	9	15
Weißenburg 613	1982	5	21
Weißenburg 613	1987	7	21
Weißenburg 613	1996	7	21
Weißenburg 613	2002	7	21
Weißenburg 613	2009	7	21
Weißenburg 613	2016	7	21
Zusmarshausen 603	1995	2	12
Zusmarshausen 603	2000	3	15
Zusmarshausen 603	2005	4	15
Zusmarshausen 603	2010	6	15
Zusmarshausen 603	2017	6	15
Zusmarshausen 604	2000	2	3
Zusmarshausen 604	2005	2	7
Zusmarshausen 604	2010	4	9
Zusmarshausen 604	2017	4	9