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Maintenance of long-term experiments for unique insights into forest growth dynamics and trends: review and perspectives

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Abstract
In this review, the unique features and facts of long-term experiments are presented. Long-term experimental plots provide information of forest stand dynamics which cannot be derived from forest inventories or small temporary plots. Most comprise unthinned plots which represent the site specific maximum stand density as an unambiguous reference. By measuring the remaining as well as the removed stand, the survey of long-term experiments provides the total production at a given site, which is most relevant for examining the relationship between site conditions and stand productivity on the one hand and between stand density and productivity on the other. Thus, long-term experiments can reveal the site-specific effect of thinning and species mixing on stand structure, production and carbon sequestration. If they cover an entire rotation or even the previous and following generation on a given site, they reveal a species’ long-term behaviour and any growth trends caused by environmental changes. Second, we exploit the unique data of European long-term experiments, some of which have been surveyed since 1848. We show the long-term effect of different density regimes on stand dynamics and an essential trade-off between total stand volume production and mean tree size. Long-term experiments reveal that tree species mixing can significantly increase stand density and productivity compared with monospecific stands. Thanks to surveys spanning decades or even a century, we can show the changing long-term performance of different provenances and acceleration of stand production caused by environmental change, as well as better understand the growth dynamics of natural forests. Without long-term experiments forest science and practice would be not in a position to obtain such findings which are of the utmost relevance for science and practice. Third, we draw conclusions and show perspectives regarding the maintenance and further development of long-term experiments. It would require another 150 years to build up a comparable wealth of scientific information, practical knowledge, and teaching and training model examples. Although tempting, long-term experiments should not be sacrificed for cost-cutting measures. Given the global environmental change and the resulting challenges for sustainable management, the network of long-term experiments should rather be extended regarding experimental factors, recorded variables and inter- and transdisciplinary use for science and practice.

Keywords Unthinned stands · Total stand volume production · Maximum stand density · Density-growth relationship · Mixing effects · Growth trends · Biomonitoring · Silvicultural guidelines

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disciplines. Agronomists, for instance, can test a new variant of sunflower or potato within just some 100 days. In forestry, it requires a 100 years to obtain knowledge about the productivity for one rotation in temperate and boreal forests. And it would even require at least some 100 years to follow a tree during its entire lifetime. Only a few genera such as eucalypts, pines, or poplars when growing in Mediterranean, oceanic, subtropical or tropical climates reach harvestable dimensions within less than a decade or within only a few decades; most others require much longer survey periods in order to cover their growth dynamics in full.

The founding fathers of forest science such as Bernhard Danckelmann and Adam Schwappach were convinced that trees and forest stands require long-term observation and for this purpose they established the first forest research stations beginning in 1870 (Ganghofer 1881; Landesforstanstalt Eberswalde 2001; Milnik 1999). Analogous developments proceeded in many European countries and resulted in the establishment of the research stations which care for long-term experiments till present, some represented by the authors of this review paper. In the year 1872, national organisations (VDVF 1873), and since 1892 international organisations (IUFRO 1993), emerged and developed standards for tree and stand measurements (DVFFA 1986a), definitions of silvicultural actions (DVFFA 1986b), evaluation of long-term experimental plots (DVFFA 1988; Johann 1993) and their application for growth modelling (DVFFA 2000). As a result, the experiments established in different regions of the world became comparable and suitable for overarching evaluations. Most of our scientific knowledge of tree and stand dynamics and the effects of silvicultural decisions in forest practice are based on long-term experiments; this applies to such prominent examples like the self-thinning rule (Reineke 1933; Gadow 1986; Pretzsch and Biber 2005), the density-growth relationship (Assmann 1970), yield tables (Assmann and Franz 1965; Bergel 1985; Moller 1933; Schwappach 1889) and thinning guidelines for practical decision making (Pretzsch and Zenner 2017). The knowledge compiled in most textbooks and lectures is based on long-term experiments (Assmann 1970; Kramer 1988; Wenk et al. 1990).

With the term “long-term experiments” this review summarises the following four types of experiments in a wider sense: (1) regularly dendrometrically measured plots in forests with defined experimental factors and factor levels (e.g. factor thinning, factor levels slight, moderate and heavy thinning from below). Even those without repetitions, established in the early pre-statistical times are called experiments; they are often large in plot area (up to 1 ha), long in survey (>150 years) and established as disjunct experiments. “Disjunct” means that they have only one replicate per experimental site (e.g. one A, B and C grade treatment plot at each site) but several similar setups were established along productivity gradients and kept under long-term survey. von Gadow and Kleinn (2005), von Gadow (2017) call such designs “observational studies” in order to distinguish them from experiments in a strict statistical sense.

(2) Experiments established since the middle of the twentieth century under strict statistical aspects with randomisation, replication and objectively reproducible factors and factor levels. These are experiments in a strict sense according to von Gadow (2017) or Fisher (1937).

(3) When replicated not only at one site but also established on several other sites along productivity or ecological gradients (e.g. standardised IUFRO experiments) such strict statistical designs are of special value.

(4) Finally, we address also costly experiments with e.g. free air O3-fumigation, water retention by roofs, or acid rain irrigation. Due to the high expenditure, they are often repeated a few times only, and located just on one site. Although just as weakly statistically substantiated as the early experiments of the 1850–1870ies, they can pave the way for new insights, findings and understanding. A common criterion of all types of experiments summarised by (1)–(4) is that they may measure at the tree or organ level or even deeper, but all provide stand level information such as stand mean and sum values in regular periods of one or more years.

Recently, the benefit of long-term experiments has been questioned (Gadow 1999; Nagel et al. 2012) and it is not unusual that they are sacrificed in order to cut costs. Forest areas with long-term experiments have to be left out from regular forest operations, their maintenance is costly, and having to wait more than a couple of years for the first results hardly fits the contemporary funding organisations and the rushed spirit of the age.

Long-term experiments in ecological research (LTER), agriculture and grassland (Rothamsted Research), soil science (LTE), or agroecosystems (LTAE) have similar importance (Redman et al. 2004; Blake et al. 1999; Körschens 2006; Rasmussen et al. 1998). However, long-term experiments in forests face even higher pressure due to their particular longevity and space consumption.

According to an often-heard, but misleading argument, forest inventories, that have been increasingly established during the last few decades at national or enterprise levels, will render long-term experiments superfluous (Gadow 1999). Forest inventories may provide representative data on large scales and their information potential can be exploited with big data methods such as geospatial random forests and geostatistical mixed-effects models (e.g. Liang et al. 2016). Doubtlessly, inventories are ideal for obtaining information about the status quo on a statistical basis, as this is of utmost importance for forest monitoring, which is what they are designed for. Thus, forest inventory data provide a suitable source for initialising forest growth models when doing large-scale simulations and scenario analyses.
There are, however, five main aspects, where long-term experiments by far outperform the information potential of temporary inventory plots by far. First, long-term plots are the unique way to study long-term dynamics at the tree and stand level (e.g. different volume growth patterns by provenance, dominant height growth patterns at different sites, changes in tree allometry, stratification in mixed stands, demographic changes in natural forests). Inventories hardly provide information about the stand history, and intermediate yield, a lack that can be only partly remedied by establishing permanent inventory plots which gradually provide longer time series.

Second, long-term experiments can reveal the cause-effect relationships of various treatment options at the tree and stand level as they are established under controlled, ceteris paribus conditions (stand history is known, important for evaluation of mixing, fertility, pruning effects, etc.). Inventory plots rather indicate correlations but provide no evidence for causalities as they can vary in many (even unobserved) traits beyond the factor of interest (Gamfeldt et al. 2013).

Third, long-term experiments often include unthinned and otherwise untreated variants which indicate the maximum stand density and serve as a reference for the density and growth of other treatments (e.g. thinned, mixed, or fertilised plots). In addition to the omission of any treatment, long-term experiments often comprise other extreme variants, for example solitary growing conditions obtained by extremely heavy thinning. Such extremes are usually avoided by forest practice, and thus, they are usually not covered by inventories. For a better understanding of forest dynamics, however, extremes are as important as the middle course, because they open the whole range of options to scientific scrutiny and advice for practitioners.

Fourth, long-term experiments provide complete information about the growth and yield of the remaining and removed stand, i.e. they indicate the total production since stand establishment including the intermediate yield, caused by natural mortality or/and silvicultural treatments. This detailed quantitative knowledge about the stand history, especially former interventions, is a crucial advantage against inventory plots.

Fifth, long-term experiments cover a long part of the rotation and may even include the subsequent stand generation, allowing the identification of the effects of changes in environmental conditions at tree and stand level (Spiecker et al. 1996). Long-term experiments provide time series of growth and yield data that reach further back in time for selected sites. This is because the first inventories were started far later than the first long-term experiments; an advantage of long-term experiments that could become more important over time. One could argue that long time series can always be obtained by retrospective growth ring analysis. This is, however, only true for single trees. It is not true at all for forest stands, because only the trees living at the time of sampling can be covered, not their neighbours which were removed decades ago.

The information potential of long-term experiments may further increase when these five aspects are combined, e.g. if unthinned plots are monitored over more than a rotation. In summary, it may be concluded that long-term experiments and temporary plots are rather complementary than redundant (Fukami and Wardle 2005; Nagel et al. 2012).

With this paper, we want to (1) present theoretical considerations about the unique information potential of long-term experiments, (2) show recent empirical findings from long-term experiments and their scientific and practical relevance, and (3) draw conclusions for the maintenance of existing, and the establishment of future long-term network of experimental plots in forests. Finally, we discuss that beyond their value for forest science and practice, long-term experiments monitor the anthropogenic influence on ecosystems. Long-term records of stand development can serve as an ultimate and unerring arbiter regarding the human footprint on nature and its influence on tree and stand growth. Although examples mainly cover even-aged monocultures and mixed-species stands, the same arguments, can be applied with due caution to uneven-aged stands.

**Unique features of long-term experimental plots. Theoretical considerations**

**Fully stocked, unthinned stands as an ultimate reference for quantifying the effects of silvicultural treatments**

Many long-term experiments include fully stocked unthinned stands which indicate the maximum stand density of the respective species, i.e. the carrying capacity, on a given site. Thus, they provide an ultimate reference for quantifying the effects of silvicultural treatments. In this respect, long-term experiments may provide unique insights into stand dynamics which cannot be derived from routinely managed temporary inventory plots. Figure 1a shows the self-thinning line (line 1) which is characteristic for fully stocked, unthinned stands. The decrease in the maximum tree number with increasing mean tree diameter indicates the site- and species-specific maximum stand density. From long-term experiments, we know that the steepness (slope) of this line varies around \( \alpha = -1.605 \) and its level (intercept) increases with site fertility. This line is pivotal for science (e.g. understanding self-thinning and mortality) and practice (e.g. thinning guidelines and density-growth relationships). Stands which were not thinned at all, even long ago, are difficult to find in inventory data. Plausible self-thinning
relationships may only be established if self-thinning conditions can be assumed over a large diameter range (Charru et al. 2012). Forest stands sampled by inventories or temporary studies mostly represent medium stand density conditions (line 2) and thus do not directly provide information about a site’s capacity. Inventories also lack permanently strongly thinned stands with open or solitarily grown trees (line 3). This means that inventories may provide valuable information about current growth under current silvicultural management, but they will not inform us about the whole spectrum of tree and stand dynamics; understanding these is virtually impossible without covering the extremes.

Complete information about both the remaining and removed stand, which together result in the total stand volume production, can only be provided by long-term experiments with regular measurements since stand establishment. Such information obtained for a range of different silvicultural treatments may reveal that unthinned stands certainly have the highest standing volume (Fig. 1b, upper jagged curve, black filled circle) but not necessarily the maximum total stand volume production (lowest smooth curve, black filled circle). In Fig. 1b, the medium thinning (grey diamond) results in the highest total stand volume production. The fact that both unthinned and strongly thinned stands often yield a sub-maximum total stand volume production (Assmann 1961; Corral-Rivas et al. 2018; del Río et al. 2017; von Gadow and Kotzé 2014; Pretzsch 2005) could not be revealed without long-term experiments, as unthinned stands would not be available as references and stand volume production would be only partly recorded.

Figure 1c shows a density–productivity relationship derivable from long-term experiments with unthinned stands (level of line 1.0) and different density levels and the respective total stand volume production for the different variants. Temporary plots would reflect a limited density spectrum only, and incomplete productivity records, so that only parts of the optimum curve (in this case the lower density was over-recompensed by size-growth acceleration) shown in Fig. 1c could be derived.

Permanent experiments furthermore reveal that there is an obvious trade-off between thinning intensity, stand volume production (Fig. 1c) and tree size characteristics (Fig. 1d). Increasing thinning strength results in increased diameter growth and hence shortened rotation age and price of the end product. At the same time, increased thinning results in decreased slenderness expressed by the h/d ratio, which is inversely related to individual tree stability. Comparing Fig. 1c and d shows to what extent the increase in tree size and stability due to density reduction can be practiced without losses of total stand production.
Continuous measurement of monospecific and mixed-species plots at the same site can reveal mixing effects

The quantification of mixing effects requires that monospecific and mixed-species plots are located on the same site and do not differ in any other aspects (age, site conditions, thinning) except the species mixing. Unthinned monospecific and mixed plots are especially valuable because they can reveal the mixing effect on stand density and the self-thinning line. Figure 2a shows a schematic representation of the self-thinning lines for two monospecific stands (line sp₁ and sp₂) and three hypotheses regarding the possible behaviour of the mixed-species stand (sp₁₂). Lines 1, 2 and 3 would indicate that tree species mixing increases stand density (i.e. the level of self-thinning line), leaves it unchanged or decreases it, respectively. Managed stands could not be used to analyse such effects because the artificial density reduction may have been eliminated or equalled out by differences between the maximum density of monospecific and mixed stands.

An increased productivity due to mixing of two or more species (overyielding) is often attributed to an increased crown packing density or carrying capacity due to reduced competition between complementary tree species (Bielak et al. 2014, 2015; Pretzsch 2014; Pretzsch and Biber 2016, Zhang et al. 2015). However, any mixing effects on productivity, as they are mostly caused by higher density, may be simply cancelled (“thinned-away”) by undocumented previous thinnings as is the normal case with inventory plots. Thus, thinned stands with sub-maximum density or even unknown maximum density are hardly suitable for revealing the potential over- or underyielding by tree species mixing. Measurements of the removed and remaining stand in monospecific (sp₁ and sp₂) and mixed plots (sp₁₂) in close vicinity since stand establishment (Fig. 2b) enables the comparison of mixed-species with monospecific stands under ceteris paribus conditions and to calculate over- or underyielding based on total volume production. Different thinnings may affect the productivity of the monocultures but also the extent of mixing effects (Fig. 2c). Long-term tree species mixing experiments with thinning variants including unthinned stands may reveal mixing effects which would not be detected in moderately or strongly thinned plots (Fig. 2c, from above to below).

Long-term survey can reveal ontogenetic and environmental growth trends

For testing the suitability of given species or provenances or various thinning or fertilising options, long-term observation is essential. Often the ranking between different treatment variants changes when the observation goes beyond the juvenile state. Figure 3a shows this effect in schematic representation for the total stand volume production of three treatment variants. A similar change intersection of the trajectories and change in the ranking can emerge for all kinds of stand characteristics. This questions the reliability of all extrapolations from the early performance to advanced development stages, and vice versa.

Long-term surveys can reveal growth trends and positive or negative deviations from yield tables or other references caused
by changing environmental conditions (Fig. 3b). Observations of successive generations where consecutive stands grow at the same site and are similar in provenance and silvicultural treatment has a unique indicative value. They can reveal whether the successive stands have the same total stand volume production and standing volume at a given age as the previous stands. In the example in Fig. 3c, both total stand volume production and standing volume increase from one to the next stand generation. Inventory or other temporary plots are less suitable for such biomonitoring because their history is often unknown so that changes in, e.g. provenance, silvicultural treatment, or fertilisation cannot be excluded as possible causes behind the observed changes (Charru et al. 2010). On long-term experimental plots, in contrast, genetic traits, stand establishment technique, and silvicultural treatment can be controlled, so that long-term changes in growth can be assigned to environmental changes such as dry deposition, acid rain, or climate change (Kahle 2008; Kenk et al. 1991; Pretzsch et al. 2014; Spiecker et al. 1996).

Essential empirical findings based on long-term experiments

Maximum density and productivity-density relationship

Self-thinning line and maximum stand density

Most of the classic long-term experiments include the so-called A grade plots (VDFV 1902). “A grade” is defined by VDFV (1902, § 4) as follows “This is limited to the removal of dying and dead trees, as well as any bowed pole wood […] for the purpose of delivering material for comparative growth investigations only”. In other words, on A grade plots nothing more is done than closely monitoring natural mortality and removal of dying or dead trees to prevent possible stand damage coming from dead trees (infestations by fungi or insects). A grade plots reveal the maximum stand density and self-thinning and they serve as the reference for quantifying how different levels of stand density regulation influence productivity, carbon sinks and stand structure.

Figure 4 shows the relationship between tree number (N) and mean tree diameter (d) on A grade plots (green) compared with medium (B grade) and strongly thinned plots (C grade) of Norway spruce and European beech. These kinds of data from 28 plots in fully stocked monospecific stands of European beech (Fagus sylvatica L.), Norway spruce (Picea abies (L.) Karst.), Scots pine (Pinus sylvestris L.), and sessile oak (Quercus petraea (Matt.) Liebl.), systematically surveyed since 1848, were used to answer a question which was open since the 1930s, namely whether there exist species-specific allometric exponents (= slopes) of the self-thinning line, or if there is only one single overarching value of $\alpha = -1.605$, as proposed by Reineke (1933). Although the four species’ allometric exponents are remarkably close to Reineke’s postulate, the data exposed significant species-specific deviations (Pretzsch and Biber 2005), which reveal different strategies of species-specific self-tolerance (Zeide 1985). Beyond, precise knowledge of self-thinning lines from long-term plots is useful for developing self-thinning
trajectories (del Río et al. 2001; Ningre et al. 2016) as an upper boundary and base line in developing silvicultural guidelines (Bégin et al. 2001), for further development of allometric rules and theory (Enquist et al. 1998; Enquist and Niklas 2001), and for modelling tree mortality (Coomes and Allen 2007; Hara 1985; Monserud et al. 2004).

Productivity-density relationship

Better knowledge of self-thinning lines enables improved calculations of the stand density index SDI (Reineke 1933), which in turn can serve as a reference for investigating unbiased productivity-density relationships. Figure 5 shows the productivity of thinned stands in relation to unthinned plots at different stand ages. Hereby the Standardised Stand Density Index, SSDI, a given SDI divided by the corresponding maximum value, is used for describing stand density (i.e. SSDI = 1 represents maximum density).

As evident from Fig. 5, a unimodal relationship between stand density and productivity can be shown for Norway spruce and European beech on long-term thinning trials under survey since 1848. This relationship is an essential feature in many stand growth models and silvicultural guidelines.

The data from the thinning trials shown in Fig. 5 allowed calibrating a detailed model of the density-productivity relationship (Pretzsch 2005). It predicts the RPAI, i.e. the periodic annual increment of merchantable wood as a function of the SSDI, the site index SI, i.e. the mean height (m) at age 100, and the quadratic mean stand diameter \( d_q \) (Fig. 6). Besides revealing opposing-site-quality-related behaviour between both species, the model reflects the apparently paradoxical fact that a thinning which keeps a stand at maximum periodic increment does not guarantee a maximum total stand production at the end of a rotation (Zeide 2001, 2004). Suppose a young beech stand \( (d_q = 10 \, \text{cm}, \, SI = 32 \, \text{m}) \) is kept on SSDI = 0.50 by heavy thinnings. According to the model, this will accelerate the periodic annual increment (PAI) to 123% of the value at maximum stand density. However the accelerated stand growth also leads to a faster

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Fig. 4 Long-term development of tree number over mean tree diameter (\( \ln(N) - \ln(d_q) \) - relationship) for thinning trials in even-aged stands of (a) Norway spruce \( (n = 9) \) and (b) European beech \( (n = 9) \) for untreated, fully stocked plots (A grade), medium (B grade) and strong thinning (C grade). Reference lines \( \ln(N) = \ln(b) - 1.605 \times \ln(d_q) \) in accordance with Reineke (1933) where \( \ln(b) = 11, 12, 13 \) (after Pretzsch and Biber 2005)

Fig. 5 Periodic annual increment (PAI) plotted over the standardised SDI, SSDI, for selected (a) Norway spruce and (b) European beech experiments (Sachsenried 02 and Fabrikschleichach 15, respectively). Stand ages, sorted corresponding to A-grade PAI’s are arranged to the right of the respective surveys (open circle, filled circle, open triangles = thinning grades A, B and C). As the A grades represent maximum density, their SSDI is always 1. SSDI: a given SDI divided by the corresponding maximum value (Modified after Pretzsch 2005)
physiological aging as evident by a quicker increase in $d_q$. Thus, the stand grows quicker through its highly productive life stages and arrives earlier at less productive ones. This response pattern explains why the total stand production of older B and C grade plots differs little from the A grade in the end, although PAI can be increased considerably by B and C grade thinning.

Using a Scots pine experiment as an example (combined spacing and thinning experiment Weiden 611, observed since the middle of the last century), Fig. 7 shows how different stand density reductions can reduce total stand production but increase mean height and diameter as well as the mean individual tree stability (indicated by the ratio of dominant stand height and diameter $h_d/d_q$) up to a stand age of 50 years. The characteristic trade-off between area related stand productivity and (mean) tree size development becomes obvious; strong thinnings may accelerate tree size at the expense of the production per hectare and year (del Río et al. 2017). If such relationships are not known, silviculture operates without reference.

### Tree species mixing effects

#### Tree-species mixing and stand productivity

Tree species mixing effects on stand growth are among the most hotly debated issues since the origins of forest science. Mixing effects are commonly quantified by comparing the productivity (or other stand characteristics of interest) of the mixed plot of a long-term experiment with the weighted mean productivity of neighbouring, monospecific plots with the same age, site conditions and silvicultural treatment. Weights are then equal to the proportion of the species in the mixed stand. In this context, the term “overyielding” means that the mixed stand is more productive than the weighted mean of the monocultures. The term “transgressive overyielding” means that the mixed stand’s productivity comes off even better than the most productive of the monoculture reference stands (Pretzsch and Schütze 2009).

Figure 8 shows the results of a meta-analysis on overyielding of various species assemblages based on long-term experiments in Central Europe (Dieler et al. 2017). It revealed a significant mean overyielding of 19% for Norway spruce and European beech (Fig. 8a), 24% for sessile oak and European beech (Fig. 8b) and 20% for a species combination of Norway spruce, silver fir (Abies alba Mill.), and European beech (Fig. 8c).

Despite these significant overyielding effects, the plots in Fig. 8 also show a broad variation in mixing effects. Pooling long-term experiments from several Central European institutions revealed a pattern that explained a large part of this variation (Pretzsch et al. 2010). Overyielding for a given species combination was the stronger the poorer the site conditions were in mixtures of European beech with either Norway spruce or sessile oak. This is important information for practitioners. In contrast, spruce–fir mixtures in south-west Germany and in Switzerland appear to have higher mixing effects on more productive sites. So do several other types of mixtures, such as mixtures with N fixers, where stands with the highest monoculture productivity (high rainfall, high soil P, but low soil N) have the highest mixing effects (Forrester 2014; Hao et al. 2018; Jactel et al. 2018).

To assist forest practice, Pretzsch (2016) and Pretzsch and Forrester (2017) published a comprehensive overview of mixture effects on productivity which is shown in Table 1. It
summarises the overyielding of common two-species assemblages in Central Europe and underlines the fact that the mixing effects are not only scientifically evident but also practically relevant. The long-term experiments show that in relation to the weighted mean of the monospecific stands, mixed-species stands produce 11–30% more stem volume (Pretzsch 2016). Combinations of ecologically more similar species (e.g. Norway spruce and European beech, Norway spruce and silver fir) result in lower overyielding than complementary species combinations (e.g. Scots pine and European beech, European larch \( \text{Larix decidua} \) Mill. and European beech) which can more efficiently share available space and resources (Kelty 1992, Nord-Larsen and Meilby 2016).

In addition to the mean overyielding and standard error, Table 1 shows conservative correction factors which may be used to estimate mixed stand productivity based on the productivity of neighbouring monocultures. The correction factors indicate that the productivity of monocultures should be multiplied by 1.10–1.20 to estimate the productivity of the respective mixed-species stands. They apply to fully stocked mixed-species stands, individual mixing to group-wise mixing patterns and mixing proportions of about 50:50.

**Tree-species mixing and stand density**

In pure and mixed stands of Norway spruce and European beech the reduction in spruce tree numbers \( (N) \) with increasing mean diameter \( (d) \) due to self-thinning occurs more strongly in mixed stands (slope of the \( \ln(N) - \ln(d) \)-line \( \alpha_{N,d} = -2.76 \)) than in monospecific stands \( (\alpha_{N,d} = -1.97) \), whereas beech is released by mixing \( (\alpha_{N,d} = -1.59 \text{ vs } -1.669) \) (Fig. 9a, b). Figure 9c shows this pattern for a broad set of mixed stands all containing beech. In this data set, self-thinning rates for beech are at a maximum in monospecific stands \( (\alpha_{N,d} = -1.52) \) and this species is continuously released when growing in mixture with spruce \( (\alpha_{N,d} = -1.25) \), oak \( (\alpha_{N,d} = -1.12) \), or pine \( (\alpha_{N,d} = -0.51) \). It seems that intraspecific competition is high and results in steep self-thinning slopes in monospecific beech stands,
Fig. 8 Comparison of the stand productivity of mixed versus mono-specific forest stands based on long-term experimental plots in Central Europe. a Norway spruce and European beech, b sessile oak and European beech, c mixed mountain forests of Norway spruce, silver fir, and European beech. On average, the mixed stands produced 119, 124, and 120%, respectively, of the weighted mean of the neighbouring monocultures. All three analyses revealed a broad variation in mixing effects including underyielding and strong overyielding among the single plots. The entry “Wiedemann” in Fig. 8a refers to the results of a study by Wiedemann (1942) about the growth of mixed versus monospecific stands of Norway spruce and European beech (after Dieler et al. 2017).

Table 1 Mixing effects on stand productivity of various tree species mixtures in Central European forests derived from long-term experiments according to Pretzsch and Forrester (2017) (after Pretzsch 2016). The relative overyielding (%) refers to the productivity of the mixed-species stands in relation to the weighted mean of the neighbouring monospecific stands. The correction factors may be used to conservatively adjust the stand productivity of monospecific stands to the expected stand productivity of the respective species assemblages within the studied forest regions.

| Species combination | Norway spruce/ European beech | Scots pine/ European beech | sessile oak/ European beech | European beech/Douglas-fir | Scots pine/ Norway spruce | European larch/ Norway spruce | Norway spruce/silver fir |
|---------------------|--------------------------------|---------------------------|-----------------------------|----------------------------|----------------------------|----------------------------|--------------------------|
| Overyielding (± SE) in % | 21 (± 3) | 30 (± 9) | 20 (± 3) | 11 (± 8) | 21 (± 11) | 25 (± 6) | 13 (± 6) |
| Corr. factor | 1.10 | 1.20 | 1.10 | 1.10 | 1.20 | 1.20 | 1.10 |
whereas in mixture, competition turns against the admixed species and reduces mortality of beech.

Based on triplets of fully stocked and unthinned long-term plots of mixed-species stands and neighbouring mono-cultures, Pretzsch and Biber (2016) revealed higher densities of the mixed-species stands on the basis of the self-thinning line, i.e. the stand density index SDI (Reineke 1933). The evaluation with mixed linear models showed that in mixed stands maximum density was on average 16.5% ($p < 0.0001$) higher than in neighbouring monospecific stands. Species mixtures including Norway spruce, the most important commercial species in Central Europe, significantly exceeded densities of monospecific stands by 8.8% ($p < 0.05$) on average. Individual species mixtures showed a significant density effect of +29.1% ($p < 0.01$) for Norway spruce mixed with European larch, and +35.9% ($p < 0.0001$) for Scots pine in association with European beech, both being very complementary species combinations (Fig. 10). All other species assemblages, when analysed in isolation (except European larch/European beech where only one observation was available), showed higher, albeit non-significant densities between 4% and 21% in the mixed stands compared to the monocultures (Fig. 10).

While species mixing clearly raised the level of the self-thinning line, the slope remained the same. This shows that mixing can reduce tree mortality of the total stand so that their self-thinning line can be significantly higher (Bravo-Oviedo et al. 2018; Ducey et al. 2017), indicating a higher carrying capacity of a given area when stocked with mixed stands.

Mixing effects may become more pronounced in denser stands and they may be cancelled out by wide spacing or strong thinning. For a 12-year-old 50:50 mixed plantation of Douglas-fir and western hemlock, Amoroso and Turnbull (2006) showed the importance of stand density for the relationship between the productivity of mixed versus monospecific stands. In terms of relative stand productivity, the fully stocked stands (1729 trees per ha) showed overyielding effects while the advantage of mixing vanished when the stands were stocked with only 1111 or 494 trees per hectare (Fig. 11a). The graph for the absolute total yield (Fig. 11b) shows that under high stand density the mixed plots even transgressively overyield, as total yield at age 12 exceeds the total yield of both neighbouring monocultures. This experiment underlines that high positive mixing responses and overyielding (even transgressive overyielding) may be more likely at medium and high density levels compared with stands where the stand density has been substantially lowered through thinning or other disturbances.

If long-term experiments are not available, temporary plots or artificial age series are often used to examine species mixing effects (Pretzsch et al. 2015). In such cases, the plots should cover a wider range of stand ages as mixing effects may change with age. Retrospective productivity analyses on such plots require increment cores which, however, can provide stand productivity for not much longer than 5 or 10 years backwards. This is due to increasing uncertainties in tracing back height growth and trees that were thinned or died, which can strongly influence any over- or underyielding. Using inventory data for such analyses may produce
misleading results, e.g. if silvicultural practice preferably establishes mixed stands on more favourable sites and monocultures on the poorer sites and sufficiently detailed site quality information is not available. In this case, mixed stands would be more productive because they dominate on better sites, thus confounding site effects with the actual ecological effects of species mixing. The overestimation of

Fig. 10 Boxplots of the ratio of stand density (RSDI = SDImixed/SDImono) for various species assemblages. Numbers above the boxes indicate the relative stand density (SDImixed/SDImono). In the cases of spruce-larch and pine-beech, the deviations of the relative stand density from the density of the monoculture (RSDI = 1.0) was significant according to linear mixed models. The central line of the boxes represents the median of the data, and the lower and the upper border of the boxes show the 25% and the 75% quantile, respectively. The whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. In case there are values beyond that range, they are displayed as single points (after Pretzsch and Biber 2016)

Fig. 11 Effect of stand density on mixing effects illustrated by cross diagrams. a Relative and b absolute yield for a 12-year-old 50:50 mixed plantation of Douglas-fir and western hemlock adapted from Amoroso and Turnblom (2006, Fig. 10). The left and right ordinates represent the productivity of the pure stands of hemlock and Douglas-fir, respectively, and the abscissa represents the mixing proportion of Douglas-fir. The broken lines illustrate the productivity of the stand as a whole and the species’ contribution in the case that mixed stands perform similar to monospecific stands. The solid lines represent the productivity of the mixed stand as a whole and the contributions of hemlock and Douglas-fir.
the mixing effects can be even higher if mixed stands are less intensively thinned and denser than monocultures.

The finding that mixing effects on stand productivity are species specific should be considered when merging large-scale inventory data sets from different parts of the world (Liang et al. 2016). Long-term experiments with defined tree species assemblages, mixing proportions and mixing patterns in contrast, control all these factors which potentially influence the species mixing effects on stand dynamics and provide species-specific results.

**Long-term changes in growth**

**Changing long-term-performance of different provenances**

The Scots pine provenance trial Schwabach 304, established in 1927, provides an example for the unique value of long-term experiments. This experiment showed the production of the provenance “Bamberg” to be inferior up to an age of 50 years (Fig. 12a) compared to the provenances “Schwabach” and “Unterfranken”. Only the continuation of observations to the present has revealed the superiority of the Bamberg provenance in the long run. If the investigation had been closed before the trees were 50 years old, neither the marked superiority of all provenances compared to the Scots pine yield tables by Wiedemann (1943, moderate thinning), nor the temporal change in the provenances’ performance ranking would have been identified. As was common at the time when experimental forestry was established, the experiment Schwabach 304 does not contain replications, and consequently the results cannot be backed with statistics.

In the case of the Douglas-fir provenance trial Kösching 95 (established 1961, first survey 1961, latest survey 2015), all provenances performed very similarly during the juvenile stand development. With increasing age, however, the difference in total stand growth between the poorest and best performing provenance becomes a remarkable 500 m³ ha⁻¹ (Fig. 12b). This trial also includes plots of Norway spruce which performs similarly to Douglas-fir initially, but lags behind most of the Douglas-fir provenances at advanced ages. The deviations from the reference yield tables are negligible in the beginning but accumulate strongly with increasing stand age.

The long-term changes in ranking and trend depicted in Fig. 12 underpin that the choice of silvicultural options (e.g. tree species, provenance, and/or thinning regime) should not be based just on early tests, but on long-term observation. Real times series of observations cannot simply be replaced with artificial time series, which attempt to derive the development over age by measuring and combining stands of different ages on the same site. When the history, the site conditions, the treatment and genetic properties of such space for time series are not sufficiently similar, their use as a substitute for real time series is questionable (Pretzsch 2010, S. 145–148). The need for longer surveys as a prerequisite to practical decision making is of special importance for

![Fig. 12](image_url)

**Fig. 12** Long-term observations can reveal changes in the performance ranking of different trial variants as well as deviations of their growth and yield characteristics from the prediction by yield tables. a On the Scots pine provenance trial Schwabach, 304 initially low-performing provenances finally have superior total production. After 20 years all three provenances surpass the level of the yield table. b Douglas-fir provenance trial Kösching 95 where some Douglas-fir provenances significantly excel the others and the total production of the Norway spruce reference plots in advanced age. The yield tables for Scots pine by Wiedemann (1943, yield classes I-III.) and for Douglas-fir by Bergel (1985, yield class I.) and Norway spruce by Assmann and Franz (1965, O 40) were used as reference.
new introduced species, provenances, species combinations or thinning regimes in order to avoid misinterpretations of their performance.

**Long-term trends in growth caused by environmental change**

Comparison of growth between subsequent rotations of the same species grown at the same site allows for diagnoses of long-term changes in the growth behaviour over multiple generations (Kenk et al. 1991; Pretzsch et al. 2014; Röhle 1994, 1997; Wiedemann 1923). Obviously, the analysis over such a large time span requires an exceptionally extensive database with consistent surveys of the present and previous generation, which might easily date back 200 years. Few long-term experimental plots provide such valuable data, so that stem analysis combined with statistical analysis to filter out influencing factors (e.g. ontogeny) has also been proposed as an approach (Bontemps et al. 2012). However, if appropriate long-term plots are available, the comparison can be carried out for all covered stand characteristics, of which stand height is especially useful as it remains almost unaffected by stand silvicultural treatment.

In an early study, Wiedemann (1923) detected an impeded height growth of Norway spruce, which he attributed to silvicultural and climatic effects. Comparing the height growth behaviour of stands established in 1700–1730 with the subsequent generation established in 1825–1845, he proved a degradation in the site fertility by two levels of Schwappach’s (1890) yield tables for Norway spruce (Fig. 13).

More recently, for Norway spruce stands on poor to medium sites, Kenk et al. (1991) detected a site index improvement by up to seven meters of dominant height at age 100, referenced with the Assmann and Franz yield tables (1963). The time span between the establishment of the previous stands (1820) and the subsequent stands (1950) was similar as in the study by Wiedemann (1923). Spiecker et al. (1996), Pretzsch et al. (2014) and Bontemps et al. (2012) confirmed that forest stand growth dynamics in Central and Western Europe have accelerated since 1870.

For a close analysis of the growth trends in this review, we compiled a data set of several hundred long-term experiments from Austria, Denmark, England, France, Germany, Poland, Spain, Sweden, and Switzerland. For illustration in Fig. 14 and evaluation in Fig. 15, we selected 577 fully stocked and unthinned or just moderately thinned long-term experiments of Norway spruce \((n=202)\), Scots pine \((n=189)\), European beech \((n=97)\), and common and sessile oak \((n=89)\).

On many plots, the total stand volume production develops more rapidly than suggested by the reference yield tables and finally even exceeds the maximum values of the yield tables with as much as 500–1000 m³ ha⁻¹. Further analyses showed that a similar acceleration and transgression of the yield tables applies for the development of other stand variables such as height, mean diameter, standing and total stand basal area. As reference, we used the yield tables (yield classes I. and IV.) for Norway spruce by Wiedemann (1936/1942), Scots pine by Wiedemann (1943), European beech by Schober (1967), and sessile oak by Jüttner (1955) as they represent the growth and yield expected for Central Europe (Fig. 14). The upper yield classes of these tables represent the performance of the respective species when growing in the last century under optimal conditions.

We analysed the same data with generalised additive mixed models (GAMM) in order to test for possible relocations of the age trajectories of total stand volume production and related variables with the year of stand establishment. The trends we identified are shown in Fig. 15 for Scots pine. They reveal how total stand volume production, standing volume, absolute and relative cumulative volume that was reached at a given age, changed during the last 150 years. Remarkably, the same total stand production and standing stock in an old stand is reached 50 years earlier today than for stands that were established 100 years before the former. At an age of 75 years, the intermediate yield (i.e. the cumulative removed volume) is 200 m³ ha⁻¹ today while it was just 75 m³ ha⁻¹ for stands that were established 100 years earlier, which means an increase by 150%. Similar trends where found for all other main species. Based on a part of the German plots Pretzsch et al. (2018) showed that wood density has decreased by 8-12% since 1900. While stand
and trees grow much faster with respect to wood volume, stand biomass increment increased 9–24 percentage points less compared to volume increment. The decreasing wood density goes along with an increased early wood fraction, and suggests the observed extension of the growing season and fertilisation effect of dry deposition as the main causes of the observed growth trends.

Changes in growth dynamics as shown in Figs. 13, 14, 15 have far-reaching consequences for many aspects of forest science, inventory, planning, silvicultural guidelines and

Fig. 14 Acceleration of stand growth revealed by the development of the total volume production on long-term experiments of a Norway spruce (n = 202), b Scots pine (n = 189), c European beech (n = 97), and d sessile oak (n = 89) in Europe established between 1848 and 2010. The measured trajectories strongly exceed the common yield tables (yield classes I. and IV.) for Norway spruce by Wiedemann (1936/1942), Scots pine by Wiedemann (1943), European beech by Schober (1967), and sessile oak by Jüttner (1955). The German experimental plots were provided by the Forest Research Station of Baden-Württemberg (BW), the Research Station of Lower Saxony in Goettingen (GOE) and the Chair for Forest Growth and Yield Science at the Technical University of Munich (MUE)
measures, and also for forest utilisation, wood processing, and even the establishment and management of long-term experiments. The growth trends shown in Figs. 14 and 15 indicate changes in growth conditions in terms of a rise in temperature, extension of the growing season, a rise in atmospheric CO₂-level, nitrogen deposition, and abandonment of nutrient exporting treatments like litter raking (Pretzsch et al. 2014).

Detailed analyses of the growth trends show that tree and stand allometry remain the same as in the past, just the growth rates increase. This means that stand structure still looks the same as in the past; however, a given structure or development phase is simply achieved earlier than in the past, i.e. the forests’ life cycle is accelerated. Thus, yield tables and other models which are built upon basic allometric relationships mainly require adjustments to the time related growth rates (Pretzsch 2016). However, this could be only done efficiently based on empirical data delivered by long-term experiments plots.

At a given stand age, removed volume can nowadays be higher, stand density or basal area can be higher, and the annual cut can be raised compared to the situation decades ago. Practitioners might want to thin monospecific stands more frequently than in the past in order to avoid very high densities. In mixed stands, the regulation of species interactions might have to become more intensive due to the accelerated dynamics relating to interspecific suppression processes. Accelerated stand dynamics mean higher mortality in unthinned stands, higher quantities of removed volume in thinned stands, more nutrient export, and shorter rotation periods. The increase in potential sustainable harvest means an increased carbon sequestration due to wood utilisation. Stands will probably also move faster through or into the typical phases of high wind and storm risk than in the past.

In other regions and under other conditions, environmental changes can be of course also detrimental for growth rates and slow down stand dynamics. A recent study about tree growth in forests and urban areas revealed that the beneficial effects of climate change can turn into growth decrease and losses in regions with limited water and nutrient availability (Pretzsch et al. 2017a). Again, without long-term experiments our knowledge of these processes would be strongly biased or blurred if available at all.
Conclusions and perspectives

Conclusions

Long-term forest experiments provide a record of forest stands with known history regarding establishment, silvicultural treatment, and disturbances. They offer time series of stand development for biomonitoring in managed and unmanaged forests, development of silvicultural treatment, modelling and demonstration and training. Because of their high and irreplaceable potential of information for science and practice, long-term forest experiments shouldn’t be given up, although their costs might temporarily seem to outweigh benefits. In the long run, with changing scientific questions, silvicultural preferences, political conditions, and environmental impacts such as acid rain, nitrogen deposition, or climate change, they have provided information far beyond the purposes they were originally established for.

Abandoning plots is a quick action, but re-establishing a comparable source of information would require another century or more, not to mention a break in time series that cannot be compensated for by any means. Even if plots no longer contribute to answering the original research question (e.g. effect of various grades of thinning or fertilisation on stand productivity), they have more often than not served as a valuable basis and reference for other purposes, especially in the context of global change impacts (del Río et al. 2017). Thus, in contrast to giving up long-term experiments, new urgent questions (tree species mixing, drought resistance, provenances, foreign species, new introduced species, heterogeneously structured stands) call for an even more intensive maintenance and even extensions of existing experimental networks (Seynave et al. 2018). Analogous to the LTER, LTE, LTAE, and Rothamsted Research initiatives and networks mentioned in the introduction, the institutions responsible for long-term experiments in forest stands should strive for an even better cooperation, standardised data storage and exchange and common funding platform. With the DESER-Norm (Johann 1993) the German Association of Forest Research Institutes, DVFFA, (in German: “Deutscher Verband Forstlicher Forschungsanstalten”), has made an important step towards such a standardisation. Recent works taking into account the DESER standards in new evaluation software (Biber 2013) and DVFFA initiatives for defining common XML-based data exchange formats point into the same direction. However, internationalisation is still below its possibilities.

The course of forest growth as observed during more than a century reveals site and species-specific reactions on various disturbances and may contribute to a less emotional but more objective discussion of the human influence on tree growth, forest dynamics, and long-living ecosystems in general. While the public debate about forests and especially their provision of ecosystem services is rapidly changing, long-term experiments provide differentiated and consolidated information about a wide range of aspects on forests. Hence, the knowledge gained may facilitate a nuanced perspective and ultimately provide optimum support to future forest management.

Perspectives

The European network of long-term experiments was established by researchers who knew that they themselves would not benefit from the results but that the experiments would make up an invaluable resource of information for future research. As described above, we are now, and have been for a long time, exploiting this treasure of data for making fundamental conclusions on long-term tree and stand growth. Because previous generations of forest researchers have given us this opportunity, it would be strongly unethical not to pass on new long-term experiments to future researchers. Therefore, resources should not just be allocated for maintaining existing experiments but also for establishing new experiments in order to answer questions that can be anticipated to be important during the coming century.

By emphasising the importance of long-term experiments in the preceding paragraphs, we do not mean to imply that we do not see additional requirements and perspectives for future development. One important point is that the existing long-term experiments are not even close to sufficiently representing mixed-species stands. Newly established long-term experiments should cover the most important species assemblages in a systematic way. Besides unthinned monocultures and mixed plots, such experiments should include variants of density reduction, mixing proportions, and mixing patterns (individual tree mixture, group and clusters). Common quantitative standards for mixing regulation still need to be defined.

In addition, new and urgent topics require long-term experiments, such as non-native tree species, agroforestry systems, new silvicultural approaches such as transformation from homogeneous monocultures to complex uneven-aged mixed stands, natural regeneration approaches such as shelterwood or group selection systems. This is also valid in the case of strictly protected natural forests. In this case, the observations on long-term plots allow us to better understand their demography dynamics, growth and yield, and to finally answer the question to which extent they can serve as models or benchmarks for sustainable and multifunctional forestry. There is also a need for clone and clone mixture trials, as well as for long-term disturbance trials such as lowering ground water levels, ozone and thawing salt applications, or motorway impacts. Such disturbances become increasingly frequent so that model examples for assessing
their long-term effects are required for damage assessment, judicial evidence, and compensation payments.

Existing long-term experiments originally aimed at providing the best possible scientific information about forest growth and yield. Along with the gradual extension of the sustainability paradigm to a broad range of ecosystem services beyond pure wood production (Biber et al. 2015), the variable list to be measured and evaluated on experimental plots extended to—among many others—wood quality, non-wood forest products, carbon sequestration, forest structure, biodiversity, habitat properties and recreation value, and in a psychological context, even spiritual characteristics. So, more and more variables for quantifying many ecosystem traits, functions and services are measured on existing plots. This significantly increases their value for monitoring silvicultural practices. In the case of new experiment establishments, the protocols must include such variables and measurement installations from the very beginning. More detailed measurements of the site-specific environmental factors and resource supply are also required for deepening the insights into cause–effect relations in forest dynamics. As this is rather costly, future long-term experiments require an optimised placement in terms of sites covered and environmental gradients.

Forest stands nowadays often grow faster in temperate and boreal climates and produce more than in the past, and therefore the intervals of sampling, measuring, and regulating measures must be reconsidered. The replacement of one generation by the next becomes more frequent and the costs for managing a network of experimental plots increase if stand development should be traced with the same intensity and accuracy as in the past. New measurement technology should be developed both for reducing the cost of sampling and maintenance but also to provide new kinds of data for future analyses. Examples of new possible technologies are terrestrial and air-borne laser-scanning, monitoring of soil–water availability and measurement of leaf-area index.

Long-term experiments with a continuous treatment or non-treatment over entire rotations or even beyond normal rotation age are valuable for demonstration, education, and training. They demonstrate the long-term effect of treatments on tree and stand dynamics and may serve for correcting exaggerated expectations towards realism. For example, long-term thinning plots show that trees react strongly to thinning initially, but with increasing size their growth rates decrease. So, there is no guarantee at all that promising results obtained in the short term will last in the long term. Ontogenetic drift may even let early and strongly promoted trees fall below the growth rates of unthinned neighbouring stands in the long run. To develop new silvicultural guidelines, long-term experimental plots are frequently used as model examples for which stand structures should be aimed for or avoided. Most ecological laws and rules of tree and forest stand dynamics, as well as yield tables and other models, were derived from long-term experiments; so more than ever they must be actively integrated in teaching and training in order to bring theory, numbers and visual perceptions together.

Most long-term experiments were established, regulated and evaluated following similar protocols and standards, e.g. thinning definitions (VDFV 1902) and evaluation algorithms (Johann 1993). These definitions have become widely adapted even beyond the countries that were historically influenced by the German tradition of forest science. Nowadays, this facilitates the internationalisation of long-term experimental networks. As could be seen from some of the results presented above, pooling research plot data from several countries leads to an enormous added value in terms of relevant insights. Overarching analyses, e.g. of growth reactions on site conditions, climate change, or matter export by different thinning intensities, cover far wider gradients than regionally limited data. Thus, the chances to see and understand the full spectrum of possible forest stand dynamics under controlled experimental conditions and known past development have never been as high as they are today.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest
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