

Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests

A. Fichtner^{1*}, K. Sturm², C. Rickert¹, W. Härdtle³ and J. Schrautzer⁴

¹Institute for the Conservation of Natural Resources, University of Kiel, Olshausenstr. 75, 24118, Kiel, Germany;

²Community Forest Lübeck, Kronsforder Hauptstraße 80, 23560, Lübeck, Germany; ³Institute of Ecology, University of Lüneburg, Scharnhorststr. 1, 21335, Lüneburg, Germany; and ⁴Institute for Ecosystem Research, University of Kiel, Olshausenstr. 75, 24118, Kiel, Germany

Summary

1. New forest management approaches aim to ensure high biodiversity and climatic adaptability. Silvicultural practices can alter tree–tree interactions and thus influence forest structure and composition. However, knowledge of the interacting effects of competitive and abiotic stress in tree communities is still limited.

2. We assessed growth dynamics of European beech *Fagus sylvatica* in oligo- to eutrophic lowland beech forests by quantifying variation in the importance and intensity of competitive interactions among adult trees along a productivity gradient defined by nutrient availability and hydrological characteristics. We further predicted changes in competition indices with various levels of crowding for different forest types. Basal area growth of 1819 canopy trees was analysed using forest inventory data.

3. Competition response of adult trees was inconsistent among forest types. For small timber trees, the intensity (absolute effect) and importance (effect relative to abiotic constraints) of competition decreased with increasing abiotic stress. Growth responses of medium and large timber trees, however, revealed an opposite trend. Thus, in tree communities, competition effects did not follow a general pattern, because tree maturation altered the responsiveness of trees to environmental stress.

4. Resource dependency of competition effects was most pronounced for large timber trees, with lowest sensitivity to changes in crowding conditions occurring on fertile sites. For small and medium timber trees, however, competition effects were strongest in dense stands, with lowest sensitivity to changes in crowding conditions on resource-limited sites.

5. *Synthesis and applications.* Tree–tree interactions in beech forests showed a clear pattern which depended on tree maturation and resource supply. This highlights the importance of considering tree size-related changes along environmental gradients in regional growth models. Our findings indicate that management practices could facilitate both timber production and nature conservation demands by adapting thinning approaches to age- and resource-related tree growth patterns. We propose a distinct reduction in thinning intensity, particularly for larger beech trees growing on sites with optimum below-ground resources. This would increase the permanent stand volumes and promote natural stand dynamics, which in turn would benefit biodiversity typical of old-growth beech forest ecosystems.

Key-words: basal area increment, competition, plant interaction, size asymmetry, stress gradient hypothesis, sustainable forest management, thinning

*Corresponding author. E-mail: afichtner@ecology.uni-kiel.de

Introduction

Competition among trees is one of the main drivers determining the structure and composition of tree communities (Oliver & Larson 1996). Thus, it is important to understand the mechanisms mediating inter- and intraspecific competition of trees from both an ecological and economical point of view (Nord-Larsen *et al.* 2003). The interpretation of competition effects, however, largely depends on the way competition is assessed (Freckleton & Watkinson 1999).

Adult tree growth is strongly affected by crown competition and competition for resources. Although all trees compete for nutrients, competition for light is particularly important for smaller trees (Coomes & Allen 2007). Furthermore, competitive effects are assumed to be altered by changing levels of abiotic stress (Bertness & Callaway 1994). Resource supply has a stronger influence on light competition on fertile sites than on nutrient-poor sites (Pretzsch & Biber 2010). However, the interactions between tree size and resource availability have rarely been analysed (Schwinning & Weiner 1998). Although the underlying stress gradient hypothesis (SGH) is debated (Maestre *et al.* 2009; Smit, Rietkerk & Wassen 2009), numerous experimental studies on herbaceous plants or juvenile trees have shown that competition among individuals becomes less severe with increasing abiotic stress (e.g. Callaway *et al.* 2002; Lortie & Callaway 2006) and shifts from below-ground to above-ground competition with increasing resource supply (see Tilman 1982 for the underlying theoretical model). In this context, the distinction between the absolute impact of competition (competition intensity) and the impact of competition in relation to other processes along an abiotic gradient (competition importance) plays a crucial role in assessing plant interactions (Welden & Slauson 1986; Brooker & Kikvidze 2008). A refined version of the SGH additionally suggests that the plant responsiveness along abiotic stress gradients should be related to the stress type (resource vs. non-resource) and the stress tolerance of the interacting species (Maestre *et al.* 2009). Apart from studies on herbaceous plants or juvenile trees, little quantitative non-manipulative information is available on plant–plant interactions along environmental gradients (Callaway 1998; Coomes & Allen 2007; Baribault & Kobe 2011), and studies assessing the competition's relative impact are scarce (Kunstler *et al.* 2011).

Thinning is an important silvicultural method to promote the growth and quality of residual trees by reducing competitors although growth acceleration patterns largely depend on site quality and stand age (Assmann 1970). Moreover, thinning intensity is negatively related to forest integrity (e.g. carbon storage, structural complexity and species diversity; Mund & Schulze 2006; Brunet, Fritz & Richnau 2010). In this context, a better understanding of tree responsiveness to varying levels of competitive and abiotic stress becomes crucial to support management

decisions with regard to changing environmental conditions. Competition response of trees in uneven-aged mixed stands, however, is largely unknown, because most competition analyses are based on data from long-term thinning experiments in even-aged stands. These data can help to evaluate growth responses to varying levels of competition reduction under defined growing conditions in typically even-aged and mono-species stands on smaller scales (e.g. European beech, Utschig & Küsters 2003; Pretzsch 2005), but might not hold for more complex tree–tree interactions in uneven-aged, mixed tree communities on larger spatial scales (e.g. growth districts and areas). In contrast, data derived from non-manipulative sample plot inventories provide an alternative dynamic approach. Such data allow the development of flexible growth models which can gradually replace the commonly used yield tables in forestry and will reflect tree growth under changing environmental conditions more accurately (Hasenauer 2006; Pretzsch 2009).

To assess competition effects on tree growth, we used inventory data from lowland beech forest communities. We focused on the following hypothesis: (i) Competition intensity and importance is highest at sites with low levels of abiotic stress. (ii) Competition effects remain unaltered during tree maturation. Furthermore, we evaluated (iii) the implications of the SGH for near-natural management approaches.

Materials and methods

STUDY SITES AND DESIGN

For this study, a total of 597 plots were selected in European beech *Fagus sylvatica* forests of the forest districts Stadtwald Lübeck (53°47' N, 10°37' E) and Stadtwald Mölln (53°38' N, 10°42' E), which are located in the moraine landscapes of Schleswig-Holstein, Northwest Germany. The forest areas are dominated by deciduous trees (Lübeck: 72%; Mölln: 41%) with total area of 4297 ha (Lübeck) and 1150 ha (Mölln). Elevation ranges from 0 to 90 m asl. The study area is characterized by a suboceanic climate with a mean annual precipitation between 580 and 871 mm and a mean annual temperature of 8.3 °C (Gauer & Aldinger 2005).

Forests are managed according to a low-impact approach based on the protection of natural disturbance regimes within managed stands (Sturm 1993; Westpahl *et al.* 2004) and are certified according to the Forest Stewardship Council (FSC). We included unmanaged, crowded stands in the modelling data set as regional reference areas to ensure that a comprehensive gradient of stand density was used. Structurally, the investigated stands are multi-layered and uneven-aged (see Fig. S1, Supporting Information).

To test large-scale (regional) edaphic effects on tree growth, we stratified the plots according to their geological substrate. The resulting three beech forest types were characterized by a productivity gradient based on nutrient and water availability: (i) 'GF-till' meso- to eutrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) on moderately moist to moist recent moraine soils originating from the Weichselian glaciation. Soil texture consists

of till (clay/sandy loam) with varying carbonate content, providing an optimal nutrient and water supply. The predominant soil types are (pseudogleyic) Luvisols and Cambisols. (ii) 'GF-clay' mesotrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) on hydromorphic recent moraine soils. The strong stagnant water influence is induced by basin clay deposits which are covered with silt or sand of varying thickness. These soils have a deficit in aeration during periods of excess water, which in turn increases the abiotic stress for tree growth. The prevailing soil types are strongly pseudogleyic Cambisols and Planosols. (iii) 'DF' oligotrophic beech forests (*Deschampsio-Fagetum*; EU habitat code: 9110) on recent moraine soils which consist of glacial sand deposits of the Weichselian glaciation. A low retention capacity for nutrients and water is caused by a high sand content, which increases the risk of trees suffering drought during summer. The soils are rather acidic (pH 3.5–5.0) compared to the recent moraine. The predominant soil types are podsollic Cambisols.

Optimal growing conditions (lowest level of abiotic stress) are associated with GF-till sites, whereas suboptimal situations are characterized by low top soil aeration during wet periods (GF-clay) or additive effects of summer drought and low nutrient availability (DF). The gradient of decreasing productivity is expressed by the significant decline in site index values, which is a proxy for the growth potential at a given site (Table 1). Thus, the abiotic stress level increases within the series GF-till – GF-clay – DF.

INVENTORY DATA

We used tree and stand data from sample plot inventories, conducted in 1992 and 2003 (Lübeck) as well as in 1999 and 2009 (Mölln). Measurements were taken in a regular spatial resolution of 180 × 130 m (Lübeck) and 100 × 200 m (Mölln), respectively. Within circular plots (Mölln, plot size: 250 m²) or concentric circular plots (Lübeck, total plot size: 500 m²), all living trees > 7 cm diameter at breast height (*DBH*) were considered. For each tree, the species, social status and *DBH* were determined. *DBH* values represent the average tree size derived from 2 cross-measurements at 1.3 m. Tree height was measured for a subset of 2–4 trees of each species and layer. Annual basal area growth (*BAI*) was calculated as the difference between the tree basal areas (cm²) at the end and beginning of the sample period divided by the number of vegetation periods.

For the growth analyses, we randomly selected 1819 beech trees (target trees) from 250-m² (Lübeck) and 125-m² (Mölln) circular subplots, placed at the centre of the sample plots to account for edge effects. Only dominant and co-dominant target trees of the upper layer (canopy trees) were considered (classes 1–3 according to Kraft 1884).

DATA ANALYSIS

Preliminary analyses indicated nonlinear *BAI-DBH* and *BAI-BAL* relationships. We therefore applied generalized additive mixed models (GAMMs) with a log link function and gamma distribution to assess growth patterns along the productivity gradient (Wood 2006). Study site and plot were used as random factors, accounting for the intraclass correlation at the site and plot level. To address the skewed response and heteroscedasticity of the *BAI* data, a gamma probability distribution was preferred, because it retains the structure of the data while accounting for a

Table 1. Mean (±SD) tree and stand characteristics of the investigated forest types and the associated stress gradient. 'GF-till' meso- to eutrophic beech forests (*Galio-Fagetum*) on moderately moist to moist recent moraine soils; 'GF-clay' mesotrophic beech forests (*Galio-Fagetum*) on hydromorphic recent moraine soils; 'DF' oligotrophic, acidophytic beech forests (*Deschampsio-Fagetum*) on sandy recent moraine soils. Data represent initial inventory values of the modelling data set. The soil nutrient status of the study plots was classified according to the German forest site mapping system (Arbeitskreis Standortkartierung 1996). This index ranges from 1 (very low nutrient availability) to 6 (very high nutrient availability)

	GF-till	GF-clay	DF
Abiotic stressor			
Nutrient-based	–	–	Nutrient deficiency
Water-based	–	Temporal water excess	Temporal water deficiency
Soil nutrient class (<i>n</i> plots)			
Eutrophic sites (index 5–6)	173	27	–
Mesotrophic sites (index 3–4)	139	151	–
Oligotrophic sites (index 1–2)	–	–	107
Site index* (m)	33.3 ^a ± 4.4	31.2 ^b ± 3.9	29.6 ^c ± 4.0
Tree age (year)	71.1 ± 36.7	74.9 ± 40.2	94.0 ± 46.7
Tree diameter (cm) at 1.30 m	28.6 ± 15.0	29.6 ± 17.0	31.7 ± 16.3
Tree height (m)	22.7 ± 8.1	21.9 ± 7.6	23.6 ± 7.4
Basal area growth (cm ² year ⁻¹)	22.4 ± 15.8	20.7 ± 16.8	25.8 ± 19.9
Relative radial growth rate† (%)	6.08 ± 8.2	4.61 ± 5.5	4.42 ± 4.1
Basal area all trees (m ² ha ⁻¹)	27.6 ± 11.8	28.2 ± 10.1	27.3 ± 11.8
Basal area larger trees (m ² ha ⁻¹)	15.8 ± 10.3	18.7 ± 10.3	12.2 ± 9.9
Proportion beech trees (%)	76.6 ± 24.8	64.2 ± 28.6	73.8 ± 28.5
<i>n</i> (forests)	17	10	1
<i>n</i> (plots)	312	178	107
<i>n</i> (trees)	1046	553	220

*Mean height of the 100 largest beech trees, different letters indicate significant differences among forest types (Tukey's HSD test: GF-till vs GF-clay: $P = 0.001$; GF-till vs DF: $P < 0.001$; GF-clay vs DF: $P < 0.05$).

†Basal area growth-basal area ratio.

heteroscedastic error structure and avoiding biased inferences associated with logarithmic transformations (see Gea-Izquierdo & Cañellas 2009).

Basal area increment was modelled as a basic function of tree size (*DBH*) and tree's competitive status. Basal area of larger trees (*BAL*) was used as a distance-independent measure of crowding (Wykoff, Crookston & Stage 1982) and calculated as the total basal area of trees larger than the subject tree within a plot. To account for variation in the effect of species composition (inter- versus intraspecific competition), we calculated the proportion of beech trees within a plot (*PBT*) as the percentage of basal area composed of beech tree individuals. The resulting GAMM is:

$$BAI_{ijk} = \exp(\alpha + f_1(DBH_{ijk}) + f_2(BAL_{ijk}) + \beta(PB_{ij}) + b_i + b_{ij} + \varepsilon_{ijk}) \quad \text{eqn 1}$$

where BAI_{ijk} is the mean basal area growth, α is the intercept, $f_{1,2}$ are smoothing functions (thin plate regression splines) of tree size and crowding effects and β is a parametric coefficient of the beech proportion effect. $b_i + b_{ij}$ denote the random effects of forest site_{*i*} and plot_{*j*} and ε is the residual error of the *k*-th tree. The optimal amount of smoothing was determined by cross-validation (Wood 2006). To test for size dependency of crowding effects, we additionally considered a two-way interaction term $f(DBH, BAL)$. All models were fitted for each beech forest type separately. Additionally, we compared our semi-parametric model with a log-transformed parametric growth function and normal probability distribution, but the GAMM resulted in a better statistical fit (see Appendix S1, Supporting Information).

Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC). Only models with an AIC difference (ΔAIC) < 4.00 (compared with the best fit model) were considered as models with substantial support (Buhrnham & Anderson 2002). The optimal random effects structure was based on restricted maximum likelihood (REML) estimation, the optimal fixed effects structure was identified by maximum likelihood (ML) method. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur *et al.* 2009). Model accuracy was judged according to the adjusted coefficient of determination (R^2_{adj}) and mean error. The relative influence of the predictors was determined by calculating the percentage change in R^2_{adj} owing to the inclusion of the subject predictor in the model.

To evaluate competition effects, we used two different competition measures: Competition intensity (C_{int}) and competition importance (C_{imp}). For each beech forest type, we predicted the radial growth (G) of a focal tree based on our best-fitted models, either in the presence (+) or in the absence (−) of larger competitors. We used the average value of beech proportion along the productivity gradient, while varying tree size and crowding conditions.

C_{int} was quantified as the response ratio between the growth of a target tree in a low- and a high-density stand (Brooker *et al.* 2005):

$$C_{int} = (G_- - G_+)/\max(G_-, G_+) \quad \text{eqn 2}$$

where G_- and G_+ are the basal area growth of a target tree experiencing a low level of crowding (BAL was set at $0 \text{ m}^2 \text{ ha}^{-1}$) and a high level of crowding (BAL was set at $30 \text{ m}^2 \text{ ha}^{-1}$). Accordingly, higher indices were taken to be those with greater absolute competition impact. As we were interested particularly in management implications, we further analysed changes in C_{int} with various levels of crowding (BAL varied between 1 and $30 \text{ m}^2 \text{ ha}^{-1}$) by predicting the proportion of growth decline because of crowding. The crowding response (CR) was calculated as:

$$CR = 1 - ((G_- - G_{+,i})/\max(G_-, G_+)) \quad \text{with } i = 1, \dots, 30 \text{ m}^2 \text{ ha}^{-1} \quad \text{eqn 3}$$

To determine significant changes in C_{int} with tree size and stand density, we applied a recursive partitioning approach

using the function *ctree* implemented in the R library *party* (Hothorn, Hornik & Zeileis 2006). The resulting splits (threshold values) indicate a significant shift in growth reduction in relation to competition intensity. We used the threshold as a management-related indicator for the effectiveness of thinning, because it reflects the balance between maximum growth acceleration and growing stock capacity. The 95% confidence intervals for the thresholds were calculated based on 1000 bootstrap samples.

C_{imp} can be described as the impact of competition in relation to the total environment (competition and abiotic constraint, Brooker *et al.* 2005):

$$C_{imp} = (G_- - G_+)/(\max G_- - \min(G_-, G_+)) \quad \text{eqn 4}$$

where $\max G_-$ is the maximum value of G_- along the investigated gradient. Accordingly, higher indices were taken to be those with greater competition impact incorporating the role of other processes. Similarly to C_{int} , we predicted the crowding response (CR) to analyse the density dependence effects on competition importance using eqn 4.

To test tree size-related effects at low and high crowding levels, trees were stratified into three timber tree size classes and competition indices were calculated for each size class separately: (i) small timber trees: DBH 20–35 cm, (ii) medium timber trees: DBH 36–50 cm and (iii) large timber trees: DBH 51–70 cm. Differences in competition indices between forest types were tested by analysis of variance (ANOVA) followed by a post hoc performance (Tukey's HSD test).

Finally, we calculated for each forest type the relationship between the basal area of all trees (BA) and the basal area larger trees (BAL) to facilitate practical management implications.

All statistical analyses were performed using R (R Development Core Team 2009, version 2.10.1). The nonlinear models were fitted using the *gamm* function from the *mgcv* library.

Results

GROWTH PATTERN

Tree size, crowding condition and level of intraspecific competition explained between 43% (GF-till, GF-clay) and 47% (DF) of the variation in log-basal area growth. At GF-till sites, the effect of canopy tree crowding on radial growth depended on tree size, while the crowding–diameter relationship was consistent across the observed diameter range of GF-clay and DF (Table 2). DBH was a much stronger predictor than BAL or PBT . Canopy tree crowding accounted for 4–18%, which underlines the high importance of tree size as an indicator for the tree's past competition status in uneven-aged stands (Prévosto & Curt 2004). For all forest types, increasing intensity of intraspecific competition was negatively related to tree growth. An increase in beech proportion by 10% resulted in an average growth reduction of 5% (GF-till −4.1%; GF-clay −4.7%; DF −4.2%). Graphical model validation plots indicated no trends in the residuals (Fig. S2, Supporting Information), and parameter estimates of the final models are summarized in Table S1 (Supporting Information).

Table 2. Results of the model selection for the basal area growth of canopy trees (*Fagus sylvatica*) using Akaike's information criterion (AIC). Models were fitted by generalized additive mixed models (GAMMs) for each forest type separately. Tree size at 1–30 m (DBH), basal area larger trees (BAL) and proportion of beech trees (PBT) were included as fixed effects, forest site and study plot as random factors. The best-fitted model structure is highlighted in bold, and the corresponding adjusted coefficient of determination (R^2_{adj}) and mean error are given. The relative influence of the predictors was calculated as the percentage change in R^2_{adj} when the subject predictor was included in the model. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests

Predictor variables	GF-till	GF-clay	DF
DBH + BAL + PBT	1774.0	1134.1	392.0
DBH + BAL	1785.1	1142.2	395.8
DBH + PBT	1828.1	1146.9	404.0
BAL + PBT	2002.8	1317.3	454.8
DBH + BAL + PBT + DBH * BAL	1767.0	1138.0	414.5
R^2_{adj} best model	0.434	0.426	0.469
Relative influence DBH (%)	75	83	88
Relative influence BAL (%)	18	4	9
Relative influence PBT (%)	7	13	3
Mean error ($\text{cm}^{-2} \text{ year}^{-1}$) best model	0.8	1.9	1.8

COMPETITION INTENSITY

Tree growth was negatively affected by increasing competition. However, the intensity strongly varied between forest types (Fig. 1). In GF-till, the effects of density reduction were most influential for smaller trees (20–40 cm), while the sensitivity to local crowding of large timber trees (>50 cm) was negligible. Absolute differences

between tree sizes were largest in medium- and high-crowded stands (BAL, 15–30 $\text{m}^2 \text{ ha}^{-1}$; BA, 26–38 $\text{m}^2 \text{ ha}^{-1}$, Fig. S3, Supporting Information). Crowding response of GF-clay and DF was negatively related to stand density, with absolute differences between tree sizes being comparably small.

The amplitude of mean C_{int} values significantly differed along the productivity gradient across all diameter classes (Fig. 2). The response of small timber trees (20–35 cm) to competition reduction was significantly higher in GF-till than in GF-clay and DF ($P_{adj} < 0.001$). An opposite trend was obvious for medium (36–50 cm) and large (>50 cm) timber trees, with highest values in GF-clay and DF ($P_{adj} < 0.01$). Large trees in GF-till showed a fourfold weaker effect than those in GF-clay or DF. Moreover, the threshold analysis for thinning efficiency indicated that C_{int} significantly declined at DBH 42 cm in GF-till ($P < 0.001$, 95% CI: 37–51 cm; Fig. S4, Supporting Information), at DBH 27 cm in GF-clay ($P < 0.001$, 95% CI: 24–39 cm; Fig. S5, Supporting Information) and at DBH 45 cm in DF ($P < 0.001$, 95% CI: 38–50 cm; Fig. S6, Supporting Information). However, it should be noted that thresholds for GF-clay and DF represent marginal changes (see Fig. 2). There was no distinct effect of crowding intensities on the thresholds (Table S2, Supporting Information).

COMPETITION IMPORTANCE

On average, competition response was much stronger in GF-clay and DF than in GF-till (Fig. 3). Tree size effects on C_{imp} were inversely related to C_{int} , with effects being strongest for largest trees and weakest for smallest trees. Differences in the magnitude of tree size effects, however, increased with increasing abiotic stress. Regardless of

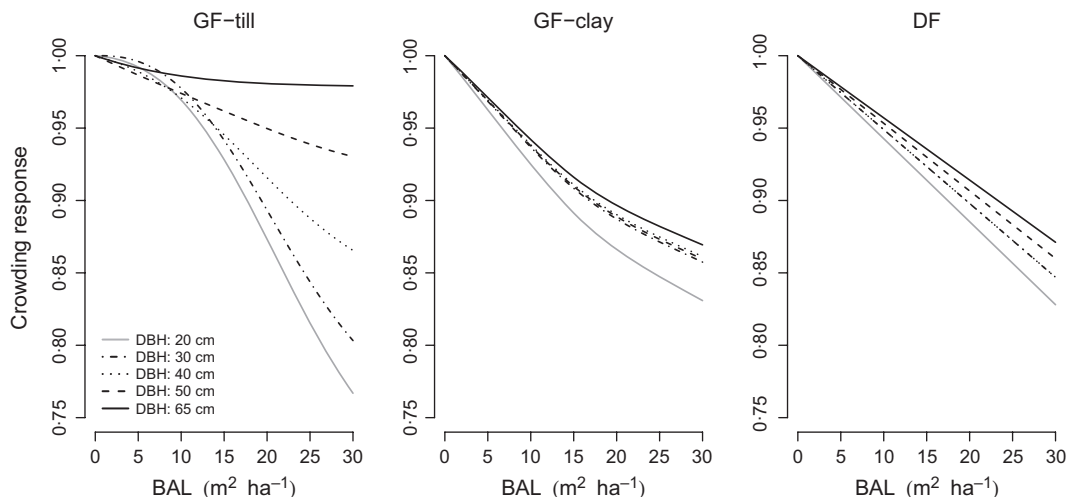


Fig. 1. Effect of tree size (DBH) on the competition intensity–crowding relationship. The response index ranges from 0 (maximal response) to 1 (no response) and indicates the percentage change in growth reduction because of crowding. Crowding condition (BAL) is described as the basal area of larger canopy trees within a study plot. Regression lines represent the predicted response pattern of *Fagus sylvatica* obtained by generalized additive mixed models. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

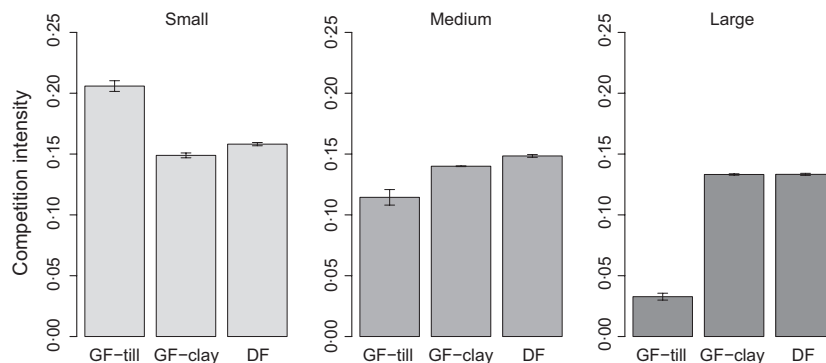


Fig. 2. Change in competition intensity during tree maturation for three timber tree size classes (small 'DBH 20–35 cm'; medium 'DBH 36–50 cm' and large 'DBH 51–70 cm'). The competitive interaction index ranges from 0 (no competition) to 1 (maximal effect of competition) and indicates the impact of competition on the radial growth of *Fagus sylvatica* in a specific abiotic environment (forest type). Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences ($P_{adj.} < 0.01$) among forest types. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

resource availability, density-dependent growth reductions in small and medium timber trees were generally stronger in dense stands, whereas especially for mature trees (>65 cm), C_{imp} was high almost over the entire investigated density range (*BAL*, 10–30 m² ha⁻¹; *BA*, 20–39 m² ha⁻¹).

Changes in the mean C_{imp} values along the productivity gradient were similar to C_{int} (Fig. 4).

Discussion

THE ROLE OF COMPETITION IMPORTANCE AND INTENSITY IN LOWLAND BEECH FOREST COMMUNITIES

We hypothesized that competition becomes less important with increasing abiotic stress (Bertness & Callaway 1994),

which is supported by the declining relative influence of *BAL* (see Table 2). Likely, this trend was linked to the decreasing competitiveness of beech with increasing water (e.g. waterlogging, severe drought) or nutrient stress (Peters 1997; Härdtle, von Oheimb & Westphal 2003). When considering variations in tree size, however, for adult trees along a productivity gradient, no consistent pattern was obvious. Contrary to our expectations, the stress gradient hypothesis (SGH) seemed to hold for small timber trees, while competition effects on medium and large timber trees were strongest in resource-limited environments, thus contradicting the SGH predictions. This might be in accordance with the increasing adaptation capacity of *F. sylvatica* during tree maturation and thus reduced resource restrictions. The higher adaptation

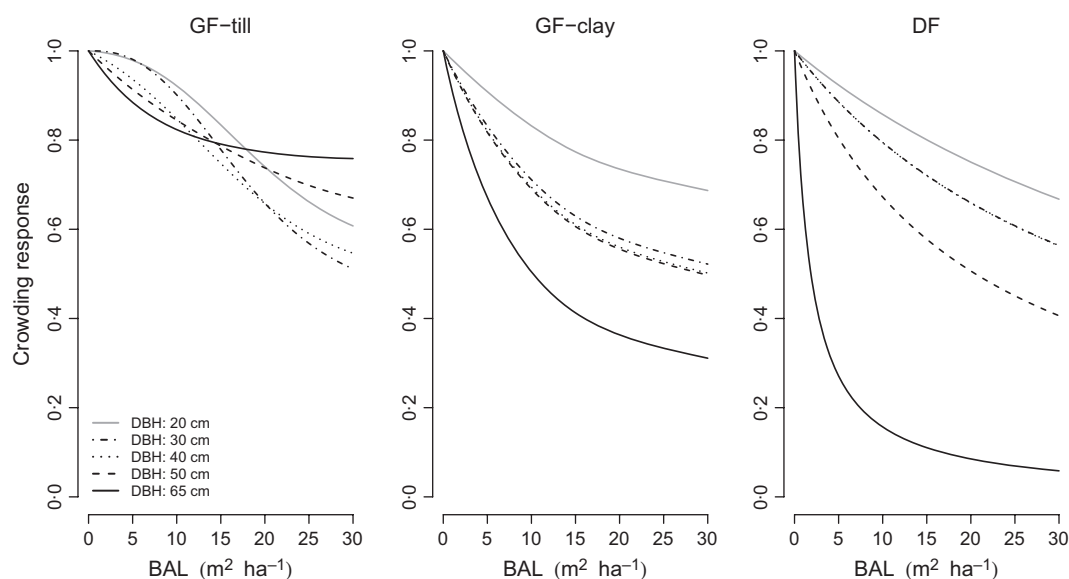


Fig. 3. Effect of tree size (DBH) on the competition importance–crowding relationship. Crowding condition (*BAL*) is described as the basal area of larger canopy trees within a study plot (see Fig. 1 for more details). 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

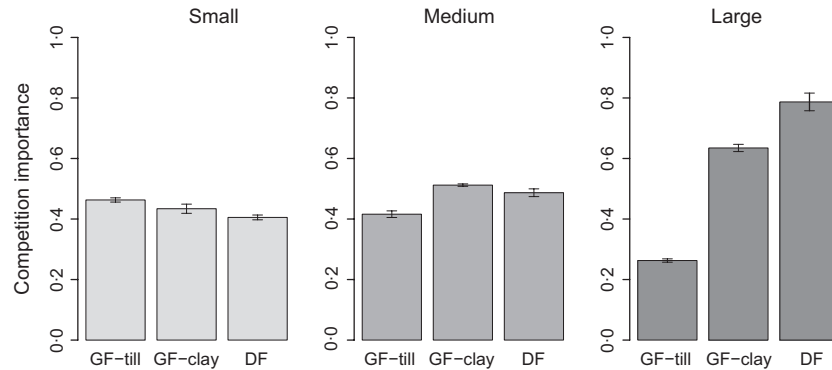


Fig. 4. Change in competition importance during tree maturation for three timber tree size classes (small 'DBH 20–35 cm'; medium 'DBH 36–50 cm' and large 'DBH 51–70 cm'). The competitive interaction index ranges from 0 (no competition) to 1 (maximal effect of competition) and indicates the impact of competition in relation to the total environment (competition and abiotic constraint). Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences ($P_{adj.} < 0.01$) among forest types. 'GF-till' meso- to eutrophic beech forests on moderately moist to moist soils; 'GF-clay' mesotrophic beech forests on hydromorphic soils; 'DF' oligotrophic, acidophytic beech forests.

capacity of larger individuals in resource-limited environments is probably linked to a deeper root system and thus to an improved water and nutrient access (Dawson 1996). Furthermore, larger trees might be able to pre-empt growth resources and become more competitive (Schwinning & Weiner 1998) or develop root densities in favourable zones and thus compensate the high sensitivity of *F. sylvatica* to hydromorphic soils (Diekmann *et al.* 1999). Consequently, tree size-related growth patterns seemed to gain relevance in uneven-aged tree communities, and the SGH might not be universally applicable for tree growth under near-natural growing conditions.

Moreover, we found evidence that competitive interactions were affected by different crowding intensities. For large trees, competition was equally important in dense and less crowded stands, with effects being more pronounced on sites with moderate and low resource availability. In contrast, competition was most important for small- and medium-sized trees in dense stands, with highest sensitivity for changes in crowding conditions on fertile sites (GF-till). Thus, the resource dependency of competition effects appeared to be variable during tree maturation. This contradicts findings from Pretzsch & Biber (2010), who could not observe resource- and tree size-related competition effects for *F. sylvatica* along a fertility gradient. Our results demonstrate that competitive interactions shift in importance during tree maturation, most likely due to tree size-specific allocation pattern and temporal variations in the strength and duration of competition (Niinemets 2010).

The effect of increasing intraspecific competition on tree growth was generally negative. As *F. sylvatica* represents the most competitive tree species in forest ecosystems of Europe, a reduction in beech proportion can be assigned to an overall decreasing competitive stress within the stand. Accordingly, the niche theory predicts that competition becomes less important as niche differences increase (Chesson 2000). Thus, different ecological strategies alter crown space occupancy patterns and crown competition,

which in turn favour radial tree growth (Assmann 1970; Pretzsch & Schütze 2005).

In a recent study, Kunstler *et al.* (2011) found evidence that competition importance in tree–tree interactions supports the assumptions of the SGH. Adult trees (e.g. of *F. sylvatica*) responded with increasing C_{imp} to increasing values of bioclimatic growth determinants. However, the authors did not observe significant changes along climatic gradients regarding C_{int} . This is partly consistent with our findings, whereas the discrepancy between the study of Kunstler *et al.* (2011) and ours may be explained by altitude differences (mountain vs. lowland forests) and the investigated diameter range, because the average diameter generally declines with altitude. Mean diameter of *F. sylvatica* trees in mountain forests was 22 cm (maximum DBH: 56 cm), while mean diameters of trees in the present study were 29 cm (GF-till, maximum DBH: 80 cm), 30 cm (GF-clay, maximum DBH: 92 cm) and 32 cm (DF, maximum DBH: 83 cm), respectively. Thus, Kunstler *et al.* (2011) could hardly predict the response of mature beech trees (>50 cm) in relation to density-dependent effects. However, our results suggest additionally that both C_{imp} and C_{int} vary notably with tree maturation. The distinct decline of C_{int} with tree maturation in environments without abiotic constraints might be a result of differences in biotic stress tolerance (Liancourt, Callaway & Michalet 2005), because we observed the highest tolerance towards competition for large and vigorous trees on fertile sites. Furthermore, growth efficiency of dominant trees is likely to increase in crowded stands on edaphically optimal sites (Utschig & Küsters 2003). We emphasize that our results do not hold for tree growth pattern in sparsely stocked stands (<20 m² ha⁻¹), because under such growing conditions even large-sized trees respond with high radial growth acceleration to growing space expansions (Wilhelm, Letter & Eder 1999).

In this context, it is worth mentioning the indirect assessment of the underlying abiotic stress gradient in our

study, because we could not directly relate our results to measured or modelled soil parameters over longer periods. However, the trophic–hydrologic gradient investigated in our study corresponds with the most important lowland beech forest ecosystems in Europe (Leuschner, Meier & Hertel 2006). Our results suggest that tree–tree interactions along abiotic gradients do not follow a simple pattern (Maestre, Valladares & Reynolds 2006; Maestre *et al.* 2009), because the magnitudes of C_{imp} and C_{int} vary during tree (i.e. size) and stand (i.e. crowding level) development. Thus, for tree communities, the SGH might be refined by consideration of maturation aspects.

IMPLICATIONS FOR NEAR-NATURAL FOREST MANAGEMENT

Both C_{int} and C_{imp} could be considered as criteria for near-natural management strategies, which in turn would allow more flexible adjustments to varying growing conditions in the future. C_{int} indicates growth reduction because of competition at a specific level of resource availability, and thus the growth acceleration potential, whereas C_{imp} indicates how environmental stress alters growth patterns along abiotic gradients. For example, our results suggest that tree size-dependent competition effects might become more important with regard to changing environmental stress, rather than differences in crowding intensities. This is particularly important, because trees with low competition tolerance are predisposed to additional temporary abiotic stress (Linares, Camarero & Carreira 2010).

To our knowledge, this is the first study to quantify tree size-dependent effects on tree–tree interactions along abiotic stress gradients. The identified thresholds for thinning efficiency indicate that growth acceleration decreased during tree maturation, with strongest impacts for tree growth under optimum growing conditions (from an edaphic point of view). Thinning effects declined within the series GF-till_{20–40 cm} – GF-clay/DF_{20–50 cm} – GF-clay/DF_{> 50 cm} – GF-till_{> 40 cm}. A crucial result was that radial growth of canopy trees with a $DBH > 40$ cm seemed to be hardly affected by competition (absolute impact) in GF-till. As a consequence, competitor removal in such diameter dimensions would result in a strong reduction in timber volume in relation to timber increment and in a higher probability of cutting damages. Because natural stand dynamics in beech forests are characterized by small-scale variation in forest development stages (Piovesan *et al.* 2005), it seems feasible for uneven-aged stands to apply thinning strategies to specific diameter classes and forest development stages. Reduced thinning intensities shift diameter distribution towards more complex stand structures with higher permanent growing stocks, which in turn represent a key factor for realising sustainability on stand level.

Our findings are of considerable relevance, because they directly relate to practical aspects of forest biodiversity

and management strategies. Forest management guidelines require simple but ecologically effective key values (Moning & Müller 2009), among which stem diameter range and stand volume are considered appropriate surrogates that can easily be integrated in management schemes. Linking competition responses with thinning intensity and growing stocks, we propose the following low-impact management strategies for lowland beech forests:

1. Thinning interventions should be exclusively performed in a diameter range of 20–40 cm, particularly on sites with optimum nutrient and water supply (GF-till). Interventions in later developmental stages should be restricted to harvest cuts. On sites with restricted below-ground resources (GF-clay, DF), thinning strength could be increased by *c.* 25%, because absolute thinning effects are lower compared with fertile sites. This contrasts commonly applied thinning strategies in beech stands, which include continuous treatments throughout the development stages until the harvest cut (e.g. Nagel & Spellmann 2008).

2. For GF-till, we suggest permanent stand volumes of 600 m³ ha⁻¹, which represents 80% of the growing stock of mature stands in unmanaged reference areas (Fichtner 2009). For GF-clay and DF, permanent stand volumes should be adjusted to the natural growth potential and can amount to 450 m³ ha⁻¹. These values exceed by far recommended permanent stand volumes for uneven-aged beech forests (e.g. plenter forests, Schütz 2006).

The management strategies proposed above will facilitate both timber production and nature conservation demands. There is evidence that intensive logging, particularly in old stands, reduces species diversity at stand and landscape scale, mainly due to homogenization of forest structures and loss of microhabitats (Paillet *et al.* 2009). Particularly, affected forest species are characterized by low dispersal abilities (Brunet & von Oheimb 1998), or are stenotopic and require microhabitats related to old-growth stands (e.g. old or large trees, snags, coarse woody debris; Brunet, Fritz & Richnau 2010). Decreasing management intensity in combination with a prolonged rotation age will favour natural stand dynamics (e.g. lesser soil disturbance, accumulation of biomass, extension of senescent processes, formation of dead wood), and thus biodiversity patterns characteristic for old-growth stands. This was recently demonstrated for several forest-dwelling species across different taxonomic groups (Moning & Müller 2009; Paillet *et al.* 2009). As a consequence, stands subjected to low-impact management practices may not only host more forest-dwelling species, but may also serve as source biotopes for other stands (Moning & Müller 2009).

In conclusion, our results provide important additional insight into competitive interactions in tree communities along environmental gradients. Although our 10-year study may be limited with respect to long-term growth dynamics, the bias of the present regional individual-tree growth models is much smaller compared with those derived from long-term thinning experiments (e.g. yield

table models, Pretzsch 2009). Future research based on long-term non-manipulative inventory data would help to generalize our observations to other forest communities. Nevertheless, it seems that the identified growth response to competition might hold for other shade-tolerant tree species (Kunstler *et al.* 2011), even if the authors did not test tree size effects. We found strong divergence in tree growth response to competition among the investigated beech forest types. Therefore, management practices should be adjusted to the specific growth dynamics and potentials. Implementing ecological theory into management strategies, and thus increasing the benefit of natural productivity and self-regulation would be a further step towards near-natural forest management. A dynamic, low-impact management approach that favours high permanent stand volumes and stand age, respectively, seems to be a possibility to link ecological (e.g. biodiversity, carbon storage) and economical (e.g. quality timber production) concerns in forest management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Diameter distribution of the study stands.

Fig. S2. Residual plots of the final generalized additive mixed models.

Fig. S3. GAM predicted relationship between basal area all trees and basal area larger trees.

Fig. S4. Conditional inference tree for the GF-till data.

Fig. S5. Conditional inference tree for the GF-clay data.

Fig. S6. Conditional inference tree for the DF data.

Table S1. Parameter estimates of the final generalized additive mixed models.

Table S2. Variation in threshold values with varying crowding intensities.

Appendix S1. Comparison of different growth functions.

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