Crown size-growth relationships of European beech (*Fagus sylvatica* L.) are driven by the interplay of disturbance intensity and inter-specific competition

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ABSTRACT

Crown size is considered one of the most important traits that affect radial tree growth, but it remains unclear how (anthropogenic) disturbance intensity affects crown size-radial growth relationships. This knowledge, however, is crucial for a better comprehension and prediction of community dynamics, and thus to support management decisions. We analyzed changes in stem and crown characteristics of dominant canopy European beech (*Fagus sylvatica*) trees along an anthropogenic disturbance gradient based on the duration of non-forestry use. We further investigated the dependency of basal area increment on crown surface area and linked this relationship to growth efficiency. Crown efficiency (basal area growth per unit crown surface area) was used as an indicator for the effectiveness of tree growth. Further stand attributes included stand density and tree species composition. Changes in crown efficiency with tree and stand attributes were assessed using generalized additive models (GAMs). Tree morphology sensitively responded to disturbance intensity. However, the indicative value of crown surface area for basal area increment decreased with increasing duration of non-forestry use and stand density. We found that the interplay between disturbance intensity and species composition modulates crown efficiency of dominant beech trees. Inter-specific competition enhanced crown efficiency in unmanaged stands, whereas managed stands showed an opposite trend. Consequently, crown efficiency significantly increased with decreasing disturbance intensity and intra-specific competition. Thus the widely accepted close correlation between crown size and radial increment needs reconsideration for trees growing under (near-) natural conditions. We hypothesize that carbon allocation in densely stocked stands can be adapted to an efficient trunk-crown relation, which in turn weakens crown size-radial growth relationships as known from managed stands. The importance of continuity in tree-tree interactions therefore imposes significant constraints on the generality of crown traits as radial growth determinants in beech forests. Our findings indicate that a higher structural complexity and stand productivity might be achieved in managed stands by a wider variety of crown size classes and tree species assemblages. Hence, stand dynamics can benefit from lowering anthropogenic disturbances and favouring self-regulation, which would be a further step towards near-natural forest management.

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1. Introduction

Crown size is positively related to the light interception of a tree, and thus to tree's carbon budget (Sterck et al., 2001; Hemery et al., 2005). Therefore, it is regarded as an important indicator for individual tree growth assessments, and individual-based growth models that include crown traits are commonly applied in forestry (Hasenauer, 2006; Pretzsch, 2009).

Crown traits respond sensitive to changes of crowding conditions, hence reflecting tree's cumulative competition status within a stand (Davi et al., 2008; Lintunen and Kaitaniemi, 2010; Thorpe et al., 2010). Increasing competition alters the resource acquisition capacity of a tree by reducing crown length and diameter (Short and Burkhart, 1992; Brown et al., 2004; Lang et al., 2010), which in turn results in a lower biomass production (on the tree individual level). For this reason, growing space extensions by thinning are frequently used in forestry to promote lateral crown growth of residual trees and thereby favour radial increment (Hasenauer

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and Monserud, 1996; Drobyshev et al., 2007). Various studies, however, have demonstrated that intensive biomass removal in forest ecosystems (e.g. by thinning) contradict climate and biodiversity objectives (e.g. Bauhus et al., 2009; Brunet et al., 2010; Verkerk et al., 2011; Schulze et al., 2012). Furthermore, size-asymmetric competition response of European beech (*Fagus sylvatica* L.) alters the effectiveness of thinning effects, particularly on fertile sites (Fichtner et al., 2012). Consequently, an understanding of the mechanisms underlying density-dependent tree growth pattern (e.g. competition for canopy space) is crucial for a better comprehension and prediction of community dynamics, and thus to support management decisions (Purves et al., 2007; Davi et al., 2008).

Crown size is considered one of the most important traits that affect radial tree growth and crown efficiency is commonly used as a proxy to assess tree vigor (Assmann, 1970). There is evidence that thinning positively affects crown efficiency of deciduous (e.g. *F. sylvatica*: Pouderouxa et al., 2001) and coniferous trees (e.g. *Pinus ponderosa*: Mainwaring and Maguire, 2004). Numerous studies from thinning experiments showed that crown efficiency increases with crown dominance (Hamilton, 1969; Roberts and Long, 1992; O'Hara, 1996), whereas within a given crown class, trees with smaller crowns tended to be more efficient (Assmann, 1970; O'Hara, 1988; Sterba and Amateis, 1998). Contrarily, Reid et al. (2004) found an opposite pattern, suggesting suppressed coniferous trees to be more efficient than dominant ones. Thus, stand level productivity is linked to a complex vertical crown size distribution (O'Hara, 1989). However, the vast majority of thinning experiments have been conducted in rather small-sized plots and mono-species stands or uneven-aged coniferous stands (O'Hara, 1996; Maguire et al., 1998). In contrast, studies on the relationship between crown size and radial increment for deciduous trees in multi-layered, uneven-aged natural tree communities are scarce (Norton et al., 2005). The specific objectives of this study therefore are (i) to assess shifts in crown morphology of *F. sylvatica* with various levels of natural stand development and stand densities, (ii) to re-evaluate the indicative value of crown size for radial tree growth under (near-) natural growing conditions, and (iii) to evaluate crown efficiency (basal area growth per unit of crown surface area) in response to anthropogenic disturbance. We used non-manipulative data from mature managed and unmanaged lowland beech forests, which represent an important beech forest ecosystem type within the European range of beech (Bohn et al., 2002/2003).

2. Methods

2.1. Study area

The study was conducted in meso- to eutrophic beech forests (*Galio-Fagetum*; EU habitat code: 9130) of the forest district Stadtwald Lübeck (53°47′N, 10°37′E), which is located in the moraine landscapes of Schleswig–Holstein, Northwest Germany. The forest area is dominated by deciduous trees (72%) and comprises 4297 ha. The dominant tree species is *F. sylvatica*, and the predominant phytocoenoses are affiliated to the *Fagion sylvaticae* alliance. Elevation ranges from 0 to 90 m asl. The study area is characterized by a sub-oceanic climate with a mean annual precipitation between 580 and 871 mm and a mean annual temperature of 8.3 °C (Gauer and Aldinger, 2005). Edaphic conditions of the forests investigated are characterized by 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 for tree growth. The predominant soil types are (pseudogleyic) Luvisols and Cambisols.

2.2. Disturbance levels and field data

The study was based on an anthropogenic disturbance gradient across 42 mature beech stands with various proportions of other trees, such as pedunculate oak (*Quercus robur*), European hornbeam (*Carpinus betulus*), European ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), wild cherry (*Prunus avium*) and silver birch (*Betula pendula*). The gradient included stands managed according to a low-impact approach based on the protection of natural disturbance regimes (e.g. Sturm, 1993) and unmanaged stands from two large and coherent forest nature reserves (48 ha and 184 ha). Structurally, the investigated stands are multi-layered and uneven-aged and developed from natural regeneration (Fichtner, 2009). Disturbance intensity (DI) was derived from the duration of non-forestry use, ranging from 'currently managed' to long-term (>50 years) abandonment. We defined three levels of disturbance: (i) 'M' managed stands, (ii) 'U12' short-term (12 years) unmanaged stands, and (iii) 'U50' long-term (>50 years) unmanaged stands.

We randomly selected 60 dominant beech trees (hereafter target trees) of the upper layer (canopy trees; classes 1–2 according to Kraft, 1884) from 500 m^2 plots. The plots were established in 1992 and 2004, and are part of a systematic sample plot inventory network (180 × 230 m grid). For each target tree diameter at breast height (DBH at 1.30 m), tree height, crown radius, crown length and crown position were measured in 2007. Crown length was defined as the vertical distance from the lowest leaf to the top leaf and crown position as the height of the lowest crown leaf. Crown radius was determined as the average value of radii measurements in six different directions (N, E, S, W, maximum and minimum crown radius). Additionally, we calculated the following architectural traits: Stem slenderness (tree height–tree diameter ratio), crown ratio (crown length–tree height ratio), crown projection area (using the formula for an ellipse) and crown surface area (hereafter crown area). Crown area (CA) was calculated as (Kramer, 1988):

$$CA = \pi CR/6CL^2[(4CL^2 + CR^2)^{\frac{3}{2}} - CR^3)] \qquad (1)$$

where CR is crown radius and CL is crown length. Crown area as defined here (i.e., including crown length) is a more accurate representation of the potential light interception experienced by a target tree than crown projection area, particularly when comparing tree growth in managed and unmanaged stands (Courbaud, 2000).

We further determined stand density and species composition of each study plot by: (i) summing the basal area of all living trees (DBH > 7 cm) within a plot, and (ii) calculating the proportion of beech trees (PBT) within a plot as the percentage of basal area composed of beech individuals.

2.3. Data analysis

Variation in tree morphology with disturbance intensity was evaluated by analysis of dissimilarity (ADONIS, 1000 permutations) followed by a Bonferroni adjustment (Anderson, 2001). The analysis was performed on a matrix of Bray-Curtis dissimilarities based on standardized (Wisconsin double standardization) architectural traits: crown radius, crown length, crown position, crown ratio and stem slenderness. Differences in architectural traits and stand characteristics among disturbance levels were tested by analysis of variance (ANOVA) with a Post Hoc performance (Tukey HSD test).

A basic parametric growth function was selected to analyze the dependency of annual basal area growth (BAI) on crown area:

$$\log(BAI_{ij}) = \alpha + \beta \log(CA_{ij}) + \varepsilon_{ij} \qquad (2)$$

where α describes the mean annual basal area growth of tree i in plot j, β the crown area effect on growth and ε is the residual error. 15-year basal area growth was calculated as the difference between the tree basal area (cm^2) of 2007 and 1992 divided by the number of vegetation periods. Basal area values of 1992 were derived from inventory data for the corresponding trees. Separate models were fitted for the three disturbance levels.

To understand disturbance intensity related changes in tree growth pattern, we used crown efficiency (CE) as an indicator for the effectiveness of tree growth (Reid et al., 2004). Crown efficiency was calculated as the basal area increment per unit crown area. To investigate the effect of species composition (inter- vs. intra-specific competition) on crown efficiency, we used an index of inter-specific competition (CI) computed as CI = 1 − (PBT/100). The index ranges from 0 (no inter-specific competition) to 1 (maximum inter-specific competition).

We estimated crown efficiency using generalized additive models (GAMs, Hastie and Tibshirani, 1990) with a Gaussian distribution and identity link based on a function of crown area (log-transformed), inter-specific competition index and disturbance intensity. We additionally considered two interaction terms (CA × DI and CI × DI), which allowed us to test for shifts in community compositional-specific and crown area-specific growth response with different disturbance intensities (Zuur et al., 2009). The basis dimension was set to $k = 3$ to allow some complexity in the growth function, while avoiding over-fitting the data (Wood, 2006). The general model structure is:

$$CE_{ij} = \alpha + f_1 \log(CA_{ij}) + f_2(CI_j) + \beta DI_j + \varepsilon_{ij} \tag{3}$$

where α denotes the mean crown efficiency, $f_{1,2}$ are nonlinear smoothers estimated as thin plate regression splines describing the crown area and inter-specific competition effects on crown efficiency of tree i in plot j, β is a parametric coefficient for the effect of disturbance intensity, and ε is the residual error. Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC). Only models with an AIC difference (ΔAIC) < 2.00 (compared with the best fit model) were considered as models with substantial support (Buhrnham and Anderson, 2002). We additionally tested a model with a random plot effect, but the likelihood ratio test indicated no substantial between-plot variation ($L = 0.44$, $p = 0.51$).

To quantify the interplay between disturbance intensity and inter-specific competition index on the effectiveness of tree growth, we further predicted crown efficiency for each target tree based on our best-fitted model. We used mean values of crown area along the disturbance gradient, while varying inter-specific competition indices. Differences between disturbance intensities were tested by ANOVA followed by a Post Hoc performance (Tukey HSD test).

All statistical analyses were performed using R (R Development Core Team, 2012, Version 2.14.2).

3. Results

3.1. Stand characteristics

Stand density varied among disturbance levels with significantly higher values in U50 (44 m^2 ha^{-1}) compared to M (32 m^2 ha^{-1}) and U12 (35 m^2 ha^{-1}; Table 1). Differences in species composition, however, were not significant. Mean proportions of beech trees ranging from 80% (U12, U50) to 81% (M; Table 1). Q. robur was the most dominant accompanying species in both, managed and unmanaged stands, followed by C. betulus and F. excelsior. The high proportion of oak can be primarily attributed to human facilitation in the past.

3.2. Tree morphology

ADONIS indicated that disturbance intensity was a strong predictor for the variation in tree morphology of F. sylvatica (F: 6.64, $p < 0.001$). Trees growing in M and U12 had significantly different architectural traits than those in U50 (M vs. U50: $p_{adj} < 0.001$; U12 vs. U50: $p_{adj} < 0.05$). Growth performance in M and U12 was similar (M vs. U12: $p_{adj} = 0.13$). On average, tree morphology of individuals in U50 was characterized by small, shallow and high positioned crowns and slender stems, respectively, whereas the opposite was found for trees in M (Table 1). A significantly lower crown radius and higher crown position only occurred after long-term abandonment of forest management. In contrast, crown length and crown ratio were most sensitive to disturbance

Table 1
Variation in stand and tree characteristics across the anthropogenic disturbance gradient. Values refer to dominant beech (*Fagus sylvatica*) trees growing in mature lowland beech forests (*Galio-Fagetum*). Superscript letters indicate significant differences between means (at the $\alpha = 0.05$ level; Tukey's HSD post hoc test). M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands; CV: coefficient of variation.

|	M		U12		U50	
	Mean (SE)	CV	Mean (SE)	CV	Mean (SE)	CV
Stand attributes						
Stand volume (m^{-3} ha^{-1})	467.56[a] (31.96)	30.57	544.19[a] (32.55)	26.74	714.18[b] (47.03)	29.44
Stand density (m^{-2} ha^{-1})	31.65[a] (2.23)	31.53	34.95[a] (1.42)	18.15	44.01[b] (1.95)	19.83
Proportion beech trees (%)	81.33 (4.66)	26.61	76.98 (5.11)	32.00	80.45 (5.33)	29.64
Target tree attributes						
Tree age (years)	115.85[a] (1.13)	4.36	130.95[b] (2.27)	7.75	125.60[b] (2.40)	8.54
Diameter at 1.30 m (cm)	51.44 (3.14)	27.32	48.51 (2.85)	26.35	46.36 (2.95)	28.52
Height (m)	33.09[ab] (1.36)	18.32	32.46[b] (0.93)	12.76	35.98[a] (1.18)	14.70
Stem slenderness	0.67[a] (0.03)	19.72	0.71[ab] (0.04)	23.48	0.82[b] (0.04)	23.83
Crown radius (m)	6.21[a] (0.37)	26.97	5.65[a] (0.34)	27.01	4.29[b] (0.40)	41.61
Crown length (m)	17.22[a] (1.39)	36.14	13.48[b] (0.54)	18.11	13.94[b] (0.85)	27.37
Crown position (m)	17.87[a] (0.71)	17.71	18.95[a] (0.64)	15.06	22.04[b] (0.93)	18.95
Crown ratio	0.53[a] (0.04)	37.23	0.42[b] (0.01)	12.15	0.39[b] (0.02)	21.52
Crown surface area (m^2)	491.10[a] (56.98)	51.89	350.48[ab] (31.49)	40.18	274.04[b] (37.18)	60.68
Crown projection area (m^2)	121.70[a] (14.50)	53.28	104.85[ab] (11.74)	50.08	65.46[b] (14.07)	96.14
Basal area growth (cm^2 year^{-1})	33.76[a] (3.83)	50.72	33.16[ab] (4.11)	55.44	22.63[b] (3.32)	65.59
Crown efficiency (cm^2 m^{-2} year^{-1})	0.075 (0.01)	34.90	0.094 (0.01)	41.14	0.093 (0.02)	52.65
No. (plots)	18		14		10	
No. (trees)	20		20		20	
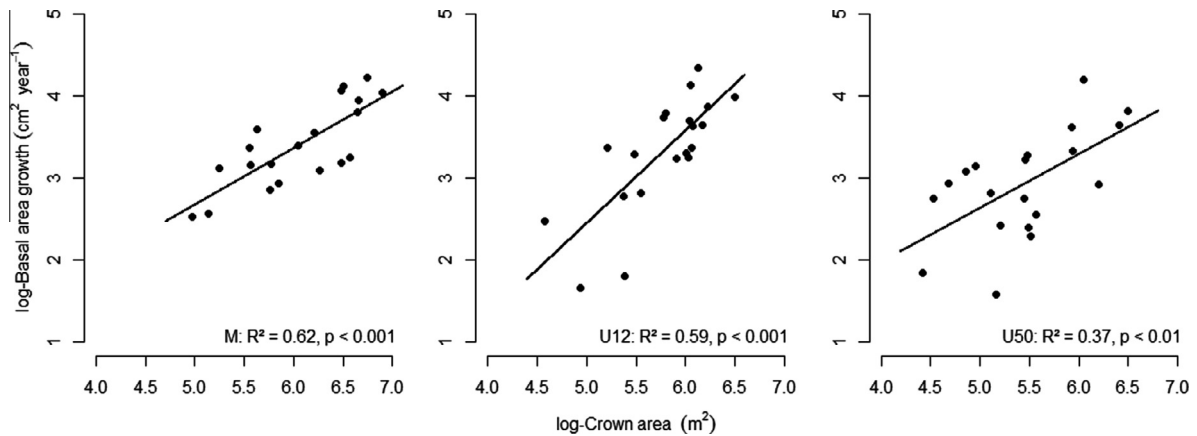
Fig. 1. Shifts in crown area-basal area growth relationship with anthropogenic disturbance intensity in mature beech forests. M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands.

intensity with significantly lower values in unmanaged stands, even after short-term abandonment of forest management. Stem slenderness increased with decreasing disturbance intensity.

3.3. Crown size effects on radial growth

On average, crown area significantly declined with decreasing disturbance intensity (Table 1). Mean values of trees growing in unmanaged stands were 29% (U12) to 44% (U50) lower than in managed stands. Basal area increment also decreased in unmanaged stands compared to M (by 2% in U12 and 33% in U50). However, there was weak statistical support for differences in mean basal area growth not only between M and U12 (p_{adj} = 0.99), but also between M and U50 (p_{adj} = 0.10). This can be primarily attributed to the increasing individual variability in growth rates in unmanaged stands (coefficients of variation: M = 51%, U12 = 55%, U50 = 66%; Table 1).

Basal area growth was positively related to crown area for each disturbance level (Fig. 1). However, the importance of crown area as growth predictor distinctly declined with decreasing disturbance intensity. The proportion of explained variance was 40% lower in U50 compared to M. U50-trees with large-sized crowns corresponded to high growth rates, whereas U50-trees with small- or medium-sized crowns showed a highly variable and thus tree-specific growth pattern.

Table 2
Model selection statistics for different candidate models describing crown efficiency as a function of disturbance intensity (DI), inter-specific competition index (CI) and crown area (CA). The Akaike's Information Criterion (AIC), difference in AIC relative to the best-fitted model (ΔAIC) and degree of freedom (d.f.) are presented. The best-fitting model is highlighted in bold. Parameter estimates for the best-fitted model are given at the bottom of the table.

Model terms	AIC	ΔAIC	d.f.
DI + CI	−217.41	9.36	5.00
DI + log-CA	−217.98	8.79	5.00
DI + log-CA + CI	−221.26	5.51	6.45
DI + log-x CA + CI + log-CA × DI	−222.84	3.93	9.51
DI + log-CA + CI + CI × DI	**−226.77**	**0.00**	**9.12**
	Estimate/edf	t/F	P
Parametric terms			
Intercept	0.138	3.81	0.0004
U12	0.024	1.66	0.1028
U50	0.054	5.10	<0.001
log-CA	−0.021	−2.33	0.0238
Smooth terms			
f (DI × M)	1.886	4.52	0.0148
f (D × U12)	2.071	9.76	0.0001
f (DI × U50)	2.154	9.61	0.0001

3.4. Crown efficiency

The model that best explained variation in crown efficiency included a linear crown area effect and nonlinear inter-specific competition effects varying with different levels of disturbance (Table 2). The interaction between CI and DI was the strongest predictor, with an asymptotic (U50) or exponential (U12) increase of crown efficiency in response to decreasing intra-specific competition in unmanaged stands (Fig. 2). An opposite trend with a weak linearly decreasing pattern was obvious for M. The effect of log-crown area was comparatively small (β = −0.02, p < 0.05). Accordingly, crown efficiency in mixed stands differed significantly among disturbance intensities (F: 83.14, p < 0.001). Average values increased with decreasing disturbance intensities and ranged from 0.07 (M) to 0.11 (U50). In contrast, disturbance intensity had no significant effect on crown efficiency in pure stands (F: 1.64,
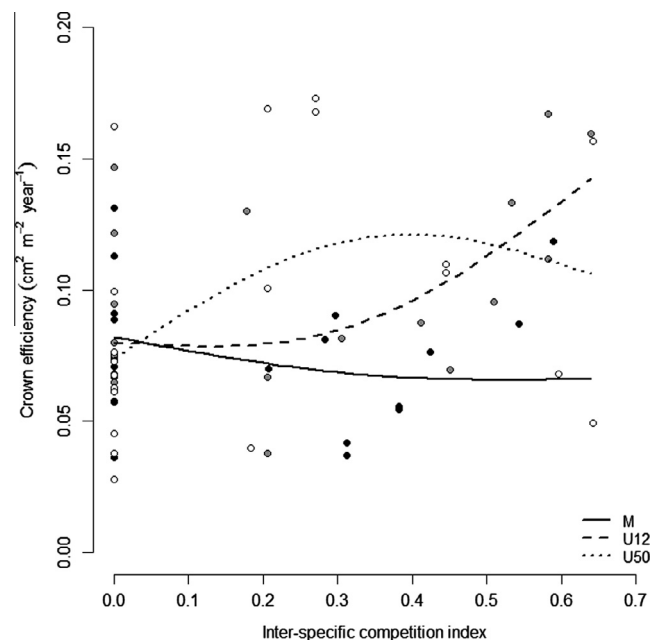

Fig. 2. Disturbance-related variation in crown efficiency with different levels of inter-specific competition. The competition index ranges from 0 (no inter-specific competition) to 1 (maximum inter-specific competition). Crown area was kept constant at the corresponding means. Smooth curves were obtained by fitting a generalized additive model. M: managed stands (black circles); U12: short-term (12 years, grey circles) unmanaged stands; U50: long-term (>50 years, open circles) unmanaged stands.
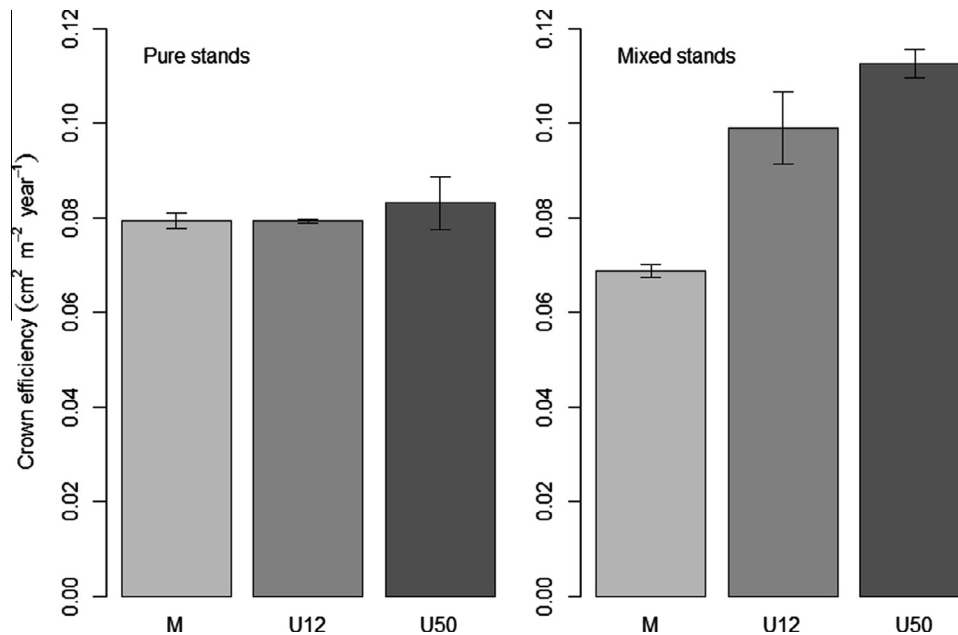
Fig. 3. Changes in mean crown efficiency in pure and mixed stands across different disturbance levels. Predictions were derived from the growth pattern presented in Fig. 2. Error bars represent 95% confidence intervals. Non-overlapping confidence intervals indicate significant differences (p_{adj} < 0.001) among disturbance levels. M: managed stands; U12: short-term (12 years) unmanaged stands; U50: long-term (>50 years) unmanaged stands. Pure stands were defined as CI ranging between 0 and 0.1.

p = 0.23, Fig. 3). Overall, trees in unmanaged forests showed a considerably more effective tree growth (in terms of radial increment) than those in managed stands (U12: +36%, U50: +54%).

4. Discussion

4.1. Efficient resource utilization of F. sylvatica in response to disturbance intensity

The importance of crown size as growth determinant was found to be inconsistent among managed and unmanaged forests. Given the close correlation between crown area and basal area growth in managed stands, trees with larger crowns are assumed to be those with higher growth rates (e.g. Assmann, 1970; O'Hara, 1988; Drobyshev et al., 2007). In contrast, our results demonstrate that crown size becomes less important in undisturbed tree communities.

Tree morphology of shade-tolerant species is optimized for light capture (Aiba and Nakashizuka, 2009), and morphological traits such as crown size are mainly determined by the competition for light and space (Grams and Andersen, 2007). Consequently, tree growth largely depends on light interception (e.g. King et al., 2005; Kunstler et al., 2005). We found evidence, however, that basal area growth of trees in long-term unmanaged, crowded stands was much less affected by crown area than that of trees growing in managed and regularly disturbed stands. We hypothesize that this discrepancy results mainly from contrasting crown efficiencies (e.g. tree vigor), rather than differences in photosynthetic capacities. Particularly in uneven-aged stands effectiveness of tree growth is strongly determined by light conditions (O'Hara, 1996; Maguire et al., 1998). Constant disturbances such as the removal of trees with small and medium-sized crowns prevent morphological adjustments and thereby diminish individual differences in growth potentials. Yet, morphological adjustments enable trees to reduce competitive pressure from neighbors, and thus improve their carbon acquisition, particularly in mixed-species forests (Lang et al., 2010, 2012; Seidel et al., 2011; Dieler and Pretzsch,

2013). Significant morphological differences in our study indicate that trees in unmanaged stands are able to modify their architecture, and thus alter growth strategies to optimize their growth pattern. Accordingly, competition for canopy space may become less important in long-term unmanaged, dense stands.

Natural stand dynamics are strongly altered by silvicultural practices, since thinning interventions aim to promote the growth and quality of residual trees by reducing competitors (Oliver and Larson, 1996). As a result, basal area growth in managed stands was strongly related to crown area, because after growing space extension target trees allocate assimilates primarily to lateral crown growth (Hemery et al., 2005). In contrast, the variation in growth rates of trees in unmanaged stands increased with decreasing crown area. This suggests that assimilate acquisition depends more strongly on individual-specific morphological adjustments than on potential light availability. Vieilledent et al. (2010) demonstrated for (half-) shade tolerant coniferous species that individual variability in tree allometry (e.g. crown traits) is a major driver that explains differences in light resource exploitation. Moreover, the high importance of individual-specific growth traits in unmanaged forests can be partly explained by the high morphological plasticity of F. sylvatica (Schröter et al., 2012). In their study of an old-growth, long-term unmanaged beech forest, the authors conclude that this high plasticity allows beech's light resource utilization to become highly effective by reducing intra-specific competition, which in turn provides the maintenance of high stand productivity, even in densely stocked stands. Neglecting natural individual variability in tree growth strategies thus restricts conclusions on tree-tree interactions in forest communities.

We could not observe distinct disturbance-related variations in crown efficiency for trees experiencing a high level of intra-specific competition (cf. Fig. 3). Moreover, it seems that the interplay between disturbance intensity and species composition modulates crown efficiency of dominant canopy trees. Accordingly, long-term species coexistence in unmanaged forests may shift carbon allocation pattern towards a more pronounced trunk-storage, and thus may compensate for lower light interception. Recently, Zhang et al. (2012) showed that species trait variation (e.g. shade

tolerance) is a key factor determining forest productivity. Hence, the pattern observed here is likely to be attributed to increased heterogeneity of niche differences induced by the duration and intensity of inter-specific competition. This, in turn, allows tree species to become more efficient with regard to light resource allocation (Aiba and Nakashizuka, 2009; Coomes et al., 2009), because increasing growth efficiency might be related to increasing crown efficiency. Moreover, niche differentiation alters crown space occupancy patterns and crown competition, which in turn are related to radial tree growth (Pretzsch and Schütze, 2005).

4.2. Implications for forest community structure

Understanding the impacts of anthropogenic disturbances on tree growth patterns is crucial for forest ecology, because growth is directly related to forest structure and biomass, which in turn affects ecosystem functionality. Our study showed that *F. sylvatica* in unmanaged forests is able to achieve similar growth rates by smaller crown sizes compared to beech trees in managed stands. This indicates that carbon allocation in densely stocked stands can be adapted to an efficient trunk-crown relation, and thus meets management and conservation objectives. Consequently, a higher structural complexity in managed stands can be achieved by a wider variety of crown size classes and tree species assemblages, which in turn would benefit primary productivity in temperate forests (Morin et al., 2011) as well as biodiversity patterns (Brunet et al., 2010). A high variation in crown characteristics leads to a high heterogeneity of light conditions over time, which is particularly important in densely stocked stands (Vieilledent et al., 2010). Additionally, an increasing variability in crown structures might ensure a higher resilience towards stochastic natural disturbances (Seidl et al., 2011) and an improved adaptation to crowding (Pretzsch and Dieler, 2012). Both, management and conservation strategies with a focus on natural stand attributes could therefore benefit from lowering anthropogenic disturbance intensity (e.g. crown thinning) in beech forests.

5. Conclusions

We hypothesized that radial growth is strongly related to crown size. Instead, no consistent pattern was obvious for dominant canopy trees along an anthropogenic disturbance gradient. The increasing effectiveness in tree growth with increasing duration of natural stand dynamics suggests that this interrelation is largely induced by management, and needs reconsideration for trees growing under (near-) natural conditions. Hence, there is no universally applicable crown area-growth relationship. Instead, the application of crown size as an indicator for tree growth largely depends on the continuity in tree-tree interactions (e.g. niche differentiation), and thus does not universally reflect the growth potential of dominant canopy trees in beech forest ecosystems. This is particularly important, because changes in tree allometry potentially affect forest structure and allow species coexistence along vertical and horizontal light gradients over time (Aiba and Nakashizuka, 2009). Therefore, our understanding of tree-tree interactions might be refined by the consideration of the continuity of ecological processes. We are aware that our analyses might be limited by the relative small sample size. However, the observed growth patterns should motivate further studies to link growth mechanisms and species traits to disturbance gradients.

Acknowledgements

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