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# Trees grow modulated by the ecological memory of their past growth. Consequences for monitoring, modelling, and silvicultural treatment

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A B S T R A C T

The growth of forest trees under given environmental conditions is assumed to depend mainly on their age, stem and crown size, and competitive position in the stand. The current stem and crown size are commonly recognized as adequate proxy markers for the tree's ecological memory of the past. In contrast, tree ring structure, crown whorl morphology, or other biographical patterns are rarely used for predicting growth. Here, we asked how the latter affect tree growth.

Our main hypothesis was that the growth in the longer past significantly co-determines the present growth. To test this hypothesis we derived metrics which quantify the social position, course of growth, and annual variation of trees in their past. We further selected variables for quantifying the trees' present stem and crown size and competitive status. Finally, we selected the approximately 200-years-old thinning experiment in European beech (*Fagus sylvatica* L.) Fabrikschleichach 15 in South Germany as our study object because it provided all required information.

To examine the dependency of the current growth on the present growing conditions and the past tree development more closely, we applied linear mixed models. They revealed that (i) trees with similar age, size, crown and competitive status at present grew better if they were subdominant in the past. (ii) Ceteris paribus, slow starting trees with progressive growth trajectories were associated with higher growth than quick starting trees with degressive growth trajectories. (iii) Trees with lower interannual variations of growth in the past had significantly higher growth rates at present than trees with higher interannual variations of growth in the past. (iv) Including information about the trees' past reduced the RSME of the diameter growth model by 17–27% and increased the $R^2$ by 15–30%. Thus, the diameter growth model could achieve $R^2$ values of 0.76–0.79. (v) The contribution of past information for estimating present growth was higher in periods without thinning.

We suggest that in the analysed European beech stands, even at parity of stem diameter or crown size, different courses of growth created different internal stem structures and crown morphologies. Such past structural and morphological formations may affect the tree's light interception and hydraulic conduction. These differences in structure may cause specific differences in the present tree functioning and growth. Of course these findings based on only one long-term experiment should not yet be generalized. However, the revealed relationship between the past and present growth deserves further investigations. We discuss the relevance of the ecological memory embedded in the past growth and in the tree ring pattern. We stress the consequences of the ecological memory for the monitoring, inventory, and modelling of tree growth and its implications for the development of silvicultural prescriptions.

## 1. Introduction

Which factors determine the growth of a tree is of high interest for both forest science and forest management. Knowledge of the main factors of tree growth is essential for understanding, modelling, predicting, and steering silvicultural interventions and practices toward appropriate tree and stand development. Classical concepts posit that individual tree growth depends mainly on environmental conditions, competitive status, and current age.

The growth of trees depends mainly on the resource supply and environmental factors. The individual tree's competition as an additional external factors of tree growth got in the focus with the transition

to individual tree measurement and modelling. Many competition indices (Biging and Dobbertin 1992, 1995) were developed to better quantify individual tree local environment and growing space (Webster and Lorimer 2003) and to estimate the trees' resource supply and growth. The strong dependence of tree growth on both size and resource supply was confirmed, among others, by Magin (1959) and Preuhsler (1979, pp. 158-175) who analyzed trees with different suppression times in the mountain forests of the Alps. They found that the trees' growth rates depended mainly on the duration of overshading, i.e. on the light supply.

Under given external conditions tree growth may be predicted depending on age (Backman, 1943, Richards 1959). However, age is not a mechanistic driver of growth for modular organisms like trees. Trees grow by continuously producing multiple copies of discrete units (e.g., tree rings, branches, twigs, roots). This keeps their latest modules juvenile. The cells in the tissue of the stem and branch modules built in the more distant past are often shut down, e.g., by heartwood formation. Thus, the older modules serve as useful scaffolds for the younger modules, but require only low or even no maintenance respiration. In this context, there is little evidence for genetic aging, at least at time scales relevant for human purpose (e.g., rotation time). In fact, tree vitality may be increased over decades through epigenetic acclimation (Rico et al. 2014, Bose et al. 2020). Hence, while tree growth may be plotted over time, in contrast to human beings and animals, neither time nor age are driving growth. Approaches to predict tree growth depending on time, e.g., introduced by Backman (1943) and Weck (1948), were inadequate (Assmann 1961, p. 42-44). Tree growth is mechanistically depending on resource supply and environmental factors and on the present plant size, rather than on tree age or on time. The bigger the present size the more extended the meristems for building new cells and the higher the growth rate. In the past, many studies have been published on the subject of the course of tree growth depending on tree size (von Bertalanffy, 1951, Coomes and Allen 2007). Tree growth theory (von Bertalanffy, 1951, Wenk et al. 1990) and corresponding growth equations (Zeide 1993) have used tree volume or mass as predictors of growth (Pretzsch 2020a). An estimation of the metabolic rate and growth, according to the model by West, Brown and Enquist (1997) (WBE model), i.e. only based on body size or mass, is useful for a simplified assessment of the productivity when detailed predictors are not available. However, the WBE model approach may be an over-simplification, especially in heterogeneous stands with a wide variation of stem and crown allometries (Kozłowski and Konarzewski 2004, Muller-Landau et al. 2006).

Beyond by resource supply and size, tree growth can also be determined by antecedent growing conditions. Past conditions may affect growth via epigenetic (Rico et al., 2014; Bose et al., 2020), transcriptional, proteomic, and metabolic (Fleta-Soriano and Munné-Bosch, 2016) changes, and also through physiological adjustments (Peltier and Ogle, 2019) and the created plant structure (Netzer et al., 2019). The internal structure of the trunk (Fleta-Soriano and Munné-Bosch, 2016, Netzer et al. 2019), the tree ring pattern (Ogle et al. 2015, Camarero et al. 2018), and the crown morphology (Mäkelä and Valentine 2006, Duursma et al. 2010) may represent an ecological memory and determine a tree's growth and vitality in the future. A description based on present mass or size and environmental conditions neglects individual differences in their morphology (e.g., ring pattern, whorl distances, root length). The trees' development from their early beginning on is still manifested in their internal structure and external morphology in advanced ages. And the manifested structure may determine the functioning, the processes, and the growth. This suggests that explanation of tree growth in dependence on time, mass or external characteristics such as crown size is inevitably insufficient. So far, only a few studies addressed the dependency of growth on internal stem traits (e.g. tree ring pattern, amount of sapwood) or inner crown structure (e.g. whorl structure, dead branch frequency, leaf area) on tree growth and stress response (Zweifel and Sterck, 2018, Zweifel et al. 2020). There are many

studies about the relevance of internal traits like rot, pruning, frost cracks on wood quality (Nikolova et al. 2009, Seifert et al. 2010, Pretzsch and Rais 2016). However, how internal traits of the stem, crown, or root modify the functioning of the tree and determine its current or future growth rate is hardly known (de Kort 1986, Borghetti et al. 1998, Ryan and Yoder 1997, Pretzsch 2005).

We used the thinning experiment in European beech (*Fagus sylvatica* L.) named Fabrikschleichach 15 (FAB 15) to examine to what extent past growth trajectories of trees modify present und future tree growth. The long-term thinning experiment FAB 15 in South Germany offers information about the past and current growth and morphology for a large number of trees (Pretzsch et al. 2019). FAB 15 provided the necessary data base to analyse the ecological memory effect of growth and structure recorded in the past on present and future growth. The state-of-the-art concept is that the present stem size, tree mass, crown size, and competive status adequately represent the trees' history when modelling and predicting tree growth (Pretzsch 2009, Weiskittel et al. 2011, Burkhart and Tomé 2012). Here, we questioned how tree growth is further modulated by the ecological memory in terms of the structural memory imbedded in the tree ring pattern of the stem. Specifically, we analysed how the current tree growth was modified by the social position in the long past, the long-term course of growth, and the interannual variation of growth. Further, we quantified how this information about the past can improve the prediction of present and future growth, and how the revealed ecological memory effect is modulated by thinning effects on growth. Finally, we discussed the implications of the ecological memory effect for the monitoring, modelling, and management of trees and forest stands.

## 2. Material and methods

### 2.1. Material

To analyse how the history of a tree determines its current growth in addition to classical predictors, we selected the long-term thinning experiment in European beech Fabrikschleichach 15 (FAB 15) with A-, B-, and C-grade plots (see explanation below for the grade's definition). FAB 15 provided the necessary database required for this analysis. The rectangular, approximately 0.4 ha sized A-, B-, and C-grade plots of FAB 15 were established in 1870–1871 in a 48-year old, even-aged European beech stand. The stands on the three plots originated from natural regeneration by shelterwood cutting (Burschel and Huss 1987, p. 90-92) of a beech stand in 1822. FAB 15 is located 1 km east of the village Fabrikschleichach at 10.62° E longitude and 49.95° N latitude. It belongs to the ecoregion 5.2 Steigerwald (Arbeitskreis Standortskartierung 1985) and to the forest enterprise Ebrach. The annual precipitation is 820 mm (420 mm in the growing season), the mean annual temperature 7.5 °C (14.5 °C in the growing season), and the length of the growing season is 150 days. The natural vegetation in this region would be submountane European beech-sessile oak forests. Soils are mainly brown soils of Coburg sandstone (Semionoten sandstone).

Like most of the classic long-term experiments, FAB 15 comprises so called "A-grade plots" (VDFV 1902). "A-grade" is defined by VDFV (1902, § 4) as follows (translated from German into English) "This is limited to the removal of dying and dead trees, as well as any bowed pole wood .[…]. for the purpose of delivering material for comparative growth investigations only". In other words, on A-grade plots nothing more is done than the close monitoring of natural mortality and the removal of dying or dead trees to prevent possible stand damage through dead trees (infestations by fungi or insects). B- and C-grades represent moderate and heavy thinning from below (VDFV 1902, § 4) as they moderately and heavily reduce stand density (mainly by removing small trees). Tall trees are removed only when they are of poor quality.

## 2.2. Methods

### 2.2.1. Dendrometric measurements

All trees included in this experiment have been measured 18 times since the first survey in 1870. From the first survey at age 48 years in spring 1871 to the fifth survey at age 77 in autumn 1899 the tree measurements were registered in tally-sheets. In the course of the sixth survey in 1904, at a stand age of 82 years, the trees were individually numbered. Since that time the individual tree size development is known and can be analysed. This is why the stand characteristics can be reported since 1871 but the individual tree characteristics only since 1904. For the present analyses we used the 13 continuous full inventories of stem diameters, tree heights and crown length since 1904. For 1980, at age 158, we have detailed records of all stem positions and crown radii in addition to the standard inventory of diameter, height, and crown length. The crown radii were measured in 8 cardinal directions by the projection method using a plummet (Röhle and Huber 1985). Thus, the growth in 1980–1990 can be linked to the tree status at the beginning of this growth period but also to the more distant past from 1904 to 1980. For the year 2000 we obtained a second detailed measurement of 8 crown radii that may be related to the growth in the past and in the period from 2000 to 2010. In 2000, the B- and C-grade plots were thinned. Hence, the growth in the period 2000–2010 can be used to analyse the effects of past and present conditions on thinning reactions.

The repeated measurements (Fig. 1) covered the diameter at breast height ($d_{1.3}$, cm) and tree height ($h$, m), as well as the height to crown base ($hcb$, m). Several surveys included the measurement of the crown radii projection of the trees in the eight cardinal directions (N, NE, E, SE, S, SW, W, NW) according to standards described by Pretzsch (2009, pp. 115-118) and Röhle and Huber (1985). The eight radii were used to calculate the crown projection area in $m^2$ $cpa = \overline{cr}^2 \times \pi$ with $\overline{cr} = \sqrt{(r_1^2 + r_2^2 + \cdots + r_8^2)/8}$.

FAB 15 provided surveys in 1871s, 1884s, 1889a, 1894a, 1899a, 1904a, 1909a, 1924a, 1929a, 1936 s, 1950a, 1958a, 1968a, 1978s, 1981s, 1991s, 2000a, and 2010a (s = survey in spring, a = survey in autumn). A survey in spring (e.g. 1981 s) means that the growth of that



**Fig. 1.** Visualisation of the variables used in this study to quantify tree structure and crown morphology. The course of growth and tree ring patterns was reconstructed using the repeated mesurements dating back to 1904. d stem diameter at height; h, tree height; hcb, height to crown base; cl, crown length; cr, crown radius; cpa, crown projection area.

year (i.e. 1981) was not yet included due to the measurement before the start of the growing season in that year. In contrast, a survey in autumn (e.g. 2000a) includes the growth of that year (i.e. 2000). Accordingly, the terms survey 1981 or period 1981–2000 may suggest that the survey 1981 includes the growth in 1981 and that 1981–2000 covers a duration of 19 years. However, the survey 1981 does not include the annual growth of the year 1981 and the period from spring survey 1981 to autumn survey 2000 covers 20 years. To avoid confusion we named surveys according to the calendar year of the last included growth period, i.e., 1871 s = 1870, 1889a = 1889, … etc.

The repeated surveys yielded data suitable to calculate all common stand characteristics for each of the 18 successive survey periods since 1870 (Biber 2013). Table 1 provides an overview over the stand characteristics at the last survey in 2010. The reported stand level data was derived from the diameter and height records as well as from the removal trees. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (in German "Deutscher Verband Forstlicher Forschungsanstalten") (Johann 1993). To estimate the merchantable tree volume of European beech we used the approach by Franz et al (1973) with the equations and coefficients published by Pretzsch (2002, p. 170, Table 7.3).

The mean heights at age 100 (Table 1) indicate a site index of I.-II. according to the yield table of Schober (1967, 1975, moderate thinning). Thus FAB 15 represents good to very good site quality and productivity. This is corroborated by the main stand charateristics of the three plots at the last survey (Table 1). The stand density, represented by the tree numbers, N, stand basal area, BA and standing stem volume (merchantable wood >7 cm at the smaller end), V, decreased continuously from the A- to the C-grade due to the thinning interventions. This stand density reduction created more growing space for the remaining trees and had a strong positive effect on their stem diameter growth, d. The current and mean annual stand volume growth, and the total yield were increased by the thinning on the long term. The last two columns in Table 1 show that the removed volume was approximately twice as high on the C-grade compared to the removed volume on the A-grade plot. Notice that on the A-grade plots only trees that were already dead or dying due to self-thinning were removed. The percentage of removed stand volume in relation to the total yield at age 188 were increased by the active thinning from 21.2% (A-grade) to 38.2% (C-grade).

Table 2 shows the mean tree characteristics of the A-, B-, and C-grade plots at the last survey in autumn 2010 at the stand age of 188 years. It reflects that the stem dimensions d, h, and v, at the last survey were much higher in moderately and heavily thinned stands than on the A-grade plot. The positive effect of thinning on the crown dimensions, cr, cl, and cpa was even stronger. The increased size on the B- and C-grade plots is associated with higher stem diameter and stem volume growth in the last survey period. Regarding all variables the effect size of thinning was much stronger for the transition from A- to B- grade than from B- to C-grade. For more details about this long-term experiment see works by Assmann (1950, 1970) and Kennel (1972) regarding thinning reactions, by Franz et al. (1993) and Pretzsch et al. (2019) regarding long-term survey, and by (Pretzsch 1999, Pretzsch et al., 2014) with respect to indication of environmental changes and quantification of growth trends.

### 2.2.2. Quantification of the trees' current and past competitive status

To characterise the trees' competitive or social status, spatially dependent competition indices (Biging and Dobbertin 1992, 1995) are the most appropriate. However, for inventories dating back many years or decades, the stem positions and crown characteristics required for such indices are commonly unavailable. To quantify the trees' competitive status in the longer past we used the diameter percentile of the trees as a spatially independent competition index. The stem diameter percentiles (from 0 = lowest to 100 = predominant) were calculated for all stand surveys from 1904 to 2010 based on the ranking of the trees in the
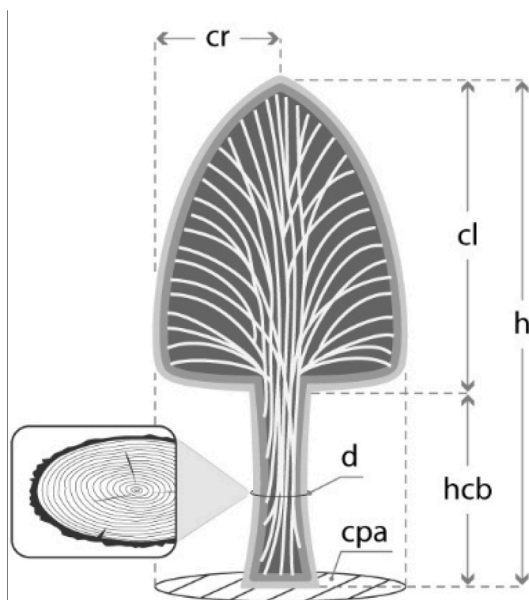
**Table 1**
Stand characteristics of the A-, B-, and C-grade plots at the last survey in autumn 2010 at the stand age of 188 years. N, tree number per hectare; dq quadratic mean stem diameter; hq, height of the tree with the quadratic mean diameter; BA stand basal area; V standing stem volume; Current annual volume growth, stand volume growth in terms of merchantable wood (>7 cm at the smaller end) in the last survey period 2000–2010; Mean annual volume growth, average stand volume growth per year since stand establishment; Total yield, total stand volume growth since stand establishment; Removed volume, volume removed (dead trees on A-grade plot; thinned trees on B- and C-grade plots); Intermediate yield, removed stem volume/total yield $\times$ 100. The Intermediate yield indicates how much of the total yield were already removed by preliminary harvest until age 188.

| Thining grade | Stand age yr | N ha$^{-1}$ | dq cm | hq m | BA m$^2$ ha$^{-1}$ | V m$^3$ ha$^{-1}$ | Current annual volume growth m$^3$ ha$^{-1}$ yr$^{-1}$ | Mean annual volume growth m$^3$ ha$^{-1}$ yr$^{-1}$ | Total volume yield m$^3$ ha$^{-1}$ | Removed volume m$^3$ ha$^{-1}$ | Intermediate yield % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A-grade | 188 | 381 | 44.1 | 36.1 | 58.4 | 1120 | 8.3 | 7.8 | 1460 | 308 | 21.1 |
| B-grade | 188 | 194 | 54.0 | 39.8 | 43.5 | 920 | 13.4 | 9.1 | 1715 | 607 | 35.4 |
| C-grade | 188 | 128 | 62.4 | 41.5 | 39.3 | 865 | 12.9 | 8.8 | 1655 | 633 | 38.2 |

**Table 2**
Characteristics of the trees on the A-, B-, and C-grade plots at the last survey in autumn 2010 at the stand age of 188 years. The variable abbreviations are d, stem diameter at breast height; h, tree height; v, stem volume; cr, crown radius; cl, crown length; cpa, crown projection area; stem diameter increment; stem volume increment; id, mean periodical annual increment of stem diameter; iv, mean periodical annual increment of stem volume.

| Thinning grade | d cm | h m | v m$^3$ | cr m | cl m | cpa m$^2$ | id 2000–2010 cm yr$^{-1}$ | iv 2000–2010 dm$^3$ yr$^{-1}$ |
|---|---|---|---|---|---|---|---|---|
| A-grade | 42.7 | 35.8 | 2.68 | 2.88 | 15.14 | 27.38 | 0.11 | 141 |
| B-grade | 52.2 | 39.8 | 4.49 | 3.37 | 16.99 | 38.10 | 0.21 | 320 |
| C-grade | 58.9 | 41.2 | 5.92 | 3.99 | 19.51 | 53.03 | 0.24 | 468 |

diameter distribution of the whole stand. For the statistical analyses we used all trees' percentiles of the surveys in 1904, 1980, and 2000.

Fig. 2a shows the change of the position in the tree diameter distribution from 1904 to 2010 using the example of three selected trees (a quickstarter, a latecomer, and a mean tree). The individual trees' position was used for calculating their percentiles in the diameter distribution at each survey. In the example in Fig. 2a the quickstarter had percentiles of 99, 94, and 90% in 1904, 1980, and 2000, respectively. The mean tree developed from 62 to 85, and 86%. The latecomer started with percentile 41% in 1904 and increased to the diameter percentiles 72 and 89% until the surveys in 1980 and 2000, respectively. This means that quickstarters have high diameter percentiles first and lose in the

ranking later, whereas latecomers start subdominantly and later often improve their ranking.

The trees' competitive status for the surveys 1980 and 2000 for which stem positions and crown characteristics were available was further calculated based on the local stand density index (SDI). This competition index is distant-dependent and easy to interprete (Pretzsch and Biber 2010). The local SDI indicates, for each tree, the number of competitors in a defined search radius around its position. The detected tree number in the search radius is scaled up to a hectare and referred to an index diameter of $d_q = 25$ *cm* according to Reineke (1933). To calculate the local SDI we defined around the position of each tree an influence zone by a circle with radius r and area a. All trees within the
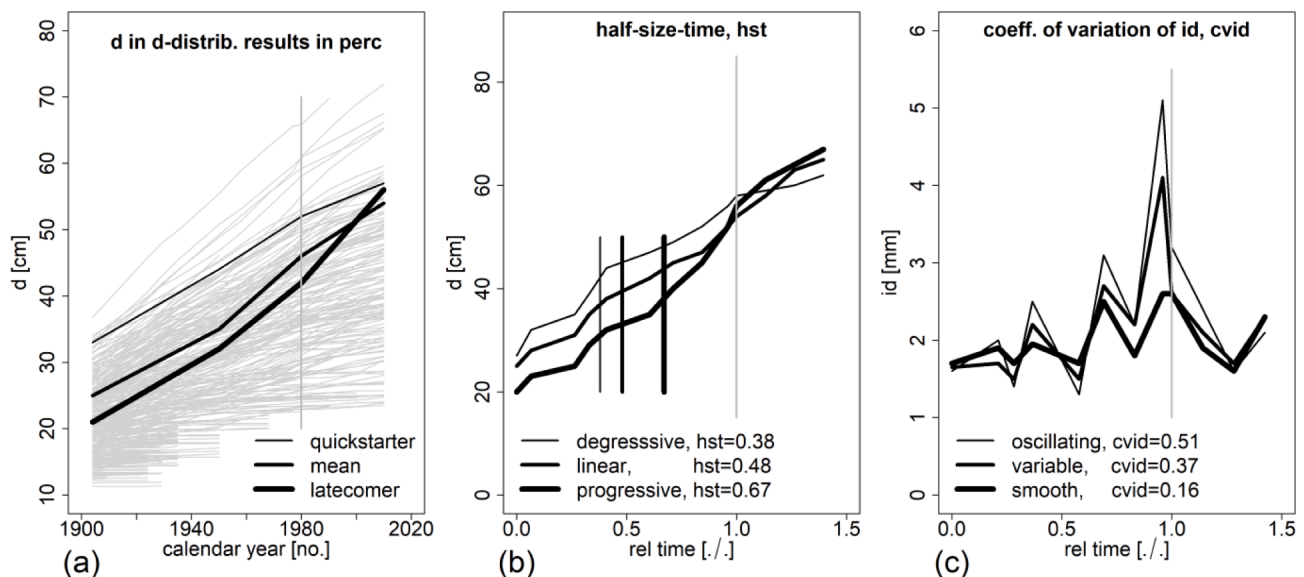


**Fig. 2.** Metrics for a tree's past development in schematic representation. (a) Change of the ranking of three model trees in the stem diameter distribution from the beginning to the end of the survey period 1904–2010. (b) half-size-time, hst, for characterizing the progressive, linear, or degressive growth trajectory. The light grey, grey and black vertical lines indicate at which points in time (from left to right: 0.38, 0.48, and 0.67) the degressively, linearly, and progressively developing trees, respectively, reach the half-size-time. (c) coefficient of variation for the diameter increment, cvid. The grey vertical lines in (a), (b), and (c) reflects the end of the imprinting period 1904–1980 for calculation of hst, and cvid. Further explanation of hst and cvid provided in the section "Characterization of the trees' past growth trajectory".

circle were used to calculate the local density n on circle area a. $N = 10.000/a \times n$ was the respective tree number upscaled to one hectare. For the n trees we calculated the quadratic mean stem diameter $d_q$ and based on this the local density $SDI = N \times (25/d_q)^{-1.789}$ around each individual tree. The circle radius, r was set to 5 m as test runs showed that this radius yielded the best correlation with the diameter increment. The local SDI was calculated using the species-specific allometric exponent of $-1.789$ for European beech derived by Pretzsch and Biber (2005). Notice, that the latter allometric exponent was based on the data of A-grade and unthinned plots of long-term beech experiments in South Germany. It deviates from the species-overarching exponent of $-1.605$ propose by Reineke (1933). In summary, we tried to make the most of the available data by using the distant-dependent competition index SDI where tree coordinates and crown measurements were available. For the early stand development phase for which stem coordinates were unavailable we used the diameter percentiles as distant-independent competition indices (Pretzsch 2009, pp. 305-314).

### 2.2.3. Characterization of the trees' past growth trajectory

We further quantified whether the past course of diameter development was degressive, linear, or progressive (Fig. 2b). We quantified the respective pattern by the half-size-time, hst, at which the tree achieved half of the size growth from the beginning to the end of the respective growth period. Fig. 2b shows in schematical representation that the trees with the degressive, linear, or progressive course reach the half-size-time at $t_{rel} = 0.38, 0.48, 0.67$, respectively. For quantification of the hst we calculated the half-size value $d_h = (d_e - d_b)/2$ and then read off the respective $t_{rel}$ from the x-axis. The trajectory of quickstarters with degressive development is indicated by low hst values, as the half of the diameter in a given period is achieved early. Latecomers are indicated by high hst values. They follow progressive courses of growth and reach the hst late. A continuous, linear development would result in $hst = 0.5$ (Fig. 2b).

### 2.2.4. Variation of the tree diameter growth

Based on the mean periodical diameter increment, id, in the past survey periods, the coefficient of variation $cvid = sd_{id}/\overline{id}$ was calculated using the standard deviation, $sd_{id}$, and mean, $\overline{id}$, of the id values. The more irregular the ring width pattern of a tree is, the higher is $cvid$ (Fig. 2c). For the calculation of cvid we used the surveys 1904a, 1909a, 1924a, 1929a, 1936s, 1950a, 1958a, 1968a, 1978s, 1981s, 1991s, 2000a, and 2010a and the respective growth periods. Following the explanation in the section "Dendrometric measurements" we called the surveys according to the calendar year of the last included growth period, i.e., 1904a = 1904, 1909a = 1909, 1924a = 1924, 1929a = 1929, 1936s = 1935, 1950a = 1950, 1958a = 1958, 1968a = 1968, 1978s = 1977, 1981s = 1980, 1991s = 1990, 2000a = 2000, and 2010a = 2010.

### 2.2.5. The growth periods selected for analysing the ecological memory effect

Measurements of the stem dimensions were available for all successive surveys, whereas records of the crown sizes were only available for the two surveys 1980 and 2000. To analyze the ecological memory effect, we needed the crown information at the beginning of the respective growth periods. To this aim, we selected two points in time for the following statistical analyses, 1980 and 2000. The survey 1980 and the subsequent growth period 1980–1990 represented a period without thinning. The decreasing diameter and volume growth of some trees in the 1980–1990 could be attributed to the drought years in the late 1970ies (Supplement Figures 1 and 3). In the year 2000 the B- and C-grade plots were thinned. Thus the subsequent growth period 2000–2010 represented a period with thinning effects. The thinning caused a growth increase of most of the trees on the treatement plots (B- and C-grade plots) in 2000–2010 (Supplement Figures 1 and 3, b and c).

### 2.3. Statistical models

In order to analyse and visualize the dependency of the tree diameter growth, id, on various tree attributes y we applied the regression model

$$id = a_0 + a_1 \times y + \varepsilon_k \qquad \text{Model 1.}$$

Using this general linear regression model we analysed the relationship between the annual increment of stem diameter and the stem diameter, mean crown radius, crown projection area, crown volume, percentiles of the diameter distribution in 1904, 1980 and 2000, local stand density index, half-size-time, and coefficient of variation of the diameter increment in the past.

Model 1 was fitted to two datasets. Firstly, we fitted it to the stem diameter increment data in the period 1980–1990 and the tree characteristics at the beginning of this period in 1980. Secondly, it was fitted to the stem diameter increment data 2000–2010 and the tree characteristics at the beginning of this period in 2000.

Models 2 and 3 were applied for exploration in more detail how the mean annual tree diameter growth in the periods 1980–1990 and 2000–2010, respectively, were determined by tree attributes of the present state and past development of the trees. For this purpose, we pooled the data of A-, B-, and C-grade plots. The indexes i, j, k in the following equations refer to the levels of experimental plot, tree within plot, and single observation, respectively. In both models the random variable $b_i$ accounts for correlation between the trees on plot i, and the random variable $b_{ij}$ accounts for the correlation among the observations of tree j on plot i.

$$id_{1980-1990\,ijk} = a_0 + a_1 \times d_{ijk} + a_2 \times cv_{ijk} + a_3 \times percd1980_{ijk} + a_4$$
$$\times percd1904_{ijk} + a_5 \times hst_{ijk} + a_6 \times cvid_{ijk} + b_i + b_{ij}$$
$$+ \varepsilon_{ijk} \qquad \text{Model 2.}$$

$$id_{2000-2010\,ijk} = a_0 + a_1 \times d_{ijk} + a_2 \times cv_{ijk} + a_3 \times percd1904_{ijk} + a_4 \times hst_{ijk}$$
$$+ a_5 \times cvid_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \qquad \text{Model 3.}$$

The selection of the fixed effects variables and the random effects on the intercept at the tree and plot level was based on the Akaike information criterion (AIC). The most performing model was chosen on the basis of the AIC values. This resulted in the full models 2 and 3. We also calculated models with tree diameter only

$$id_{ijk} = a_0 + a_1 \times d_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \qquad \text{Model 4.}$$

and with tree diameter, crown and competition variables but without information about the past growth

$$id_{ijk} = a_0 + a_1 \times d_{ijk} + a_2 \times cv_{ijk} + a_3 \times percd1980_{ijk} + b_i + b_{ij}$$
$$+ \varepsilon_{ijk}) \qquad \text{Model 5.}$$

In this way we could assess the added explanation value of information about the crown and the tree's past (see Sections 3.3 and 3.4).

For all calculations we used the statistical software R 3.6.3. We in particular used the libraries nlme (Pinheiro et al. 2018), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), and MuMIn (Barton 2009).

## 3. Results

### 3.1. Overview of the long-term development of the stem diameter

The courses of the stem diameter growth were an essential basis for the subsequent analysis. In Fig. 3, a-c, the green trajectories represent the remaining trees in the stands. The red trajectories reflect the trees that dropped out by self-thinning on the A-grade plots and those that were removed by moderate and heavy thinning from below on the B- and C-grade plots. Comparison between the trajectories on the thinned and unthinned plots (Fig. 3, b and c versus a) evinced that thinning
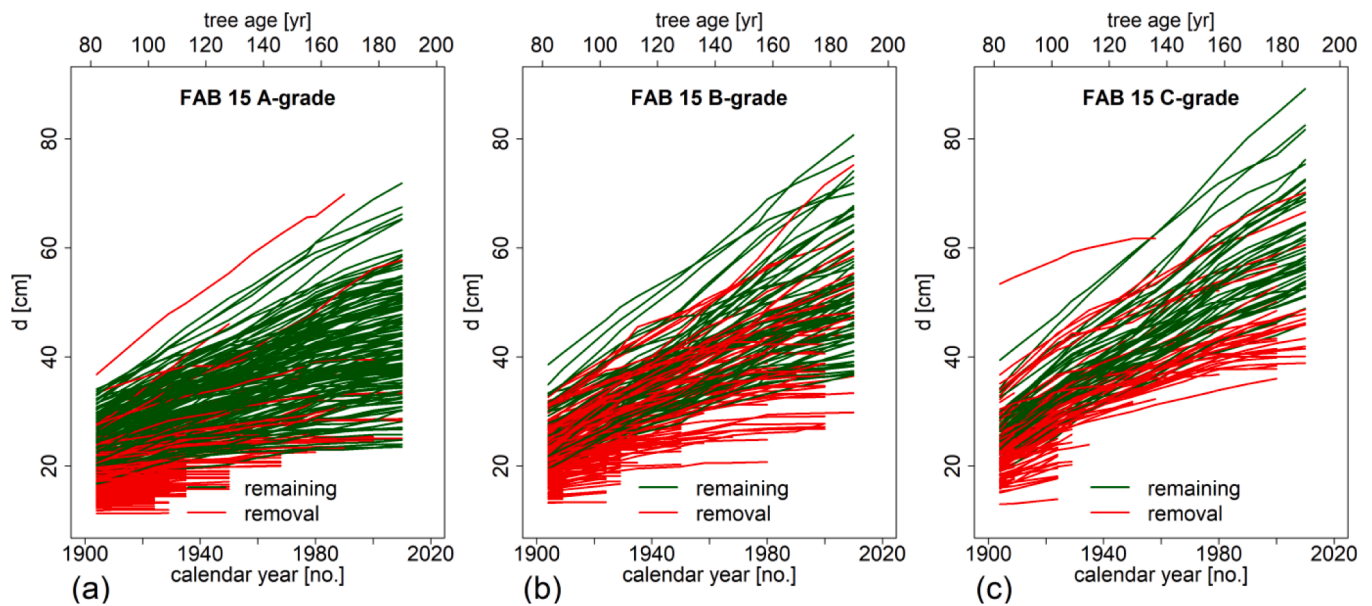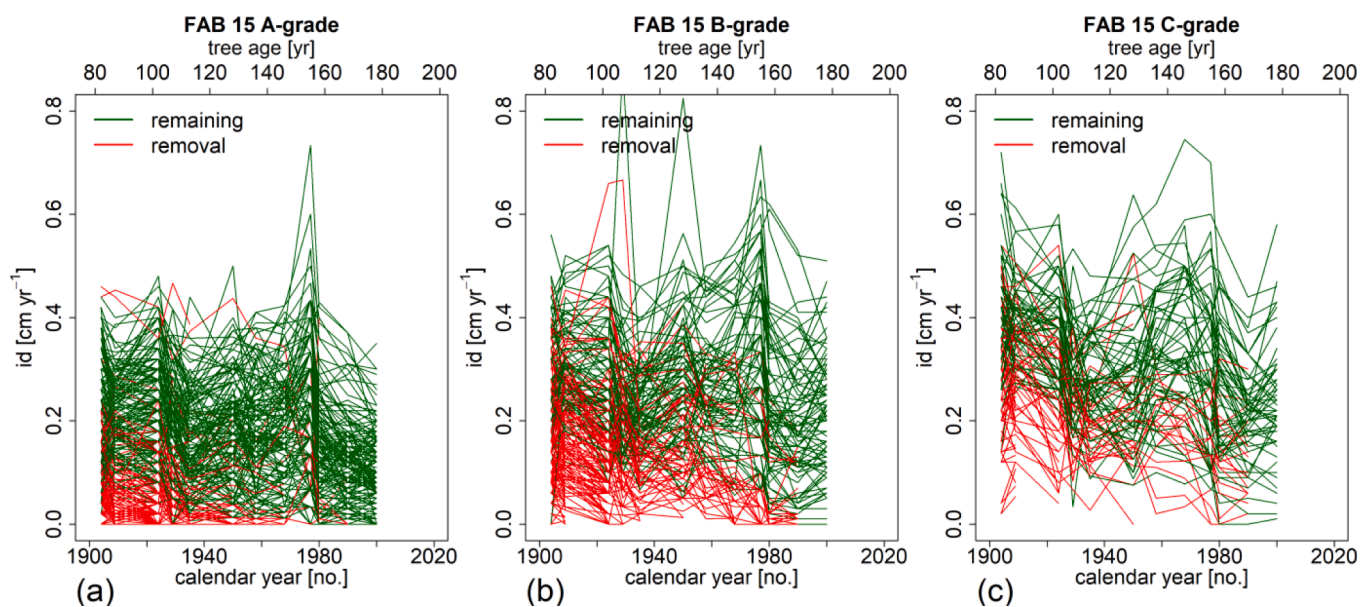
**Fig. 3.** Stem diameter growth of remaining (green) and removal (red) trees on the A-, B-, and C-grade plots (a-c) of the thinning trial in European beech, Fabrikschleichach 15, shown for the period 1904–2010 (age 82–188 years, see upper abscissa). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

accelerated the diameter growth. The range of stem diameters at the last survey was about 20–70 cm on the A-grade and 40–90 cm on the C-grade plots. Except the suppressed and removal trees (red lines) the courses of diameter development proceeded rather linear until the end of the shown period 1904–2010 although the trees were nearly 200 years old (Fig. 3 and Supplement Figure 1). The trajectories intersected in many cases; i.e., the size ranking changed with progressing stand development.

Fig. 4 shows that the mean periodical annual diameter growth developed more or less in parallel to the x-axis from middle to advanced tree ages. This general trend was similar on all three plots. The absolute level of growth was lower on the A-grade compared with the B- and C-grade plots (Fig. 4, from left to right).

### 3.2. The bivariate correlations between present and past tree characteristics and current diameter increment in 1980–1990

The bivariate correlations (Fig. 5) between the mean periodical diameter increment, id, in the period 1980–1990 and various current and past tree characteristics confirmed common knowledge but also revealed new insights. The finding that the id increased with (a) the stem diameter at the beginning of the respective growth period, d, with (b) increasing crown catio, cr, (c) crown projection area, cpa, (d) crown volume, cv, and (e) the social status of the individual trees, perc d1980, was not new. It is also well known that the id decreases with an increasing local competition index SDI (f). Certainly, competition reduces growth.



**Fig. 4.** Periodical mean annual stem diameter increment of remaining (green) and removal (red) trees on the A-, B-, and C-grade plots of the thinning trial in European beech Fabrikschleichach 15 show from 1904 to 2010 (age 82–188 years, see upper abscissa). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
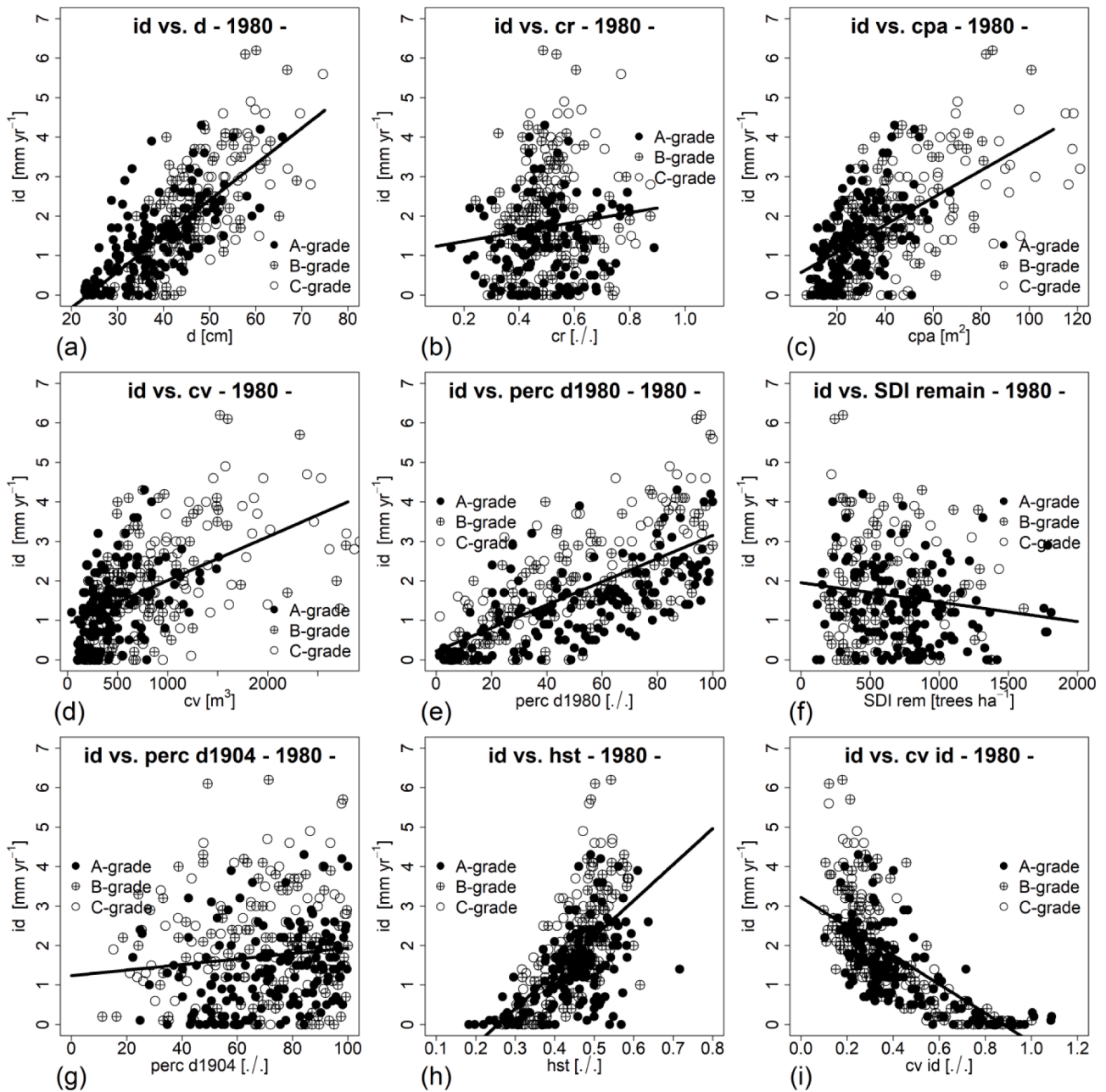
**Fig. 5.** The effect of various present and past tree characteristics on the current mean annual diameter increment, id, on the A-, B-, and C-grade plots (black dots, dots with a cross, and empty dots) of FAB 15. The id in the period 1980–1990 ist plotted over (a) the stem diameter, d, in 1980, (b) the crown ratio, cr, in 1980, (c) the crown projection area, cpa, in 1980, (d) the crown volume, cv, in 1980, (e) the stem diameter percentile, perc d1980, in 1980, (f) the local SDI of the remaining stand in 1980, (g) the stem diameter percentile, perc d1904, in 1904, (h) the half-size-time, hst, between 1904 and 1980, and (i) the coefficient of variation, cvid, of the diameter increment in the period 1904–1980. The straight lines show the linear regression between id and the respective independent variables, var, fitted to the model $\ln(id) = a_0 + a_1 \times \ln(y)$ (see respective statistics in Table 3).

More interesting were the findings in parts (g) - (i), in the last row of Fig. 5. The percentile in the diameter distribution in the long past, perc d1904, had only a low effect on the present growth. In combination with other variables perc d1904 even had a negative effect on id (see Section 3.3). The half-size-time raised the id (h); i.e., the lower the growth in the youth, the higher it was in the advanced age. And the quicker the growth in the youth, the lower was the growth in future. Furthermore, the diameter growth strongly decreased with the coefficient of variation of the diameter increment in the past (i). Latter means that the more variable the diameter growth was in the past, the lower was the growth at present. Smooth growth trajectories in the past, in contrast, resulted in higher growth rates at present. The respective statistical characteristics

of the linear regression lines included in Fig. 5 are presented in Table 3. The linear, bivariate regression analyses indicated significant ($p < 0.05$ to $< 0.001$) relationships between id and all analysed variables.

### 3.3. The multivariate effects of present and past tree characteristics on diameter increment in the non-thinning period 1980–1990

The multivariate model for predicting the diameter growth in the period 1980–1990 depending on the tree characteristics in 1980 and in the past also revealed some new insights. The results based on Model 2 (Section 2.2) are shown in Fig. 6 and Table 4. We found significantly positive effects of the initial tree diameter, social position of the tree and

**Table 3**
Statistical characteristics of the relationship $id = a_0 + a_1 \times y$ fitted to the data of all three plots of FAB 15. For explanation of variables see Fig. 1, for the applied model see Section 2.2. As variables y we analysed stem diameter, d, crown ratio, cr, crown projection area, cpa, crown volume, cv, percentile in the stem diameter distribution in 1980, perc d1980, local SDI of the remaining stand in 1980, SDI remain, percentile in the stem diameter distribution in 1904, perc d1904, half-size-time from 1904 to 1980, hst, and coefficient of variation of id from 1904 to 1980, cvid.

| Variable | n | $a_0$ | $SE(a_0)$ | p-value | $a_1$ | $SE(a_1)$ | p-value | $R^2$ | p-value |
|---|---|---|---|---|---|---|---|---|---|
| d | 321 | −2.143 | 0.198 | <0.001 | 0.091 | 0.005 | <0.001 | 0.54 | <0.001 |
| cr | 321 | 1.116 | 0.273 | <0.001 | 1.210 | 0.526 | <0.05 | 0.02 | <0.05 |
| cpa | 321 | 0.398 | 0.100 | <0.001 | 0.035 | 0.002 | <0.001 | 0.41 | <0.001 |
| cv | 321 | 0.093 | 0.009 | <0.001 | 0.00011 | 0.000 | <0.001 | 0.32 | <0.001 |
| perc d1980 | 321 | 0.219 | 0.102 | <0.05 | 0.102 | 0.029 | <0.001 | 0.45 | <0.001 |
| SDI remain | 321 | 1.951 | 0.152 | <0.001 | −0.001 | 0.0001 | <0.05 | 0.02 | <0.001 |
| perc d1904 | 321 | 1.137 | 0.230 | <0.001 | 0.007 | 0.003 | <0.05 | 0.01 | <0.05 |
| hst | 321 | −2.335 | 0.279 | <0.001 | 9.122 | 0.616 | <0.001 | 0.39 | <0.001 |
| cvid | 321 | 3.219 | 0.098 | <0.001 | −3.667 | 0.208 | <0.001 | 0.47 | <0.001 |
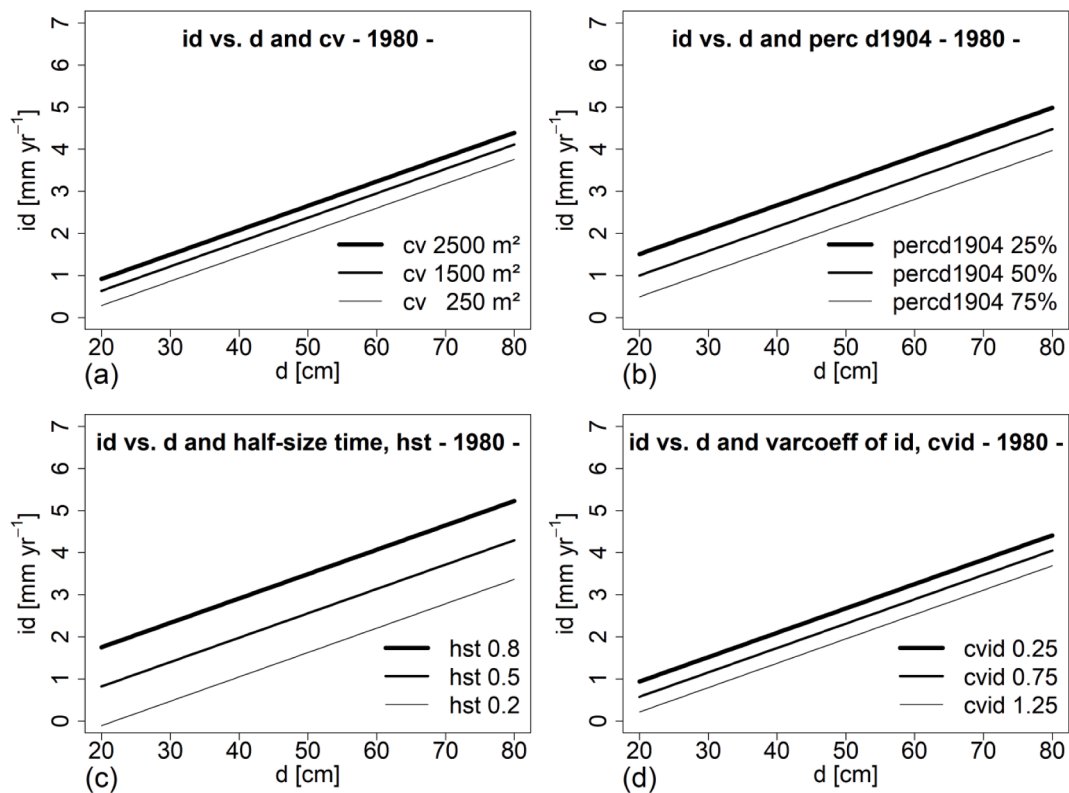


**Fig. 6.** Effect of (a) crown volume, cv, (b) diameter percentile in 1904, perc d1904, (c) half-size time in 1904–1980, hst, and (d) coefficient of variation of id, cvid, in 1904–1980 on the id ~ d relationship in the period 1980–1990. In each of the graphs the respective variables d, cv, perc d1904, hst, and cvid were varied, whereas the other variables were mean centered (see statistical model characteristics in Table 4 as basis for this graph).

the crown volume on growth, indicated by the coefficients $a_1 - a_3$ (Fig. 6a and Table 4). Beyond these variables that represent the current status of the tree, also the past characteristics of the tree perc d1904, hst, and cvid characteristically contributed to predict growth in 1980–1990 (see coefficients $a_4 - a_6$ in Table 4). In contrast to the positive effect of the social position in 1980, represented by perc d1980, the social position of the tree in 1904, perc d1904, negatively influenced the present tree growth (Fig. 6b). The present growth was significantly higher, the lower the trees' social position was in 1904. This means that trees had the chance to leave their past subordinate social position. The higher the half-size-time of the individual tree in 1904–1980, the higher its growth. Early and fast starters in 1904–1980, indicated by low hst values in Fig. 6c, had a lower growth rate in 1980–1990 than slow starters, indicated by high hst values in Fig. 6c. Furthermore, the growth variation in 1904–1980 reduced the growth in 1980–1990 (Fig. 6d). Trees with smooth courses of diameter growth in the past (1904–1980), indicated by low cvid values, had higher growth rates (1980–1990) than

trees with high interperiodical variation of growth in the past, indicated by high cvid values in Fig. 6d.

The full model for 1980 shown in Table 4 and visualized in Figs. 6 and 7 had a RMSE = 0.4596 and an adjusted $R^2$ = 0.7883. The respective results for the model without the historic information (without prec d1904, hst and cvid) were RMSE = 0.6287 and $R^2$ = 0.6049. The model only with stem diameter 1980 yielded RMSE = 0.6343 and $R^2$ = 0.5984. This means that the RMSE was reduced by 27% and that the $R^2$ was increased by 30% by including the information about the tree history (prec d1904, hast, and cvid).

Fig. 7 summarizes the effects of perc d1904, hst, and cvid on the diameter growth, id in 1980–1990. The effect of social dominance in the past was negative (Fig. 7a). The effect of lagging growth in the past, represented by high hst values, was positive (Fig. 7b). Growth variation caused negative effects (Fig. 7c). The combined effect of hst and cvid (Fig. 7d) suggests that, ceteris paribus, tree growth in 1980–1990 strongly benefited from decelerated juvenile growth and smooth

**Table 4**
Results of fitting the linear mixed effect model of tree diameter increment in the period 1980–1990 depending on variables characterizing the present status and the past development of the trees on the A-, B-, and C-grade plots. The underlying model 2 (Section 2.2) was $id_{1980-1990ijk} = a_0 + a_1 \times d_{ijk} + a_2 \times cv_{ijk} + a_3 \times percd1980_{ijk} + a_4 \times percd1904_{ijk} + a_5 \times hst_{ijk} + a_6 \times cvid_{ijk} + b_i + b_{ij} + \varepsilon_{ijk}$. AIC comparisons suggested using random effects at the plot and tree level. Number of observations = 321.

| Fixed Effect Variable | Fixed Effect Parameter | Estimate | Std. Error | p |
|---|---|---|---|---|
| intercept | $a_0$ | −1.1871 | 0.4543 | <0.01 |
| d | $a_1$ | 0.0579 | 0.0099 | <0.001 |
| cv | $a_2$ | 0.0003 | 0.0001 | <0.05 |
| perc d1980 | $a_3$ | 0.0111 | 0.0030 | <0.001 |
| perc d1904 | $a_4$ | −0.0203 | 0.0024 | <0.001 |
| hst | $a_5$ | 3.1030 | 0.5493 | <0.001 |
| cvid | $a_6$ | −0.7229 | 0.2355 | <0.01 |
| | Random Effect | Std. Dev. | | |
| Plot level | $b_i$ | 2.4495 | | |
| Tree level | $b_{ij}$ | 0.5394 | | |
| | Residuals | Std.Dev. | | |
| | $\varepsilon_{ik}$ | 0.1583 | | |

courses of growth. Fig. 7 corroborated that even when all other external tree characteristics were similar, the trees' past, reflected in their past development or inner structure, strongly mattered.

New was the negative effect of the social position in 1904 on the id in 1980–1990. This indicated that, ceteris paribus, dominance in the long past had a negative effect on tree growth even if trees have currently the same dimension. Interesting was also the positive effect of the half-size-time on the growth. Trees with quick starting growth in the longer past showed degressive growth trajectories and low growth at present. Trees with slow starting growth showed progressive growth trajectories and

superior growth at present. The negative sign of $a_6$ (Table 4) indicated that id variation in the trees' past reduced their growth rates at present. Smooth curves, ceteris paribus, enabled higher growth rates. This suggested a similar total growth for all trees, when looking at a tree's lifetime. There was a continuous growth compensation for initially slow growing trees in later years, and vice versa for initially fast growing trees.

In each of the graphs the respective variables perc d1904, hst, and cvid were varied, whereas the other variables were fixed to their overall means (see model in Table 4 as basis for this graph).

### 3.4. The multivariate effects of present and past tree characteristics on diameter increment after thinning in 2000–2010

The bivariate correlations between the mean annual id from 2000 to 2010 and the trees' present and past tree characteristics (see Fig. 8 and Table 5) showed similar tendencies as the analogous evaluation for the survey period 1980–1990 (see Fig. 4 and Table 3). However, the correlation and $R^2$ values were predominantly lower. Notably, the trees' percentile in the diameter distribution in the long past, perc d1904, had little effect on present growth. In combination with other variables, perc d1904 even had a negative effect on id (see Table 5). The half-size-time raised the id. The lower the growth in the youth, the higher it was in the advanced age. The diameter growth strongly decreased with the variation coefficient of diameter increment in the past. Smooth courses of growth, in contrast, resulted in higher growth rates. The statistical characteristics of the linear regression lines included in Fig. 8 are presented in Table 5. The linear regression analyses indicated significant (<0.001 to p < 0.05) relationships between id and all analysed variables except perc d1904. The correlations between the selected predictors and the id in the past-thinning period 2000–2010 were generally lower than in the non-thinning period 1980–1990.

For the following multivariate analysis AIC comparisons suggested using d, cv, perc d1904, hst and cvid as independent variable and
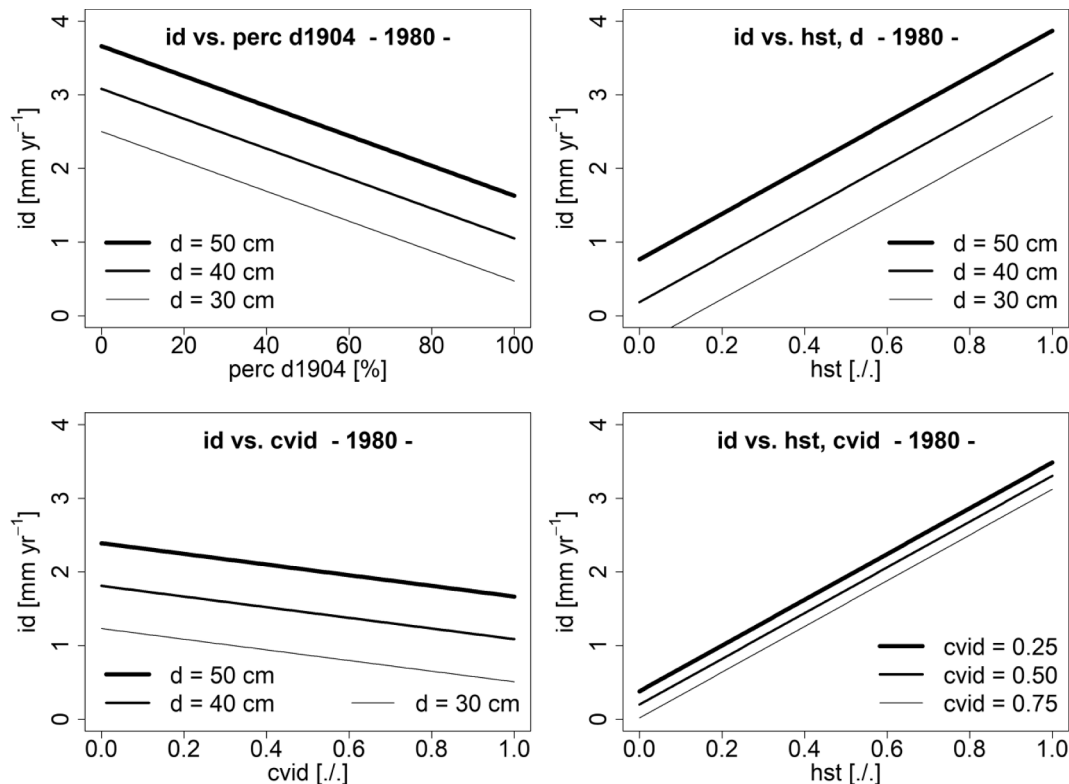


**Fig. 7.** Effect of tree history represented by the diameter percentile in 1904, perc d1904, the half-size-time 1904–1980, hst, and the variation of the diameter increment cvid in 1904–1980 on the stem growth in the growth period 1980–1990.
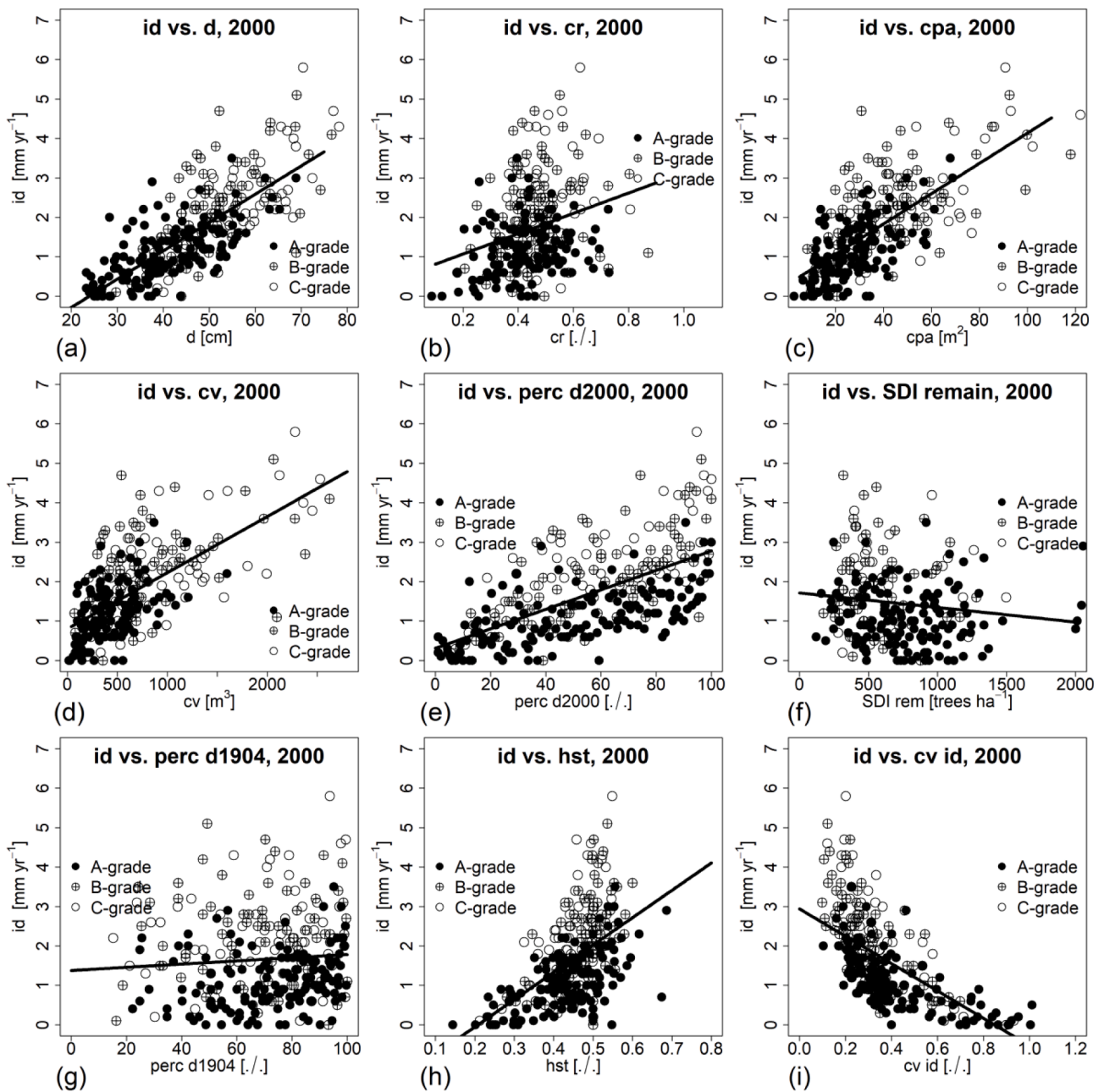
**Fig. 8.** The effect of various present and past tree characteristics on the current mean annual diameter increment, id, on the A-, B-, and C-grade plots (black, grey, and empty symbols) of FAB 15. The id in the period 2000–2010 is plotted over (a) the stem diameter, d, in 2000, (b) the crown ratio, cr, in 2000, (c) the crown projection area, cpa, in 2000, (d) the crown volume, cv, in 2000, (e) the stem diameter percentile, percd2000, in 2000, (f) the local SDI of the remaining stand in 2000, (g) the stem diameter percentile, percd1904, in 1904, (h) the half-size-time, hst, between 1904 and 2000, and (i) the coefficient of variation, cvid, of the diameter increment in the period 1904–2000. The straight lines show the relationships between id and the respective independent variables, y, fitted to the model $\ln(id) = a_0 + a_1 \times \ln(y)$ (see respective statistics in Table 5).

random effects on the intercept at the tree and plot level (Table 6). For the full model shown in Table 6 we calculated RMSE = 0.4371 and an adjusted $R^2 = 0.7548$. A tentative model without past information yielded RMSE = 0.5300 and an adjusted $R^2 = 0.6580$. And another tentative model id ~ d with d as predictor only we calculated RMSE = 0.5248 and an adjusted $R^2 = 0.6568$. This means that by including historical information the RMSE was reduced by 17% and the $R^2$ was increased by 15% compared to classic models with tree dimension and competition as predictor variables.

The model results based on the history from 1904 to 2000, the tree status of 2000, and the growth in the post-thinning period 2000–2010 differed in some aspects from the results reported in the previous Section

3.3. For the growth after the thinning the status of the tree in terms of perc d2000 and other tree variables was less relevant. However, the variables characterizing the past of the tree, perc d1904, hst in 1904–2000, and cvid in 1904–2000 had a highly significant effect on the growth after thinning. The coefficients of model 3 (Table 6) show that all three variables that characterize the trees' past, perc d1904, hst, and cvid had a significant effect on the tree diameter growth in the post-thinning period 2000–2010. All three variables significantly determined the tree growth beyond the status variables d, crown size at the beginning of post-growth period. Thus the results are in line with those found for the evaluation for 1980 without thinning (Section 3.3). The variables diameter and crown size are even less relevant for explaining

**Table 5**
Statistical characteristics of the relationship $id = a_0 + a_1 \times y$ fitted to the data of all three plots; id was the mean periodical diameter increment in the period 2000–2010. For visualization of the results see Fig. 8. As variable y we analysed stem diameter, d, crown ratio, cr, crown projection area, cpa, crown volume, cv, percentile in the stem diameter distribution in 2000, perc d2000, local SDI of the remaining stand, SDI remain, percentile in the stem diameter distribution in 1904, perc d1904, half-size-time from 1904 to 2000, hst, and coefficient of variation of the id in the period 1904–2000, cvid.

| variable | n | $a_0$ | SE($a_0$) | p-value | $a_1$ | SE($a_1$) | p-value | $R^2$ | p-value |
|---|---|---|---|---|---|---|---|---|---|
| d | 272 | −1.718 | 0.178 | <0.001 | 0.072 | 0.004 | <0.001 | 0.57 | <0.001 |
| cr | 272 | 0.554 | 0.247 | <0.05 | 2.578 | 0.528 | <0.001 | 0.08 | <0.001 |
| cpa | 272 | 0.299 | 0.092 | <0.01 | 0.038 | 0.002 | <0.001 | 0.51 | <0.001 |
| cv | 272 | 0.801 | 0.008 | <0.001 | 0.001 | 0.00009 | <0.001 | 0.44 | <0.001 |
| perc d2000 | 272 | 0.310 | 0.112 | <0.05 | 0.025 | 0.002 | <0.001 | 0.39 | <0.001 |
| SDI remain | 272 | 1.715 | 0.146 | <0.001 | −0.0004 | 0.0002 | <0.05 | 0.02 | <0.05 |
| perc d1904 | 272 | 1.376 | 0.229 | <0.001 | 0.004 | 0.003 | <0.20 | 0.01 | <0.20 |
| hst | 272 | −1.440 | 0.298 | <0.001 | 6.929 | 0.655 | <0.001 | 0.28 | <0.001 |
| cvid | 272 | 2.939 | 0.104 | <0.001 | −3.467 | 0.248 | <0.001 | 0.41 | <0.001 |

**Table 6**
Results of fitting the linear mixed effect model of tree diameter increment in the period 2000–2010 depending on variables characterizing the present status and the past development of the trees on the A-, B-, and C-grade plots. The underlying model 3 (Section 2.2) was $id_{2000-2010ijk} = a_0 + a_1 \times d_{ijk} + a_2 \times cv_{ijk} + a_3 \times percd1904_{ijk} + a_4 \times hst_{ijk} + a_5 \times cvid_{ijk} + b_i + b_{ij} + \varepsilon_{ijk}$. AIC comparisons suggested using random effects at the plot and tree level. Number of observations = 272.

| Fixed Effect Variable | Fixed Effect Parameter | Estimate | Std. Error | p |
|---|---|---|---|---|
| intercept | $a_0$ | −0.8110 | 0.4366 | <0.10 |
| d | $a_1$ | 0.0578 | 0.0072 | <0.001 |
| cv | $a_2$ | 0.0003 | 0.0001 | <0.05 |
| perc d1904 | $a_3$ | −0.0124 | 0.0021 | <0.001 |
| hst | $a_4$ | 1.9904 | 0.6079 | <0.01 |
| cvid | $a_5$ | −1.2519 | 0.3096 | <0.001 |
| | Random Effect | Std. Dev. | | |
| Plot level | $b_i$ | 0.2870 | | |
| Tree level | $b_{ij}$ | 0.5037 | | |
| | Residuals | Std.Dev. | | |
| | $\varepsilon_{ik}$ | 0.1603 | | |

id than in 1980. Obviously the ecological memory of the past is more important than the present state for explaining the tree growth after thinning.

The effect of the tree history represented by the diameter percentile in 1904, perc d1904, the half-size-time 1904–2000, hst, and the coefficient of variation of the diameter increment cvid in 1904–2000 on the stem growth in the growth period 2000–2010 are visualized in Figs. 9 and 10.

## 4. Discussion

Forest tree growth is primarily explained, modelled, and predicted depending on environmental conditions, competitive status in the stand, and current tree age or size. The accumulated size is commonly used as a proxy for a tree's past development. In line with recent studies our results suggest that antecedent conditions may also impact present growth. The growth performance in the past may be embedded in the ring width structure of the stem. Such structural properties obviously contain valuable unspecific information regarding the past and represent a structural and ecological memory. They may impact present growth in addition to epigenetic, transcriptional, proteomic, metabolic and physiological changes.

### 4.1. Considerations regarding the ecological memory effect and its further exploration

The current diameter growth of trees that were similar in stem diameter, crown size, and competitive status strongly varied depending

on their growth trajectory in the longer past (Figs. 6 and 7). Progressive courses of stem diameter growth with low inter-periodical variation in the past were associated with higher diameter growth rates at present. Degressive courses and high variation of stem diameter growth in the past led to lower diameter growth rates at present. Because of the allometric relationships between stem diameter and crown and root growth, the development of tree dimensions such as tree height, branch diameter, branch length, root diameter may follow a similar pattern as the stem growth. Thus, at parity of accumulated stem, crown and root diameter, this may result in a different internal stem and crown structure and root morphology due to different courses of growth. Different courses of growth may result in specific tree ring patterns of the stem and whorl architectures of the crown as schematically shown in Fig. 11. Different courses of growth in the past may also shape the present root structure. Such patterns may represent a structural memory imbedded in stem, crown, and root and may affect the trees' functioning and growth. It may affect among others the light interception, hydraulic conduction, or water and nutrient uptake. Thus, the differences in structure may cause specific differences in the functioning and growth curve pattern. Degressive courses with widest rings close to the pith were triggered by early dominance and may result from advantageous hydraulic conductance in the youth followed by disadvantages growth due to more narrow rings in advanced age (Fig. 11). Slow starters with narrow rings first and wide rings later may have an advantageous structure and morphology in higher ages. In advanced ages trees are bigger and inner pipeline systems are more challenged (Fig. 11) because of longer water transport length and advanced tree heights. A stronger variation of the diameter growth may indicate alternating growing conditions and higher need for physiological and morphological acclimation. The acclimation to a varying competitive status may leave less photosynthates for stem growth.

The dying of branches at the base of and within the crown and subsequent heartwood formation may have proceeded differently in the past depending on the growth velocity. They may result in different crown morphologies even if the stem and crown size are similar at present. As reflected by recent empirical studies (Ogle et al. 2015, Camarero et al. 2018, Zweifel et al. 2020) and functional structural models (Sievänen et al. 2000, 2008), pattern of tree rings, crown morphology, or root structure (Pretzsch et al. 2012) may determine the water conduction, light interception and nutrient uptake, respectively. In this way, trees may ecologically memorize their past development. Thus they also grow in dependence on internal structures in addition to their dependency on well analysed external factors such as size, competition and site conditions.

One of the bottlenecks for better understanding the combined effect of both external and internal factors on tree growth are empirical datasets. Unraveling the external and internal effects on tree growth requires information of both the tree structure and morphology at a given point in time and the growth before and after this point in time. Such information is scarce in general. This lack of a combination of long-
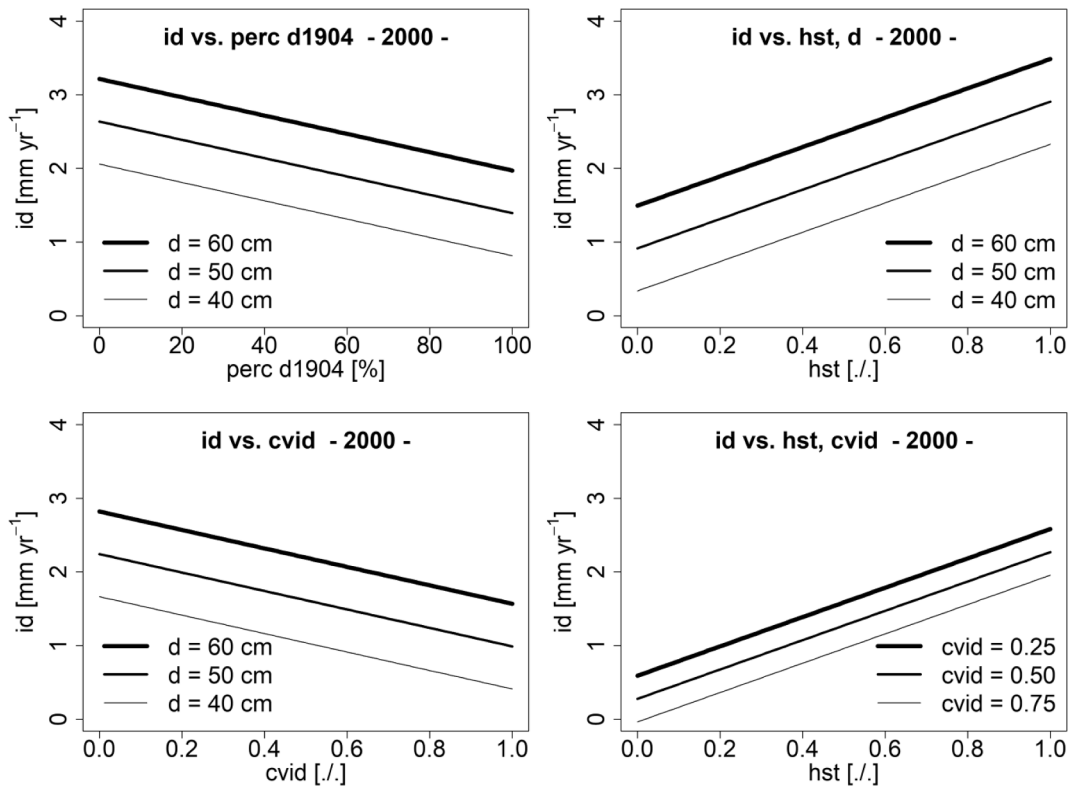
**Fig. 9.** Effect of the tree history represented by the diameter percentile in 1904, perc d1904, the half-size-time 1904–2000, hst, and the coefficient of variation of the diameter increment, cvid, in 1904–2000 on the stem growth in the growth period 2000–2010. In each of the graphs the respective variables perc 1904, hst, and cvid were varied, whereas the other variables, d and cv, were fixed to their overall means (see model in Table 6 as basis for this graph).
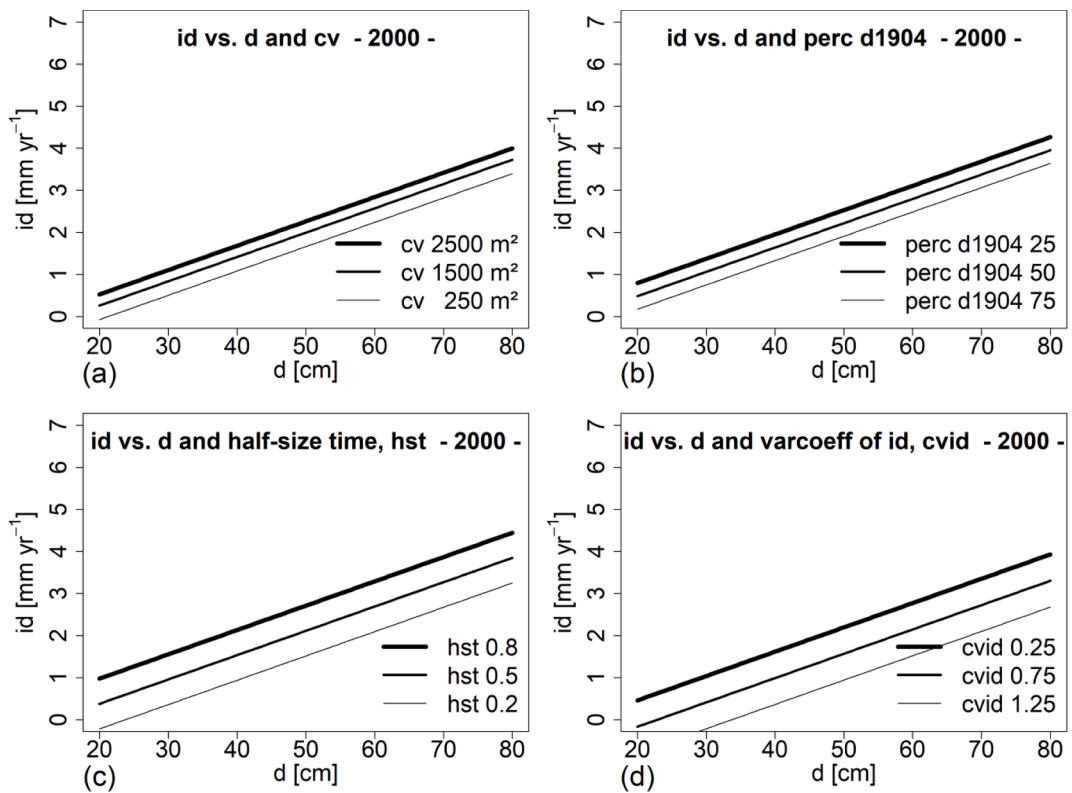


**Fig. 10.** Effect of (a) crown volume, cv, (b) diameter percentile in 1904, (c) half-size-time in 1904–2000, hst, and (d) coefficient of id variation in 1904–2000 on the id ~ d relationship in the period 2000–2010. In each of the graphs the respective variables d, cv, perc d1904, hst, cvid were varied, whereas the other variables were fixed to their overall means (see model 3 in Section 2.2 and model characteristics in Table 6 as basis for this graph).
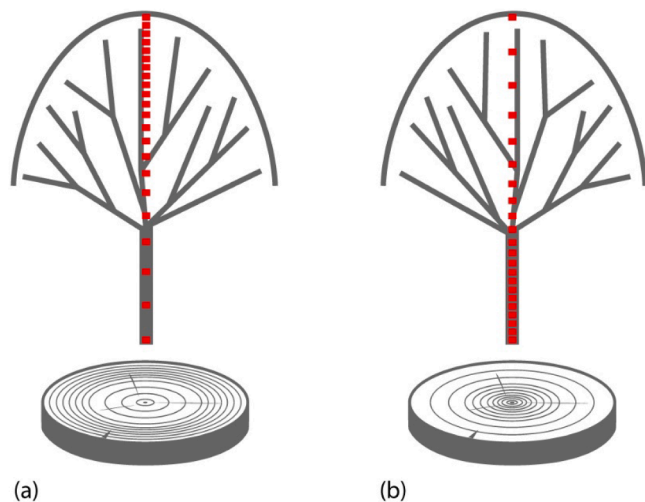
**Fig. 11.** Trees with similar stem and crown size but differing internal stem structure and crown morphology in schematic representation. (a) tree with growth acceleration in the juvenile and deceleration in the advanced age. (b) slow growth first and higher growth rates later.

term courses of growth and detailed measurement of internal and external tree and crown characteristics may be one of the reasons why the ecological memory effect has been assumed (Camarero et al. 2018, Zweifel and Sterck, 2018) but often neglected or called into question so far (Cvrčková et al. 2009). A positive exception are experiments with long time series of repeated survey of growth and morphology of trees, as presented and harnessed in this study.

To improve the knowledge about ecological memory effects, forest and tree mensuration are challenged to better measure the crown morphology. Appropriate methods have been proposed, among others, by Hussein et al. (2000), Bayer et al. (2013, 2017), or Jacobs et al. (2020). They enable the assessment and quantification of tree allometry beyond mere tree size (Niklas 1994, Pretzsch and Schütze 2005). To what extent different courses of growth (A- and B-types) in the same stand result from differences in genetics has been analysed for Scots pine (Kräuter 1965), but yielded no clarity (Hertel and Kohlstock 1994) and is still open for debate (Wenk et al. 1990, p. 41). More detailed measurements of the crown morphology may reveal the different history and explain the differences in the present growth.

We found considerable variation in the growth trajectories even in the even-aged, rather uniformly thinned European beech monocultures. The variation of trajectories is probably even higher in uneven-aged, multi-layered, and more selectively thinned stands. Such kind of stands are presently promoted throughout Europe (Bravo-Oviedo et al. 2014, Pach et al. 2018, Torresan et al. 2020) and also far beyond Europe (O'Hara 2014). This means that the consideration of the ecological memory effect of the past development on the present and future growth may deserve even more attention in future forest stands. A further corroboration of this kind of memory effect would suggest far-reaching consequences for monitoring, modelling, and management of trees and forest stands.

### 4.2. Consequences for monitoring and analysing tree growth

That the past development of presently equally sized trees had a strong effect on their current and future growth should be considered when monitoring or experimentally analyzing tree growth. Trees selected for the monitoring of environmental stress and associated growth losses (Eckmüllner and Sterba 2000, Wulff 2002) should be matched for their past development. Otherwise, damages and growth reduction, though co-determined by the past treatment, may be falsely attributed to present environmental conditions. Growth trend analyses

in the course of climate change research might be misleading if current tree growth is compared with historical growth of trees with a different treatment history (Bowman et al. 2013). In contrast, reliable results may be achieved if present tree and stand growth are compared to historical data of trees and stands with similar silvicultural treatment. For this purpose such analyses should be based on long-term experiments with the same defined and standardized silvicultural treatments in the past and at present (Assmann 1970). If growth trend analyses are based on increment cores at individual trees, different trajectories in the past may be accounted for if not only pre-dominant tree but also co- and sub-dominant trees are sampled. This study comprised trees with different histories and different current and future growth potential.

If experimental plots, e.g. for analysing thinning, species mixing, or provenances of a species, differ in their stand history, the measured present growth reactions might be flawed due to a co-determination by the past stand development. The past stand development may have shaped the inner structure and morphology of the trees and embedded an ecological memory effect. Growth reactions in mixed versus mono-specific stands were so far interpreted as direct mixing effects due to modified resource supply and uptake at present. However, mixing effects may also be co-determined by different past growth trajectories of the respective tree species compared with mono-specific stands. A measured growth superiority of the trees in mixed stands may be at least partly an ecological memory effect of differences in the past development. In this case mixing effects would be rather an indirect effect of the mixture caused in the past, than a direct effect of the current external growth conditions.

The tree' ability of growth response to thinning might also strongly depend on the trees' past. Even if tree size and tree density (number of a trees of a given size per unit area) are similar, the growth reaction may be different. It may be co-determined by the treatment history of the stand. In stands of the same age and stocked by trees with similar tree diameters the thinning reaction may be much stronger in stands with moderate and slow opening up in the youth compared to stands with strong crop tree thinning in the past. A way to avoid any bias by the past development and to consider the ecological memory effect may be the further development of indicators for the past tree or stand development. In this study we proposed indicators such as hst or cvid based on the past growth pattern. They may be further developed based on the growth rhythm reflected and stored in tree ring, crown structure, or root morphology pattern. Future thinning studies may use this kind of indicators to select tree and stand that are more appropriate and similar regarding their past development.

### 4.3. Implications for tree growth modelling

Growth models should consider the trees' history as start values beyond tree age, size, crown characteristics and competitive position. Permanent sample plots of forest inventories, for example, provide continuously improving information about the past growth with each repeated survey. Growth records from forest inventories are so far used for model parameterization (Sterba and Monserud 1997, Sterba et al. 2002) and validation (Pretzsch et al. 2002). In future such data may be also used for quantifying the ecological memory effect and for considering the trees past in the course of model initialization for a given stand.

Dendrometrically based individual tree simulators commonly predict the tree growth in time-steps of 1 or 5 years from the young until the mature age. They generate and store the individual tree trajectories. Future models might harness this accumulated information to improve the prediction of current and future growth. Eco-physiologically based models, addressing the structural-functional relationships, may better consider the effects of tree structure on the hydraulic conduction, light interception, and water and nutrient uptake. The internal stem structure and crown morphology represent the structural basis for many processes and thus determine the plant growth (Ogle et al. 2015, Fleta-Soriano and Munné-Bosch, 2016, Netzer et al. 2019).

## 4.4. Consequences for silviculture

The study showed that beech growth proceeded on a high level generally longer as expected and did not yet show a clear age-related reduction as assumed by textbooks by among others Bruce and Schumacher (1950, p. 377), Assmann (1961, p. 80), Kramer (1988, p. 66), Mitscherlich (1970, p. 83), and Wenk et al. (1990, p. 74). The study further showed that characteristics of the tree history such as, e.g., subdominance, progressive growth trajectory, low inter-annual growth variation in the past, may even extend this long persisting upward trend of growth. Economical aspects (timber, wood quality, dimension, inner rot, decreasing timber value, decreasing net present value) may object to exploiting this long continuation of growth. This may be one of the reason why the long continuation of European beech growth was neglected by forest science in the past. Understanding the course of growth and its dependency on silvicultural treatment are important for improving many ecosystem functions and services (e.g., C-sequestration, biodiversity, protection, recreation). The consideration of the ecological memory effect revealed in this study is of special relevance for silvicultural concepts such as thinning from above with holding of the understorey (Vuokila 1977), structural thinning and threshold diameter thinning (Sterba and Zingg 2001), Z1/Z2 crop tree thinning (Schröpfer et al. 2009), and selection forest systems (Schütz 2002, Drozdowski et al. 2014, O'Hara 2014). The finding, that competition in the youth may create slowgrowers or even latecomers, whereas early opening results in quickstarters and earlier asymptotic bending of the growth curve, means an enrichment of the silvicultural options of stand management. If all trees are released from relative early beginning on (e.g., future crop tree thinning) they grow quick and decrease simultaneous and earlier. Continuously dense stands, in contrast, may create simultaneously developing slow starters and latecomers. A mixture of both, resulting from structured two- or multilayered forest, may create a composition of slow and fast growing trees. Such a mixture of different individual behaviours means a high ability to respond to silvicultural inferences and disturbances and enables a long lasting stand growth on high level. Slow starters and latecomers may better react to and compensate for the opening up of stands by human or natural disturbances. They are highly important for growing resistant and resilient forests.

## 5. Conclusions

The strong effect of the trees' past development on their future growth uncovered here highlights the relevance of goal oriented, far-sighted, and quantitatively based silvicultural steering. In addition to the current stem and crown size and competion, the individual tree treatment and development in the longer past contributed significantly to explain the current growth. We found this association both in periods with and without thinning. Our findings suggest that reactions to e.g., mixture, drought, or fertilization may also depend on the respective tree history. For instance, wide initial spacing or repeated strong thinnings could result in wide tree rings and large xylem vessels that enhance water conduction and growth under normal conditions, but increase the risk of embolism under drought in the long term. This suggests to rethink low-density silvicultural prescriptions that have become very common in forest management (Pretzsch 2020b, Sohn et al. 2016). Tree history may be reflected in the tree ring pattern or the crown morphology. Both can be measured much more easily than in the past through mobile Computed Tomography (CT) (Habermehl and Ridder 1993, Beaulieu and Dutilleul, 2019) and Terrestrial Light Detection and Ranging (TLidar) (Metz et al. 2013, Blanchette et al. 2015, Olivier and Robert, 2017). Such measurement techniques may reveal in which other tree structures past growing conditions are stored. Furthermore, successive surveys of permanent inventory plots may accumulate and provide information of the individual trees' past development in terms of the mean periodical diameter increment. Each successive inventory increases the available data concerning the trees' past. This information may be harnessed for a

continuously better understanding of the ecological memory effect on tree and stand growth. Our findings were based on a well known and representative European beech stands. However, our analysis was based on only one long-term experiment. Further research is needed before a generalization of the results. In future studies we will extend our investigations to additional sites as done by Itter et al. (2019) and to other species, mixed stands, and stands repeatedly affected by drought as shown by Ogle et al. (2015) and Peltier and Ogle (2019). Such research will provide the basis for a better understanding and modelling of tree growth. It may enable a more goal-oriented steering of individual tree development in order to enhance growth, wood quality, vitality, and stress resistance.

## 6. Author contributions statement

HP initiated and conceptualised the study, evaluated the data, wrote and revised the manuscript.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118982.

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