Genetic diversity reduces competition and increases tree growth on a Norway spruce (*Picea abies* [L.] KARST.) provenance mixing experiment

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A B S T R A C T

Many recent studies address that diversification of tree species and stand structure can increase the level and stability of growth and other forest functions and services to mitigate natural and human disturbances. Most studies so far focussed on the diversification of tree species mixing and stand structure. The potential of intra-specific genetic diversification in terms of provenance mixture was hardly explored so far.

Here we analyse how a mixing of species provenances of Norway spruce (*Picea abies* [L.] KARST.) affects the competition between neighboring trees and their growth. We based our study on the 40-years-old provenance-mixing experiment Vohenstrauß 622 in the Upper Palatinate Forest in South Germany. Here 21 different provenances from clonal propagation of Norway spruce across Germany were combined in individual tree mixture, replicated in different spacing, and thinning. Our main objective was to analyze how the individual tree competition, tree growth, and stand productivity were affected by neighboring trees of different provenances.

First we show that at an tree age of 43 years the different provenances strongly vary between 10 and 27% in their crown diameter, cd, stem diameter, d, crown length, cl, and tree height, h, with a ranking $cv_{cd} > cv_d > cv_{cl} > cv_h$ in the coefficient of variation, cv. We found significant differences of the stem and crown allometry between the provenances; e.g. the range of the allometric exponents of $h \propto d^\alpha$ was $\alpha = 0.12–0.58$ and of $cd \propto d^\alpha$ $\alpha = 0.47–0.84$.

Second we found that different provenances in the neighborhood reduced the inter-individual competition and increased the stem diameter growth. Having 10 different provenances in the neighborhood increases the diameter growth of a tree on average by 28 % compared with having only 5 provenances in the neighborhood. Stem diameter followed a saturation curve with increasing number of provenances.

Third we showed that an increasing number of provenances also increased the productivity at the stand level. The effects on stand growth are not only determined by the number of different provenances per area but also by their spatial mixing pattern.

The inter-provenance complementarity of tree allometry is discussed as main cause of the revealed reduction of competition and increase of growth. We further discuss how spatially explicit individual tree models may incorporate tree structure as proxy of provenance characteristics. We conclude that genetic diversification in terms of provenance mixture can increase and stabilize tree and stand growth analogously to tree species mixing and may be further explored and considered as seminal silvicultural option.

1. Introduction

Research into forest stands with diversity of species and structure revealed that diverse neighborhood can cause facilitation (del Río et al. 2014, Cavard et al. 2011) and competition reduction (Williams et al. 2017, Kelty 1992), and that diversity can result in overyielding of mixed versus mono-specific stands (Zeller and Pretzsch 2019, Fichtner et al. 2018, Jactel et al. 2018, Pretzsch 2005). Thus mixed stands have the

potential to increase wood production and carbon storage (Liang et al. 2016) and at the same time maintain or even improve other provisioning and regulating services of forests (Schwaiger et al. 2018, Dieler et al. 2017). Here, we scrutinize whether also a mixture of different provenances of the same species provides similar advantages as mixed-species stands.

Probably the facilitation by humus layer improvement (Augusto et al. 2002), hydraulic lift (Caldwell et al. 1998), atmospheric nitrogen

fixation (Forrester et al. 2006) or barrier building against pathogens (Malézieux et al. 2009, Jactel and Brockerhoff 2007) which are well know for mixed-species stands will be less efficient in mixtures of provenance. The inter-provenance differences in the trees' physiological traits, their ways of resource aquisition and modification of the environment can be assumed to be rather small compared with the big differences in inter-specific mixtures. So, the preconditions for growth increase by inter-provenance facilitation may be restricted. However, the preconditions for competition reduction may be given, due to morphological diversity (Barbeito et al. 2017), reduced crown shyness (Onoda and Bando 2021) due to provenance-specific structure, space occupation and canopy packing density (Čortan et al. 2019, Gandour et al. 2007). In addition provenances may differ in the intra-annual and long-term temporal pattern of resource acquisition, and this may improve growth (Knutzen et al. 2015, Pretzsch 2014, Gratani et al. 2003, Chmura and Rozkowski 2002). This suggests that intra-specific but inter-provenance mixture may cause competition reduction, increase the maximum stand density, and tree growth under given density compared to stands that consist of similar provenances. This would mean analogous interactions in provenance mixtures as in species mixtures with structural or temporal niche complementarity (Williams et al. 2017).

Analyzing and comparing various provenances of tree species based on generative or vegetative propagation is very common in forest science since long (Beuker 1994, Günzl 1979, Schober 1961). The main objective is to provide forestry with genotypes that are superior in terms of vitality and growth, wood quality, and resistance against disturbances (Schober 1961). A special focus was on the selection of suitable provenances of foreign tree species, e.g., on analyzing provenances of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Eilmann et al. 2013) or English walnut (*Juglans regia* L.) (Kerr 1993) as a knowledge basis for their successful establishment in forestry in Europe. Recently, provenance research also considered succeptibility to drought (Atzmon et al. 2004), warming (Arend et al. 2011), and other disturbances such as ozone exposure (Paludan-Müller et al. 1999) or herbivorous insects (Sinclair et al. 2015) in order to prepare and stabilize forests to environmental changes (Aitken et al. 2008, Matyas 1996). Most provenance experiments analysed and compared different provenances based on a number of mono-provenance plots (Schober 1961). In many cases similar experiments with the same provenances were established at different locations in order to reveal how the performance is co-determined by the site conditions (Liesebach et al. 2001). Mixed-species experiments are still rare (Pretzsch and Schütze 2021) and mixed-provenenance trials are even rarer. However, alike mixed-species trials offered insight into species interactions, provenance mixing trials may offer insight into interactions and effects on growth and yield of mixed- compared to mono-provenance stands. Genetic diversity, no matter whether due to mixture of species or provenances, may cause benefical effects based on a variety of niches, diversity of traits, and the resulting stabilisation of productivity and risk distribution (Aussenac et al. 2019, Jucker et al. 2014, Chmura and Rozkowski 2002).

Analyzing any pros and cons of genetic diversity requires long-term survey as the phenotypical plasticity, canopy space occupation, and stand density effects need time to develop (Pretzsch 2014). Provenance experiments based on clones (Spellmann and Brokate 1991) may better maintain the desired genetic traits than provenance trials based on generative propagation. Thus, the middle aged, 40-year-old clone-based mixed-provenance experiment Vohenstrauß 622 in the Upper Palatinate Forest in South Germany which is underl`ying this study, is very suitable and rather unique for research into the inter-provenance interactions. On this experiment 21 different provenances from clonal propagation of Norway spruce across Germany were combined in individual tree mixture, replicated in different spacing, and thinning.

This study analyzed how a mixing of provenances of Norway spruce (*Picea abies* [L.] Karst.) modifies the competition between neighboring trees and their growth. The main question was how the individual tree competition and tree and stand growth were affected by mixing of provenances until the present stand age of 40 years, when the mean stand height was about 20 m. In detail the hypotheses were as follows.

H I: The Norway spruce provenances differ in size growth, stem allometry, and crown allometry.

H II: Mixing of provenances decreases the inter-provenance competition and increases the tree growth.

H III: At parity of age, stand density, and silvicultural treatment stand productivity increases with the diversity of provenances.

2. Material and methods

2.1. The background and rational of the provenance trial Vohenstrauß 622

The high relevance of Norway spruce is reflected by its share of about 20 % of the 177 million hectare of the forest area of Europe (Brus et al. 2012). The natural range of Norway spruce reaches from Scandinavia to middle and south Europe, from the Pyrenees to Siberia and the Central European highlands to the high altitudes of up to 1800 m a.s.l. in the Alps and Carpathain Mountains (Leuschner and Ellenberg 2017, Schmidt-Vogt 1986). A special feature of Norway spruce is its cultivation far beyond the natural range in the European lowlands due to its fast growth, high productivity, and valuable and versatile wood. However, beyond its natural range Norway spruce is prone to natural disturbanes; most common are damages by windthrow, bark beetle, ice-breakage, and drought (Knoke et al. 2021, Pretzsch et al. 2020). Forest management strives for appropriate thinning, species mixing, and optimal provenance selection in order to keep productivity, quality, and stability and stress resistance on a high level even on sites beyond the natural range.

Vohenstrauß 622 (VOH 622) is part of an transregional study that established 22 different Norway spruce provenances on various sites across Germany to analyse the performance of different provenances in terms of growth, quality, and resistance (Spellmann and Brokate, 1991). Identical experimental designs were realized in Bavaria, Lower Saxony, and Schleswig-Holstein. Here, we explain the setup of VOH 622 in Bavaria which is the basis of this evaluation. Notice that the provenance with code number 7 (Table 1) was planted in other experiments of the transregional study across Germany but not in VOH 622, thus VOH 622 comprises 21 provenances.

VOH 622 has the following special features that makes it appropriate for this study. It includes a wide variety of Norway spruce provenances from all over Germany (lowlands, highlands, Alps) obtained by cloning. Trees of the different provenances were planted in individual tree mixtures on plots with different spacing and thinning. The experiment has been established in 1978 with 3-years-old plants, so that the trees were 43 years at the last survey in 2018. Thus, this experiment is one of the oldest existing clone-based provenance mixing experiments and provides much more substantial knowledge compared to new experiments that are only a few years old.

2.2. The experimental setup of VOH 622

The provenance mixing trial Vohenstrauß 622 (location 49° 41′ N, 12° 26′ E) has been established 1978 in Southern Germany 10 km northeast of the city of Vohenstrauß/Bavaria in the Upper Palatinate Forest, close to the German/Czech border. It is located at 720–740 m a.s. l. on a slightly inclined northern exposed slope. The soils are nutrient rich slightly podsolic loamy braunsoil of basal gneiss with rich biotit content. The average precipitation is 904 mm in the year and 375 mm in the growing season. The temperature is 6 °C on average, 12–13° in the 120–130 days lasting growing season, and the annual temerature amplitude is 19 °C. In this region the natural vegetation would be European beech/silver fir forests (Walentowski et al. 2004). The experiment lies in the ecoregion 10.4 Inner Upper Palatinate Forest, according

Table 1

Overview of the Norway spruce provenances analyzed in this study. Clone number and provenance names according to Spellmann and Brokate (1991), altitudinal range of the occurrence of the respective provenance, number of sample trees in this study, code number of the provenance used in this study. The number of sample trees refers to the provenances available at the first survey in 1993. Notice that the provenance with code number 7 was planted in other experiments of the transregional study across Germany but not in VOH 622.

Clone no.	Provenance name	Altitude meter a. s. l.	Number of sample trees	Code number in this study
1–460	Bavarian Forest	> 1100	181	1
461–690	Upper Harz mountain	300–600	41	2
691–990	Western German highlands	300–600	15	3
1154–1604	Western German highlands	< 300	147	4
1605–1762	Western German highlands	<600	112	5
1763–1930	Harz foreland, Westerhof	900–1300	112	6
1980–2134	South Bavaria, Upper Swabia, Lake Constance	<700	269	8
2135–2252	Western German highlands	300–600	150	9
2253–2313	South Bavaria	300–700	81	10
2314–2530	South Bavaria, Upper Swabia, Lake Constance	<900	213	11
2531–2569	Swabian Alb, Bavarian Jurassic Alb	>700	12	12
2570–2744	other Southern Bavaria	300–700	128	13
2745–2976	Bavarian Forest	<1100	106	14
3001–3471	Western German highlands	<300	7	15
3472–3535	other Southern Bavaria	300–700	14	16
3536–3675	Western German highlands	300–600	23	17
3676–3727	Upper Harz mountains	300–600	20	18
3728–3826	Harz foreland, Westerhof		34	19
3827–3954	South Bavaria, Upper Swabia, Lake Constance	<900	53	20
3955–4027	Swabian Alb, Bavarian Jurassic Alb	>700	44	21
4082–4289	South Bavaria, Upper Swabia, Lake Constance	<900	25	22

to Arbeitskreis Standortskartierung (1985). The site index based on the height of the dominant trees was 38 m at age 100 according to the yield table by Assman and Franz (1965). It indicated a very good productivity of the Norway spruce stands.

VOH 622 consists of 9 plots that were planted in 1978 with 3-years-old spruce clones. The plants were 44.7 cm high and based on cuttings of plants from 21 different regions in Germany (see Table 1). Alltogether we used 427 different clones from 21 different provenances. All plots are 30 m × 35 m, i.e. they have an area of 0.105 ha (Fig. 1). They all are surrounded by buffer zones that were planted and treated similarly to the core area. The total area of the experiment is 2.8 ha, the measuring area covered by clones of different provenances is 0.945 ha. The clones were planted with a spacing of 1.25 × 1.25 (one plot), 1.25 × 2.50, 2.50 × 2.50, 2.50 × 5.00, and 5.00 × 5.00 (two plots each). The initial tree numbers were 400, 800, 1600, 3200, and 6400 per hectare, depending on the spacing.

The different provenances were planted in individual tree mixture in a way that two similar provenances were never established in direct neighborhood (Fig. 1). One replication of the 1.25 × 2.50, 2.50 × 2.50, 2.50 × 5.00, and 5.00 × 5.00 plots remained unthinned and was used as reference. The other 5 plots were thinned from above after selection of 400 future crop trees per hectare (Spellmann and Brokate 1991). On the treatment plots with an initial density > 400 trees per hectare up to three thinnings were applied. These density reductions were based on set curves of tree numbers depending on top height. The curves arrive at 400 trees per hectare at a top height of 28 m. On the plots with the initial spacing of 5.00 × 5.00 m there were only 400 trees per hectare from the beginning on and no thinnings applied.

2.3. Measurements

At the first survey in 1993 all tree coordinates were measured as in some cases their were minor deviations of the tree positions from the spacing scheme due to, e.g., stumps or stones. The stands were inventoried five times until now (1993, 1997, 2002, 2007, 2018). The inventories comprised the measurement of all stem diameters by tape measurement. On each plot 30 trees distributed over the stem diameter range were selected for measuring tree height and height to the crown base by Vertex hypsometer (Haglöf, Sweden). The survey in 2002 comprised measurement of eight crown radii per tree (N, NE, E, SE, S, SW, W, NW) by crown mirror and branch diameter measurements at height 1.3 and 5 m by caliper. The eight radii were used to calculate the crown radius $cr = \sqrt{(r_1^2 + r_2^2 + \cdots + r_8^2)/8}$. The crowns were only measured of those provenances that were still present on all plots in 2002; thus the information base for stem allometry is better than for crown allometry.

2.4. Dendromeric evaluation at the stand and tree level

Testing the hypotheses H I- H III required calculation of the following dendrometric characteristics at the tree and stand level.

2.4.1. Tree level evaluations

For analysing the effects of the competition and inter-provenance neighborhood on the stem diameter growth of each tree we constructed a circle with radius $sr_1 = 0.50 \times h_1$ around its stand point; with h_1 being the height of the central tree. Within the constructed circles, there were 16.5 trees on average at the last survey in 2018. We fixed the search radius to the half of the height of the respective central tree as other search radii resulted in lower correlations between growth of the central tree and the number of provenances within this radius. By choosing the search radius depending on tree height we took into consideration that in even-aged stands the influence zone around a tree increases with progressing size development (Pretzsch, 2009, p. 295–296). All trees within the constructed circle were used to quantify local competition and provenance mixing.

To quantify the competitive status of each individual tree we calculated the local Stand Density Index, sdi. Note that sdi refers to the stand density at the individual tree level, whereas SDI is the density calculated at the stand level (see section *2.4.2 Stand level evaluations*). The calculation of sdi was based on all trees in the search radius sr, except the central tree; sdi served as a proxy for the local density and competition. We used the concept of the stand density index, SDI, by Reineke (1933) for this purpose. The SDI is a measure of relative density. It provides the stand density in terms of trees per hectare for a stand with an index quadratic mean stem diameter of 25 cm.

For calculating sdi all trees within the circle except the central tree were used to calculate the local density n on circle area a. $N = 10.000/a \times n$ was the respective tree number upscaled to one hectare. For the n trees, we calculated the quadratic mean stem diameter d_q; based on N and d_q we then calculated the local density $sdi = N \times (25/d_q)^\alpha$ around
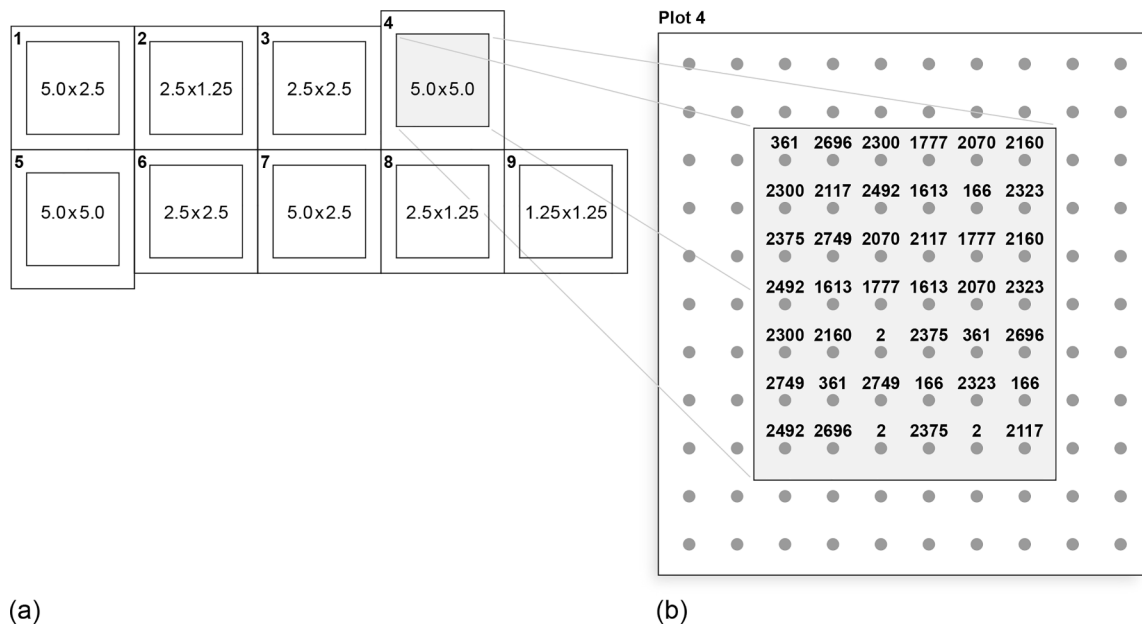
Fig. 1. Design of the Norway spruce provenance mixing experiment Vohenstrauß 622. (a) On nine plots in total the effect of 21 provenances and five plant spacing variants on the growth of Norway spruce is tested. (b) For plot 4 (5 m × 5 m) the basic design is presented with the numbers of the clones. Each of the individual plots contains clones from different provenances with three replicates, e.g. clones number 361, 2696 etc. are replicated three times on plot 4 (b).

each individual tree. The local sdi was calculated using the species-specific allometric exponents of $\alpha = -1.664$ derived by Pretzsch and Biber (2005). Note that this exponent α was derived on unthinned and A-grade plots of long-term experiments in South Germany that are located in the same area as VOH 622. The used exponent $\alpha = -1.664$ deviated from the species-overarching exponent of -1.605, as proposed by Reineke (1933). The resulting competition index sdi is distant-dependent and easy to interpret. The local sdi values were calculated for the competitive constellation before and after thinning, i. e. with and without the removed trees for all circles and all surveys. In this way we could calculate the competition relief by thinning (Δsdi = sdi$_{before}$-sdi$_{after}$). In the result section we reported both sdi$_{before}$, sdi$_{after}$, and also the Δsdi values. In the models only the sdi values of the remaining stand at the end of the survey period after thinning were significant.

To quantify the number and diversity of provenances within the local neighborhood of the individual trees (within the search circle) and at the stand level (on the plot) we used the three measures R, D, and H. These indices were calculated for each circle for the individual tree level evaluation and for each plot for the stand level evaluation. R, D, and H were used in section 3.1 for characterization of the inter-provenance mixture at the tree and plot level. In the statistical analysis we only used the number of different provenances R, as this variable had the largest explanatory contribution.

R is the number of different provenances. In a provenance mixing experiment with 10 provenances on the plot or in search radius applies R = 10.

D is an index of genetic diversity introduced by Gregorius (1978, 1987) with $D = \left(\sum_{i=1}^{S} p_i^2 \right)^{-1}$. D considers the number and frequency of the species present. If all S occurring genotypes have the same frequency of occurrence, then the diversity D is at a maximum.

H is the well known index by Shannon (1948) $H = -\sum_{i=1}^{S} p_i \times \ln(p_i)$. H is also a measure for the diversity, i.e., the richness weighted by frequency. H has been developed by Shannon and Weaver for use in information theory and was successfully transferred to the description of species diversity in biological systems (Shannon, 1948)

In the indices D and H p_i is the relative frequency of the provenances, $\ln(p_i)$ is the relative frequence in logarithmic representation. S represents the number of provenances present. The proportion p_i of a prov-

enances in the population ($p_i = n_i/N$) results from the number n_i of individuals belonging to provenance i, and the total number of individuals N.

Before calculating the local sdi values and mixing proportions for neighborhood analysis, we established a toroidal shift of the plot to all eight directions of the plot periphery for edge bias compensation (Pretzsch, 2009; Pommerening and Stoyan, 2006; Radtke and Burkhart, 1998). This was necessary as in several cases the search radius reached even beyond the buffer zone around the individual plots (Fig. 1). The plot edges were located in the middle distance between the planting rows. By the toroidal shift we extended the same planting pattern and distances in all eight directions and avoided any overdensity as it can be produced by other techniques such as reflection via a reflecting line through the edge trees or a random arrangement of interior trees around the plot (Radtke and Burkhart 1998).

By modelling the relationship between height, stem diameter, and age, we calculated the height of each tree. To estimate the individual tree height (h) depending on the stem diameter (d), and tree age (age) we parameterised Equation (1) using all available measurements of tree heights, stem diameters, and tree ages. In order to reflect the specific height growth on each treatment variant the model was fitted for all 9 plots separately.

$$\ln(h) = a_0 + a_1 \times \ln(d) + a_2 \times \ln(age) + a_3 \times \ln(d) \times \ln(age) \quad (1)$$

All regression coefficients were significant, at least at the level of $p < 0.05$; the R^2-values ranged between 0.85 and 0.98. For the model parameters, see Supplementary Table 1.

2.4.2. Stand level evaluations

To give an overview of the nine plots and analyse the effect of provenance richness on stand growth, we also derived common dendrometric stand charateristics. The stand level characteristics were derived from the successive inventories of the stem diameters, tree heights, and records of the removal trees. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (in German "Deutscher Verband Forstlicher Forschungsanstalten") (Johann 1993, Biber 2013). For estimating the merchantable stem volume in dependence on tree diameter, tree height and form factor, we used the approach by Franz et

al (1973) with the stem form equations and coefficients published by Pretzsch (2002, p. 170, Table 7.3).

The results encompassed all common stand characteristisc such as the quadratic mean diameter and height of the mean and dominant trees, the stand basal area, standing stem volume, basal area growth, stem volume growth, and total stem volume yield. All variables were calculated for total stand, the remaining and removal stand (see Table 2). The Stand Density index was calculated analogously to the local sdi at the tree level (see section 2.4.1 Tree level evaluations). Whereas at the tree level the central tree was excluded, the calculation of the SDI at the stand level included all trees. The stand data was used for introducing the stand and for stand level analysis (H III).

2.5. Statistical models

For testing H I we calculated the coefficient of variation for the tree characteristics stem diameter, tree height, crown diameter, and crown length. The analyses of the stem and crown allometry of the provenances focused on the variation of the intercept (allometric factor) and slope (allometric factor) of the relationships h ~ d, cl ~ d, cd ~ d, and cl ~ cd. For this purpose we calculated the individual allometric relationships for all provenances with n≥20 measurement in order to quantify and visualize the allometric variability and phenotypic plasticity. For this purpose we applied the double-logarithmic model 2 $\ln(y) = a_0 + a_1 \times \ln(x_k) + \varepsilon_k$. For each provenance was analysed separately the allometric

Table 2
Overview of the main measurement variables and metrics at the (i) tree and (ii) stand level used in this study.

Variables' and metrics' names	Abbreviation	Explanation and Indication
(i) tree level variables		
stem diameter	d	indication of tree present size
tree height	h	determination of radius for competition analysis
height to crown base, to lowest branch	hcb	indication of bole length, used for visualization
crown radius	cr	$cr = \sqrt{(r_1^2 + r_2^2 + \cdots + r_8^2)/8}$
crown diameter	cd	cr × 2
crown length	cl	$cl = h - hcb$, used for visualization
stem slenderness	hd	h/d, indicator of stem shape and stem stability
crown ratio	cratio	cl/h, relative lenth of crown
crown percentage	cperc	cratio × 100
search radius for neighborhood analysis	sr	$sr_1 = 0.25 \times h_1$ for analyzing
annual stem diameter increment	id	periodical diameter increment/ period length
local competition, trees ha^{-1}	sdi	stand basal area in the circle before selection cut
competition relief by thinning, tree ha^{-1}	Δsdi	stand basal area remove by selection cut
Number of provenances	R	number of provenances in search radius
Diversity index	D	Index of provenance diversity
Shannon index	H	Index of provenance diversity
(ii) Stand level variables		
quadratic mean sten diameter	dq	calculated species-overarching
mean tree height	hq	height of the tree with dq
stem slenderness ratio	hq/dq	indicator for stem stability
tree number per hectare	N	density measure
Stand basal area	BA	density measure
Stand density index	SDI	density measure
standing stem volume	V	merchantable volume > 7 cm at the smaller end
stand stem volume growth	IV	current periodical annual stem volume growth
Mean annual stem volume growth	MAI	mean annual stem volume growth
Total yield	TY	total yield since stand establishment

relationship between height, h, and stem diameter, crown length and stem diameter, crown diameter and stem diameter, and crown length and crown diameter.

$$\ln(h) = a_0 + a_1 \times \ln(d_k) + \varepsilon_k \tag{2a}$$

$$\ln(cl) = a_0 + a_1 \times \ln(d_k) + \varepsilon_k \tag{2b}$$

$$\ln(cd) = a_0 + a_1 \times \ln(d_k) + \varepsilon_k \tag{2c}$$

$$\ln(cl) = a_0 + a_1 \times \ln(cd_k) + \varepsilon_k \tag{2d}$$

For testing H II we applied the linear mixed effect model

$$d_{ik} = a_0 + a_1 \times \ln(R_{ik}) + a_2 \times \ln(init_{ik}) + a_3 \times \ln(sdi_{ik}) + a_4 \times \ln(R_{ik}) \\ \times \ln(init_{ik}) + b_i + \varepsilon_{ik} \tag{3}$$

to the individual tree data of the latest survey in 2018 of VOH 622 (n = 384). In this way we analysed the accumulated effect of the number of provenances, the initial spacing, and the current local sdi on the individual stem diameter at the last survey in 2018. For this evaluation we used the variable init as it represents the best the effect of the initial stand density. We used the variables R and sdi from the last survey as they represent the best the prevailing neighborhood constellation of the trees; the use of periodical means of R and sdi did not improve the prediction of d. The indexes i and k represent the kth tree on the ith plot. The random effect b_i $N(0, \tau^2)$ was introduced in order to cover correlations of the observations on plot level. With ε_{ik} $N(0, \sigma^2)$, we denoted independently and identically distributed errors.

For testing H III we applied the model

$$IV_{ik} = a_0 + a_1 \times \ln(SDI_{ik}) + a_2 \times \ln(R_{ik}) + b_i + \varepsilon_{ik} \tag{4}$$

to the stand survey data of VOH 622. It reveals the dependency of the periodical stand stem volume growth, IV, on the stand density index, SDI, and the number of provenances at the beginning of each included survey period.

In Equation (4), indexes *i* and *k* represent the kth observation of the ith plot. With the random effect b_i $N(0, \tau^2)$, we cover the correlation between the single observations at the plot level. With ε_{ik} $N(0, \sigma^2)$, we denoted independently and identically distributed errors. In both, Equation (3) and (4), a$_0$, ..., a$_n$ are the parameters of the fixed effects.

For all calculations, we used the statistical software R 4.1.0 (R Core Team, 2021), and we used the libraries nlme (Pinheiro et al., 2021) and lme4 (Bates et al., 2015).

3. Results

3.1. Descriptive results. Overview of structural and growth characteristics of the provenances at the tree and stand level

Table 3 shows the mean tree characteristics in terms of tree dimensions and neighborhood. Especially the stem diameters and crown characteristics show a very strong variation. The crown length e.g. ranges from 5.30 − 22.60 m and the crown diameter from 0.99 to 4.40 m.

Because of the different initial spacing and thinning the local density sdi ranges between 226 and 845 trees per hectare and the competition relief by thinning between 0 without thinning and 248 with strong thinning from above. Important for the subsequent evaluation are the high mean values of R, D, and H and their broad variation within the search radius. The variation was large for the number of provenances (R = 1–15), the diversity index (D = 1–13.44), and also for the Shannon index (H = 0.30–2.65).

On the nine provenance mixing plots included in this study the number of mixed provenances strongly varies between 9 and 21 due to the different initial tree numbers (400–6400 trees per hectare) and respective range in the initial growing space (1.56–25 m^2 per plant).

Table 3

Overview of the main data for analyzing the dependency of the annual stem diameter growth, id, on characteristics of trees and their neighborhood. Shown are the characteristics mean, standard deviation, minimum and maximum values (n = 560). The overview is based on the survey in 2018, respectively in 2002 in case of the crown characteristics. For variable explanation see Table 2.

Variable	Unit	Mean	Sd. dev.	Min	Max
id	$cm\ yr^{-1}$	0.37	0.09	0.11	0.71
d	cm	27.68	6.37	8.00	52.20
cd	m	2.33	0.63	0.99	4.40
h	m	22.08	2.27	10.00	27.50
cl	m	14.69	3.12	5.30	22.60
hd	$m\ cm^{-1}$	0.78	0.14	0.48	1.27
cratio	$m\ m^{-1}$	0.66	0.11	0.34	0.92
sdi before	ha^{-1}	590.40	100.09	225.67	844.99
sdi after	ha^{-1}	547.27	102.77	225.67	844.99
Δsdi	ha^{-1}	43.13	53.11	0.00	247.89
R	number	7.01	3.88	1.00	15.00
D	./.	5.32	2.84	1.00	13.44
H	./.	1.52	0.88	0.30	2.65

Thus the potential number of provenance per unit area is simply higher if there were more plants per area (Table 4). We found a strong variation of the quadratic mean stem diameter between the plots, whereas the height was rather similar. Accordingly, the slenderness hd/dq showed a strong variation between 62 and 85 m/cm. Due to the different initial spacing the stand density in terms of stand basal area, BA, stand density index, SDI, and standing volume, V, varied strongly between the plots. Because of the close relationship between standing stock and growth, the current stand volume growth, the mean annual growth, and the total yield showed similar variations and dependencies on the initial stand density and spacing.

The current stem volume growth of $16.70\ m^3\ ha^{-1}\ yr^{-1}$, mean annual growth of $10.80\ m^3\ ha^{-1}\ yr^{-1}$, and total yield of densely and fully stocked plots of $474\ m^3\ ha^{-1}$ reflect the level of the site index of O 38 (dominant tree height h_{100} = 38 m at age 100) according to yield table by Assmann and Franz (1963, 1965) and indicate very good growing conditions for Norway spruce. The still lower level of growth on the other plots is mainly the effect of the lower initial stand densities.

3.2. Structure and allometry of the various provenances (H I)

The coefficient of variation was cv_d = 23.01% for stem diameter, cv_h = 10.28 % for tree height, cv_{cd} = 27.04 % and cv_{cl} = 21.24 % for crown length (see underlying means and standard deviations in Table 3). Thus, the ranking in terms of crown characteristic variation between the different provenances was $cv_{cd} > cv_d > cv_{cl} > cv_h$. The variation of the crown diameter or length was>2-fold compared with the variation of

Table 4

Overview of some stand characteristics of the nine plots of the provenance mixing trial Vohenstrauß 622. The table reflects the mean, standard deviation, minimum, and maximum of the main stand characteristics for the last survey in 2018. For variable explanation see Table 2.

Variable	Unit	Mean	Sd. dev	Min	Max
number of prov.	ha^{-1}	15.22	4.69	9	21
initial tree number	ha^{-1}	2044.44	1953.91	400	6400
initial growing space	m^2	10.59	9.04	1.56	25
dq	cm	29.19	3.39	25.30	35.60
hq	m	22.16	1.03	19.80	23.90
hq/dq	m/cm	76.20	7.87	62.00	85.00
N	ha^{-1}	441.70	89.95	286.00	514.00
BA	$m^2\ ha^{-1}$	28.81	3.68	24.49	35.27
SDI	ha^{-1}	552.62	67.97	470.79	655.50
V	$m^3\ ha^{-1}$	295.20	45.25	255.00	383.00
IV	$m^3\ ha^{-1}\ yr^{-1}$	12.37	2.15	9.80	16.70
MAI	$m^3\ ha^{-1}\ yr^{-1}$	9.10	1.45	6.50	10.80
total yield	$m^3\ ha^{-1}$	400.00	63.85	286.00	474.00

the tree height. This means that the different provenances arrived at a rather similar tree height at age 43. The crown characteristics such as crown diameter, cd, and crown length, cl, varied considerably between the provenances. The crown diameter and crown length indicate the size and space requirement of the trees. Especially the crown diameter and the respective crown projection area, cpa ($cpa = cd^2/4 \times \pi$) reflects the growing area requirement of trees and the potential number of trees per hectare N ($N = 10.000/cpa$). Thus the variation of crown diameter indicates the strong variation of the growing area requirement and possible stand densities between the provenances.

Fig. 2 visualizes selected tree characteristics of the various provenances on the provenance mixing experiment Vohenstrauß 622 as box plots. The results are based on the survey in 2018, respectively in 2002 in case of the crown measurement. The vertical lines represent the overall mean and serve as references. As the crowns were only measured of those provenances that were still present on all plots in 2002 the information base for stem allometry (a and b) is better than for crown allometry (c and d).

For analyzing the variation of stem and crown allometry (h ~ d, cl ~ d, cd ~ d, and cl ~ cd) between the provenances we applied models 2a-2d with the following results. Fig. 3 and Table 5 show that the provenances differed strongly in the stem and crown allometry in terms of the allometric factor a_0 and the allometric exponent a_1. For example, the range of the allometric exponent of $h \propto d^\alpha$ was α = 0.12–1.21 and the range of the allometric exponent of $cd \propto d^\alpha$ was α = 0.47–0.84. The wide range of provenance-specific stem and crown allometry visualized in Fig. 4 underlines the strong variation in vertical and lateral crown extension and growing area requirement of the different provenances.

The allometric relationships in Fig. 4 show strong differences between the provenances. Fig. 4, a and b show the allometric relationship at the survey 2018; the different curves represent different provenances covered by the measurements (see Table 5). The evaluation of the stem and crown allometry in Fig. 4, c and d, refers to the crown measurements in 2002. The relationship between individual crown diameter, cd, and stem diameter, d, for example, varied strongly between the different provenances (Fig. 4c). The relationship between the crown dameter and stem diameter which Assman (1970, p. 112) called growing space factor indicates the space requirement of each provenance. The higher the crown diameter at a given stem diameter the more space consuming the trees belonging to a given provenance. Trees with a stem diameter of 30 cm, for example, had on average a crown diameter of 3.5 m and a crown projection area of 9.6 m^2. However, the inter-provenance range of crown diameters was 2.9–4.0 m and of the crown projection area 7.0–13.0 m^2. This means at parity of stem diameter, the crown area and growing area requirements of the provenance with the widest crown allometry was by 85% higher compared to the provenance with the slimmest crowns. Another important aspect was the variation of the crown shape reflected by the allometry between crown length and crown diameter under the same density (Fig. 4d). A given crown diameter can be associated with very short but also with very long crowns, reaching nearly to the ground. Latter emphasizes the strong morphological variation in both, width and length of the crown of trees with given stem diameters.

3.3. Tree growth depending on neighborhood conditions (H II)

All fitted models were subject to the usual visual residual diagnostics. For all models, the residuals were plotted against the fitted values. In no case the plots suggested a violation of variance homogeneity. Likewise, normality of errors was verified by making normal q-q plots of the residuals. Both diagnostic plots are provided for the relationship between the tree growth depending on the neighborhood conditions (model 3). We provided the same diagnostic plots also for the second core relationship conveyed in this paper, the relationship between the stand growth and the number of provenances (model 4) (see Supplementary Figures 1 and 2).
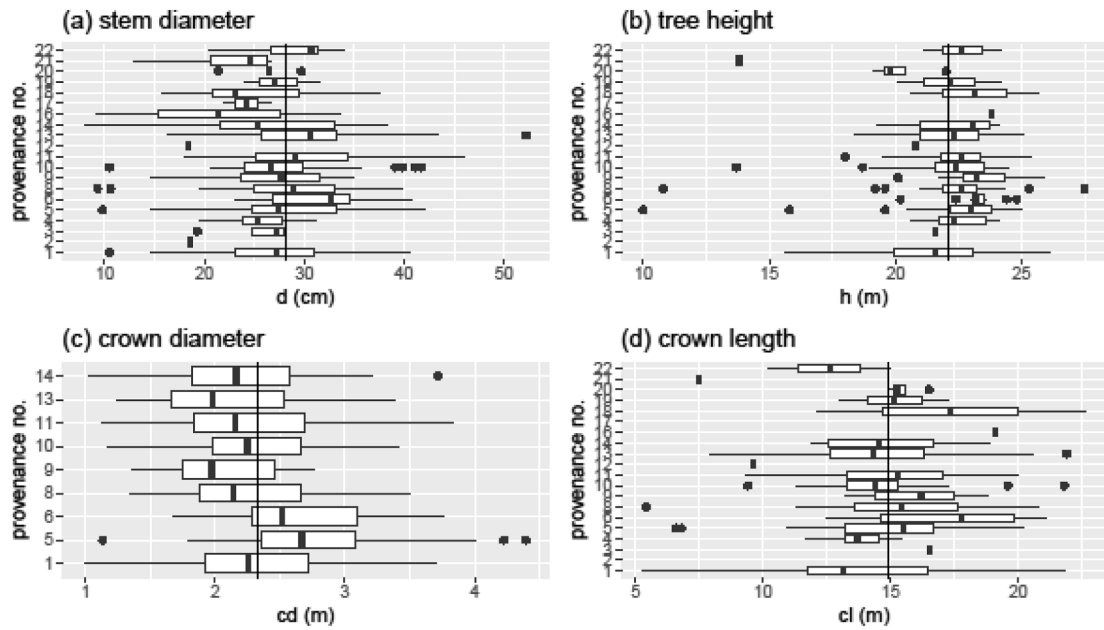
Fig. 2. Tree characteristics of various provenances on the provenance mixing experiment Vohenstrauß 622 visualized as box plots. Based on the survey in 2018, respectively in 2002 in case of the crown diameter the graphs show (a) stem diameter, (b) tree height, (c) crown diameter, and (d) crown length. The vertical lines represent the overall mean and serve as references.
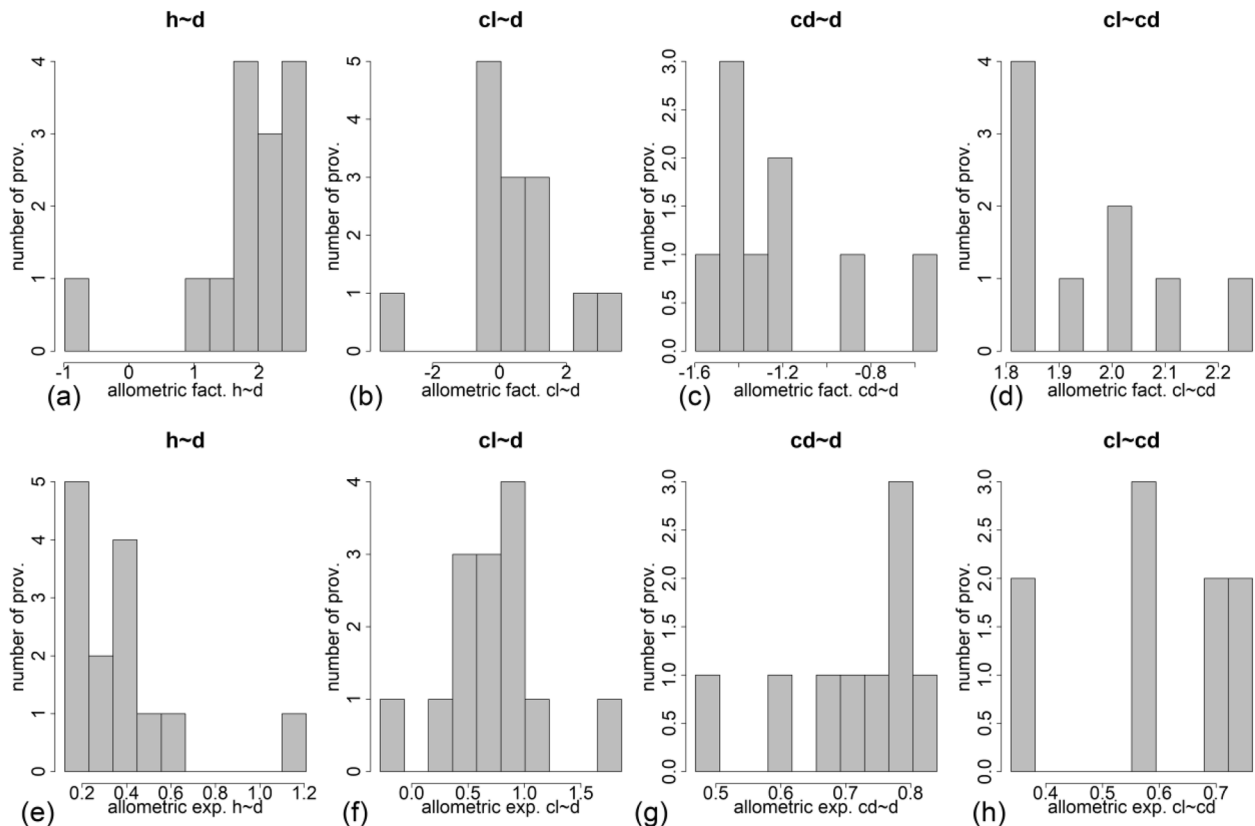

Fig. 3. Allometric variation between the Norway spruce provenances in terms of the respective allometric factors (a_0, above) and allometric exponents (a_1, below) of models 2a-2d. Visualized are the results for the stem allometry h ~ d (a and e), the crown allometry cl ~ d (b and f), the crown allometry cd ~ d (c and g) and cl ~ cd (d and h).

Model 3 revealed that the stem diameter at the last survey in 2018 at tree age 43 increased significantly with the number of provenances in the neighborhood of the trees (Fig. 5). A doubling of the provenance number (e.g., increase of the richness from R = 5 to R = 10) caused an increase in stem diameter of >5 cm. In addition, the diameter growth decreased with increasing local competition sdi, in the vicinity of the trees (in the search circle) and increased with the initial growing area, init.
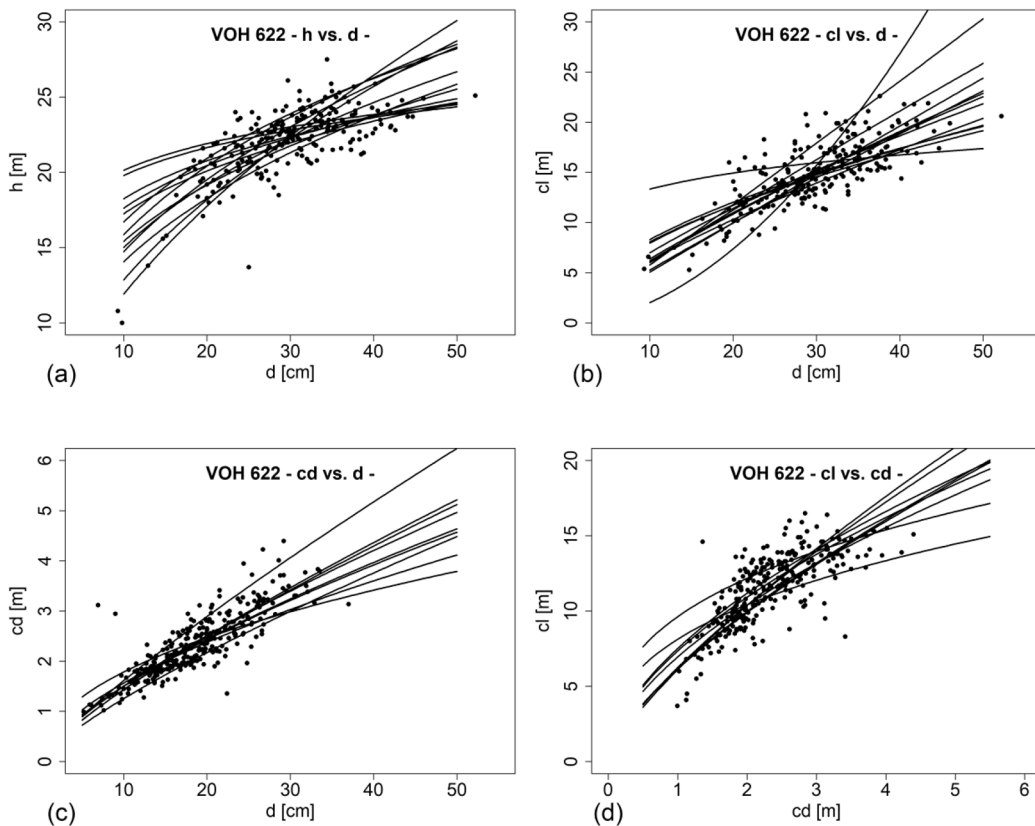
Table 5
Allometric factors (intercepts), a_0, and exponents (slopes), a_1, derived by double-logaritmic linear regression model 2a-2d $\ln(y) = a_0 + a_1 \times \ln(x)$ for each provenance separately (see also Fig. 3).

Allometry	Number of provenances	Coefficient	Mean	Sd. dev	Min	Max
h ~ d	14	a_0	1.82	0.93	−0.98	2.72
h ~ d	14	a_1	0.38	0.27	0.12	1.21
cl ~ d	14	a_0	0.23	1.61	−3.57	3.65
cl ~ d	14	a_1	0.73	0.48	−0.28	1.86
cd ~ d	9	a_0	−1.24	0.34	−1.60	−0.50
cd ~ d	9	a_1	0.72	0.12	0.47	0.84
cl ~ cd	9	a_0	1.94	0.16	1.81	2.26
cl ~ cd	9	a_1	0.59	0.15	0.34	0.76

We found a significant interaction between the provenance richness and the initial spacing (Table 6, coefficient a_4). The number of provenance in a given circle was higher if the spacing was narrow (e.g. 1.25 m × 1.25 m) with many plant within the search radius. In this case the probability of the establishment and survival of a larger number of provenances was higher than for wide spacing (e.g. 5 m × 5 m).

3.4. Provenance number and stand growth (H III)

The periodical stand stem volume growth increased with the number of provenances and the stand density index; i. e. those plots that carried a high number of provenances and were kept dense produced the highest stem volume growth (Fig. 6a, Table 7). The periodical stand stem volume growth increased with the number of provenances per plot (Fig. 6b). AIC comparisons suggested using the year of survey as random variable. An interaction term between SDI and R was eliminated as it was not significant.

4. Discussion

At an age of 43 years the trees of different Norway spruce provenances strongly varied in stem and crown allometry. The inter-provenance neighboorhood reduced competition and increased the stem diameter growth. An increasing number of provenances also increased the productivity at the stand level. Thus, both tree growth and stand productivity increased with the number of represented provenances.

4.1. Competition reduction in neighborhood

Living in neighborhood can have various negative but also positive effects on the function, structure, and growth of plants (del Rio et al. 2017, Pretzsch 2017, Vandermeer 1992). Neighboring trees may, for example, protect their neighbors against sun radiation or drought stress by sun shading (Pretzsch et al. 2018) but also may reduce or even shut off their supply with water (Pretzsch et al. 2020, Goisser et al. 2016). Positive and negative effects can occur simultaneously and are hardly to separate (Vandermeer 1992), and they can also vary over time (del Río et al. 2014, Wichmann 2001). The measured growth reactions represent the net effect of the interaction between positive and negative effects of neighborhood and show the balance of competition, competition reduction, and facilitation (Pretzsch and Schütze 2009, Pretzsch and Schütze 2021). The effects of inter-specific neighborhood such as shading (Magin 1959, van Hees 1997), atmospheric nitrogen fixation (Forrester et al. 2006), hydraulic redistribution (Caldwell et al. 1998, Hafner et al. 2019), soil improvement (Rothe and Binkley 2001, Augusto et al. 2002), or crown shyness (Fish et al. 2006, Meng et al. 2006, Hajek et al. 2015) and their results in terms of growth were studied intensively. Much less is known about positive and negative interactions between neighbors of the same species. Some few studies revealed that trees growing in group structures in the alpine zone compete for light but their neighbors also protect them against snow and wind, so that they
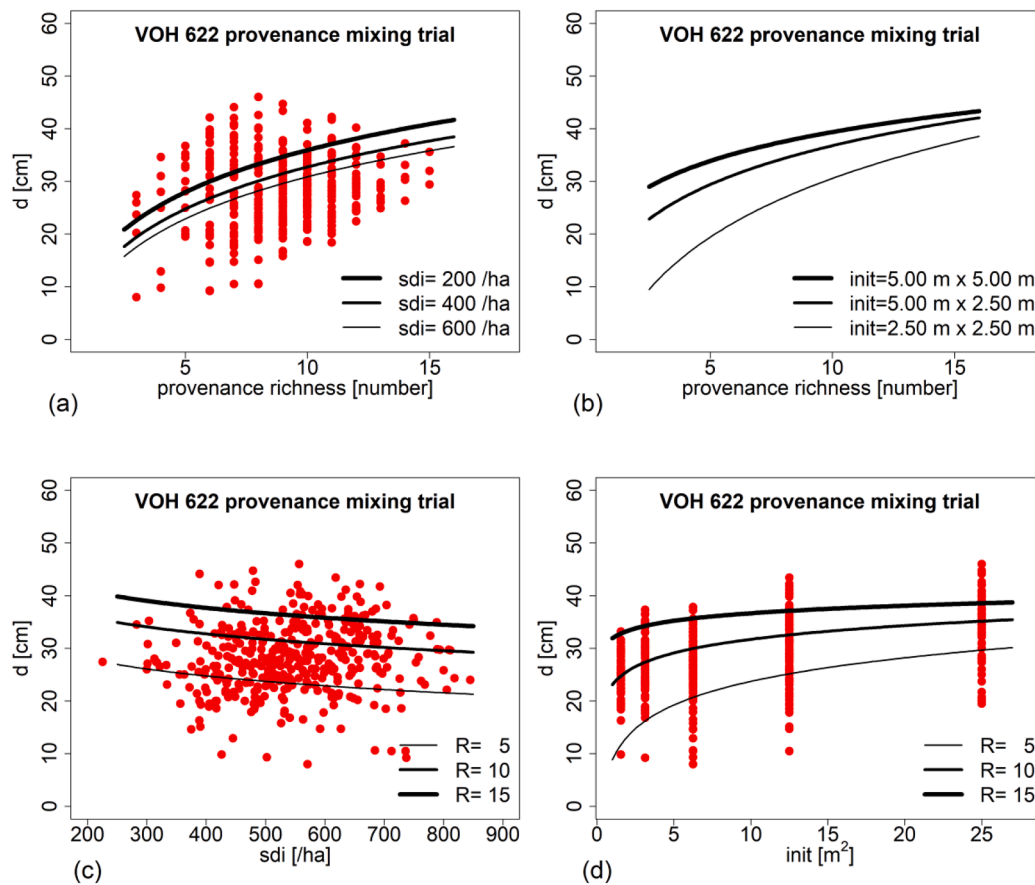

Fig. 4. Variation of the stem and crown allometry of Norway spruces on the experiment VOH 622. The regression curves show how the sampled provenances differ in their allometric relationships between various stem and crown characteristics. Visualized are the relationships between (a) stem diameter and tree height, (b) stem diameter and crown length, (c) stem diameter and crown diameter, and (d) crown diameter and crown length. The underlying model equations and allometric factors and exponents (intercepts and slopes) are presented in Fig. 3 and Table 5.

Fig. 5. Individual stem diameter, d, at age 43 (survey 2018) in dependence on provenance richness in the neighborhood, local stand density, sdi, and initial spacing, init. The relationship between d and provenance richness is shown for (a) different levels of sdi, (b) different levels of init. (c) Stem diameter in 2018 as co-determined by (c) sdi and R, and (d) init and R. Other independent variables were set to the overall mean. Visualization according to model 3 (see Table 6).

Table 6

Results of fitting the linear mixed effect model 3 $d_{ik} = a_0 + a_1 \times \ln(R_{ik}) + a_2 \times \ln(init_{ik}) + a_3 \times \ln(sdi_{ik}) + a_4 \times \ln(R_{ik}) \times \ln(init_{ik}) - + b_i + \varepsilon_{ik}$ to the individual tree data of the latest survey in 2018 of VOH 622 (n = 384). AIC comparisons suggested using the plot as random variable.

Fixed Effect Variable	Fixed Effect Parameter	Estimate	Std. Error	p
	a_0	42.17	12.92	0.0012
$\ln(R)$	a_1	15.48	2.97	<0.0001
$\ln(init)$	a_2	−1.08	3.50	0.7659
$\ln(sdi)$	a_3	−9.52	1.68	<0.0001
$\ln(R) \times \ln(init)$	a_4	3.24	1.41	0.0223
plot	Random Effect	Std. Dev.		
	b_i	4.21		
	Residuals	Std.Dev.		
	ε_{ij}	4.67		

frequently benefit from being associated and grow more than solitary trees. Forest management occasionally makes use of intra-specific facilitation by planting trees in groups or clusters known as "Rotten" in the alpine zone (Strobel 1995) and "Nester" in the lowlands (Saha et al. 2012).

As reviewed in the section *Introduction*, many studies deal with the structure of growth of different provenances, their performace under different environmental conditions and silvicultural treatment. However, we found very few studies about how different provenances of the same species affect each other when growing in close neighborhood (Boyden et al. 2008). The advantage of living in inter-provenance neighborhood that we showed in Fig. 6 and Table 5 means, e.g., that

having 10 different provenances in vicinity increases the stem diameter growth on average by 28 % compared with having only 5 provenances in the neighboodhood. This results from the following model calculation based on equation (3) and the model parameters in Table 6. For a setup of sdi = 400 trees ha^{-1} and an initial spacing of 12.5 m^2 (800 trees ha^{-1}) the model predicts a stem diameter of d = 26.2 cm for R = 5 and d = 33.6 cm for R = 10 provenances. The order of magnitude of this growth increase by 28 % is similar to the effect of competition reduction and stem diameter growth increase in mixed compared with monospecific stands (Pretzsch and Schütze 2021). Probably, the positive diversity-productivity relationship found for tree species mixtures (Jactel et al. 2018, Liang et al. 2016) can be transfered to provenance mixtures. Interactions between different genotypes may be determined by complementary morphology, different phenotypical plasticity, and asynchrony in functioning and growth (Boyden et al. 2008, Forrester 2017, Kelty 1992, Vandermeer 1992).

Probable benefits of provenance mixing might be a reduction of competition for space and light due to differences in tree structure (Čortan and Šijačić-Nikolić 2019) and functioning (Chmura and Rozkowski 2002) similar to inter-specific conditions (Pretzsch 2014, 2021). The crown shyness may become lower due to complementary crown shapes as shown for inter-specific competition (Barbeito et al. 2017, Pretzsch 2017) and the potential canopy packing density may become higher (Pretzsch 2014, Jucker et al. 2015). Analogously the differences between the morphological traits of provenances may cause a more diverse root system and separated resource aquisition below ground as shown for mixed speceis stands (Wiedemann 1942, Schmid and Kazda 2002). Beyond these structural diversification their may be a temporal diversification in sprouting, light assimilation, and water uptake due to
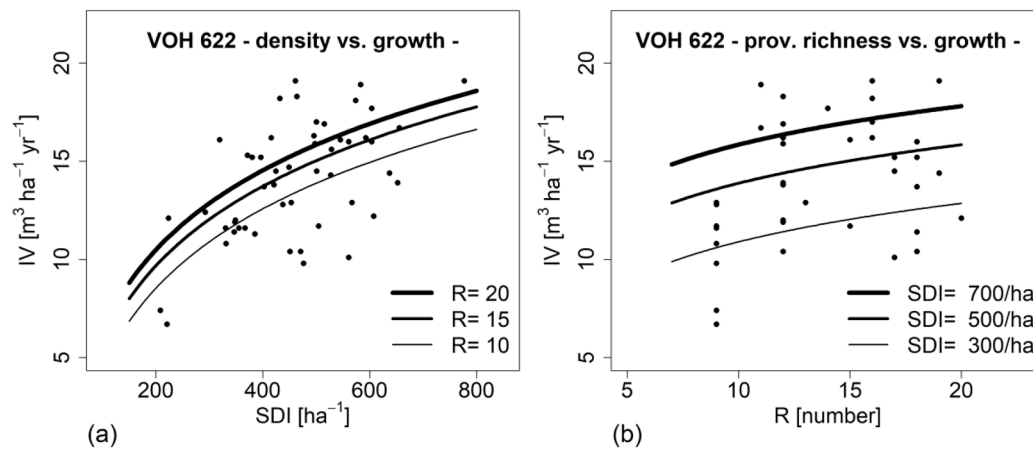
Fig. 6. Periodical stand stem volume growth depending on (a) stand density and (b) number of different provenances per plot. The included regression lines are based on model 4 (see Table 7).

Table 7

Results of fitting the linear mixed effect model 4 $IV_{ik} = a_0 + a_1 \times \ln(SDI_{ik}) + a_2 \times \ln(R_{ik}) + b_i + \varepsilon_{ik}$ to the stand survey data of VOH 622. AIC comparisons suggested using the year of survey as random variable (n = 42).

Fixed Effect Variable	Fixed Effect Parameter	Estimate	Std. Error	p
	a_0	−28.95	7.33	0.0004
ln(SDI)	a_1	5.84	1.34	0.0001
ln(R)	a_2	2.83	1.23	0.0279
year of survey	Random Effect	Std. Dev.		
	b_i	1.84		
	Residuals	Std.Dev.		
	ε_{ij}	1.81		

asynchrony between the provenance-specific functioning (Chmura and Rozkowski 2002) as in mixed-species stands (Torresan et al. 2020, del Río et al. 2014, Goisser et al. 2016, Schäfer et al. 2018). Asynchrony in the provenances' phenology, e.g. differences in the bud formation, sprouting, leaf shedding (Chmura 2006, Worrall 1975) may contribute to a complementary resource use, a competition reduction, and productivity increase of provenance mixtures compared with mono-provenance stands.

We hypothesize that mainly structural differences between the provenances enable the competition reduction and growth increase in inter-provenance neighborhood. This is based on our findings that the provenances varied strongly in stem and crown allometry. In addition different provenances may have different root systems. We assume that the structural diversity triggers an improved light absorption, reduced mechanical abrasion, crown shyness, modified pre-emption of water and light by neighbors, modified water uptake and within stand bioclimatic conditions compared with the mono-provenance setup. From the combination of provenances may also emerge diversified and stabilizing root-associated mycorrhizal and microbial networks (Nickel et al. 2018, Steidinger et al. 2019) and holobiontic interactions above and below ground similar to mono-specific stands (Matyssek and Lüttge 2013, zu Castell et al. 2019).

Interestingly, we found an increase of tree growth with provenance richness at the tree level (Fig. 5) and also at the stand level (Fig. 6). This means that stem diameter growth was generally higher when trees grew in neighborhood of different provenances. Inter-provenance competition reduced the competition and promoted stem growth. That stand productivity similar to tree growth increased with provenance richness is not self-evident. At the stand level not only the absolute number of provenances but also their spatial mixing pattern matters. Suppose a given number of provenance would be distributed in clusters, growing

separated from each other, the interaction and also any benefit of stand productivity would be low. However, on the analysed plots the different provenances were planted in individual tree mixture in a way that two similar provenances were never established in direct neighborhood (section *2.2 The experimental setup of VOH 622*). The various provenances were planted randomly distributed across the plot under the condition that similar provenances do not occur as direct neighbors (Pretzsch and Schütze 2021, Bieng et al. 2013). In this way the provenances are intensively intermingled with each other, so that any positive effects of competition reduction may be at maximum.

4.2. Silvicultural implications of the growth increase by genetic diversity

On the provenance mixing experiment stem diameter increased with increasing number of provenance in the neighborhood of a tree. This mean that a given stem diameter can be achieved under higher density if the neighbors are diverse in terms of provenance and respective structure (Fig. 5). This further means that analogously to the findings in many mixed-species stands (Pretzsch and Schütze 2021) mixed provenances can raise growth and yield. If we interpret growth as an indicator of vitality (Dobbertin et al. 2005) provenance mixing contributes to risk prevention and growth increase and stabilization. At parity of age and stand density, provenance mixing can be highly beneficial in terms of tree and stand growth. In view of the rather narrow range of provenances (only from regions across Germany) the provenance richness effect on growth was rather strong. It may be even stronger if provenances across a larger or the whole range of the natural distribution of Norway spruce would have been represented in the mixtures.

This finding for a provenance mixture is analogous to the dependency of overyielding from the spatial pattern of the tree species mixture (Pretzsch et al. 2012, Williams et al. 2017, Fichtner et al. 2018). The mixing effects are based on a strong intermingling between species or provenances in close neighborhood. The benefits are the strongest when 5–10 provenances are present in the neighborhood of trees and increase less when more provenances are aggregated. This means that a representation of only the number of provenances at the stand level is not sufficient for achieving an overyielding. Positive interactions require a mixing of provenance in close vicinity to come into effect. Similarly, 2 or 3 species per stand will not come into effect if the species are growing in separation. It rather requires that they are strongly intermingled in individual tree mixture to benefit from the complementary in canopy space and light use, reduced crown shyness, or complementary in root space exploration. The finding suggests the relevance of the spatial pattern and arrangement for exploiting the potential of mixing species as well as mixing provenances.

The currently very popular paradigm of close-to-nature forestry with

continuous forest cover and mainly naturally regenerated stands mainly maintaines and copies the restricted set of local provenances. Thus it does not harness the potential of growth and stability improvement by genetic diversification. Our results suggest that an enrichment by additional provenances may be advantageous. This could be achieved by combining natural generation with planting of suitable non-local provenances.

4.3. Implications for tree and stand modelling

Individual tree models may be adapted to different provenances by provenance-specific parameterization of the model functions for stem diameter, height, mortality etc., analogously to the model parameterization und calculation for different tree species. The plots of this study and other provenance trials offer the appropriate database for such model adaptions. Here, we used mainly the tree sizes of the currently last survey for analyzing of interactions between the provenances. However, the repeatedly recorded developments at the tree and stand level could also be used for exploring and modelling the provenance-specific course of tree growth. For example, the distant dependent individual tree model SILVA 3.0 (Pretzsch et al. 2002), originally developed for simulation of monospecific and mixed-speceis stands, has been tentatively complemented with a program module that enables the simulation of the effects of intra-specific genetic variation on growth and allometry (Röder et al. 2005).

Our analysis showed that the provenances differed strongly in stem and crown allometry. So, if the genetic code is not explicitly available, the structural characteristics might be suitable substitute model variables. This study showed that the provenances significantly differed in the tree structures and allometries, and these differences probably co-determine tree growth. This suggests that part of the impact of the different provenance may be caused by their different structural traits and the effects of the structure on the tree growth. So, a part of the genetic variation can be captured in models by the structural variability. A structural and morphological characterization and modelling approach has the advantage that it is suitable for silvicultural prescriptions as structural effects of management as e.g., stem stabilization, crown extension, or self-pruning are visible and accessible. The genetic code, in contrast, is only rarely available; exceptions are well analysed and documented long-term experiments.

To improve the knowledge about phenotypical and genotypical differences, tree mensuration are challenged to better measure the crown morphology. Appropriate methods have been proposed, among others, by Hussein et al. (2000), Bayer et al. (2013, 2017), or Jacobs et al. (2020). The proposed methods allow for an assessment and quantification of tree allometry beyond the tree size (Niklas 1994, Pretzsch and Schütze 2005). More detailed measurements of the crown morphology may reveal the different history and explain the differences in the present growth of trees. A common example is the relationships between the crown shape of Scots pine (A- and B-types according to Kräuter 1965) and the course of tree growth. To what extent different courses of growth (A- and B-types) in the same stand result also from differences in genetics has been analysed for Scots pine (Kräuter 1965), but yielded no clarity (Hertel and Kohlstock 1994) and is still open for debate (Wenk et al. 1990, p. 41). Further studies into the relationship between genetics, tree allometry, and growth are highly recommended as they can pave the way to better design of genetic and structural diversity in favour of stand growth stability.

4.4. The preliminary character of the results

As the analyzed stands are only 40 years old, our results have still preliminary character. Many studies showed that the course of tree growth (Binkley et al. 2002, Dobbertin 2005), the allometry (Genet et al. 2011), and stress reactions (Ding et al. 2017, Zang et al. 2012) can considerably change with age and size. Thus from the ranking of

seedlings of young trees of different species or provenances in terms of vitality, quality, or resilience should not be infered their performance in the mature age. Pretzsch et al. (2019) showed examples how provenances can change their relative performance with increasing age. 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 m^3 ha^{-1}. This trial also included plots of Norway spruce, which performed similarly to Douglas-fir initially, but lagged about 30% behind the total stand growth of most of the Douglas-fir provenances at advanced ages even though Douglas-fir is an introduced species. Such long-term changes in ranking and trend underpin that the choice of silvicultural options (e.g., provenance, thinning, tree species) should not be based only on early tests, but on long-term observations.

On VOH 622 the stem and crown allometry differed between the provenances (Fig. 4) and the differences increased wth increasing tree size (see cd ~ d and cl ~ cd in Fig. 4, c and d). With increasing age, the species or provenances can continuously adapt to their individual growth constellation in the stand and continuously reveal their phenotypic variability. Compared to often wide spacing in young stands, the survival in higher stand densities requires an adaption to increasing crowding and competition. Thus, with progressing age and mean tree dimension the provenances' ranking in terms of performance may change.

With a stand age of 40 years and a mean height of about 20 m the experimental stands currently enter the development phase of high risk and increased tree drop out caused by storm, snow-breakage, bark-beetle, or root rot (Knoke et al. 2021, Müller 2002, Peltola et al. 2000). Especially, less stress acclimated and adapted provenances may drop out in the coming years and impair the stand growth and productivity. Suppose a very stress susceptible provenance with a share of 10 % would drop out, this would cause severe growth losses especially if this provenance was planted clustered in groups or mono-provenance stands. In case of individual tree mixture, as realized on VOH 622, the gaps caused by damages would be small in size and might cause less growth losses. Analogously to canopy openings by thinning, many small removals spread over the whole stand area can be better buffered, closed, and compensated by the growth of the remaining trees, than large gaps. Latter need much longer to be closed again.

It is unlikely that the essential finding of growth increase with increasing number of provenances will change with progressing stand age. We rather assume that the differentiation and diversity of structure which co-determines the growth increase will become more effective so that the superiority of provenance-diverse compared with similar neighborhood will even increase with progressing stand age.

5. Conclusions

The finding that inter-provenance mixtures can significantly increase tree growth and stand productivity based on only one rather unique provenance mixing experiment. The promising results suggest a further clarification of the impacts of inter-provenance mixtures as the results are highly important for silviculture. A combination and mixing of provenances may cause an increase of the level and stabilty of growth analogous to the growth increase by tree species mixture. The common close-to-nature forestry, although very advantages in terms of mitigation of climate change and adaptation to disturbances at present, may curtail the genetic diversity on the long term. A combination of both natural regeneration that maintains local provenances and planting of the same species for a widening of the genetic diversity may be beneficial. Next steps for improving the respective knowledge base may be the evaluation of further existing and the establishment of new provenance mixing experiments.

Author contributions statement

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

Declaration of Competing Interest

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

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119498.

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