Eur J Forest Res (2005) 124: 193–205
DOI 10.1007/s10342-005-0068-4

ORIGINAL PAPER

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Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.): evidence from long-term experimental plots

Received: 1 May 2004 / Accepted: 15 February 2005 / Published online: 25 August 2005

Abstract On the basis of nine Norway spruce (*Picea abies* (L.) Karst.) and ten European beech (*Fagus sylvatica* L.) thinning experiments in Germany, for which both residual and removed stock had been registered first during 1870, I scrutinize how moderate and heavy thinning from below (B-, C-grade) affects the production of merchantable volume compared with light thinning (A-grade). In relation to A-grade, cumulative merchantable volume (CV) of B- and C-grade amounts in average to 103–107% in juvenile and to 97–102% in mature Norway spruce stands. The corresponding findings for European beech are 101–106% and 94–102%. CV of individual stands varies between 89% and 130% for Norway spruce and 73% and 155% for European beech (CV of A-grade = 100%). These findings are substantiated by the relation between stand density (SDI) and periodic annual increment (PAI). On the B- and C-grade plots of spruce and beech, respectively, SDI was reduced down to 41–91% and 31–83% of the A-grade. When SDI is reduced in young stands, PAI follows a unimodal curve. Norway spruce's PAI culminates in 109% if SDI is reduced to 59%; European beech's PAI culminates in 123% when density is reduced to 50%. Whereas Norway spruce's growth reacts most positively on thinning under poor site conditions and with increment reduction on favourable sites, European beech behaves oppositely. With stand development the culmination point of the unimodal relation moves towards maximum density, so that in older stands PAI follows the increasing pattern, which is the left portion of a unimodal curve. A model is presented which apparently unifies contradictory patterns of stand density–growth reactions by integrating relative stand density, average tree size and site fertility effects, and makes the findings operable for forest management.

Keywords Thinning · Stand density · Merchantable volume growth · Density–growth relationship · Permanent plots

Communicated by Peter Biber

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Introduction

The question whether stand volume production can be raised by silvicultural thinning or is at maximum under self-thinning conditions challenges forest science since its beginning. By the end of the seventeenth century much of the forests of central Europe were over-exploited. The "Age of Enlightenment" with its glorification of nature, together with the forest ownership reform in the wake of revolutions led to a new appreciation of forests, their reconstruction and protection. For economic as well as ecological reasons, the previously exploited forests were replaced by densely stocked stands, under the assumption that they would guarantee maximum growth. In accordance with Rousseau's philosophy that "nature" is synonymous with "rationality" (Rousseau 1762) and his credo that things develop best when left to the hands of the creator, whereas everything inevitably degenerates in the hands of man, it was only consequent to assume that the highest yield would be achieved in undisturbed stands. So the prevailing opinion was that untreated stands would produce maximum volume, while any reduction in density would cause growth losses (Fig. 1, curve 1).

Hartig (1795, p. 17) and Cotta (1828, p. 103) were persuaded that a periodical removal of surpressed trees increases volume production and strongly contradicted the above views. Reventlow (1879, pp. 79–81) considered the thinning propagated by the founding fathers of forest science Hartig and Cotta as too light; however, the pioneer of heavy thinning was convinced of the validity of an optimum relationship (Fig. 1, curve 2) between density and growth.

Will untreated stands produce maximum growth while thinning causes a reduction? The resulting density-growth curve 1 (Fig. 1) is quoted as increasing pattern or asymptotic curve in the following. Or may maximum growth be expected at sub-maximal densities, as postulated by Hartig and Cotta, while natural density may lead to growth reduction? In the following I call density–growth curve 2 (cf. Fig. 1) unimodal or optimum curve.

Long-term thinning experiments, established in Central European countries from 1870 onwards by the Forest Research Stations promised clarification (von Ganghofer 1881). However, the otherwise progressive evaluations by Schwappach (1908, 1911), Wiedemann (1932) and Schober (1972) considering pure Norway spruce and European beech stands from the thinning experiments by the Prussian Forest Research Station, which produced contradictory findings of the density–growth relationship. For instance, in European beech stands, increment was raised by up to 40% as a consequence of heavy thinning in comparison to light or moderate thinning. This result was reflected in Schwappach's two differing yield tables for European beech (Schwappach 1911, Table A and B). Table A of Schwappach (1911), which was developed for stands with loose canopy closure reports a considerably superior growth compared with Table B for normal canopy closure. In his evaluation of the same experimental plots and after another two decades of observation, Wiedemann (1932, p. 87) came to the conclusion that "... the assumed great superiority of heavier degrees of thinning was not confirmed in the course of the long-term experiment". Schwappach agreed with Wiedemann's statement that growth superiority through heavy as against moderate or

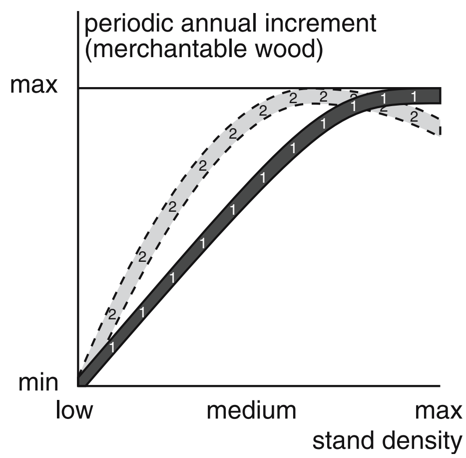

Fig. 1 Hypotheses on the relationship between stand density and production of merchantable wood in schematic representation: asymptotic increasing pattern (*curve 1*) versus unimodal optimum pattern (*curve 2*)

light thinning had been overestimated on account of temporary growth acceleration: in the long run it amounts to a mere 2–15%. A third evaluation of the same data by Schober (1972), 60 years after Schwappach's first evaluation, was not very conclusive as regards to the question whether thinning will lead to an expected increase in growth. Due to the alterations in treatment concept or irregular thinnings on the reference plots, only 6 out of the 37 test series permit the comparison between light and moderate thinning.

In contrast, varied thinning experiments including lightly thinned plots were consistently maintained in South Germany. On the basis of this experimental data, Assmann (1953, 1956, 1970) showed both, an optimum as well as an increasing pattern of density–growth relationship, depending on stand age and site fertility. He defined critical and optimal degrees of stocking (Assmann 1970, pp. 229–233) on the basis of thinning experiments in which light, moderate and heavy thinning was consistently applied in accordance with the recommendations of the Association of German Forest Research Stations (Verein Deutscher Forstlicher Versuchsanstalten 1902). Assmann's results (1953, 1956, 1970) underpinned by similar findings by Bryndum (1978, 1980, 1987), Dittmar (1959, 1961), Hamilton (1976), Kennel (1972), Kramer (1978, 1988), Langsaeter (1941), Mar:Møller (1945), and Schober (1972, 1979, 1980) formed European forester's prevailing understanding of growth reaction on thinning: In principle, moderate thinning can increase or reduce a stands cumulative merchantable volume (CV) and periodical annual increment (PAI) of merchantable volume; however, occurrence and extent of growth acceleration or reduction caused by thinning depends on stand properties, in particular on stand age and site fertility. In others words, both reaction patterns in Fig. 1 can occur.

While considering the results of new experiments, Curtis et al. (1997) question the occurrence of an optimum relation between density and growth again. In view of this return to an opinion prevailing before Hartig und Cotta, Zeide (2001, p. 21) fears an endless loop in the attempts at understanding the density–growth relationship.

With this article I want to promote the transition from a qualitative to a quantitative approach to density–growth relations and integrate apparently contradictory patterns of density–growth reactions in a generalizable model. For this purpose I

1. analysed density–growth relationship of long-term thinning experiments for Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.),
2. scrutinized how physiological age and site fertility influence the pattern of the density–growth relationship, and
3. developed a simple model for periodical annual increment of merchantable volume that includes increasing pattern as part of underlying unimodal curve (Fig. 1, curve 1 and 2, respectively).

Materials and methods

In the lowlands or sub-alpine parts of Southern and Central Germany, 19 long-term thinning experiments (Fig. 2, Table 1) were selected from pure stands of Norway spruce and European beech, these being the tree species in Germany that occupy 54% of the forested area. The oldest of these experiments have been under observation since the mid-nineteenth century when growth and yield research was first introduced. Characteristic of most experiments from the pre-statistics era in the nineteenth century is a design without replication. However, this shortcoming is mitigated to some extend by the considerable size of the plots (0.25–0.5 ha). The majority of the experiments are being surveyed by the Chair of Forest Yield Science of the Munich Technical University; the Norway spruce experiment Paderborn 697/Westphalia and the European beech experiments Haiger 333 and Saar Forst Süd 1606/Saarland belong to the former Prussian Network of Forest Experiments, today being monitored by the Lower Saxony Forest Research Station in Göttingen.

Establishment of the experiments

With the exception of the North-Rhine-Westphalian experiment Paderborn 697, the Norway spruce plots are all located in the pre-alpine area of South Bavaria, the South Bavarian lowlands and Swabia (cf. Fig. 2, Table 1). They are concentrated on the South German pleistocene in the natural habitat of Norway spruce. The excellent site fertility is reflected by site classes of I and II based on yield tables by Wiedemann (1936/42) (moderate thinning). The stands were artificially established, the trial areas Sachsenried 03 and Sachsenried 07 by seeding, and all others by planting. Plot sizes range from 0.25 ha to 0.5 ha. Tree spacing in the individual trials was uniform, but sizes amongst the trial areas varied from 0.9 m×0.9 m, 1.2 m×1.2 m to 1.4 m×1.4 m. The experiments Denklingen 05, Eglharting 72 and Eglharting 73 are re-afforestations after clear-cutting while all other areas were originally first afforestations of arable land and pastures. The included European beech experiments represent sites with average to very good fertility on red marl and red sandstone soils in Central Germany.

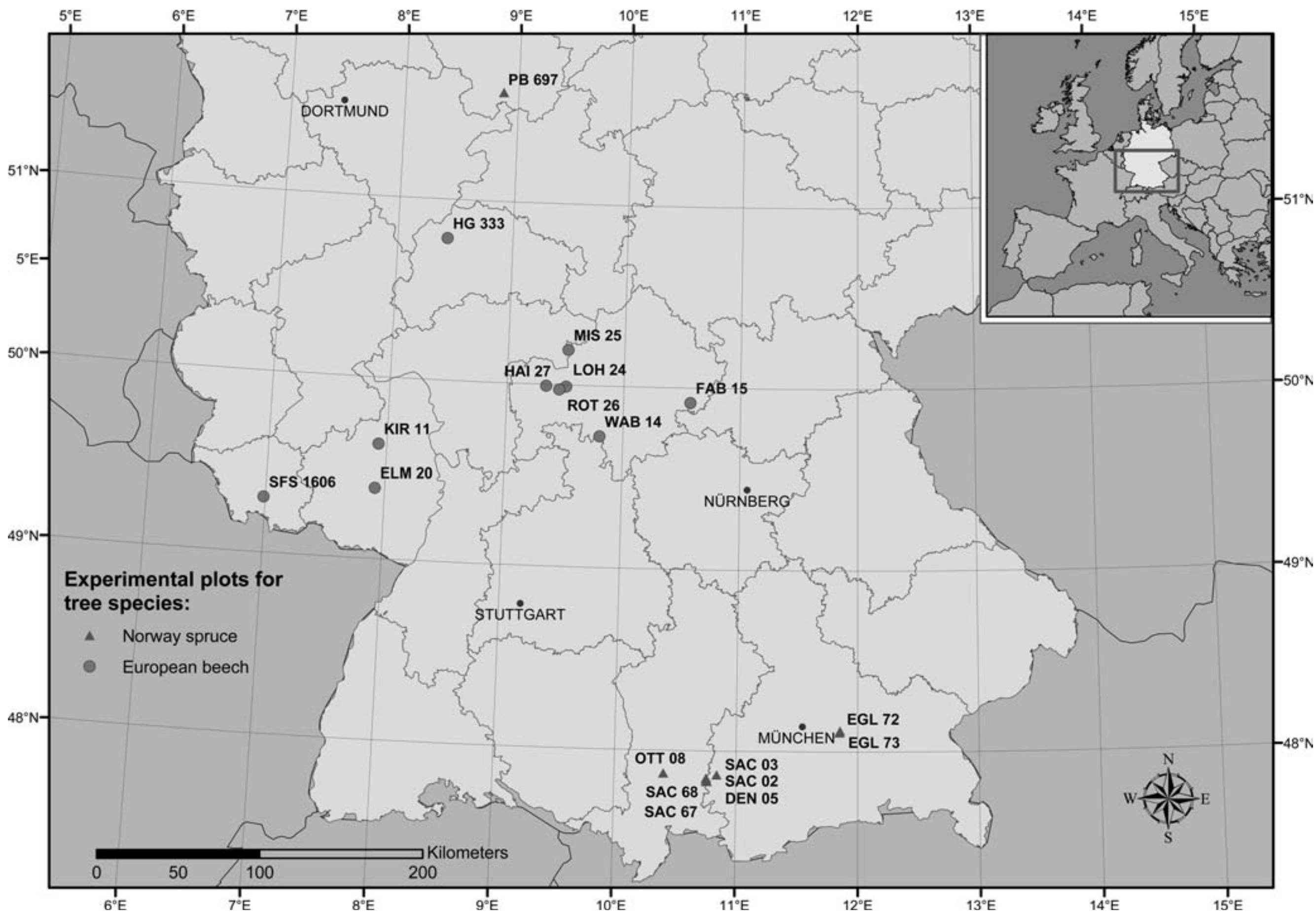

Fig. 2 Map with the distribution of the 19 thinning experiments in Central and Southern Germany. The 19 long-term thinning experiments included in the present study are mainly located in Central and Southern Germany. Experiments for the species European beech and Norway spruce are marked by *different symbols*. Abbreviations nearby the symbols refer to location and number of the experiments and indicate the plot number within the experiment

Table 1 Degree of longitude and latitude, elevation and meteorological data (vegetation period = degree-days above 10°C), listed separately for all 19 experimental plots, included in the presented study

Species	Experiments (loc, nr)	Longitude (degree)	Latitude (degree)	Elevation (m)	Temperature		Precipitatioqn	
					Mean (°C)	Veget. per. (°C)	Annual sum (mm a^{-1})	Veget. per. (mm a^{-1})
Norway	SAC 02	E 10° 45′ 16″	N 47° 51′ 01″	820	6.2	13.3	1200	700
spruce/	SAC 03	E 10° 45′ 21″	N 47° 51′ 11″	820	6.2	13.3	1,200	700
Picea abies	DEN 05	E 10° 50′ 32″	N 47° 52′ 16″	780	6.8	13.9	1,110	650
(L.)	OTT 08	E 10° 24′ 14″	N 47° 52′ 38″	820	7.0	14.2	1,100	600
Karst.	SAC 67	E 10° 45′ 49″	N 47° 50′ 03″	840	6.2	13.3	1,200	700
	SAC 68	E 10° 45′ 18″	N 47° 50′ 03″	840	6.2	13.3	1,200	700
	EGL 72	E 11° 51′13″	N 48° 07′08″	533	7.6	14.9	1,010	580
	EGL 73	E 11° 50′ 59″	N 48° 06′ 32″	533	7.6	14.9	1,010	580
	PB 697	E 08° 52′ 08″	N 51° 36′ 06″	340	8.0	14.0	830	380
European	KIR 11	E 07° 55′ 51″	N 49° 37′ 56″	610	7.0	14.0	660	320
beech/	WAB 14	E 09° 48′ 10″	N 49° 43′ 20″	360	8.5	16.5	710	350
Fagus	FAB 15	E 10° 34′ 16″	N 49° 55′ 07″	470	7.5	14.5	820	420
sylvatica L.	ELM 20	E 07° 55′ 07″	N 49° 23′ 27″	400	8.0	15.0	780	330
	LOH 24	E 09° 30′ 22″	N 49° 59′ 28″	430	7.5	15.5	960	410
	MIS 25	E 09° 30′ 55″	N 50° 11′ 42″	505	7.0	15.0	1,020	450
	ROT 26	E 09° 26′ 49″	N 49° 58′ 27″	475	7.0	15.0	1,050	460
	HAI 27	E 09° 20′ 05″	N 49° 59′ 33″	420	7.0	15.5	1,080	480
	HG 333	E 08° 25′ 58″	N 50° 47′ 05″	560	6.5	13.0	900	405
	SFS 1606	E 06° 59′ 15″	N 49° 48′ 22″	310	8.8	15.1	925	390

Abbreviations preceding the experiments' number refer to nearby place names: *SAC* Sachsenried, *DEN* Denklingen, *OTT* Ottobeuren, *EGL* Eglharting, *PB* Paderborn, *KIR* Kirchheimbolanden, *WAB* Waldbrunn, *FAB* Fabrikschleichach, *ELM* Elmstein, *LOH* Lohr, *MIS* Mittelsinn, *ROT* Rothenbuch, *HAI* Hain, *HG* Haiger, *SFS* Saar Forst Süd

Height growth reflects site classes from I to III according to Schober (1972) (moderate thinning). The stands are the result of natural regeneration following cutting according to Hartig's (1791) compartment shelterwood system, resulting in consistently even-aged stands despite natural regeneration. Plot sizes vary between 0.25 ha and 0.4 ha.

Applied thinning methods

Thinning of the experiments followed the concept defined by Verein Deutscher Forstlicher Versuchsanstalten (1902, p. 180–184), after which A-, B- and C-grade are carried out by elimination of defined tree classes. These classes combine social status and stem quality of a tree (cf. §2, p. 180–181) and differ from the tree classes by Kraft (1884), which are exclusively based on a tree's height and crown size. Thinning grades were assigned randomly at the beginning and subsequently applied consistently to the installed plots. Light thinning (A-grade) is restricted to the removal of dead, dying and unsound trees and serves as a reference. Moderate thinning (B-grade) removes trees of class 5 (dying and dead individuals), class 4 (suppressed but still vital trees) and parts of class 2 (dominant trees with abnormal crown development or bad stem shape). Heavy thinning (C-grade) gradually removes all trees from classes 2 to 5 (2 = stems with abnormal crown development or bad stem shape, 3 = retarded trees with unsheltered crowns, 4 = suppressed but still vital trees, 5 = dying or dead trees). In order to establish a regular spatial distribution of class 1 trees (dominant trees with normal crown development and good stem shape), this type of thinning also removes individual trees from class 1 when competing with neighbours of the same class. Thus, after heavy thinning, the final stand contains only trees from class 1 in the most regular distribution possible, with room on all sides for their crowns to develop freely, but without permanent disruption of crown closure (Verein Deutscher Forstlicher Versuchsanstalten 1902).

I quantified these historically qualitative thinning rules with respect to kind, severity and intensity of the applied thinning (Assmann 1970, p. 213–217). I calculated quotient q_D (= quadratic mean diameter of removed trees/remaining trees) to quantify the kind of thinning. In this and all subsequent calculations, quadratic mean diameter $D = \sqrt{\sum_{i=1}^{n} d_i^2 / n}$ is used as average stand diameter. The more the thinning interferes in the middle and upper storey, the higher the q_D is. For Norway spruce on A-, B-, and C-grade plots, respectively, q_D is 0.63, 0.70 and 0.74 in average and 1.04 at maximum. The corresponding q_D mean values for European beech are 0.59, 0.71 and 0.76 and the maximum is 0.94. Some q_D values transgressing 1.0 indicate that the thinning on the plots is not entirely from below. Following §4 of Verein Deutscher Forstlicher Versuchsanstalten (1902, p. 181), B- and C-grade remove also stems from classes 1 and 2. Thus, the plots represent a kind of thinning that works on principle from below, but reaches in the upper stand layer. A suitable measure for the severity of thinning is the standardized stand density index SSDI at the beginning of the relevant observation period. The A-grades mean diameter D and tree number N are used to estimate SDI_A, whereupon the SDI of the thinned plots (SDI_B, SDI_C) is set in relation to SDI_A (e.g. $SSDI = SDI_C/SDI_A$). For Norway spruce mean SSDI (min–max) is 0.88 (0.66–1.00) for B-grade and 0.71 (0.41–0.91) for C-grade. The corresponding SSDI values for European beech are 0.77 (0.58–0.94) and 0.60 (0.31–0.83). Stand density index $SDI = N(25/D)^r$ (Reineke 1933) was calculated with the r-values of the respective A-grade instead of using Reineke's generalized exponent $r = -1.605$. The experiment-specific r-values were estimated on the basis of the A-grade's mean diameter-stem number trajectories by OLS regression and were in average (min–max) $r = -1.660$ (-1.593 to -1.757) and $r = -1.757$ (-2.027 to -1.581) for Norway spruce and European beech, respectively. These and all subsequent calculations were done using SPSS (Version 11.5). The intensity of thinning can be quantified by the beginning and average frequency of thinnings. Thinning began in Norway spruce and European beech stands, at age 32–43 and 38–66, respectively. The average frequency is 6.0 and 6.7 years.

Basic evaluation methods

On an average, 15 (min. 12, max. 18) successive inventories per plot were available for Norway spruce and 13 (min. 10, max. 16) for European beech. These successive inventories, where the removed and residual trees of the plots were measured, impart time series of volumes removed during thinning, the response of the remaining stand and, consequently, the CV production of the plots. Thus mortality is included in the merchantable volume production; tree volume at the time of death was approximated by the volume of the tree when it was last measured alive. For the basic evaluation, the course from diameter and height measurements to PAI and CV, I followed the norm DESER, which was established by the German Union of Forest Research Organizations in order to standardize the evaluation of long-term growth and yield experiments (cf. Johann 1993; Pretzsch 2002, p. 139–197). The following results are discussed in detail:

1. Cumulative merchantable volume (CV) = merchantable volume of remaining stand at a given age + merchantable volume of all thinnings and self-thinnings in the past.
2. Periodic annual increment (PAI) = periodic annual increment of merchantable volume over a defined period. Especially, short survey periods (<5 years) are susceptible to sampling errors, due to low increment in proportion to the mensuration error. They produced outliers concerning PAI and RPAI in several cases and were excluded from the evaluation.
3. Removed volume (RV) = removed merchantable volume of all thinnings and self-thinnings since establishment of the stand.

Ratios RCV, RPAI, and RRV stand for CV, periodic annual volume increment and removed merchantable volume of the B- and C-grade in relation to the corresponding A-grades. All volumes refer to $m^3\ ha^{-1}$ merchantable wood (i.e., over 7 cm minimum diameter at the smaller end).

Growth and yield characteristics

Due to their uniquely long time-series, the thinning experiments were used for the development of silvicultural treatment rules and yield tables and subject of numerous publications on growth and yield for Norway spruce (e.g., Assmann 1953, 1970; Kramer 1988; Pretzsch and Utschig 2000; Röhle 1994; Schmidt-Vogt 1986; Schober 1979, 1980) and European beech (Foerster 1993; Franz et al. 1993; Kennel 1972; Pretzsch 2002; Schober 1972). So this report is confined to the experiments' essential growth and yield characteristics at age 100 (Table 2). The mean heights at age 100 show Norway spruce to grow on sites with good to excellent fertility (30.1 m to 36.6 m) and European beech on sites with average to very good fertility (23.1 m–31.8 m). Up to age 100 the repeated inventories of residual and removed trees result in CVs of 1,170–1,967 $m^3\ ha^{-1}$ and 400–806 $m^3\ ha^{-1}$ for Norway spruce and European beech, respectively. If we compare the RV with the CV, the relative removed volume (RRV) in Norway spruce stands amounts to 31.6, 35.5 and 41.8% for grades A, B and C respectively, and in European beech stands it amounts to 20.0, 32.6 and 46.6%. These mean values result from the last three columns in Table 2. CV, standing merchantable volume (SV) and RRV are presented for the respective survey, closest to age 100, in order to make the experiments' performance comparable. The exact reference ages range from 97 years to 108 years. This slight variation in age is explained by the fact that not all of the plots were inventoried at age 100, since the experiments were started at different stand ages and inventory rotation varied from experiment to experiment.

Results

In the course of the observation period the experiments develop mean diameters ranging from 8.6 cm to 60.7 cm for Norway spruce and 5.7–58.6 cm for European beech. These and the subsequent pairs of numbers represent the overall minimum value on the A-, B- and C-grade plots at the onset of their survey, respectively, the overall maximum value at the last measurement. Stem numbers range from 232 to 7,428 trees ha^{-1} for Norway spruce and from 88 to 11,242 trees ha^{-1} for European beech. Basal areas and standing merchantable volume vary from 23.9 to 89.5 $m^2\ ha^{-1}$ and 118 to 1,637 $m^3\ ha^{-1}$ for Norway spruce and from 13.0 to 48.3 $m^2\ ha^{-1}$ and 47.6 to 795 $m^3\ ha^{-1}$ for European

Table 2 Growth and yield characteristics for nine Norway spruce and ten European beech thinning experiments at age around 100 years. (Abbreviations preceding the experiments' number cf. Table 1)

Experiment	Thinning grades	Period of survey a = autumn s = spring	Age span	Height age 100 (m)	CV age 100 (m^3 ha^{-1})			SV age 100 (m^3 ha^{-1})			RRV age 100 (%)		
					A	B	C	A	B	C	A	B	C
Norway spruce													
SAC 02	A,B,C	1883a–1973a	32–122	35.4	1,841	1,948	1,819	1,234	1,230	1,108	33.0	36.9	39.1
SAC 03	A,B,C	1883a–1965s	33–116	35.3	1,692	1,711	1,570	1,227	1,163	986	27.5	32.0	37.2
DEN 05	A,B,C	1883a–1991a	35–143	34.4	1,572	1,667	1,560	1,095	1,111	946	30.3	33.4	39.4
OTT 08	A,B,C	1882s–1964a	32–113	36.6	1,967	1,956	1,966	1,264	1,195	1,077	35.7	38.9	45.2
SAC 67	A,B,C	1902s–1990s	43–131	36.4	1,803	1,925	1,861	1,210	1,218	1,002	32.9	36.7	46.2
SAC 68	A,B,C	1902s–1990s	42–130	36.3	1,818	1,808	1,799	1,243	1,162	964	31.6	35.7	46.4
EGL 72	A,B,C	1907a–1990s	36–120	30.5	1,229	1,369	1,170	841	1,004	816	31.6	26.7	30.3
EGL 73	A,B,C	1906s–1970s	42–106	30.1	1,225	1,319	1,181	818	748	569	33.2	43.3	51.8
PB 697 +	A, C	1928s–2000a	42–113	32.8	1,356		1,282	970		762	28.5		40.6
European beech													
KIR 11	A,B,C	1871s–1936s	49–114	29.0	676	786	806	541	563	422	20.0	28.4	47.6
WAB 14	A,B,C	1871a–1968a	48–145	26.8	502	566	597	459	436	355	8.6	23.0	40.5
FAB 15	A,B,C	1871a–2001s	48–179	28.7	586	664	641	509	474	315	13.1	28.6	50.9
ELM 20	A,B,C	1871s–1967s	49–145	29.7	568	500	467	475	329	243	16.4	34.2	48.0
LOH 24	A,B,C	1871s–1967s	66–162	25.7	480	525	560	414	340	251	13.8	35.2	55.2
MIS 25	A,B,C	1871a–1982a	42–153	23.1	464	400	409	322	266	238	30.6	33.5	41.8
ROT 26	A,B,C	1871s–1967s	48–144	29.3	629	646	555	520	450	335	17.3	30.3	39.6
HAI 27	A,B,C	1870s–2001s	38–169	31.8	643	705	621	506	482	374	21.3	31.6	39.8
HG 333	A,B,C	1952a–1999s	56–104	27.0	713	648	595	577	394	241	19.1	39.2	59.5
SFS 1606	A,B,C	1891s–2002s	48–159	27.8	749	689	618	455	398	349	39.3	42.2	43.5

Thinning grades A, B, C: light, moderate and heavy thinning from below
Period of survey and age span: Observation time in calendar years and stand age in years; a and s behind the period of survey denote inventories in spring and autumn, respectively
Mean height age 100: average height of the stem with mean diameter at age 100
CV, SV, RRV: Cumulative merchantable volume, standing merchantable volume and relative removed volume (all volumes refer to merchantable wood > 7 cm minimum diameter at the smaller end)
Exact reference ages for listed CV, SV and RRV are for Sachsenried 02 to Paderborn 697: 101, 102, 104, 98, 98, 97, 100, 99, 98 years; for Kirchheimbolanden 11 to Saar Forst Süd 1606: 103, 102, 102, 103, 100, 101, 101, 97, 99, 108
+ In the experimental area Paderborn 697, a B-grade plot is lacking

beech. In order to characterize maximum stand density SDI_{max} on the experimental plots, the SDI values were determined for all surveys of any experiment. Hence SDI_{max} is max(SDI_i = 1... n). The range and mean of SDI_{max} found out on the lightly thinned plots is 1,246–1,549 trees ha^{-1} (1,395) for Norway spruce and 796–1,013 trees ha^{-1} (885) for European beech. PAI amounts in average (min–max) to 19.3 m^3 ha^{-1} $year^{-1}$ (6.7–28.8) and 9.3 m^3 ha^{-1} $year^{-1}$ (4.2–18.0). At the latest inventory, when Norway spruce and European beech are up to 143 and 179 years old, RRV of the A-grades amounts to 31.4% and 31.8%, respectively. This means that out of the CV of stemwood production, over 30% are eliminated through light thinning and about 70% remain standing. The B-grades' average percentages of relative removed merchantable volume (RRV) are 38.1% for Norway spruce and 38.7% for European beech; for C-grades they amount to 44.0% and 48.2%, respectively.

Mean diameter-stem number trajectories and CV development

Figure 3 displays the development of stem numbers per hectare over mean diameter D for A-, B- and C-grade plots. The A-grade plots (black lines) approximate the upper boundary relation. The plotted straight lines with the slope −1.605 delineate the reduction in stem numbers according to the stand density rule by Reineke under conditions of self-thinning in untreated stands (Reineke 1933). As a consequence of the applied thinning the stem number-diameter trajectories for the B-grade (broken lines) and the C-grade (dotted lines) remain permanently at a low level.

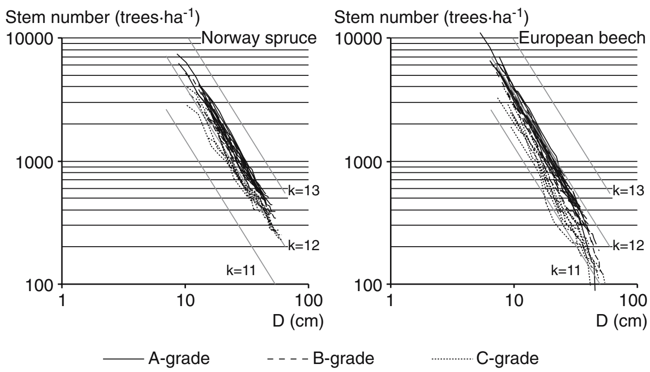

Fig. 3 Relationship between stem number and quadratic mean diameter D for Norway spruce and European beech experimental plots under study. The *plotted straight lines* represent $\ln(N) = k + r \ln(D)$ with Reineke's (1933) slope $r = -1.605$ and intercepts $k = 11$–13 as reference

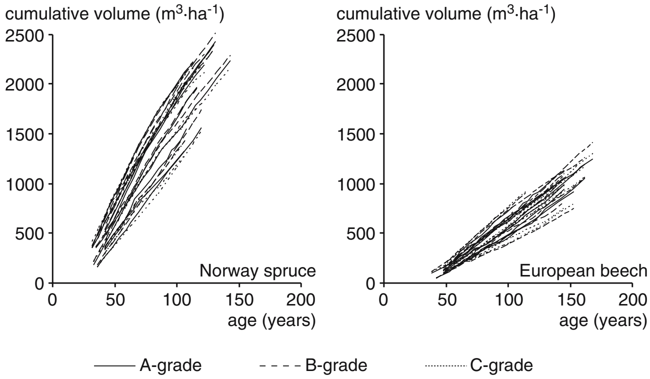

Fig. 4 Development of CV recorded for nine Norway spruce and ten European beech long-term thinning experiments

For the merchantable volume production of Norway spruce, data was available for ages ranging from 32 years to 143 years (Fig. 4). The linear rise of CV in the first half of this age range is followed by a very slight flattening out. The curvature is concave (seen from below) and ends with values of up to 2,500 $m^3\ ha^{-1}$. The corresponding age-cumulative merchantable volume curves for European beech cover a range from 38 years to 179 years and are convex (seen from below) (Fig. 4). At 179 years of age, CV amounts to about 1,400 $m^3\ ha^{-1}$. Both curve groups cover a wide spectrum of volume production for given ages, which can be explained by the considerable variation of the site fertility covered by the experiments (see Table 1). Plots subjected to light, moderate and heavy thinning (continuous, broken and dotted lines, respectively) are not grouped together, e.g., a specific thinning grade is not concentrated on the lower or upper range of the curve spectrum.

Stand density and CV

The long time series of up to 131 years can be used to detect whether CV growth can be raised by thinning. For that purpose CV of B- and C-grade plots was set in relation to the corresponding A-grade (Fig. 5). First-age class comprises stands up to 39 years (to 49 years in the case of European beech), the following age is divided into 10-year classes 40–49, 50–59 years etc., last-age class comprises stands with age ≥ 130 (age ≥ 140 in the case of European beech). Moderate thinning (B-grade) increases the performance of Norway spruce by 7% (compared to the A-grade) in age class 30–39 and the response tapers off to 2% in ages ≥ 130 (Fig. 5, left). During the whole survey period mean CV of the B-grade is significantly ($P < 0.05$) higher than the A-grade. C-grade thinning raises CV by 3–5% in age class 30–39; in the subsequent decades it falls by 2–3% below CV of the corresponding A-grade. The C-grade's superiority to the A-grade is significant ($P < 0.05$) until age 39; its inferiority is significant from age 80–130.

European beech's reaction on B-grade resembles that of Norway spruce (Fig. 5, right). In average RCV amounts to 6% and 2% in young and old stands, respectively. However, the variation of the reaction (and resulting SE of RCV) is much higher than for Norway spruce. C-grade raises CV by 1–3% (compared with A-grade) in juvenile phase and lowers it by 4–6% in mature stands; again the comparatively high variation of thinning reactions is obvious.

Additional to the presented means and SE, the range of individual stands reaction (min–max) of −11% to +30% (CV compared with A-grade) for Norway spruce and −27% to +55% for European beech gave evidence of the occurrence of both, decrease and increase of CV by thinning. Grouping of the stands with respect to site fertility revealed for Norway spruce the following: most positive RCV under moderate thinning on unfavourable sites, and most severe reduction of increment in heavily thinned stands on favourable sites. Compared with this, European beech benefits maximally from moderate thinning on favourable sites, whereas on poor sites heavy thinning causes CV fall below the level of the A-grade.

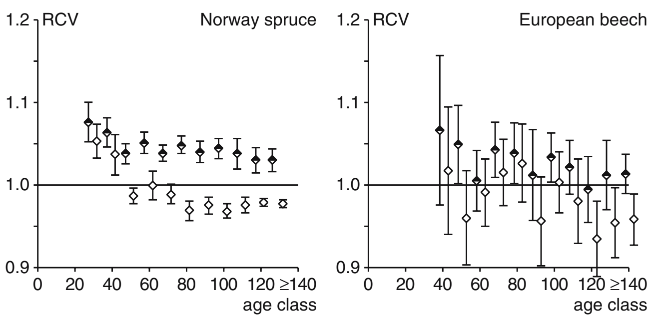

Fig. 5 Mean and standard error of RCV over 10-year-wide age classes for B- and C-grade (*half filled and empty symbols*, respectively) in relation to the corresponding A-grade

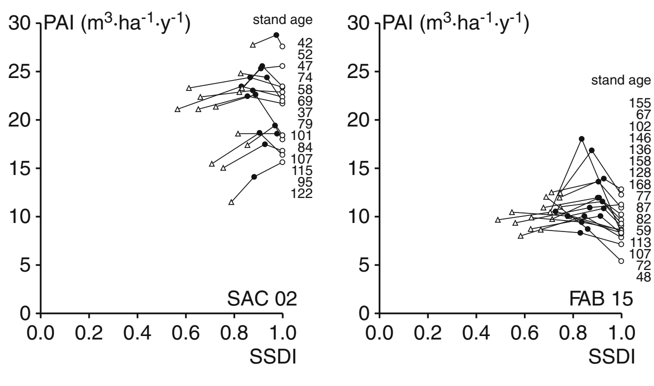

Fig. 6 Periodic annual increment (PAI) plotted over SSDI for selected Norway spruce and European beech experiments (Sachsenried 02 and Fabrikschleichach 15, respectively). Endperiod ages, sorted in correspondence with A-grade's PAI are arranged to the right of the respective surveys (*open circle, filled circle, open triangles* = grades A, B and C)

Stand density and PAI

Figure 6 shows two selected experiments of both considered species for the development of the density–growth relationship from the start of the experiment in the years 1870 to 1907 up to the very last survey. PAI–SSDI value pairs from the same survey were joined by lines, in order to emphasize the shape of the density–growth relationship. In most periods, an optimum relationship between density and growth is apparent. The PAI increases from the A- to B-grade and decreases by transition to grade C. The peakedness of the optimum curve is pronounced at the beginning of the survey, in the juvenile phase of the stand, and becomes flatter in middle-aged and mature stands.

Is the overall superiority of CV of the B-grade to the A-grade also reflected in the PAI of the individual growth periods? For examination of this question a total of 301 and 290 PAI–SDI value pairs for Norway spruce and European beech, respectively, were available. The relative periodic annual increment RPAI (e.g. RPAI = PAI_B/PAI_A) and SSDI (SSDI = SDI_B/SDI_A) form the basis of the subsequent calculations (cf. Materials and methods). For all subsequent calculations I used PAI from periods with length ≥ 5 years, exclusively.

The experiments for Norway spruce cover a closer spectrum of densities and growth reactions compared with European beech, although the applied thinning grades B and C were the same for both species (Fig. 7). However, both scattergrams cross the 1.0-line, which represents RPAI on A-grade plots. Low densities reduce RPAI below 1.0, medium densities can cause both, acceleration or reduction of RPAI. The fact that, in moderate and heavy thinned stands of Norway spruce and European beech, respectively, RPAI still transgresses in 40% and 46% of the cases 1.0 whereas only 60% and 54% fall below 1.0, gives evidence of the occurrence of both, negative and positive growth response on thinning.

In order to elucidate the influence of site conditions (SI) and mean diameter (*D*) [as an indicator for the stand's stage of development] on the density–growth relationship, the RPAI dataset of each species was grouped as follows (1) SI < SI50, *D* < *D*50, (2) SI < SI50, *D* ≥ *D*50, (3) SI ≥ SI50, *D* < *D*50, and (4) SI ≥ SI50, *D* ≥ *D*50. As thresholds for the grouping, I used the species specific 50% percentiles of SI and *D* of the dataset (Norway spruce and European beech, respectively *D*50 = 29.6 cm and 25.0 cm, SI = 35.3 m and 28.7 m). Within these groups I separated three SSDI classes with approximately equal sample size: SSDI < 0.65, SSDI = 0.65–0.75 and SSDI > 0.75. Figure 8 displays RPAI (mean ± 95% CI) for SI-D-groups (1) to (4). Within the groups the SSDI classes are arranged in a way, that density raises from left to right (low, medium and high density is represented by empty, half-filled and filled symbols). With one exception means of RPAI are lying below 1.0 for the heavily thinned stands and increase in parallel with density. The 95% CI show both, significantly ($P < 0.05$) positive and negative deviations from the 1.0-line in several cases. When growing on unfavourable sites [groups (1) and (2)], young stands of Norway spruce transgress RPAI = 1.0 significantly on moderately thinned plots (filled symbols) and overcompensate even heavy thinning (half-filled symbols). On favourable sites [groups (3) and (4)] ability to compensate for lowering of density is much lower, especially in old stands. The ability to buffer or even overcompensate for thinning is more pronounced in young compared with old stands, and on poor sites compared with better ones. Regarding the age effect, European beech behaves similar to Norway spruce; while growth of young stands [groups (1) and (3)] is hardly lowered or even significantly ($P < 0.05$) raised by thinning, mature stands [groups (2) and (4)] show a significant ($P < 0.05$) fall below 1.0-line. Though in the case of European beech, the effect of site fertility on density–growth relation seems to be opposite to that of Norway spruce. European beech gains in RPAI much

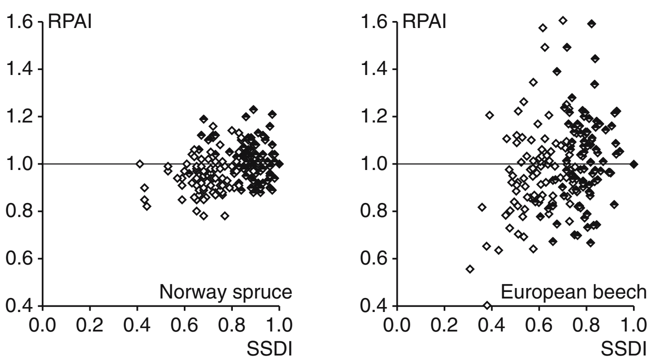

Fig. 7 Relative periodic annual merchantable volume increment (RPAI) over SSDI on thinned plots of Norway spruce and European beech. RPAI of B-, and C-grade are represented by *half filled and empty symbols*, respectively. For A-grades SSDI = 1.0 and RPAI = 1.0

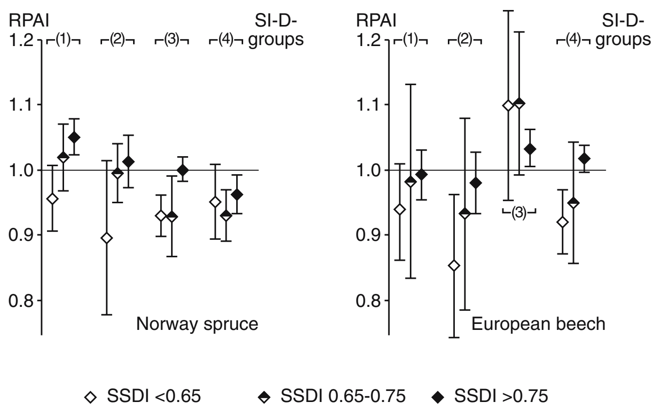

Fig. 8 RPAI (mean ± 95% CI) for SSDI classes SSDI < 0.65, 0.65–0.75, and > 0.75 (*empty, half filled, filled symbols*, respectively). In order to reveal the effect of SI and *D*, stands are grouped (1) SI < SI50, *D* < *D*50, (2) SI < SI50, *D* ≥ *D*50, (3) SI ≥ SI50, *D* < *D*50, and (4) SI ≥ SI50, *D* ≥ *D*50. SI50 and *D*50 represent the 50% percentiles of SI and *D* in the dataset

more on favourable sites and shows severe increment losses after heavy thinning on unfavourable sites. Range of mean values and CI of RPAI is much wider in European beech stands compared with Norway spruce. In order to scrutinize the particular effect of moderate thinning (B-grade) on RPAI, I evaluated slope $\mathrm{SLOPE_{A,B}} = (\mathrm{SSDI_A}-\mathrm{SSDI_B})/(\mathrm{RPAI_A}-\mathrm{RPAI_B})$ for each pair of A- and B-grades of the available surveys. This brings to focus how relative the PAI reacts on the removal of trees of classes 5, 4 and 2 (cf. Materials and methods). Mean (±SE) of $\mathrm{SLOPE_{A,B}}$ is −0.0293 (±0.1030) and −0.0429 (±0.1157) for Norway spruce and European beech, respectively, still it varies considerably between −2.57 to +3.37 and −4.46 to +3.55 (min–max). In average $\mathrm{SLOPE_{A,B}}$ is not significantly different from zero, as positive and negative slopes cancel each other. But if I separate $\mathrm{SLOPE_{A,B}}$ of young and old stands and on favourable and unfavourable sites from each other, we get a clear tendency, which is species specific. In Norway spruce stands Pearson's correlation coefficient **r** is positive for $\mathrm{SLOPE_{A,B}}$ versus age (**r** = 0.435, $P<0.01$), $\mathrm{SLOPE_{A,B}}$ versus D (**r** = 0.446, $P<0.01$) and $\mathrm{SLOPE_{A,B}}$ versus SI (**r** = 0.333, $P<0.01$). For European beech I found for $\mathrm{SLOPE_{A,B}}$ versus age (**r** = 0.263, $P<0.05$), $\mathrm{SLOPE_{A,B}}$ versus D (**r** = 0.270, $P<0.05$) and $\mathrm{SLOPE_{A,B}}$ versus site index (**r** = −0.434, $P<0.01$). Age and D affect $\mathrm{SLOPE_{A,B}}$ of both species significantly positively, site fertility raise $\mathrm{SLOPE_{A,B}}$ of Norway spruce and lowers $\mathrm{SLOPE_{A,B}}$ of European beech. OLS regression analysis of the model

$$\mathrm{SLOPE_{A,B}} = a + bD + c\mathrm{SI} \tag{1}$$

yields for Norway spruce estimates (± SE) a = −4.051 (±1.483), b = 0.03342 (±0.009), c = 0.08992 (±0.45) with n = 85, $\mathbf{r}^2$ = 0.218, F = 12.833, $P<0.001$. For European beech I found a = 3.248 (±0.948), b = 0.03353 (±0.012), c = −0.147 (±0.033), with n = 76, $\mathbf{r}^2$ = 0.251, F = 13.703, $P<0.001$. In this and all subsequent analyses only variables with significant regression parameters ($P<0.05$) were included in the model.

Model for PAI in dependence on stand density

In order to integrate the revealed influence of stand properties on PAI and to make this knowledge operable for prognosis and management, I formulate and parameterize the following model for Norway spruce and European beech

$$\mathrm{RPAI} = e^{(d+e\,\ln(\mathrm{SSDI})+f\mathrm{SSDI}+g\,\ln(D)\ln(\mathrm{SSDI})+h\,\ln(\mathrm{SI})\ln(\mathrm{SSDI}))}, \tag{2}$$

in logarithmic transformation

$$\ln(\mathrm{RPAI}) = d + e\,\ln(\mathrm{SSDI}) + f\mathrm{SSDI} + g\,\ln(D)\ln(\mathrm{SSDI}) + h\,\ln(\mathrm{SI})\ln(\mathrm{SSDI}). \tag{3}$$

RPAI is the relative periodic annual increment of merchantable wood, SSDI the standardized stand density index at the beginning of the particular survey period, SI the mean height at age 100 (m) as an indicator for site fertility, and D is mean diameter (cm) at the beginning of the particular survey period (cf. Materials and methods). The model is flexible enough to represent both, an asymptotic as well as an unimodal density–growth curve for SSDI ≤ 1.0 (cf. Fig. 1). Apart from the direct influence of SSDI on RPAI, the model considers the interaction terms $\ln(D)\times\ln(\mathrm{SSDI})$ and $\ln(\mathrm{SI})\times\ln(\mathrm{SSDI})$, which represent the modification of the density–growth relationship by further stand properties.

The model parameters (Table 3) were estimated on the basis of Eq. 3 by OLS regression. Figure 9 displays the model behaviour for the stands of different mean diameters D (above) and site fertility SI (below). Whereas both species' density–growth curves exceed the 1.0-line in the juvenile phase and become shallower with increasing age (above), they react differently on site conditions. The better the site conditions, the shallower the density–growth curve of Norway spruce is. In young stands a 10% increase of RPAI above the level expected under light thinning can be induced by moderate and heavy thinning (SSDI = 0.7–0.8) on medium and unfavourable sites, while on favourable sites such treatment would cause 5–10% losses of increment. European beech reacts the other way around; the better the site conditions, the higher is the level of density–growth curve and the benefit of RPAI after thinning. For European beech a decrease of site fertility is combined with shallower density–growth curves; which is equivalent with a lower ability of such stands to buffer or even overcompensate for lowering of stand density.

In order to underpin these findings quantitatively I ascertain the first derivative of Eq. 2 with respect to SSDI

$$\mathrm{RPAI}' = \frac{e}{\mathrm{SSDI}} + f + \frac{g\,\ln(D)}{\mathrm{SSDI}} + \frac{h\,\ln(\mathrm{SI})}{\mathrm{SSDI}} \times e^{(d+e\,\ln(\mathrm{SSDI})+f\mathrm{SSDI}+g\,\ln(D)\ln(\mathrm{SSDI})+h\,\ln(\mathrm{SI})\ln(\mathrm{SSDI}))}$$

Table 3 Estimated parameters, standard errors (SE) and test statistic for model equation $\ln(\mathrm{RPAI}) = d + e\,\ln(\mathrm{SSDI}) + f\mathrm{SSDI} + g\,\ln(D)\ln(\mathrm{SSDI}) + h\,\ln(\mathrm{SI})\ln(\mathrm{SSDI})$, with RPAI (relative periodic annual merchantable volume increment), SSDI (standardized stand density index), D (quadratic mean diameter at the beginning of the relevant growth period), and SI (mean height at age 100)

Species	df	d ± SE	e ± SE	f ± SE	g ± SE	h ± SE	r^2	P-tail sign
Norway spruce	301	0.851 ± 0.299	−2.639 ± 0.932	−0.845 ± 0.302	0.191 ± 0.051	0.810 ± 0.304	0.21	0.000***
European beech	290	1.332 ± 0.329	2.309 ± 0.949	−1.332 ± 0.335	0.365 ± 0.069	−0.717 ± 0.293	0.23	0.000***

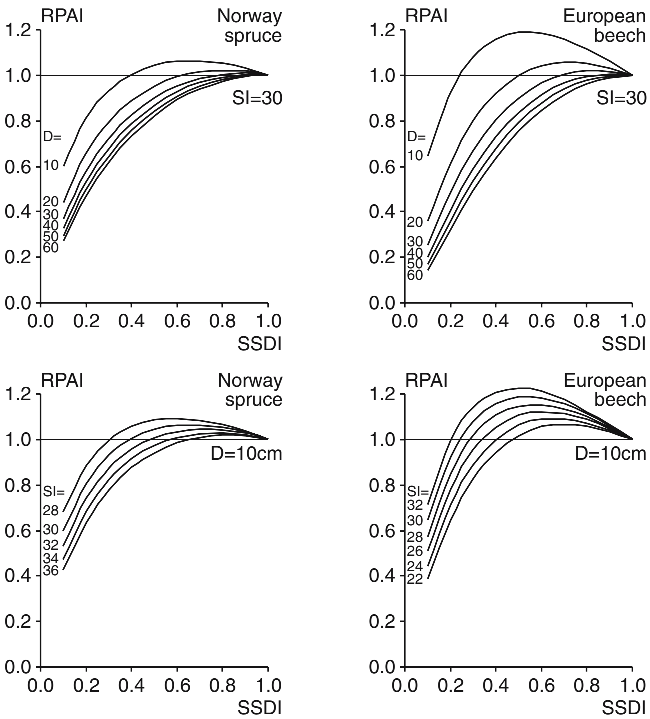

Fig. 9 Relationship between stand density SSDI and increment RPAI for stands of different mean diameter D and site index SI. Effect of diameter D (10–60 cm), if SI = 30 m (above). Effect of SI (22–36), if D = 10 cm (below)

and equate it with 0. In this way I detect optimal stand density $SSDI_o$, which causes maximum PAI of merchantable volume. In the following the optimal density, i.e., density where increment is at maximum, is named $SSDI_o$; the corresponding optimal increment is $RPAI_o$. Rearrangement of $(e/SSDI + f + g\ln(D)/SSDI + h\ln(SI)/SSDI) = 0$ results in

$$SSDI_o = \frac{e + g\ \ln(D) + h\ \ln(SI)}{-f}. \quad (4)$$

Insertion of species-specific parameters in Eq. 4 yields $SSDI_o = (-2.639 + 0.191\ \ln(D) + 0.810\ \ln(SI))/0.851$ for Norway spruce and $SSDI_o = (2.309 + 0.365\ \ln(D) - 0.717\ \ln(SI))/1.332$ for European beech. Parameter g in Eq. 4 is positive for both species and reflects that RPAI's maximum shifts to the right (i.e., towards higher stand densities) within stand development. Parameter h is positive for Norway spruce but negative for European beech, i.e., the better the site conditions (SI) the more $SSDI_o$ is shifted to the right in Norway spruce stands and to the left in European beech stands.

Discussion

For clarification whether total biomass growth of a stand can be raised by thinning, inventory of complete shoot and root biomass is indispensable. Therefore this evaluation is restricted on the production of merchantable stem volume.

Evidence of transgressive growth in thinned compared with unthinned stands

Cumulative merchantable volume of moderate and heavy-thinned Norway spruce and European beech stands, can amount to 131% and 155%, respectively at age 50 and still to 112% and 122%, respectively past age 100 (A-grade = 100%). On other plots CV falls on 96% and 81% in age 50 and 90% and 76% past age 100. These findings correspond to Assmann (1970), Schmidt-Vogt (1986), Schober (1979, 1980), and Kramer (1988), who gave evidence that CV of Norway spruce stands, moderately thinned from below, on the long run is up to 10% superior to A-grade, whereas heavy thinning from below causes CV losses of up to 14% (light thinning = 100%). European beech buffers the lowering of density even more than spruce: CV can be raised up to 15% and transgress the reference plots even on heavily thinned plots and under accretion thinning (Kennel 1972; Schober 1972).

These findings concerning CV are substantiated by analyses of the relationship between stand density and PAI. In young stands the relationship between density and PAI follows a unimodal optimum curve. PAI of Norway spruce and European beech, respectively, culminates in 109% and 123% if density is reduced to 59% or 50% (A-grade = 100%). The comparatively higher peak and broader curvature of beech's density–growth relationship reflects the species ability to buffer thinning effects. Bryndum (1978), Dittmar (1959), Hamilton (1976), and Kramer (1978) confirm that in young Norway spruce stands PAI can be accelerated up to 25% at maximum (compared with light thinning) and falls back within stand development. Benefit of thinning is more distinct on soils with poor water and nutrients supply than on rich soils (Assmann 1970; Dittmar 1961; Hamilton 1976). Heavy thinning causes severe losses of increment, especially in older stands on favourable soils. Henriksen (1951) and Assmann (1970) report PAI acceleration by thinning in young European beech stands up to 50% and PAI's tapering off with progressing age (Bryndum 1980, 1987; Assmann 1970; Schober 1972). Impact of site index on density–growth relation for European beech is hardly understood to date (Foerster 1993; Franz et al. 1993; Kennel 1972).

Since the increment can rise sharply first, but tapers off only a few years after a thinning, the detected level of growth acceleration depends on the respective length of the survey period. Post-thinning survey periods of 2–3 years (Henriksen 1951) yield more pronounced reactions than of 5- to 7-year-periods (Assmann 1970). That is why reports about CV vary less than those about PAI.

In addition to the evidence of transgressive growth caused by thinning, application of model $SLOPE_{A,B} = a + bD + cSI$ (cf. Eq. 1) reveals, why this benefit occurs in some cases, while not in others. The stands included in the analysis cover mean diameters from $D = 10$–60 cm and site indices from SI = 29–36 m in the case of Norway spruce, from SI = 22–32 m in the case of European beech. Applying the Norway spruce's model with variables D (10 cm,..., 60 cm) and SI (28 m,..., 36 m) makes clear that in stands with $D \leq 30$ cm and SI ≤ 32, $SLOPE_{A,B}$ is negative, in other words moderate thinning raises PAI compared to A-grade. In contrast, if $D \geq 40$ cm and SI > 32 m $SLOPE_{A,B}$ is positive, and indicates that moderate thinning causes a decrease of PAI under the level of A-grade. In European beech stands with $D \leq 30$ cm and SI ≥ 32, $SLOPE_{A,B}$ is negative, whereas combinations of $D \geq 50$ cm and SI ≤ 32 yield $SLOPE_{A,B} > 0$. So when stand density is reduced by thinning, PAI increases to some extent in young Norway spruce stands on poor sites, while it decreases in old stands on unfavourable sites. European beech reacts differently insofar as PAI increases predominantly in young stands on favourable site, whereas it goes down on unfavourable sites.

From verbal description to a quantitative model

Hartig (1795), Cotta (1828) and Reventlow (1879) founded their opinion about optimal density on personal experience, Schwappach (1908, 1911) provided the first evidence of a growth increase through thinning by experiments. Numerous long-term experiments followed, some of them confirming others refuting the existence of an optimum curve (Assmann 1970; Kramer 1988; Langsaeter 1941; Pardé 1979; Schober 1972, 1979, 1980). To date we have hardly gone further than just describing and to some extent systematising growth reaction patterns caused by thinning qualitatively (Oliver and Larson 1996, p. 352 ff, Smith et al. 1997, pp. 84–85). Based on Douglas fir thinning trials (*Pseudotsuga menziesii* Mirb.) in the Pacific Northwest of the USA, Curtis et al. (1997) even generally rejects the existence of the optimum density–growth relationship. Zeide (2001) pleads for a transition from verbal description to a quantitative model in order to solve apparently contrary findings concerning this century-old issue.

Since the underlying experiments cover a wide spectrum of development stages and sites, the presented model (cf. Eq. 2) incorporates a bunch of reaction patterns in a continuity which were so far detected only in succession in stands at different ages (Nelson 1961) or separately in stands of different site fertility (Assmann 1970). The revealed relationship follows a unimodal curve in principle; but depending on i.a. observed range of density, stage of stand development, and site fertility of the stand, we perceive only a particular (increasing or culminating) portion of the curve.

These facts can be reflected for Norway spruce and European beech by $SSDI_o$ and $RPAI_o$ for the combinations of D and SI (Tables 4, 5), calculated on the basis of Eqs. 2 and 4. The stairline separates combinations yielding $SSDI_o < 1.0$ from those with $SSDI_o \geq 1.0$. In other words it separates constellations where a unimodal density–growth curve is prevailing (curve 2) from those with a increasing pattern (curve 1). A location of $SSDI_o$ below 1.0 is equivalent to $RPAI_o > 1.0$, and vice versa. In young Norway spruce stands ($D = 10$ cm) on poor soils (SI = 28 m), RPAI can be increased up to 109% by reducing stand density to $SSDI_o = 0.59$. Within the range of observed site indices (SI = 28–36 m) and dimensions ($D = 10$–60 cm), $SSDI_o$ and $RPAI_o$ approach 1.0 the more, the older the stand and the better the site fertility is. In young European beech stands ($D = 10$ cm) with good site fertility (SI = 32 m), $RPAI_o$ amounts to 123% if stand density is reduced to $SSDI_o = 0.50$.

The database is a prerequisite as well as a restriction for the model. More than 100-years-long time series enable incorporation of the age effect. Although the data covers only medium to favourable site qualities, the integration of site effect on growth–density pattern proved to be extremely important. By just pooling data for the statistical analysis, without separation between favourable and unfavourable sites, positive and negative effects cancel each other (Assmann 1970), which conceals the reaction pattern's site and species dependency. SI is a rather unspecific indicator for site fertility and should be replaced by more specific quantitative site

Table 4 Stand density $SSDI_o$ where RPAI is at maximum

SI	$D = 10$	20	30	40	50	60
$SSDI_o$						
Norway spruce						
28	0.59	0.75	0.84	0.90	0.96	1.00
30	0.66	0.81	0.91	0.97	1.02	1.06
32	0.72	0.88	0.97	1.03	1.08	1.12
34	0.78	0.93	1.03	1.09	1.14	1.18
36	0.83	0.99	1.08	1.15	1.20	1.24
European beech						
22	0.70	0.89	1.00	1.08	1.14	1.19
24	0.65	0.84	0.95	1.03	1.09	1.14
26	0.61	0.80	0.91	0.99	1.05	1.10
28	0.57	0.76	0.87	0.95	1.01	1.06
30	0.53	0.72	0.83	0.91	0.97	1.02
32	0.50	0.69	0.80	0.88	0.94	0.99

$SSDI_o$ is listed for the range of D and SI, covered by the thinning experiments

Table 5 $RPAI_o$ predicted by Eq. 2 for optimal density $SSDI_o$ (cf. Table 4)

SI	$D=10$	20	30	40	50	60
$RPAI_o$						
Norway spruce						
28	1.09	1.04	1.02	1.01	1.01	1.01
30	1.06	1.02	1.01	1.01	1.01	1.01
32	1.04	1.01	1.01	1.01	1.01	1.01
34	1.03	1.01	1.01	1.01	1.01	1.01
36	1.02	1.01	1.01	1.01	1.02	1.03
European beech						
22	1.07	1.01	1.00	1.00	1.01	1.02
24	1.10	1.02	1.00	1.00	1.01	1.01
26	1.12	1.03	1.01	1.00	1.00	1.01
28	1.16	1.04	1.01	1.00	1.00	1.00
30	1.19	1.06	1.02	1.01	1.00	1.00
32	1.23	1.08	1.03	1.01	1.00	1.00

variables in future (e.g. precipitation, temperature, nutrients supply). The model describes growth reaction on thinning from below. Its comparatively low $\mathbf{r}^2$ is due to the rather narrow range of stand densities, where thinning from below covers by definition (Verein Deutscher Forstlicher Versuchsanstalten 1902).

The model approach uses SDI and SSDI as a measure of density, as these measures take into account the allometric development stage of the stand. By using the site-specific *r*-exponents of Reineke's (1933) relationship, derived from corresponding A-grade plots, I got a more adequate and stable measure of density than from that of the basal area (Zeide 2002, 2004; Avery and Burkhart 2002). A-grade plots merely approach maximum density; yet dead, dying and unsound trees are removed (cf. Materials and methods). It means completely undisturbed stands can transgress SSDI of 1.0 to some extent. The corresponding increment RPAI for SSDI > 1.0 can be extrapolated by the model.

The dependence of a stands growth reaction on physiological stand age is represented by *D* at the beginning of the relevant growth period. Compared to stand age, *D* was preferred as steering variable, as even at same actual stand age, *D* varies considerably depending on growth acceleration caused by thinning (Assmann 1970). *D* therefore characterizes more appropriate a stands allometric phase and ability to react on thinning. Unlike actual age, *D* contributes significantly ($P<0.05$) to the estimation of RPAI in model equation. In addition *D* is more appropriate for practical application, as *D* is mostly measured by inventories, whereas stand age is often only estimated.

Conclusion

The presented model reflects the apparently paradox fact (Zeide 2004) that a thinning which keeps a stand permanently at maximum periodical increment RPAI not at all ensures a maximum CV. Let us suppose if a young beech stand ($D=10$ cm, SI = 32 m) is thinned heavily by reducing SSDI on 0.50, then PAI is accelerated up to 123% (cf. Tables 4, 5). This transgressive PAI is equivalent with an increased growth of *D* and causes the stand's potential of thinning-induced growth acceleration to taper off earlier; due to a faster physiological aging. The more intense the induced-growth acceleration, the quicker the stand is driven through the system of reaction curves (Fig. 9), which passes the phase of high absolute increment and looses the ability to buffer or even overcompensate thinning by growth reaction of remaining stand. This outlined reaction pattern explains, why CV of older B- and C-grade plots differs little in the end, although PAI can be increased considerably by B- and C-grade thinning. *D* therefore is more appropriate to reveal this feedback between growth and density, than stand age would be.

The revealed reaction pattern, especially the transgressive growth of moderate compared with lightly thinned stands tempts into a causal explanation (Zeide 2001). Assmann (1970) and Mar:Møller (1945) assume that light deficiency makes suppressed trees less efficient than dominant trees in using water and nutrients for the fixation and retention of carbon. Assmann (1970, p. 233) suggests that resources made available when suppressed trees are removed are being used more efficiently by dominant trees to boost their growth. Furthermore, it is conceivable that competition processes may cause reduced growth due to the increased formation of secondary metabolic substances. Perhaps, a tree under stress finds itself in the same dilemma as described by Herms and Mattson (1992) for plants, which defend themselves against stress from parasites or pathogens. Growth loss under increasing competitive pressure may be attributable to increased energy consumption in an attempt to produce allelopathic or toxic effects on neighbours (Tubbs 1973). Another conceivable cause could be the stress-related emission of hydrocarbons, which could amount to a few thousandth of percent, or in some cases to 10, 20 or even 50% of the assimilated carbon (Kesselmeier and Staudt 1999). The revealed reaction pattern paves the way for such causal explanations; however, further clarification of the density–growth issue requires complicated full biomass growth analysis on long-term plots.

Acknowledgements The author wishes to thank Deutsche Forschungsgemeinschaft for providing funds for forest growth and yield research as part of the Sonderforschungsbereich 607 "Growth and Parasite Defense" and the Bavarian State Ministry for Agriculture and Forestry for the permanent support of the growth and yield research project W 07. Prof. Dr. Hermann Spellmann of the Lower Saxony Forest Research Station in Göttingen complemented the Bavarian data set with 3 experimental plots from the former Prussian Forest Research Station. The authors also thank Prof. Dr. Boris Zeide, University of Arkansas at Monticello, for inspiring discussion; Hans Herling, for conscientious preparation of graphs; and anonymous reviewers, for constructive criticism.

References

Assmann E (1953) Bestockungsdichte und Holzerzeugung. Forstw Cbl 72:69–101

Assmann E (1956) Natürlicher Bestockungsgrad und Zuwachs. Forstw Cbl 75:257–265
Assmann E (1970) The principles of forest yield study. Pergamon Press Ltd, Oxford, New York, Toronto, Sydney, Braunschweig
Avery TE, Burkhart HE (2002) Forest measurements. McGraw-Hill, New York
Bryndum H (1978) Der Einfluß verschiedener Durchforstungsstärken auf Massen- und Wertleistung der Fichte am Beispiel der dänischen Versuchsflächen. Forstw Cbl 97:302–313
Bryndum H (1980) Der Buchen-Durchforstungsversuch im Waldort Totterup. Forstl Forsögsv Danmark 38:1–76
Bryndum H (1987) Buchen-Durchforstungsversuch in Dänemark. Allgem Forst Jagdztg 158:115–122
Cotta H (1828) Anweisung zum Waldbau. Arnoldische Buchhandlung, Dresden, Leipzig
Curtis RO, Marshall DD, Bell JF (1997) LOGS. A pioneering example of silvicultural research in coast Douglas-fir. J For 95:19–25
Dittmar O (1959) Zur Frage des "Wuchsbeschleunigungseffektes" durch starke Durchforstung im jungen Fichtenbestand. Arch Forstwesen 8:923–945
Dittmar O (1961) Zuwachs und Ertrag langfristiger Fichten-Durchforstungs-versuchsflächenreihen des Thüringer Waldes und des Harzes in Abhängigkeit von Bestockungsdichte und Standort. Arch Forstwesen 10:458–476
Foerster W (1993) Der Buchen-Durchforstungsversuch Mittelsinn 025. Allg Forstzeitschrift 48:268–270
Franz F, Röhle H, Meyer F (1993) Wachstumsgang und Ertragsleistung der Buche. Allge Forstzeitschrift 48:262–267
Ganghofer A (1881) Das Forstliche Versuchswesen. Schmid'sche Buchhandlung, Augsburg
Hamilton GJ (1976) The Bowmont Norway spruce thinning experiment 1930–1974. Bull For Comm London 54:109–121
Hartig GL (1791) Anweisungen zur Holzzucht für Förster. Neue akademische Buchhandlung, Marburg
Hartig GL (1795) Anweisung zu Taxation der Forsten oder zur Bestimmung des Holzertrags der Wälder. In: Kommißion bei Buchhändler Heyer
Henriksen HA (1951) Durchforstungsversuch in jungem Buchenbestand. Forstl Forsögsv Danmark 20:387–401
Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335
Johann K (1993) DESER-Norm 1993. In: Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwachstumskundlichen Dauerversuchen, Jahrestagung 1993 der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten, Unterreichenbach-Kapfenhardt, Proceeding, pp 96–104
Kennel R (1972) Die Buchendurchforstungsversuche in Bayern von 1870 bis 1970. Forstliche Forschungsberichte München, 7, 264 p
Kesselmeier J, Staudt M (1999) Biogenic volatile organic compounds (VOC): an overview on emission, physiology and ecology. J Atmos Chem 33:23–88
Kraft G (1884) Beiträge zur Lehre von den Durchforstungen, Schlagstellungen und Lichtungshieben. Klindworth's Verlag, Hannover
Kramer H (1978) Der Bowmont-Durchforstungsversuch. Forstw Cbl 97:131–141
Kramer H (1988) Waldwachstumslehre. Paul Parey, Hamburg, Berlin
Langsaeter A (1941) Om tynning i enaldret gran- og furuskog Maddel. Det Norske Skogforoksvesen 8:131–216
Mar:Møller C (1945) Untersuchungen über Laubmenge, Stoffverlust und Stoffproduktion des Waldes. Kandrup und Wunsch, Kopenhagen
Nelson TC (1961) Loblolly pine growth as related to site, age, and stand density. Soc Am Foresters Proc 1960:12–14
Oliver CD, Larson BC (1996) Forest stand dynamics. Wiley, New York
Pardé J (1979) Entwicklung, Stand und Zukunft der Forschungen über die Durchforstung in Frankreich. Forstw Cbl 98:110–119
Pretzsch H (2002) Grundlagen der Waldwachstumsforschung. Blackwell, Berlin
Pretzsch H, Utschig H (2000) Wachstumstrends der Fichte in Bayern. Mitt Bay Staatsforstverw München 49:1–170
Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638
Reventlow CDF (1879) Forslag til en forbedret Skovdrift grundet, paa Undersogelser over Traeernes Vegetation I Danmarks og Slesvigs Skove. In: Kjobenhavn, 1879, Ed. in English 1960: A treatise of forestry, Society of Forest History, Horsholm Denmark
Röhle H (1994) Zum Wachstum der Fichte auf Hochleistungsstandorten in Südbayern. Habilitationsschrift Forstwissenschaftliche Fakultät, Universität München, p 249
Rousseau J-J (1762) Du Contract Social. German Ed. 1977: Gesellschaftsvertrag, Reclam, Stuttgart
Schmidt-Vogt H (1986) Die Fichte. Bd. II/1. Verlag Paul Parey, Hamburg
Schober R (1972) Die Rotbuche 1971. J.D. Sauerländer's Verlag, Frankfurt
Schober R (1979) Massen-, Sorten- und Wertertrag der Fichte bei verschiedener Durchforstung. Teil 1, Allgem. Forst Jagdztg 150:129–152
Schober R (1980) Massen-, Sorten- und Wertertrag der Fichte bei verschiedener Durchforstung. Teil 2, Allgem. Forst Jagdztg 151:1–21
Schwappach A (1908) Die Kiefer. Wirtschaftliche und statische Untersuchungen der forstlichen Abteilung der Hauptstation des forstlichen Versuchswesens in Eberswalde. Verlag Neumann, Neudamm
Schwappach A (1911) Die Rotbuche. Wirtschaftliche und statische Untersuchungen der forstlichen Abteilung der Hauptstation des forstlichen Versuchswesens in Eberswalde. Verlag Neumann, Neudamm
Smith DM, Larson BC, Kelty MJ, Ashton PMS (1997) The practice of silviculture: applied forest ecology. Wiley, New York
Tubbs CH (1973) Allelopathic relationship between yellow birch and sugar maple seedlings. For Sci 19:139–145
Verein Deutscher Forstlicher Versuchsanstalten (1902) Beratungen der vom Vereine Deutscher Forstlicher Versuchsanstalten eingesetzten Kommission zur Feststellung des neuen Arbeitsplanes für Durchforstungs- und Lichtungsversuche. Allg Forst Jagdztg 78:180–184
Wiedemann E (1932) Die Rotbuche 1931. Mitt. der Preußischen Forstl. Versuchsanstalt. Verlag M. & H. Schaper, Hannover
Wiedemann E (1936/42) Die Fichte 1936. Verlag M.& H. Schaper, Hannover
Zeide B (2001) Thinning and growth: a full turnaround. J For 99:20–25
Zeide B (2002) Density and the growth of even-aged stands. For Sci 48:743–754
Zeide B (2004) How to measure stand density. Trees 19(1):1–14