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Wood density reduced while wood volume growth accelerated in Central European forests since 1870

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ABSTRACT

Forest stand growth dynamics in Central Europe have accelerated since 1870 due to a rise in temperature, extended growing seasons, and other components of climate change. Based on wood samples from the oldest existing experimental plots in Central Europe, we show that the dominant tree species Norway spruce (*Picea abies* (L.) H.KARST.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), and sessile oak (*Quercus petraea* (MATTUSCHKA) LIEBL.) exhibit a significant decrease in wood density since more than 100 years. While stand and trees grow faster with respect to wood volume, we can show that wood density decreased by 8–12% since 1900. These results object a naïve direct transformation of volume growth trends into an accelerated biomass production. Since 1900, stand biomass increment increased 9–24 percentage points less compared to volume increment (29–100% increase reduces to 20–76%). For a given stem diameter and annual ring width, tree stability against windthrow, wood strength, energy content and C sequestration are even reduced under recent conditions. The generally decreased late wood density, partly going along with an increased early wood fraction, suggests the observed extension of the growing season and fertilization effect of dry deposition as the main causes.

Our results indicate that current increased wood volume growth rates must not be straightforwardly converted into sequestrated C and biomass harvest potentials assuming historic values for wood density. This should be taken into account in monitoring, modeling, and utilization of carbon and biomass in forests under global change.

1. Introduction

Recent studies provide a growing body of evidence on acceleration of forest growth dynamics in Central Europe and worldwide caused by environmental changes (Bussotti et al., 2014; Fang et al., 2014; Kauppi et al., 2014; Pretzsch et al., 2014a, 2014b; Reyer et al., 2014; Boisvenue and Running, 2006). While drought events may temporarily cut down growth rates (Hartmann, 2011; Pretzsch and Dieler, 2011; Rötzer et al., 2013), the overall level is still unprecedentedly high. Recently, most of the authors of this study authored a paper which clearly substantiated these trends for Norway spruce and European beech in Central Europe, the most important coniferous and broadleaved tree species in that region (Pretzsch et al., 2014b). Based on long term observations of a rather unique set of research plots with first observations dating back as far as the 1870ies, an accelerated forest stand growth in terms of wood volume was shown to be statistically significant. Corresponding scenario analyses with the ecophysiological forest model BALANCE (Grote and Pretzsch, 2002) suggested that mainly the rise in temperature and extended growing seasons contribute to the observed growth acceleration, in particular on fertile sites. The study also gave a rough estimate of the additional C sequestration in Central Europe due to the substantiated growth trends in wood volume. However, this estimate assumed a constant wood density. This assumption must be questioned as climatic factors have shown to be among the most important determinants of wood properties (Zhu et al., 2015; Roderick and Berry, 2001), and as several publications identified links between climate change and wood density (Franceschini et al., 2012, 2010; Bouriaud et al., 2005; Jacoby and D'Arrigo, 1995).

The study at hand strives to clarify if the wood density of important Central European tree species can be legitimately taken as a long-term constant or if it undergoes systemic temporal trends in a similar way as could be shown for wood volume growth. We chose the tree species Norway spruce (*Picea abies* (L.) H.KARST.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), and sessile oak (*Quercus petraea*

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(MATTUSCHKA) LIEBL.) as they represent roughly ¾ of Central Europe's forest area with Norway spruce and Scots pine accounting for about 25% each, European beech 15% and sessile oak 10%. Besides their ecological importance, these species also dominate the market of domestic timber. Systematic trends in their wood density would not only relate to ecological issues like resistance against wind breakage, biomass accumulation and C sequestration, but also to economic and technical matters like the usability of wood for constructive and energetic purposes.

For this study we took an extensive sample of increment cores from long-term forest research plots which are among the longest observed ones worldwide. For the species Norway spruce and European beech these plots largely overlap with those, where Pretzsch et al. (2014b) showed recently accelerated growth as mentioned above. These cores were used to measure wood density and related properties together with stem diameter growth on an annual basis for more than a century back before the sampling date.

We analyzed our data with respect to the questions, whether a tree ring's (i) mean wood density, (ii) earlywood density, (iii) latewood density, and (iv) early wood fraction depend on the calendar year.

2. Materials and methods

2.1. Long term research plots sampled for this study

We chose altogether 41 long term forest growth and yield trials in Southern Germany for taking the samples required for this study. The plots are maintained and regularly surveyed under responsibility of the first author and his group. Among them are the oldest forest research plots worldwide, e.g. the European beech trial Fabrikschleichach (FAB 15) is under continuous observation since 1870. For Norway spruce and European beech, there is a broad overlap with the trials used by Pretzsch et al. (2014b) for substantiating accelerated stand and tree volume growth. From each trial we selected the plot which was fully stocked and had undergone either no or only minor silvicultural treatment in the past. With this selection procedure we made sure not to include confounding effects on wood density which might come from treatment or especially from treatment changes. The 41 plots which were eventually selected break down to 13 in Norway spruce stands, 11 in Scots pine 9 in sessile oak and 8 in European beech. All stands are monospecific, even aged and were established either by planting or by seeding, their ages at the time of sampling – after the growing season of 2014 – were between 31 and 194 years. The plots cover a range of northern latitudes between 47.852° and 50.375°, and eastern longitudes between 7.750° and 13.308°. Their altitude above sea level are between 320 m and 820 m (Table A.1). The spatial distribution of the plots (Fig. A.1) mirrors typical site and climate conditions for the occurrence of the four investigated species in Central Europe. The Norway spruce plots are mostly in the south and east parts of Southern Germany, while Scots pine plots concentrate in the north east part. Most beech and oak plots are in the north and extreme west part of the region.

The long term mean annual temperature of all plots together is between 5.7 °C and 8.4 °C, the mean annual precipitation ranges between about 500 mm and 1400 mm (Table A.2). The DeMartonne aridity index (calculated as $P/(T+10)$ with P being the mean annual precipitation in mm and T being the mean annual temperature in °C) covers a range of 30 up to almost 90. While this indicates a considerable variation, even the smallest value stands for humid conditions; only index values of 20 and below would mean an arid climate (Blüthgen, 1980).

As can be taken from Table A.2, the pine plots are generally growing under lowest precipitation, highest temperatures and consequently under the least humid conditions when compared with the other species. The opposite is true for Norway spruce, which is associated with pronouncedly more humid climates. A similar, albeit less distinct difference is visible for sessile oak and European beech, where the beech plots generally show more humid conditions than the oak plots.

Following the nomenclature of the German forest site classification system (Arbeitskreis Standortskartierung, 1985), the plots are distributed among 13 ecoregions and 17 sub-ecoregions (Table A.3). Most frequently, the plots are covered with clayey or sandy soils. Hereby, the pine and oak plots tend to be associated with the more sandier sites, whereas the spruce and beech plots cover the more clayey sites. With regard to soil types, the oak and beech plots are dominated by brown soils, the pine plots growing on pseudogleys or podzols, and the spruce plots were most often established on parabrown soils and brown soils.

2.2. Sampling procedure, sample preparation and measurements

All the selected plots are embedded in a buffer zone, where the silvicultural treatment (including omission of treatment) is the same as on the plot itself. In this zone around each plot, we sampled about ten dominant trees following the social tree class definitions by Kraft (cited after Assmann, 1961), see Table A.4 for the precise sample sizes. This social class of trees (class #2 after Kraft) contributes most to wood volume and increment in even-aged stands. From each tree we took a core at breast height (1.3 m) with a standard increment borer (Haglöf Mora Coretax, diameter 5.15 mm), attempting to hit the centre of the stem in order to cover as many growth rings as possible. The stem diameter at breast height (dbh) and total tree height of the standing tree were measured in addition (girth tape, Haglöf Vertex IV height measuring instrument). In order to prepare the cores for the subsequent wood density measurements, they were air-dried and accurately glued, with the vessels pointing in vertical direction, onto wooden slides. After that, they were honed first with a belt sander, then by hand, and sand paper down to a grain size of 1200 in order to achieve a surface as even as possible. Abrasive dust was carefully removed using a compressed air cleaner.

For the wood density measurements we used a LIGNOSTATION™ high frequency densitometer. The measurement method relies on the principle that electromagnetic waves propagate differently in dielectric materials like wood, depending on the material's density. To this end, an extremely small high frequency transmitting and receiving electrode system (Fig. A.9) is moved along the wood sample of interest. The transmitting electrode emits a 10 MHz sinusoidal signal which partly propagates through the wood sample to the receving electrode. The strength of the received signal is positively correlated with the local density of the wood sample (Spiecker et al., 2003). While high frequency densitometry is a simple and fast measuring method, the quality of the sample surface, which has to be absolutely plane, is crucial for achieving usable results (Wassenberg et al., 2014). Therefore, the above-mentioned sample preparation and all other steps were executed with painstaking care.

The measurement procedure yielded a wood density profile for each core with a resolution of 1/100 mm. Growth rings were detected by a combination of an algorithm implemented in the LIGNOSTATION software, which evaluates wood density gradients, with visual assessment. Besides the growth ring widths, we used the density profiles to calculate the mean wood density (MWD) per growth ring, as well as the earlywood density (EWD) and the late wood density (LWD) respectively. According to the LIGNOSTATION standard procedure, the earlywood-latewood border was defined as the point, where the local wood density was 50% of a given growth ring's maximum wood density. Besides the density values above, this allowed us to calculate the earlywood ratio (EWR) which is the width (in growth direction) of a growth ring's earlywood divided by the total ring width. An overview of sample sizes, mean values and the range of the above-mentioned variables is given in Table 1. The species-wise distributions of the backwards calculated diameters at breast height and corresponding growth ring widths are visualized as boxplots in Fig. 1.

Table 1
Overview of the sampled growth ring data. Diameter at breast height, tree height, and age relate to the time of sampling. The site index is the expected stand mean height at an age of 100 years according to standard yield tables. On average, 79 growth rings could be evaluated per tree (max. 171, min. 16).

Species	n		Diameter at breast height (mm)	Tree heigth (dm)	Age (years)	Ring width (1/100 mm/a)	Earlywood density (mg/cm^3)	Latewood density (mg/cm^3)	Mean wood density (mg/cm^3)	Earlywood ratio	Site index (m)
Norway spruce	127	min	216	222	45	3	75	90	85	0.05	25.0
		mean	437	314	89	263	376	512	416	0.68	36.8
		max	804	459	167	1433	592	739	611	0.99	44.7
Scots pine	103	min	135	134	44	10	139	172	168	0.07	22.0
		mean	380	265	122	148	470	661	539	0.63	26.0
		max	637	410	171	832	706	917	846	0.93	33.1
European beech	63	min	271	265	75	3	122	130	126	0.06	28.1
		mean	443	336	135	175	679	753	716	0.50	30.7
		max	580	402	194	751	881	969	913	1.00	36.2
Sessile oak	99	min	129	151	31	2	131	195	187	0.00	25.1
		mean	427	295	134	144	506	778	683	0.36	28.7
		max	732	394	180	1011	959	1192	1026	0.93	32.0

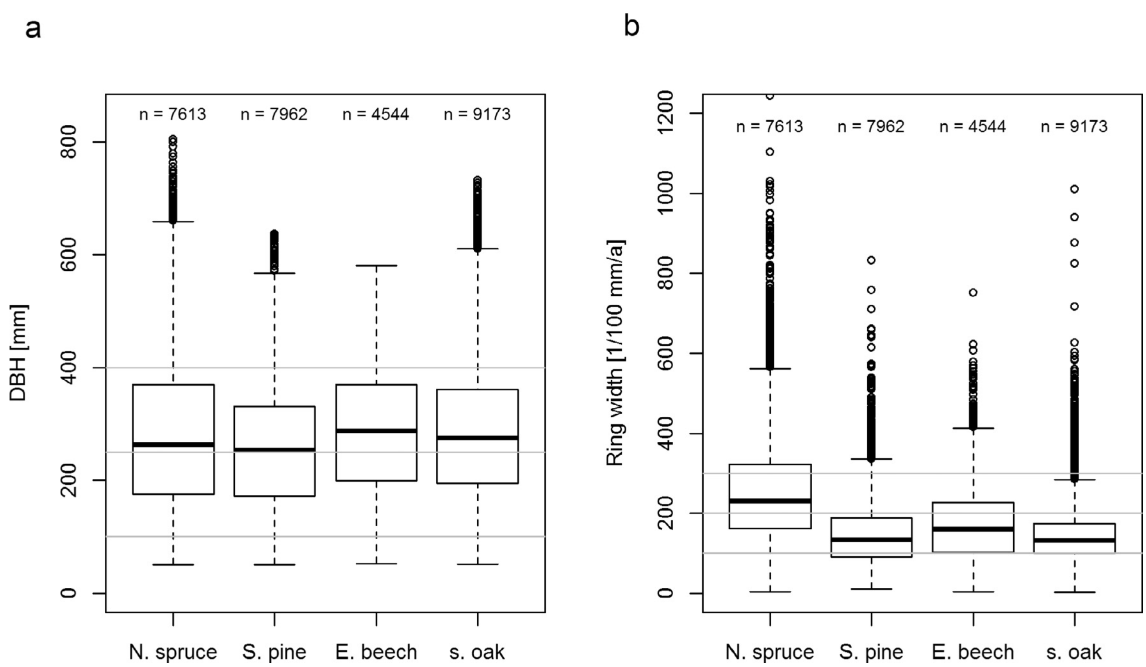

Fig. 1. Species-wise distributions of the backwards calculated diameters at breast height (a) and growth ring widths (b). The horizontal grey lines indicate diameters of 10, 25, and 40 cm (diagram a), and growth ring widths of 1, 2, and 3 mm.

2.3. Statistical analyses

In order to test for a calendar year effect on the mean wood density *MWD* (mg/cm^3), we applied the following model for each tree species separately:

$$MWD_{ijkt} = \beta_0 + \beta_1 \cdot YEAR_t + \beta_2 \cdot RW_{ijkt} + \beta_3 \cdot DBH_{ijkt} + \beta_4 \cdot YEAR_t \cdot RW_{ijkt} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (1)$$

The variables *YEAR*, *RW*, and *DBH* mean the calendar year, the tree ring width (1/100 mm) and the diameter at breast height (mm), measured in 1.3 m above the forest floor. The indexes *i*, *j*, *k*, and *t* represent the levels of a trial, a plot in a trial, a tree in a plot, and observation (point in time), respectively. The parameters β_0, ..., β_4 quantify the fixed effects, while b_i, b_{ij}, b_{ijk} are random effects on trial, plot, and tree level. These random effects are assumed to be normally distributed with an expectation of 0 ($b_i \sim N(0,\tau_1^2)$, $b_{ij} \sim N(0,\tau_2^2)$, $b_{ijk} \sim N(0,\tau_3^2)$). The errors ε_{ijkt} are i.i.d. with $\varepsilon_{ijkt} \sim N(0,\sigma^2)$.

We chose this model structure because it incorporates, besides the calendar year itself, the ring width and the diameter at breast height as a proxy for tree size in general, which both must be considered to correlate with wood density. As the correlation of ring width with wood density may have a calendar year dependent trend itself, the interaction between both variables, *RW* and *YEAR*, was explicitly introduced in the model. By introducing random effects on all data nesting levels higher than a single observation, we take care for possible autocorrelation issues, including site-specific variation.

The same model was applied for early wood density (*EWD*), late wood density (*LWD*), and the early wood ratio (*EWR*), which is the fraction of early wood in a growth ring, as the dependent variables:

$$EWD_{ijkt} = \beta_0 + \beta_1 \cdot YEAR_t + \beta_2 \cdot RW_{ijkt} + \beta_3 \cdot DBH_{ijkt} + \beta_4 \cdot YEAR_t \cdot RW_{ijkt} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (2)$$

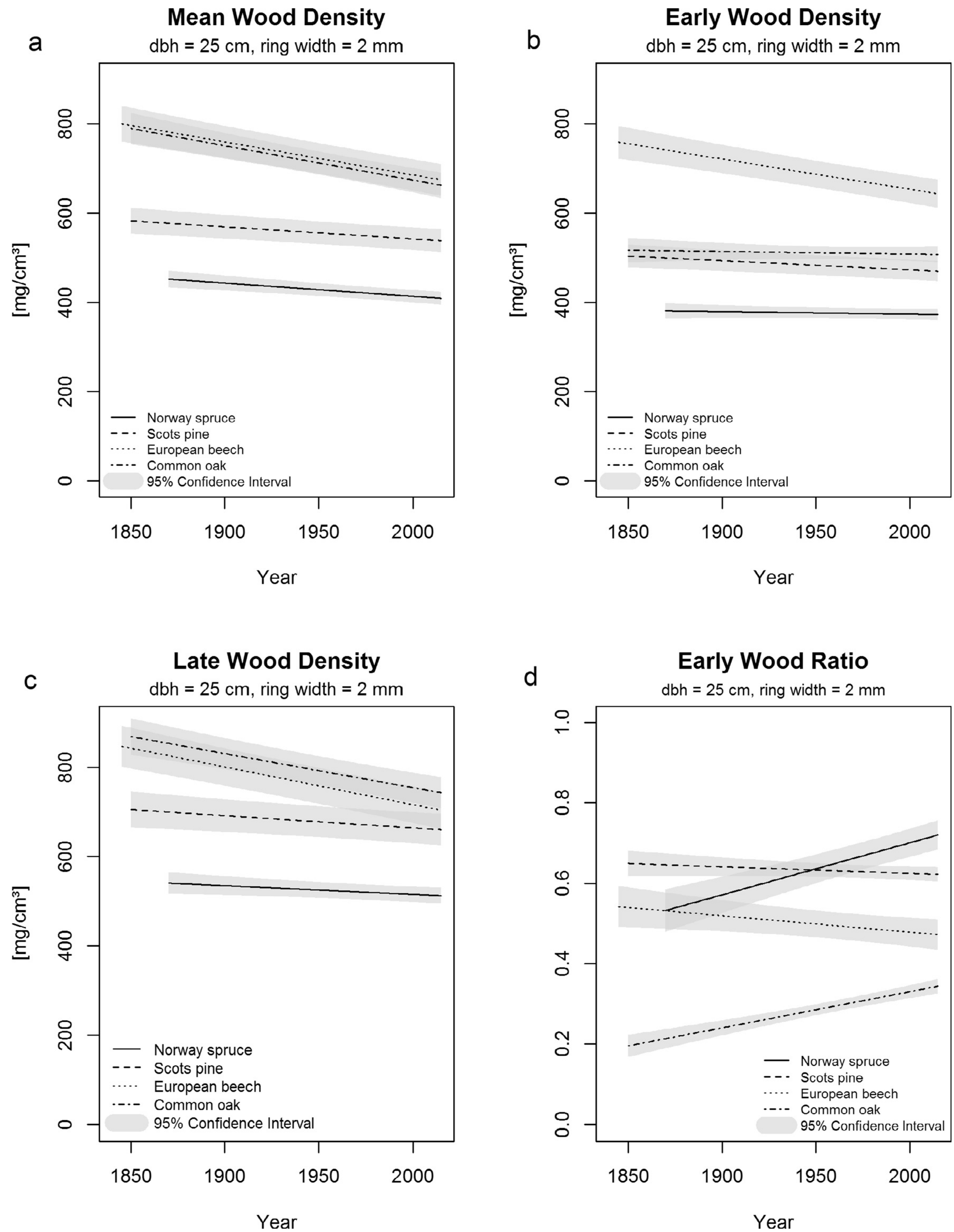

Fig. 2. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 25 cm and 2 mm/a (standard tree) for these predictions.

$$LWD_{ijkt} = \beta_0 + \beta_1 \cdot YEAR_t + \beta_2 \cdot RW_{ijkt} + \beta_3 \cdot DBH_{ijkt} + \beta_4 \cdot YEAR_t \cdot RW_{ijkt} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (3)$$

$$EWR_{ijkt} = \beta_0 + \beta_1 \cdot YEAR_t + \beta_2 \cdot RW_{ijkt} + \beta_3 \cdot DBH_{ijkt} + \beta_4 \cdot YEAR_t \cdot RW_{ijkt} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \quad (4)$$

3. Results

Our fitted models for Mean Wood Density (MWD, Eq. (1), see Table A.5 for parameter estimates) show significant influences for all input variables (calendar year, growth ring width, diameter at breast height) and the considered interaction between calendar year and ring width (mostly $p < 0.001$) across all four tree species. Consistently, MWD generally decreased from earlier to recent calendar years, and

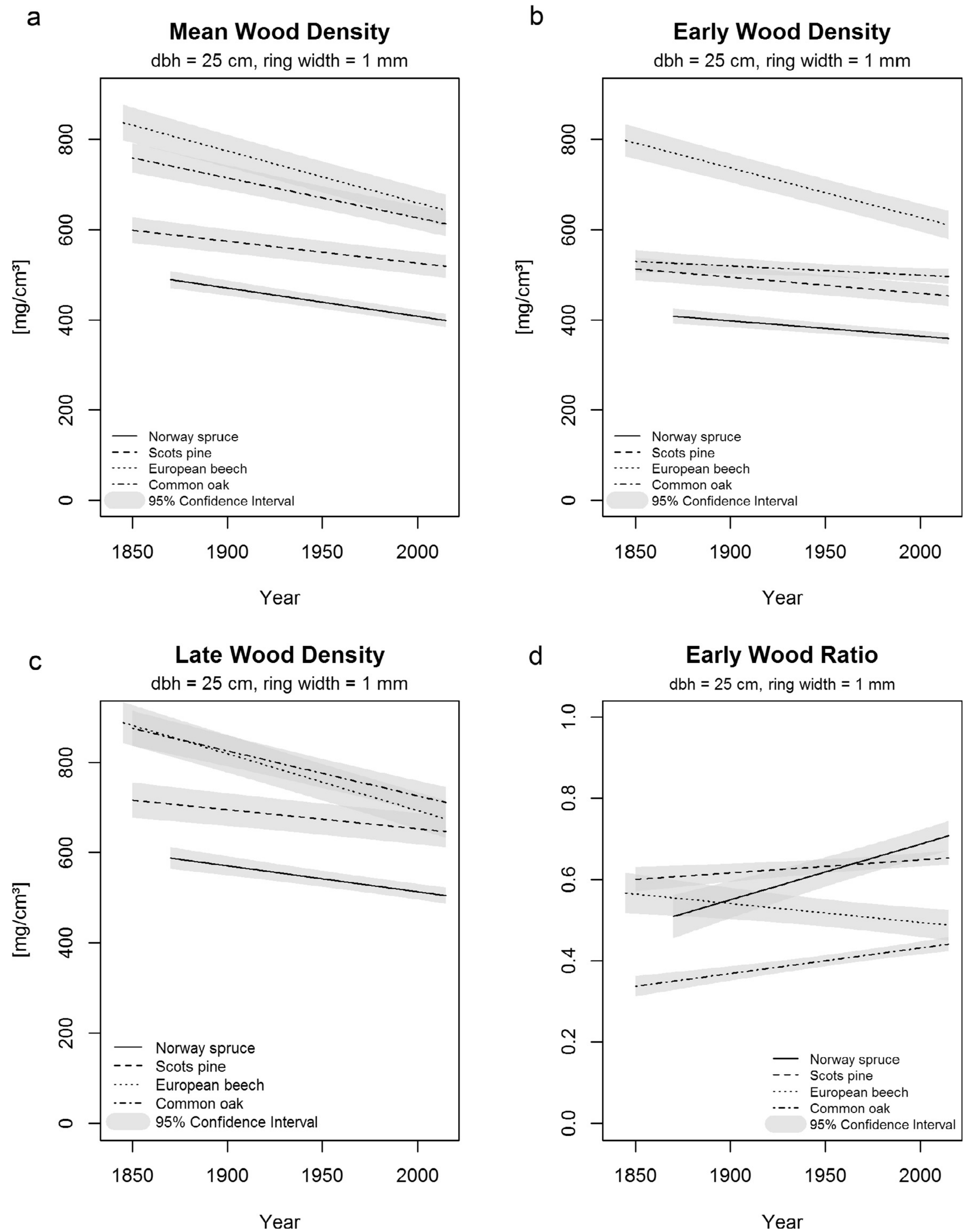

Fig. 3. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 25 cm and 1 mm/a for these predictions.

decreased with increasing ring width. In all cases these calendar year and ring width effects are to some extent counteracted by a significant interaction between calendar year and ring width.

Decreasing wood density with increasing ring width does not come as a surprise for the conifer species Norway spruce and Scots pine, where broader growth rings typically mean more earlywood with low density. However, it was interesting to find this also for the diffuse-porous hardwood European beech and the ring-porous hardwood sessile oak, where broader growth rings usually mean a higher share of the dense latewood. With greater stem diameters at breast height, in addition, mean wood density has a significant tendency to increase.

In order to obtain a clear view, we visualized the model outcomes over time for certain combinations of diameters at breast height and three ring widths. The choice we made was due to the distribution of our DBH and RW data as visualized in Fig. 1. As can be taken from Fig. 1a, the stem diameters of all four species are very similarly distributed around a median near 25 cm, and the range between 10 and 40 cm covers evidently more than 50% of the data. The distribution of

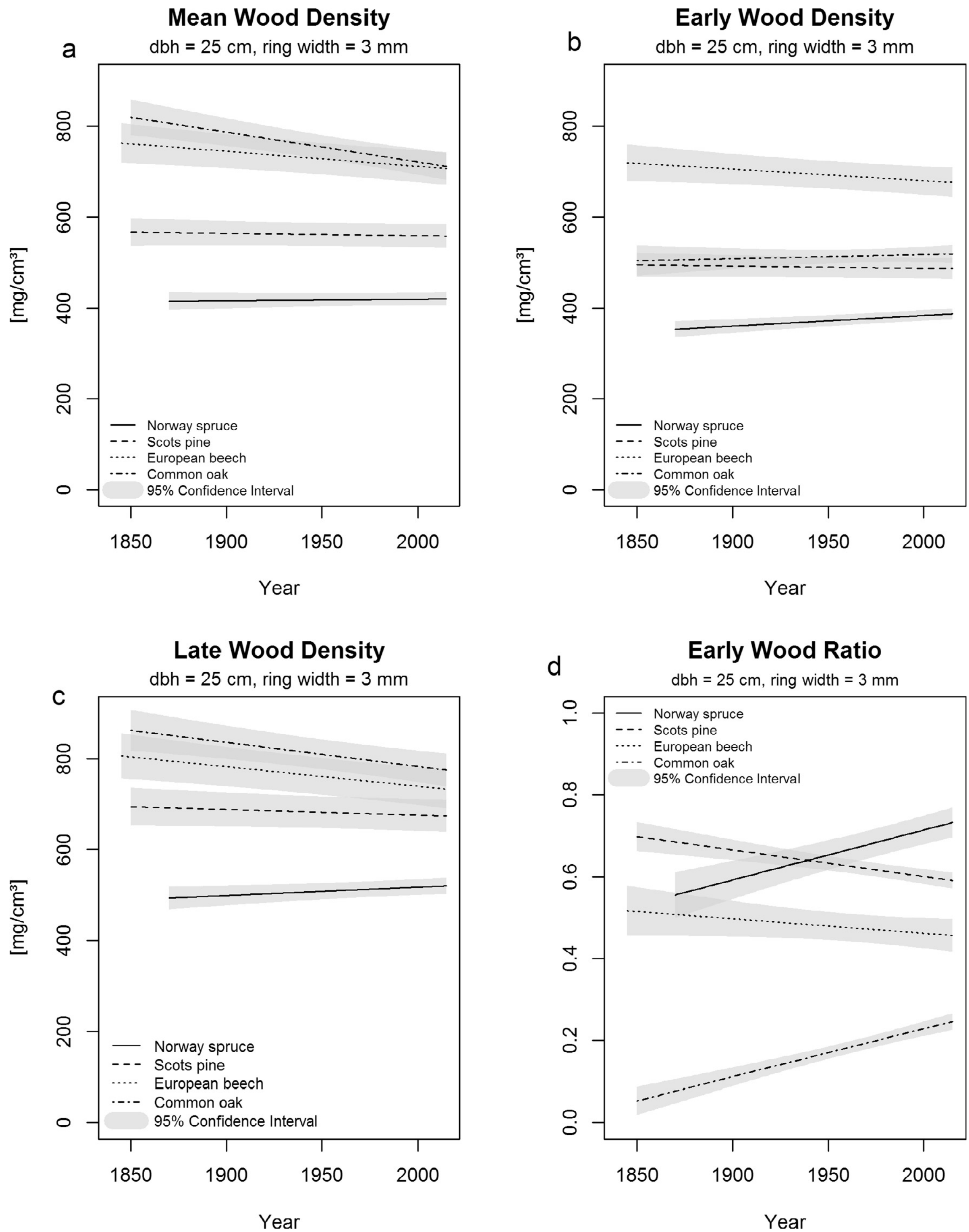

Fig. 4. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 25 cm and 3 mm/a for these predictions.

Table 2
Relative changes of wood density variables from 1900 to 2015. The values were estimated based on linear mixed models fitted to our data (Eqs. (1)–(4), Tables A.5–A.8) for a standard tree with DBH = 25 cm and a growth ring width of 2 mm/a. Values in parentheses are estimated standard errors of the percentages.

Species	Mean wood density		Early wood density		Late wood density		Early wood ratio	
Norway spruce	−7.7%	(2.5)	−1.7%	(2.3)	−4.2%	(2.5)	26.1%	(3.7)
Scots pine	−5.4%	(3.4)	−4.8%	(3.4)	−4.5%	(3.9)	−2.9%	(2.2)
European beech	−11.2%	(3.8)	−10.8%	(3.4)	−12.1%	(4.4)	−9.1%	(5.9)
sessile oak	−11.8%	(3.1)	−1.3%	(2.5)	−10.6%	(3.5)	43.1%	(3.9)

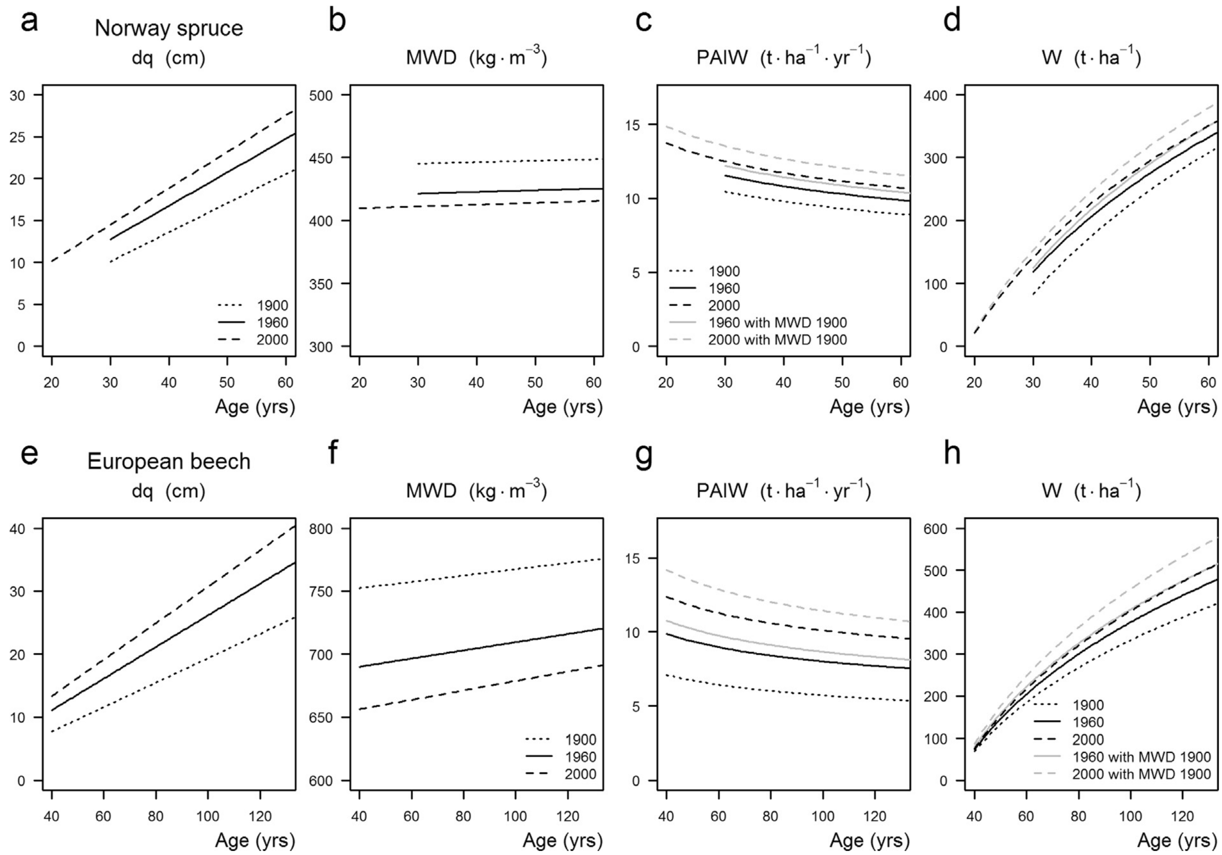

Fig. 5. Conversion of stand volume growth trends reported by Pretzsch et al. (2014b) into above ground wood biomass. Trends in quadratic mean stand diameter dq taken from Pretzsch et al. for Norway spruce (a) and European beech (e). Corresponding mean wood density MWD estimated with the linear mixed models fitted in this study for Norway spruce (b) and European beech (f). Periodical annual increment of above ground stand wood biomass PAIW (c: spruce, g: beech) calculated from the wood densities shown in (b) and (f) and the trends of stand volume increment shown by Pretzsch et al. (2014b). Standing above ground stand woody biomass W (d: spruce, h: beech) calculated from the wood densities in (b) and (f) and the stand volume growth trends reported by Pretzsch et al. (2014b). Grey lines in (c), (d), (g), (h) indicate PAIW and W trends assuming mean wood density MWD keeping the same levels as in 1900, i.e. no calendar year trends in MWD.

the ring widths (Fig. 1b) is for all species, except Norway spruce, distributed around a median of 1.5 mm with about 50% of the data being inside the range of 1–2 mm/a. The ring width distribution of Norway spruce is on a somewhat higher level; the median is slightly above 2 mm/a, and the range of 1–3 mm/a covers about the central 50% of the data.

In order to work with round numbers, we defined a “standard tree” with DBH = 25 cm and RW = 2 mm/a, based on the information shown above. The ring width of 2 mm/a is close to the median ring with of Norway spruce, and close to the 75% quantile for the other species. As our parameter estimates (Table A.5) show, the negative calendar year effects on mean wood density are the stronger the narrower the growth rings are. Thus, visualizing the model outcome for a ring width of 2 mm/a should be close to average conditions for Norway spruce and provide conservative trend estimates for the other species. While the following presentations focus on this standard tree, we show the model outcomes as well for ring widths of 1 and 3 mm/a in addition for the sake of a broader view which is still well covered by our data (Figs. 2–4). While in our models the diameter at breast height does influence the level of wood density but not its calendar year trend, we provide model visualisations for additional diameters (10 and 40 cm) in combinations with ring widths of 1, 2, and 3 mm/a in the appendix only (Figs. A.2–A.7).

As evident in Fig. 2a, European beech and sessile oak exhibit a very similar behavior for standard tree (DBH = 25 cm, RW = 2 mm/a), with wood densities about 800 mg/cm^3 in the 1850ies decreasing to less than 700 mg/cm^3 in the early 2000 s. Both conifer species show a similar, but weaker trend on lower levels of wood density (about 600–550 mg/cm^3 for Scots pine, and 450–400 mg/cm^3 for Norway spruce). Related to the time span between 1900 and 2015 this means a decrease of wood density by 5.4% (Scots pine), 7.7% (Norway spruce), 11.2% (European beech), and 11.8% (sessile oak), see Table 2.

Due to the interaction of ring width and calendar year, these trends towards a decreasing wood density with calendar year are pronouncedly stronger for all tree species when growth rings are narrower, as shown in Fig. 3a for a ring width of 1 mm/a. Consequently, the effect is weaker when growth rings are wider, shown in Fig. 4a for a ring width of 3 mm/a. Interestingly, at about this ring width our models suggest no more calendar year trend in wood density for both coniferous species Norway spruce and Scots pine.

The same main effects of calendar year and ring width become evident for Early Wood Density (EWD, Eq. (2), see Table A.6 for parameter estimates) and Late Wood Density (LWD, Eq. (3), see Table A.7 for parameter estimates). Trends and significances for LWD are virtually the same as for mean wood density (MWD), albeit obviously on a higher level of wood densities than for MWD (Fig. 2b, c). In EWD the influence of the stem diameter is less unambiguous and not significant in two cases (Scots pine, sessile oak). Compared to LWD, where the standard tree’s wood density decreases with calendar year for all four species (Fig. 2c), the standard tree’s EWD does not change with the

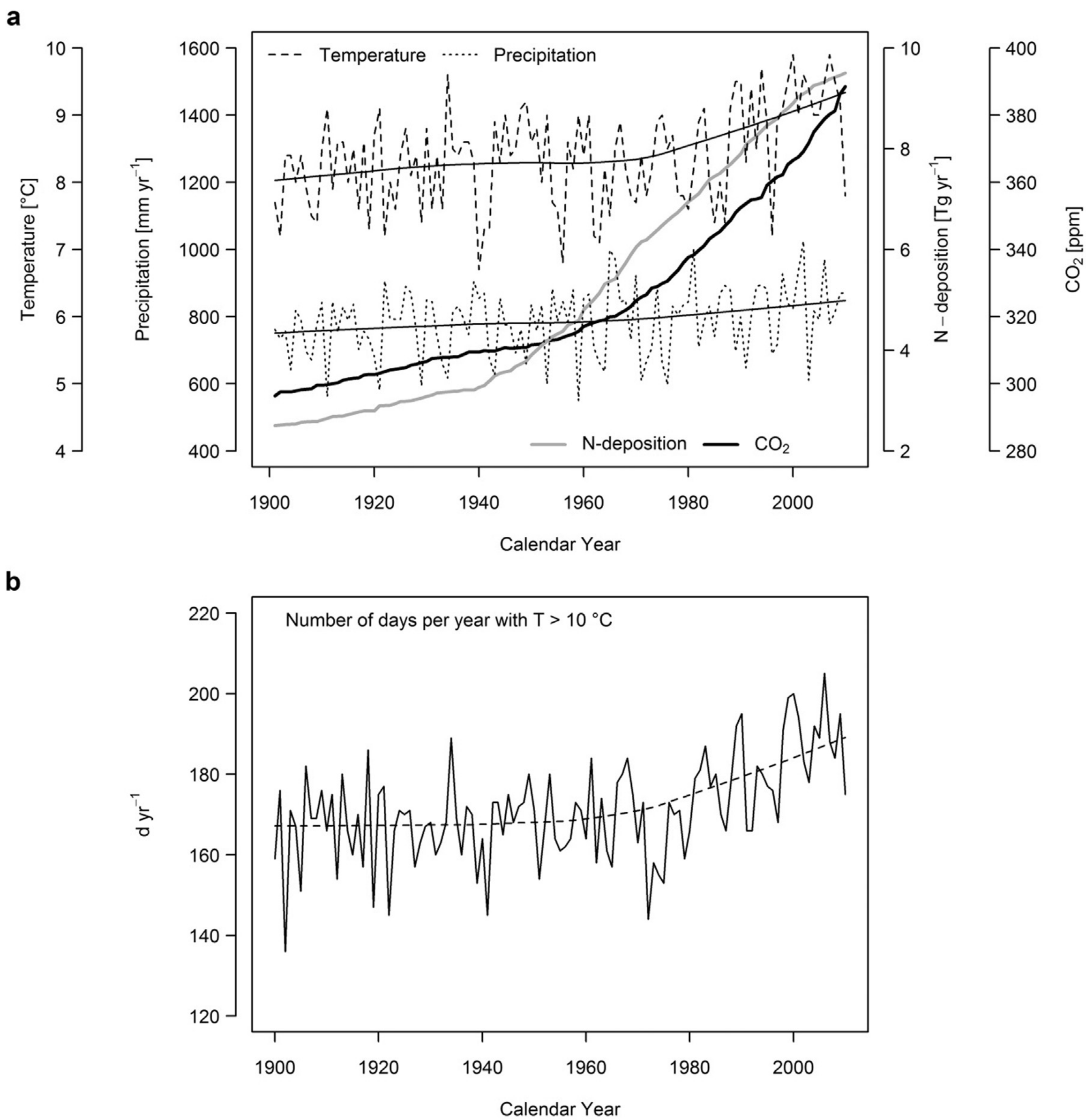

Fig. 6. Change in growth conditions for Central Europe since 1900 (taken from Pretzsch et al., 2014b). (a) Trend in mean annual air temperature (dashed), annual precipitation (dotted), atmospheric CO2-concentration (bold black line), and N-deposition (bold grey). For better trend visualization loess smoothers for temperature and precipitation have been added (thin solid lines). (b) Extended annual growing season, expressed by the number of days per year with a mean temperature > 10 °C. The dashed line represents a loess smoother. Data sources: (Churkina et al., 2010; Schönwiese et al., 2005).

calendar year for sessile oak and Norway spruce. MWD, EWD, and LWD in Fig. 2a–c show the typical traits of the different wood types: The diffuse-porous wood of European beech does not have remarkable density differences between MWD, EWD, and LWD; the time trends of all three variables are virtually the same. In contrast, LWD is considerably higher than EWD for the conifers Scots pine and Norway spruce, with the latter exhibiting almost no time trend for EWD. Sessile oak with its ring-porous wood represents the other extreme. Here, we see the low-density early wood without a meaningful time trend coming along with a high-density late wood undergoing a strong time trend.

Compared to these observations for the standard tree, the trend of decreasing EWD and LWD with calendar year is evidently stronger when a ring width of only 1 mm/a is assumed (Fig. 3b, c). Vice versa, the trend weakens for broader growth rings; at 3 mm/a (Fig. 4b, c) it is almost not existent for Scots pine, and even slightly reverted, i.e. increasing EWD and LWD for Norway spruce.

As not only the densities of early wood and late wood but also their shares in a growth ring explain mean wood density, it is worth looking at the trends we found for the early wood ratio (EWR, Eq. (4), see Table A.8 for parameter estimates). In contrast to MWD, EWD, and LWD, far less of the considered explaining variables were significant, with calendar year being the only significant variable across all species. For Norway spruce and sessile oak the regression models indicate a clear increase of EWR with time, while the same main effect in Scots pine is counteracted by a significant interaction of calendar year and ring width (Table A.8). With European beech in contrast, we observe an unambiguous tendency of decreasing EWR with time. For the standard tree (dbh = 25 cm, ring width = 2 mm), Fig. 2d depicts only a slight decrease of the EWR in Scots pine (about 0.65 down to 0.62), and a more pronounced decrease (0.55 to 0.45) in European beech. Norway spruce, in contrast had a very strong increase of EWR from about 0.55 up to 0.70. On the low EWR level which is typical for a ring-porous wood, we also see a pronounced EWR increase with time for sessile oak (0.20 up to 0.32).

Considering a smaller ring width of 1 mm/a (Fig. 3d) shows the same increasing EWR trend for Norway spruce and sessile oak, however, on a higher level for oak and a lower level for spruce. For broader ring widths (3 mm/a, Fig. 4d), we observe again the same trend – increasing EWR with calendar year – however on a high level for Norway spruce and on a low level for sessile oak. Having low EWR with broader growth rings in general is typical for ring-porous species like oak, while the opposite as observed for Norway spruce is typical for coniferous species.

Compared to the standard tree with a growth ring width of 2 mm/a the EWR time trend is more complex for Scots pine. When growth rings are narrow (1 mm/a), EWR is slightly increasing with the calendar year (Fig. 3d), but pronouncedly decreasing for broader rings (3 mm/a, Fig. 4d). European beech, in contrast, as to be expected from a diffuse-porous wood, shows virtually the same time trend, independent from the growth ring width (Figs. 2d, 3d, 4d).

Thus, EWR turns out as an important driver for the time trend and general level of mean wood density in Norway spruce and sessile oak. Albeit the early wood density (EWD) does decrease with time for both species only when narrow growth rings are narrow (Fig. 3b) and even slightly increase for broader growth rings (Fig. 4b), it is considerably lower than late wood density (LWD). Thus, an often decreasing density of LWD is complemented with an increasing share of low-density early wood.

For Scots pine decreasing EWR only slightly counteracts the overall trend of decreasing mean wood density in case of the standard tree. For narrow growth rings in Scots pine the increasing EWR seems to be behind the decreasing overall wood density (Fig. 3), while its decrease with time is part of the mechanism that keeps mean wood density constant for broader growth rings (Fig. 4). Mostly independent from the ring width, the decreasing EWR of European beech does not cancel out the general decrease of mean wood density over time.

Recently reported growth trends in European forests by Pretzsch et al. (2014b) were measured in (above ground) wood volume, not in wood biomass. The results of this study suggest that, due to time trends in wood density, such results must not be straightforwardly considered to be the same for (above ground) wood biomass. As Pretzsch et al. (2014b) also show trends for mean stand diameter growth (Fig. 5a, e), our mean wood density models obtained for Norway spruce and European beech by fitting Eq. (1) can be used for estimating a typical mean stand tree's mean wood density MWD growing under the conditions of 1900, 1960, and 2000 (corresponding to Pretzsch et al., 2014b). This is shown in Fig. 5b (Norway spruce) and 5f (European beech). While MWD increases only slightly with tree age for spruce, this age trend is much stronger for beech, but this age trend takes place on pronouncedly decreasing levels of MWD from 1900 to 2000. As a consequence of the previously presented results (Table 2, Figs. 2–4) the calendar year trend in MWD visible in Fig. 5b and f is stronger for European beech compared to Norway spruce.

As evident from Fig. 5c and 5g, the MWD trend does not cancel out the growth trends of stand volume increment when periodical annual stand biomass increment PAIW is considered. When the decreasing wood density is taken into account, however, the PAIW trend is considerably dampened compared to the assumption that there is no calendar year trend in wood density since 1900. In numbers, a 75 year old typical Norway spruce stand would, under the conditions of 2000 have its PAIW accelerated by 29% compared to 1900 without any calendar year trend in wood density. This acceleration is reduced to 20%, i.e. by 9 percentage points, when the actual wood density trends are taken into account. For European beech the analogous numbers are 100% (PAIW acceleration with trend-free wood density), 76% (PAIW acceleration with time trend in wood density), and 24 percentage points of reduced acceleration.

The same is true for standing wood biomass (Fig. 5d, 5h). Without a time trend in wood density, a 75 year old spruce stand growing under the conditions of 2000 would accumulate 19% more biomass compared to such a stand growing under the conditions of 1900. Applying the time trends identified in this study, this increased accumulation reduces to 10%, i.e. 9 percentage points less. When applied to European beech, the same assumptions lead to 35% (increased accumulation without trends in wood density), and 19% (increased accumulation with time trend in wood density) which means a slow-down by 16 percentage points.

When applied to the above ground wood biomass and biomass increment of a typical mean stand tree (Fig. A.8), the dampening effects obviously show the same tendency; due to the very strong volume growth trends on the mean tree level found by Pretzsch et al. (2014b), their absolute effect is less strong than on the level of the whole stand. Although the calendar year trends of wood density are small compared to the volume growth trends reported in the above-mentioned study, they are not negligible. The values given in Table 2 and the fitted models shown in the study at hand might be useful when correspondent corrections are required.

4. Discussion

4.1. Generalizability of the identified trends

As mentioned in the Materials and Methods section, the site and climate conditions covered by our plots represent the typical environments where the four tree species of interest are growing in Central Europe. Thus, we are confident that the informative value of our results is not limited to the plot locations as shown in Fig. A.1. As they are, the plots are distributed across an area of roughly 7,000,000 ha. We deem it quite improbable that such consistent results obtained under typical Central European conditions would not be valid for the rest of Central Europe as well. Nonetheless, we strongly suggest similar studies with a wide spatial scope, maybe coupled to the spatial design of existing National Forest Inventories, although there is usually not much known about the treatment history, if at all. However, as we can exclude treatment effects as possible reasons for the trends in wood density, this would strongly support that similar findings from such designs are due to environmental changes as well.

Our models suggest that the trend of declining wood density is strongest for narrow and lowest for broad growth rings. From the model parameters for mean wood density (Table A.5), it can be derived that the interaction effect of calendar year and ring width cancels the trend of decline at ring widths of about 3 mm/a for Norway spruce and Scots pine, almost 4 mm/a for European beech and more than 8 mm/a for sessile oak. As can be taken from Fig. 1, the span of ring widths up to these critical values covers about ¾ of the data for Norway spruce and almost the whole data set for the other three species. As our models are linear in structure, they suggest an increasing wood density trend with the calendar year for growth ring widths beyond these values. However, if this is a real trend, it is only relevant for a small share of the data, and probably an artifact due to the simplification coming along with linear models; when studying literature for possible reasons for our findings (see below), we did not find any hint for such a trend inversion.

In any case, as the strength of the wood density effect depends on ring width, this raises a highly interesting issue: It should be possible to mitigate or even cancel out the wood density decline on single tree level by maintaining low stand densities, i.e. heavy thinnings that cause broad growth rings in the remaining trees. However, lower stand densities will at some point lead to pronouncedly reduced productivity on stand level. Such tradeoffs might be explored by way of simulation studies with dynamic forest growth models where wood density trends have been incorporated.

4.2. Growth and growth trend analyses so far mostly based on tree and stand volume growth

Numerous studies show substantial effects of climate change on the growth of forest systems (Bussotti et al., 2014; Pretzsch et al., 2014b; Reyer et al., 2014; Boisvenue and Running, 2006; Keenan, 2015). Kauppi et al. (2014) stated an increased tree and stand growth in boreal forests, Fang et al. (2014) in Japanese forests and Pretzsch et al. (2014b) and Spiecker et al. (1996) in temperate forests in Central Europe. Similar findings for tropical forests were reported by Lewis et al. (2009), and Baker et al. (2004). Obviously, there is a change in environmental conditions fostering growth up to date regardless of climate zone and land classification. Global warming (Pachauri et al., 2014), going along with an extension of the growing season (Chmielewski and Rötzer, 2001), higher atmospheric CO_2-concentration (Pachauri et al., 2014; Churkina et al., 2010) and fertilization through N-deposition (Churkina et al., 2010) are discussed as possible drivers. Fig. 6, taken from Pretzsch et al. (2014b), illustrates these trends for average Central European conditions. Despite possible negative effects of global change on tree growth, such as drought events which reduce tree and stand growth (Hartmann, 2011; Pretzsch and Dieler, 2011; Rötzer et al., 2013), or even cause a die off (Griess and Knoke, 2011; McDowell et al., 2008), beneficial effects seem to predominate trees' growth reactions so far.

All those studies of growth trends were based on tree and stand volume growth. However, a series of papers (Bouriaud et al., 2005; Franceschini et al., 2010, 2012; Jacoby and D'Arrigo, 1995) discussed effects of climate change also on the wood density of trees. We base this study of wood density partly on the same long-term experiments which were used before to substantiate accelerated stand volume growth in Central Europe since 1870 (Pretzsch et al., 2014b). In this way we can show that the volume growth increase since 1900 (in terms of periodical annual volume increment) of Norway spruce since 1900 (+19%), (+35%) is coupled with a decrease of wood density by 7.7% and 11.8% for Norway spruce and European beech, respectively. Additional studies (Pretzsch, 2016; Pretzsch et al., 2014a) suggest similar volume growth accelerations for sessile oak and Scots pine which, according to the results at hand, go together with wood density reductions of 11.2% (sessile oak) and 5.4% (Scots pine).

For all these analyses we chose fully stocked stands which were always unthinned or not more than moderately thinned, young and old stands on the same sites, and in several cases even initial and subsequent stands of the same provenance. Thus, we can largely exclude other factors than environmental changes as causes for the revealed increase of volume growth and decrease of wood density. We further statistically eliminated the species-specific effects of growth ring width and tree size on wood density. Thus, we can show considerable trends also in terms of biomass growth and carbon sequestration since 1900 (see above); the earlier reported volume growth trends (Pretzsch, 2016; Pretzsch et al., 2014a, 2014b) are counteracted by decreasing wood density. But, as shown above, the volume increase strongly exceeds the decrease of wood density, resulting still in substantially accelerated biomass growth.

Beyond assessing growth for quantifying impacts of environmental changes, our results indicate that volume based forest productivity assessments must be done with caution. Ceteris paribus, the same volume growth in cubic meters per ha and year means a lower productivity in primary units like tons of biomass per ha and year today compared to decades earlier. E.g. when developing quantitative models for understanding forest productivity (cf. Keeling and Phillips, 2007) using volumes instead of the produced mass itself must be expected to yield biased results. This is especially true, when observations from long-term experiments which cover time spans of several decades and more are pooled. The same considerations apply when working on the principles of plant allometry (Ernest et al., 2003), or ecological theory, the dynamics of interspecific competition and facilitation (Kelty, 2006; Vanclay, 2006) and ecophysiological stress reactions (Bréda et al., 2006) being promiment examples.

4.3. Causes for the decreasing wood density

In our study region atmospheric CO_2-concentrations rose from 295 ppm in 1901 to 390 ppm in 2010 (Churkina et al., 2010; Solomon et al., 2007). Throughout Central Europe, the average N-deposition increased from approximately 2.5 kg ha^{-1} yr^{-1} in 1900 to more than 9 kg ha^{-1} yr^{-1} in the first decade of the 21st century (Fig. 6a, Churkina et al., 2010). During the 20th century, mean annual air temperature and annual precipitation increased by 1.0 °C and 9%, respectively (Fig. 6a, Matyssek and Sandermann, 2003). Temperature data indicated the length of the growing season throughout Central Europe increased during the last 110 years by 22 days (Fig. 6b). Based on statistical evaluations and model calculations Pretzsch et al. (2014b) explained the volume growth acceleration mainly by the present rise in temperature, extended growing season and improved nitrogen supply via atmospheric deposition.

We hypothesize that the decrease of wood density is mainly caused by the significant increase of N-deposition from the late 19th to the early 21st century together with the increase of temperature and the length of the growing season. From many fertilization trials it is well known that added nitrogen supply can strongly reduce wood density (Jozsa and Brix, 1989; Cao et al., 2008; Mäkinen et al., 2002). Lundgren (2004) reported reductions in wood density of Norway spruce by 30 kg/m^3 after thinning, which are very similar to our finding for spruce of about 35 kg/m^3 since 1900. Less probable is an effect of the increased CO_2 concentration; many studies showed no (Norby et al., 2002) or even positive effects (Kilpeläinen et al., 2005) of an elevated CO_2 concentration on wood density. Precipitation effects are rather unlikely as well, because precipitation did not substantially change within the last century (Fig. 6a). However, temperature effects on wood density in general and late wood density in particular are well known (Bouriaud et al., 2005; Thomas et al., 2004; D'Arrigo et al., 1992). Our observation that decreasing late wood densities strongly contribute to the overall wood density decrease supports the idea of increasing temperatures as an important driver in addition to fertilization effects due to Nitrogen deposition. The latter is in line with Franceschini et al. (2010) who analyzed wood density trends throughout the 20th century and found a decrease by 5% for Norway spruce which is in the same order of magnitude as our results (Table 2).

4.4. Potential influences of secondary wood property changes

Despite the strong arguments for steadily increasing N-depositions and temperatures as the main cause for the decreasing trend in wood density mentioned in the previous paragraph, one could argue that secondary wood property changes are the real reasons for our observations. One could hypothesize that the transition from sapwood to heartwood, occurring years or decades after ring formation, goes along with a considerable increase of wood density. This would, however, be an exception, not the rule (Desch and Dinwoodie, 1981, p. 76). We found no publication that would report such effects for the species in focus of this study in a relevant order of magnitude. While Vansteenkiste et al. (2007) observe mineral inclusions partly occurring during the heartwood formation of Sessile oak, they also mention that typically the inorganic mass share of woods from temperate zones is 1% at maximum. Thus, the density variation caused by such effects can be hardly the reason for the trends we show in this study.

From a methodological point of view, telling apart such tree-internal effects from external calendar year related effects would require adding the actual age of a tree ring, i.e. the time elapsed since its formation, into our statistical models. However, as all trees used in this study were sampled at the same time (after the end of the growth period 2014), this definition of ring age is just a linear transformation of the variable calendar year. As such, it is neither technically feasible nor logically reasonable to add it into the models. Consequently, from a mere technical point of view, a distinction between both kinds of effects is not possible with our data. However, significant density changes due to heartwood formation would not happen continuously over time, so that the oldest ring always had the highest density, but during the short period when a sapwood ring becomes heartwood. Therefore, neither inside the heartwood, nor inside the sapwood there should be meaningful ring age effects, just potentially a density jump from sapwood to heartwood. For none of the investigated tree species we did find such patterns of abrupt wood density changes in our data. While literature, as shown above, strongly supports the hypothesis of Nitrogen and temperature effects, tree internal wood ageing effects as potential reasons are supported neither by our data nor by literature.

We should mention that a large body of literature reports wood density trends related to the *cambial age* of the tree rings. However, the cambial age of an annual tree ring is its number counted from the pith and as such not at all an indicator for the age of the wood. E.g. Diaconu et al. (2016), and Franceschini et al. (2010) report slight density increases with increasing cambial age, while Bouriaud et al. (2004) find the opposite trend. As our models include the stem diameter, which closely correlates with cambial age, as a fixed effect, and a tree level random effect in addition, all such phenomena are taken into account with our approach.

4.5. Consequences for the mechanical stability of trees and forests stands

A decrease of wood density generally means a higher risk of forest damage by snow (Peltola et al., 1999) and wind (Meyer et al., 2008; Dunham and Cameron, 2000; Putz et al., 1983). The lower the wood density, the weaker the wood in terms of stiffness (Evans and Ilic, 2001; Lachenbruch et al., 2010) and strength (Hoffmeyer and Pedersen, 1995), which both are essential for mechanical stability and risk prevention of individual trees (Pretzsch and Rais, 2016). A reduction of overall wood density by 5.4–11.9 % and of late wood density by 4.2–12.1 % since 1900 suggests a substantial decrease in mechanical stability and increase of susceptibility to damage while Schelhaas et al. (2003) showed a strong increase of snow and storm damage in European forests for the same time period. Experiments (Gardiner et al., 1997) as well as simulation studies (Cucchi et al., 2005) demonstrate the significant role of wood density for mechanical tree stability. Thus, decreasing mechanical stability might, among others, be one important reason for the fact that forest damages by natural disturbances increase. For such a vulnerable species as Norway spruce damage-induced harvests already amount up to 50% of the total harvest (Schröpfer et al., 2009). If decreasing wood densities are indeed an important reason for the increasing damages, then even higher risks have to be expected in the future. The mature trees of today have accumulated more dense and therefore more stable wood during the past decades, while the young trees of today already begin their growth under conditions which induce lower wood density and therefore less mechanical stability. Besides, if storm damages become more frequent, this will reduce the mean carbon stock on landscape level. Such an effect of reduced wood densities might become a strong counteracting factor against carbon stock accumulation due to accelerated forest growth.

4.6. Timber and bioenergy use

In North America and Europe, approximately 15% of the harvested timber is used for energy production. According to the Food and Agriculture Organization of the United Nations (FOREST EUROPE et al., 2011), the majority of harvested wood, however, goes to the industry to produce sawn timber and veneers (approximately 60% in North America and Europe). The reduction of stiffness and strength as a consequence of the decrease of wood density by 5.4–11.9 % applies especially for construction and furniture wood (Lachenbruch et al., 2010; Hoffmeyer and Pedersen, 1995). In addition to the general decline of technical wood properties with lower density, the decreasing homogeneity within wood products due to the observed trends in wood density may create problems for many kinds of usage (Pretzsch and Rais, 2016).

In case of laminated wood products these disadvantages may be eliminated; however, the general tendency towards slim and solid wood products in architecture may be challenged (Schulz et al., 1988). The 11.2% wood density decrease of European beech calls for special attention. Because of the transition to close-to-nature forests with high shares of European beech (Ammer et al., 2008; Pretzsch et al., 2010), wood quality and wood utilization of this species will become an important issue in the coming decades (Hapla and Militz, 2008; Schmidt and Glos, 2010). In some cases there might be also positive trade-offs of the decreasing density for wood utilization; production of sliced veneer from oak wood requires low density and will benefit by the decrease of wood density and increase of soft early wood proportion (Zhang et al., 1993).

In view of the present tendency to use wood more and more for energy supply the decreasing wood density means less calorific and thermal value per unit volume. Compared with the reference year 1900 a cubicmeter of wood has by 32–94 kg less mass at present. Except minor species specific variations (Lamlom and Savidge, 2003) the C content of wood is approximately 50% (Thomas and Malczewski, 2007). As both, the calorific value and thermal value of wood are proportional to the C content (Hartmann et al., 2009) the decrease of wood density by 5.4–11.9 % applies also to the energy content. In this regard the percent values given in Table 2 may be used as reduction factors for calculating unbiased species-specific calorific and thermal values based on volume yield.

4.7. Consequences for C-sequestration

Based on their findings about accelerated wood volume increment Pretzsch et al. (2014b) roughly estimated the sequestration rate assuming an additional annual volume growth of 3 m^3/ha/a (~0.75 tC) on the 45 × 10^6 ha area, which is about the forest-covered area of Central Europe. This is equivalent to 34 × 10^6 tC additionally sequestrated per year. The relative wood density reductions given in Table 2 translate into a wood density decrease of about 8% from 1900 to the present day, given the above-mentioned area shares of the investigated four species in Central Europe. For including this wood density decrease, we assume that, since 1900, the annual wood volume increment increased (by 3 m3/ha/a) from 8 to 11 m^3/ha/a (which is the current value reported by the latest German Federal Forest Inventory, covering a large share of Central Europe's forests). So, under the conditions of

1900 the annual carbon sequestration would be $8\,m^3/ha/a \times 0.25\,tC/m^3 \times 45 \times 10^6\,ha = 90 \times 10^6\,tC/a$. Under recent conditions, without any wood density reduction however, we would expect $11\,m^3/ha/a \times 0.25\,tC/m^3 \times 45 \times 10^6\,ha \approx 124 \times 10^6\,tC/a$, the difference being $124 \times 10^6\,tC/a–90 \times 10^6\,tC/a = 34 \times 10^6\,t\ C$ as mentioned above. However, if we reduce the value for recent conditions by 8%, accounting for the decreased wood density, the result is $124 \times 10^6\,tC/a \times (1–0.08) \approx 114 \times 10^6\,tC/a$ only. The additional amount of C sequestrated due to the increased volume growth therefore decreases to $114 \times 10^6\,tC/a–90 \times 10^6\,tC/a = 24 \times 10^6\,tC/a$ in contrast to the originally estimated $34 \times 10^6\,tC/a$. Despite the roughness of these estimates they show nevertheless that the identified time trends of wood density are not negligible for the purpose of forest carbon balance calculations with other than short term-scope.

5. Conclusions

Our study suggests that the identified trend in wood density is an area-wide phenomenon. Based on fully stocked long term plots we could exclude silvicultural treatment as the reason behind. This clarified should encourage further studies to sample trees from systematic large-area forest inventories to statistically investigate such trends from regional up to national or even larger levels. This would be important for considering about how to cope with the implications for forest science, silviculture, and wood utilization as discussed above.

Author contributions

HP initiated the study, interpreted the data and wrote the paper. PB performed the statistical analyses, interpreted the data and wrote the paper. GS compiled the data. JK conducted the sampling, wood density measurements and contributed to the statistical analyses. EU contributed to the sampling, interpreted the data and revised the manuscript.

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Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Appendix A

See Figs. A1–A9 and Tables A1–A8.

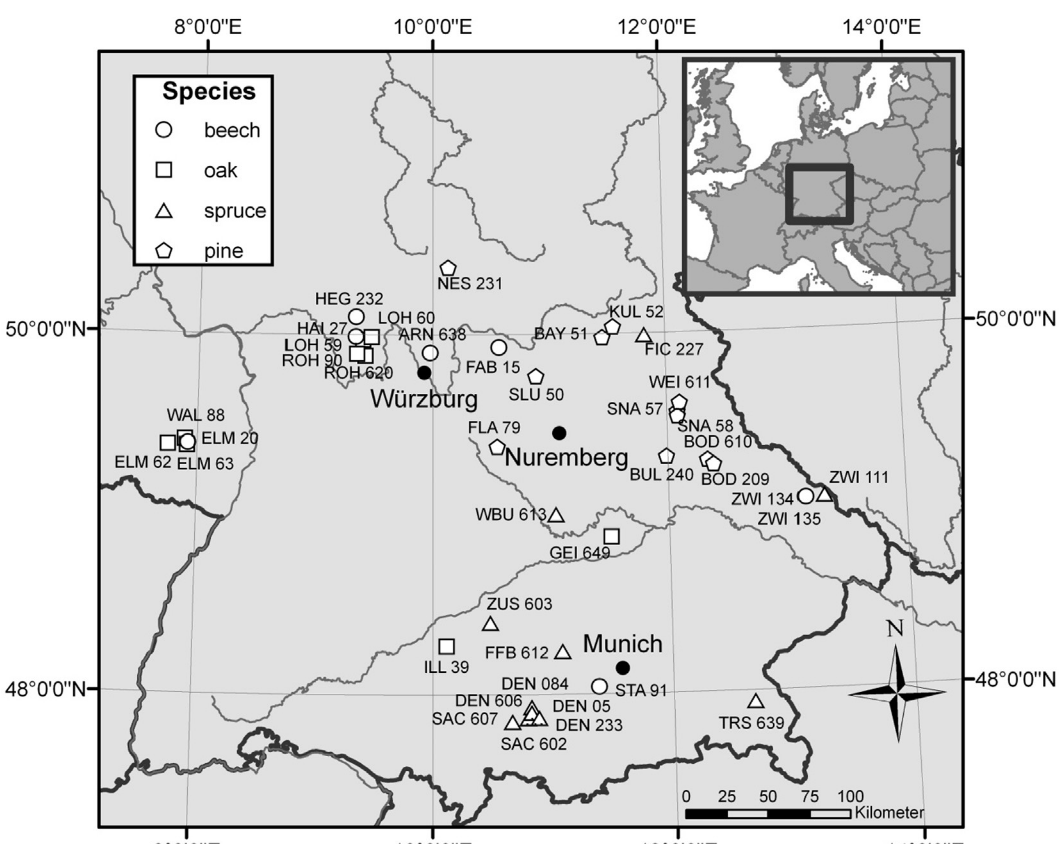

Fig. A.1. Locations of the long-term growth and yield trials sampled in this study.

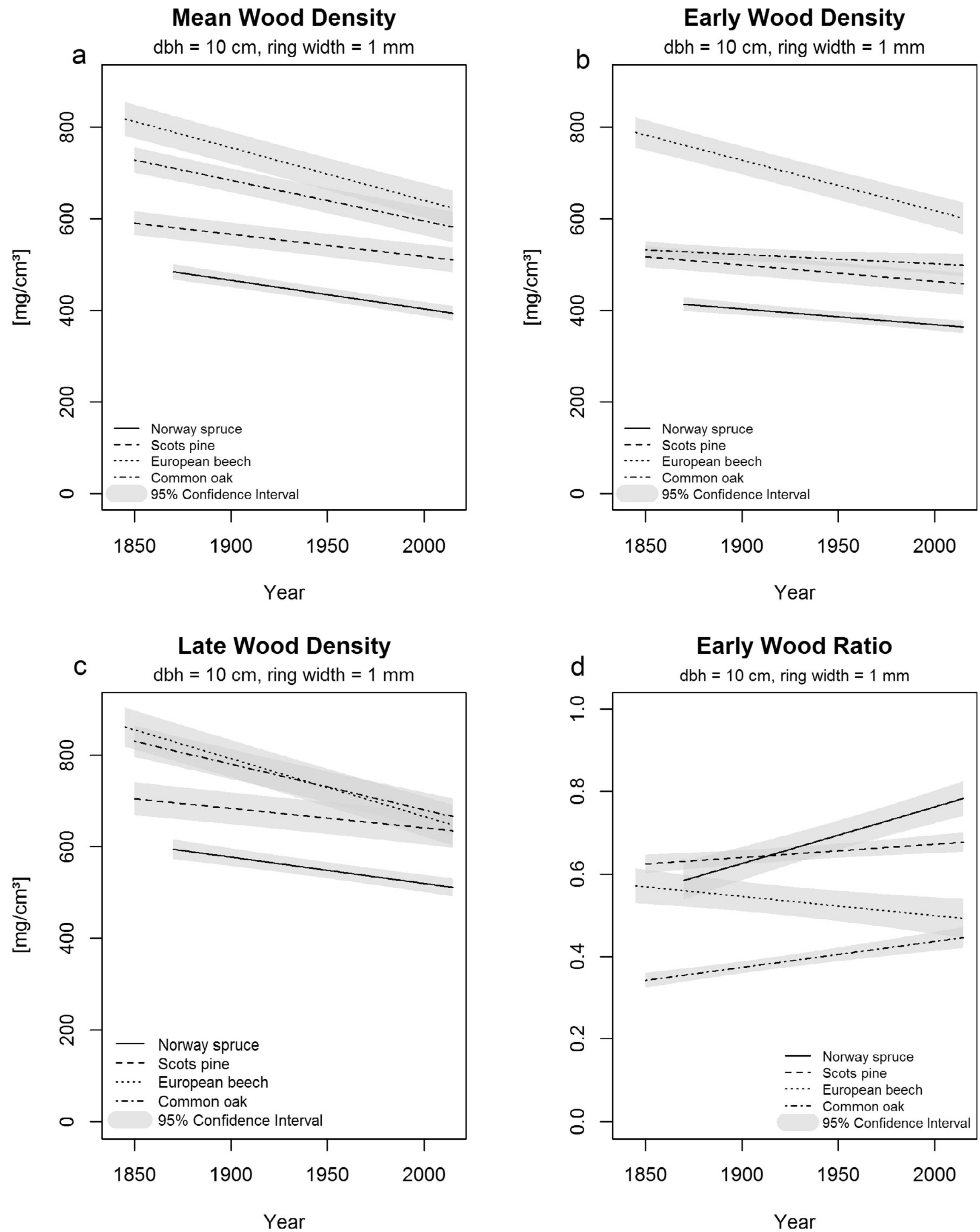

Fig. A.2. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 10 cm and 1 mm/a.

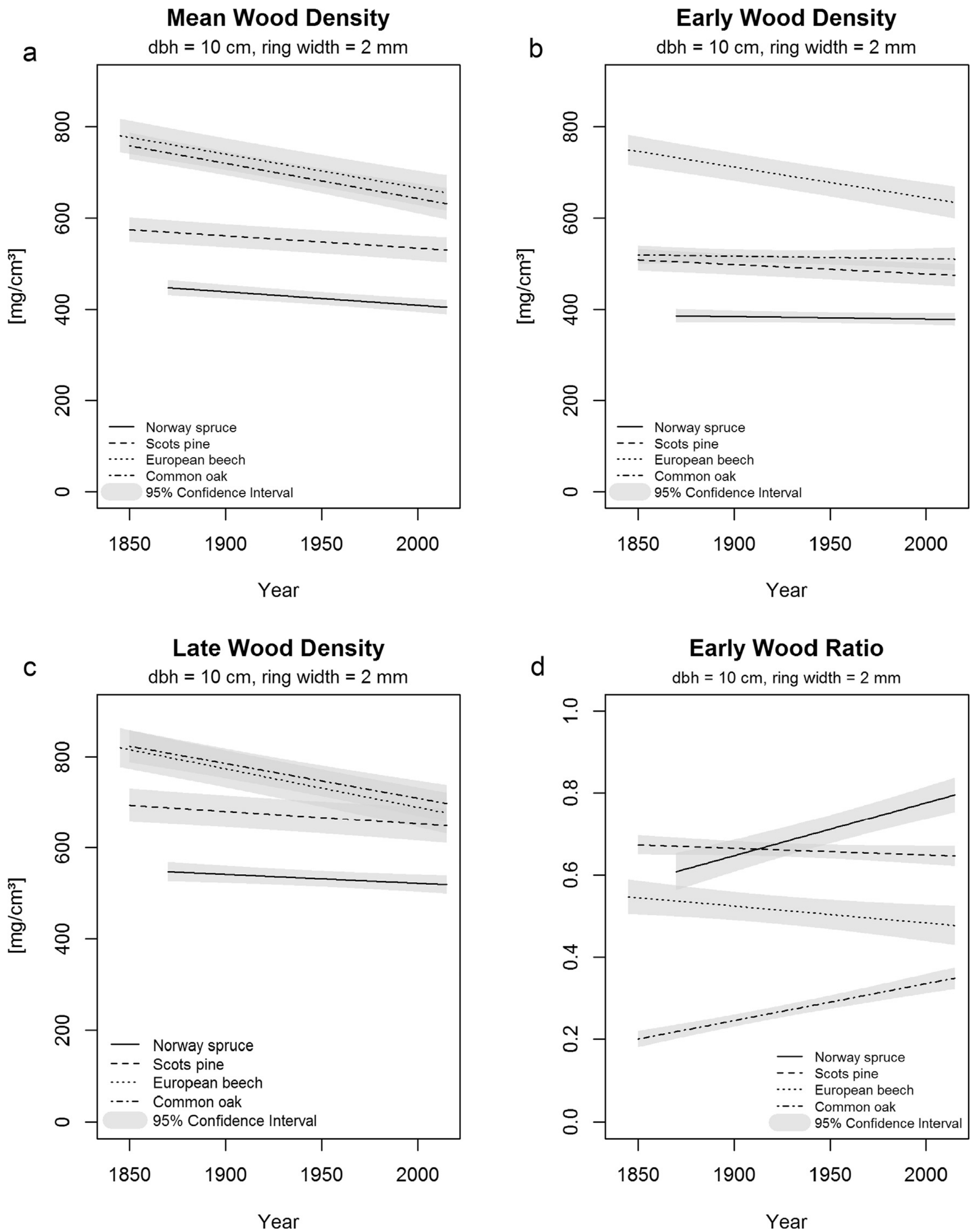

Fig. A.3. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 10 cm and 2 mm/a.

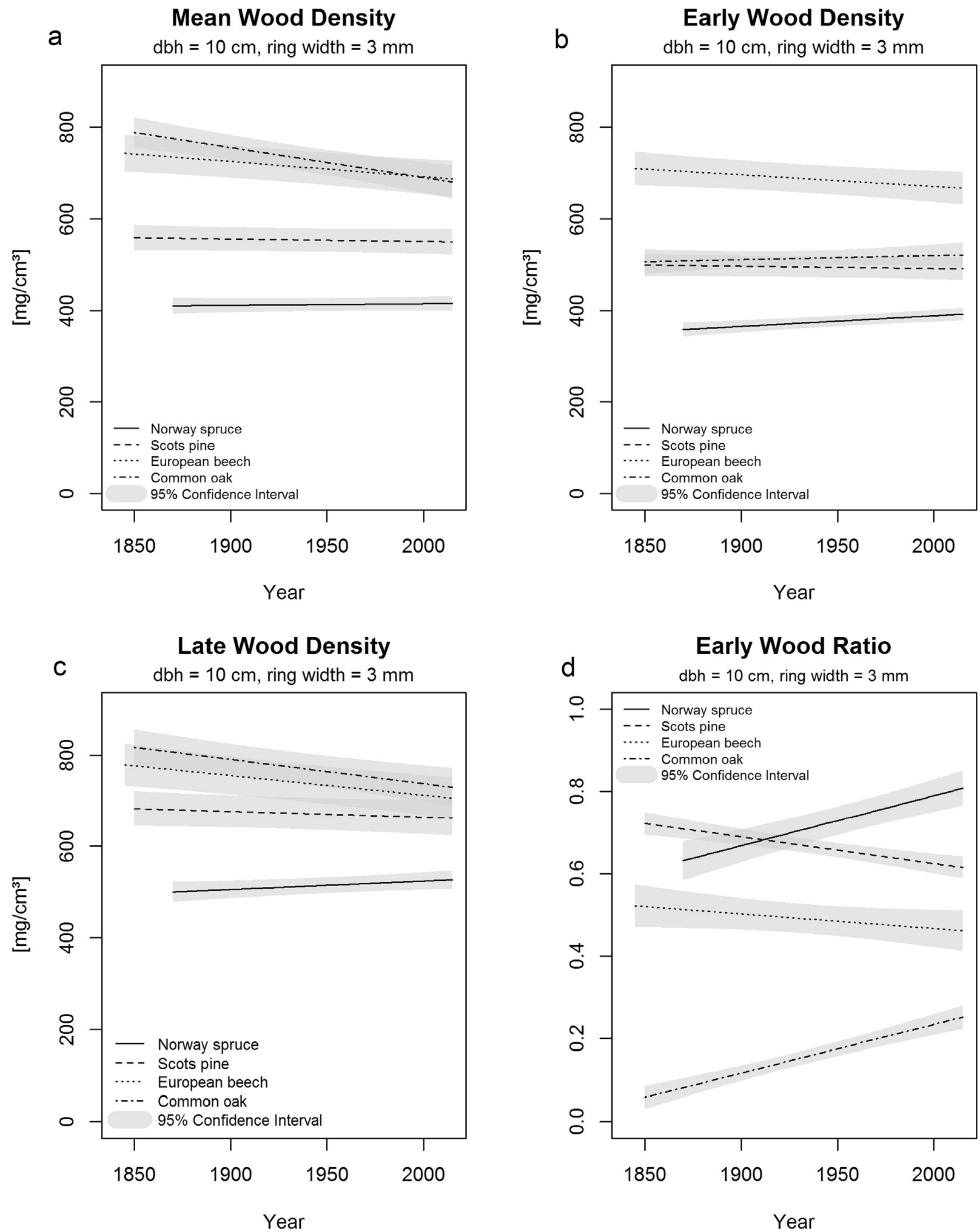

Fig. A.4. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 10 cm and 3 mm/a.

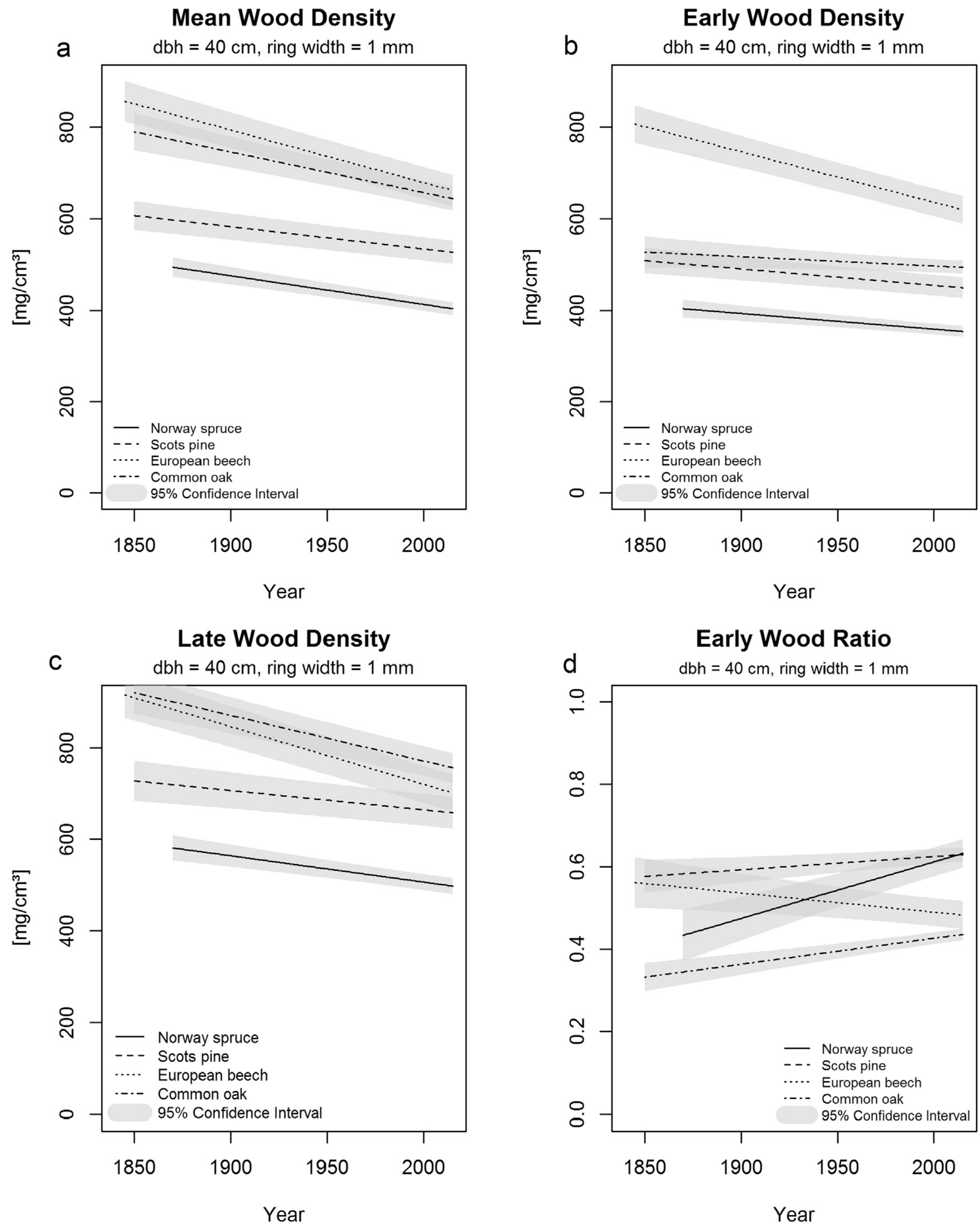

Fig. A.5. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 40 cm and 1 mm/a.

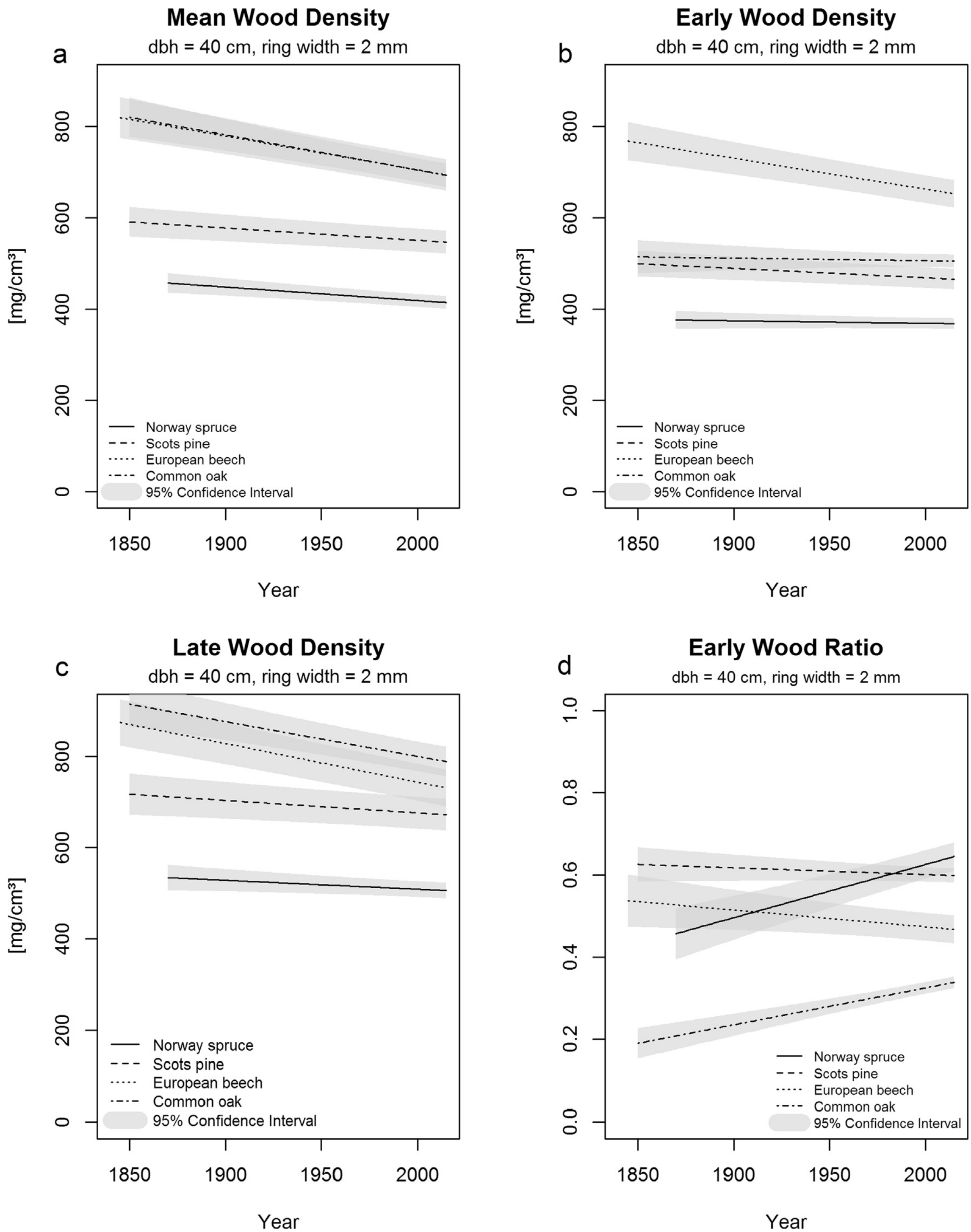

Fig. A.6. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 40 cm and 2 mm/a.

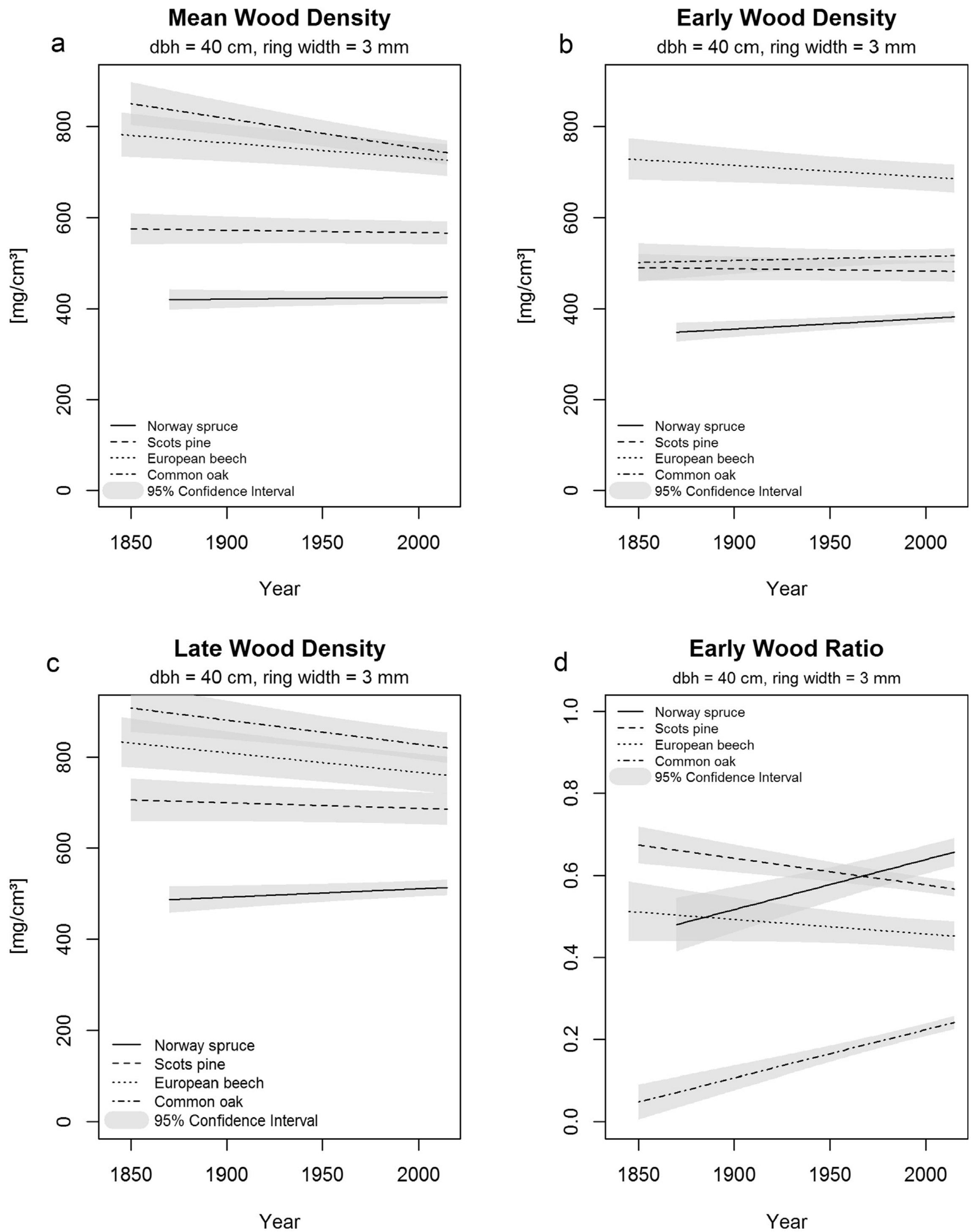

Fig. A.7. Time related development of the four wood density related variables Mean Wood Density (a), Early Wood Density (b), Late Wood Density (c), and Early Wood Ratio (d) as described with the mixed linear models fitted in this study (Eqs. (1)–(4)). Tree diameter at breast height (dbh) and growth ring width were kept constant at 40 cm and 3 mm/a.

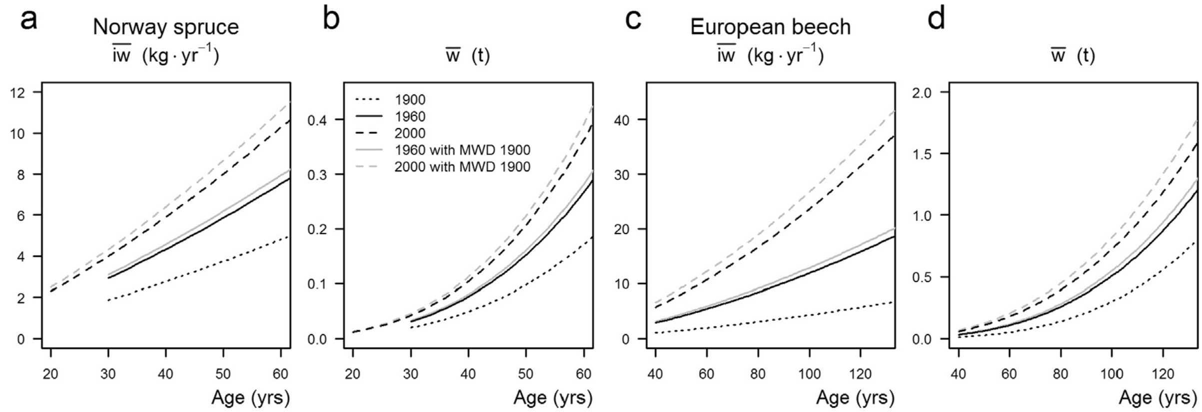

Fig. A.8. Conversion of mean stand tree volume growth trends reported by (Pretzsch et al., 2014b) into above ground wood biomass. Mean tree biomass increment $\overline{iw}$ (a: Norway spruce, c; European beech). Mean tree biomass $\overline{w}$ (b: Norway spruce, d: European beech). Black lines consider the effect of the observed trends of mean wood density on $\overline{iw}$ and $\overline{w}$. Grey lines indicate the same trends assuming mean wood density MWD keeping the same levels as in 1900, i.e. no trends in MWD.

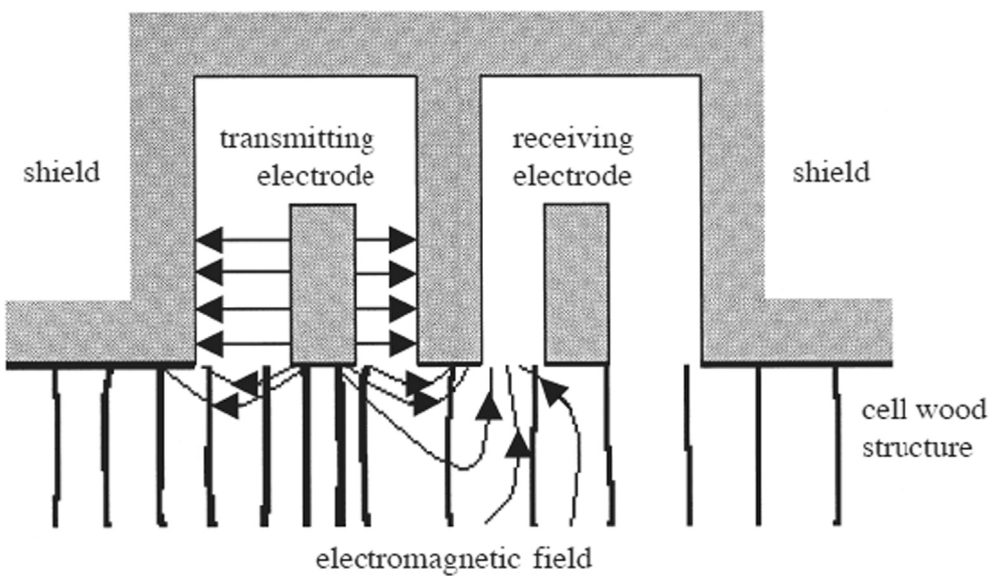

Fig. A.9. Schematic representation of the electrode system used for high frequency wood densiometry in the LIGNOSTATION™ (after Spiecker et al., 2003).

Table A.1
Geographic locations, altitude above sea level, and stand age at sampling time (2014) of the plots sampled in this study.

Observational plot: location/plot number	Species	Eastern Longitude (°)	Northern Latitude (°)	Altitude (m a.s.l.)	Stand age at sampling time (years)
Denklingen 5/1	Norway spruce	10.842	47.871	780	167
Denklingen 84/2		10.835	47.870	780	134
Zwiesel 111/5		13.308	49.069	765	119
Zwiesel 134/4		13.271	49.065	725	103
Fichtelberg 227/3		11.824	49.994	750	111
Denklingen 233/1		10.786	47.873	790	116
Sachsenried 602/1		10.760	47.852	820	52
Zusmarshausen 603/2		10.480	48.397	510	51
Denklingen 606/3		10.824	47.869	750	61
Sachsenried 607/3		10.823	47.867	775	61
Fürstenfeldbruck 612/19		11.085	48.236	540	45
Weißenburg 613/2		11.038	49.003	560	98
Traunstein 639/1		12.673	47.940	590	45
Schlüsselfeld 50/1	Scots pine	10.884	49.769	320	141
Bayreuth 51/1		11.459	49.980	355	171
Kulmbach 53/2		12.552	50.039	370	154
Schnaittenbach 57/1		12.088	49.559	395	157

(continued on next page)

Table A.1 (*continued*)

Observational plot: location/plot number	Species	Eastern Longitude (°)	Northern Latitude (°)	Altitude (m a.s.l.)	Stand age at sampling time (years)
Schnaittenbach 58/2		12.089	49.536	397	148
Flachslanden 79/2		10.549	49.379	470	128
Bodenwöhr 209/13		12.335	49.290	380	125
Neustadt 231/2		10.133	50.375	440	109
Burglengenfeld 240/1		11.986	49.313	445	108
Bodenwöhr 610/2		12.385	49.263	393	62
Weiden 611/3		12.108	49.610	398	44
Fabrikschleichach 15/1	European beech	10.571	49.962	470	192
Elmstein 20/1		7.919	49.391	400	194
Hain 27/1		9.336	49.992	420	182
Starnberg 91/2		11.378	48.039	620	87
Zwiesel 111/4		13.308	49.069	765	138
Zwiesel 135/1		13.269	49.065	695	86
Heigenbrücken 232/4		9.342	50.096	480	127
Arnstein 638/1		9.978	49.905	330	75
Illertissen 39/1	sessile oak	10.115	48.270	520	172
Lohr 59/1		9.400	49.973	460	180
Lohr 60/1		9.473	49.988	500	156
Elmstein 62/1		7.893	49.410	430	152
Elmstein 63/1		7.911	49.375	430	152
Waldleiningen 88/2		7.750	49.379	420	128
Rohrbrunn 90/1		9.422	49.884	475	150
Rohrbrunn 620/4		9.350	49.895	450	88
Geisenfeld 649/5		11.506	48.872	475	31

Table A.2
Long-term climate data of the trials sampled in this study.

Observational plot: location/plot number	Species	Mean annual precipitation (mm)	Mean annual temperature (°C)	De Martonne Aridity index
Denklingen 5/1	Norway spruce	1110	6.8	66.1
Denklingen 84/2		1110	6.8	66.1
Zwiesel 111/5		1369	5.7	87.2
Zwiesel 134/4		1369	5.7	87.2
Fichtelberg 227/3		1073	5.9	67.5
Denklingen 233/1		1110	6.8	66.1
Sachsenried 602/1		1200	6.2	74.1
Zusmarshausen 603/2		800	7.5	45.7
Denklingen 606/3		1110	6.8	66.1
Sachsenried 607/3		1110	6.8	66.1
Fürstenfeldbruck 612/19		830	7.5	47.4
Weißenburg 613/2		800	7.0	47.1
Traunstein 639/1		1200	7.3	69.4
Schlüsselfeld 50/1	Scots pine	669	8.4	36.4
Bayreuth 51/1		676	7.7	38.2
Kulmbach 53/2		697	7.7	39.4
Schnaittenbach 57/1		650	7.0	38.2
Schnaittenbach 58/2		650	7.0	38.2
Flachslanden 79/2		680	8.0	37.8
Bodenwöhr 209/13		644	6.9	38.1
Neustadt 231/2		760	7.5	43.4
Burglengenfeld 240/1		536	7.7	30.3
Bodenwöhr 610/2		644	6.9	38.1

(*continued on next page*)

Table A.2 (*continued*)

Observational plot: location/plot number	Species	Mean annual precipitation (mm)	Mean annual temperature (°C)	De Martonne Aridity index
Weiden 611/3		676	7.5	38.6
Fabrikschleichach 15/1	European beech	820	7.5	46.9
Elmstein 20/1		780	8.0	43.3
Hain 27/1		1080	7.0	63.5
Starnberg 91/2		1040	7.5	59.4
Zwiesel 111/4		1369	5.7	87.2
Zwiesel 135/1		1369	5.7	87.2
Heigenbrücken 232/4		1160	7.0	68.2
Arnstein 638/1		670	8.0	37.2
Illertissen 39/1	sessile oak	850	7.5	48.6
Lohr 59/1		980	7.0	57.6
Lohr 60/1		1000	7.0	58.8
Elmstein 62/1		770	7.5	44.0
Elmstein 63/1		770	7.5	44.0
Waldleiningen 88/2		770	7.5	44.0
Rohrbrunn 90/1		1120	7.0	65.9
Rohrbrunn 620/4		1120	7.0	65.9
Geisenfeld 649/5		706	7.8	39.7

Table A.3
Ecoregions (after Arbeitskreis Standortskartierung, 1985) and soil properties of the growth and yield trials sampled in this study.

Observational plot: location/plot number	Species	Ecoregion	Sub-Ecoregion	Soil Texture	Soil type
Denklingen 5/1	Norway spruce	Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	parabrown soil-brown soil
Denklingen 84/2		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	pseudogley-parabrown soil
Zwiesel 111/5		Bayerischer Wald	Innerer Bayerischer Wald	loam	brown soil
Zwiesel 134/4		Bayerischer Wald	Innerer Bayerischer Wald	loam	brown soil
Fichtelberg 227/3		Frankenwald, Fichtelgebirge und Steinwald	Fichtelgebirge	loam	podsolized brown soil
Denklingen 233/1		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	parabrown soil-brown soil
Sachsenried 602/1		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	pseudogley-(para-) brown soil
Zusmarshausen 603/2		Tertiäres Hügelland	Mittelschwäbisches Schotterriedel- und Hügelland	sand	brown soil
Denklingen 606/3		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	parabrown soil-brown soil
Sachsenried 607/3		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	parabrown soil
Fürstenfeldbruck 612/19		Schwäbisch-Bayerische Schotterplatten und Altmoränenlandschaft	Landsberger Altmoräne	fine loam	parabrown soil
Weißenburg 613/2		Frankenalb und Oberpfälzer Jura	Südliche Frankenalb u. Südlicher Oberpfälzer Jura	loam	pseudogley-parabrown soil over terra fusca
Traunstein 639/1		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	pseudogley
Schlüsselfeld 50/1	Scots pine	Fränkischer Keuper und Alpenvorland	Nördliche Keuperabdachung	stratified loam	(pseudogley-) brown soil
Bayreuth 51/1		Oberfränkisches Triashügelland	Obermainhügelland	loam	brown soil over gley
Kulmbach 53/2		Oberfränkisches Triashügelland	Obermainhügelland	sand	podzolized brown soil
Schnaittenbach 57/1		Oberpfälzer Wald	Vorderer Oberpfälzer Wald	loamy sand	weak pseudogley
Schnaittenbach 58/2		Oberpfälzer Wald	Vorderer Oberpfälzer Wald	loamy sand	podzolized brown soil
Flachslanden 79/2		Fränkischer Keuper und Albvorland	Frankenhöhe	loamy sand	brown soil-pseudogley
Bodenwöhr 209/13		Oberpfälzer Wald	Vorderer Oberpfälzer Wald	sand	podzol
Neustadt 231/2		Fränkische Platte	Nördliche Fränkische Platte	stratified sand	podzol-brown soil and podzol
Burglengenfeld 240/1	Scots pine	Frankenalb und Oberpfälzer Jura	Oberpfälzer Jurarand	stratified loam	podzol-pseudogley
Bodenwöhr 610/2		Oberpfälzer Wald	Vorderer Oberpfälzer Wald	loamy sand	podzol-brown soil
Weiden 611/3		Oberpfälzer Becken- und Hügelland	Oberpfälzer Becken- und Hügelland	loamy sand	podzol
Fabrikschleichach 15/1	European beech	Fränkischer Keuper und Albvorland	Steigerwald	sandy loam	brown soil
Elmstein 20/1		Pfälzerwald	Mittlerer Pfälzerwald	loamy sand	brown soil
Hain 27/1		Spessart-Odenwald	Bundsandsteinspessart	sand	brown soil

(*continued on next page*)

Table A.3 (*continued*)

Observational plot: location/ plot number	Species	Ecoregion	Sub-Ecoregion	Soil Texture	Soil type
Starnberg 91/2		Schwäbisch-Bayerische Jungmoräne und Molassevorberge	Oberbayerische Jungmoräne u. Molassevorberge	loam	(para-) rendzina, parabrown soil
Zwiesel 111/4		Bayerischer Wald	Innerer Bayerischer Wald	loam	brown soil
Zwiesel 135/1		Bayerischer Wald	Innerer Bayerischer Wald	loam	brown soil
Heigenbrücken 232/4		Spessart-Odenwald	Bundsandsteinspessart	loam	brown soil
Arnstein 638/1		Fränkische Platte	Südliche Fränkische Platte	sande	(pseudogley) brown soil
Illertissen 39/1	sessile oak	Tertiäres Hügelland	Mittelschwäbisches Schotterriedel- und Hügelland	sandy loam	brown soil
Lohr 59/1		Spessart-Odenwald	Bundsandsteinspessart	sand	brown soil
Lohr 60/1		Spessart-Odenwald	Bundsandsteinspessart	sand	brown soil
Elmstein 62/1		Pfälzerwald	Mittlerer Pfälzerwald	loamy sand	brown soil
Elmstein 63/1		Pfälzerwald	Mittlerer Pfälzerwald	loamy sand	brown soil
Waldleiningen 88/2		Pfälzerwald	Mittlerer Pfälzerwald	loamy sand	brown soil
Rohrbrunn 90/1		Spessart-Odenwald	Bundsandsteinspessart	sand	(podsolized) brown soil
Rohrbrunn 620/4		Spessart-Odenwald	Bundsandsteinspessart	sand	(podsolized) brown soil
Geisenfeld 649/5		Frankenalb und Oberpfälzer Jura	Südliche Frankenalb u. Südlicher Oberpfälzer Jura	silty clayey loam	parabrown soil-pseudogley

Table A.4
Number of sampled trees per plot.

Observational plot: location/plot number	Species	Number
Denklingen 5/1	Norway spruce	5
Denklingen 84/2		8
Zwiesel 111/5		5
Zwiesel 134/4		10
Fichtelberg 227/3		9
Denklingen 233/1		10
Sachsenried 602/1		10
Zusmarshausen 603/2		20
Denklingen 606/3		10
Sachsenried 607/3		10
Fürstenfeldbruck 612/19		8
Weißenburg 613/2		15
Traunstein 639/1		7
		127
Schlüsselfeld 50/1	Scots pine	10
Bayreuth 51/1		9
Kulmbach 53/2		8
Schnaittenbach 57/1		10
Schnaittenbach 58/2		6
Flachslanden 79/2		10
Bodenwöhr 209/13		10
Neustadt 231/2		10
Burglengenfeld 240/1		10
Bodenwöhr 610/2		10
Weiden 611/3		10
		103
Fabrikschleichach 15/1	European beech	5
Elmstein 20/1		7
Hain 27/1		10
Starnberg 91/1		10
Zwiesel 111/4		6
Zwiesel 135/1		9
Heigenbrücken 232/4		6
Arnstein 638/1		10
		63
Illertissen 39/1	sessile oak	8
Lohr 59/1		6
Lohr 60/1		10
Elmstein 62/1		9
Elmstein 63/1		10
Waldleiningen 88/2		16
Rohrbrunn 90/1		10
Rohrbrunn 620/4		10
Geisenfeld 649/5		20
		99
		392

Table A.5
Mean Wood Density model fit results (Eq. (1)). Significant ($p < 0.05$) parameter estimates are printed in bold.

Norway spruce					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**2303.7850**	122.5576	0.0000
	YEAR	β_1	**−0.9549**	0.0629	0.0000
	RW	β_2	**−6.5370**	0.3328	0.0000
	DBH	β_3	**0.0328**	0.0132	0.0126
	*YEAR * RW*	β_4	**0.0033**	0.0002	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.0807		
	Plot	b_{ij}	20.5151		
	Tree	b_{ijk}	50.8185		
	Residual	ε_{ijkt}	39.1729		
Scots pine					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1901.1385**	104.3664	0.0000
	YEAR	β_1	**−0.7029**	0.0547	0.0000
	RW	β_2	**−4.1665**	0.3520	0.0000
	DBH	β_3	**0.0554**	0.0212	0.0090
	*YEAR * RW*	β_4	**0.0022**	0.0002	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	32.5923		
	Plot	b_{ij}	17.4543		
	Tree	b_{ijk}	63.9746		
	Residual	ε_{ijkt}	43.8186		
European beech					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**3713.7733**	195.4022	0.0000
	YEAR	β_1	**−1.5563**	0.1015	0.0000
	RW	β_2	**−7.9099**	0.8266	0.0000
	DBH	β_3	**0.1295**	0.0294	0.0000
	*YEAR * RW*	β_4	**0.0041**	0.0004	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	28.8959		
	Plot	b_{ij}	28.8959		
	Tree	b_{ijk}	57.2759		
	Residual	ε_{ijkt}	71.3210		
Sessile oak					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**2532.2835**	184.7845	0.0000
	YEAR	β_1	**−1.0026**	0.0977	0.0000
	RW	β_2	**−1.8473**	0.7803	0.0179
	DBH	β_3	**0.2066**	0.0372	0.0000
	*YEAR * RW*	β_4	**0.0012**	0.0004	0.0034
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.2488		
	Plot	b_{ij}	33.8098		
	Tree	b_{ijk}	71.6386		
	Residual	ε_{ijkt}	73.7837		

Table A.6
Early Wood Density model fit results (Eq. (2)). Significant ($p < 0.05$) parameter estimates are printed in bold.

Norway spruce					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1619.8793**	119.0345	0.0000
	YEAR	β_1	**−0.6289**	0.0611	0.0000
	RW	β_2	**−5.6429**	0.3248	0.0000
	DBH	β_3	**−0.0325**	0.0127	0.0107
	*YEAR * RW*	β_4	**0.0029**	0.0002	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.1531		
	Plot	b_{ij}	15.5329		
	Tree	b_{ijk}	46.9147		
	Residual	ε_{ijkt}	38.2798		
Scots pine					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1478.8574**	89.5437	0.0000
	YEAR	β_1	**−0.5135**	0.0469	0.0000
	RW	β_2	**−2.9410**	0.3018	0.0000
	DBH	β_3	−0.0290	0.0182	0.1105
	*YEAR * RW*	β_4	**0.0015**	0.0002	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	31.9700		
	Plot	b_{ij}	7.8756		
	Tree	b_{ijk}	54.9699		
	Residual	ε_{ijkt}	37.5555		
European beech					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**3637.4083**	194.8118	0.0000
	YEAR	β_1	**−1.5264**	0.1013	0.0000
	RW	β_2	**−8.2151**	0.8266	0.0000
	DBH	β_3	**0.0618**	0.0293	0.0349
	*YEAR * RW*	β_4	**0.0042**	0.0004	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	24.5299		
	Plot	b_{ij}	24.5299		
	Tree	b_{ijk}	55.3518		
	Residual	ε_{ijkt}	71.3399		
Sessile oak					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1191.7320**	202.1563	0.0000
	YEAR	β_1	**−0.3488**	0.1062	0.0010
	RW	β_2	**−2.8371**	0.9238	0.0021
	DBH	β_3	−0.0160	0.0357	0.6538
	*YEAR * RW*	β_4	**0.0015**	0.0005	0.0018
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	11.5071		
	Plot	b_{ij}	0.1974		
	Tree	b_{ijk}	54.5632		
	Residual	ε_{ijkt}	91.9274		

Table A.7
Late Wood Density model fit results (Eq. (3)). Significant ($p < 0.05$) parameter estimates are printed in bold.

Norway spruce					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**2428.9548**	163.4302	0.0000
	YEAR	β_1	**−0.9536**	0.0839	0.0000
	RW	β_2	**−7.5629**	0.4447	0.0000
	DBH	β_3	**−0.0433**	0.0175	0.0134
	*YEAR * RW*	β_4	**0.0038**	0.0002	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.1627		
	Plot	b_{ij}	23.2489		
	Tree	b_{ijk}	69.3130		
	Residual	ε_{ijkt}	52.3760		
Scots pine					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1765.9265**	146.4729	0.0000
	YEAR	β_1	**−0.5721**	0.0768	0.0000
	RW	β_2	**−2.8803**	0.4948	0.0000
	DBH	β_3	**0.0778**	0.0297	0.0089
	*YEAR * RW*	β_4	**0.0015**	0.0003	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	50.9079		
	Plot	b_{ij}	0.3158		
	Tree	b_{ijk}	83.8754		
	Residual	ε_{ijkt}	61.6054		
European beech					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**3973.7205**	209.8171	0.0000
	YEAR	β_1	**−1.6745**	0.1089	0.0000
	RW	β_2	**−8.0688**	0.8860	0.0000
	DBH	β_3	**0.1809**	0.0316	0.0000
	*YEAR * RW*	β_4	**0.0041**	0.0005	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	34.8034		
	Plot	b_{ij}	34.8034		
	Tree	b_{ijk}	60.6913		
	Residual	ε_{ijkt}	76.4388		
Sessile oak					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**3079.2276**	193.9512	0.0000
	YEAR	β_1	**−1.2287**	0.1026	0.0000
	RW	β_2	**−4.3781**	0.8120	0.0000
	DBH	β_3	**0.3024**	0.0394	0.0000
	*YEAR * RW*	β_4	**0.0023**	0.0004	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.4520		
	Plot	b_{ij}	44.7636		
	Tree	b_{ijk}	80.0230		
	Residual	ε_{ijkt}	76.3711		

Table A.8
Early Wood Ratio model fit results (Eq. (4)). Significant ($p < 0.05$) parameter estimates are printed in bold.

Norway spruce					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**−2.0966**	0.3989	0.0000
	YEAR	β_1	**0.0014**	0.0002	0.0000
	RW	β_2	0.0016	0.0011	0.1342
	DBH	β_3	**−0.0005**	0.0000	0.0000
	YEAR * *RW*	β_4	0.0000	0.0000	0.1727
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.0555		
	Plot	b_{ij}	0.0001		
	Tree	b_{ijk}	0.0842		
	Residual	ε_{ijkt}	0.1303		
Scots pine					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**−0.9029**	0.2002	0.0000
	YEAR	β_1	**0.0008**	0.0001	0.0000
	RW	β_2	**0.0095**	0.0007	0.0000
	DBH	β_3	**−0.0002**	0.0000	0.0000
	YEAR * *RW*	β_4	$\mathbf{-4.8603 \cdot 10^{-6}}$	0.0000	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.0003		
	Plot	b_{ij}	0.0241		
	Tree	b_{ijk}	0.0430		
	Residual	ε_{ijkt}	0.0953		
European beech					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	**1.5607**	0.3781	0.0000
	YEAR	β_1	**−0.0005**	0.0002	0.0081
	RW	β_2	−0.0013	0.0016	0.4406
	DBH	β_3	0.0000	0.0001	0.5643
	YEAR * *RW*	β_4	0.0000	0.0000	0.5067
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.0281		
	Plot	b_{ij}	0.0281		
	Tree	b_{ijk}	0.0521		
	Residual	ε_{ijkt}	0.1431		
Sessile oak					
Fixed effects	Variable	Parameter	Estimate	Std. Error	p
	Intercept	β_0	−0.1759	0.2095	0.4013
	YEAR	β_1	**0.0004**	0.0001	0.0011
	RW	β_2	**−0.0064**	0.0010	0.0000
	DBH	β_3	0.0000	0.0000	0.3568
	YEAR * *RW*	β_4	$\mathbf{2.7061 \cdot 10^{-6}}$	0.0000	0.0000
Random effects	Level	Parameter	Std. Dev.		
	Trial	b_i	0.0002		
	Plot	b_{ij}	0.0168		
	Tree	b_{ijk}	0.0406		
	Residual	ε_{ijkt}	0.0963		

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