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Long-term stand dynamics of managed spruce–fir–beech mountain forests in Central Europe: structure, productivity and regeneration success

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With a total area of several million hectares, mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) connect the beech-covered lowlands and spruce-dominated alpine regions and still represent the most natural though managed forests in Europe. For sustaining their unique functions and services, their natural gap dynamics are emulated by the combined shelterwood–femel-coupe system. In the 1970s, 22 long-term experimental plots were established in the Bavarian Alps in order to substantiate the formerly mainly experience-based silvicultural prescriptions. After more than 40 years of successive surveys including the integrated evaluation of the old stands and the measurement of natural regeneration, analyses reveal: (1) The reduction of overstorey density is generally associated with a proportional reduction of the overstorey stand growth. So, the recommended 20–40 per cent density reduction of a combined shelterwood–femel coupe may reduce the mean annual increment also by ~20–40 per cent, but part of this loss is compensated by the additional growth of the regeneration. (2) Over time, the natural regeneration is continuously augmented by new recruitment of seedlings and saplings. (3) However, even 40 years after initiating regeneration, spruce is rare in the regeneration compared with fir, beech and other broadleaved species. Further observation will show whether spruce will catch up with the other species or whether it requires either larger disturbances than gap and femel coupes, or possibly planting. Based on these findings, a refined shelterwood–femel-coupe system is proposed and its advantages and disadvantages are discussed.

Introduction

Characteristics and relevance of alpine spruce–fir–beech mountain forests in Europe

Mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) connect the lowland beech forest communities and spruce-dominated alpine forest types. They represent a valuable forest resource with high provision of ecosystems services. While forests in the lowlands were exploited much more intensively and mostly converted into the age-class-systems by clearcutting, forests in the submontane and montane (600–1400 m a.s.l.) altitudes were managed using a continuous cover management system which kept the species composition much closer to the natural composition (Magin, 1959). The main reasons that mountain forests are often lower in productivity include their accessibility for logging and their role in protection against alpine risks like avalanches, landslides or rockfall (Bebi *et al.*, 2001). A rough estimate of the area covered by these mixed mountain forests based on Brus *et al.* (2011) and EUFORGEN (2011) is at least 3 million hectares. Thus, spruce–fir–beech mountain forests which are managed in order to sustain their functions and services as risk prevention, promotion of biodiversity, wood supply and recreation cover a significant forest area in Europe.

To sustain these unique functions and services the natural gap dynamics of mountain forests are often emulated by silviculture (e.g. Acevedo *et al.*, 1996; McCarthy, 2001; O'Hara, 2001; Ciancio *et al.*, 2006). In this context, the most common silvicultural prescription for management is the combined shelterwood–femel-coupe system, which comprises several stages (Figure 1): mature stands of spruce, fir and beech at the age of 100–120 years (Figure 1a) are slightly opened up homogeneously over the whole stand area (Figure 1b) to promote natural regeneration (shelterwood coupe). Above these patches of upcoming regeneration the canopy is opened up continuously (femel coupe) (Figure 1c). With progressing regeneration of all three species, the gaps are gradually extended by cuttings at the edges in the course of femel coupe (Figure 1d). Modern cable crane logging systems triggered a tendency towards larger extended gaps aligned with the slope, designed to

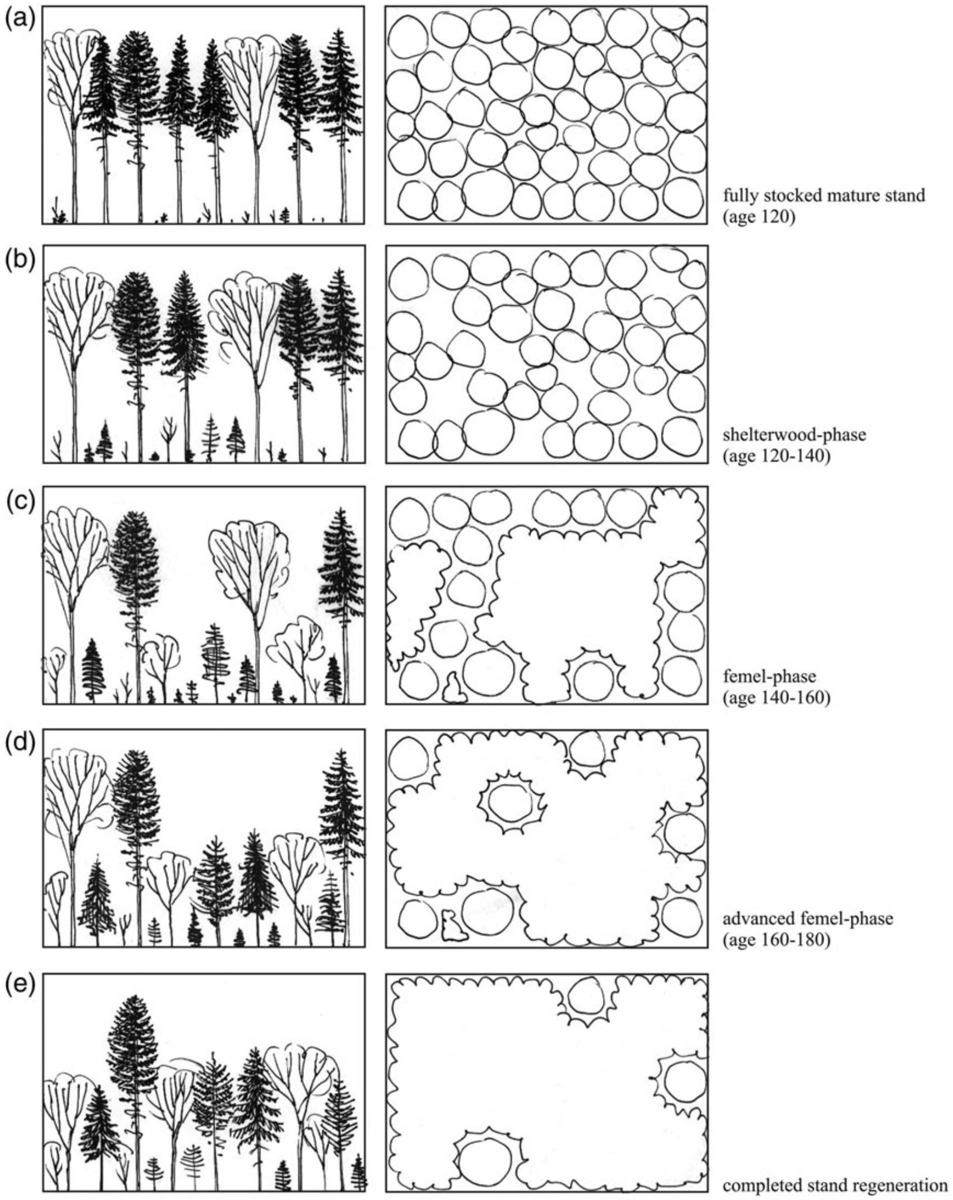

Figure 1 Combined shelterwood- and femel-coupe system for management of spruce–fir–beech mountain forests in Europe. The regeneration process can be characterized by (a) the fully stocked phase at age 100–120, (b) the shelterwood-phase at age 120–140 for promoting regeneration, (c) the femel-phase with progressing regeneration, (d) the advanced regeneration phase after cutting at the edges of the femel gaps and (e) the growing together of the patches so that the whole stand is regenerated ~40–80 years after the first opening up. (a) Fully stocked mature stand. (b) Shelterwood-phase. (c) Femel phase. (d) Advanced femel-phase. (e) Completed stand regeneration.

increase the volume harvested per operation in order to augment the rate of return. By removing the overstorey step by step, 40–60 years after the first harvest, the whole stand area is regenerated as the regeneration patches grow together (Figure 1e).

Although rather common, this combination of a shelterwood phase for initiating natural regeneration, followed by a femel- or gap phase for fostering the seedlings and saplings by a 20–40 per cent opening up of the overstorey, needs further quantitative evaluation. The system has not been analysed in terms of productivity, regeneration success and interaction between the overlapping generations (overstorey and understorey). Crucial issues for better understanding the stand dynamics of spruce–fir–beech mountain forests in the regeneration phase are: (1) the relationship between the overstorey stocking density and growth of the overstorey, (2) the effect of the overstorey density on regeneration establishment and development (3) and the effect of the regeneration on overstorey growth.

Relationship between overstorey density and growth

Stand structure and species composition strongly determine how silvicultural interventions (thinning, regeneration cuts) and other structural disturbances (windthrow, snow-breakage, bark beetle damage) in the overstorey affect its productivity. As a canopy becomes vertically deeper and multi-layered, it develops higher growth resilience to structural disturbances (Pretzsch, 2003). The relationship between stand density and growth in even-aged stands follows a unimodal or asymptotic curve; i.e. with the lowest productivity level at low densities, increasing productivity when stand density increases and a slight decrease of productivity when approaching maximum stand density. The resilience of stand growth to silviculturally induced density reductions is higher for species that are shade tolerant and that respond well to release such as beech and fir in contrast to larch and pine, and the resilience usually decreases with stand age (Assmann, 1970; Pretzsch, 2005).

If mixed stands have a multi-layered canopy, thinnings or selection cuts cause productivity reductions only under heavy density reductions. This is because the trees in the medium and lower canopy layers can compensate for losses in the upper layer. The range of stand densities where productivity is rather stable has been reduced is also called the saddle of the density–growth relationship (Langsaeter, 1941). This saddle is particularly wide in selection forests. Here, the effects of structural disturbances within the overstorey on stand growth are efficiently buffered due to their pronounced multi-layered, uneven-aged structure (Mitscherlich, 1952; Pretzsch, 2003). Productivity losses, due to overstorey harvest or by overstorey tree losses in the course of damaging events, can be moderated by the presence of a second or third layer of trees which might immediately use the resources previously used by the removed or lost trees.

However, in mixed spruce–fir–beech mountain forests, Preuhsler (1989) found growth to decrease even after slight density reductions and proportionally decreasing growth with increasing density reduction in the canopy. This is different from the reaction usually observed in mixed stands. Reasons might be that the non-productive gaps caused by felling close more slowly due to the advanced tree age, or the generally lower growth rate of mountain forests.

Overstorey effects on regeneration

The effect of the overstorey stand structure on seedfall, germination, seedling, sapling development and ingrowth into the main stand has been studied for understanding old-growth and natural forest dynamics, and also as a basis for management systems that emulate natural dynamics. Mosandl and El Kateb (1988) showed that seed production in such stands as studied here is at its maximum when they have a full unbroken canopy, and that the germination success is independent from overstorey density. Even in rather closed stands, temperature and light supply seem to be sufficient for germination and temporary seedling survival. However, for successful establishment of regeneration and ensuring its proper development, improving temperature and light conditions by opening the canopy is a requirement.

In general, the relationship between overstorey density and establishment and growth of the regeneration significantly depends on the site conditions. On fertile sites where overstorey stand density and therefore shading is higher, regeneration establishment requires heavier density reductions. On poor sites, in contrast, the overstorey canopy is often transparent enough for regeneration establishment and survival even at maximum stand density (Larsen and Johnson, 1998; Drever and Lertzman, 2001).

In mixed mountain forests, the species composition of regeneration is influenced by the pattern and intensity of canopy opening (Firm *et al*., 2009). Compared with beech or fir, regeneration of Norway spruce is more sensitive to site conditions. It generally germinates on thick humus layers, dead wood and on mineral soils but seedling development is heavily limited by competing weeds (Baier, 2006). Consequently, Norway spruce is rare in stands established by cutting small gaps but more common after larger disturbances, where it can more easily outgrow competing weeds.

Regeneration effects on overstorey growth

The growth distribution between the trees in forest stands changes during stand development. In young and dense stands, competition causes a concentration of growth on the dominant trees, while the canopy gaps in mature and old stands can favour the growth of smaller trees (Binkley, 2004; Binkley *et al*., 2006). The growth distribution between small and tall trees in forest stands can also vary spatially (Pretzsch and Dieler, 2011) and temporally (Wichmann, 2002) with site conditions. On fertile sites and in years with optimum conditions, growth concentrates strongly on the tall trees as they can better intercept light and suppress smaller neighbours. On poor sites and in less favourable years, competition and growth distribution is less size-asymmetric (Pretzsch, 2010; Pretzsch *et al*., 2012). Under such conditions, smaller trees grow more in relation to their taller neighbours, as the limited supply of water and nutrients reduces the advantage of taller trees in light competition (Schwinning and Weiner, 1998; Wichmann, 2002). Knapp (1991) showed that European beech regeneration on sandy soils in the north-eastern German lowlands can even reduce the growth of overstorey Scots pine; the lower the soil moisture and the higher the stand density, the stronger the growth reduction effect. Such an effect could be relevant for forest management, but has not been demonstrated in European mixed mountain forests.

Aims and objectives of the study

In the context of the above, an opportunity to study the stand dynamics of mixed mountain forests arose based on a set of long-term research plots located on sites of the Northern Limestone Alps. The questions examined in these stands were: (i) how the density of the mature overstorey affects its own growth rate, (ii) how the growing stock of the regeneration and the density of the overstorey affect the stem density, height and biomass of the regeneration and (iii) whether there are interactions between the understorey in terms of growing stock and the growth of the overstorey. Based on the answers, assets and drawbacks of the combined shelterwood–femel-coupe system are discussed and a further refinement is suggested.

Materials and methods

The mixed mountain forest trials Kreuth 120–126

Our study uses data from seven long-term monitoring trials known as Kreuth (KRE) 120, 121, 122, 123, 124, 125, 126 (Preuhsler, 1979). In total, they encompass 22 single plots, which were established between 1973 and 1975. All plots are located within a catchment of the Northern Limestone Alps in Bavaria (Southern Germany) near the town Kreuth close to the German–Austrian border between 11.63° E to 11.81°E and 47.60° N to 47.66° N (Figure 2 and Table 1). The plot sizes in horizontal projection vary between 1584 and 1773 m^2, except for the two plots of KRE124.

Here, topographic variability allowed plot sizes of 900 m^2 only. Plot locations were carefully chosen to represent typical stand structures.

Geologically, the area is shaped by sediments from the later Upper Triassic and early Jurassic (Lias) periods, providing Main Dolomite, Fleckenmergel-Facies and Koessen layers as basis for soil development. According to the world reference base for soil resources (IUSS Working Group WRB, 2014) the prevailing soil types are loamic cambisols. Locally, soils vary in humus amount in top soil and in groundwater influence resulting in phaeozems and gleysols, respectively.

All plots are situated in montane altitudes between 850 and 1240 m a.s.l. with northwest, northeast and south-facing aspects. Slopes range from moderate (~6°) to steep (up to 36°). The natural forest communities belong to the *Abieti-Fagetum* group (Preuhsler, 1979). The average mean annual temperature varies between 4 and 5°C for a 30-year mean and average annual precipitation is between 1600 and 2000 mm (see Table 1 for more details).

Most of the stands originated from clearcuts and artificial reforestation in the mid-nineteenth century, when wood was mainly used for the local salt exploitation process. Those harvests left some smaller trees, leading to a considerable variation in the current age distribution of these stands.

The Kreuth trials were established as artificial time series to represent different stages of the regeneration process at the same time. In 1975, when the plots were installed, the average stand age ranged between ~110 and 250 years with a broad age range at the plot level (Table 2). Only two plots were established in virtually untreated natural forests, which had been preserved due to limited accessibility.

The trials KRE 120–122 were designed to test different overstorey stand densities for their effect on regeneration establishment. Thus, their treatment followed a strict thinning regime with different intensities of basal area reduction, beginning in 1975. While one plot was always kept unthinned, reflecting undisturbed conditions and thus serving as a reference (plot number 3 in each trial), the other three plots were thinned to 80 per cent, 60 per cent and 40 per cent of the reference plot's basal area. For the 80 per cent type a shelterwood-coupe system was applied. In the cases of the 60 per cent and 40 per cent variants, regeneration was initiated by femel coupes of different sizes (Figure 1). The trials KRE 123–126 were established in stands that had previously had undergone a femel-coupe treatment in the mid-1960s. The idea behind these trials was to represent the locally applied silvicultural approach. According to local practice, thinning intensity depended on stand accessibility and the condition of existing regeneration. Subsequent plot management continued this approach without following compulsory thinning rates. Fellings were repeated every 10 years starting in 1975.

Key characteristics of the main stand and regeneration are described in Tables 2, 3 and 4, respectively. The dominant tree species in the main stand at the time of plot establishment were Norway spruce, silver fir and common beech accompanied by other broadleaved tree species including sycamore maple (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.) and whitebeam (*Sorbus aria* (L.) CRANTZ). In terms of stand basal area, Norway spruce accounted for the largest proportion at the time of plot establishment in 1975 (Table 2). The same was mostly true at the last survey in 2004, except that; in some cases silver fir made up the largest proportion (Table 3). The stand volumes in 1975 exhibited a broad range (75–908 m^3 ha^{-1}) which reflects the range of the applied treatments (Table 2). This range is quite similar to the last survey (129–1115 m^3), albeit on a somewhat higher level (Table 3). Mean annual volume increments at the time of the last measurement reflect the variety of stand densities with values between 3.6 and 15.2 m^3 ha^{-1} yr^{-1} (Table 3).

In 1975, tree density of regeneration >50 cm in height ranged between ~1000 and more than 6000 trees per ha, mostly dominated by common

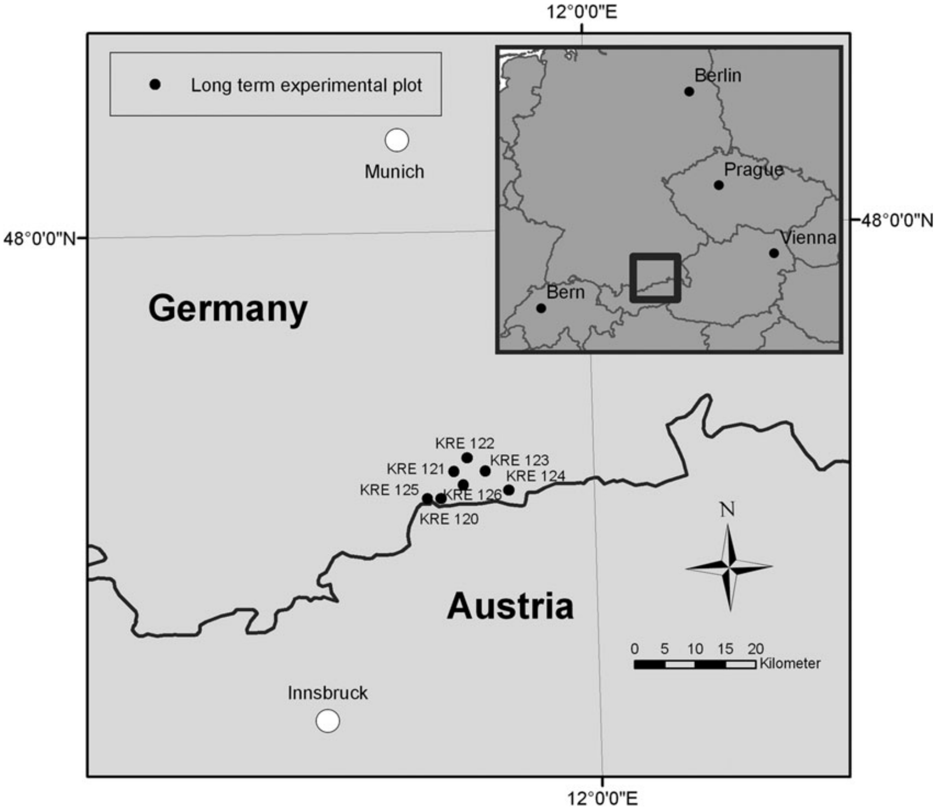

Figure 2 Geographic location of the long-term experimental plots Kreuth (KRE) 120–126.

Table 1 Long-term trials and plots used in this study – geographic, climatic and ecologic characteristics

Trial	KRE 120	KRE 121	KRE 122	KRE 123	KRE 124	KRE 125	KRE 126
Number of plots, *n*	4	4	4	3	2	3	2
Geographical position (°)	11.66 E, 47.60 N	11.69 E, 47.64 N	11.72 E, 47.66 N	11.76 E, 47.64 N	11.81 E, 47.61 N	11.63 E, 47.60 N	11.71 E, 47.62 E
Mean annual precipitation (mm a^{-1})	1600–2000						
Mean annual temperature (°C)	4–5						
Altitude (m a.s.l).	1080	1220	1240	1040	970	1040	850
Aspect	NW	NO	S	NW	S	NW	NO
Slope (°)	6–16	26–30	14–28	10–36	26	10–16	13–19
Geology	Main dolomite	Lias-Fleckenmergel	Koessen layers	Main dolomite			
Soil type	Brown soil	Oxigley (brown Soil)	Brown Soil	Brown Soil	Brown Soil Rendzina	Rendzina Terra fusca	Rendzina brown Soil
Natural plant association	Adenostylo-Glabrae-Abieti-Fagetum	Asperulo-Abieti-Fagetum	Asperulo-Abieti-Fagetum	Adenostylo-Glabrae-Abieti-Fagetum	Adenostylo-Glabrae-Abieti-Fagetum	Adenostylo-Glabrae-Abieti-Fagetum	Adenostylo-Glabrae-Abieti-Fagetum

beech and even more by other commercial broadleaved species, mainly sycamore maple; however, there were no differences in height among these species at that time (Table 4). Regeneration density in 2004 was mostly >10 000 trees per ha, ranging between 1300 and 44 000 with similar dominance relationships as mentioned before (Table 5). Average tree heights in the regeneration have approximately doubled since establishment (Tables 4 and 5).

Measurements

Four surveys (1975, 1985, 1995, 2004) were conducted on each plot. All trees with a diameter at breast height (dbh) >6.5 cm were defined as the main stand for which stem positions were recorded. At each survey, dbh was measured on all trees, while tree heights and height to crown base were recorded from representative samples. Each overstorey tree's crown radii were measured in all four cardinal directions on all plots in 1975 and 1985, and in 2004 on the plots 120/1 and 120/3 only.

Each main stand survey was accompanied by a full regeneration survey that included any tree with a dbh <6.5 cm. For the regeneration surveys the plots were divided into 5 × 5 m (1975) or 2.5 × 2.5 m (1985, 1995, 2004) squares, forming a grid that gaplessly covered the entire plot. Height of the regeneration was measured using 50-cm height classes (>0–50 cm, >50–100 cm, >100–150 cm, …). The surveys 1975 and 1985 subdivided the lowest class (>0–50 cm) into the classes >0–25 cm and >25–50 cm. Thus, the regeneration surveys yielded estimates of stem density, species and height class.

Standard plot evaluation

The DESER-standards (Johann, 1993) were applied to quantify wood volume V ($m^3\ ha^{-1}$), basal area BA ($m^2\ ha^{-1}$), quadratic mean diameter d_q (cm), mean height h_q (m) corresponding to d_g, dominant tree diameter d_{100} (cm), dominant height h_{100} (m), as well as periodic annual basal area and wood volume increment PAIBA ($m^2\ ha^{-1}\ yr^{-1}$) and PAIV ($m^3\ ha^{-1}\ yr^{-1}$), respectively. In addition, Reineke's (1933) stand density index, SDI for each survey was calculated. By averaging all SDI's from a given survey backwards to the survey when the first felling for promoting regeneration took place, the mean SDI, MSDI during the regeneration phase was obtained. MSDI expresses, in other words, the mean stand density under which regeneration developed from its origin up to a given survey. Mean basal area, MBA for the regeneration phase was obtained by the same averaging procedure as with MSDI. Main stand crown cover percentage CC was calculated for all appropriate surveys by plotting crown maps with crown shape approximations by cubic splines and taking the area covered by tree crowns from these maps.

For the purpose of this study, regeneration data were aggregated and summarized by plot, survey, species and height class. Species-specific and overall mean regeneration heights HR were then calculated by assuming all trees in one height class have the same height which was the middle height of the class. Regeneration stem density per hectare NR was obtained by summing up tree numbers across all height classes and dividing by the plot size in ha. In order to solely include well-established regeneration, only the height classes above 50 cm were taken into account in all calculations and evaluations.

Above-ground woody tree biomass for all overstorey trees was obtained by first estimating total above-ground tree volume v after Grundner and Schwappach (1952), i.e. using the following function which had been fitted to match the Grundner–Schwappach table values

$$\ln(v) = \alpha_0 + \alpha_1 \cdot \ln(\text{dbh}) + \alpha_2 \cdot \ln(h) + \alpha_3 \cdot \ln(\text{dbh}) \cdot \ln(h) \qquad (1)$$

with dbh as the diameter in breast height and h being total tree height. The species-specific parameters $\alpha_{0,\ldots,3}$ are listed in Supplementary data 1. Subsequently, these tree volumes were multiplied with species-specific dry wood densities as given by Trendelenburg (1939) resulting in above-ground

Table 2 Main stand characteristics of the trials KRE 120–126 at plot establishment in 1975

Trial		120				121				122			
Plot		1	2	3	4	1	2	3	4	1	2	3	4
Size (m^2)		1613	1652	1600	1592	1638	1639	1642	1635	1602	1560	1773	1740
Age (yr)		86–262	99–143	63–252	63–252	77–147	77–149	77–137	77–134	81–143	57–135	60–128	60–128
	Spruce	137	137	127	127	130	128	128	128	116	109	121	121
	Fir	137	137	127	127		128	128	128	116	109	119	119
	Beech	126	126	107	107	120	118	112	112	115	104	109	109
	Other bl species	126	126	107	107		118	112		115			
N/ha	Spruce	74	139	288	258	134	61	177	232	206	173	361	270
	Fir	56	54	181	88		6	12	12	12	13	85	57
	Beech	93	36	300	63	85	140	152	232	131	218	147	69
	Other bl species	62	103	125	144		18	6		12			
	Total stand	285	332	894	553	219	225	347	476	361	404	593	396
CC (%)		0.59		0.77	0.67	0.5	0.61	0.61	0.64	0.76	0.78	0.72	0.66
h_{100} (m)	Spruce	33.9	35.8	31.7	33.1	34.3	33.3	34.0	34.7	30.7	30.7	32.3	32.0
	Fir	28.8	29.1	29.1	30.1		18.8	34.5	30.7	25.6	28.6	32.0	32.3
	Beech	25.3	15.7	27.1	25.4	25.1	24.3	27.3	25.2	22.2	23.2	20.3	18.7
	Other bl species	23.5	20.4	21.2	24.3		22.4	23.3		17.8			
d_{100} (cm)	Spruce	51.0	54.8	48.4	49.5	62.8	57.2	61.1	65.0	48.4	48.1	57.7	55.5
	Fir	42.9	38.9	42.9	44.6		21.2	64.1	46.0	33.8	41.2	53.6	54.9
	Beech	33.2	20.8	35.2	27.5	36.7	33.9	45.8	37.0	26.0	28.5	21.8	19.1
	Other bl species	28.0	28.6	28.9	26.9		37.6	46.3		18.5			
BA (m^2 ha^{-1})	Spruce	13.0	25.2	27.2	28.2	31.3	14.1	36.0	46.2	24.4	22.1	56.3	43.5
	Fir	3.0	3.2	12.0	5.7		0.2	2.1	1.8	0.7	1.3	8.6	8.1
	Beech	2.4	0.7	7.2	1.2	4.6	6.6	9.8	10.8	3.5	4.8	2.6	0.8
	Other bl species	2.3	3.4	4.2	4.7		1.8	1.0		0.3			
	Total stand	20.8	32.4	50.6	39.8	35.8	22.7	48.9	58.8	28.8	28.1	67.5	52.5
V (m^3 ha^{-1})	Spruce	194.9	381.3	356.4	394.2	448.4	202.9	512.7	655.3	324.5	297.4	771.2	597.6
	Fir	35.5	39.7	141.6	69.0		2.1	31.8	26.2	8.1	17.1	116.9	115.7
	Beech	23.6	3.9	73.4	11.2	51.3	72.3	117.6	115.0	31.7	43.3	19.4	5.2
	Other bl species	23.2	30.3	40.6	46.0		20.1	12.4		2.4			
	Total stand	277.4	455.3	612.0	520.6	499.7	297.4	674.5	796.5	366.7	357.8	907.5	718.5

Trial		123			124		125			126	
Plot		1	2	3	1	2	1	2	3	1	2
Size (m^2)		1620	1600	1600	900	900	1600	1600	1701	1584	1602
Age (yr)		82–264	87–275	85–270	136–342	136–387	100–181	64–220	67–220	98–186	98–195
	Spruce	181	181	181	260	260	158	142	161	148	162
	Fir	181	181	181		260	158	142	161	148	162
	Beech	156	156	156	183	183	164	166	166	134	143
	Other bl species	156	156	156	183	183		166	166	134	143
N/ha	Spruce	62	94	250	44	78	94	69	206	101	50
	Fir	37	19	50		133	31	69	47	13	6
	Beech	49	69	131	22	67	25	150	41	246	275
	Other bl species	25	6	12	22	44		25	6	13	106
	Total stand	173	188	443	88	322	150	313	300	373	437

CC (%)		0.44	0.4	0.79	0.2	0.47	0.3	0.39	0.7	0.65	0.65
h_{100} (m)	Spruce	27.3	26.0	32.2	20.5	24.8	32.2	26.0	31.7	31.0	31.8
	Fir	24.9	27.8	27.9		25.5	32.3	29.1	32.5	21.6	28.5
	Beech	24.0	23.4	31.2	20.7	23.3	22.7	22.3	20.9	22.9	23.3
	Other bl species	22.1	21.8	22.2	18.2	19.6		27.0	24.1	25.9	24.4
d_{100} (cm)	Spruce	41.8	38.8	56.2	33.5	44.7	51.4	34.8	49.8	46.9	50.2
	Fir	43.7	52.2	52.3		46.9	54.3	47.2	54.6	29.5	58.3
	Beech	36.0	34.8	53.4	38.4	44.7	34.5	33.2	29.5	33.2	34.2
	Other bl species	35.4	34.3	36.1	26.9	31.0		39.3	32.5	39.1	34.7
BA (m^2 ha^{-1})	Spruce	4.9	6.4	32.8	3.7	5.9	15.3	3.5	25.4	12.2	6.3
	Fir	4.8	4.0	4.3		10.0	6.0	9.2	6.0	0.8	1.7
	Beech	2.2	3.1	15.0	2.6	7.2	1.5	6.3	1.3	9.2	8.7
	Other bl species	2.3	0.6	1.2	1.2	2.8		2.8	0.5	1.4	7.1
	Total stand	14.2	14.1	53.3	7.5	25.9	22.9	21.7	33.2	23.6	23.7
V (m^3 ha^{-1})	Spruce	59.1	71.6	422.3	36.5	60.7	214.0	35.8	338.5	164.5	86.1
	Fir	56.7	55.0	46.0		103.0	89.3	118.7	81.6	9.2	21.8
	Beech	28.3	35.7	218.4	27.5	79.4	16.1	61.0	11.2	88.3	81.7
	Other bl species	25.4	6.4	13.7	11.1	26.7		38.0	6.0	18.9	80.2
	Total stand	169.5	168.7	700.4	75.2	269.8	319.4	253.5	437.4	280.9	269.8

Age = stand age; N = tree number; bl = broadleaved; CC = crown coverage; h_{100} = dominant height; d_{100} = dominant diameter; BA = basal area; V = stand volume.

woody tree biomass. Stand biomass W and its periodic annual increment PAIW were then obtained by totalling tree biomass per survey and calculating differences between subsequent surveys, respectively.

The same procedure was, in principle, applied to the regeneration, assuming that the height of regeneration trees was the middle height of the height class to which they belonged. As regeneration trees' dbh was not available from measurements, we used an allometric equation of the form

$$\ln(\mathrm{dbh}) = \alpha_0 + \alpha_1 \cdot \ln(h) \tag{2}$$

that had been previously fitted for a large set of regeneration trees down to heights of 1.3 m (the species-specific parameter values for $\alpha_{0,\,1}$ are listed in Supplementary data 2). Depending on the species, this results in estimates of dbh = 1.1 cm (Norway spruce, silver fir) and 0.5 cm (European beech) which is fully plausible and in line with the data used for fitting. Although dbh is technically not defined for trees lower than 1.3 m, we extrapolated equation (2) to the smaller heights represented in our data and obtained diameters (pseudo-dbh) which, of course, cannot be interpreted as dbh anymore. However, we considered them allometrically plausible stem diameters.

Using the volume function given by equation (1) – which represents a three-dimensional plausible allometric relationship – for heights below 1.3 m together with the corresponding stem diameter estimates, leads us to reasonable volume estimates given the available information. Our approach profits from the fact that dbh, due to its fixed measurement height, is only an approximate fundamental allometric scaling variable. Thus, strictly speaking, the allometric relationship between dbh and h (equation (2)) would require a slight (practically mostly irrelevant) non-allometric correction if any possible bias in dbh estimation should be avoided, as the allometry described in equation (2) demands dbh to converge towards zero when h converges towards zero. The same is true for allometric volume estimations based on dbh as shown above (equation (1)). Insofar, our pseudo-dbh acts as a fundamentally allometric stem diameter which leads to plausible allometric volume estimates.

Multiplying these volumes with species-specific wood densities as described above yielded biomass estimates which were in line with allometric theory and were, after several comparisons with available data, accepted as realistic. Aggregating this information we obtained summaric regeneration biomass WR and its periodic annual increment PAIWR. Although our regeneration biomass estimates are based on several assumptions, and even if there is some bias involved, this would not affect our statistical results on stand level. This is because the volume estimation and subsequent biomass conversion is based on the fundamental principle of allometry, which ensures biological plausibility in terms of size–volume–biomass relations and the estimates' order of magnitude.

Statistical methods

All statistical evaluations presented in this study were conducted with mixed linear models of the following form:

$$\begin{aligned} y_{ijk} &= \beta_0 + \beta_1 \cdot x_{1_{ijk}} + \beta_2 \cdot x_{2_{ijk}} + \ldots + \beta_{n_{ijk}} \cdot x_{n_{ijk}} + b_i + b_{ij} + \varepsilon_{ijk} y_{ijk} \\ &= \beta_0 + \beta_1 \cdot x_{1_{ijk}} + \beta_2 \cdot x_{2_{ijk}} + \ldots + \beta_{n_{ijk}} \cdot x_{n_{ijk}} + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned} \tag{3}$$

Here, y is the response variable, and $x_1, \ldots, x_n$ are the explanatory variables. The indices i, j, k represent the trial level (e.g. KRE 120, 126, …), the plot-in-trial level (e.g. plot 1 in trial KRE 120), and the survey level (e.g. survey, 1975 of plot 1 in trial KRE 120), respectively. The fixed-effects parameters are $\beta_0, \ldots, \beta_n$, where b_i and b_{ij} represent trial and plot specific random effects ($b_i \sim N(0;\, \sigma_1^2)$, $b_{ij} \sim N(0;\, \sigma_2^2)$), and ε_{ijk} are i.i.d errors ($\varepsilon_{ijk} \sim N(0;\, \sigma_3^2)$). This mixed model formulation avoids biased results that might result from the nested error structure of the data.

Specifically, for analyzing the relationship of stand biomass W and stand crown cover CC with the periodic annual stand biomass increment PAIW

Table 3 Main stand characteristics of the trials KRE 120–126 at the last survey in 2004

Trial		120				121				122			
Plot		1	2	3	4	1	2	3	4	1	2	3	4
Age (yr)	Spruce	166	166	156	156	161	157	157	157	145	138	150	150
	Fir	166	166	156	156		157	157	157	145	138	148	148
	Beech	155	155	136	136	151	147	141	141	144	133	138	138
	Other bl species	155	155	136	136	20	147	141		144			
N/ha	Spruce	37	67	144	138	92	37	97	122	93	160	254	149
	Fir	49	48	100	69		6	6	6	12	13	62	34
	Beech	55	24	256	50	37	55	49	183	106	154	141	52
	Other bl species	105	91	106	126	61	42	6		68			
	Total stand	246	230	606	383	190	140	158	311	279	327	457	235
h_{100} (m)	Spruce	34.1	36.2	32.1	33.5	38.5	39.0	38.2	39.1	35.6	36.1	38.1	37.7
	Fir	30.0	30.3	28.2	31.7		20.9	39.8	34.9	30.2	31.4	35.8	35.6
	Beech	26.3	24.9	29.7	30.6	29.7	28.9	29.5	28.8	23.3	23.6	21.4	19.0
	Other bl species	27.3	20.8	21.5	26.8	13.5	25.7	27.0		11.8			
d_{100} (cm)	Spruce	51.7	58.1	49.5	51.0	66.9	69.0	65.5	69.5	54.6	56.9	67.0	65.0
	Fir	45.4	47.1	41.0	48.4		25.8	73.4	53.1	44.4	48.3	66.4	65.5
	Beech	35.0	33.3	42.4	37.9	44.9	41.2	43.7	40.8	34.8	35.8	28.8	23.3
	Other bl species	34.1	32.0	31.7	30.8	13.7	43.6	52.0		16.9			
BA (m^2 ha^{-1})	Spruce	6.5	16.5	17.4	18.3	29.9	13.7	29.3	35.2	16.0	29.9	60.8	40.9
	Fir	4.8	4.7	7.4	5.9		0.3	2.6	1.4	1.0	1.8	9.3	8.8
	Beech	2.8	1.4	10.2	2.1	4.0	4.7	4.5	11.9	6.6	6.0	3.5	1.3
	Other bl species	2.9	3.0	5.1	5.6	0.4	2.7	1.3		0.5			
	Total stand	17.0	25.7	40.1	32.0	34.3	21.4	37.6	48.5	24.2	37.8	73.6	51.0
V (m^3 ha^{-1})	Spruce	98.7	252.3	237.0	263.0	475.8	220.0	465.3	557.3	243.3	460.2	950.5	645.2
	Fir	65.5	64.2	90.3	77.3		3.4	45.0	22.1	14.1	26.3	136.7	138.0
	Beech	34.9	15.8	126.3	28.2	58.5	67.0	64.3	157.6	72.7	59.3	28.0	9.6
	Other bl species	34.6	28.5	52.1	64.8	1.8	34.1	18.4		2.0			
	Total stand	233.7	360.8	505.7	433.3	536.1	324.6	593.1	737.0	332.1	545.9	1115.2	792.8
PAIBA (m^2 ha^{-1} yr^{-1})	Spruce	0.1	0.1	0.1	0.1	0.4	0.2	0.3	0.3	0.2	0.4	0.6	0.5
	Fir	0.1	0.1	0.1	0.1		0.0	0.0	0.0	0.0	0.0	0.1	0.1
	Beech	0.1	0.0	0.1	0.0	0.0	0.1	0.1	0.2	0.2	0.1	0.0	0.0
	Other bl species	0.0	0.0	0.1	0.1		0.0	0.0		0.0			
	Total stand	0.3	0.3	0.3	0.3	0.4	0.3	0.4	0.5	0.5	0.5	0.7	0.6
PAIV (m^3 ha^{-1} yr^{-1})	Spruce	1.2	1.7	1.4	2.0	7.8	3.9	6.5	7.7	4.1	7.6	12.8	10.4
	Fir	1.4	1.3	1.0	1.5		0.1	0.8	0.6	0.8	0.4	2.0	2.3
	Beech	1.6	0.5	2.2	0.7	1.0	1.1	1.5	3.1	2.7	1.1	0.4	0.3
	Other bl species	0.5	0.4	0.6	0.8		0.6	0.4					
	Total stand	4.8	3.9	5.2	5.1	8.7	5.8	9.1	11.4	7.6	9.1	15.2	13.0

Trial		123			124		125			126	
Plot		1	2	3	1	2	1	2	3	1	2
Age (yr)	Spruce	210	210	210	289	289	187	171	190	177	191
	Fir	210	210	210		289	187	171	190	177	191
	Beech	185	185	185	212	212	193	195	195	163	172
	Other bl species	185	185	185	212	212	30	195	195	163	172
N/ha	Spruce	99	106	119	378	78	50	62	106	57	37
	Fir	43	88	19		122	206	62	53	13	
	Beech	167	457	75	678	56	137	162	111	195	212
	Other bl species	223	162	12	266	33	350	44	12	26	94
	Total stand	532	813	225	1322	289	743	330	282	291	343
h_{100} (m)	Spruce	29.9	31.0	31.8	25.1	28.2	32.5	29.2	29.9	34.6	34.9
	Fir	28.9	31.6	30.6		29.4	32.0	31.7	31.3	28.9	
	Beech	28.5	29.1	31.4	24.7	27.1	21.7	23.0	22.8	27.2	27.7
	Other bl species	22.8	23.3	23.6	20.6	21.4	16.3	24.5	23.4	27.8	27.0
d_{100} (cm)	Spruce	48.7	52.4	55.1	45.4	56.4	52.9	29.2	45.0	54.8	56.7
	Fir	55.8	66.6	62.2		58.8	57.2	31.7	53.1	48.3	
	Beech	46.1	47.7	54.0	48.5	55.7	33.1	23.0	39.4	40.7	42.7
	Other bl species	38.4	41.0	42.3	34.5	38.0	13.7	24.5	35.1	47.3	42.1
BA (m^2 ha^{-1})	Spruce	6.2	11.9	17.7	5.5	9.9	8.3	5.1	12.2	9.2	5.0
	Fir	8.3	6.9	3.2		16.2	9.1	11.4	7.1	2.3	
	Beech	4.4	9.1	13.2	7.5	9.8	1.1	11.0	2.5	10.8	13.8
	Other bl species	3.6	1.7	1.5	3.1	3.0	1.9	3.5	0.6	2.1	9.8
	Total stand	22.7	29.6	35.6	16.1	38.9	20.5	30.9	22.5	24.4	28.6
V (m^3 ha^{-1})	Spruce	75.2	153.6	233.5	40.8	112.8	118.7	59.7	158.7	137.0	74.0
	Fir	110.0	94.3	41.5	65.2	197.1	121.2	164.9	100.9	31.2	
	Beech	57.3	106.4	210.5	65.2	131.2	7.7	120.9	24.7	138.7	177.7
	Other bl species	34.8	14.3	17.4	23.4	31.6	9.1	43.4	6.9	30.4	131.8
	Total stand	277.4	368.6	502.9	129.4	472.7	256.6	388.9	291.1	337.4	383.5
PAIBA (m^2 ha^{-1} yr^{-1})	Spruce	0.1	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Fir	0.1	0.1	0.1		0.3	0.1	0.1	0.1	0.1	0.0
	Beech	0.1	0.1	0.1	0.0	0.1	0.1	0.2	0.0	0.2	0.2
	Other bl species	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.1
	Total stand	0.3	0.5	0.4	0.1	0.5	0.3	0.4	0.3	0.4	0.4
PAIV (m^3 ha^{-1} yr^{-1})	Spruce	1.1	4.6	2.5	0.8	1.8	2.1	1.0	2.2	2.4	0.1
	Fir	2.3	1.3	1.0		4.0	0.9	1.9	0.9	1.0	0.0
	Beech	1.0	2.1	2.6	0.7	1.9	0.9	2.1	0.5	3.4	0.2
	Other bl species	0.1	0.0	0.1	0.1	0.1			0.0	0.4	0.1
	Total stand	4.6	8.0	6.2	1.6	7.9	3.9	5.0	3.6	7.3	0.4

Age = stand age; *N* = tree number; bl = broadleaved; h_{100} = dominant height; d_{100} = dominant diameter; BA = basal area; *V* = stand volume; PAIBA, PAIV = periodic annual basal area and volume increment.

Table 4 Regeneration characteristics (tree height >50 cm) of the trials KRE 123–126 at plot establishment in 1975

Trial	Plot	Year	Avg. age	Tree number per hectare						Mean tree height (m)					
				Total	Spruce	Fir	Beech	Commercial broadleaved	Other broadleaved	Average	Spruce	Fir	Beech	Commercial broadleaved	Other broadleaved
123	1	1975	10	6401	31	25	901	5420	25	0.91	0.75	0.75	0.86	0.92	1.13
123	2	1975	10	7150		31	3675	3406	38	0.85		0.75	0.85	0.85	0.83
124	1	1975	16	3822	56		1089	1967	711	0.87	0.75		0.77	0.92	0.88
124	2	1975	16	1056	89		56	667	244	0.83	0.75		0.75	0.88	0.77
125	1	1975	15	2900	38	238	856	1506	263	0.85	0.75	0.76	0.76	0.90	0.94
125	2	1975	15	1038	13	25	281	531	188	0.79	1.00	0.75	0.75	0.78	0.85
125	3	1975	15	1552			553	847	153	0.77			0.77	0.76	0.83
126	1	1975	10	5133	158	6	3504	1389	76	0.95	0.87	0.75	1.00	0.84	1.00
126	2	1975	10	3446	506		1567	1336	37	0.93	1.06		0.95	0.85	1.00

The trials KRE 120–122 are not listed as there was no regeneration higher than 50 cm in 1975.

Table 5 Regeneration characteristics (tree height >50 cm) of the trials KRE 120–126 at the last survey

Trial	Plot	Year	Avg. age	Tree number per hectare						Mean tree height (m)					
				Total	Spruce	Fir	Beech	Commercial broadleaved	Other broadleaved	Average	Spruce	Fir	Beech	Commercial broadleaved	Other broadleaved
120	1	2004	29	32 343	787	1258	7328	22 951	19	1.29	1.09	1.05	1.41	1.27	1.25
120	2	2004	29	19 752	593	2397	1071	15 666	24	1.25	0.97	1.02	1.43	1.28	1.50
120	3	2004	29	7719		25	1769	5925		0.95		0.75	0.83	0.98	
120	4	2004	29	15 917	107	760	6539	8511		1.50	0.96	0.93	1.30	1.71	
121	1	2004	29	7910	107	18	4213	3573		1.39	0.86	0.75	1.20	1.63	
121	2	2004	29	10 866	61	12	4625	6168		1.54	0.95	0.75	1.38	1.67	
121	3	2004	29	16 985	12	30	6888	10 055		1.20	1.00	0.75	1.05	1.30	
121	4	2004	29	8899		18	5058	3823		1.08		0.75	1.01	1.17	
122	1	2004	29	6660	1254	368	2378	2559	100	1.72	1.21	1.53	1.29	2.39	1.78
122	2	2004	29	4506	122	212	1308	2865		1.33	0.83	0.95	1.09	1.49	
122	3	2004	29	2059	11	152	632	1263		1.05	1.00	1.10	0.98	1.08	
122	4	2004	29	1328	213	454	167	494		1.22	0.82	0.89	1.09	1.74	
123	1	1995	30	31 975	1667	889	7772	21 463	185	1.92	1.17	1.12	1.78	2.06	1.98
123	2	1995	30	27 113	1081	1694	10 769	13 488	81	1.99	1.12	1.26	2.30	1.90	3.87
124	1	1995	36	35 944	1600	78	19 456	12 722	2089	2.12	2.35	0.96	2.05	2.08	2.94
124	2	1995	36	12 167	767	11	6989	3000	1400	1.23	1.26	0.75	1.05	1.34	1.88
125	1	1995	35	29 413	1025	2894	8150	15 731	1613	1.90	1.20	1.44	1.97	1.91	2.68
125	2	1995	35	43 631	856	1569	19 588	20 163	1456	1.39	0.98	0.91	1.53	1.26	1.92
125	3	1995	35	26 520	400	1922	10 306	12 228	1664	1.83	0.98	0.97	1.94	1.81	2.42
126	1	1995	30	22 487	549	202	9905	11 528	303	1.24	0.94	0.88	1.41	1.10	1.95
126	2	1995	30	28 483	1142	162	13 596	12 672	911	1.34	1.01	0.92	1.42	1.23	2.08

from the period subsequent to a given survey, two different regression models were used:

$$\mathrm{PAIW}_{ijk} = \beta_0 + \beta_1 \cdot W_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \quad (4)$$

$$\ln(\mathrm{PAIW}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(\mathrm{CC}_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (5)$$

The same analysis was also conducted with stand volume V, crown cover CC and the periodic annual stand volume increment PAIV:

$$\mathrm{PAIV}_{ijk} = \beta_0 + \beta_1 \cdot V_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \quad (6)$$

$$\ln(\mathrm{PAIV}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(\mathrm{CC}_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (7)$$

In order to link overstorey density with variables that express the stage of regeneration establishment, several regression models were developed to relate regeneration stem density NR, mean regeneration height HR and regeneration biomass WR to the main overstorey's density index MSDI during the regeneration phase and the corresponding duration of the regeneration phase ΔT up to the observation of interest. Those models were:

$$\ln(\mathrm{NR}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(\mathrm{MSDI}_{ijk}) + \beta_2 \cdot \ln(\Delta T_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (8)$$

$$\ln(\mathrm{HR}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(\mathrm{MSDI}_{ijk}) + \beta_2 \cdot \ln(\Delta T_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (9)$$

$$\ln(\mathrm{WR}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(\mathrm{MSDI}_{ijk}) + \beta_2 \cdot \ln(\Delta T_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (10)$$

The dependency of the overall and species-specific regeneration tree numbers NR from main stand biomass W and ΔT was analysed with

$$\ln(\mathrm{NR}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(W_{ijk}) + \beta_2 \cdot \ln(\Delta T_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (11)$$

The relationship between the regeneration's biomass increment PAIWR, the main stand's biomass W and its own biomass WR was analysed as follows:

$$\ln(\mathrm{PAIWR}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(W_{ijk}) + \beta_2 \cdot \ln(\mathrm{WR}_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (12)$$

Analogously, the main stand's biomass increment PAIW was related to its own biomass W and the regeneration's biomass WR:

$$\ln(\mathrm{PAIW}_{ijk}) = \beta_0 + \beta_1 \cdot \ln(W_{ijk}) + \beta_2 \cdot \ln(\mathrm{WR}_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \quad (13)$$

These models were selected from our theoretical understanding of the system's behaviour rather than empirical investigations of the data. Note that the models described by equations (4) and (6) have PAIW and PAIV

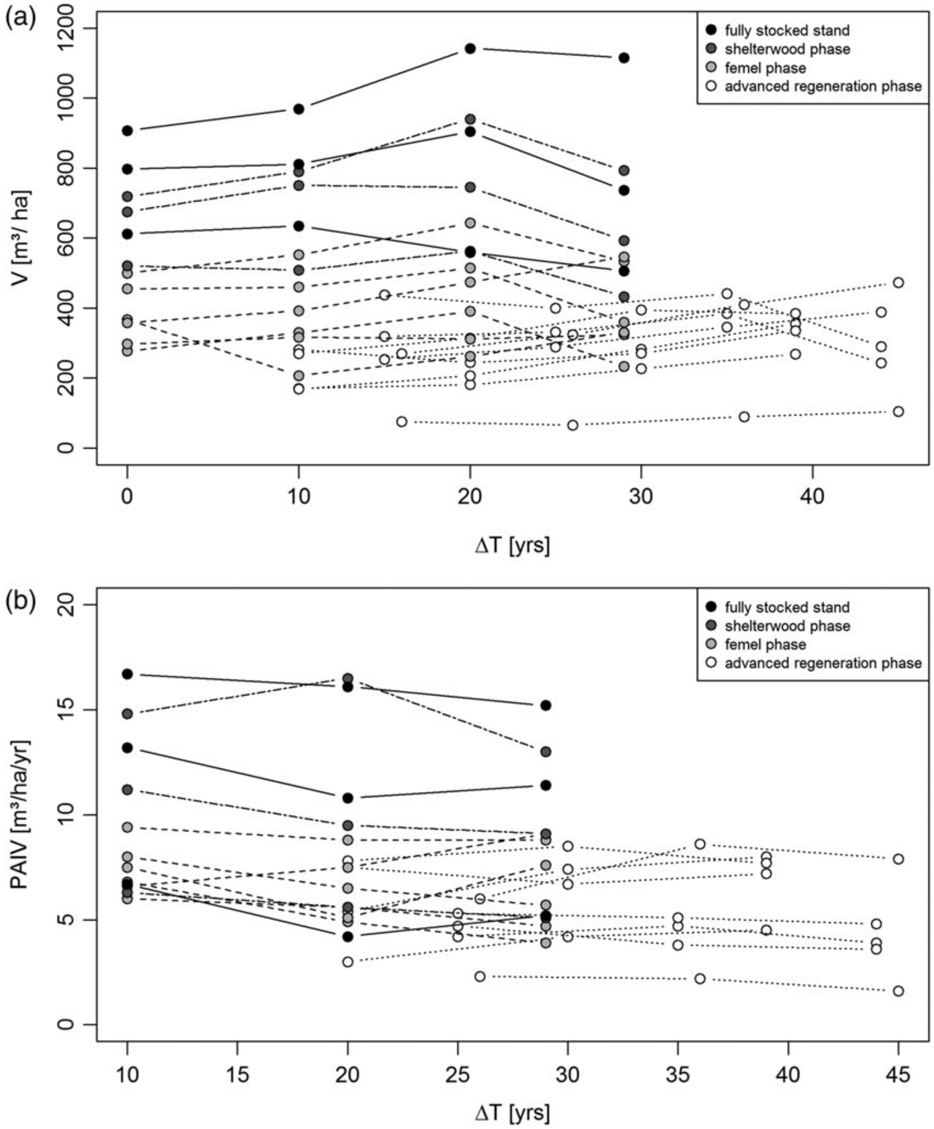

Figure 3 Development of the standing overstorey volume (a) V and (b) mean periodic annual overstorey volume growth PAIV on the experimental plots KRE 120–126 over the time ΔT since the start of the regeneration process in 1975. The trajectories represent the performance for plots in the unthinned phase (black circles), shelterwood phase (dark grey), femel-coupe phase (light grey) and advanced regeneration phase (white).

Table 6 Regression results for stocking density and growth of the main stand (equations (4)–(7))

Equation no.	β_0	β_1	σ_1^2	σ_2^2	σ_3^2	n
4	**1.3321** (0.3337)***	**0.0099** (0.0011)***	0.3284	0.1966	0.1660	66
5	**−1.6752** (0.5287)**	**0.7224** (0.1347)***	0.0327	0.0372	0.0101	24
6	**2.5882** (0.7500)**	**0.0102** (0.0011)***	1.8976	0.9802	0.8668	66
7	−0.9559 (0.5667)	**0.7256** (0.1437)***	0.0627	0.0322	0.0184	24

Significance levels P for $\beta \neq 0$: *$P < 0.05$. **$P < 0.01$. ***$P < 0.001$. Significant parameter estimates are given in bold. Standard errors for the fixed-effect estimates are given in parentheses.

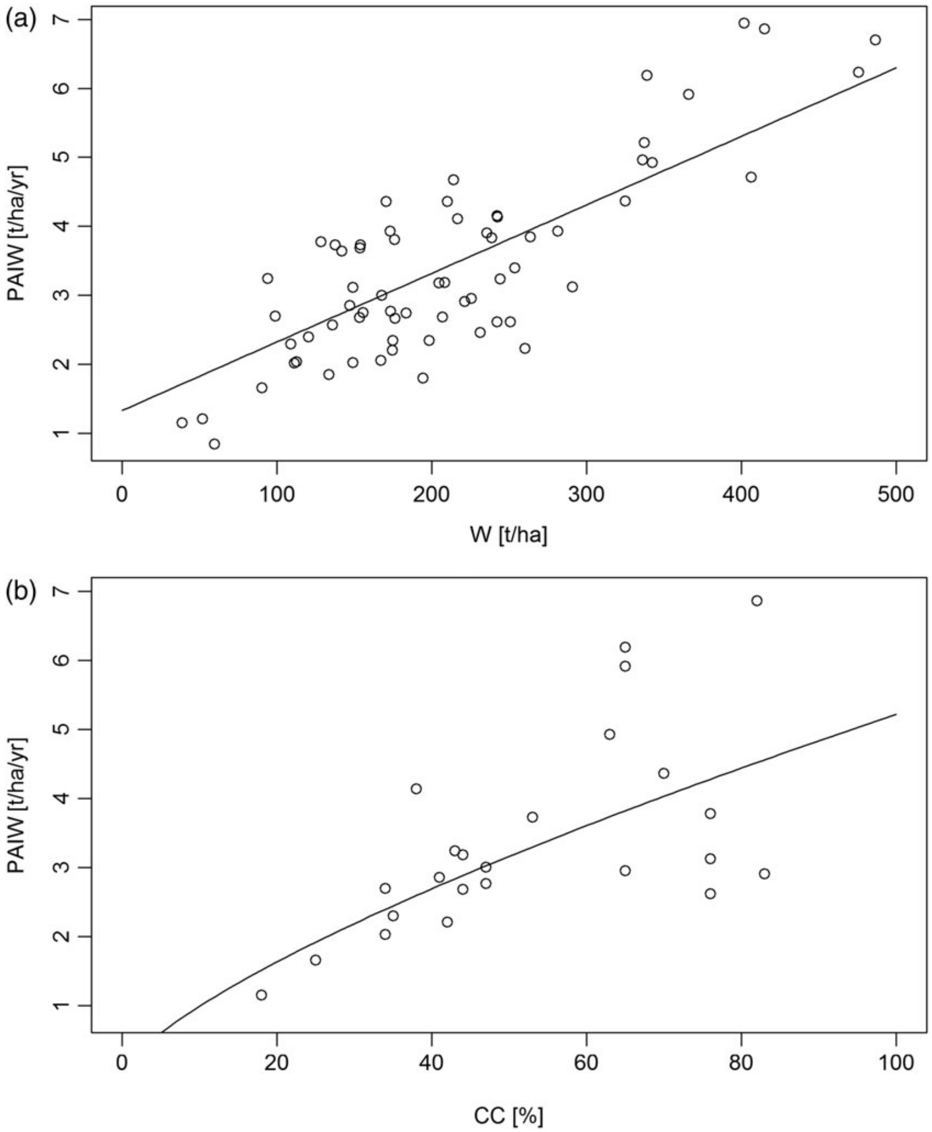

Figure 4 Density and growth of the overstorey on the experimental plots KRE 120–126. The periodic annual biomass increment PAIW decreases nearly linearly with both (a) stand biomass *W* of the overstorey and (b) canopy cover percentage CC on the plots. The former relationship was fitted with a linear model (equation (4)), the latter with a log-linear one (equation (5)). See Table 6 for the parameter estimates and significances.

as the dependent variables, while in equations (5), (7) and (13) their logarithms are used. From a theoretical point of view, this is a contradiction, because the former assumes an additive error structure while the latter assumes a multiplicative one. However with our data a decision for one of both assumptions was not substantiated, as in both cases the obtained residuals did not give a clear indication of departure from the assumptions of normality. Thus, we decided on a case-by-case basis which model best described the relationships of interest.

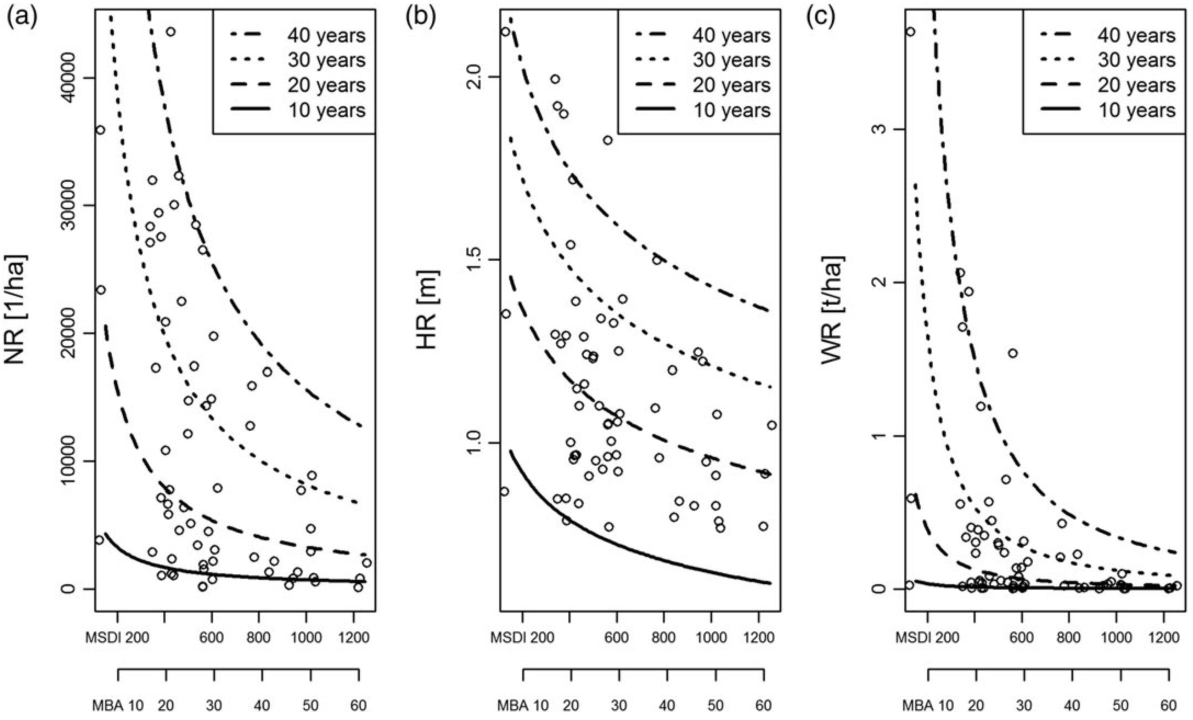

Figure 5 Effect of the overstorey stand density (represented by mean SDI and MBA per hectare during the regeneration phase, MSDI and MBA) and length of the regeneration period (10–40 years) on (a) regeneration tree number NR, (b) mean regeneration tree height HR and (c) standing biomass of the regeneration WR. The observed regeneration progress (empty circles) is modelled in dependence from stand density and length of the regeneration period (see equations (8)–(10), parameter estimates in Table 7). The presented regeneration variables refer to the sum and the mean over all tree species, respectively; for species-specific results, see Figure 7.

Table 7 Regression results for regeneration variables depending on main stand's density and duration of the regeneration phase (equations (8)–(11))

Equation no.	Regeneration species	β_0	β_1	β_2	σ_1^2	σ_2^2	σ_3^2	n
8	All	**8.0399** (1.2259)***	**−0.9675** (0.1741)***	**2.2498** (0.1432)***	0.7945	0.0000	0.2309	63
9	All	−0.2436 (0.4281)	**−0.2188** (0.0606)***	**0.5720** (0.0546)***	0.0037	0.0052	0.0155	63
10	All	−3.0557 (1.7356)	**−1.6223** (0.2493)***	**3.5735** (0.2069)***	1.0407	0.0000	0.4824	63
11	All	**5.5459** (1.0047)***	**−0.7514** (0.1752)***	**2.3541** (0.1515)***	0.6825	0.0130	0.2557	63
11	Norway spruce	0.5921 (2.3267)	−0.6602 (0.4509)	**2.5684** (0.3144)***	1.1039	0.4460	0.6993	50
11	Silver fir	**−8.0870** (2.5237)**	0.6586 (0.4929)	**2.9553** (0.2300)***	2.2425	1.4881	0.2768	48
11	European beech	**3.8284** (1.5317)*	**−0.9187** (0.2665)**	**2.7898** (0.2480)***	1.0449	0.0000	0.6888	63
11	Commercial broadleaved	**5.4771** (1.1842)***	**−0.7333** (0.2189)**	**2.1350** (0.1472)***	0.7189	0.0926	0.2388	63
11	Other broadleaved	−0.7823 (1.9774)	0.0330 (0.3442)	**1.9099** (0.3786)***	0.6034	0.0000	1.0277	48

Significance levels P for $\beta \neq 0$: *$P < 0.05$. **$P < 0.01$. ***$P < 0.001$. Significant parameter estimates are given in bold. Standard errors for the fixed-effect estimates are given in parentheses. Variance values of 0.0000 are to be understood as rounded to four decimals.

All analyses were conducted using the free software R version 3.0.3 (R Core Team, 2014), namely the package nlme (Pinheiro *et al.*, 2013) for fitting mixed models.

Results

Stocking density and growth of the main stand

The stocking density on the 22 plots had a constantly wide range and provided a good basis for the analysis of overstorey and regeneration interactions (Figure 3a). The standing volume amounted to >1000 m^3 ha^{-1} on the fully stocked plots and decreased to <100 m^3 ha^{-1} on plots in the advanced regeneration phase. The mean periodic volume growth varied between 17 m^3 ha^{-1} yr^{-1} on the fully stocked plots and 2.5 m^3 ha^{-1} yr^{-1} in the advanced regeneration phase (Figure 3b). Compared with the mean growth rate of all forests in Southern Germany of 11.9 m^3 ha^{-1} yr^{-1} (Bayerische Landsesanstalt für Wald und Forstwirtschaft, 2014), the mountain forests in this study represent highly productive ecosystems when fully stocked in their mature phase. The decline in standing volumes or volume increments on some of the unthinned plots reflects storm and bark beetle damages that occurred in the region in the 1990s (Röhle, 1997). Continuous increases in both variables despite repeated thinnings on some of the other plots reflect widespread positive growth trends in the pre-alpine forest ecosystems since the 1980s (Pretzsch *et al.*, 2014).

The decrease in overstorey growth when overstorey stocking density is gradually reduced during the regeneration process was analysed on the basis of both volume and biomass (equations (4)–(7); see Table 6 for parameter estimates and significances). The results that are based on biomass eliminate the effects of the species' different shoot morphologies and wood gross density. Decrease in standing biomass reduces growth linearly in these stands (Figure 4a, equation (4)); removal of 100 t ha^{-1} results in a growth reduction of ~1 t ha^{-1} yr^{-1}. Figure 4 shows the growth reaction over canopy cover percentage which was modelled by a log-linear approach (equation (5)). When canopy cover decreases by 1 per cent the growth rate decreases only by 0.7 per cent (see regression parameters for equation (5) in Table 6). That means overstorey growth decreases linearly with a reduction of standing biomass, but non-linearly by a reduction of standing canopy cover. Although this is a seemingly subtle effect only, it is nevertheless significant and indicates that a cover reduction has less impact on the growth rate at higher canopy cover values than in situations when the canopy cover is already low. With our parameter estimates (Table 6) inserted in equation (5), a canopy cover reduction from 80 to 60 per cent leads to an expected increment reduction by 0.83 t ha^{-1} yr^{-1}, while the increment reduction is 1.06 t ha^{-1} yr^{-1} when reducing canopy cover from 40 to 20 per cent. In both cases the reduction amounts to 20 per cent points. This reflects that a removal of overstorey trees reduces the degree of stocking in terms of biomass, volume and basal area stronger than the canopy cover (Assmann, 1970). Canopy cover buffers density reductions most efficiently when starting at higher levels of canopy cover (Figure 4b), because after thinning, trees can extend their crown radii and crown volume quickly, through accelerated lateral growth and changing branch angles (Bayer *et al.*, 2013). Especially slight cover reductions at comparatively high canopy cover levels may be fully compensated after a short time. Growth reaction in terms of compensation of removed biomass or volume takes much longer.

The same analysis with overstorey volume and its growth as the dependent variables instead of biomass (equations (6) and (7), parameter estimates in Table 6) produces virtually the same result. In all cases, growth decreases significantly ($P < 0.001$) with thinning. Seen from another perspective, growth increased most significantly with stand density. The estimates of the slope parameter β_1 are remarkably similar between the biomass based equations and their volume counterpart (Table 6, equations (4) and (6), and (5) and (7), respectively). Evidently, species-specific morphology and wood densities obviously did not play a major role in the presented relationships.

Main stand density and natural regeneration establishment

In the early phase of regeneration, the overstorey stocking density in a stand does not affect the total stem density, mean tree height and standing biomass of the regeneration. Especially for stem density and regeneration biomass, only small differences under heavily thinned as well as fully stocked stands were found (Figure 5a, c). However, as the duration of the regeneration phase increases, stem density (Figure 5a), mean tree height (Figure 5b) and standing biomass (Figure 5c) increase considerably under a heavily and moderately opened overstorey, but only negligibly under a fully stocked main stand. During the 40-years-long

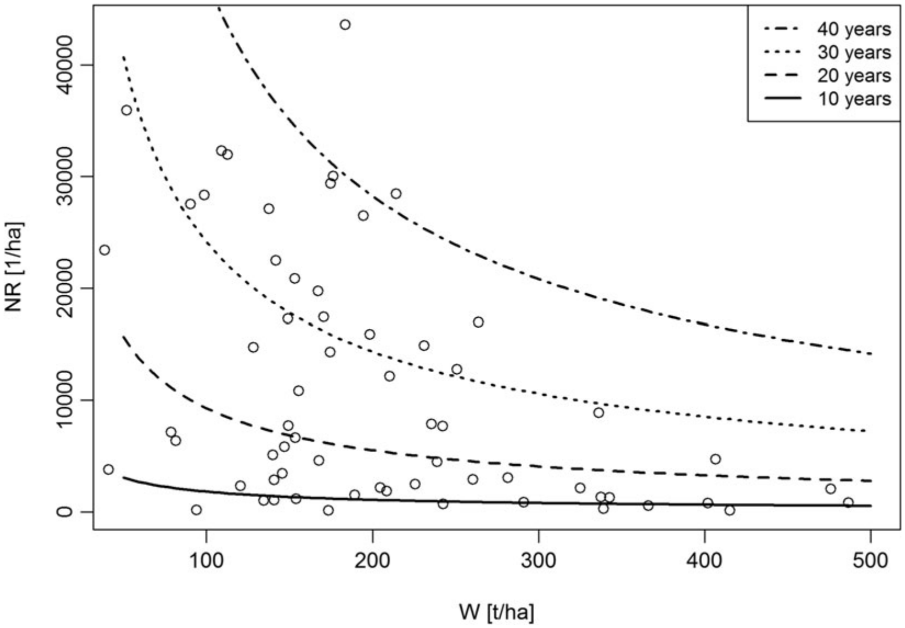

Figure 6 Relationship of regeneration stem density NR with the stand biomass *W* and the duration of the regeneration period (10–40 years). The observed progress of the regeneration (empty circles) is modelled depending on the stand biomass and the length of the regeneration period (see equation (11), parameter estimates in Table 7).

regeneration process, the number and the size of upcoming trees continuously increased and filled up the understorey when the canopy had been opened up heavily or moderately. Under a slightly opened or closed canopy in contrast, regeneration stem density and tree size are developing so slowly that a new stand generation might not be established even after 40 years.

In the respective statistical models (equations (8–10), parameter estimates in Table 7), both overstorey MSDI and length of the regeneration period show a significant effect on the development of the regeneration. The course of the regression lines in Figure 5 underlines that a substantial regeneration success may be promoted by a strong and long-term reduction in the SDI of the overestorey.

With progressing regeneration time period and opening of the canopy (cf. equation (11) and Table 7), total regeneration stem density increases up to 40 000 stems per hectare (Figure 6). However, the species' proportions are rather different (Figure 7). The regeneration is dominated by European beech and other commercially valuable broadleaved species such as sycamore maple and European ash. Both groups show a significant increase in regeneration stem density with progressing regeneration time and canopy opening. The tendency is similar for Norway spruce, however, its stem density amounts to only about a tenth compared with common beech and other commercially valuable broadleaved species, and the influence of stand density is not significant. Conversely, regeneration stem density of silver fir and other broadleaved species do not significantly depend on overstorey density (cf. Table 7); however, with progressing length of the regeneration process, a considerable number of trees become established under both dense and closed canopies. The ability of silver fir to establish and keep a considerable number of regeneration trees despite being found beneath dense overstoreys and mixed with dense regeneration of other species is a key reason for the typical species combination in these spruce–fir–beech mixed mountain forests.

Interaction between overstorey growth and regeneration growth

The biomass growth of the regeneration in relation to its biomass stock follows the same allometric slope independent from overstorey density (Figure 8, based on equation (12), parameter estimates in Table 8). However, the denser the overstorey, the lower is the relationship, which suggests that regeneration growth is

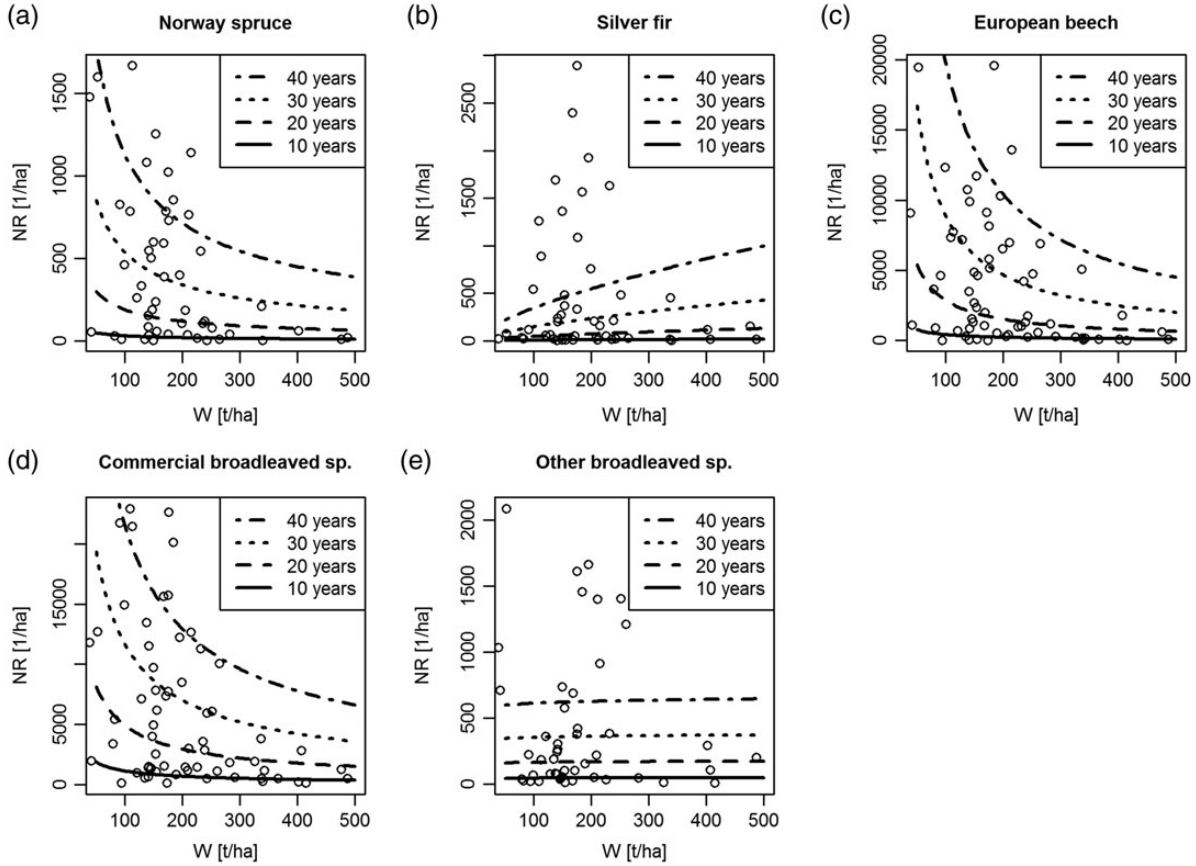

Figure 7 Relationship between regeneration stem density by species NR from the stand biomass *W* and the length of the regeneration period (10–40 years) displayed for (a) Norway spruce, (b) silver fir, (c) European beech, (d) other commercially valuable broadleaved species such as sycamore maple and European ash and (e) other broadleaved species such as whitebeam and aspen. The observed progress of the regeneration (empty circles) is modelled depending on the stand biomass and the length of the regeneration period (equation (11), parameter estimates and significances in Table 7). Note that the scale of the ordinate (stem density) varies by species. Also note that only the time effect (not the biomass effect) is significant for Norway spruce, silver fir, and other broadleaved species. For all other species both, time effect and biomass effect are significant.

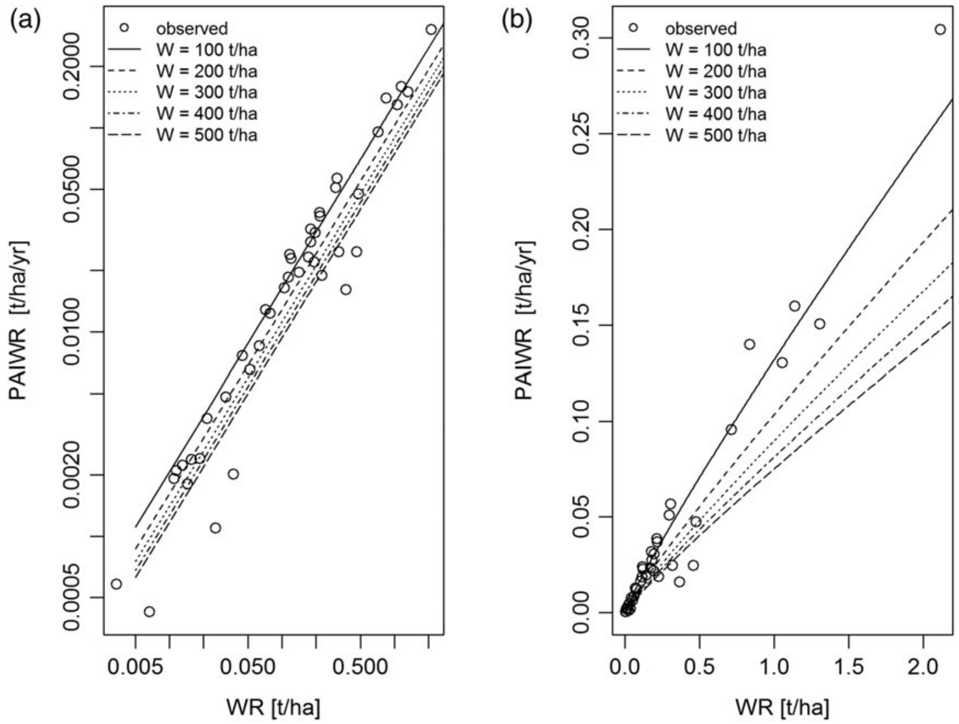

Figure 8 Regeneration biomass growth PAIWR over regeneration biomass WR in (a) double logarithmic and (b) linear representation. Left: The relationship between PAIWR and WR follows the same allometric slope for all densities of the overstorey (W). However, the denser the overstorey, the lower is the intercept of the allometric relation. Right: Significant increase of PAIWR with both WR and reduced density (expressed through *W*) of the overstorey. For model functions and parameters see equation (12) and Table 8

Table 8 Regression results regeneration's and main stand's biomass increment against main stand's and regeneration's biomass (equations (12) and (13))

Equation no.	β_0	β_1	β_2	σ_1^2	σ_2^2	σ_3^2	*n*
12	−0.4123 (0.7198)	**−0.3504** (0.1494)*	**0.9023** (0.0530)***	0.0130	0.0000	0.1414	42
13	**−2.0900** (0.4557)***	**0.6165** (0.0876)***	0.0019 (0.0209)	0.0560	0.0191	0.0148	42

Significance levels *P* for $\beta \neq 0$: $^{*}P < 0.05$. $^{**}P < 0.01$. $^{***}P < 0.001$. Significant parameter estimates are given in bold. Standard errors for the fixed-effect estimates are given in parentheses. Variance values of 0.0000 are to be understood as rounded to four decimals.

significantly reduced by competition from above. This becomes even more evident when the relationships are displayed along untransformed coordinate axes (Figure 8b) and when the overstorey biomass is used for the abscissa (Figure 9a).

Thus, regeneration growth is significantly modified by the overstorey biomass as well as by the regeneration biomass stock in the respective survey period. Both modify regeneration growth significantly but in different ways. The effect of the overstorey is clearly negative: an overstorey stock increase from 100 to 500 t ha^{-1} approximately halves the regeneration growth rate (Figure 8b). In contrast, a regeneration biomass increase from 0.1 to 1.3 t ha^{-1} more than doubles the regeneration growth on both plots with sparse as well with full overstorey (Figure 9a). In other words, the regeneration growth is clearly limited by the overstorey but not regeneration density itself. The latter can even be increased ~10-fold without any negative effect on the productivity of the regeneration per hectare. The parameter estimate $\beta_2 = 0.90$ in equation (12) (Table 8) with 1 being inside the estimate's 95 per cent confidence interval indicates a virtually linear increase of regeneration growth with regeneration biomass.

The regeneration biomass stock has no significant effect on overstorey growth (Figure 9b, equation (13), parameter estimates in Table 8); at all levels of overstorey density the relationship between overstorey biomass growth and regeneration biomass runs virtually parallel to the horizontal axis. The hypothesis that regeneration affects the overstorey either positively (e.g. by improving the upper soil layer or accelerating nutrient turnover) or negatively (e.g. by competition for mineral nutrients or water) does not appear to be supported by our data.

The growth rate of the overstorey increases significantly but subproportionally with the main stand's biomass (Figure 9b, equation (13), parameter estimates in Table 8). An increase in overstorey growing stock of 100 t ha^{-1} is, in sparsely stocked stands, coupled with an increase in overstorey biomass growth by ~1 t ha^{-1} (lower

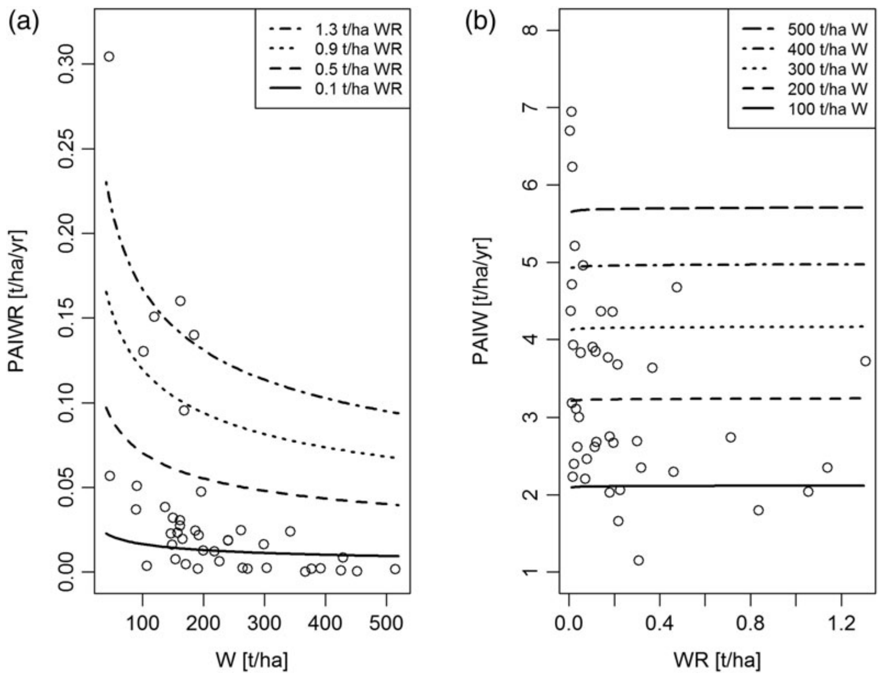

Figure 9 Relationships affecting the productivity of overstorey and regeneration on the experimental plots 120–126. (a) Effect of the overstorey biomass *W* and the regeneration biomass WR on the growth of the regeneration PAIWR. (b) Effect of the regeneration biomass WR and the overstorey biomass *W* on the overstorey productivity PAIW (for model functions and parameters see equations (12), (13) and Table 8).

two lines in Figure 9b). With progressing growing stock accumulation from 100 to 500 t ha^{-1}, the additional growth decreases.

Discussion

Overstorey growth and feedback between overstorey and understorey as crucial system attributes

The key growth processes in the period of generation overlap are shown as a system diagram in Figure 10. The obvious fact that the overstorey growth is mainly determined by the overstorey stock is depicted by the feedback loop overstorey stock → overstorey growth → overstorey stock. Results from this study show that overstorey growth decreases almost proportionally when the overstorey stock is reduced. This matches earlier findings by Preuhsler (1989) but is different from the post-thinning reaction patterns usually identified in pure even-aged stands as well as in selection forests, where growing stock reductions can be buffered in a way that growth does not decrease before the stock is strongly reduced (Mosandl and El Kateb, 1988). From our point of view this is due to the different spatial impact of conventional thinnings in contrast to gap cutting for initiating regeneration as conducted on our research plots Typically, thinnings are more or less homogeneously performed across a stand; they do not create large open patches in the canopy, which enables a rather quick canopy closure after the treatment. By concentrating on delimited spots, gap-cutting creates longer-lasting openings with less potential to recover by understorey or lateral crown extension from the remaining overstorey trees. Results from this study underline that the feedback between understorey stock and understorey growth is also positive; the denser and more advanced the understorey, the greater its growth.

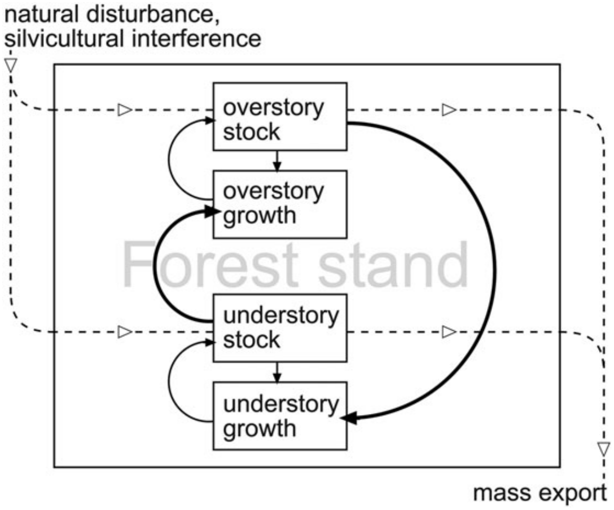

Figure 10 Development of overstorey and understorey with feedback between both represented in a system diagram. Growth in both, overstorey and understorey, depends primarily on the current growing stock in both cohorts (feedback loops stock → growth→ stock, depicted by thin arrows). Beyond this, the overstorey stock may affect the understorey growth and the understorey stock may affect the overstorey growth (feedback overstorey stock → understorey growth and understorey stock → overstorey growth depicted with bold arrows).

However, the cause–effect relationship between overstorey stock and the growth of the understorey in terms of its tree number, tree height and biomass development is negative. This effect, which is probably caused mainly by competition for light, is crucial for understanding and regulating the stand dynamics in the phase of generation overlap. Any influences of the understorey stock on the overstorey growth which might be caused by competition for water or mineral nutrients were not significant. This would have closed a negative feedback loop (overstorey stock → understorey growth → understorey stock → overstorey growth → overstorey stock) which might lead to equilibrium-like conditions between overstorey and understorey stocks. Results of previous work (Knapp, 1991) suggest such a loop being in effect on less fertile sites where light is not the main limiting resource. It is assumed that the supply of water and nutrients in the ecosystems studied is sufficient for both layers, and that light rather than the soil-bound resources limits growth.

The prevailing shading effect of the overstorey on size growth, density and species composition of the natural regeneration in temperate forests is well documented for early gap phases (Lertzman, 1992;1995; Drever and Lertzman, 2001;2003; Baier *et al*., 2007). The same applies for the competition between the understorey trees (Ammer, 1996). In contrast, an effect of forest floor vegetation, tree regeneration and understorey density on overstorey growth has been tested very rarely for lowland forests (Knapp, 1991; Messier *et al*., 1998; Booth, 2004) and not at all for multi-layered mountain forests. Even less is known about the long-term growth and structure dynamics of overstorey and understorey and the resulting growth and yield characteristics per hectare. Many short term studies emphasize the need for long-term results and their relevance for better understanding the ongoing dynamics (Mosandl and El Kateb, 1988), for modelling (Bugmann, 2001; Wehrli *et al*., 2005) and for the full assessment of silvicultural concepts (Mosandl and El Kateb, 1988). However, to our knowledge the present study is the only one that analyses the outcome of the combined shelterwood–femel-coupe concept in mountain forests from the beginning to the end of the regeneration phase.

Artificial and true time series as research basis

Research plots that represent an artificial age series, sometimes called growth series, are a traditional design for working with pure stands, but have been increasingly applied to mixed, rich-structured stands as well (Pretzsch, 2009). In the absence of long-term experimental plots, where age development is documented in long-term observations (real-time series), artificial time series can be constructed from adjacent stands spanning the desired spectrum of stand development phases (Figure 11, vertical chronosequence). For this purpose, a series of plots are set up under comparable, previously defined site conditions. After establishment, a complete inventory of each plot is carried out, which may include the extraction of core samples for reconstructing past growth. The sample plots cover the entire age spectrum of interest (e.g. age of plot 1 ≙ 40 years, age of plot 2 ≙ 90 years, . . ., age of plot 6 ≙ 150 years) so that the plots together represent the stand development over time.

The plots used in this study were established in the 1970s as an artificial time series, because long-term observations (Figure 11, horizontal sequence) of overstorey and regeneration development in mixed mountain forests were not available at that time (Preuhsler, 1979). With continued plot surveys now covering 40 years of development, the originally artificial time series has essentially become a real-time series study.

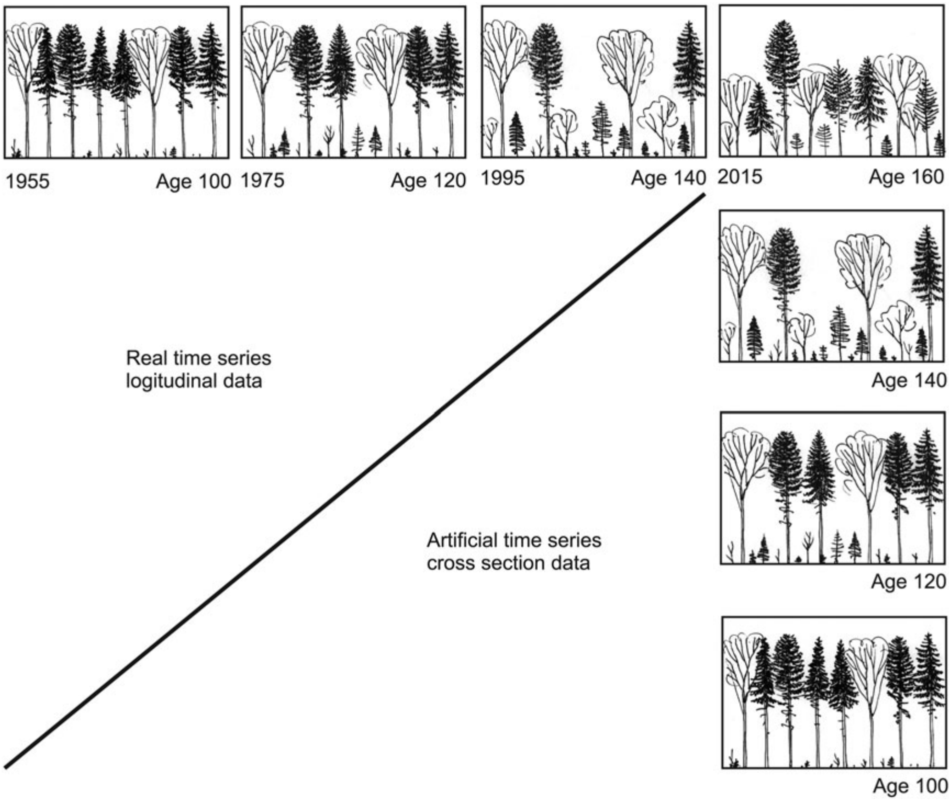

Figure 11 Concept of the artificial time series for analyzing dynamics of the main stand, regeneration and interaction between over- and understorey.

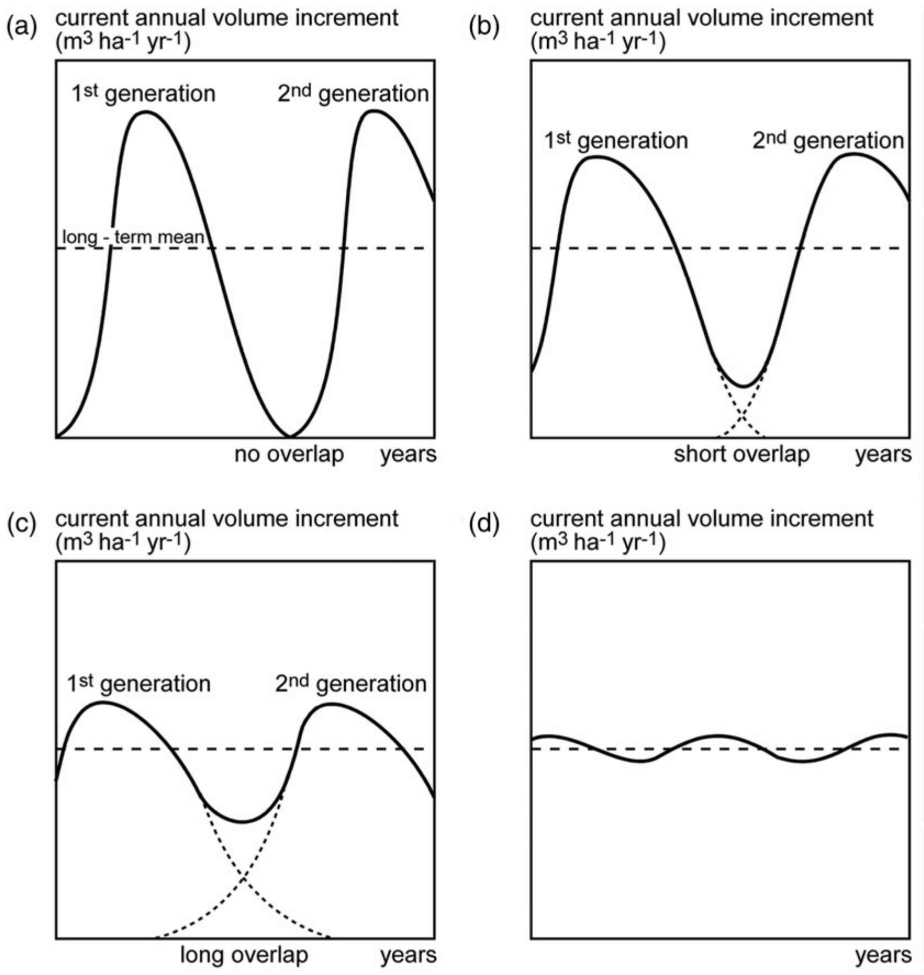

Figure 12 Schematic representation of the current volume increment for four different silvicultural model procedures: (a) Clearcut system without generation overlap, (b) short overlap, (c) long generation overlap between successive stand generations and (d) selection forest system. The longer the overlap between trees or cohorts of different ages and sizes the more steady the course of current volume increment (adapted from Assmann, 1970, p. 473).

This transition from artificial to real-time series overcomes the problem that, by using pure artificial time series data, one might confound the effects of treatment and the ongoing change of site conditions. The younger stands in the series probably grow under site conditions different from those prevailing when the older stands were at the same age (Pretzsch *et al*., 2014). By combining artificial and true time series data we can cover and analyse all phases of the 40–60 years lasting shelterwood- and femel-coupe procedure already after 40 years of survey. This approach which required application of mixed linear models with trial and plot specific random effects is a model example of how to quickly achieve preliminary answers to questions coming from silvicultural practice.

Ecological implications

The silvicultural model usually applied in mixed mountain forests lies in the continuum spanned and restricted by the extremes of the age-class model on the one hand (Figure 12a) and the selection forest on the other hand (Figure 12d). In age-class forests (Figure 12a) the current volume increment follows a unimodal curve over time and decreases to zero at the time of transition to the next forest generation. In the selection forest (Figure 12d) the combination of trees of many age classes, sizes and species results in a rather steady course of current volume increment, as the stand area is continuously covered at rather a high level of stand density and growth.

Giving that the overlap between the overstorey and the next generation lasts ∼40–60 years, the stands in this study lie in between these borderline cases (Figure 12b, c). During the time of generation overlap, volume increment of regeneration and overstorey add up. Thus, compared with an age-class forest, the total volume increment's oscillations are much less distinct. The more multi-layered a stand, and the more horizontally diverse it is, the higher is its growth resilience to natural and silvicultural interferences. In our stands, the long-term average volume increment amounts to ∼10 $m^3 ha^{-1} yr^{-1}$ which is rather similar to nearby selection forests on comparable sites (Pretzsch, 2009, p. 74).

Implications for forest management

Forty years of overstorey and regeneration survey allow a first assessment whether the applied silvicultural concept is appropriate for emulating the natural regeneration dynamics of spruce–fir–beech mountain forests. Assessment criteria are the regeneration success in terms of species composition and size, stand stability in the transition phase and productivity in the overlap phase. Without human interference, the natural regeneration of spruce–fir–beech mountain forests would be set off on small gaps caused by the death of a single tree or small cohort of trees, and on larger gaps that result from disturbances like landslides, avalanches or bark beetle calamities.

Our data show that natural regeneration establishment in these forests requires patience. Even when overstorey density had been reduced by >50 per cent, regeneration density (not >5000–20 000 plants per hectare) and regeneration heights are still rather low 10–20 years after the initial shelterwood coupe. However, albeit slowly, continuous seed production, seedling establishment and sapling ingrowth permanently fills the regeneration stock, so that 20–40 years after start 15 000–40 000 stems per hectare, mostly beech and other deciduous species, have become established. The portion of silver fir is sufficient as it grows rather independently from stand density, but even at that time Norway spruce regeneration is still rather sparse with 500–1500 trees per hectare. Probably, there are not enough spots with adequate soil conditions for successful spruce establishment, and the rare individuals often get outcompeted by either weed or more shade tolerant tree species. The recent decades' large-regional growth acceleration reported especially in European beech (Pretzsch *et al*., 2014), could have changed the competitive relationship in favour of beech on our plots.

Re-thinking the combined shelterwood- and femel-coupe system on the basis of the long-term survey results

The low frequency, small size and unbalanced species composition of the natural regeneration still 20 years after the initiation of the shelterwood coupe (see Figures 6 and 7) suggests that the applied light opening up is too cautious. Effectively stimulating regeneration seems to require higher canopy opening rates. This calls into question the benefit of the 10–20-year shelterwood phase. Leaving out the shelterwood phase and starting directly with a stronger opening up of the canopy at two to four selected spots per hectare in mature stands would probably accelerate the regeneration dynamics. This strategy may even better emulate the natural gap dynamics of this mountain forest ecosystem. Larger gaps and their continuous extension within the advanced femel phase will also improve the light conditions, and initiate and maintain any upcoming regeneration inside the still closed parts of the stand. Concentrating harvest more than before on gaps may improve soil conditions and create a more favourable light ecology for Norway spruce regeneration, will accelerate the size growth of all species, and shorten the regeneration process by one or two decades. As the upcoming of silver fir is neither impeded by overstorey nor by the understorey, all species in the regeneration might benefit from stronger and more concentrated gap creation. However, the linear reduction of overstorey growth with the decrease of overstorey stand density (Figure 4a) suggests that implementing this type of management will be to some extent on the expense of the remaining overstorey's productivity. However, a more rapidly developing understorey will provide better balance for any overstorey growth reduction.

Conclusions

About 50 years after inducing natural regeneration and based on 40 years of continuous measurements, the following conclusions for silvicultural practice can be drawn from this study: it is advisable to start the regeneration process in closed stands with stronger density reductions compared with the presently applied light shelterwood cuts. These density reductions of ∼20–40 per cent should be concentrated on 2–4 larger gaps per hectare. A lower or more homogenously distributed basal area reduction will make the available seedlings disappear again as deep shade recurs in the stand. Conversely, a stronger basal area reduction risks weed development in a way that the desired natural regeneration might get outcompeted. Reduction of the overstorey density is coupled with roughly a proportional overstorey growth reduction. Consequently, a reduction by 20–40 per cent may reduce the mean annual overstorey increment by ∼20–40 per cent, but part of this loss is counterbalanced by an additional growth of the upcoming understorey. In summary, the timespan needed for a complete stand regeneration may be shortened by 1–2 decades by skipping the shelterwood phase, establishing stronger initial femel coupes with faster subsequent gap widening.

On our plots, over a 40-year period after the initial shelterwood coupe, the natural regeneration is continuously restocked with new seedlings and saplings. However, even decades after initiating regeneration, Norway spruce is likely to be rare in the regeneration compared with fir, beech and other broadleaved species. Further observation will show whether spruce will catch up on the long run or whether additional conceptual changes like larger disturbances than gap and femel coupes or even planting will be required.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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