



Effects of competition reduction on intra-annual radial growth of European beech (*Fagus sylvatica* L.) at stem base and crown base

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Key message In beech stands, thinning affects growth differently along tree stems, with higher and longer duration increment at stem base than at crown base while unmanaged stands depict opposite patterns.

Abstract Forest management affects individual tree growth dynamics at different levels of the tree bole. Here, we assessed stem-growth patterns as a function of bole height (stem base and crown base) and competition reduction using high-resolution dendrometer records. We measured radial increments throughout the vegetation periods of 2015 and 2016 in two differently managed European beech (*Fagus sylvatica* L.) stands in central Germany. In one stand, trees had been repeatedly released from competition while the other had remained unmanaged for about 40 years. To assess different temporal phases of diameter increment, we fitted Weibull growth curves to dendrometer data. Stem basal area and crown base area increments of trees in the managed stand were always higher than in the unmanaged stand. In the managed stand, crown base and stem base monthly diameter increments were highly correlated until July when diameter increment at stem base surpassed the diameter increment at crown base. Conversely, in the unmanaged stand, monthly diameter increment at the stem base was often lower than at crown base. In both stands, diameter growth started earlier at crown base than at stem base. However, stem base growth in the managed stand began earlier and lasted longer than in the unmanaged stand. Our results confirm that competition reduction affects diameter increment along the stem differently than in unmanaged stands and increases growth duration. Future research is needed to test whether different growth patterns and tapers of residual trees in managed and unmanaged stands have implications for biomass and carbon storage modeling.

Keywords Stem growth dynamics · Thinning · Beech · Forest management · Dendrometer · Competition

Introduction

Stem growth is closely related to management practices (e.g., thinning from above) and the environmental changes that result (Köcher et al. 2012; Larson 1963; Tardif et al.

2001), because they alter the competition status of individual trees. Managed and unmanaged stands react differently in terms of radial growth (Assmann 1961). For example, when trees that reach their target diameter are harvested (Miller 1993), resource availability increases. Thus, the remaining trees benefit from the removal of neighboring trees through increases in solar radiation, water, and nutrients (Thibodeau et al. 2000; Purahong et al. 2014). Increased resource availability in the residual stand usually leads to increased radial stem increment after a time delay (Girona et al. 2017).

In the past, tree growth analyses have focused mainly on records of radial increment at standard height, i.e., at stem base or breast height (1.3 m above soil surface) (Assmann 1961; Hoffmann et al. 2018a). These studies found that in managed stands with lower individual tree competition (Lang et al. 2010; van der Maaten 2013; Fichtner et al. 2013), growth response at stem base was higher than that of trees growing in dense unmanaged stands. Growth at stem base is, therefore, slower in dense stands compared to stands

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with more open canopies where light can penetrate further (Oliver and Larson 1996). However, much less is known about how tree growth at different stem heights is influenced by forest management practices (Girona et al. 2017); the growth reaction in the upper part of the stem remains unexplained (Chhin et al. 2010; Chhin and Wang 2005). In managed stands, the physiological responses at the stem base and the crown base of trees are stimulated and growth is initiated at both levels almost at the same time (Olson et al. 2014). In contrast, in unmanaged stands growth at stem base may be delayed, resulting in marked differences in growth onset at respective heights.

The few studies on this subject suggest that the effects of thinning on temperate tree species result in growth responses that differ along stem height, with greater stimulation of growth at the stem base compared to the upper part of the tree (Thomson and Barclay 1984; Valinger 1992; Hoffmann et al. 2018b). Further investigation is needed, especially in terms of mitigating climate change; calculations of above-ground carbon storage in trees and stands depend on actual tree biomass allocation. In fact, model-related uncertainties are important sources of uncertainty for carbon estimation (Sileshi 2014). The contribution of variables diameter increments and thus carbon sequestration in stem biomass at different stem height has not yet consistently been investigated and considered in biomass regression models. The effects of thinning on the allocation of growth along the stem have, to our knowledge, rarely been studied in temperate deciduous forests. Detailed knowledge on the relationship between stem increment at the commonly used breast height and stem increment at other stem heights would be particularly relevant for ecologically and economically important species such as European Beech (*Fagus sylvatica* L.) which would, under natural conditions, be the dominant tree species in Central Europe (Jarčuška 2009; Puriņa et al. 2017). Moreover, understanding individual tree biomass allocation is crucial for selecting and controlling silvicultural treatments that are compatible with management goals.

Two phases of stem circumference variation are usually distinguished: a diurnal or reversible phase and an irreversible one. The reversible changes in stem circumference depend on water flow through uptake by the roots and water release by transpiration, and on cells' osmotic pressure (Zweifel 2016). Downes et al. (1999) already differed between the two reversible circumference changes shrinkage and swelling (also called recovery). Shrinkage was described as a period with decreasing circumference, starting from a daily maximum observed early in the morning, and swelling as an increase in the stem circumference, back to the initial morning maximum value. The irreversible change in stem circumference, which reflects stem growth resulting from cells' multiplication and expansion in the cambium, is quantified as the difference between the excess circumference value measured until a subsequent

maximum, and the maximum value measured in the morning (Oberhuber et al. 2015). Two approaches can be used to calculate stem growth from the described diurnal cycles: daily approach (metrics calculated as one value per day) and stem-cycle approach (dissociation of the real growth from the shrinking/swelling-induced radial change) (Deslauriers et al. 2003, 2007).

Long-term intra-annual tree circumference increment in mature temperate forests has long been investigated (Deslauriers et al. 2007; Oberhuber et al. 2015), but studies of different phases of intra-annual growth (onset, termination, and duration) of tree species remain rare (Metz et al. 2020; Vospernik et al. 2020). However, assessing biomass allocation through individual tree growth measurements encompasses a strict methodology of data acquisition (Bowman et al. 2013). Empirical procedures have involved destructive tree felling and stem sectioning (Konôpka et al. 2021), followed by caliper-measurement of above and below bark diameter in several directions for each section (Bouriaud et al. 2005; Chhin et al. 2010; Valinger 1992); inter-annual growth assessment through radial core extraction for ring width measurement has also been applied (Girona et al. 2017). More accurate techniques for stem circumference growth assessment have emerged over the years, with the advantages of being less invasive, non-destructive and providing continuous high-resolution measurements under specific environmental conditions (Deslauriers et al. 2003; Köcher et al. 2012; Mencuccini et al. 2017; Wang et al. 2016). In the present study, high-resolution automatic dendrometers were used.

This study investigated how above-ground biomass is allocated throughout the vegetation period at the stem base (breast height) and at the crown base under two different management conditions. The objective was to specifically assess the effects of competition reduction on the growth response at different stem heights during the growing season of dominant and codominant European beech trees exposed to different management regimes. We hypothesized that the area/diameter increment (absolute and relative) varies significantly between managed and unmanaged stands. Absolute and relative radial increments throughout the vegetation period were expected to be higher in the managed stand compared to the unmanaged. We also hypothesized that area increment at stem base and at crown base correlate more closely in the managed stand compared to the unmanaged stand. Finally, we hypothesized that releasing trees from neighborhood competition affects growth onset and duration of the remaining trees.

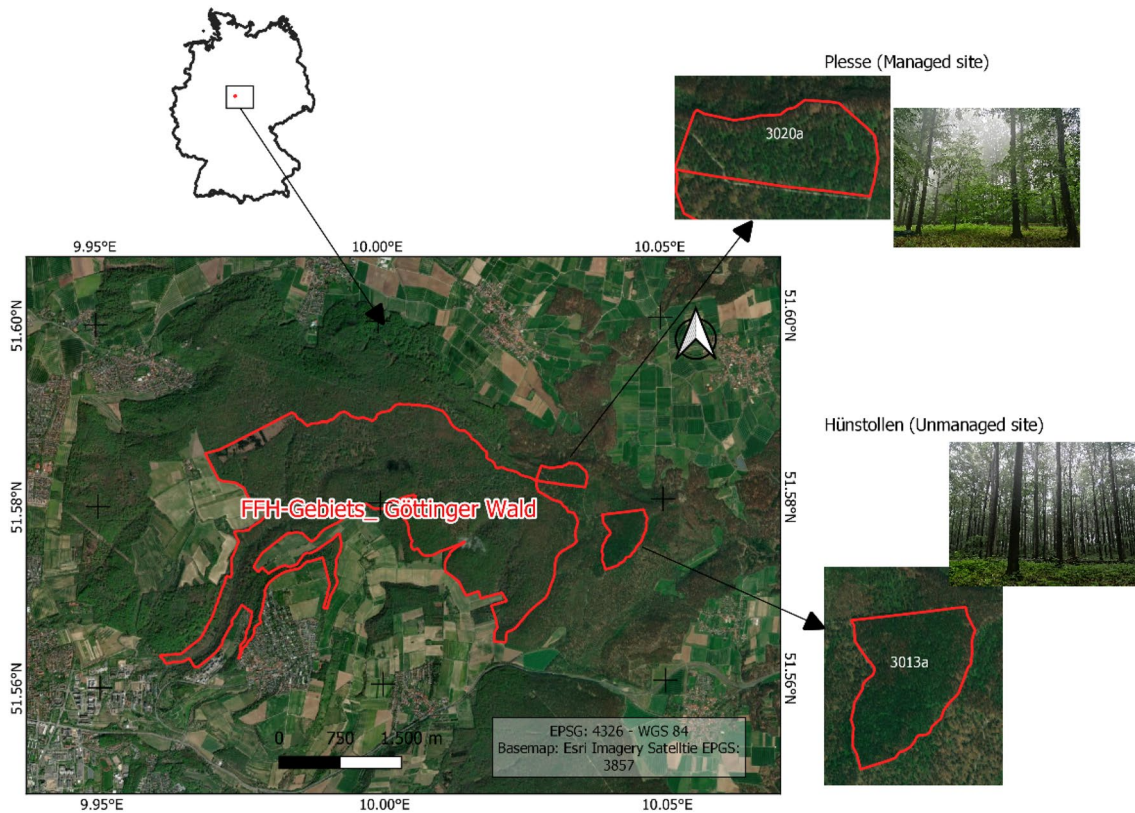


Fig. 1 Geographic location of the two study sites (Plesse_section 3020a and Hünstollen_section 3013a)

Methods

Site description and study design

The experimental sites (Fig. 1) considered for this study were the forests of Hünstollen/section 3013a (latitude: 51° 34' 35.83" N, longitude: 10° 2' 38.10" E, 401–450 m.a.s.l) and Plesse/section 3020a (latitude: 51° 34' 57.21" N, longitude: 10° 2' 0.53" E, 401–450 m.a.s.l), both part of the Göttinger Wald, one of the FFH (Fauna–Flora–Habitat) zones in Lower Saxony, Central Germany (Forstamt-Reinhausen 2021; Heinrichs et al. 2014). The two sites were located close to each other (approximately 900 m) and, therefore, comparable in soil type, geology and vegetation composition, but different in structure (e.g., basal area, gap portion, and canopy openness) (Table 1) and microclimate (e.g., light availability at the forest floor) resulting from their respective management histories. While the stand at Hünstollen was designated a natural reserve and has remained unmanaged since 1972, the Plesse stand has been managed by shelterwood cuttings, i.e., removing evenly distributed trees once they have reached their target diameter. The last harvest operation was performed 3 years prior to measurements. Due to their proximity to each other, the two sites have almost identical climate, with average annual temperature

and precipitation of 7.4 ± 0.8 °C and 410 ± 156 mm, respectively (Panferov et al. 2009). The main difference between the two stands is the stocking density.

Trees were older and taller at Hünstollen compared to Plesse. In the following, we will refer to the two stands as “managed” for Plesse and “unmanaged” for Hünstollen.

Radial stem increment measurements with high-resolution dendrometers

High-resolution electronic circumference dendrometers (DC2 dendrometers of 0.3–3.6 μm resolution, Ecomatik GmbH, Munich, Germany) (Metz et al. 2020) were installed on thirty (30) dominant and codominant trees (15 *F. sylvatica* in Hünstollen and 15 *F. sylvatica* in Plesse), selected to represent comparable diameter ranges. Stem radial increments were recorded from 1st April 2015 to 30th September 2016. Dendrometers were positioned at the NW-exposition side of each tree to limit direct irradiation (van der Maaten 2013). Prior to data collection, calibration was performed according to Metz et al. (2020). Circumference increment at two different positions on the stem, i.e., at stem base (1.3 m above the soil) and at crown base, i.e., below the first major branch, was recorded every 30 min for a total of 48 daily records per dendrometer. At crown base, the goal was to

Table 1 General characteristics of the study sites of Hünstollen and Plesse

	Hünstollen Section 3013a (unmanaged)	Plesse Section 3020a (managed)
Stand age in 2022 (years)	Upper canopy: 159 (more or less even-aged)	Upper canopy: 135 (two age classes)
Relief	Moderately to barely fresh site of plain, very shallow slope, broad ridge; plateau well supplied with nutrients (Forstamt-Reinhausen 2021)	
Geology/soil	Soil type: Rendzic Leptosols and Calcaric Cambisols (Mölder et al. 2014); thick limestones, mixed loam soils, with loess overlays or loess admixture, less to strongly skeletal in the top soil (Forstamt-Reinhausen 2021)	
Vegetation	Dominated by European beech (<i>Fagus sylvatica</i> L.)—89%, abundance of wild garlic (<i>Allium ursinum</i>) Other species: <i>Fraxinus excelsior</i> , <i>Acer pseudoplatanus</i> and <i>Acer platanoides</i>	Dominated by European beech (<i>Fagus sylvatica</i> L.)—92% abundance of wild garlic (<i>Allium ursinum</i>)
Management	Unmanaged since 1972	Managed as a regular shelterwood system
Dominant height (m)	38.9	33.6
Canopy cover (gap) percentages and stand structure	98.6% (1.4% gap) Abundance of dead wood/branches and litter on the floor, some standing dead trees	73.1% (26.9% gap) Abundance of dead wood/branches and litter on the floor, some standing dead trees
Basal area (m ² ha ⁻¹)	26.7 (23.6 for <i>F. sylvatica</i>)	12.6 (11.6 for <i>F. sylvatica</i>)
Last thinning	Unmanaged since 1972	In 2012 with removal of 47 trees ha ⁻¹

place the dendrometers at the closest possible position to the canopy, which resulted in variable heights (height varying between 8.4 m and 18 m above the forest floor) (Fig. 2) between investigated trees. Tree selection was based on diameter classes with a focus on dominant and codominant trees (32 cm < diameter at breast height < 74 cm); the healthiest individuals were also targeted by visual assessment; finally, after installation of dendrometers, no treatment was applied to the stands.

Data processing and analysis

The statistical language “R” version 4.1.1 (R Core Team 2021) was used to structure, analyze, and plot stem increment patterns and correlations over space and time. Time series datasets were restricted to the vegetation period (1st April to 30th September) for each considered year (2015 and 2016). Values recorded included both irreversible and reversible radial stem growth, the latter induced by the alternating actions of swelling and shrinking (van der Maaten 2013;

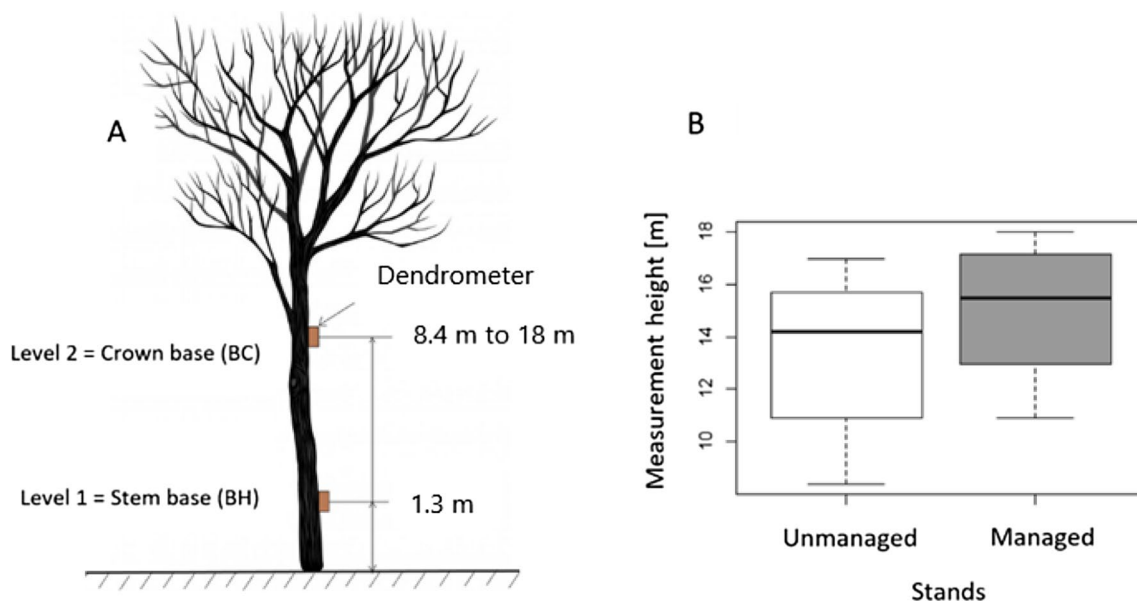


Fig. 2 (A) The position of dendrometers on the support tree. Two levels per tree were considered: stem base (BH) and the crown base (BC). (B) Box plot opposing the crown base heights observed

between the managed and unmanaged sites. Statistical analyses revealed no significant difference between the two sites ($p > 0.05$)

Chan et al. 2016; Zweifel et al. 2016). Calculation of effective stem growth was thereafter performed following the *daily approach*, consisting of a single daily average reading (Deslauriers et al. 2007; Tardif et al. 2001) at considered measurement heights. We used the package *DendrometeR* (van der Maaten et al. 2016) in R to visualize stem cyclic patterns, daily aggregations, and gaps at each measurement height for each tree and across the vegetation period of the considered years. Aberrant values of stem radial increment, resulting from field damages, were checked by plotting time series patterns, and correction of wrongly shifted values were performed whenever possible. When a gap in a dataset was too large or when the shifting direction was impossible to identify, data were deleted. Of 120 datasets expected from 30 initial trees (i.e., 15 records at stem base and 15 at crown base of trees within each stand and each year), 112 were suitable for analyses. Values on the 1st of April 2015 and the 1st of April 2016 were set to zero as a starting level reference for cumulative radial growth.

Absolute and relative area increment were calculated for the vegetation period (1st April to 30th September) and for three subperiods: 1st April to 31st May, 1st June to 31st July, and 1st August to 30th September, for each stand and at each considered measurement height in 2015 and 2016. Total area increments at stem base and at crown base were calculated for all trees by subtracting the initial area value of 1st April from the final area increment of 30th September at the respective heights. The absolute area at a specific point in time was computed by converting circumferences to cross-sectional area by radius assuming a circle. In addition to absolute values, relative area at stem base area and at crown base were computed for the three subperiods (1st April to 31st May, 1st June to 31st July and 1st August to 30th September) relative to the total area accumulated across the vegetation period (1st April to 30th September). For each considered sub-period, total absolute area increment in four categories (treatments' combination here called *MH*) was considered for further comparison: Managed stand_stem base (BH), Managed stand_Crown base height (BC), Unmanaged stand_BH and Unmanaged stand_BC. We used the *lme4* (linear mixed-effects) package (Bates et al. 2015) introducing the variable *Tree* as the random effect to test the significance of difference in area increment between the four categories. The model was elaborated as follows:

$$y = \mu + MH + T + \varepsilon \quad (1)$$

where y is the response variable (basal area increment), μ is the overall mean, MH are the four treatment combinations (listed above), T represents the random effect and ε is the residual error. We then applied a *Tukey HSD* test to assess pairwise differences. Furthermore, the correlation between absolute total area increments at the stem base and crown base was plotted and modeled with a simple linear function;

the strength of correlation was assessed with the coefficient of determination (R^2) and the regression function ($y = b + ax$). We did not include a random effect here because this analysis was conducted at single tree level. The slope coefficients a were also derived from the latter linear models at respective stands and years and compared using a t test. Calculation of area increment additionally to diameter increment values was necessary to reduce the risk of underestimation of actual tree productivity. We calculated average monthly diameter increments for management types and height levels. The *npar.t* test of *nparcomp* package (Konietschke et al. 2015) was applied to check the significance of differences in monthly average diameter increment between the two measurement heights.

We modeled intra-annual diameter change measured in each tree using the cumulative Weibull function (Weibull 1951; van der Maaten 2013; Metz et al. 2020), a non-linear regression model integrated in the *nls2* package (Grothendieck 2022). Parameters of the Weibull function were computed with the formula:

$$y = 1 - e^{-\left(\frac{t}{T}\right)^m} \quad (2)$$

where y represents the relative change in diameter to the total diameter growth over the vegetation period; T is the scale parameter defining when 63% of growth is reached and m is the shape parameter (van der Maaten 2013); and t represents the number of days elapsed since the reference day for growth start (1st April). Time series analyses of tree girth increment enabled the differentiation of different growth phases (onset, termination and duration) contributing to the characterization of trees' reaction to environmental conditions. Onset (*Ons.*), duration (*Veg. per*) and termination (*Term.*) of the vegetation period were derived through the inverse Weibull function:

$$f(y, T, m) = T * (-\log(1 - y))^{(1/m)} \quad (3)$$

$$\text{and then, } \textit{Ons.} = f_{y,T,m}(0.05, T, m) \quad (4)$$

$$\textit{Term.} = f_{y,T,m}(0.95, T, m) \quad (5)$$

$$\textit{Veg.per} = \textit{Term.} - \textit{Ons.} \quad (6)$$

with *Ons.*, *Term.* and *Veg. per* representing the number of days corresponding, respectively, to 5%, 95% and 100% of cumulated diameter increment throughout the vegetation period. The growing phases were determined for each tree and then averaged by stand (managed and unmanaged), by measurement height (stem base and crown base) and by year (2015 and 2016). Average Weibull parameters were plotted on sigmoid functions as relative diameter increment across the vegetation period.

Results

Effect of thinning on stem area increment

Total area increment differed significantly between the managed and the unmanaged stands, most notably in 2015. Interestingly, the difference between the two measurement heights (BH and BC) was significant only in the managed stand (Fig. 3). Maximum basal area increment was on average higher in the managed stand (average \pm standard error = 59 ± 4.2 cm² in 2015 and 44 ± 2.8 cm² in 2016) compared to the unmanaged stand (27.9 ± 2.6 cm² in 2015 and 28.1 ± 3.4 cm² in 2016). Average maximum crown base area increment was higher in the managed stand (38 ± 2.4 cm² in 2015 and 32 ± 3.4 cm² in 2016) compared to the unmanaged stand (25 ± 2.0 cm² in 2015 and 23 ± 2.1 cm² in 2016) as well.

Correlation between stem base and crown base radial increment

In 2015, the relationships of stem Basal Area Increment (BAI) to Crown base Area Increment (CAI) in the managed

($R^2 = 0.57$) and unmanaged stands ($R^2 = 0.74$) were both high and the main difference observed was a higher BAI at the managed compared to the unmanaged stand. In 2016, however, there was a stronger relationship between BAI and CAI in the managed ($R^2 = 0.71$) compared to the unmanaged stand ($R^2 = 0.36$). BAI in the managed stand was substantially reduced in 2016, while BAI in the unmanaged stand was only slightly reduced. The slope between BAI and CAI at the unmanaged site in 2015 was steeper (0.71 ± 0.13) than at the managed site (0.45 ± 0.10), whereas in 2016, the slope at the managed site became steeper (1.01 ± 0.18) when compared that of the unmanaged stand (0.65 ± 0.26) (Fig. 4). However, the slopes were not significantly different for years ($p > 0.05$ in 2015 and 2016).

The average monthly cumulative diameter increment (stem base diameter increment $BH_{incr.}$ and crown base diameter increment $BC_{incr.}$) considered for all trees were higher in the managed stand compared to the unmanaged stand (managed_2015: $BH_{incr.} = 6.3 \pm 0.06$ mm and $BC_{incr.} = 5.3 \pm 0.04$ mm; unmanaged_2015: $BH_{incr.} = 3.1 \pm 0.05$ mm and $BC_{incr.} = 3.2 \pm 0.03$ mm; managed_2016: $BH_{incr.} = 5.02 \pm 0.06$ mm and $BC_{incr.} = 4.5 \pm 0.08$ mm; unmanaged_2016: $BH_{incr.} = 3.3 \pm 0.05$ mm and $BC_{incr.} = 3.3 \pm 0.04$ mm)

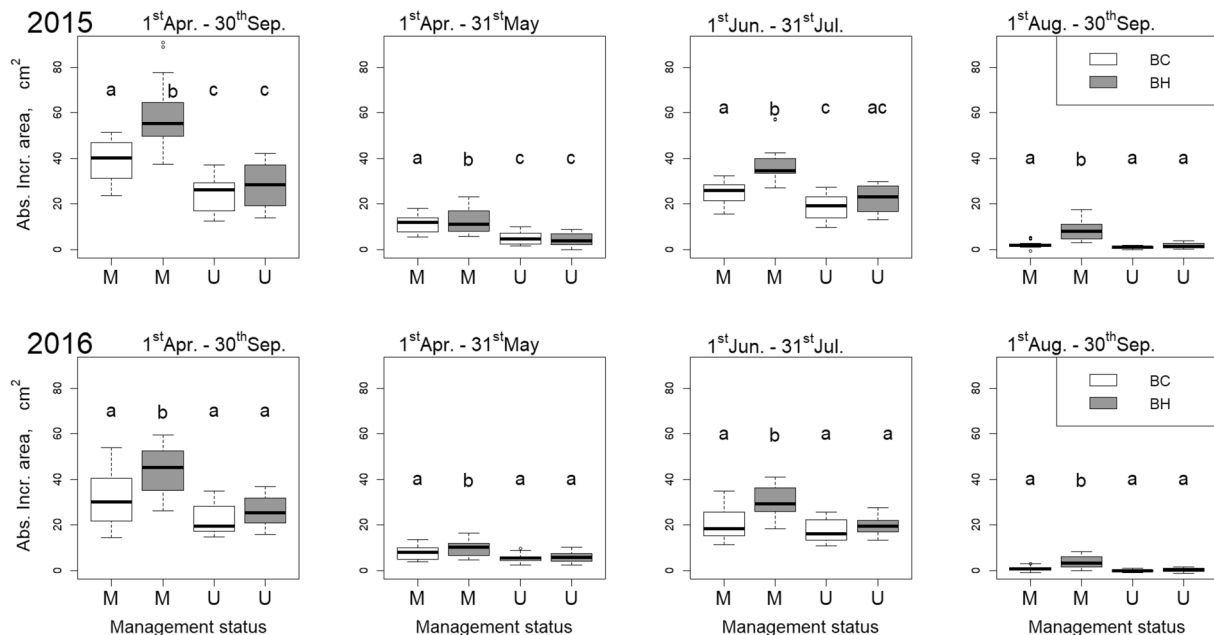


Fig. 3 Influence of management status and measurement heights on absolute intra-annual area increment (cm²) in 2015 (top row) and 2016 (bottom row). Two management conditions (*M* Managed and *U* Unmanaged) and two measurement heights (*BH* stem base, and *BC* crown base) were compared. Four periods were considered (April to

September, April and May, June and July, August and September). The letters a, b and c indicate the significance of differences between the variables on the *x*-axis. The variables carrying at least one common letter are not significantly different. The box plot represents raw data, while test results are corrected for the random effect

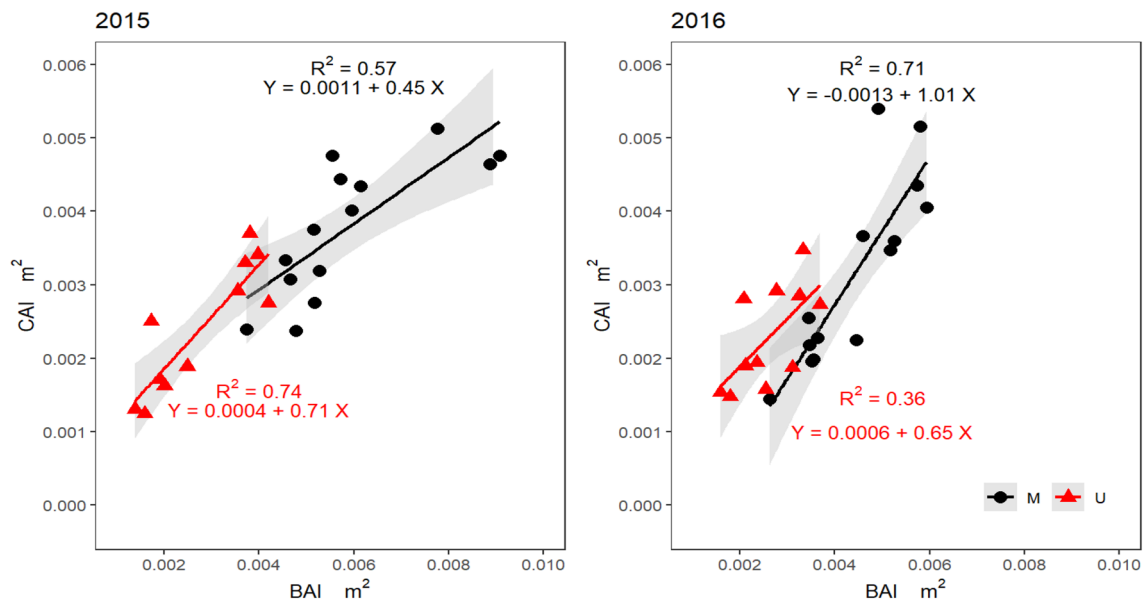


Fig. 4 Relationship between basal area increment (BAI) in m^2 and crown base area increment (CAI) in m^2 per tree in two years (2015 and 2016). Black circles represent data from the managed stand (M)

and red triangles from the unmanaged stand (U). The grey-shaded area represents the confidence interval around the predicted values

(Fig. 5). In the managed stand, the difference between radial increments at the stem base and crown base resulted from different patterns in late summer (July to September). Patterns in the unmanaged stand differed from those in the managed stands; here, differences between $BH_{incr.}$ and $BC_{incr.}$ had already been observed by mid-summer but in contrast to the trees in the managed stand, $BC_{incr.}$ was always higher than the $BH_{incr.}$ (Fig. 5). In the managed stand, $BH_{incr.}$ and $BC_{incr.}$ during the late summer were in 2015 higher than in 2016.

Phases of radial growth at two levels

In the managed stand, tree growth started earlier and terminated later, resulting in a longer vegetation period compared to the unmanaged stand (Fig. 6; Table 2). The latter differences in days of onset and cessation between the two stands were always significant except in 2016 for the onset at stem base ($p=0.129$). In the managed stand (2015), growth terminated earlier at crown base compared to the growth at stem base. In contrast, in the unmanaged stand (2015), crown base growth lasted longer than stem base growth (Table 2).

Discussion

Effects of competition reduction on diameter growth

Absolute basal area increment (BAI) and crown base area increment (CAI) in the managed stand were higher compared to the unmanaged stand, which confirms our first hypothesis. Our results are in line with other studies such as that of van der Maaten (2013) who observed a prolonged growth duration due to reduced competition through thinning of European beech in wet and dry years. It has been known for decades that releasing trees from neighborhood competition can enhance their basal area increment substantially (Assmann 1961). In line with our findings, this positive thinning effect has been confirmed repeatedly for beech (Boncina et al. 2007; Diaconu et al. 2015; Pretzsch 2005; Utschig and Küsters 2003). In stands of *Pinus taeda* and *Pinus elliottii* with different densities, Will et al. (2001) observed a decreasing response in stem volume growth to increasing stocking density as light interception was reduced and competition increased. These retrospective studies suggest that thinning provides favorable microclimate conditions (i.e., light, temperature) for residual trees, resulting in increased resource availability and growth (Aussenac 2000; Chase et al. 2016; Giuggiola et al. 2016). However,

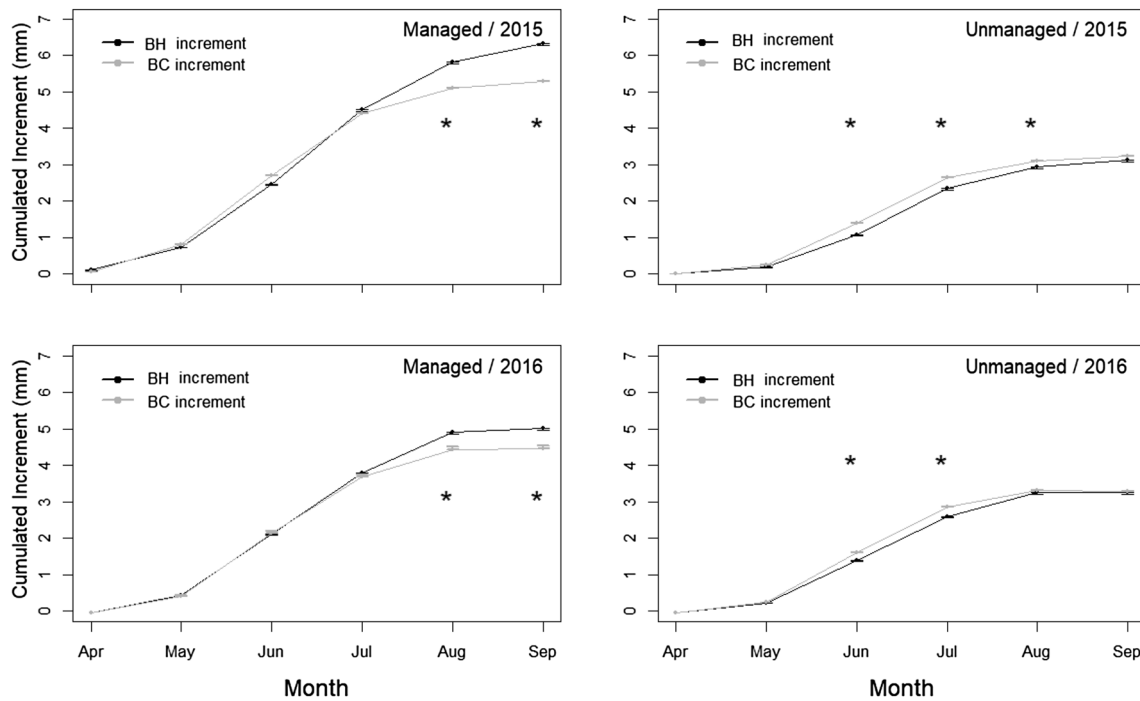


Fig. 5 Monthly average increment considered at two height levels (diameter at stem base (BH increment) in black and crown base (BC increment) in grey), in two stands (Managed and Unmanaged) in

2015 and 2016. Standard error bars are indicated. Asterisks indicate significant differences between the two levels (BH and BC) ($p \leq 0.05$)

the positive response of tree growth to repeated thinnings has almost exclusively been studied solely at stem base (i.e., diameter at breast height). If trees respond differently to competition reduction at different tree heights, estimates of total above-ground biomass production when tree growth is monitored at the tree base only, as is usually done, may be inaccurate (Schweingruber et al. 1990).

Growth response at different stem heights

Our second hypothesis suggested that the relationship between BAI and CAI is stronger in the managed stand. The

results in Fig. 4 support this view only in 2016 but not in 2015. The marked reduction of BAI in the managed stand between 2015 and 2016 suggests a greater sensitivity of the managed stand to weather conditions (temperature, precipitation, wind, etc.), which is typical of managed stands (Mausolf et al. 2018). This is in contrast to unmanaged stands where BAI decreased slightly between the two years. Directional patterns of CAI between 2015 and 2016 were not so distinct at either stand, suggesting less sensitivity to weather conditions at crown base compared to the tree base. Although trees in the unmanaged stand were taller, BAI was substantially lower than that of trees in the managed stand;

Table 2 Average starting and ending day of growth with standard error (se) for each category (managed and unmanaged sites, crown base (BC) and stem base (BH) levels

Year	Management	Level	Average day of year_growth start (day and month) ± se	Average day of year_growth end (day and month) ± se	Average duration of the growing period (number of days)
2015	Managed	BH	127 (7th May) ± 2	234 (22nd August) ± 2	107
2015	Managed	BC	123 (3rd May) ± 1	216 (4th August) ± 2	93
2015	Unmanaged	BH	137 (17th May) ± 2	217 (5th August) ± 2	80
2015	Unmanaged	BC	131 (11th May) ± 1	213 (1st August) ± 1	82
2016	Managed	BH	129 (8th May) ± 1	215 (3rd August) ± 2	86
2016	Managed	BC	128 (7th May) ± 1	206 (25th July) ± 2	78
2016	Unmanaged	BH	131 (10th May) ± 1	204 (23rd July) ± 2	73
2016	Unmanaged	BC	132 (12th May) ± 1	198 (17th July) ± 2	66

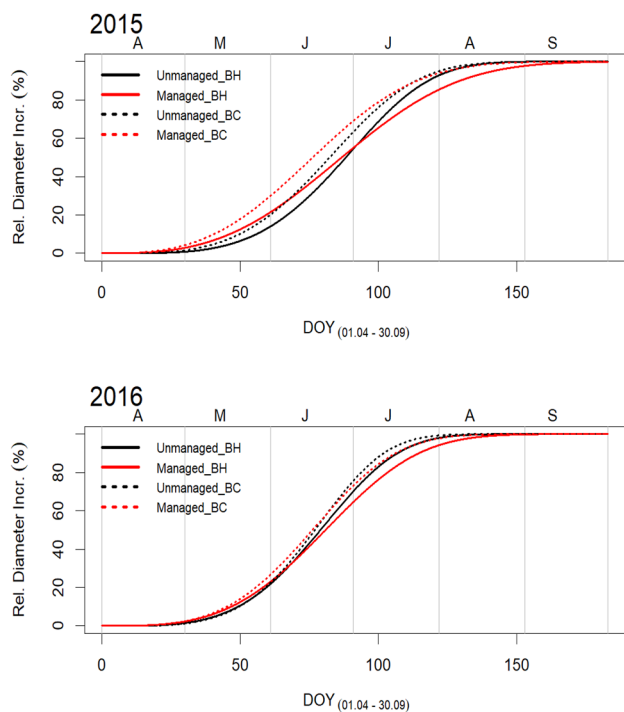


Fig. 6 Weibull functions of tree growth fitted based on Weibull parameters (time and shape parameters) averaged for all measured trees in 2015 and 2016. Two management strategies (managed/red and unmanaged/black) and two height levels (Stem base/BH/plain line and Crown base/BC/dashed line) were considered. The grey vertical lines mark the limit between the investigated months (beginning April to end September/A to S on the top x -axis)

stronger competition for light in the unmanaged stand and the absence of a particular need for stem stabilization could explain these observations. Our results contribute to the discussion whether field-based biometric estimations of carbon pools (see for example Mund et al. (2020)), or Eddy covariance flux-based estimations (see for example Tamrakar et al. (2018)), yielded more reliable results. In fact, in the same stand (Hainich National Park, Germany) Mund et al. (2020) recorded $2.01 \pm 80 \text{ tC ha}^{-1} \text{ year}^{-1}$ of living and dead biomass and organic matter around the footprint eddy tower, whereas Tamrakar et al. (2018) obtained $4.87 \pm 57.8 \text{ tC} \cdot \text{ha}^{-1} \text{ year}^{-1}$, values averaged for a 14-year records. The higher value recorded by Tamrakar et al. (2018) could be related to “an underestimation of the heterotrophic respiration rates” (Mund, 2004). However, since the calculations by Mund et al. (2020) were based on diameter at breast height only, they may have underestimated carbon sequestration. Further research is recommended, with a greater sample size, and where diameters at two different heights are measured, to get better estimates of carbon storage.

In the unmanaged stand, diameter growth at crown base was equal to or higher than at stem base in both years (Fig. 5). However, it should be noted that identical diameter

increments at stem base and crown base does not mean identical area increment at both heights; the latter is strongly influenced by the initial diameter (Diaconu et al. 2015). In the managed stand, lower diameter increments at crown base compared to the diameter increment at stem base may reflect a limited carbon gain at crown base, possibly due to the necessity of trees to increase their stability, as the trees in open stands are more exposed to wind. In fact, Yücesan et al. (2015) found that light thinning, by exposing stands to wind hazards, promoted stability of beech trees. Bruchert and Gardiner (2006) assessed the effect of wind exposure on the architecture of *Picea sitchensis* and found that exposed trees expressed their resistance mechanism to wind through a higher taper; this resulted from greater rigidity and larger diameter at stem base compared to the crown base. It is assumed that once tree stability is secured by carbon allocation at the base, the stabilizing mechanism continues to the upper part of the tree. In the managed stand, growth was more stimulated at the stem base compared to the crown base, and was more limited in the unmanaged stand. In the managed stand diameter growth at crown base followed similar patterns as observed at tree base for the first months of the vegetation period. Figure 5 illustrates that from April to July, the monthly averages of cumulative radial increment of trees in the managed stand were almost equivalent between both levels, and differences between the two started only in July. Thus, it seems that the positive effect of competition reduction simultaneously facilitates tree growth at both heights in the beginning of the growing period. However, in late summer, trees in the managed stand seemed to invest more carbon in the lower part of the stem. We can only speculate, but it may be for stability reasons. Valinger (1992) found, when investigating stem increment in 45-year-old *Pinus sylvestris* trees, that thinning had a greater positive effect on increment at stem base compared to the upper part. Such results had been observed by Farrar (1961) and Myers (1963) after thinning in a *Pinus ponderosa* stand and by Thomson and Barclay (1984) in a *Pinus menziesii* stand.

Investigation of stem-growth onset, duration and termination

During the vegetation periods of 2015 and 2016, growth started on average in early May (3rd to 8th May in the managed stand, 10th to 17th May in the unmanaged stand), peaked around end June (23rd June to 4th July in both stands) and ceased by mid-July to mid-August (25th July to 22nd August in the managed stand, 17th July to 5th August in the unmanaged stand), resulting in a longer growing period in the managed stand. The growing patterns observed at the two study sites resembled the wood formation phases of beech trees as investigated by Čufar et al. (2008) and Metz et al. (2020). Considering that the differences in growth

phases between our two stands were for the most part significant, our third hypothesis, suggesting that releasing trees from neighborhood competition affects the growth phases of the remaining trees, was confirmed. The latter observation indicates that resource limitations in the unmanaged stand significantly delayed growth at both stem heights, except at stem base in 2016. This single exception might reflect specific microclimate conditions in early spring 2016 resulting in similar physiological responses of trees at both stands, i.e., air temperature in early spring 2016 may have caused the growth onset at stem base in the unmanaged stand. Similar investigations from deciduous forests are rare, but observations from conifers exist. For example, Drew and Downes (2018), when assessing the timing of *Pinus radiata* growth, found that growth onset at thinned and unthinned stands were generally very similar, differing from our observations. Drew and Downes' (2018) observations, opposite from ours, could be related to the investigated species (*Pinus radiata*) which is known to have a lower adjustment potential compared to beech (Knoke et al. 2008). In fact, the adaptability of beech to changing environmental conditions is linked to its attempt to stabilize, reflected in its earlier stem base growth in the exposed (managed) stand compared to the unmanaged stand. Drew and Downes (2018) also found that growth duration was longer in the managed stand compared to the unmanaged, which agrees with our findings. These observations suggest that the significant differences in total area increments, accumulated over the vegetation period between the managed and unmanaged stands, are closely related to the timing of growth (onset and termination) observed between the two sites.

We found that at both sites, tree growth started earlier at crown base compared to stem base (Fig. 6). The closer position of the crown base to the carbon source compared to the stem base as demonstrated by Lacoite (2000) may serve as a first potential explanation. The carbon captured by the leaves gradually builds the tree from the top to the bottom as shown by Larson (1963). A distance-related model relative to the crown is, however, only a single model among others (Lacoite 2000) and might not exclusively explain the earlier start of growth at crown base. In fact, carbon allocation patterns are controlled by sources and sinks (Dickson 1989; Gower et al. 1997), supporting the proposal that nutrients/water uptake from the soil may also determine stem growth. Furthermore, it was found that stem growth is not restricted by carbon limitation (Schulze et al. 1994; Skomarkova et al. 2006; Mund et al. 2010) suggesting that other external factors such as weather conditions might also determine tree growth (Mund et al. 2010, 2020). Other assumptions explaining the earlier growth onset at crown base than at stem base arise from a physiological perspective. Important

phytohormones such as cytokinin and auxin are involved in cell division, morphogenesis and thus cambial development (Nieminen et al. 2008). It is well known that phytohormones play an important role in the regulation of cambial growth, and the growth in spring starts from the top of trees (Sorice et al. 2013; Bhalerao and Fischer 2017). In addition, more studies confirm that diffuse-porous species such as beech start cell division at the crown base earlier than at stem base (Schmitt et al. 2000; Sprengel et al. 2018). In fact, diffuse-porous species are characterized by the presence of vessels of more or less equal sizes and evenly distributed in the annual ring, that are primarily formed at bud base and then gradually downward to the stem base (Takahashi et al. 2013).

Conclusions

Our study demonstrated that competition reduction affects stem growth differently at two considered stem heights, which can be explained by changes in environmental conditions (i.e., light and resource availability). Growth termination and thus duration throughout the vegetation period were extended due to the management effect. This was of particular importance at stem base, since in the unmanaged stand growth duration at crown base was longer. The great potential of beech to adjust its stem morphology to environmental changes explains the observed patterns in the managed stands. Our results underscore the role of tree removal as an efficient management strategy to control biomass allocation at various stem heights in beech stands. We recommend further investigations into the contribution of diameter growth at upper parts of the stem to develop more accurate biomass estimation models.

Author contribution statement LSD, PS and CA designed and conceptualized the study; PS collected the data; LSD did the data curation; LSD, CA, MM and PS led the formal data analyses; LSD wrote the original draft. LSD, CA, PS, MM and AK contributed to the critical review of the drafts and approved the final manuscript.

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Availability of data and materials The datasets analyzed during the current study are available from the corresponding author on request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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