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ORIGINAL PAPER

Growth response of advanced planted European beech (*Fagus sylvatica L.*) after storm-caused loss of shelterwood

Johannes Weidig[1] · **Sven Wagner**[1]

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Abstract

Outcomes after an abrupt, storm-caused loss of spruce shelterwood (*Picea abies* L. Karst.) overstories on advanced planted beech (*Fagus sylvatica L.*) were investigated, including effects of developmental stage and beech stand density on growth after release. Six years after overstorey loss by storm Kyrill in January 2007, heights and root collar diameters were measured, along with annual length of the main shoot and ring widths of the stem and strongest branch. No significant difference in the total height of released and sheltered beeches was found at six years after shelter loss, but annual growth of the main shoot of released beeches increased from the second year after release. Overall growth patterns of released and sheltered beech differed significantly. Diameter growth and that of the strongest branch increased strongly after shelter loss. Height-to-diameter ratio (H/RCD) indicated that sheltered beeches with higher densities were slenderer. However, no differences were found in growth response between young stands and beech in the thicket live stage. Overall, advanced planted beech beneath a spruce shelterwood of medium canopy closure showed vigorous height growth and a qualitatively desired form. Sudden release of the planted beech enhanced diameter growth of stem and branches, which is undesirable for timber quality. Findings suggest that advanced planted beech should not be released by abruptly cutting the shelterwood. Instead, with stepwise canopy opening beech should gradually adapt to the open conditions.

Keywords Beech · Advanced planting · Thicket life stage · Shelter loss · Growth reaction · Tree ring analysis · Branch growth

Introduction

European beech (*Fagus sylvatica* L.) has a high shade tolerance (Niinemets and Valladares 2006; Ewald 2007; Jarcuska 2009; Annighöfer et al. 2017). Also, protection from extreme climatic events, such as late frost and drought, is of major importance in early developmental stages (Brown 1951; Otto 1994; Niinemets and Valladares 2006). Optimal conditions for young beech are found under moderate canopy cover, and this is taken into consideration in artificial regeneration of the species. In forest conversion of Norway spruce (*Picea abies* L. Karst.) monocultures, advanced planting of beech beneath thinned spruce shelters is common (Spellmann and Wagner 1993; Otto 1995; Hering et al. 1999; Butter 2001; Leitgeb et al. 2005; Eckardt and Arenhövel 2006; Röhrig et al. 2006; Löf et al. 2010). Spruce shelter also serves as a silvicultural tool to regulate resource availability for regeneration (Ammer 2000; Löf et al. 2007) and to control growth and quality development of beech regeneration by partial cutting of shelterwood. Canopy cover densities should ensure continuous, vigorous height growth of young beech, while limiting diameter and branch development. Under appropriate conditions, high proportions of well-formed phenotypes are expected (Leonhardt and Wagner 2006; Hertrampf 2009; Linnert 2009).

Against the background of climate change and the associated rise in the frequency of extreme weather events, such as storms and droughts (Thomasius 1991; Beniston et al. 2007; Majunke et al. 2008; Usbeck et al. 2010), uncertainties about the required durability of thinned spruce shelters exist. Thus, the growth and quality control of advanced planted beech beneath a shelter of spruce, is questionable. Recent

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✉ Johannes Weidig
Johannes.Weidig@forst.hessen.de

[1] Institute of Silviculture and Forest Protection, Technische Universität Dresden, Pienner Str. 8, 01737 Tharandt, Germany

experiences showed that mature spruce stands are particularly prone to storm damage (Bräunig and Dieter 1999; Dobbertin et al. 2002; Löf et al. 2010; Schmidt et al. 2010) that can result in a sudden loss of overstorey that protects the advanced planted beech. Then half-shade-adapted beeches are immediately exposed to substantially different environmental conditions (Aussenac 2000), and effects on development of the planted beech remain uncertain.

Morphological plasticity is a well-studied characteristic of *Fagus spec.* Beech species show remarkable stature adaptations to variation in gap dynamics and changes in light regime beneath canopy covers (Canham 1988; Beaudet and Messier 1998; Planchais and Sinoquet 1998; Cao 2001; Valladares et al. 2002; Curt et al. 2005; Kunstler et al. 2005; Collet et al. 2011; Schall et al. 2012). Nevertheless, it remains unknown how young beech, adapted to half-shade, reacts to abrupt environmental changes, i.e. total shelter removal. A few insights are provided by Collet et al. (2001), Beaudet et al. (2007), Barna et al. (2009) and Annighöfer (2018). These studies, however, only refer to naturally regenerated beech which grew beneath dense canopy cover before overstorey removal. No studies regarding growth reactions or quality development of advanced planted beech related to abrupt loss of a shelterwood cover are known. To address that knowledge gap we studied the growth and quality development of advanced planted beech after mature spruce shelters were blown down by the storm KYRILL in January 2007. The following questions were addressed:

- Are there detectable differences in diameter and height between released and still sheltered advanced planted beech six growing seasons after the storm event?
- What is the pattern of annual height and diameter increment after shelter loss?
- How does abrupt release affect the diameter growth of branches and, thus, the quality of beech regeneration, and what is the relationship between the increments of branch and stem?
- How does developmental stage (young stand *vs.* thicket life stage) and density (intraspecific competition) of advanced planted beech affect growth and quality development after shelter loss?

This study contributes to an understanding of the adaptive capacity of young beech in the case of sudden changes in environmental conditions. A linkage between growth and quality development is established. Based on these findings, recommendations are made for the silvicultural management of mature spruce stands above advanced planted beech.

Methods

Study site and stands

Two regions in the low mountain range of Thuringian and Saxonian state forest (Germany) have site characteristics commonly for forest conversion of mature spruce stands through advanced planting of beech (Fig. 1). Here the climatic conditions are humid, with an annual mean temperature of 6.6–8.8 °C and total annual precipitation of 750–1100 mm. The bedrock consists of granite, gneiss, slate or porphyry, in part with loess evolved (podsol) cambisols of (low) moderate trophic level and medium water supply. Based on site and stand characteristics, 29 representative stands were selected. Seventeen had lost the shelterwood overstorey during January 2007. The remaining stands, still sheltered, served as a reference (Table 1). In case of four stands affected by storm, portions escaped damage, and the overstorey shelterwood remained intact. We used these as reference stands. In other parts, the shelterwood was lost and we used these as released stands. Overall, the difference in height between sheltered and released beech was not significant at time of shelter loss (Table 1), which supports the thesis of previously equal growing conditions across the stands before shelter loss.

For the reference stands, overstorey canopy closure was visually estimated. Previous studies showed that canopy closure of 40–50% is the best compromise between vigorous growth and quality development of advanced planted beech (Weihs and Klaene 2000; Hertrampf 2009). Therefore, reference plots were established under spruce stands within this range of canopy closure only.

Each advanced planting was characterized by its developmental stage. These stages represent the natural age of advanced planted beech at the time of shelter loss and are independent from actual tree age. The differentiation criteria

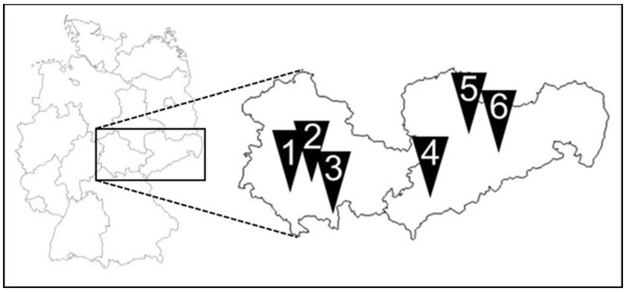

Fig. 1 Location of the six state forest enterprises in which the study was carried out in the German federal states of Thuringia (1: Oberhof, 2: Frauenwald, 3: Sonneberg) and Saxony (4: Eibenstock, 5: Chemnitz, 6: Bärenfels). Maps modified from: https://d-maps.com/carte.php?num_car=17879&lang=de

Table 1 Characteristics of investigated stands at time of storm Kyrill in January 2007 in relation to developmental stage and canopy cover

		Sheltered	Released
Young stands stage	Age of spruce canopy	57–147 a	57–113 a
	Stocking level of spruce	15–35 m^2 ha^{-1}	24–35 m^2 ha^{-1}
	Age of beech	7–15 years	7–12 years
	Mean height at release (SD)	2.1 m (0.8)	2.0 m (0.7)
	Number of stands[1]	11	8
	Number of plots	49	59
Thicket live stage	Age of spruce canopy	72–118 a	82–105 a
	Stocking level of spruce	21–27 m^2 ha^{-1}	21–38 m^2 ha^{-1}
	Age of beech	10–20 years	10–20 years
	Mean height at release (SD)	4.3 m (1.2)	4.1 m (1.5)
	Number of stands[1]	5	9
	Number of plots	39	57

Height of advanced planted beech was reconstructed by backward measurement of annual main shoot length for period 2007 to 2012. *SD* standard deviation (m)

[1] In four stands, shelterwood was wind thrown on a part of the stand area only. So these stands were separated in two investigation stands and included as released and sheltered once both

included crown closure of the advanced planted beech, incipient natural pruning and average height of more than 3 m. Beech plantings with these criteria were characterized as “thicket live stage”. Others were designated as “young stand stage” (Table 1).

Because of heterogeneous conditions within the advanced plantings, a grid design was used to determine sample units for measurement within the stands. Each grid square was 20 m wide, with the grid intersection points used as the centre of 19.95 m^2 sample plots (radius: 2.52 m). In total, 204 representative plots were selected. Within these plots, the stand density of advanced plantings was determined and extrapolated to stem number ha^{-1}. We found a range of 500 to 12.000 ha^{-1}.

Measurements

Data collection focused on the most vigorous individuals (potential target trees). The six tallest trees per plot were selected. If the total number of trees was less than six in a given plot, then all trees were considered. In all, 895 individual trees were sampled. Data collection was carried out after the growing season of 2012—six years after loss of shelterwood.

Quantification of height and diameter growth focused on two aspects: stand characteristics showing the results of growth six years after shelter loss, and those describing increment patterns as a dynamic process. Tree height (cm) was measured along a perpendicular line between ground level and the base of the terminal bud using a telescopic measuring stick. Root collar diameter (mm) was determined by crosswise measurement 10 cm above ground level, using digital Vernier callipers. Height-to-diameter ratio (H/RCD) was calculated as the quotient of height (m) and root collar diameter (RCD, cm).

The annual increment of the main shoot (cm) within the last eight growing seasons (2005–2012) was measured, allowing us to compare reactions directly associated with shelter loss (2007–2012) and the growth before shelter loss (2005 and 2006). The annual main shoot length was measured between shoot scars (Roloff 1986; Gruber 1998; Collet et al. 2002; Dammann et al. 2009), using a folding rule. Shoot scars mark the borderline between annual internodes, and due to the smooth bark of beech, these remain visible for many years (Roloff 1986).

Using these data, tree heights at time of shelter loss (January 2007) could be calculated by subtracting annual main shoot lengths (2007–2012) from tree height measured in fall 2012.

The tree height, as a measure of intra- and interspecific competition (Ammer et al. 2004), is of interest in our study. However, the annual increment was measured as the distance between the shoot scars along the main shoot. In terms of method, this corresponds more to a measurement of the increase in length than in height (Ammer et al. 2004). However, since beech trees exposed to favourable light conditions showed an orthotropic growth in both the open field and beneath the shelterwood, this approach is appropriate here.

Tree ring analysis

Information about responses of a tree to environmental changes is reflected within the annual rings (Spiecker 2002; Bowman et al. 2013). Analysis would show the changes in the patterns of radial increment of advanced planted beech stems and their branches as consequence of canopy cover loss.

Since the tallest, predominant trees often have bad forms (e.g. very strong branches), they are not representative in growth and quality (*big-tree selection bias*, cf. Brienen et al. 2012). Therefore, only the second-tallest beech in each plot was analysed. Tree ring analysis was conducted on 93 individuals from 14 stands in the Thuringia region. Samples were taken in October 2012, six growing seasons after shelter loss. Trees were felled by chainsaw, and one disc from the stem (10 cm above ground) and one from the thickest living branch (5 cm from stem insertion) were cut out. In all, 186 samples were analysed. Samples were dried for 4 h at 60 °C in a compartment drier to improve visibility of the annual rings after subsequent sanding of the dried wood.

We measured the width of each annual ring. Where possible, the analysis period covered the past 13 years (2000–2012). Four radii were measured perpendicular to each other on each stem and branch disc, using binocular (Nikon SMZ-1B, max. magnification 3.5x). Uncertainties caused by irregularities in growth, such as spurious rings, could thereby be minimized (Bontemps et al. 2010). Furthermore, growth variations within an annual ring could be taken into account.

The computer-based system encompassed the software TSAP-Win™ Professional (RINNTECH, Version 4.69), while a linear-micrometer-measurement-table (isel-automation, Eiterfeld Germany) and a binocular were used for the measurement of tree ring width, with an accuracy of 0.01 mm.

Statistical analysis

Static analysis

Linear mixed models (LMM) were used for analysis. LMM incorporate fixed and random effects and can cope with a nested design with inhomogeneous variance structures. LMM may use specific correlation structures to consider correlated measurement errors between the individuals within a group (Pinheiro and Bates 2000).

LMM were chosen to describe relationships for tree height, root collar diameter and height-to-diameter ratio, which were measured only once. Building the best model is an iterative process and is described in more detail by Pinheiro and Bates (2000) and Zuur et al. (2009). Because the experimental design is characterized by hierarchical nesting, error structure that takes into account several levels of correlation was built into the model. Thus, canopy cover (categorial, 1: released *vs.* 2: sheltered), stand density (covariate, range 500 to 12.000 ha^{-1}) and developmental stage (categorial, 1: young stand stage *vs.* 2: thicket live stage) are fixed effects. As these variables are on very different scales, stand density was z- or log-transformed prior to computations. Plot (214 plots), experimental site (38 stand level), forest district (14 areas of different forest rangers), forest enterprise (7 state forest enterprises), and region (Thuringia *vs.* Saxony) are random effects. First, nested design was completely considered in the random term. In the next step, random effects without significant explanatory contribution (tested by *a Likelihood Ratio Test*) were removed from the model.

Statistical analysis was carried out using the open-source software R (R Core Team 2019) and package “lme4” (Bates et al. 2020). The level of significance was 0.05.

Time series analysis

When modelling the increment of height/length and of diameter of stem or branches in time series, we generally followed Zeide (1993) and Schröder et al. (2002), i.e. we utilized an age-independent linear approach in a mixed model framework.

To do so, we log-transformed the ring width and height increment data and established a time series of diameter outside bark and of height. Predictor variables were z-transformed to ensure similar scaling (Deichsel and Trampisch 1985). The method centres and scales the columns of a numeric matrix. Centering is done by subtracting the column means (omitting NAs) of $x(\bar{x})$ from their corresponding columns, and scaling is done by dividing the (centred) columns of x by their standard deviations (s):

$$z_i = \frac{x_i - \bar{x}}{s}$$

As we wanted to test the hypothesis that tree growth differs before and after Kyrill by the most parsimonious approach, we fitted a “segmented” model (Fortin 2014), which divides the data into two segments regarding time. Location of the joint was the year 2006, i.e. the year before storm event Kyrill. However, residuals were checked for an effect of “year”. This was done by computing pairwise multiple comparisons of mean rank sums between year levels according to Dunn (1964). The method for adjusting p values then was the Bonferroni correction. As the residuals of the simple segmented models showed clear effects of “year”, year was included as a categorical crossed random effect. In the height increment model, an interaction of “shelter” and “year” built the crossed random effect.

Corresponding to this, nested random effects were in place for “stand” in both models and for “plot” in the height increment model additionally, as there were several trees on one plot for which height measurements were taken. AIC and BIC values were computed, and an ANOVA procedure was implemented to test for significant differences between models, e.g. models having different random or fixed effects.

The general model formula was

$$\log(y+1) = X\boldsymbol{\beta} + \boldsymbol{u} + \boldsymbol{\varepsilon}$$

where y is the increment value of height or diameter, X is the design matrix of the model, $\boldsymbol{\beta}$ is a vector of estimable parameters, $\boldsymbol{u}$ is a vector of random effects such that $\boldsymbol{u} \sim N\left(0, \sigma_u^2\right)$, $\boldsymbol{\varepsilon}$ is the vector of the residuals such that $\boldsymbol{\varepsilon} \sim N\left(0, \sigma_\varepsilon^2\right)$, with σ_u^2 and σ_ε^2 the variance of the random effects and the residuals, respectively.

The models in detail were

$$\begin{aligned}\log\left(\Delta height_{i,j} + 1\right) = &\beta_0 + \beta_1 height_{i,j-1} + \beta_2 height_{i,j-1}^2 + \beta_3 segment\\ &+ \beta_4 height_{i,j-1} \times segment + \beta_5 height_{i,j-1}^2 \times segment\\ &+ \beta_6 standdensity + \beta_7 developmentalstage + \beta_8 canopycover\\ &+ \beta_9 canopycover \times segment + u_k + u_{l|k} + u_j + \varepsilon\end{aligned}$$

The random effect parameter u_k relates to the kth stand, $u_{l|k}$ relates to the lth plot within the kth stand, and u_j relates to canopy cover x year$_j$.

$$\begin{aligned}\log\left(\Delta diameter_{i,j} + 1\right) = &\beta_0 + \beta_1 diameter_{i,j-1} + \beta_2 segment\\ &+ \beta_3 diameter_{i,j-1} \times segment + \beta_4 standdensity + \beta_5 developmentalstage\\ &+ \beta_6 stem.branch + \beta_7 stem.branch \times segment + \beta_8 canopycover\\ &+ \beta_9 canopycover \times segment + u_k + u_j + \varepsilon\end{aligned}$$

The random effect parameter u_k relates to the kth stand, and u_j relates to "year$_j$".

See Tables 2 (for height growth model) and 4 (for radial growth model) in results for the variables, interaction of variables and parameter estimates.

Back-transformation of the log-scale predicted values was done according to Calama and Montero (2005). We included the bias correction multiplicative factor and took the total variance as the residual variance plus the variance components associated with the random effects into account (see tables in Results).

Table 2 Variance and standard deviation of random effects and the residuals for LMM predicting annual main shoot length of beech during period of 2005 to 2012 (Table 3)

Groups	Name	Variance	std. dev
Plot × stand	Intercept	0.0239	0.1545
Stand	Intercept	0.0282	0.1680
Year	Intercept	0.0177	0.1330
	Canopy cover	0.0067	0.0817
Residual		0.1505	0.3880

Results

Height and diameter of beech

At the time of release in January 2007, beech in the young stand stage averaged 3.02 m in height, assuming an average stand density of 6000 ha^{-1} (the median of investigated range of stand densities and therefore used as a standard of comparison). Beech in the thicket life stage was 1.27 m taller in average (Table 5). We found no significant differences in the pre-storm height levels between released and sheltered plots for the two developmental stages. The stand density of advanced plantings, represented by the number of plants per hectare, showed a positive and highly significant relationship to beech height. Across the range of beech stand density from 500 to 12,000 ha^{-1}, tree height increased from 1.99 m by 0.05 m for every additional 1000 beeches planted per hectare. This relationship was independent of developmental stage.

Six years after shelter loss, beech height had increased generally, as reflected by the model intercepts for 2006 and 2012. Stand density and developmental stage were the only significant factors. Canopy cover showed a significant effect on height only in interaction with stand density ($p = 0.0131$*, Table 5), suggesting a greater promoting effect of stand density on the growth of released than unreleased trees (Fig. 2). Assuming an average stand density of 6000 ha^{-1}, released beech in the young stand stage had reached a height of 5.72 m. Under the same conditions, sheltered beeches were 5.39 m. Thus, height increased by 2.70 m and 2.37 m over six years, respectively. Under the same conditions, beech trees in the thicket live stage had reached a height of 7.36 m and 7.03 m, with an increase of 3.07 and 2.74 m, respectively.

Within six years, beech on wind thrown sites showed significantly larger root collar diameter (RCD, Table 5) than those under the unaffected shelterwood (Fig. 3). In released

Table 3 LMM predicting annual main shoot length of beech during period of 2005 to 2012 and the effect of shelter loss as function of initial height, canopy cover, stand density, developmental stage and segment (divides the data into two segments regarding time before and after release)

Fixed effects		Parameter	Standard error	*p* value
β_0	Intercept	3.8170	0.1069	0.0000***
β_1	Height	0.9040	0.0551	0.0000***
β_2	Height^2	− 0.6297	0.0739	0.0000***
β_3	Segment (after 2006)	− 0.1679	0.1108	0.1787
β_4	Canopy cover	− 0.0614	0.0763	0.4075
β_5	Developmental stage	− 0.1236	0.0533	0.0236*
β_6	Stand density	0.0052	0.0150	0.7300
β_7	Height × segment (after 2006)	− 0.2428	0.0541	0.0000***
β_8	Height^2 × segment (after 2006)	0.3244	0.0718	0.0000***
β_9	Segment (after 2006) × canopy cover	− 0.0382	0.0705	0.9584

The intercept refers to advanced planted beeches released in young stand stage

Table 4 Variance and standard deviation of random effects and the residuals for LMM predicting annual ring width of beech during period of 2000 to 2012 (Table 6)

Groups	Name	Variance	std. dev
Plot × stand	Intercept	0.0809	0.2845
Stand	Intercept	0.0262	0.1618
Year	Intercept	0.0262	0.1618
Residual		0.2772	0.5265

young stands with a density of 6000 ha^{-1}, the RCD was 7.87 cm, compared with 5.18 cm for sheltered beech. The LMM confirmed that canopy cover had the greatest effect on RCD. For stand densities of 6000 ha^{-1}, the difference in RCD between developmental stages was 1.93 cm.

Initially, the RCD decreases with increasing stand density, regardless of canopy cover. By stand densities of 4000 ha^{-1} the effect reversed and the RCD increased with a further increase in stand density. This effect is more pronounced

Table 5 Linear mixed models (LMM) for height, root collar diameter (RCD) and H/RCD value. Intercept refers to advanced planted beeches released in developmental stage “young stand”

Fixed effects		Parameter	Standard error	*p* value
Height 2006 (m)				
β_0	Intercept	− 0.59265	0.9026	0.5122
β_1	Canopy cover	− 0.09366	0.1757	0.5945
β_2	Log(stand density)	0.41501	0.1064	0.0001***
β_3	Developmental stage	1.26762	0.2569	0.0000***
Height 2012 (m)				
β_0	Intercept	5.2784	0.3641	0.0000***
β_1	Canopy cover	− 0.3306	0.2106	0.1180
β_2	z(stand density)	0.6303	0.1087	0.0000***
β_3	Developmental stage	1.6331	0.3029	0.0000***
β_4	Canopy cover × z(stand density)	− 0.4053	0.1621	0.0131*
RCD 2012 (cm)				
β_0	Intercept	23.2223	3.8964	0.0000***
β_1	Canopy cover	− 2.6937	0.3293	0.0000***
β_2	Log(stand density)	− 1.8609	0.4733	0.0001***
β_3	Developmental stage	1.9277	0.4534	0.0000***
β_4	Released × z(stand density)	1.1851	0.3224	0.0003***
β_5	Sheltered × z(stand density)	0.7903	0.3259	0.0161*
H/RCD 2012 (m/cm)				
β_0	Intercept	0.7341	0.0350	0.0000***
β_1	Canopy cover	0.2665	0.0233	0.0000***
β_2	z(stand density)	0.0594	0.0092	0.0000***
β_3	Developmental stage	0.0458	0.0362	0.2080

Level of significance: $p \leq 0{,}05$*; $p \leq 0{,}01$** and $p \leq 0{,}001$***

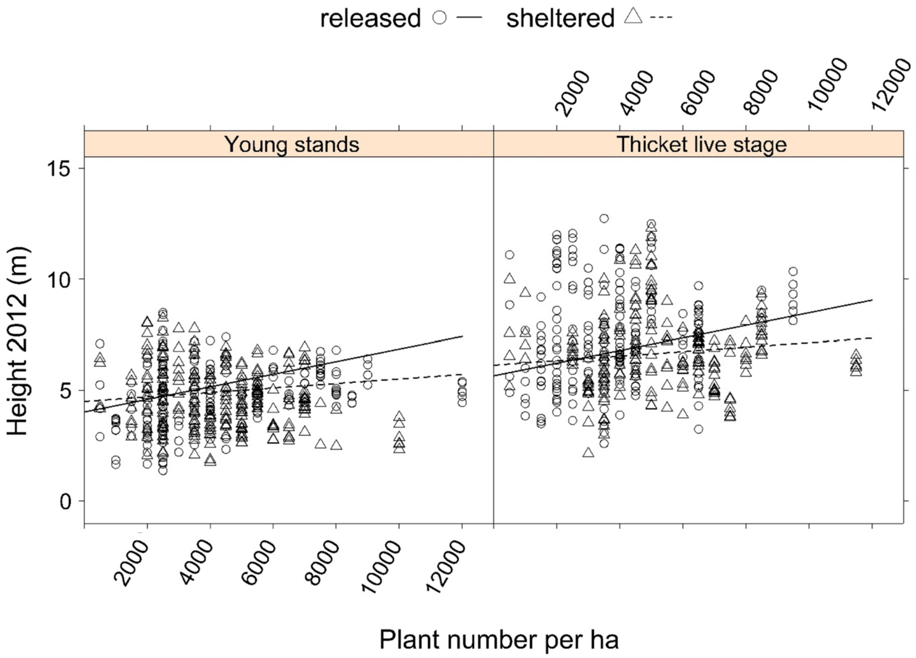

Fig. 2 Height of beech in 2012, six years after loss of shelterwood, in relation to stand density, developmental stage and type of canopy cover

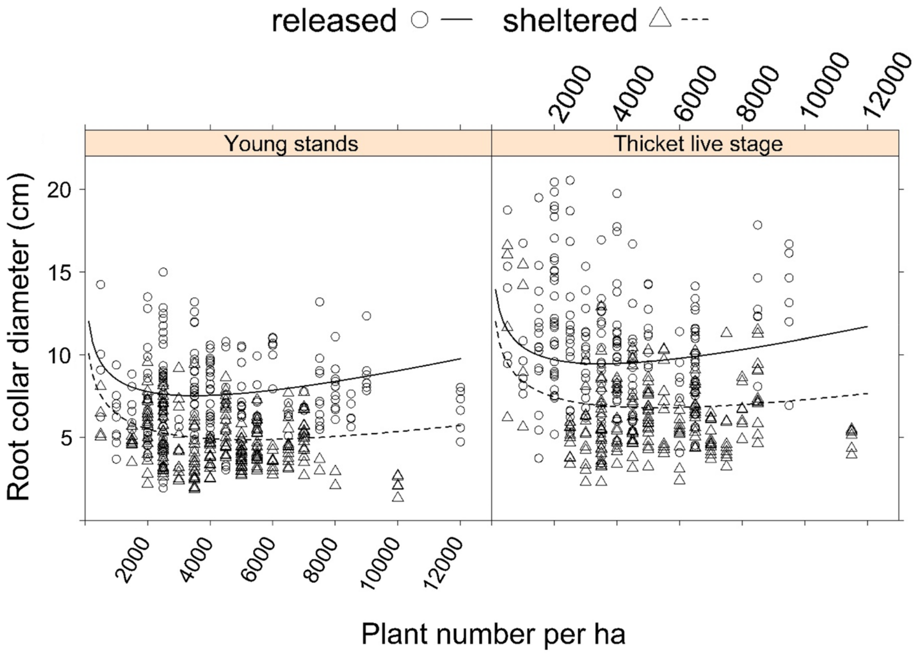

Fig. 3 Root collar diameter of beech (RCD) in relation to stand density, developmental stage and type of canopy cover

for released beech trees than for sheltered ones. As a result, the difference in the RCD between the two types of canopy cover increases with stand density. Overall, for RCD the effect of stand density is of minor importance compared to the loss of shelterwood.

In contrast to beech height and RCD, the H/RCD ratio in 2012 showed less scatter and a clear relation to the investigated factors (Table 5). First, data show a strong reduction of H/RCD values in the case of shelter loss. Based on a stand density of 6000 ha^{-1}, the H/RCD of released and sheltered beech in young stands is 0.78 and 1.04, respectively. Yet regardless of canopy cover, the H/RCD increased by 0.03 with an increase in stand density of 1000 ha^{-1}. The effects of canopy cover and stand density on H/RCD were independent of developmental stage.

Response of height increment to loss of shelterwood

As individual effects, neither canopy cover nor stand density of advanced planted beech showed a significant effect on the height increment of beech. The observed height growth pattern of beech during the period 2005–2012 can be well described by a polynomial of second degree (Fig. 4 and Table 3). Two phases distinguish the diverging development of the main shoot length: the period to 2006 and from 2007 to 2012. There is a significant difference in annual height growth between these two segments. In the period from 2007 to 2012, the annual growth varied more than in previous years. Depending on the canopy cover, the effects on the height growth changed annually. Thus, in 2007 the first growing season after shelter loss, sheltered beech trees show increased growth in relation to released beech trees. Starting in 2008, released beech trees increased their height growth for three consecutive years. For beech stands under spruce shelterwood, the growth in this period is more balanced. As a result, the released beech trees achieved significantly greater annual height growth in 2010 than sheltered beech trees. In the following year 2011, there was a strong decline of height increment in all variants. However, it was much more pronounced for released beeches. In 2012 the growth of beech trees increased again, regardless of the canopy cover. However, for released beech trees, the growth increased stronger. Therefore, released beech trees achieved significantly greater annual growth by 10–15 cm than sheltered beeches in 2010 and 2012 again.

Generally, beech trees in the thicket live stage showed significantly greater annual height growth by 10 cm than beech trees in the young stands stage.

Response of radial growth to loss of shelterwood

Basically, there is a significant linear relation between the radial growth and the trees RCD in the previous year (Table 6). Based on model predictions, the radial increment of permanently covered advanced planted beech in the young stand stage varied between 0.9 and 1.9 mm year^{-1}, with an annual radial increment of up to 2.9 mm year^{-1} during the

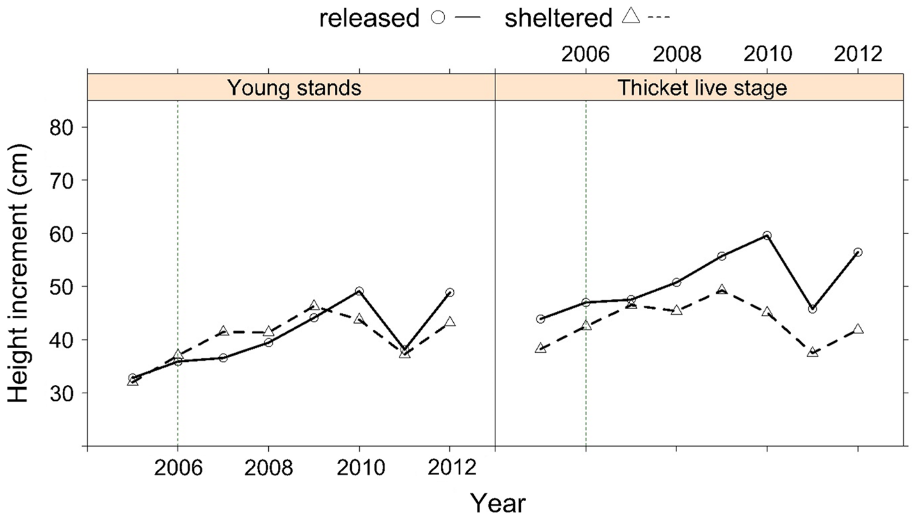

Fig. 4 Prediction of LMM for annual main shoot length for period 2005 to 2012, in relation to type of canopy cover and developmental stage. In this graph, the year random effect is taken into account. The dotted vertical line marks the time of storm KYRILL in January 2007

Table 6 LMM for tree ring width of stem and strongest living branch for period of 2000 to 2012 in relation to diameter (RCD) of previous year, canopy cover, stand density and developmental stage

Fixed effects		Parameter	Standard error	*p* value
β_0	Intercept	4.3980	0.1271	0.0000***
β_1	Diameter (year -1)	0.4646	0.0153	0.0000***
β_2	Segment (after 2006)	0.4733	0.0943	0.0003***
β_3	Canopy cover	0.0404	0.0219	0.0654
β_4	Developmental stage	0.1145	0.1536	0.4703
β_5	Stand density	0.0164	0.0082	0.0442*
β_6	Stem.branch	0.5751	0.0217	0.0000***
β_7	Diameter (year -1) × segment (after 2006)	−0.2374	0.0155	0.0000***
β_8	Segment (after 2006) × canopy cover	−0.6720	0.0250	0.0000***
β_9	Segment (after 2006) × stem.branch	0.1785	0.0270	0.0000***

The intercept refers to values for stem of beech released in young stand stage thicket life stage (Fig. 5). Growth patterns of the strongest living branch were similar, but with a significantly lower radial increment compared to the stem. Average values for the branches were between 0.5 and 0.9 mm year^{-1} for young stands and up to 1.8 mm year^{-1} for thicket live stage.

We found no significant effect of canopy cover for the period before shelter loss. However, there is a significant difference in growth between the periods before and after the storm event. For released beech trees, a significant increase of ring width began immediately after release in 2007 (Table 6; interaction segment (after 2006): canopy cover, $p < 0{,}01$). During the third growing season after storm Kyrill in 2009, annual rings of released trees reached width mean increment of 3.8 mm year^{-1} in young stands and 5.6 mm year^{-1} in the thicket life stage (Fig. 5). Compared to the growth pattern before shelter loss, this is a mean increase of 160–180% within three years.

Response patterns of the strongest living branch to release were similar to those for stems, but not as strong. This is shown by LMM model, which generated parameter for the interaction of segment (after 2006) and the factor characterizing stem or branch. Average annual branch ring widths reached 1.8 mm year^{-1} in young stands and 2.7 mm year^{-1} in the thicket life stage for 2009, or approximately 40–50% of stem radial growth. Compared to initial values before shelter loss, radial growth of the strongest living branch increased by 100–135%.

Discussion

Analysing growth response

If the growth reaction of young beech is analysed and interpreted a few years after a sudden change in environmental conditions, (static) growth variables and (dynamic) increment parameters must be examined separately. Increment parameters are measured annually and thus always represent a pattern of current growth. They have high sensitivity to environmental impacts and potential environmental changes (Dittmar et al. 2003; Eichhorn et al. 2008; Grundmann et al. 2008) and are particularly suitable for analysis of short-term growth reactions (Collet et al. 2001; Spiecker 2002; Bowman et al. 2013). In contrast, static growth parameters summarize the cumulative growth during a plant's life and have a crucial disadvantage in the context of this study: recent changes in growth are hard to detect, because they do not have immediately apparent effects on static parameters.

Height growth

Total tree height showed no statistically significant differences in relation to canopy cover, neither in 2006 nor in 2012, but there are slight differences (2012: $p = 0.1180$). This does not mean that height growth is not affected by a spruce shelter. Rather, the shelters were similar across

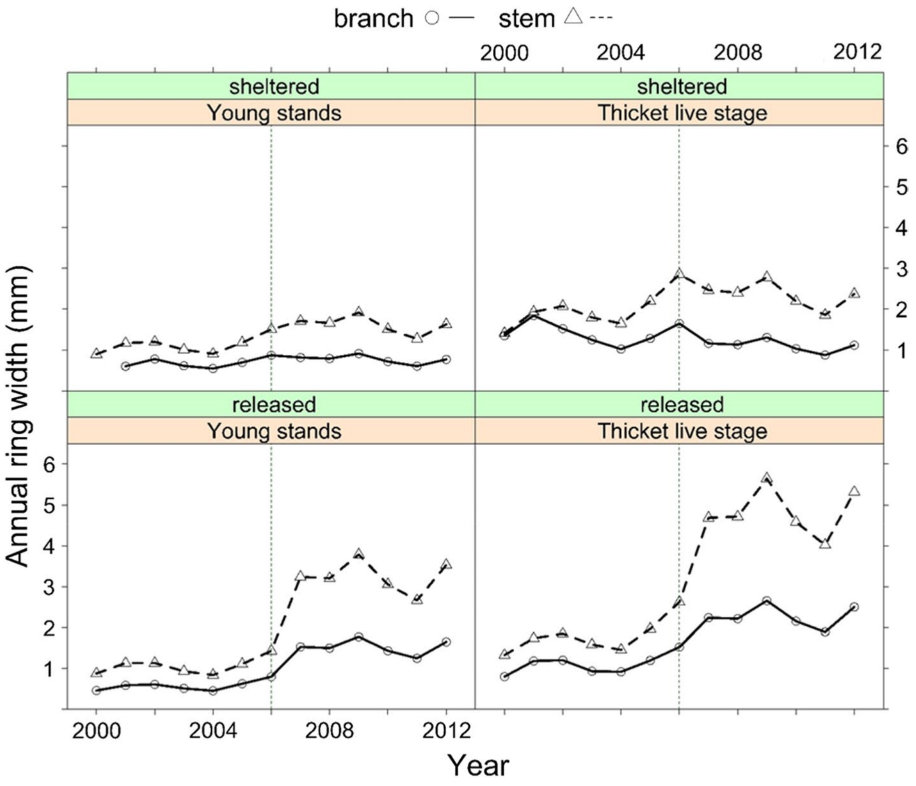

Fig. 5 Prediction of LMM for tree ring width of beech stem and strongest living branch within the period 2000 to 2012. In this graph, the year random effect is taken into account. Illustration is separated by developmental stage and canopy cover. The dotted vertical line marks time of storm Kyrill in January 2007

studied sites before release, with comparable height growth of beech during the time before release. Because many of the advanced plantings were older than 10 years at the time of release, an observation period of six years after release was not sufficient to statistically validate differences in total tree heights. In addition, the growth increase in height after release starts with a delay of one year and was very moderate compared to the increase in diameter. This is a reason why there was a trend, but no statistically significant difference in total height between sheltered and released beeches in 2012. Therefore, the results are consistent.

Competition by a spruce shelterwood affects both above and below ground resources (Wagner 1999; Ammer 2000; Petritan et al. 2011), and the reduced relative irradiation beneath the shelter is an appropriate proxy for complex overstorey competition (Wagner et al. 2010). The positive correlation between light availability and the height growth of advanced planted beech has been shown repeatedly (Burschel et al. 1985; Ammer 1996, 2003; Gralla et al. 1997; Beaudet and Messier 1998; Messier and Nikinmaa 2000; Collet et al. 2002; Petritan et al. 2007; Stiers et al. 2019), whereby the light-dependent height growth of beech is characterized by a saturation: after exceeding an irradiation threshold, further increase in increment rarely occurs (Kunstler et al. 2005; Löf et al. 2007; Linnert 2009). According to Stancioiu and O'Hara (2006) this threshold lies at approximately 25% of the irradiation in an open field, but other authors did not observe saturation effects until 30–40% relative irradiation (Collet and Chenost 2006; Petritan et al. 2009).

Our study sites were selected for canopy cover similar to previous studies (cf. Irrgang 1996; Hertrampf 2009) to ensure an optimal ratio of vigorous growth and quality development of the advanced planted beech. A Diffuse Site Factor (DIFFSF) beneath a spruce shelterwood of 25–35 $m^2 ha^{-1}$ basal area amounts to 20–30% of open field irradiation (Gerold 1996; Wagner and Müller-Using 1997; Hertrampf 2009). In the case of undamaged 80–120-year-old spruce stands in the Thuringian Forest, irradiation reached 25–35% (Mitscherlich 1940). The average annual height increment of beech under the pre-storm spruce canopy in the present study was 30–50 cm $year^{-1}$, indicating that the irradiation was sufficient for vigorous growth. Nevertheless, a further increase to 50–60 cm $year^1$ could be attained if beech was released, even if initial growing conditions are good (Martens and Preißler 2010).

No reaction in shoot growth occurred during the first growing season after shelter loss (2007), but shoot elongation was increased in 2008, consistent with some previous studies showing a one-year delay in the reaction of height growth to environmental changes (Collet et al. 2001; Beaudet et al. 2007; Jarcuska 2009; Caquet et al. 2010). In other studies, shoot length increased considerably after two years of acclimatization (Martens and Preißler 2010) or from the third year after canopy gap creation (Annighöfer 2018). A continuing effect of the shelterwood cover on released beech height growth for up to two years was reported by Collet and Chenost (2006), due to a strong dependency between shoot length increment and microclimatic conditions of the prior (sheltered) year (Welander and Ottosson 1997; Aussenac 2000; Hertrampf 2009), and because shoot and leaf primordium are formed during the previous year (Roloff 1986; Eschrich et al. 1989; Ammer 2003). Thus, for our study, the main shoot from 2007 (after shelter loss in January 2007) was fully determined by the ecological conditions (under spruce shelterwood) in summer 2006, resulting in a one-year delay before an increase of main shoot growth.

Although the shelter loss occurred in winter when the beech had no foliage, leaves that formed in 2007 also exhibited properties of shade leaves, suggesting that the delayed reaction may have resulted from inhibited photosynthesis rates (Eschrich et al. 1989; Tognetti et al. 1998; Valladares et al. 2002). An effect of climate--induced damage to the main shoot meristem cannot be excluded (Roloff 1986). Nevertheless, distinct adaptations to changes in light regime become obvious, either within the first year after such events, or during leaf flush in the following year (Tognetti et al. 1994; Aranda et al. 2001; Robakowski and Antczak 2008).

The first period of annually increasing height growth lasted for three years, reaching a maximum in the 4th year after release in 2010. This is consistent with previous studies (Collet et al. 2001; Beaudet et al. 2007). Barna et al. (2009) earlier showed significant differences in height two years after shelter loss and further increases during the next eight years. In our study, too, there was a further growth increase compared to the sheltered beech trees in 2012, the 6th year after shelter loss. Tripling or even quintupling of height growth has been observed (Collet et al. 2001; Beaudet et al. 2007), with the greatest increase occurring between the first and second growing season after release (Beaudet et al. 2007). By comparison, the noticeable increase in height growth of approximately 15–20 cm appears moderate, likely due to the pre-release crown closure of 40–50% in our study (Hertrampf 2009; Annighöfer et al. 2017). Yet this height growth was 30–40% greater than before shelter removal, perhaps related to additional resource supply compared with beech growing beneath shelterwoods of higher density (Brunner and Huss 1994). However, the sheltered beeches also showed increasing shoot lengths during the observed period. The difference between the two types of canopy cover is a maximum of 10–15 cm per year and is therefore significantly less than the comparison of the periods before and after the storm-caused shelter loss would suggest for released beeches.

Particularly in the case of unsheltered beeches, secondary shoot growth (Lammas shoot) has to be taken into account. This is caused by an above average supply of resources, resulting in an additional elongation during summer (Brown 1951; Roloff 1986; Matyssek et al. 2010), possibly extending annual shoot increment. Because distinguishing between regular and secondary shoots is difficult, particularly in case of older shoots (Gruber 1997, 1998), secondary shoots were not recorded separately. This might also explain the greater shoot lengths of released beeches (Sagheb-Talebi 1996; Petritan et al. 2010).

In 2011, shoot length decreased appreciably, particularly for released beech, probably due to climatic extremes leading to drought stress (Carlson and Groot 1997; van Hees 1997; Aussenac 2000) during May till August of the year before (c.f. Roloff 1986). June precipitation then was as much as 65% lower than the long-term average, while temperature in July 2010 was 2.5 °C higher than normal (DWD 2015). Such conditions resulted in diminished shoot length in the following year 2011 (Roloff 1986; Löf and Welander 2000). Comparable observations indicating growth depressions lasting for multiple years were made after the drought year of 2003 (Eichhorn et al. 2008). By contrast, increment has recovered the following growing season in other cases (Roloff 2001). That is consistent with present findings.

While many studies do not attribute an effect of intraspecific competition on height growth measured by competition indices (Ammer et al. 2005) or stand density (Muhle and Kappich 1979; Lanner 1985), others report a negative correlation between stand density and tree height (Bergers et al. 2006; Hertrampf 2009). Yet, some studies found a positive correlation between intraspecific competition and height (Otto 1994; Leder and Weihs 2000; Linnert 2009; Barbeito et al. 2014), which is related to the importance of tree height in the exposure to light (Ammer 2003; Ammer et al. 2005). While beeches situated in low-density advanced plantings have greater horizontal crown development, higher stand densities limit branch elongation and promote height growth (Leder and Weihs 2000; Collet and Chenost 2006). As shown by our results, this holds true mainly for released beech stands, where the trees showed greater stand density-dependent differences in tree height in 2012.

Diameter growth

Consistent with other assessments, diameter growth showed strong dependence on canopy density and its effect on light availability (Burschel and Schmaltz 1965; Brunner and Huss 1994; Petersen and Wagner 1999; Ammer 2000; Collet and Chenost 2006; Collet et al. 2011; Annighöfer 2018), with a negative correlation between canopy density and diameter increment (Cao 2001; Collet et al. 2002; Ammer 2003; Kätzel et al. 2004). After canopy thinning, diameter growth will increase linearly with differences in light until saturation is reached at a relative radiation level of approximately 35–40% (Leder and Weihs 2000; Linnert 2009; Petritan et al. 2009). Likewise, our study showed a highly significant diameter differentiation of at least 2.69 cm within six years among advanced planted beeches beneath shelter and those released by sudden overstorey removal.

The observed reaction to release is impressive compared to some research (i.e. Petritan et al. 2009), with annual ring widths increasing by 200% after shelter loss. Growth increases of this extent have been observed earlier only in the case of substantially lower initial light supply (Cao 2001; Collet et al. 2001; Beaudet et al. 2007).

It has often been reported that beech diameter growth will increase during the first year after release (Canham 1990; Collet et al. 2001; Collet and Chenost 2006; Beaudet et al. 2007; Caquet et al. 2010), and that it is essentially influenced by environmental conditions of the current year (Lanner 1985; Collet et al. 2002; Lüttge et al. 2005). Information on the duration of enhanced diameter increment is ambiguous. Some studies report increases only in the first year after release (Canham 1990; Collet et al. 2001), while others report durations of three growing seasons (Beaudet et al. 2007). In our study, the strongest increase in ring width took place in the first year after release and maximum diameter increments were observed in the third year after shelter loss, followed by decreasing tree ring widths in the subsequent two years. Similar observations were made by Beaudet et al. (2007).

Annual ring width of the strongest living branch and stem has shown a positive correlation after shelter loss, although the branch growth was not as great (Mäkinen 1996; Wagner and Röker 2000; Linnert 2009; Storch 2011; Barbeito et al. 2014). The released beech developed larger branches, compared to similar trees growing beneath a canopy (Le Tacon 1985; Leder and Weihs 2000; Annighöfer et al. 2017; Annighöfer 2018), with a markedly negative outcome for some aspects of timber quality (Röhrig et al. 2006; Kint et al. 2010).

In our study, tree ring width and root collar diameter increased slightly, but significant with stand density. This seems contradictory to other findings showing that increasing stand densities result in significantly smaller basal diameters (Lanner 1985; Leder and Weihs 2000; Rumpf and Petersen 2008; Kint et al. 2010), independent of canopy cover (Collet and Chenost 2006). Some studies confirmed such a correlation between beech annual radial increment and stand density (Rozas and Fernández Prieto 2000; Collet and Chenost 2006). A possible cause of our observation is that the sample size for higher stand densities (> 8000 ha^{-1}) is small. At the same time, these stands are older than the average of the respective stratum. We examined absolute diameter and growth. Probably, the increasing age with stand density causes increasing absolute diameters and increments at the same time.

The H/RCD value served as an indicator for competition dependent vigorousity (Wagner and Röker 2000; Hagemann 2005; Blaschkewitz 2018) and for tree stability, e. g. against breakage by heavy loads of snow (Kramer 1988; Rock et al. 2004). Released beech was characterized by H/RCD values substantially lower than those beneath shelterwoods (Weihs and Klaene 2000; Cao 2001; Linnert 2009; Petritan et al. 2009). Furthermore, evidence suggests that high stand density results in more slender trees, independent of canopy cover (Petersen and Wagner 1999; Hagemann 2005; Schulz et al. 2005). Also, Blaschkewitz (2018) reported the highest H/RCD values occur under spruce shelterwoods, because released beech shows more vigorous growth and lower H/RCD values.

Effect of the developmental stage

The developmental stage characterizes the natural age of advanced planted beech stands and can differ from actual tree age. State-oriented developmental stages suit silvicultural observations better than tree age, as the latter does not show a clear correlation with growth parameters for beech planted beneath a shelterwood (Collet et al. 2002; Collet and Chenost 2006). According to Messier and Nikinmaa (2000), height growth of beech saplings is independent of tree size, while other authors report positive correlations between initial height or diameter and the increment of trees beneath a shelterwood (Ammer 1996; Collet and Chenost 2006; Ammer et al. 2008). The latter was observed in our study, where beech had significantly greater shoot lengths during the thicket life stage, compared to the young stand stage. Yet wider annual ring widths for thicket live stage beech could not be statistically verified. The reaction to shelter loss was comparable for both developmental stages. Nor did developmental stage show significant interactions with other factors or covariates for the static and dynamic parameter analysed. If differences before release are considered, beech of both developmental stages react similarly after shelter loss (Collet et al. 2001; Collet and Chenost 2006). And while intraspecific competition should be greater during the thicket live stage, the H/RCD values demonstrate that the ratio of height and diameter increment did not differ between developmental stages.

Conclusion

Advanced planted beech grew well beneath a spruce shelter of sparse to medium canopy closure that has proven suitable for both vigorous growth and appropriate quality development (Hertrampf 2009; Petritan et al. 2009).

After sudden shelter loss, beech height growth increase was delayed and moderate, while diameter growth increased appreciably in the first year. This confirmed that a time series analyses were an appropriate method to quantify the diameter increment of beech after the environmental changes (Dittmar et al. 2003; Curt et al. 2005).

Findings revealed a distinct differentiation in diameters for released and sheltered beech by six years after shelter loss. Further, because stem and branch growth were closely correlated, the quality of released beech was negatively influenced. Findings suggest that sudden overstorey removal should be avoided and a stepwise opening up of the overstorey seems to be a better solution. As a result, the beech will gradually adapt to the periodic increase of radiation, while growth of the mature spruce stand continues (Spellmann and Wagner 1993). During these extended periods of canopy cover the advanced planted beech will reach the thicket live stage. Thus first, the canopy cover protects the beeches. As soon as they have reached the thicket live stage, the crown closure of beech stands tempering climatic conditions and protecting from extreme abiotic influences (Palmer 1985).

After shelter loss in our study, the reaction patterns of advanced plantings at different developmental stages were identical. Findings suggest that canopy closure during the thicket live stage did not protect from quality loss, as the increment of the strongest living branches was similar for both stages. Also, despite likely stronger intraspecific competition during the thicket live stage, no differences in growth were observed with differences in stand density and by the similar H/RCD values for both developmental stages. High stand densities seemed to result in relatively greater sapling heights in relation to diameter, resulting in greater slenderness and reportedly higher quality of the beech saplings (Kint et al. 2010). But at the same time, greater slenderness makes those saplings susceptible to bending under heavy loads of snow (Kramer 1988; Rock et al. 2004).

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