Biomass production dynamics for common forest tree species in Denmark – Evaluation of a common garden experiment after 50 yrs of measurements

Thomas Nord-Larsen [a,*], Hans Pretzsch [b]

[a] *University of Copenhagen, 23 Rolighedsvej, DK-1958 Frederiksberg C, Denmark*
[b] *Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany*

A B S T R A C T

Common gardens are suited for analysing the behaviour of different species in a common environment. We used a common garden experiment including 12 different tree species (*Fagus sylvatica*, *Pseudotsuga menziesii*, *Abies grandis*, *Larix kaempferi*, *Chamaecyparis lawsoniana*, *Pinus contorta*, *Pinus mugo*, *Abies procera*, *Picea abies*, *Quercus robur*, *Abies alba*, and *Picea sitchensis*) grown at 13 different sites, and representing almost 50 yrs of measurements, for answering the following questions: (i) how do the species differ in their average biomass production?, (ii) how does their performance vary in space, and (iii) how does their performance vary over time. The analyses showed that the North American conifers including *A. grandis*, and *P. sitchensis* had a significantly higher potential for biomass production than the other species. However, while *P. sitchensis* was relatively invariant to site conditions, the analysis indicated that, compared to the other species, *A. grandis* benefited more than the other species from a general improvement in growing conditions. The effectiveness of substituting fossil fuels and carbon intensive materials with woody bioenergy is highly dependent on plant growth rates. Our results may suggest a selection of species with superior biomass production and carbon sequestration.

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1. Introduction

A common garden experiment, also known as a transplant experiment, is an experiment for analysing the behaviour of different species in a common environment. An essential advantage of the common garden design compared with scattered long-term experiments including various species but in disjunct design is that they allow unimpaired comparison of the species at the given sites. Because the organisms develop in the same "garden", their environmental conditions, such as day length, sunlight, rainfall, temperature, and soil are the same. This avoids confounding effects, and allows the comparison of species behaviour under *ceteris paribus* conditions.

Common gardens were first used to analyse the behaviour of herbaceous plants (Tansley, 1917), then also of woody plants (Cheplick, 1992; Kullman, 1993), animals (Pelini et al., 2012), and other organisms (Cheplick, 2008; Wikelski et al., 2003). Common garden experiments may comprise monocultures of different species or provenances of a species, or even mixed cultures of selected species. If several common gardens are established, for instance along an ecological gradient, they may reveal the species-specific performance in dependence on the environmental conditions (Oleksyn et al., 1998). They can contribute to ecosystem understanding (e.g., site-growth relationship, adaptation, intra- and inter-specific competition and facilitation) but also to practical decision making (e.g., species or provenance selection for maximising stand productivity, quality, and resistance). As common garden experiments established across wide ecological gradients, support the selection of species and provenances suited for different climatic regimes, they currently undergo a revival in view of climate change (Reich and Oleksyn, 2008).

Although forest science and practice are commonly focused on the long term development of tree species under various site conditions, we found just a very few studies reporting about the growth and productivity from common garden experiments. Analysing *Nothofagus pumilio* in common gardens, Premoli et al. (2007) found a strong effect of altitude on morphology and phenology. A similar effect of altitude on cold resistance of *Picea abies* was observed by Oleksyn et al. (1998). Based on common garden studies, Reich and Oleksyn (2008) and Kullman (1993) found strong relationships between climate and growth and survival for *Pinus*

sylvestris and *Betula pubescens*, respectively. Although the initial intention of common gardens was the comparison of a broader set of species regarding their productivity on different sites, we did not find such evaluations except common gardens with various provenances of a given species (Aitken et al., 2008; Voltas et al., 2008).

In Denmark, a common garden trial was established in 1965 including 12 exotic and indigenous tree species at 13 locations along an productivity gradient. Today, depending on tree species and site quality, many of the stands have reached maturity and have been measured up to eight times. In view of the rather poor knowledge base of long term growth extracted so far from common gardens, our experiment appears rather unique. We use it for answering the following questions: (i) how do the species differ in their average biomass production?, (ii) how does their performance vary in space, i.e., along the productivity gradient? and (iii) how does their performance vary over time, i.e., in different survey periods? We used biomass production rather than volume growth and yield, to better capture species specific differences in biological productivity.

2. Materials and methods

The common garden experiment was established to investigate and compare the growth and health of the 12 tree species included: *Fagus sylvatica* L., *Pseudotsuga menziesii* (Mirb.) Franco, *Abies grandis* (Douglas ex D. Don) Lindley, *Larix kaempferi* (Lamb.) Carr., *Chamaecyparis lawsoniana* (A. Murray) Parl., *Pinus contorta* Douglas, *Pinus mugo* Turra var. Rostrata, *Abies procera* Rehder, *Picea abies* (L.) Karst., *Quercus robur* L., *Abies alba* Mill., and *Picea sitchensis* (Bong.) Carr. The tree species were chosen among those commonly grown or predicted to be of future importance in Danish forestry at the time.

The experiment is located on 13 sites in Denmark (Fig. 1). The sites were selected to include most typical Danish site types ranging from the sandy outwash planes and harsh Atlantic climate in the western part of the country, the gravelly tills and intermediate climate in the central parts and the clayey soils and more continental climate in the eastern parts. The former land uses of the selected sites included cropland, heathland, forest and oak scrub, with the larger part being former cropland (Table 1). The diversity of former land uses was accepted to be able to obtain homogeneous sites, each of a total size of about 3 ha.

The trials were established in the autumn 1964 and the spring 1965. At each site, 12 essentially square or rectangular plots of about 0.25 ha, one for each species (Table 2), were laid out before planting. Generally, the individual tree species were distributed randomly among the plots. For each species, the same provenance was planted across all sites. Provenances used were standard provenances according to Gøhrn (1957) and were mostly Danish land races, phenotypically selected as suitable for wood production in Denmark (Table 2). However, in some cases, the seed sources were of native foreign origin that had previously been shown to
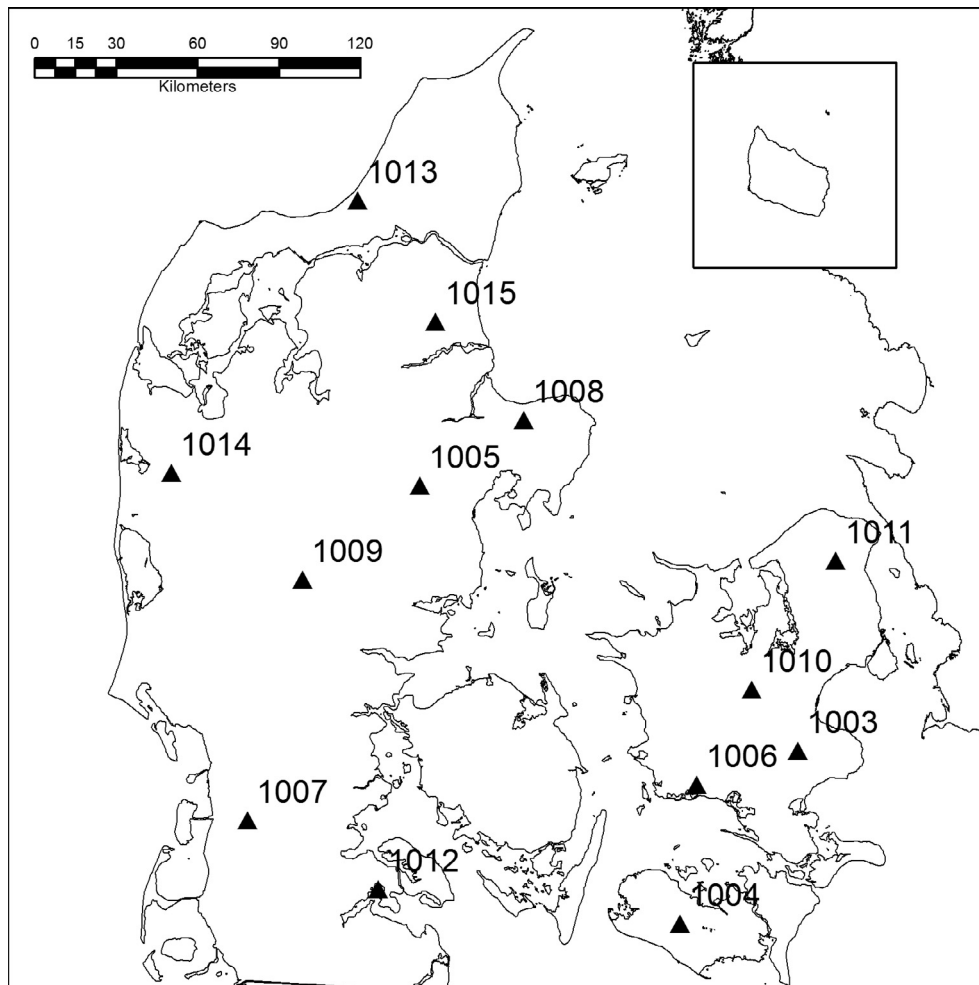

Fig. 1. Location of the field trials included in the common garden experiment. Each site included 10 conifer and 2 broadleaved species.

Table 1

Basic data for the 13 sites within the common garden experiment. Some plots were only measured few times due to poor growing conditions or destruction of the stand caused by windthrow (i.e. the forest at site 1006 was destroyed completely in the hurricane December 3, 1999).

Experiment	UTM North	UTM East	Soil type[a]	Soil texture	Former landuse	Climate	Measurement occasions[b]
1003	695279	6136415	Oxyaquic Hapludalf	Fine-loamy	Forest	Continental	6–9
1004	651929	6072566	Oxyaquic Hapludalf	Coarse-loamy	Cropland	Intermediate	7–9
1005	556085	6233934	Ultic Oxyaquic Hapludalf	Coarse-loamy	Cropland	Intermediate	7–7
1006	658182	6123847	Typic Hapludalf	Fine-loamy	Forest	Intermediate	3–7
1007	492634	6110713	Typic Quarzipsamment	Sandy	Oak scrub	Oceanic	5–11
1008	594399	6258113	Typic Oxyaquic Quarzipsamment	Sandy	Cropland	Continental	6–9
1009	512950	6199394	Aquod	Sandy	Cropland	Continental	6–9
1010	678366	6158785	Oxyaquic Hapludalf	Coarse-loamy	Cropland	Intermediate	7–9
1011	709370	6206263	Typic Hapludalf	Fine-loamy	Cropland	Intermediate	8–11
1012	540840	6085330	Typic Endoaquoll	Fine-loamy	Forest	Oceanic	8–9
1013	533226	6339015	Typic Psammaquent	Sandy	Cropland	Oceanic	6–8
1014	464584	6238767	Typic Haplorthod	Sandy	Calluna heathland	Oceanic	4–10
1015	561968	6294317	Typic Quarzipsamment	Sandy	Cropland	Continental	6–9

[a] Callesen (1993).
[b] Includes only intended measurements where all trees were measured. Measurements of minor windthrow is not included.

Table 2

Tree species included in the tree species trial. Provenances with an "F#" represent selected seed sources. Plant age is provided as *growing seasons in seedbed/growing seasons in transplant bed*. 'x' refers to species measured at the latest measurement in 2013 and '–' refers to plots lost due to calamities before the last measurement. Numbers in parenthesis refer to the number of measurements for the individual species and site combination (plot).

Latin name	Provenance	Plant age	Sites												
			1003	1004	1005	1006	1007	1008	1009	1010	1011	1012	1013	1014	1015
F. sylvatica L.	F128a, Lundsgaard	3/1	–(7)	–(7)	x(7)		x(8)	x(8)	x(6)	x(9)	x(9)	x(9)	x(7)	x(8)	x(6)
P. menziesii (Mirb.) Franco	F53a Wedellsborg	2/1	–(9)	–(8)	x(7)	–(6)	x(10)	x(9)	–(6)	x(9)	x(10)		x(7)	x(9)	x(8)
A. grandis (Douglas ex D. Don) Lindley	Comox, Vancouver Isl., B.C.	1/2	–(7)	–(7)	x(7)	–(5)	–(6)	x(9)	x(8)	x(9)	x(9)	x(9)	x(7)	x(9)	x(7)
L. kaempferi (Lamb.) Carr.	F22 Boller	2/1	–(8)	–(9)	x(7)	–(7)	x(11)	x(9)	x(9)	x(9)	x(11)	x(9)	x(8)	x(10)	x(9)
C. lawsoniana (A. Murray) Parl.	F64b Langesø	2/1 and 2/2	–(7)	–(7)		–(6)	x(9)	x(6)			–(8)	x(8)	x(6)	x(4)	x(6)
P. contorta Douglas	Gourtenay, Vancouver Isl., B.C.	2/0	–(8)	–(7)		–(3)	–(7)	–(8)	–(8)	–(7)	–(10)		x(7)	–(8)	–(8)
P. mugo Turra var. Rostrata	Aalbæk klitplantage	2/0		–(7)		–(6)	–(5)	x(7)	x(8)	–(7)	–(8)		x(6)	x(8)	–(6)
A. procera Rehder	F240b Frijsenborg	2/2 and 2/1				–(6)	–(7)	x(7)	x(6)	x(6)			x(6)	x(8)	x(9)
P. abies (L.) Karst.	F300 Rye Nørskov	2/2	–(8)	–(8)	x(7)	–(5)	–(6)	x(9)	x(8)	x(9)	x(10)	x(9)	x(7)	x(9)	x(8)
Q. robur L.	Zevenaar, Holland	2/0	–(7)	–(9)		–(7)	x(8)	x(8)	x(8)	x(9)	x(9)	x(8)	x(7)	x(8)	x(9)
A. alba Mill.	F329d Viborg	2/2		–(7)		–(7)	–(5)	x(7)	x(6)	x(8)	x(9)	x(8)	x(6)	x(8)	x(6)
P. sitchensis (Bong.) Carr.	F128a Lundsgaard	3/1	–(6)	–(8)	x(7)	–(6)	–(6)	x(8)	x(8)	x(9)	x(11)	x(9)	–(6)	x(9)	–(6)

be suitable for wood production in Denmark. Two-, three- or four-year-old plants were planted in a spacing of 1.3 × 1.3 m for conifers and 1.3 × 0.65 m for broadleaves. Some deviations regarding spacing occurred due to local conditions, but still about 6,000 and 12,000 plants were planted per ha for conifers and broadleaves, respectively. Compared to today's standards, planting numbers were high, reflecting previous practices due to lower costs. Regeneration and development during regeneration has been thoroughly described by Holmsgaard and Bang (1977).

At the time of the first thinning, sub-plots were established inside the original 0.25 ha plots, surrounded by buffer zones of 4–7 m. Gaps in the stand and similar irregularities were included in the buffer zone. At some sites, sub-plots for individual tree species were not established due to poor establishment success typically caused by frost damage, browsing or other calamities hampering the regeneration. Thinnings were conducted every 4–6 yrs depending on stand growth. Thinnings were generally carried out from below, the median thinning quotient (Q) being 0.83 ($Q = D_{g,2}/D_{g,3}$, where suffix 2 and 3 refer to the thinning and remaining crop, respectively). Thinnings were moderate to heavy, depending on stand age and species. In stands younger than 25 yrs, median thinned basal area corresponded to ~20–25% of basal area before thinning. In older stands, this value decreased from ~15% around age 30 to <10% in stands older than 45 yrs. Correspondingly, median residual basal area increased from ~17 m² ha⁻¹ at age 10–15 yrs to ~38 m² ha⁻¹ at age 45–50 yrs.

2.1. Measurements

The trees within the individual plots (including the buffer zones) were first measured at the time of the first thinning, which differed among tree species and sites due to differences in establishment success and growth. After the first thinning, the trees were measured before every thinning (every 4–6 yrs). A few plots were also measured before the first thinning and thinning due to windthrow was in some cases measured between ordinary measurements. In 2014, the plots had been measured 1–8 times since the establishment (Table 2), and many of the species were lost due to windthrows in especially 1999 and 2005.

In the plots, each row was numbered and the direction of measurements as well as the number of individual trees in each row was recorded to enable subsequent identification of individual trees. Each tree was marked permanently at breast height (1.3 m) and recorded individually in each ordinary measurement. For a few plots, trees thinned prior to the first full measurement were recorded in tally sheets to 1-cm diameter classes.

Individual tree diameters at breast height were obtained before thinning by averaging two perpendicular calliper readings (Table 3). It was further recorded whether the tree was selected for thinning and if the tree was alive or dead at the time of measurement. Before the first thinning, 50 trees per plot were selected for height measurements on standing trees. In subsequent measurements, a minimum of 30 trees per plot were measured for

Table 3
Number of measurements made on the individual sites of the species trial. The number of diameter (N_{dbh}), height (N_h) and stem volume (N_v) measurements totalled 556,163, 50,344, and 12,610, respectively.

Site	Plots	Measurements	First measurement	Most recent measurement	N_{dbh}	N_h	N_v
1003	9	70	1980	2013	31,148	3321	855
1004	11	94	1977	2013	38,492	3656	1037
1005	6	42	1985	2013	12,389	1757	336
1006	12	82	1977	2013	41,039	3633	925
1007	12	89	1974	2013	45,085	3756	1096
1008	12	97	1976	2013	50,369	4433	1129
1009	11	81	1975	2013	32,621	3459	866
1010	11	95	1977	2013	41,398	4099	1250
1011	12	116	1974	2013	50,536	6076	1173
1012	8	69	1982	2013	30,209	2853	739
1013	15	103	1982	2013	67,761	4581	965
1014	12	97	1976	2013	64,811	4544	1167
1015	12	88	1974	2013	50,305	4176	1072

height. The height measurements in connection with the first thinnings were performed using a height pole. Later measurements were carried out using a clinometer (Table 3).

At some measurement occasions, individual tree volumes of up to 25 felled trees were measured by sectioning stems (conifers and broadleaves) and branches (broadleaves)(Table 3). Stem diameters were measured by single or double (perpendicular) calliperings at 0.25, 0.75, 1.5 m above ground and subsequently at 1 m intervals. Branches were sectioned in 1 m sections from the stem node to an approximate diameter of 3 cm and remaining branches were weighed.

2.2. Calculations and analyses

Based on the pairwise measurements of diameter and height, species-specific d/h-regressions were established for each site. Subsequently, the d/h-regressions were used to estimate the height of trees not measured for height. Individual tree biomass was estimated using species specific biomass equations for beech (Skovsgaard and Nord-Larsen, 2011), Norway spruce (Skovsgaard et al., 2011), Sitka spruce, grand fir, silver fir, Douglas fir, and Japanese larch (Nord-Larsen and Nielsen, 2015). The biomass functions were in part developed on trees sampled in the common garden experiment (Nord-Larsen and Nielsen, 2015).

For all other species where no biomass equations were available, individual tree volumes were first calculated using species specific volume equations for predicting total tree (broadleaves) and stem (conifers) volumes (Madsen, 1987). When trees were measured for volume, the measured rather than the estimated volume was used. Further, when more than 10 trees were measured for volume, results were used to correct model estimated volumes by multiplying with the ratio between measured and estimated volume. Above ground (broadleaves) and stem (conifers) volumes were subsequently calculated using species specific basic densities (Moltesen, 1988). Above ground biomass for conifers was finally calculated by applying an expansion factor model for conifers developed for the Danish National Forest Inventory using the data from Skovsgaard et al. (2011) and Nord-Larsen and Nielsen (2015). Plot wise estimates of volume and biomass production were estimated by summation of individual tree estimates.

Analysis of species specific biomass production may be affected by the time of comparison as the growth of different species peaks at different ages. We analysed the production trajectory by fitting the Chapmann-Richards function to the total cumulated biomass production (P) observed at age t for the s species at the jth site: $P_{s,j} = a_j * (1 - exp(-b_j * t_{s,j}))_j^c + \varepsilon_{s,j}$. The function was fitted with non-linear regression using the MODEL procedure of SAS 9.4, and the maximum annual and maximum mean annual production

were found numerically. Species specific differences in the production and tree age at the time of maximum annual and maximum mean annual production were analysed using mixed linear regression with the MIXED procedure of SAS 9.4, including the individual sites as a random effect.

We assessed biomass productivity using basic statistics and plots showing the mean annual biomass production (MAP). We compared MAP across different sites and species using multivariate analysis of variance. Predictor variables included tree species, soil texture, and former land use. Finally, we analysed the adaptivity of individual species to different growing conditions using the approach suggested by Finlay and Wilkinson (1963). The relationship between species specific MAP versus average MAP of all species on each site for individual years was analysed using multiple linear regression:

$$MAP_{ij} = \alpha_i + \beta_i \times \overline{MAP_j} + \varepsilon_{ij}, \tag{1}$$

where MAP_{ij} is the mean annual above-ground biomass production of species i at site j, $\overline{MAP_j}$ is the average MAP of all species included from site j, α_i and β_i are the species specific intercept and slope, and $\varepsilon \sim N(0, sigma^2)$ is the residual error.

In this way, the site averages provide a numerical grading of the otherwise complex and interacting edaphic and climatic factors determining growth and regression slopes provide a measure of relative species specific adaptation or invariance to different growth conditions. As some species within individual sites were missing e.g. due to poor stand establishment or previous windthrow, the analyses included only combinations of measurement occasion, site and tree species where all species were measured on all sites.

To ease interpretation of the results, we normalised Eq. (1) by subtracting $\overline{MAP_j}$ on both sides of the equation:

$$nMAP_{ij} = \alpha_i + \beta_i^* \times \overline{MAP_j} + \varepsilon_{ij}, \tag{2}$$

where $nMAP_{ij} = MAP_{ij}^* - \overline{MAP_j}$ and $\beta_i^* = \beta_i - 1$. In this model formulation, significance of the slope parameter is equivalent to a significant deviation from unity of the slope parameter in Eq. (1). Such a deviation may be interpreted as species specific difference in the relative gain from a general improvement in growing conditions.

3. Results

In year 2013, after 48 growing seasons, stand conditions differed substantially between different species and sites. The dominant heights of the fastest growing *A. grandis* and *P. menziesii* were almost three times as tall as the most slow growing *P. mugo* and *Q. robur* (Table 4). Average basal area and growing stock of *A.*

Table 4

Mean and range of stand level variables in 2013 at stand age 48 after planting. The number of plots not terminated due to e.g. wind throw is denoted "plots". Other variables are: dominant height (H_{100}), basal area (G), mean quadratic diemeter (D_g), growing stock (V), and above-ground biomass (B_{ag}).

Species	Plots	H_{100} (m)	G (m^2 ha^{-1})	D_g (cm)	V (m^3 ha^{-1})	B_{ag} (tonnes ha^{-1})
A. alba	10	23.9	44.4	30.6	526	241
		18.5–28.8	32.7–54.7	22.1–38.9	313–754	158–326
A. grandis	8	30.4	57.7	41.2	810	332
		20.7–36.2	39.7–76.4	25.1–49.2	390–1177	185–464
A. procera	7	20.4	46.2	32.0	429	213
		15.5–24.6	38.1–55.8	21.9–41.1	243–606	134–287
C. lawsoniana	10	18.1	43.4	24.4	405	208
		13.7–21.5	34.5–58.7	19.3–29.4	286–629	153–316
F. sylvatica	12	20.9	23.6	23.1	292	168
		14.8–25.7	16.9–33.1	11.7–31.1	153–463	92–261
L. kaempferi	12	23.7	28.1	32.2	341	166
		18.1–28.2	21.4–40.9	25.1–38.5	204–530	102–261
P. abies	10	25.4	48.0	31.2	597	280
		19.7–28.5	31.3–63.3	22.4–37.1	299–832	151–377
P. contorta	3	23.9	38.2	31.8	496	233
		23.6–24.1	36.8–39.4	29.7–33.4	488–506	229–239
P. menziesii	9	27.8	44.0	37.0	526	258
		22.1–33.0	34.0–56.9	32.6–40.4	372–725	188–352
P. mugo	6	15.0	18.6	19.3	145	98
		12.8–17.1	10.0–28.8	16.5–21.1	75–238	51–160
P. sitchensis	6	29.0	45.6	36.2	634	260
		26.4–31.8	38.3–57.0	31.6–40.9	481–887	206–346
Q. robur	11	18.9	15.7	21.4	175	100
		13.0–24.0	11.0–20.5	13.4–28.8	97–275	55–157

grandis across all sites was three to four times larger than the average basal area of *P. mugo* and *Q. robur* stands. In terms of above-ground biomass, the far largest stocks were found in *A. grandis*, but the variation in biomass stocks between sites was also larger than for e.g. *P. sitchensis*.

3.1. Temporal, spatial, and species specific differences in biomass production

Total biomass production increased almost linearly for all tree species at the different sites (Fig. 2). Despite the linear appearance, analysis of the production trajectory using the Chapman-Richards growth function, showed that stand biomass production had peaked before the last measurement after 48 growing seasons for all species. The inflection point varied significantly ($P < 0.0001$) between different species, occurring earlier for *L. kaempferi* and *P. mugo* and later for *C. lawsoniana*, *F. sylvatica*, *A. alba*, and *A. grandis*. The inflection point also differed among sites ($P < 0.0001$), tending to occur later on poor, sandy soils (1005 and 1013) than on other sites. Due to the early peak of biomass production, maximum MAP had been reached for *L. kaempferi* and *P. mugo* on all locations at the time of the latest measurement. Oppositely, due to the late peaking growth, maximum MAP had not yet been reached on most locations for *C. lawsoniana*, *F. sylvatica*, *A. alba*, and *A. grandis*. However, for all other species, maximum MAP occurred around the time of the most resent measurement after 48 growing seasons. As the surface of the MAP is relatively flat, this notion enables comparison of the different species despite differences in longevity.

Mean annual biomass production (MAP) differed widely among different species and sites. At the best sites, the most productive species (*A. grandis*) reached a MAP of 13.6–14.6 tonnes ha^{-1} yr^{-1} in the first 48 growing seasons. The least productive species included *Q. robur* and *P. mugo*, which on the best sites produced 5.8–6.7 tonnes ha^{-1} yr^{-1}. The differences in MAP among species were highly significant ($P < 0.001$). After 48 growing seasons *A. grandis*, *P. sitchensis*, *P. abies* and *P. menziesii* had the highest average MAP (Table 5). *A. alba*, *L. kaempferi* and *F. sylvatica* formed an intermediate group, while *Q. robur* and *P. mugo* were the least pro-

ductive. For most species, the ranking of different tree species did not change much when considering different growth periods with *A. grandis* as a noticable exception. The MAP also differed between different soil types ($P < 0.001$), being larger on loamy soils (coarse or fine) than on sandy, and between former land uses ($P = 0.03$), being larger on former cropland than on former *Calluna* heathland and oak scrubs. The effects of soil type and former land use were similar when considering other growing periods.

3.2. Analysis of MAP and site average MAP

We analysed the relationship between MAP and site average MAP (Eqs. (1) and (2)) in 1990, 2002, and 2013. In all cases, there was a strong and positive correlation between species specific MAP and site average MAP (Eq. (1)) for all species ($P < 0.0001$), indicating that the different tree species in general benefited from improved growing conditions. The models fitted the data well, explaining 80–91% of the total variation (R^2).

In 1990, after 25 growing seasons, 10 tree species were all present at 10 different sites. The relationship between species specific MAP and site average MAP in Eq. (2) differed between species ($P = 0.028$), indicating that some species benefited more than others from improved growing conditions. For *P. abies* and *A. grandis*, the slope of Eq. (2) significantly exceeded 0 ($P \sim 0.05$), reflecting a larger than average gain in production from a general improvement in growing conditions (Table 6). Oppositely, compared to the other species, the slope for *P. contorta* was significantly smaller than 0, indicating relative indifference to improvements in growing conditions.

After 37 growing seasons and closer to the maximum of MAP for all species, 10 tree species were all present at 8 different sites (Fig. 3). Again, the slope of the relationship between species specific MAP and site mean MAP differed between species ($P = 0.006$). The slope of Eq. (2) significantly exceeded 0 for *P. abies* and *A. grandis* but was less than one for *P. mugo* (Table 6). For *P. sichensis*, the intercept of Eq. (2) was significantly larger than for the other species while the slope was not significantly different from 0. This
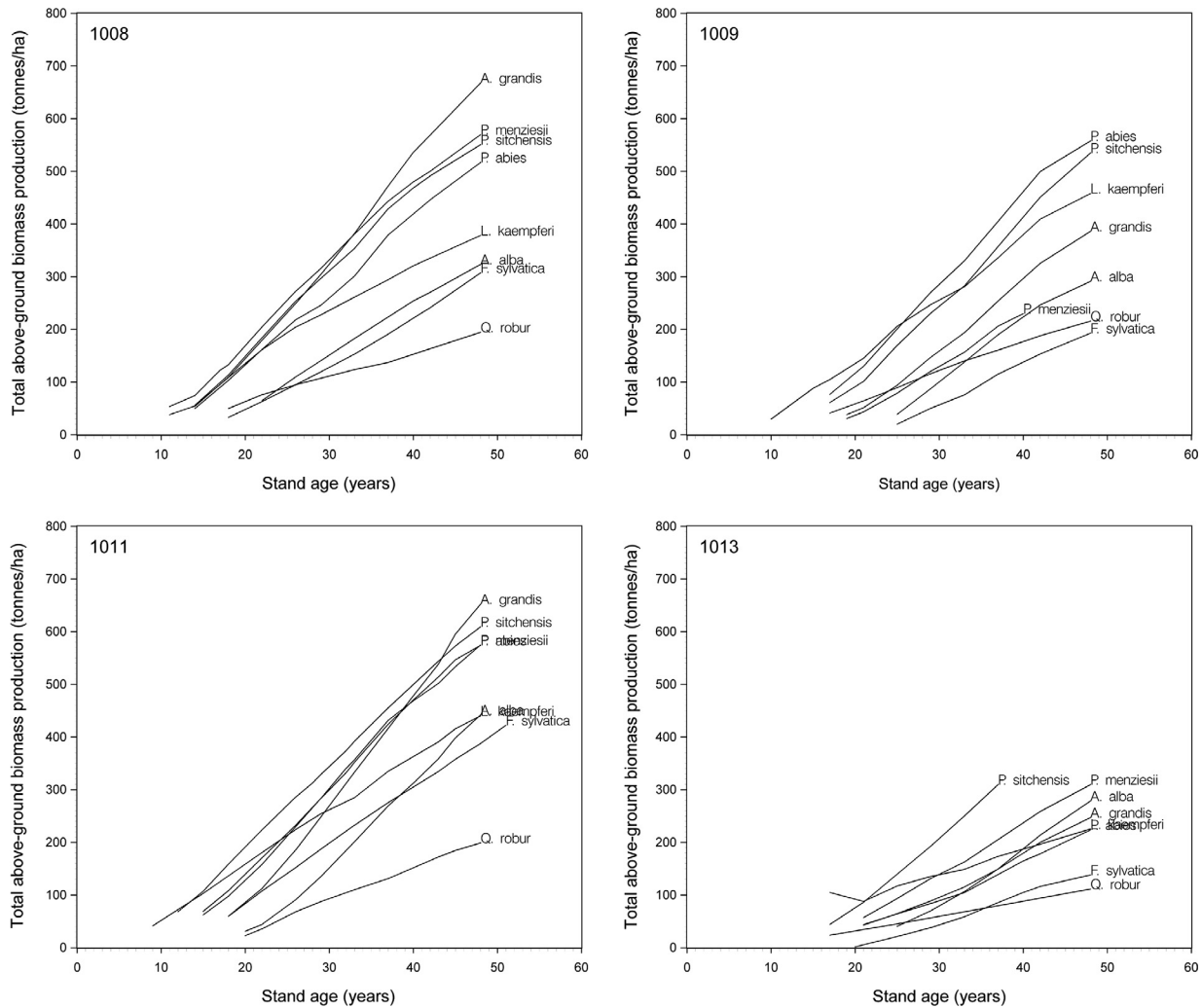
Fig. 2. Mean annual biomass production (total production/stand age) for sites 1008, 1009, 1011 and 1013. The selected sites represent the wide range of growing conditions covered by the common garden experiment as a whole.

Table 5
Average MAP across all sites and ranking of individual species after 48, 37 and 25 growing seasons. For each measurements occasion, ranks with the same letter are not significantly different, based on Duncan's Multiple Range Test.

| Species	2013 (48 yrs)		2002 (37 yrs)		1990 (25 yrs)	
	Mean	Rank	Mean	Rank	Mean	Rank
A. grandis	10.9	1[a]	9.6	2[ab]	6.5	5[b]
P. sitchensis	10.6	2[a]	10.3	1[a]	8.2	1[a]
P. abies	9.9	3[ab]	9.2	3[abc]	7.4	2[ab]
P. menziesii	9.3	4[ab]	8.6	4[bc]	6.8	3[ab]
P. contorta	8.1	5[bc]	7.8	5[cd]	6.1	6[b]
A. alba	7.4	6[cd]	6.3	7[ed]	3.8	7[c]
L. kaempferi	6.6	7[cd]	6.6	6[ed]	6.6	4[ab]
F. sylvatica	6.1	8[d]	5.2	8[ef]	3.4	9[c]
Q. robur	4.3	9[e]	4.0	10[f]	3.5	8[c]
P. mugo	3.6	10[e]	4.0	9[f]	3.4	10[c]

indicated a high MAP, relatively independent of growing conditions for this species.

At the latest measurement in 2013, after 48 growing seasons, only 8 tree species were all present on 5 different sites (Fig. 4). Contrary to the other periods analysed, the relationship between species specific MAP and site mean MAP did not differ among species (P = 0.101). However, based on the species specific analysis of

Eq. (2) showed that, despite the overall analysis, the slope was larger than 0 for *A. grandis* and near-significantly smaller than 0 for *P. sitchensis* (Table 6). Hence analysis showed that, compared to the other species, the biomass production of *A. grandis* benefited more from a general improvement in growing conditions. Oppositely, *P. sitchensis* has a large overall production as indicated by the large intercept, but benefits less from improved growing conditions.

Table 6
Parameter estimates for Eq. (2). Significance levels are as follows "ns": $P > 0.1$, $\dagger$: $0.1 \geqslant P > 0.05$, * : $0.05 \geqslant P > 0.01$, ** : $0.01 \geqslant P > 0.001$, *** : $P \leqslant 0.001$.

Species	1965–2013		1965–2002		1965–1990	
	Intercept	Slope	Intercept	Slope	Intercept	Slope
A. grandis	-3.3940^{ns}	0.9058^{*}	-5.2700^{*}	1.0740^{**}	-2.4083^{ns}	$0.5920^{\dagger}$
F. sylvatica	-5.5143^{ns}	0.5430^{ns}	$-4.1659^{\dagger}$	0.2881^{ns}	$-3.2716^{\dagger}$	0.1980^{ns}
P. contorta			3.7876^{ns}	-0.4294^{ns}	4.4825^{*}	-0.7132^{*}
P. mensiezii			0.8746^{ns}	0.1009^{ns}	0.0116^{ns}	0.2165^{ns}
Q. robur	-1.5542^{ns}	-0.2529^{ns}	-1.2734^{ns}	-0.2811^{ns}	-0.9729^{ns}	-0.228^{ns}
A. alba	-1.4167^{ns}	0.1219^{ns}	0.3596^{ns}	-0.2500^{ns}	-0.3149^{ns}	-0.2820^{ns}
P. mugo	0.4636^{ns}	-0.6071^{ns}	1.3706^{ns}	-0.6579^{*}	0.1329^{ns}	-0.4370^{ns}
L. kaempferi	3.4969^{ns}	-0.4611^{ns}	2.5005^{ns}	-0.3556^{ns}	$3.1879^{\dagger}$	-0.3464^{ns}
P. abies	-1.3314^{ns}	0.5033^{ns}	-3.6728^{ns}	0.7861^{*}	-1.7152^{ns}	0.6124^{*}
P. sitchensis	9.2501^{*}	$-0.7530^{\dagger}$	5.4891^{*}	-0.2751^{ns}	1.0891^{ns}	0.3154^{ns}
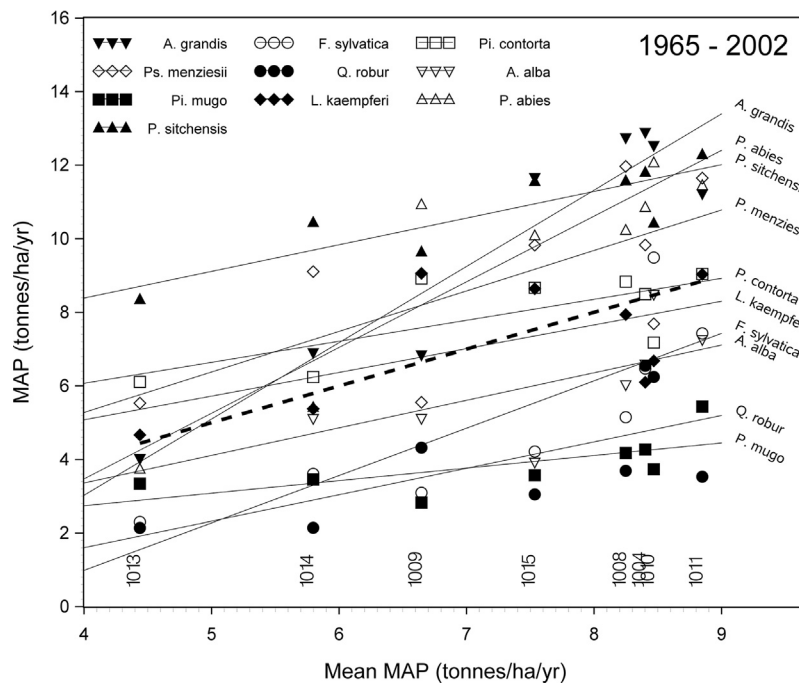
Fig. 3. Species specific mean annual biomass production (MAP) vs. site average MAP for the included species after 37 growing seasons. Individual lines represent regression linear regressions for each species. The dotted line is a 1:1 reference line, for the mean species-overarching increase of mean annual production with improving site conditions. The analysis included 8 sites and 10 species reflecting the number of plots lost due to e.g. windthrow.

4. Discussion

4.1. Methodological considerations

In contrast to many other studies based on site index (Karlsson et al., 1997; Skovsgaard and Vanclay, 2008) we used the mean annual biomass production (i.e., the total yield divided by stand age) as indicator for the site productivity and fertility. Site index, based on tree height and age would have been very much negatively biased due to the height and branch growth reducing effect of wind which is strong on many of the sites close to the coast (Hessenmoller et al., 2001; Watt et al., 2005). In addition site index represent only the vertical aspect of production and neglects the yield level, while the total yield and mean annual growth integrate both vertical and horizontal aspects of production (Assmann, 1970, p. 167).

By using biomass functions and expansion factors, developed in part on trees from the common garden experiment, we based our analyses on total yield of above-ground biomass instead of merchantable tree volume, often used as makeshift in other studies (del Río et al., 2016; Waring et al., 2006). Tree allometry can be very species-specific; e.g., the share of branches of the total bio-

mass can be much higher for broad-leaved species compared with conifers. Comparison based on biomass are more comprehensive and meaningful for comparing productivity and carbon sequestration. Unfortunately species- and site-specific allometric functions for below ground production were not available. Trees tend to change their allocation between root and shoot biomass along productivity gradients. On dry and poor soils they invest higher portions into the root for acquisition of the limited below-ground resources. On moist and fertile sites they tend to favour shoot and crown growth as light is the limiting resource (Comeau and Kimmins, 1989). This means that the reported increase of above-ground productivity along the analysed site gradient may be partly caused by a partitioning of the total tree growth in favour of shoot and on the expense of root growth (Thurm et al., 2017).

The thinning regimes applied at the individual sites in the common garden experiment were not specified but according to 'local practice'. Differences in thinning practices could potentially affect the results as e.g. heavy thinnings from above would reduce total production (Skovsgaard, 2009). However, all included stands were fully stocked and were just moderately thinned. The relationship between stand density and productivity follows a unimodal optimum curve in young stand ages and an S-shaped saturation in
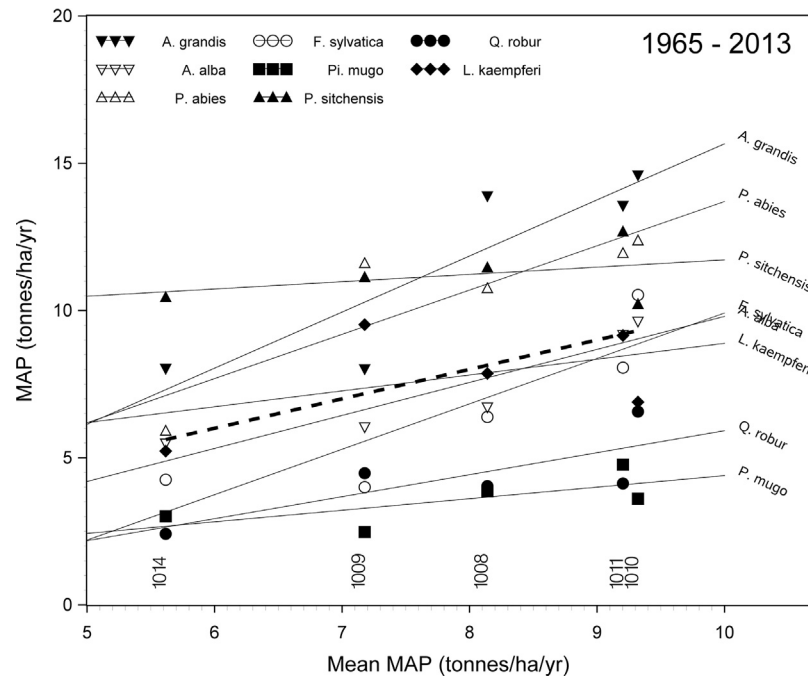
Fig. 4. Species specific mean annual biomass production (MAP) vs. site average MAP for the included species after 48 growing seasons. Individual lines represent regression linear regressions for each species. The dotted line is a 1:1 reference line, for the mean species-overarching increase of mean annual production with improving site conditions. The analysis included only 5 sites and 8 species reflecting the number of plots lost due to e.g. windthrow.

advanced stand age (Assmann, 1970), i.e., a moderate reduction of stand density as on our plots would slightly increase or just slightly decrease stand growth in the young and advanced stand age, respectively. Although thinned, we can assume that the reported mean annual productivities represent rather well the maximum productivity on the sites included into the study.

In the experimental design, care was taken to select homogenous sites and randomize placement of individual plots within sites. However, analyses of thinning experiments have previously demonstrated that considerable site productivity variation may occur in apparently homogeneous stands (Skovsgaard, 2009). Such variation obviously leads to an increased demand for replication of experimental treatments or other means to account for pre-treatment variation in site productivity. The common garden experiment reported in this study did not include such repetitions of the individual tree species within sites. In our analyses it was hence not possible to analyse and account for within-site variation in growing conditions. A possible method to deal with the lack of repetition would be to include a pre-treatment measure of site productivity, such as soil nutrient status or texture, as a covariate in the analysis. However, although a qualitative description of the soil down to 2 m's depth was collected for each plot (Callesen, 1993), quantitative soil data were only available at the site-level. An alternative approach would be to create repetitions by grouping sites with similar growing conditions, and treat these as individual blocks. However, soil texture, former land use and local climate vary to an extent that would make such grouping of the material unreasonable.

In our common garden experiment, the same provenance were used for each species across all sites, enabling comparison of tree species performance across sites. Obviously, some of the selected provenances could have a higher degree of breeding and selection than from others and hence may not express the full potential of the species. However, since provenances were selected among seed sources known as suitable for wood production, the effect of provenance selection on our results is likely small. Furthermore,

although using the same provenance across all sites on one hand enhances species comparison, some provenances may be better adapted to certain growing conditions than others (Vitasse et al., 2009), confounding our results. The effect of such provenance-site interaction on our results is unknown.

4.2. Implications for forest practice

As expected, mean annual biomass production (MAP) differed widely among different species and sites ranging between 3.5 and 13.5 tonnes ha^{-1} yr^{-1} on the three best sites and between 2.2 and 6.3 tonnes ha^{-1} yr^{-1} on the poorest. Commonly, the within site gain in maximum annual above-ground biomass production when choosing the best performing species over the poorest was 3-4-fold.

Our analyses showed a strong and positive correlation between species specific MAP and site average MAP for all species, indicating that the different tree species in general benefited from improved growing conditions. However, the slope of the relationship differed significantly between species, indicating that some species benefited more than others. In a forestry perspective, species with a high production and relatively invariant to differences in growing conditions, such as *P. sitchensis*, may be preferable at poor sites or when knowledge about growing conditions are scarce. However, there is a significant gain from choosing species with a potential to adapt to and benefit from improved growing conditions such as *A. grandis* in our analyses.

When analysing the relationship between species specific MAP and site average MAP we observed that for some species, the slope of the relationship differed between growing periods. For example after 37 growing seasons, MAP of *P. sichensis* increased faster than site average MAP (Fig. 3, while after 48 growing seasons this species seemed more invariant to growing conditions (Fig. 4). An ecological reason could be that some species may utilise available resources differently in the span of their lifetime and hence show different response to growing conditions across their life cycle.

However, in our analyses, due to the loss of species at different sites, different numbers of plots are used in the analysis of different growing periods. This renders direct comparison of the slopes impossible.

Monospecific stands located along an ecological gradient, such as our common garden experiment, allow quantification of the production optimum of a species, i.e., the level, change and maximum of the productivity. As also shown in our experiment, most species are most productive on moist and fertile sites when growing in monoculture. While they reach their production optimum on very similar sites, their ecological optimum differs considerably from the production optimum and also between the species (Körner, 2002). The ecological optimum is characterised by the sites conditions where a species reaches highest abundance under natural conditions, when growing in mixture and competing with other species. E. g. *P. abies* is very productive when promoted in monoculture but would withdraw to colder, higher altitudes or latitudes and would be replaced by *Q. robur* and *Fagus sylvatica* without human interference at lower altitudes of latitudes. This means that the found ranking of species productivity in our study applies for their growth in intra-specific competition and may strongly change when growing under inter-specific competition in mixed-species stands.

Pretzsch et al. (2014) showed that there are significant species-specific differences in nutrient content in various tree organs, however, the main differences when harvesting biomass of one or the other species is not a quality but a quantity effect. Consequently, export of the biomass out of the ecosystem by harvesting would mean much higher nutrient exports in case of the fastest growing species. For example, *A. grandis* the nutrient concentration in stem and branches may be lower than in *Q. robur*, however, when the nearly threefold amount of biomass is exported in case of *A. grandis* or *P. sitchensis*, the differences in nutrient concentration are minor in relation to the differences in the exported mass. However, importantly in relation to whole tree harvesting for forest fuel production, the nutrient-rich leaf-fraction is exported from the ecosystem for conifers but would usually be left in the stand for broadleaved species, when harvesting is carried out during fall or winter.

4.3. Relevance for carbon sequestration and bioenergy usage

Currently, the global society is putting on large efforts to mitigate climate change by reducing emissions of greenhouse gases. Several studies have demonstrated that terrestrial ecosystems can provide a cost effective, short-term buffer to reduce atmospheric CO_2 (Miner et al., 2014; Hudiburg et al., 2011). However, the potential for ecosystem uptake is limited by environmental constraints and likely not to be reached. Consequently, real long term reductions are only achieved by reducing CO_2 emissions from all sources and thus by substitution of fossil energy and carbon intensive materials with renewables, while protecting high-carbon ecosystems from human depletion (Mackey et al., 2013; Fargione et al., 2008).

The effectiveness of substituting fossil fuels and carbon intensive materials with biogenic resources is highly dependent on plant growth rates (Lamers and Junginger, 2013). Consequently, prediction of forest growth is pivotal when assessing the effect of substituting fossil energy and materials with forest biomass. Our results may suggest a selection of species with superior biomass production and carbon sequestration. The fastest growing species are certainly superior in growing space and light use efficiency. How the species come off regarding water and nutrient use requires further investigations, but the ranking of species may be influenced by climate change. Regional models predict, that due to climate change, temperatures in Europe will increase, and that

the increase will be more pronounced in Northern Europe. The climate models further predict that water availability during the summer will decrease in most of Europe and that the frequency and lengths of drought periods will increase (Olesen et al., 2014). A recent study on tree-growth responses to future climate, based in part on the common garden experiment also described in the present study, showed that the growth of most species was negatively correlated with summer drought (Huang et al., submitted for publication). For a future climate scenario, species such as *P. abies*, *F. sylvatica*, *L. decidua*, and *A. grandis* were projected to sustain growth losses of 10–16% onto 2100, while the growth of *P. menziesii*, *P. sitchensis*, and *Q. robur* was only marginally reduced or even increased.

Our study demonstrated significant differences in the potential for biomass production between tree species. However, multiple purpose forestry certainly should consider the whole spectrum of forest ecosystem services and functions (MCPFE, 1993) and how they fit to the respective objective of the forest estate as basis for species selection and management. Such considerations should also include future effects of climate change, and may be aided by knowledge from common garden experiments as demonstrated by Huang et al. (submitted for publication).

5. Conclusions

After 50 yrs survey this common garden experiment provides valuable information about timber and bioenergy production still being a core function of multi-purpose forestry. It needed the continuity of half a century continuous measurement to come to the remarkable finding that by the right match of species with site conditions the productivity and C-sequestration in terms of biomass per unit area can be about the threefold compared with the most unfavourable species selection on the same site. Regarding growing space as a resource, this means a striking increase of resource-use efficiency simply by smart species selection; notice that this by far exceeds the benefits of thinning or provenance selection. The analyses showed that the North American conifers including A. grandis and P. sitchensis had a significantly higher potential for biomass production than the other species. However, while P. sitchensis was relatively invariant to site conditions, the analysis indicated that, compared to the other species, A. grandis benefited more than the other species from a general improvement in growing conditions. The effectiveness of substituting fossil fuels and carbon intensive materials with woody bioenergy is highly dependent on plant growth rates. Our results may suggest a selection of species with superior biomass production and carbon sequestration. The experiment forms a unique basis for also testing the long term consequences of the species selection for other forest functions and services, such as e.g., ground water provision, biodiversity, or mechanical stability.

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