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Changes of forest stand dynamics in Europe. Facts from long-term observational plots and their relevance for forest ecology and management

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ABSTRACT

Nearly one and a half centuries ago, far-sighted Central European forest scientists established a network of long-term observational plots, many of them being under observation up to the present day. Especially the untreated plots reveal significant anthropogenic impacts on the structure and dynamics of forest ecosystems. Based on 14 observational plots, this study shows that tree size and stand parameters of oak (sessile oak, *Quercus petraea* (MATT.) LIEBL. and pedunculate oak, *Quercus robur* L.) presently develop much faster than in the past, which is highly relevant for forestry in Central Europe. Thus, certain threshold sizes are reached decades earlier compared with the past. Due to the accelerated stand development, stem numbers per unit area are presently lower than at the same stand age in the past, while at the same time, stand density is higher. As we can show, also the level of the tree growth rate vs. tree size allometry increased significantly. These changes have major consequences for forest ecology and management, forest modeling, and eco-monitoring.

1. Introduction

In the 1980s and 1990s, when air pollution and climate change as possible causes for a feared area-wide collapse of ecosystems dominated the public debate, scientific studies reported accelerated forest growth in Central Europe. While the evidence of positive growth trends from long-term observational plots as reported by Kenk et al. (1991), Pretzsch (1985), Röhle (1994) were perceived as exceptions at first, more and more observations at tree level (Pretzsch, 1996; Sterba, 1996), forest stand level (Spiecker et al., 1996), and national inventory level (Pretzsch, 2009, pp. 582–584) confirmed a positive growth trend for many regions in Central Europe till this day. An extension of the vegetation period (Menzel and Fabian, 1999; Myneni et al., 1997, 2001) and other effects of global warming, as well as NO_x-immissions from fuel combustion or agriculture, and increased atmospheric CO_2 concentration (IPCC, 2007) are widely discussed as possible causes. While the general trend of accelerated forest dynamics in many regions of Central Europe has become undeniable, our knowledge about the long-term effects on stand dynamics and the relevance for flexible forest management is still limited (von Gadow, 2006). Reasons for this deficit are firstly the lack of observational plots which might reflect the long-term anthropogenic effects on forests and secondly a shortage of overarching evaluations of the existing observational plot data.

This study aims at reducing this knowledge gap by compiling and evaluating data from long-term observational plots for oak (*Quercus* sp.) with respect to growth changes since the beginning of their observation in the end of the 19th century. With pedunculate and sessile oak (*Quercus* sp.), the taxon *Quercus* comprises two major representatives in Central Europe which are highly relevant for forest ecology and management. The taxonomic status of these two members of the oak group has since long been subjected to intensive discussions and repeated re-assessment. Pedunculate and sessile oak have either been described as two distinct species, *Q. robur* L. and *Q. petraea* (MATT.) LIEBL., respectively, or are currently placed within the species *Quercus robur* L. as two subspecies *Q .r. robur* and *Q. r. petraea* (Roloff and Bärtels, 2008, pp. 506–507). To avoid possible taxonomic pitfalls, we either use in the following "oak" as a generic term summarizing both members, or their colloquial names to distinguish species or subspecies with "pedunculate oak" referring to the *robur*-type and "sessile oak" to the *petraea*-type, respectively.

Common empirical backbones for analyzing long-term trends in forest growth are tree ring data (Mielikäinen and Nöjd, 1996; Schweingruber et al., 1983, 1986; Zang et al., 2011, 2012), inventory data (Elfving and Tegnhammar, 1996; Kauppi et al., 1992; Pretzsch, 1996), or long-term experiments (Dudzińska and Bruchwald, 2008;

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Kenk et al., 1991; Pretzsch, 1999; Röhle, 1994, 1997). Tree ring data obtained from increment cores, stem disks, or whole stem analysis can retrospectively provide highly valuable information about long-term growth. However, as the historic growing conditions in terms of competitive status within the stand, silvicultural treatment, or insect calamities are not available, any retrospective explanation of individual tree growth trends and association with local, regional or global environmental changes remains vague. Inventory data may provide representative information about tree and stand growth (Spiecker et al., 1996), but with a few exceptions in Northern Europe (Kauppi et al., 1992) most inventories date back for just two or three decades, which is rather short for detecting long-term changes (Tomppo et al., 2010). Long-term observation plots and experiments in forest stands deliver shorter time series than tree ring analysis and are probably less representative than inventories, but they can provide rather unique information about long-term performance on both, tree and stand level (Nagel et al., 2012). Compared with retrospective tree ring analysis and inventory data, long-term plots have the advantage that their stand history (including calamities etc.) is recorded, their experimental setup is standardized, and they often include completely unmanaged variants. Beginning in 1870, many long-term observational plots in Central Europe have been re-measured more than 20 times till present. As this study is based on long-term observational plots and exploits their information for detection of growth trends, we briefly introduce the concept behind them.

300 yr ago von Carlowitz (1713) brought the idea of sustainability into forestry and Hartig (1791, 1795), von Cotta (1828), and Pfeil (1860) developed concepts for establishing this idea in forest management. In order to procure growth and yield data as quantitative basis for sustainable forest management, farsighted researchers in the late 19th century started installing long-term observational and experimental plots (see von Ganghofer, 1881; Verein Deutscher Forstlicher Versuchsanstalten, 1873).

As the appropriate kind, severity, and intensity of thinnings was crucial information for sustainable management, most of the early experiments comprised plots in pure and mixed stands with different thinning grades as well as unthinned reference plots. They provide the data for revelation of basic principles of forest dynamics (Assmann, 1970; Gadow, 2013), for building yield tables (Assmann and Franz, 1965; Jüttner, 1955; Schober, 1967; Schober, 1975; Wiedemann, 1943) and other decision support tools (Pretzsch et al., 2002; von Gadow, 2006), and for the development and training of silvicultural guidelines for thinning, spacing, and species-mixing (Pretzsch et al., 2010, 2013). Many of the observational plots dating back to these days are still an essential part of the forest observation network in Central Europe (Dudzińska and Bruchwald, 2008). The founding fathers thought in time spans of decades or even centuries, and established the experiments for observation times of 100–200 yr in order to cover a stand's lifetime. For eco-monitoring purposes, particularly the unthinned plots of these early experiments hold a considerable value and information potential. In Europe's intensively managed forests the untreated plots represent the exceptional case of up to 140 yr' ecosystem development, where the view on growth trends is not confounded by silvicultural treatment effects.

In order to detect long-term stand growth changes in Central Europe, we used the records from 14 fully stocked observational plots in oak stands which date back till 1900. In a first step, we compare the observed development of growth and standing volume over age with common yield tables which represent the historic stand dynamics. Secondly, we analyze statistically whether stand development over age (course of mean diameter, top height, current annual stand growth, standing volume, tree number, tree mortality and other stand characteristics) changed within the last century.

Thirdly, we scrutinize whether the two mainstays of stand allometry, i.e. the relationships between tree number and mean tree volume (self-thinning line reflecting the carrying capacity), and between the mean tree's volume growth and the mean tree volume (relative growth rate reflecting the metabolic efficiency) changed since the beginning of the 20th century.

2. Materials and methods

2.1. Study sites

All of our plots were selected from experiments or other greater units which include several plots with different treatments. All plots of such a unit are located close to each other. Those units, we call them *locations* in the further text, have a geography-related name and the plots inside a unit are defined with numbers. E.g. "Waldleiningen 88/2" in Table 1 means plot number 2 at the location Waldleiningen 88.

The 14 long-term observational plots in oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) included in this study represent the growth conditions of lowland and upland regions in Southern and Central Germany and Western Poland (Fig. 1). They reach from 100 to 500 m altitude above sea level (Table 1), and in many cases they replaced a previous generation of oak stands. They were established with high stand densities of more than 10,000 individuals per hectare. Being located in the territory of two countries, they represent both atlantic and continental climate conditions. Across all plots, the range of mean temperature and annual precipitation is wide. It covers spans of 7.9–9.0 °C and 540–1,120 mm yr^{-1}, respectively. The distribution of the plots along six different eco-regions is reflected by their broad spectrum of soil conditions (Table 1).

In this study we included mature stands which were surveyed up to 18 times since 1900 but also young stands established in the last decade and only recorded twice (Table 2, Fig. 2). Hence, the plots cover both historic and present site conditions with the respective growth behaviour. The variation of stand age (26–162 yr), top height (16.2–41.7 m), tree number per hectare (106–4, 206 trees ha^{-1}) and mean tree diameter (9.3–56.9 cm) at the last survey indicates that the plots represent a broad range of stand development stages. Top height was derived from plot- and survey-specific height-diameter-curves and is the mean height of the 100 trees per hectare with the largest diameters. Standing volume (172–790 m^3 ha^{-1}) and periodic annual volume increment (7.8–16.9 m^3 ha^{-1} yr^{-1}) as well as site index (quadratic mean height ≅Lorey's height at age 100: 24.1–32.5 m) emphasize the wide spectrum of site conditions and productivity levels covered by the data. Due to the long-term survey which included exact recordings of all removal trees we can also analyze total yield which ranges from 177 m^3 ha^{-1} at an age of 26 yr to 1272 m^3 ha^{-1} at an age of 140 yr (cf. Tables 1 and 2).

Given the goal of this study we included only unthinned or A grade plots which serve as references at their locations into our analysis. According to the working plan of the Association of German Forest Research Stations from 1902 (Verein Deutscher Forstlicher Versuchsanstalten, 1902, § 4) interference on A grade plots "[] *. . . is restricted to the removal of dying and dead trees, as well as any strongly bended trees for the purpose of delivering material for comparative growth investigations only.*" In the Bavarian as well as in the Polish network of long-term research plots, these almost unthinned plots were always preserved and used as highly valuable reference for derivation of fundamental growth and yield relationships (Assmann, 1970; Bruchwald et al., 1996; Franz, 1965; Pretzsch, 2005). However, many other forest research institutions considered such plots as outdated and abandoned them. All of

Table 1
Overview on the 14 long-term observational plots in oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) included in this study. For explanation of eco-regions in Germany and Poland see Arbeitskreis Standortskartierung (1985), and Zielony and Kliczkowska (2012), respectively.

Observation plot: location/number	Country	Geographic position		Eco-region	Elevation a. s. l. (m)	Mean annual temp. (°C)	Mean annual precip. (mm yr^{-1})	Substrate
		N-latitude	E-longitude					
Waldleiningen 88/2	Germany	49°23′	07°53′	Pfälzerwald	500	8.0	850	Loamy sand
Waldleiningen 88/5	Germany	49°23′	07°53′	Pfälzerwald	500	8.0	850	Loamy sand
Rohrbrunn 90/1	Germany	49°53′	09°25′	Spessart-Odenwald	475	7.0	1120	Sand
Rohrbrunn 620/4	Germany	49°54′	09°22′	Spessart-Odenwald	450	7.0	1120	Sand
Geisenfeld 649/5	Germany	48°52′	11°31′	Frankenalb und Oberpfälzer Jura	370	7.8	706	Clayey loam
Geisenfeld 649/7	Germany	48°52′	11°31′	Frankenalb und Oberpfälzer Jura	370	7.8	706	Clayey loam
Geisenfeld 649/8	Germany	48°52′	11°31′	Frankenalb und Oberpfälzer Jura	370	7.8	706	Silty and clayey loam
Barlinek 40	Poland	52°57′	15°12′	Równina Gorzowska	103	9.0	540	Loamy silty sand
Barlinek 41	Poland	52°57′	15°12′	Równina Gorzowska	103	9.0	540	Loamy silty sand
Drawieński PN 42	Poland	53°06′	15°53′	Równina Drawska	105	7.9	592	Loamy silty sand
Drawieński PN 43	Poland	53°06′	15°53′	Równina Drawska	105	7.9	592	Loamy silty sand
Drawieński PN 44	Poland	53°06′	15°53′	Równina Drawska	100	7.9	592	loamy silty sand
Drawieński PN 45	Poland	53°06′	15°53′	Równina Drawska	102	7.9	592	Loamy sand
Wołów 54	Poland	51°22′	16°28′	Wzgórza Trzebnicko-Ostrzeszowskie	104	8.2	612	Silty loam

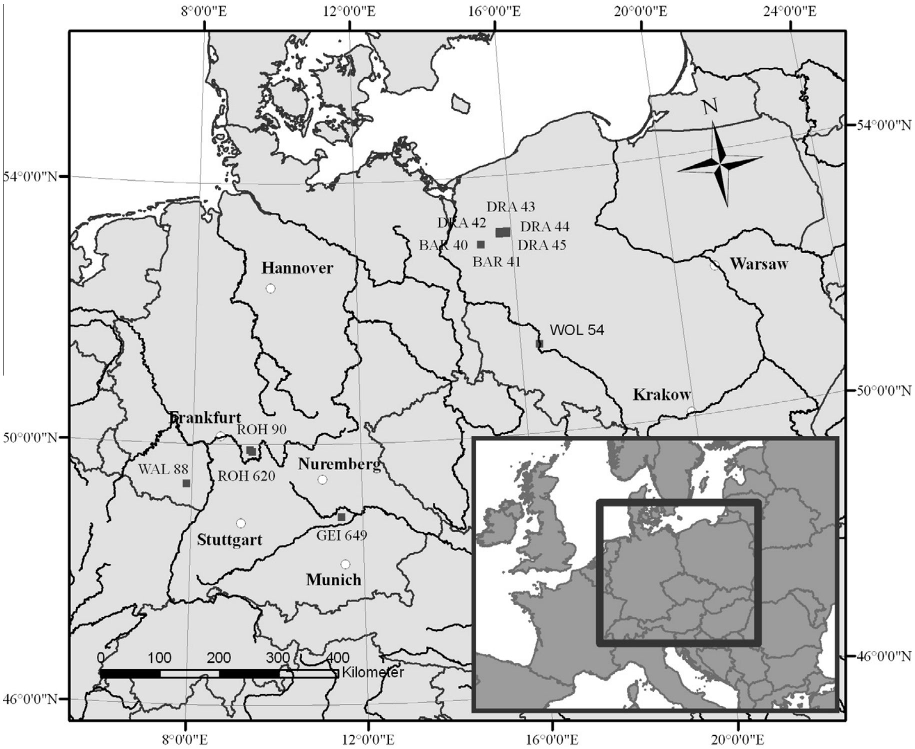

Fig. 1. Location of the 14 long-term observational plots in stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) in Germany and Poland included in this study. The plots are represented by following symbol (■).

the plots represent pure oak stands. Single beech trees (*Fagus sylvatica* L.), which occur on some of the plots, are negligible and were omitted from our evaluation in order to obtain an as much as possible conservative estimation of oak's growth and yield.

2.2. Methods

2.2.1. Standard evaluation of the observational plots

Stand characteristics were evaluated based on the definitions of the DESER-norm (Johann, 1993). Stand level surveys were carried out in intervals of several, mostly five years. For such intervals we calculated *PAI* (periodic annual increment) values which represent the mean annual growth rates over given time intervals. Between two surveys at time t_1 and t_2, the PAI is defined as follows:

$$PAI = (V_{2\text{remain}} - V_{1\text{remain}} + V_{\text{removed}})/(t_2 - t_1)$$

The total volume yield TY results from integrating *PAI*

$$\text{Total yield TY}_t = \int_{t=t_0}^{t_n} PAI\, dt$$

and standing volume V at time t is obtained from,

$$V_t = \int_{t=t_0}^{t_n} PAI\, dt - \int_{t=t_0}^{t_n} V_{removed}\, dt.$$

Table 2
Growth and yield characteristics related to the last survey for the 14 long-term observational plots in oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) included in this study.

Observation plot: location/number	Stand age (yr)	First survey (yr)	Last survey (yr)	Number of surveys	Top height (m)	Site index (m)	Tree number (ha^{-1})	Mean diameter (cm)	Standing volume ($m^3\ ha^{-1}$)	Periodic annual increment ($m^3\ ha^{-1}\ yr^{-1}$)	Total yield ($m^3\ ha^{-1}$)	SDI
Waldleiningen 88/2	103	1934	1989	9	32.1	29.9	362	30.8	426	11.1	827	506
Waldleiningen 88/5	118	1934	2004	12	34.6	29.6	419	35.2	690	11.1	994	726
Rohrbrunn 90/1	142	1934	2006	9	28.8	24.1	459	34.7	650	9.8	896	777
Rohrbrunn 620/4	83	1980	2009	6	28.8	29.8	875	24.7	574	16.0	689	858
Geisenfeld 649/5	26	2004	2009	2	16.2	32.5	2688	11.8	190	16.9	198	806
Geisenfeld 649/7	26	2004	2009	2	17.1	31.5	3563	10.1	174	14.7	180	832
Geisenfeld 649/8	26	2004	2009	2	16.4	32.5	4206	9.3	172	15.1	177	860
Barlinek 40	157	1900	2011	16	35.9	27.3	106	53.0	455	9.1	1050	355
Barlinek 41	157	1928	2011	12	36.9	29.2	125	51.1	506	10.8	1059	394
Drawieński PN 42	162	1900	2011	19	38.2	26.0	124	56.9	646	7.8	1154	464
Drawieński PN 43	162	1928	2011	15	41.7	26.9	179	50.3	773	11.0	1193	550
Drawieński PN 44	142	1928	2011	15	39.4	28.5	148	51.5	643	11.3	1057	473
Drawieński PN 45	141	1928	2011	15	40.4	30.1	275	42.2	790	14.4	1188	638
Wołów 54	140	1907	2012	18	35.2	30.2	160	50.4	597	9.7	1272	492

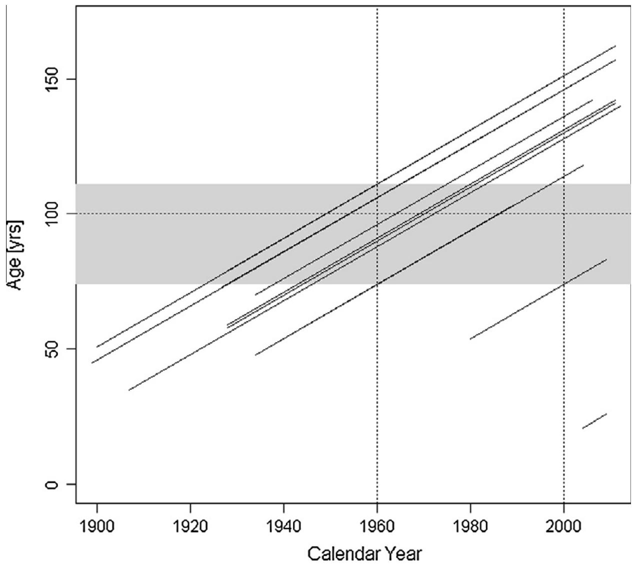

Fig. 2. Age-calendar year trajectories for our data. The grey shaded rectangle represents the age span which is covered by our plots in 1960 as well as in 2000.

Volume in this study is defined as merchantable wood (diameter over bark >7 cm).

2.2.2. Site index and stand density index

Quadratic mean height at age 100 served as site index in this study. If the age of 100 yr was inside a plot's observation time span, we linearly interpolated the actual heights. In the other cases we used the yield table by Jüttner (1955) for estimation. As a measure for stand density, we used Reineke's (1933) stand density index SDI = $N \times (d_q/25)^{1.605}$ with N as the number of trees per hectare and d_q as the quadratic mean diameter in cm. Doing so, we applied the general allometric exponent $\alpha_{N,d_q} = 1.605$ by Reineke (1933) instead of the species-specific value for oak $\alpha_{N,d_q} = 1.424$ as reported by Pretzsch and Biber (2005). The latter represents sessile oak and growing conditions in Central Europe only, and has not yet been validated for pedunculate oak and continental conditions in Poland. Reineke's original value is probably too high for oak, but using it makes our results comparable to other studies which mainly apply $\alpha_{N,d_q} = 1.605$. Table 2 shows the species-specific ranges of site index and *SDI* values on the included plots.

2.2.3. Relative mortality rate

For every interval between two subsequent surveys of a plot we calculated the mean annual relative mortality rate *MORT*. Mortality during such an interval can be understood as a geometric depreciation effect (Kouba, 2002) $N_2 = N_1 \times (1 - MORT/100)^n$ with N_2 and N_1 as the tree number at the end and at the beginning of an interval, respectively, and n as the length of the interval in years. Solving the equation with respect to *MORT* yields $MORT = (1 - \sqrt[n]{N_2/N_1}) \times 100$.

2.2.4. Regression analyses. Dependency of growth and yield variables on stand age

In order to detect long-term growth trends, we considered any stand characteristic y, in dependency from the stand age and the calendar year.

$$y = f(\text{age}, \text{year}).$$

Of course, the stand characteristics from the successive surveys (like periodic annual increment, *PAI*, standing volume, *V*, and tree mortality rate, *MORT*) depend on age. If there is an additional calendar year effect, this would be evidence for a growth trend. If this is the case, stands at a defined age perform differently in different calendar years. For that purpose, the following two basic model structures proved to be most appropriate:

$$Y_{ijt} = \beta_0 + \beta_1 \times A_{ijt} + \beta_2 \times \text{year}_{ijt} + \beta_3 \cdot A_{ijt} \times \text{year}_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \qquad (1)$$

$$Y_{ijt} = \beta_0 + f(age_{ijt}) + \beta_2 \times \text{year}_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \qquad (2)$$

In both equations, *Y* represents the stand variable of interest (stand volume, stem number, periodic annual increment, etc.) either untransformed or logarithmized, depending on what constituted a better model fit. Similarly, *A* in Eq. (1) symbolizes the stand age either untransformed, its logarithm, or its inverse. Eq. (2) contains another way of including the age trend. Here *f*(*age*) stands for a nonparametric smoothing function with the untransformed stand age as the argument.

With appropriate combinations of transformed and untransformed values of *Y* and *A* or *f*(*age*) we were able to sufficiently cover nonlinear, age-dependent relationships in the context of linear and generalized additive regression models. The second explanatory variable, the calendar year corresponding to a given observation, is indicated by the variable 'year' in both equations.

The indices *i*, *j*, and *t* represent the location a plot belongs to, the plot on a given location, and the time of a specific plot survey, respectively.

The fixed effects parameters are $\beta_0 - \beta_2$ while b_i, and b_{ij} are random effects on location, and on plot level, respectively ($b_i \sim N(0,\tau_1^2)$, $b_{ij} \sim N(0,\tau_2^2)$). With these random effects, we take care for the possible plot-specific and location-specific autocorrelation among the observations. Finally, ε_{ijt} stands for i.i.d. errors ($\varepsilon_{ijt} \sim N(0,\sigma^2)$). Thus, Eq. (1) represents a linear mixed regression model while Eq. (2) stands for a generalized additive mixed model (GAMM).

The calendar year effect and its interaction with age (represented by the parameters β_2 and β_3) were only kept in the model (Eq. (1)) when they differed statistically significant from zero. Otherwise, the model was reduced accordingly and fitted again. In case, the interaction turned out significant but not the isolated year effect, both were kept in the model (cf. Zuur et al., 2009).

2.2.5. Regression analyses. Allometric relationships between stand growth and size variables

The relationships between the mean tree's increment and mean tree size ($\overline{iv}$ vs. $\bar{v}$), and between tree number per unit area and mean size (N vs. $\bar{v}$) are keystones of mean tree and stand allometry (Pretzsch, 2006; Pretzsch and Biber, 2005; Weiner, 2004; Zeide, 1987; von Gadow, 1986). In double logarithmic form, both relationships constitute a straight line with rather general and species-overarching values for the slope b ($\ln(y) = a + b \times \ln(x)$, equivalent to $y = e^a \times x^b$). However, the lines' intercept a, is widely held to depend on environmental conditions and to be species-specific (Sackville-Hamilton et al., 1995; Skovsgaard and Vanclay, 2008; Yoda et al., 1963). We used the following mixed linear model for identifying calendar-year trends in both allometric relationships:

$$\ln(y_{ijt}) = \beta_0 + (\beta_1 + c_i + c_{ij}) \times \ln(x_{ijt}) + \beta_2 \times \mathrm{year}_{ijt} + \beta_3 \times \ln(x_{ijt}) \times \mathrm{year}_{ijt} + b_i + b_{ij} + \varepsilon_{ijt} \tag{3}$$

with y and x representing $\overline{iv}$ and $\bar{v}$, or N and $\bar{v}$, respectively. The other variable and index names mean the same as in Eq. (1). However, AIC-comparisons (Burnham and Anderson, 2004) showed that in case of the N vs. $\bar{v}$ -relationships also random effects $c_i \sim N(0, \tau_2^2)$, and $c_{ij} \sim N(0, \tau_4^2)$, which affect the slope of the allometric line had to be taken into account in addition to the intercept-specific random effects ($b_i \sim N(0,\tau_1^2)$, $b_{ij} \sim N(0,\tau_3^2)$). All statistical evaluations were carried out with R 3.0.0 (R Core Team, 2013), namely the packages nlme (Pinheiro et al., 2013) and mgcv (Wood, 2011).

2.2.6. Evaluation of the growth trends

With the fitted models (Eqs. (1)–(3)) and all random effects set to zero we estimated all stand parameters for the calendar years 1960 and 2000 at a reference stand age of 100 yr. Dividing the 2000 value by the 1960 value, we obtain the relative change caused by the calendar year effect. E.g. in case of *PAI*, that yields$PAI_{age100,\ 2000}$ and $PAI_{age100,\ 1960}$.

Thus, the ratio $RPAI_{age100,\ 2000/1960} = PAI_{age100,\ 2000}/PAI_{age100,\ 1960}$ reflects the growth trend since 1960. Many studies on forest growth trends (Kenk et al., 1991; Röhle, 1994; Spiecker et al., 1996), on the validity of common yield tables (Pretzsch, 1999; Schmidt, 1971; Sterba, 1996), and the development of the environmental conditions (IPCC, 2007; Menzel and Fabian, 1999; Schönwiese et al., 2005; Skeffington and Wilson, 1988) indicate significant changes of the long-term course since the 1970s. Therefore we use the growth in 1960 as reference for quantification of long-term changes from 1960 up to the present. The year 2000 was used to represent recent growth conditions as it is not far in the past and well covered by our data.

The reference stand age of 100 yr was chosen because it is often used as a standard reference age in forestry (e.g. for site indexing or mean annual increment estimations), and as it is more central in the age span which is covered by our plots both in 1960 and in 2000 (Fig. 2).

3. Results

3.1. Observed stand growth vs. yield table predictions

Yield tables as standard tools for forest management have been developed mainly from 1795 till 1965 (Skovsgaard and Vanclay, 2008). Being based on survey data from long-term plots, they mirror growth under past environmental conditions (Pretzsch, 1996, 1999). A comparison between observed stand characteristics yield table predictions as presented in Fig. 3 reveals this study's incentive. The majority of the periodic annual increment (*PAI*) and stand volume (*V*) values from the years after 1960 (empty symbols) exceeds the yield tables (grey shaded sections) by far. This tendency becomes most prominent at intermediate and advanced stand ages. In most cases the *PAI* persists at a rather high level even after age 100. Due to the accelerated volume growth the standing volume on stand level accumulates much more rapidly compared to the yield tables.

Especially the deviations we observe in the mature stand phase are remarkable. The measured *PAI* values amount to 7.5–15 m^3 ha^{-1} yr^{-1} while the yield tables predict such of 2.5–10 m^3 ha ^{1} yr^{-1}. The actual maximum standing volume amounts to about 800 m^3 ha^{-1} but ought to be 450 m^3 ha^{-1} according to the yield tables. Such deviations are negligible neither for ecology nor for forest management and thus justify a more thorough analysis. Note that the available yield tables which were used for this study assume moderate thinning while the observational plots represent unmanaged or just weakly thinned stands. Compared to moderate thinning, weak thinning keeps a higher standing volume but can reduce the *PAI* by 5–10% (Assmann, 1970, pp. 330–335). So, in case of *PAI* the yield table prediction must be considered somewhat optimistic which makes the superiority of the observed PAI even more remarkable. In case of standing volume the prediction for unmanaged stands would be about 10–20% higher, however, which can only explain a small part of the actual 50–100% transgression we observe.

3.2. Changes in the age trend of basic stand characteristics

For all observed stand variables except relative mortality rate *MORT* (no significance) and top height h_o (significance level $p < 0.10$), all investigated stand variables show significant calendar year trends in most cases with significance levels of $p < 0.001$ (Table 3). Mean tree diameter *dq*, top height h_o, and mean tree volume $\bar{v}$, presently grow significantly faster than in the past (Fig. 3, Table 5). The finding that height at age 100 increases by 7% from 1960 to 2000 supports the frequently reported changes in the main tree species' site index (Spiecker et al., 1996, p. 157). Considerably interesting for forest practice is the change in mean diameter (+20% at age 100) and mean tree volume (+37% at age 100). Presently, given threshold diameters are reached in much earlier stand development phases than in the past. Given the model parameter estimates shown in Table 3 with all random effects set to zero we can estimate the changed arrival time of trees and stands at a given harvest threshold size and a given target stock, respectively. A threshold diameter of 40 cm, e.g., is reached 14 yr earlier in 2000 than under the conditions of 1960. Similarly, a mean tree volume of 2 m^3 is reached about 9 yr earlier in 2000 than in the past. In general, the size growth acceleration is stronger for diameter and volume than for tree height.

Equally remarkable both, periodic annual volume increment *PAI* and mean tree volume increment $\overline{iv}$ increased significantly with progressing calendar year. At age 100, *PAI* is by 18 % higher in 2000 compared to 1960, and for $\overline{iv}$ the superiority amounts to

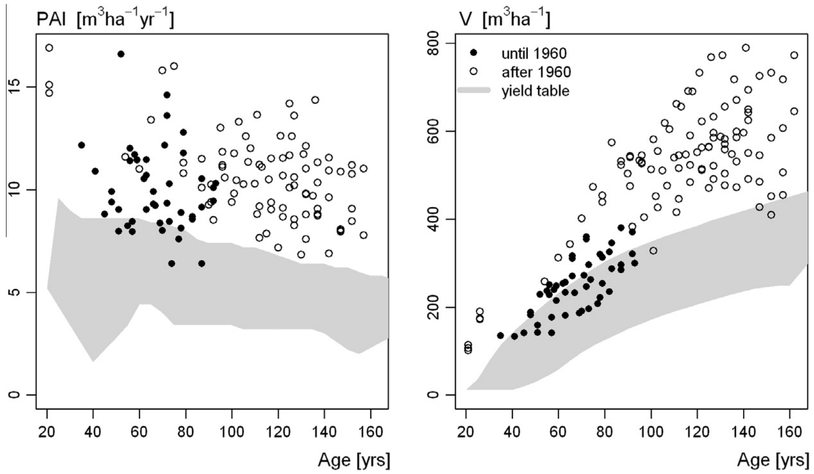

Fig. 3. Observed periodic annual volume increment, *PAI* ($m^3\ ha^{-1}\ yr^{-1}$), and standing stem volume, *V* ($m^3\ ha^{-1}$), on long term observational plots in oak. Observed *PAI* and *V* in years before 1960 (filled symbols) and after 1960 (empty symbols) are compared with the yield tables for moderate thinning for oak (Jüttner, 1955, grey shaded areas: site classes I–IV).

Table 3
Results of the mixed model regressions for age-based relationships (Eqs. (1) and (2)).

		Fixed effects				Random effects		
Response variable *Y*	Age variable *A*	β_0	β_1	β_2	β_3	τ_1^2	τ_2^2	σ^2
dq	Age	-195.372^{**} 0.0017	0.2830^{***} <0.0001	0.0991^{**} 0.0023	n.s.	13.0358	2.0633	4.8525
ln(*PAI*)	Age	-81.4896^{***} <0.0001	-0.0470^{***} <0.0001	0.0491^{***} <0.0001	n.s.	0.0001	0.5473	2.5083
V	Age	-5004.203^{***} <0.0001	46.8687^{***} <0.0001	2.5478^{***} <0.0001	-0.0215^{***} <0.0001	2033.12	4050.89	2864.47
ln(*N*)	ln(age)	21.8920^{***} <0.0001	-1.6859^{***} <0.0001	-0.0040^{*} 0.0106	n.s.	0.0728	0.0273	0.0253
h_o	Age	−56.5970 0.2365	n.p. smooth*** <0.0001	$0.0426^{\cdot}$ 0.0751	n.s.	8.7894	0.8402	1.1695
ln($\bar{v}$)	ln(age)	-81.2874^{***} <0.0001	15.0645^{***} <0.0001	0.0350^{***} <0.0001	-0.0063^{***} 0.0001	0.1145	0.0181	0.0223
ln($\overline{iv}$)	ln(age)	-25.9189^{***} <0.0001	1.3695^{***} <0.0001	0.0079^{***} <0.0001	n.s.	0.0883	0.0068	0.0385
MORT	Age^{-1}	−0.3711 0.4433	213.0834^{***} <0.0001	n.s.	n.s.	0.1676	<0.0001	3.7918

Quadratic mean diameter, *dq*; periodical annual volume increment, *PAI*; standing stand volume, *V*; tree number per hectare, *N*; top height, h_o; mean tree volume, $\bar{v}$; mean tree volume increment, $\overline{iv}$; and relative tree mortality rate, *MORT* were goal variables of mixed model regressions dependent from stand age and calendar year (see Fig. 4). Exact *p*-values are given in italics below the parameter estimates. The number of observations used was 149.
Significance levels:
$^{\cdot}$ $p < 0.10$.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

37%. Fig. 4 shows that most stands still accumulate standing stock and did not yet reach a final constant yield plateau. Our fitted model confirms that also the level of standing stock rose by 11% between 1960 and 2000 (Table 5).

Tree number *N* at age 100 is by 15% lower in 2010 while we could not substantiate any change of the relative mortality rate *MORT*. The difference in the age-related tree number is the consequence of the above-shown accelerated stand development.

3.3. Change of stand allometry

In order to achieve a better understanding of the observed changes we consider the two mainstays of stand allometry, the relationships between tree number and mean tree volume and between the mean tree's volume growth $\overline{iv}$ and the mean tree's volume $\bar{v}$ (Fig. 5, Table 4). The $\overline{iv} - \bar{v}$ – relationship significantly shifted upwards, i.e., the growth efficiency of trees of a given size increased from 1960 to 2000. Inserting the mean volumes at age 100 expected in 2000 and 1960 by our fitted age-dependent model the allometric relationship estimates an increase of $\overline{iv}$ by 28% (Table 5). The $N - \bar{v}$ relation, i. e., the self-thinning line, shifted moderately upwards within the survey period and shows a somewhat steeper slope with progressing calendar year (Fig. 5, Table 4).

In summary the stands presently grow quicker and accumulate a defined standing volume earlier than a century ago. They grow along a slightly higher and slightly steeper self-thinning line than in the past. The growth trend seems to be based on a changed relationship between tree size and tree growth, but also on a higher capacity or packing density.

Table 4
Results of the mixed model regressions for fundamental allometric relationships (Eq. (3)).

		Fixed effects				Random effects				
Response Variable y	Size Variable x	β_0	β_1	β_2	β_3	τ_1^2	τ_2^2	τ_3^2	τ_4^2	σ^2
N	$\bar{v}$	0.3362 *0.8395*	3.0114^{***} *<0.0001*	0.0030^{***} *0.0005*	-0.0018^{***} *<0.0001*	0.0168	0.0116	0.0134	0.0030	0.0063
$\overline{iv}$	$\bar{v}$	-8.8016^{***} *0.0003*	0.5559^{***} *<0.0001*	0.0025^{*} *0.0330*	n.s.	0.0164		0.0021		0.0285

N: number of trees per hectare, $\bar{v}$: mean tree volume, $\overline{iv}$: mean tree volume increment.
Exact p-values are printed in italics below the parameter estimates. The number of observations used was 149. See Fig. 5 for a visualization of the results.
Significance levels:
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 5
Percental changes of an 100 year old oak stand's growth and yield characteristics 2000 in relation to 1960 as expected from our fitted regression models (Eqs. (1)–(3)) We only report changes which are based on significant calendar year effects on the $p < 0.05$ level (bold numbers) and the $p < 0.10$ level (normal numbers). The crucial calendar year effects for a given stand attribute may result from one or two significant parameter estimates. Their exact p-values are shown in Tables 3 and 4.

Forest stand attribute	Change from 1960 to 2000 in%
Dominant tree height, h_o	+7
Mean tree diameter, dq	**+20**
Mean tree volume, $\bar{v}$	**+37**
Stand volume growth, *PAI*	**+18**
Standing volume stock, V	**+11**
Tree number, N	**−15**
Mortality rate, *MORT*	n.s.
Mean tree volume increment $i\bar{v}$	**+37**
Shift of $\overline{iv} - \bar{v}$ -allometry	**+28**
Shift of $N - \bar{v}$ -allometry	**+1.4**

3.4. Residual diagnostics

Figs. 6–9 show residual plots for the four most important model fits in this study. These are the model for (i) periodic annual volume increment *PAI*, (ii) stand Volume V, both as a function of age and calendar year (Figs. 6 and 7, cf. Table 3, Eq. (1)), and (iii) mean tree volume increment $\overline{iv}$ and iv) stem number N, both as a function of mean tree volume $\bar{v}$ and calendar year (Figs. 8 and 9, cf. Table 4, Eq. (3)). It is the time course of V and *PAI*, where the growth trends become evident on stand level, and it is the allometric relationships $N - \bar{v}$ and $\overline{iv} - \bar{v}$, whose change is behind the trends. For each model we present the residuals plotted against the fitted values and all explanatory variables as well as in a normal q–q plot for assessing normal residual distribution. All residual plots are satisfactory and show that model fits are unbiased. An exception is standing volume V (Fig. 7), where the model seems to overestimate in the range of fitted values between 300 and 400 $m^3\,ha^{-1}$, and underestimate below 100 $m^3\,ha^{-1}$. This corresponds with overestimations between the calendar years 1940 and 1960 and underestimates for calendar years earlier than 1920. Even much more flexible nonlinear models lead to virtually the same situation. However with the model predictions in the context of this study we are beyond the critical range, in case of a slight overestimation of Volume in 1960 this would tend towards a cautious estimate of the relative change between 1960 and 2000.

4. Discussion

4.1. Implications of the data structure

As can be taken from Fig. 2, which shows the age-calendar year trajectories for all our plots, there is a lack of old stands at early calendar years. Although a more balanced situation would be clearly desirable, a part of our stands had anyhow reached an age of more than 100 yr in 1960. The overrepresentation of stand ages >120 yr in the 2000nds is at least partly counterbalanced by research plots that were established in the 1980ies and the early 2000nds. Thus, the age span covered in the years after 1960 includes the age span covered before albeit with different representations. From our point of view this data constellation already allows to identify significant growth trends if there is a significant calendar year effect in addition to the mere ageing trend. By including random effects on location level and on plot level, we exclude site specific confounding influences and take care for autocorrelation.

From Fig. 3 it becomes evident that in the age span covered by observations before and after 1960, the latter consistently are at the uppermost edge of the measured stand increments (*PAI*) and volumes (V). Assuming this trend to continue in a similar way – or at least not to revert – for ages>100 yr, where we have only younger observations, seems reasonable to us. Thus, the growth trends we identify are more probably understated than overstated.

4.2. Biological and practical implications of our findings

In the following we discuss our finding that on long-term observational plots the growth rate of oak stands changed during the last century and how these changes affected tree size growth, standing volume, stand density, mortality and other stand attributes. Fig. 10 illustrates that forest stands presently develop faster in terms of tree size, stand volume growth, and standing stock. Thus, particular threshold sizes are reached considerably earlier. Due to the accelerated stand development the tree number at a given age is presently lower than in the past.

The level of the tree growth rate – tree size allometry increased and as well did the tree number – tree size allometry. That means that trees and stands nowadays grow quicker, pass more rapidly through their developmental stages, and show a higher capacity level, especially at smaller mean tree sizes.

4.2.1. From evidence to relevance of growth trends

The finding that a volume growth of about 150% compared to 50 yr ago drives oak stands faster through the yield tables' trajectories and that their growth efficiency and carrying capacity increased is new and of far-reaching relevance. Our findings go beyond previous works about growth trends (e. g., Kahle et al., 2008; Kenk et al., 1991; Spiecker et al., 1996) as we base our analyses on unmanaged observational plots and complete long-term records in terms of tree and stand characteristics. By using unmanaged observational plots we avoid a mixing of management effects with effects of environmental changes. Thanks to the available long-term records of tree and stand characteristics we can provide evidence for changes of forest stand dynamics and can quantify

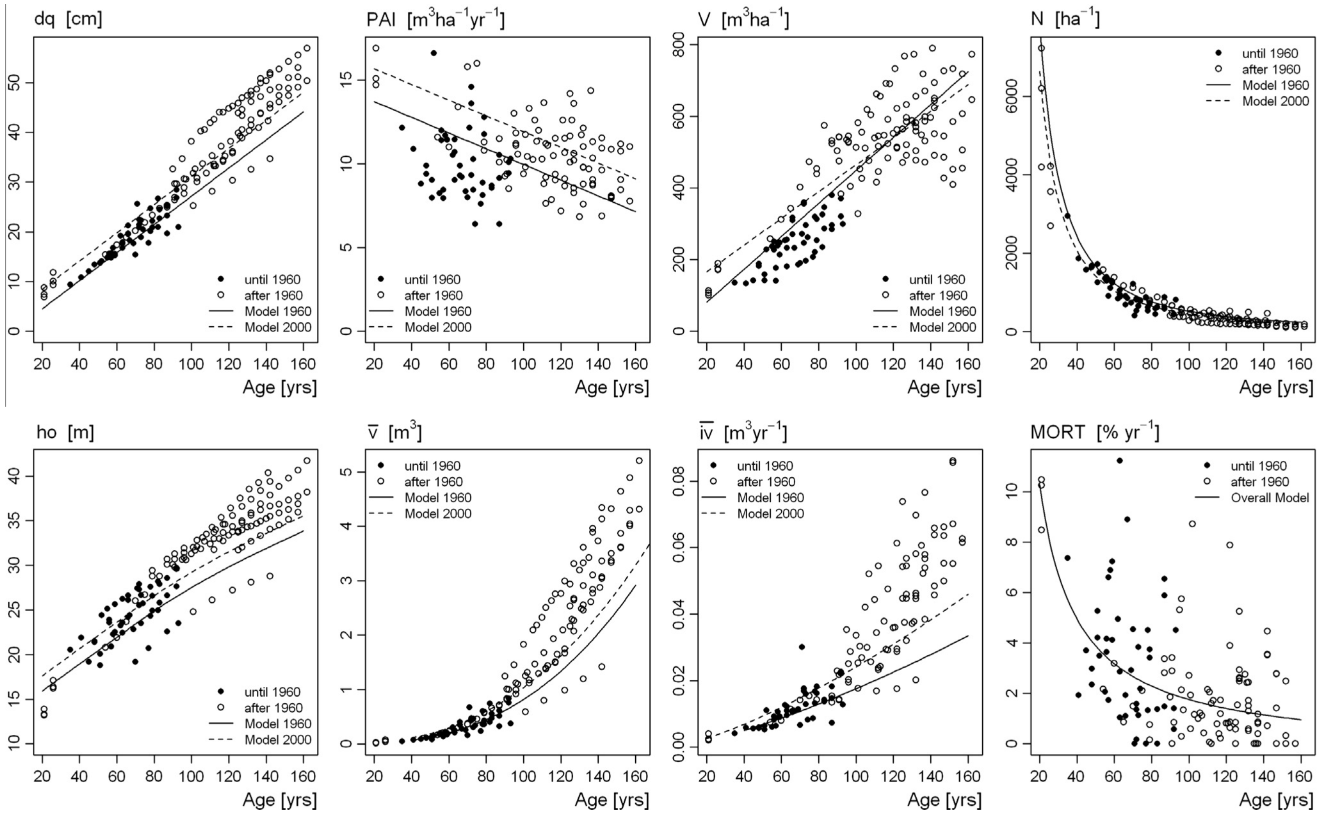

Fig. 4. Trends of quadratic mean diameter, dq; periodic annual stand volume increment, *PAI*; standing volume, *V*; tree number, *N*; top height, h_o; mean tree volume, $\bar{v}$; volume growth of mean tree, $\overline{iv}$; and mortality rate, *MORT* over age for the observational plots in oak included in this study. Observations before 1960 (filled symbols), after 1960 (empty symbols), model predictions for 1960 (solid line), and for 2000 (dashed line).

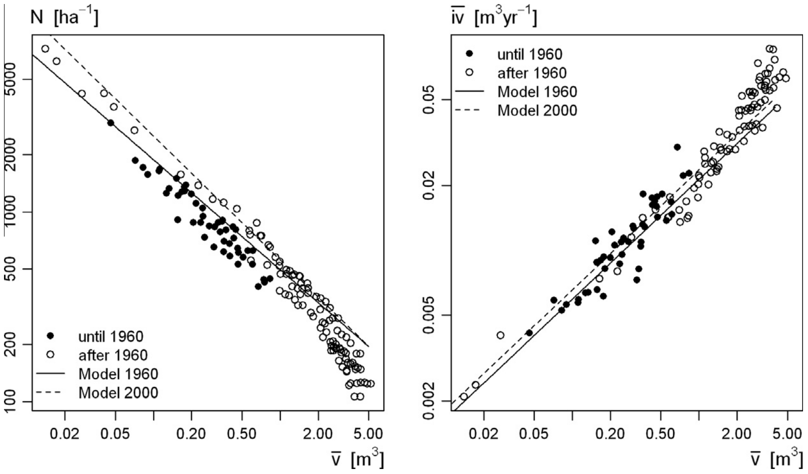

Fig. 5. Relationships between tree number, *N*; mean tree volume, $\bar{v}$; mean annual volume growth, $\overline{iv}$; mean tree volume, $\bar{v}$, in double-logarithmic scale for the observational plots in oak included in this study. Observations before 1960 (filled symbols), after 1960 (empty symbols), model predictions for 1960 (solid line), and for 2000 (dashed line).

their extent and relevance in terms of productivity changes at tree and stand level.

Many studies identified growth trends based on changes in site index (e. g., Kenk et al., 1991; Sterba, 1996) or diameter growth of individual trees (Spiecker et al., 1996, pp. 41–59). Our study confirms that height growth and diameter increment certainly changed. But based on area-related stand performance records we show that the effect of changing environmental conditions on mean tree volume, volume growth rate, and standing volume is much more pronounced.

We show that the self-thinning line which indicates the stands' carrying capacity and maximal density changed its slope and increased its level. The observed upwards shift of the self-thinning line indicates that not only the turn-over of matter has accelerated, but also the stock of resources itself. This lifted the stand's carrying capacity in terms of the number of living trees at a given size per unit area. It suggests an increase in site fertility (Long et al., 2004; Skovsgaard and Vanclay, 2008).

4.2.2. Relevance for forest ecosystem management

Faster size growth means that harvest thresholds like goal diameters or target volumes are achieved earlier which means shorter rotation times, and that due to the increased stand productivity forest managers may increase the annual cut. Besides, the

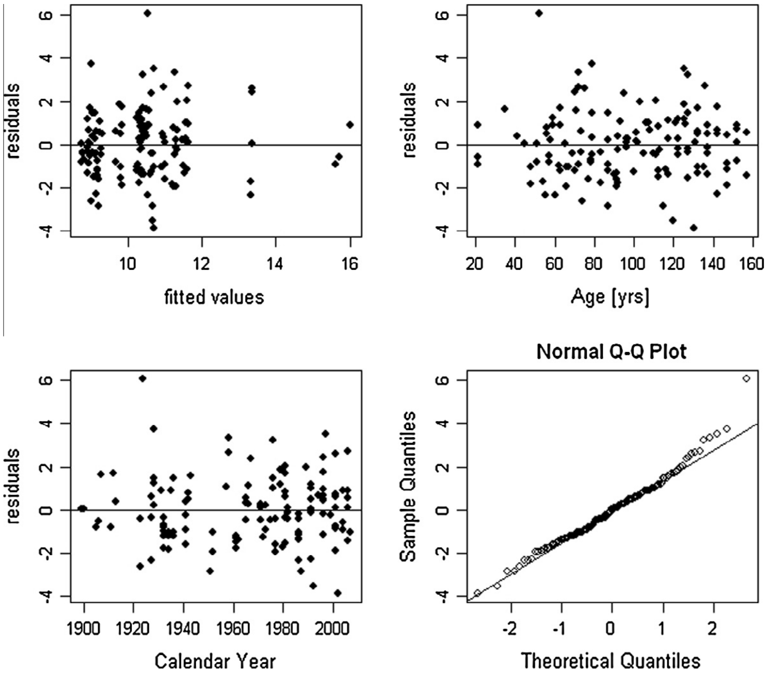

Fig. 6. Residual plots for the fitted model *PAI* = *f*(*age*, *calendar year*) (Eq. (1), Table 3, Fig. 4).

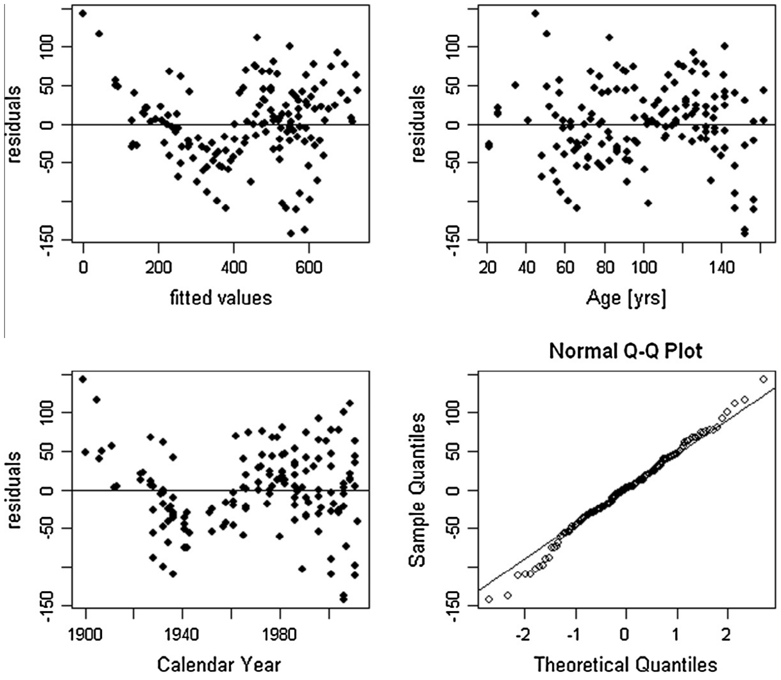

Fig. 7. Residual plots for the fitted model *V* = *f*(*age*, *calendar year*) (Eq. (1), Table 3, Fig. 4).

accelerated dynamics supposedly increased the forests' carbon sequestration, especially when the harvested wood is not burned but put into long-term uses or when it substitutes oil, gas or other mined resources. On the other hand, intensified harvest may cause new problems due to mineral nutrient export comparable to former litter raking.

4.2.3. Causal explanation of the revealed changes of forest growth

The revealed changes in stand growth and yield are just integrative and unspecific indicators for changes in system behavior and do not reveal to the underlying causes. Thus, the following considerations about relationships between changes of growth and changes of the environmental conditions remain speculative.

In the region covered by our plots, environmental and growing conditions for forests changed significantly since the end of the 19th century. Per decade, atmospheric CO_2-concentration and mean annual temperature increased by 10–20 ppm and by by 0.1 °C, respectively (IPCC, 2007; Schönwiese et al., 2005). Annual precipitation rose by 0.5–1.0 mm yr^{-1} (Schönwiese et al., 2005). The length of the growing season extended by 4–5 days per decade since the 1960 (Chmielewski and Rötzer, 2001; Menzel and Fabian, 1999). Wet N-deposition showed an increase of 0.5–1.0 kg ha^{-1} per decade and thus doubled to tripled since 1870 (IPCC, 2007; Skeffington and Wilson, 1988).

The changes in temperature, precipitation and the elongation of the vegetation period by 5–10% are hardly sufficient for explaining

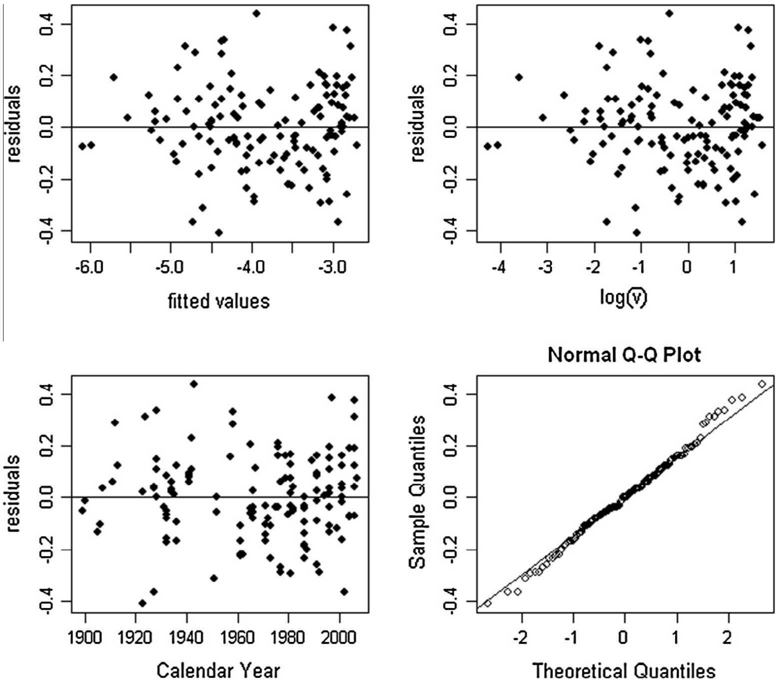

Fig. 8. Residual plots for the fitted allometric model ln($\overline{iv}$) = *f*(ln($\bar{v}$)), *calendar year*) (Eq. (3), Table 4, Fig. 5).

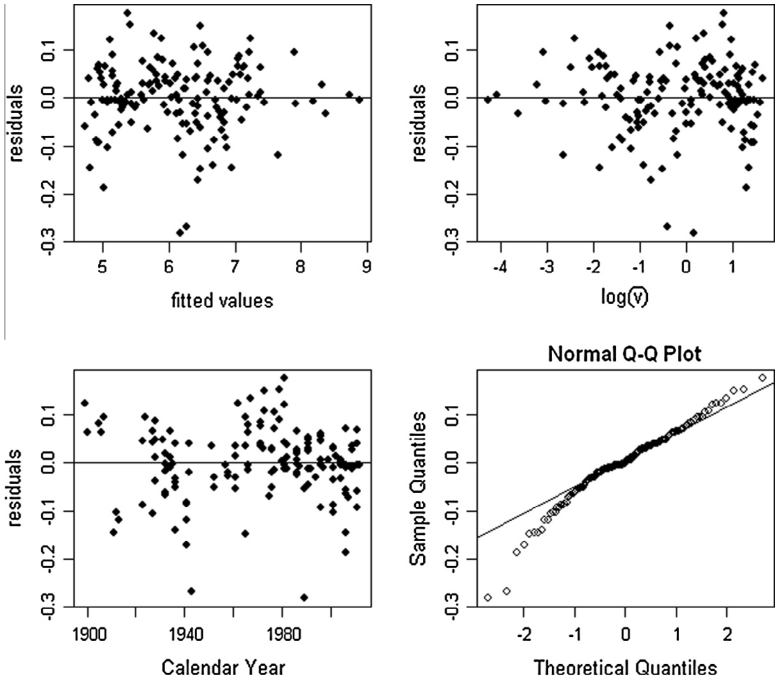

Fig. 9. Residual plots for the fitted allometric model ln(*N*) = *f*(ln($\bar{v}$), *calendar year*) (Eq. (3), Table 4, Fig. 5).

the 50% increase of tree productivity. We hypothesize that the fertilization effect by rising CO_2 levels and N-deposition are mainly behind the growth acceleration as long as no other resources as Mg or P, e.g., cause limitation (Prietzel et al., 2008). The observed increase of stand carrying capacity means that the atmospheric resource deposition not only fertilizes and accelerates the stand dynamics, but also improves the site conditions by enrichment of the nutrient stocks.

We further hypothesize that oak is rather drought resistant and can make better use of the additional resource availability than more water demanding species like Norway spruce or European beech. Both species also show an accelerated growth but not a higher carrying capacity.

4.2.4. Long-term observational plots as ultimate arbiters of human impact on forest ecosystems

While the direct effect of humans on forests, e. g. the development of the forested area and the kind of management and stock is routinely assessed by inventories, unmanaged long-term observation plots are the probate basis for assessment of the indirect effects caused by the change of climate and other environmental conditions.

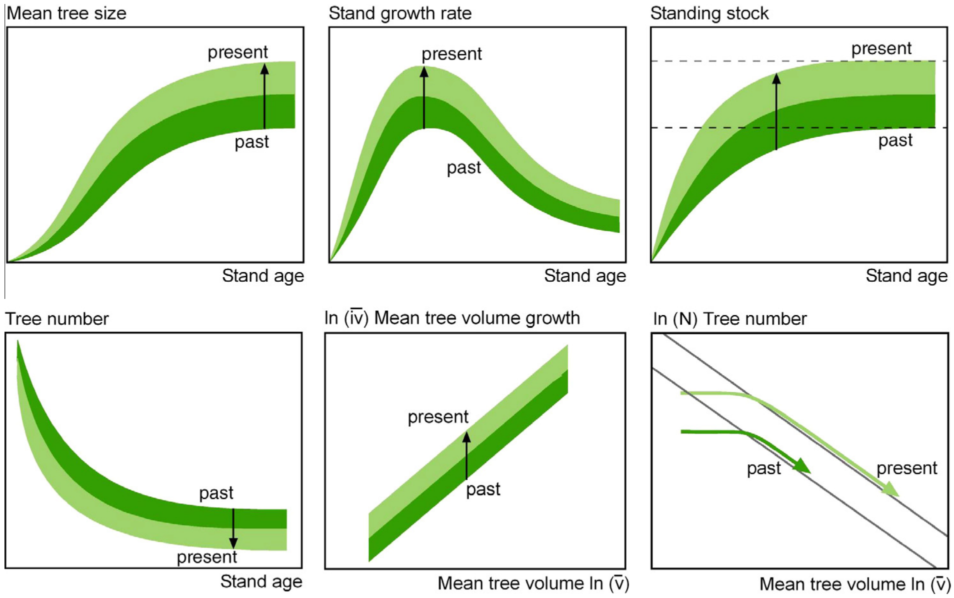

Fig. 10. Graphical abstract of the revealed growth trends of oak since beginning of the survey in 1900. Above, from left to right: Acceleration of tree size growth, stand growth rate and standing stock over stand age. Below, from left to right: Accelerated decrease of tree number over age; upwards shift of the allometric relationship between tree volume growth and tree volume; upwards shift of the self-thinning line and faster passing of stands through the tree number-tree size trajectory.

Unfortunately, most of those plots were seen as outdated, considered too expensive and abandoned when forest inventories emerged. However, in Europe's nearly completely managed forest area the unthinned plots represent the exceptional case of unmanaged ecosystem development over up to 140 yr. With our study we emphasize the still unique contribution of unmanaged long-term plots to regional but also global ecosystem monitoring, ecological research, and environmental policy. Even 300 yr after Carl von Carlowitz, long-term plots are ultimate arbiters of human footprints on forest ecosystems as they reflect whether and how forest growth is changing.

5. Conclusions

The study emphasizes the unique contribution of long-term observational plots and in particular of unmanaged plots, for indicating changes in forest ecosystems. As temporary inventory plots, artificial time series, or retrospective growth trend analysis via increment cores are hardly indicative of long-term changes of compounds, structure, functioning of forests, unmanaged observational plots should be a standard component of a country's bio-monitoring system.

Although the plots used in this study have been established in the beginning of the 20th century, long before statistical thinking and ecosystem research were common, they deliver relevant growth information for bioassay, forest ecology and management. Future observational plots should monitor both the growth and the environmental conditions and reveal the causes of changing forest dynamics.

Compared with the past, the stands presently grow quicker and accumulate a defined standing volume earlier than a century ago. They grow along modified self-thinning lines and move quicker through such trajectories than in the past. This means that silvicultural prescriptions and models depending on stand age as the main driving variable are called into question. However, guidelines and models which are size-scheduled instead are less prone to become outdated by such changes. Models which are driven by potential or actual growth rates and apart from that base on allometric instead of age-dependent relationships are probably a better choice.

In times of scarce resources and high energy costs the indicated rise of productivity has also positive consequences: growth rates are higher, stands and trees grow faster, so that rotation periods might be reduced and sustainable felling budgets might be increased. Carbon sequestration by forests might increase as well. On top of that the increase of site fertility may pave the way to multi-species, complex-structured forests which are more resilient than pure stands in the face of future environmental changes.

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