



Facilitation and competition reduction in tree species mixtures in Central Europe: Consequences for growth modeling and forest management

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ARTICLE INFO

Keywords:

Facilitation
Competition
Competition reduction
Canopy density
Niche complementarity
Individual tree model
Growth modifier

ABSTRACT

That tree species mixing may strongly affect tree structure and tree growth is so far hardly considered in tree and stand models. Hence, for a better understanding and design of mixed species stands, the inter-specific facilitation and competition needs better representation in individual tree models. Here, we show for the five most common tree species combinations in Central Europe that mixing causes facilitation and competition reduction in mixed stands and how such effects can be implemented in individual tree stem diameter growth models.

This study was based on 62 long-term experimental plots belonging to 10 chronosequences in Germany with repeated spatially explicit stand inventories from 1991 to 2016. They covered monospecific and mixed species stands of Norway spruce (*Picea abies* [L.] KARST.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* [MATT.] LIEBL.), European ash (*Fraxinus excelsior* L.), and sycamore maple (*Acer pseudoplatanus* L.). The study represented medium and high qualitative site conditions, fully stocked, or only moderately thinned stands of 22–238 years of age, and the mixing patterns ranged from individual-tree to cluster-mixtures.

Based on spatially explicit measurements, we quantified for each tree the intra- or interspecific neighborhood, local stand density, and growth. We applied mixed models to analyze how inter-specific neighborhood modified tree growth.

First, we showed that the inter-specific neighborhood can increase tree growth significantly beyond the level of open-grown trees in intra-specific neighborhoods (net facilitation). The potential growth rates of the fastest growing trees in mixed stands were 14–78% higher compared to monospecific stands matched for size, crown, and site index. The mixing effect differed between species combinations. Second, we provided evidence that mixing on average reduced competition by 16%, and that this effect increased with the mixing proportion. In four out of the five species combinations we observed a competition reduction of both associated tree species (mutualistic relationship). Third, for the mixtures of Norway spruce/European beech and sessile oak/European beech that covered a broader range of site conditions, we found a mainly positive modulation of facilitation and competition depending on site conditions.

We discussed the potential causes for the observed facilitation and competition reduction, their implementation in tree growth models, and the relevance of the findings for the design and management of mixed-species stands.

1. Introduction

The widely-used individual tree models for forest stands represent a bottom-up approach, which starts with the individuals of a system, ends at the stand level, and aims to understand and predict how a stand's properties emerge from the interaction between its trees (Weiskittel et al., 2011; Grimm 1999). The core of most of these models is a

potential-modifier algorithm (Burkhardt and Tomé 2012; Biging and Dobbertin 1995; Moore 1989; Botkin et al., 1972). The potential-modifier approach is based on the potential tree growth expected without competition, and this potential growth is modified according to the current competition by neighbors. The prediction of growth and mortality of all individuals, the ingrowth of regeneration, and the consideration of management interventions enables a

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<https://doi.org/10.1016/j.ecolmodel.2021.109812>

Received 1 May 2021; Received in revised form 29 October 2021; Accepted 2 November 2021

Available online 15 November 2021

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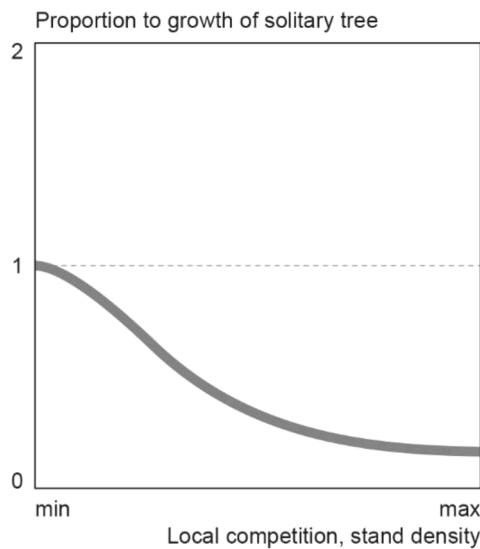


Fig. 1. Relationship between competition (measured by competition indices or local stand density) and the modifier, *mod*, for prediction of stem diameter growth of a tree according to the potential-modifier approach $id = id_{pot} \times mod$ (modified after Ek and Monserud, 1974, p. 71 and Burkhardt and Tomé, 2012, p. 314–315).

simulation of the stand dynamics in 1- or 5-year increments or other time intervals. Previous literature provides excellent overviews of such models (Weiskittel et al., 2011), their evaluation (Mette et al., 2009), and their application in science (Grimm, 1999) and forest management (Hilmers et al., 2020; Weiskittel et al., 2016; Pretzsch et al., 2002).

Since their introduction, individual tree growth models have greatly facilitated insights into the patterns and processes in forest ecosystems (Grimm 1999; Shugart 1984; Shugart and West, 1981). However, their impact on forest management was initially low due to the scarce information on initialization and parameterization, the limited computing power available for their application, and their limited added value for the mass-oriented forestry with homogeneous monocultures that was dominating in the past. Then, the following five trends substantially promoted the application of individual tree growth models in forest

management and planning over the last decades.

First, individual tree-based forest experiments, forest inventories, and remote sensing techniques strongly improved the database for analyzing and modeling individual tree growth (Nagel et al., 2012). Second, computing capacity rapidly increased, allowing for individual tree-based scenario analyses at the regional, national, or even global level, using microcomputers. Third, many forests have been transformed from homogeneous to more heterogeneous stands (del Rio et al., 2016; Reventlow et al., 2021; Pommerening and Murphy, 2004). Whereas monocultures may be abstracted by mean characteristics or frequency distribution models, multi-layered mixed-species stands are better modeled using individual tree approaches (Coates et al., 2013). Fourth, the paradigm shift from mass-oriented forestry to multipurpose approaches has been accompanied by spatially explicit individual tree models. The latter enable the prediction of structural heterogeneity, wood quality, micro-habitats, and even recreational and esthetic values (Pretzsch et al., 2006). Fifth, the individual tree approach aligns well with many innovative prescriptions to silviculturally steer complex forest stands (Bravo et al., 2019).

These five trends have resulted in a boom in the development and use of individual tree models in forest management. Examples of this development include the models HEUREKA (Wikström et al., 2011), BWINPro by Nagel et al., (2006), PROGNAUS (Ledermann 2004; Sterba and Monserud, 1997), and SILVA (Pretzsch et al., 2002; 2008). In view of the establishment and silvicultural steering of even more heterogeneous mixed forest stands, most existing individual tree models appear as an oversimplification, as they often neglect species interactions (Pretzsch et al., 2015). This study aims to contribute to the adaptation of existing individual tree models to the needs of forest science and practice. We address an improved integration of tree species mixing effects, in particular the effects of inter-specific facilitation and competition reduction.

Fig. 1 visualizes the basic relationship of the potential-modifier approach commonly used in individual tree growth models. The potential-modifier approach is competition-based and assumes that the rate of tree size growth peaks when trees grow open, solitary, and with no or only little competition. The growth rate of open-grown trees is assumed to be the potential growth and set to 1.0 in Fig. 1. The absolute level of the potential growth is certainly depending, among others, on the tree species, the respective site conditions, and the crown size.

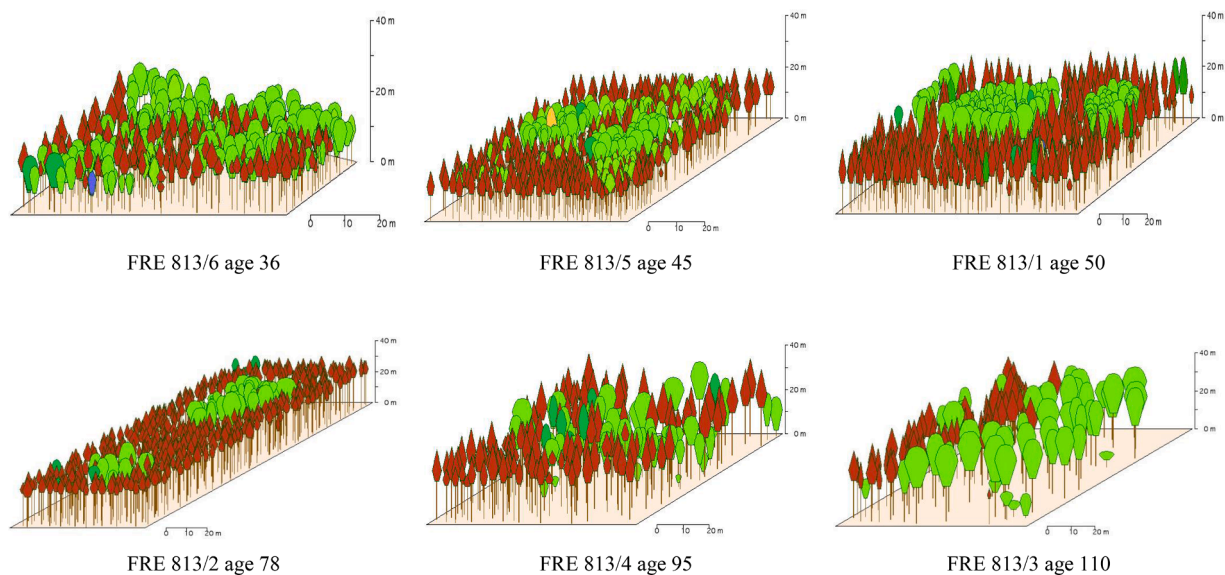


Fig. 2. Chronosequence FRE 813 with six plots in mixed stands of Norway spruce and European beech near Freising/Bavaria as an example for the setup of the 10 age series included in this study. Shown are the plots 6, 5, 1, 2, 4, and 3 ranked by age increasing from 36 to 110 years (state of the survey in autumn 1994). Crown sizes of Norway spruce are plotted in red and of European beech in green.

Table 1

Location, climate characteristics, and site conditions of the 10 age series with 62 plots included in this study. The ecoregion numbers indicate the following units: 12.8 Oberbayerisches Tertiärhügelland, 14.4.1 Westliche kalkalpine Jungmoräne, 8.1 Frankenwald, 6.2 Südlicher Oberpfälzer Jura, 2.2.1 Hochspessart, 4.1 Nördliche Fränkische Platte, 6.5 Oberpfälzer Jurarand, 4.2 Südliche Fränkische Platte (according to Arbeitskreis Standortkartierung (1985) Forstliche Wuchsgebiete und Wuchsbezirke in der Bundesrepublik Deutschland, 170 p.). N.sp., Norway spruce; E. be. European beech; s. oak, sessile oak; S. pi., Scots pine; E. ash, European ash; syc. map., sycamore maple.

Age series	Name	Species combination	Longitude °	Latitude °	Elevation a.s.l m	Annual precipitation mm yr ⁻¹	Mean temperature °C	Soil type	Substrate	Geology	Ecoregion see caption
FRE 813	Freising	N. sp., E. be.	11.66	48.42	515	814	7.7	Parabrown soil	Loam	Tertiary sand	12.8
SON 814	Schongau	N. sp., E. be.	10.77	47.87	790	1114	6.8	Brown soil	Loam	Günz-Mindel lower moraine	14.4.1
NOR 811	Nordhalben	N. sp., E. be.	11.59	50.31	590	850	5.5	Brown soil	Stony loam	Clay shale	8.1
KEH 804	Kelheim	s. oak, E. be.	11.76	48.93	455	721	7.5	Brown soil	Silt loam	Tertiary sediments	6.2
ROT 801	Rothenbuch	s. oak, E. be.	9.44	49.95	375	960	7.0	Brown soil	Silt loam	Lower sandstone	2.2.1
SWE 803	Schweinfurt	s. oak, E. be.	10.30	50.13	340	660	8.0	Brown soil	Silt loam	Lower trias	4.1
GEI 832	Geisenfeld	S. pi., E. be.	11.22	48.57	430	725	7.6	Brown soil	Soamy sand	Tertiary sand	12.8
AMB 833	Amberg	S. pi., E. be.	11.83	49.35	480	650	7.5	Brown soil	Sandy loam	Chalkstone	6.5
NEU 841	Neuburg	S. pi., N. sp.	11.22	48.56	430	725	7.6	Brown soil	Loamy sand	Tertiary sand	12.8
ARN 851	Arnstein	E. ash, syc. maple	9.94	49.99	260	670	8.0	Parabrown soil	Silt loam	Shell limestone	4.2

Table 2

Overview of main measurements variables and metrics 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	$\bar{cr} = \sqrt{(r_1^2 + r_2^2 + \dots + r_n^2)/8}$, for visualization
Crown length	cl	$cl = h - hcb$, used for visualization
searchradius 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 index	SDI	Local SDI in circle calculated without center tree
Binary variable indicating monospecific vs. mixed on circle	mfactor	$m = 0$, i.e. mixing proportion < 10% $m = 1$, i.e. mixing proportion \geq 10%
Mixing proportion in the reference circle around a tree	mportion	$m = 0$, i.e. monospecific stand, 0.1, 0.2...mixing proportions based on standardized SDI
(ii) Stand level Variables		
Stand age	age	Read off from historical stand documentation or increment cores
Quadratic mean stem diameter	dq	Calculated species-overarching
mean height	hq	Height of the tree with the quadratic mean stem diameter
Standing stem volume	V	Merchantable volume > 7 cm at the smaller end
Stand stem volume growth	IV	Periodical mean annual stem volume growth
Site index	SI	Site index based on hq at age 100 and the yield tables cited at the beginning of section "2.3 Descriptive data evaluation"

However, most models assume that any competition, quantified, e.g., by competition indices or local stand density (Grams et al., 2021; Pretzsch et al., 2015; Burkhart and Tomé, 2012; Biging and Dobbertin, 1995) reduces the tree growth. In models the potential growth rate is modified by multiplier *mod*, which decreases exponentially with increasing competition or local stand density. In Fig. 1 the decreasing curve represents the modifier function. The tree growth results from $id = id_{pot} \times mod$. The fact that neighbors (especially of other species) can facilitate growth, e.g., by atmospheric nitrogen-fixation, hydraulic lift, or nutrient upward transport from deeper soil layers, is known from scattered experiments, but rarely considered in individual tree simulation models so far.

Most available individual tree models have been parametrized using data from solitary trees in order to derive the potential growth rate (Hasenauer, 1997). They used mainly trees in monospecific stands to parametrize the modifier function (Hasenauer et al., 2006; Pretzsch et al., 2002). The application of such models to mixed stands will produce useful results only if trees behave similarly in inter- as in intra-specific neighborhoods. However, recent studies stress that mixed-species stands can be by 2–59% more productive than monospecific stands (Ruiz-Peinado et al., 2021; Steckel et al., 2019; Jactel et al., 2018) and that their maximum stand density can be by 5–25% higher (Thurm and Pretzsch, 2021; Pretzsch and del Río, 2020; Pretzsch and Biber, 2016; Binkley, 1984). Hence, it is possible to increase forest diversity by tree species mixing with a potential increase in tree growth compared to monospecific stands (Chamagne et al., 2017). Obviously, when growing together, some tree species can facilitate each other. The effect can be similar to a fertilization. One or both species may grow more due to inter-specific facilitation (Forrester, 2014; Pretzsch et al., 2013; Kely, 1992). Additionally, there may be a competition reduction when different species are mixed, leading to higher packing density. This may be caused by morphological complementarity and spatial niche separation (Pretzsch, 2014; von Felten and Schmid, 2008) or by temporal asynchrony (del Río et al., 2017; Jucker et al., 2015). Both may result in a reduction of the inter-specific compare to intra-specific competition (Metz et al., 2020; Forrester, 2017; Pretzsch, 2017; Pretzsch, 2022). Such effects of tree species mixing should be considered

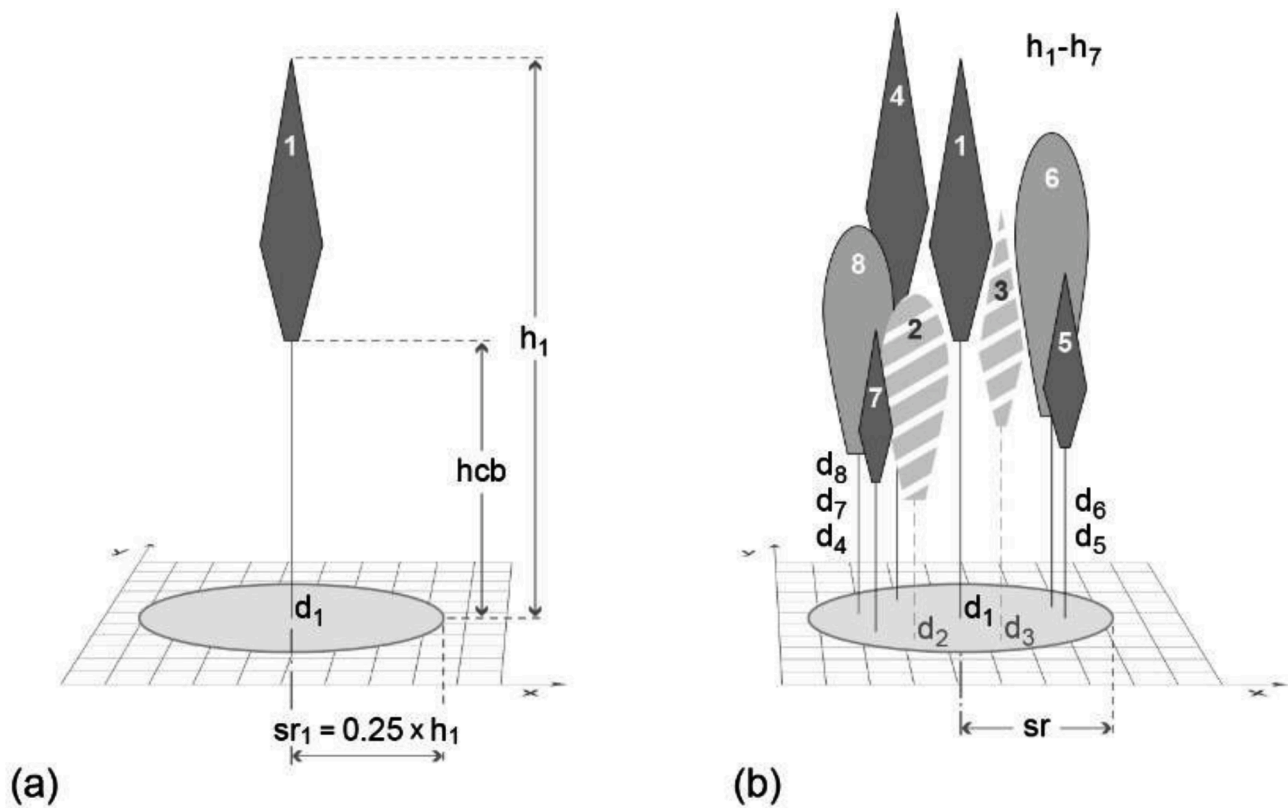


Fig. 3. Measurements (a) at the tree level and (b) setup for the evaluation of the local neighborhood of each tree.

to better model, understand, and design mixed species stands. Because of their advantageous functioning and provisioning of ecosystem services (Dieler et al., 2017), especially under changing environmental conditions (del Río et al., 2017; Jucker et al., 2014), mixed stands are presently on the rise; and suitable models, guidelines, and training plots are essential for their promotion (Coll et al., 2018).

A more detailed understanding of how an interspecific-neighborhood can facilitate tree growth and raise the potential growth rate (similarly to fertilization, but without the respective costs) may improve the nature-based design of resource-efficient forest ecosystems. Quantifying how mixing may modify tree growth efficiency is a pertinent issue in view of the increasing spread and relevance of mixed stands. Monitoring, inventories, and sampling should consider the spatial neighborhood to appropriately interpret the recorded tree growth. Models should be adapted to mixed species stands. Silvicultural prescriptions based on monospecific stands may be misleading when applied to mixed-species stands. For instance, they may neglect that mixed stands enable increased growth rates even when growing at higher stand densities. Consequently, they may prescribe overly strong stand density reductions and thereby undercut maximum stand productivity.

Here, we used a unique dataset of mono- and mixed-species growth conditions to quantify the effects of mixing on both the modification of the potential growth rate and the reduction of competition in inter-versus intra-specific neighborhoods. To address these questions we posed the following hypotheses:

H I: Inter-specific neighborhood can increase tree growth significantly above the level of open-grown trees in intra-specific neighborhoods. The potential growth rate in mixed stands can be higher compared to monospecific stands that are matched for size, crown, and site index.

H II: Tree species mixing can reduce competition. This competition reduction increases with the mixing proportion.

H III: Facilitation and competition reduction are modulated by site conditions. Facilitation and competition increase with the quality of the respective sites.

2. Material and methods

2.1. The study plots

The study based on 10 chronosequences (see example in Fig. 2) with altogether 62 long-term plots in Southern Germany with repeated stand inventories. The plots were established in the 1990ies in 18–238 years old stands. They cover the main tree species in Central Europe in intra- and interspecific neighborhood throughout the whole rotation. The plots represent the most common medium and high quality site conditions (Table 1), fully to moderately thinned stands, and mixture patterns reaching from individual-tree to cluster-mixtures. Since their establishment and first survey the chronosequences were remeasured up to 5 times. In this way the original chronosequences have become real time series of long-term survey and cover for all considered mixtures an age span of a whole rotation. The surveys cover the tree and stand growth in the time period 1991–2016.

The three-dimensional visualization of the age series FRE 813 in Fig. 2 was based on the inventory of the tree co-ordinates and species identity first recorded in 1991 and the measurements of the stem diameters, tree heights, crown sizes surveyed in autumn 1994. The plots size increases from the young to the old stands (see 20 m scale at the bottom of each plot) in order to cover representative sections of the representative stand development phases. For the sake of simplicity, we visualized the crown diameters calculated as the quadratic mean of the eight crown radius measurements.

2.2. Measurements, metrics, objective variables

Table 2 gives an overview of the main measurement variables and

Table 3
 Overview of the age 10 series with 62 plots included in this study. The number of measurements refers to the number of measured tree attributes such as stem diameters, stem coordinates, or crown characteristics at the first survey. ¹⁾ ho relates to the leading tree species mentioned at the first place in column 3. ²⁾ relates to the first survey of the youngest plot and the last survey of the oldest plot.

Age series	Name	Species combination	Site index ¹⁾ ho/Alter 100	m	Age from to ²⁾	years	Number of plots	Total plot area	m	First survey	Last survey	Number of surveys	Number of trees measured d	number	Number of trees measured h	number	Number of trees measured x, y coordinates	number	Number of trees measured crowns	number
FRE 813	Freising	N. sp., E. be.	35.1	35.1	37–168	4	6	0.48	0.48	1994	2012	4	7939	2498	2725	2020	2020	2020	2020	
SON 814	Schongau	N. sp., E. be.	37.4	37.4	50–142	5	8	0.48	0.48	1991	2011	5	14,106	4204	3619	3538	3538	3538	3538	
NOR 811	Nordthalben	N. sp., E. be.	33.3	33.3	36–126	2	5	0.44	0.44	1997	2008	2	3474	1494	1736	999	999	999	999	
KEH 804	Kelheim	s. oak, E. be.	32.7	32.7	17–165	4	7	0.45	0.45	1996	2015	4	14,587	2743	4129	1426	1426	1426	1426	
ROT 801	Rothentbuch	s. oak, E. be.	25.6	25.6	32–238	3	6	0.56	0.56	1994	2009	3	11,282	1270	3911	1389	1389	1389	1389	
SWE 803	Schweinfurt	s. oak, E. be.	27.3	27.3	21–186	2	6	0.46	0.46	1995	2005	2	6874	1813	4000	1339	1339	1339	1339	
GEI 832	Geisenfeld	S. pi., E. be.	32.0	32.0	18–214	3	6	0.35	0.35	1996	2010	3	7823	1837	2775	1029	1029	1029	1029	
AMB 833	Amberg	S. pi., E. be.	31.5	31.5	26–136	5	5	0.14	0.14	1991	2016	5	5142	1942	1869	979	979	979	979	
NEU 841	Neuburg	S. pi., N. sp.	32.8	32.8	22–118	3	6	0.41	0.41	1997	2014	3	13,433	4002	5135	1406	1406	1406	1406	
ARN 851	Arnstein	E. map., E. ash	35.0	35.0	20–94	3	7	0.28	0.28	1998	2014	3	5557	2864	5135	1241	1241	1241	1241	

metrics used in this study. From each tree on the 62 plots we recorded the species identity, measured the x-, and y- stem coordinates at the first survey and all stem diameters at each of the up to 5 surveys (Fig. 3a, Table 3). Tree height, h and height to the crown base, hcb, were sampled (>30 trees per species, sampled over the whole range of stem diameters) at each survey.

The stand age was read off from the historical documentation of the stand establishment. If such documents were not available we derived the tree age by tree-ring counting on increment cores sampled at the foot of the trunks of three trees of each species per plot. Stand ages were assumed to be identical with mean tree age in case of natural regenerated stands. In planted stands, stand age were assumed to be mean tree age minus three years to take into account the usual age of plants coming from the nursery.

2.3. Descriptive data evaluation

2.3.1. Stand level evaluation

To give an overview of the included chronosequences, we first evaluated them at the stand level using standard procedures (Biber, 2013, Pretzsch 2009, Johann, 1993). The reported stand-level data was derived from the diameter and height records, as well as from the removal of trees. The results encompassed the quadratic mean tree diameter, stand volume, and volume growth (see stand variables in Table 2 and Overview of the tree and stand characteristics of the Results section). For characterization of the site productivity we used the *hq* values and stand ages on the plots to derived the *hq* at stand age 100 as site index. For the site-indexing we applied the yield tables (moderate thinning) for Norway spruce by Wiedemann (1936/42), for Scots pine by Wiedemann (1943), for European beech by Schober (1967, 1975), sessile oak by Jüttner (1955), European ash by Volquardt (1958) and sycamore maple by Nagel (1986).

2.3.2. Tree level evaluation

Tree height estimation: As boundary and search radius *sr* for the neighborhood analyses (Fig. 3b) we used the quarter of the individual height of every tree. However, in the course of the repeated surveys the stem diameters were measured completely, the tree heights only randomly. For estimation of the individual tree height, *h*, depending on the stem diameter and tree age we parameterized the model

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

for each species on each of the 10 age series separately. For model parameters see Supplement Table 1.

The tree heights were also used for stem volume estimation in dependence on tree diameter, tree height, and form factor. For considering the stem form we used the approach by Franz et al., (1973) with the stem form equations and coefficients published by Pretzsch (2002, p. 170).

Neighborhood analyses within sample circles: To analyze the individual trees' competition indices, we used the concept of the stand density index (SDI) (Reineke 1933). For this purpose we defined around the position of each tree an influence zone by a circle with search radius $sr_1 = 0.25 \times h_1$ (see Fig. 3b). This study and a preliminar study by Pretzsch and Schütze (2021) showed that this circle size resulted in the highest correlations between the characteristics of stand structure and growth. All trees within the circle except the center 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 each individual tree. In the constructed circles, there were, on average, 8–9 trees and at least 5–6 most impactful neighbors (Prodan, 1968a, b). The local SDI was calculated using species-specific allometric exponents derived by Pretzsch and Biber (2005). They were applied for the component

species in intra- and interspecific neighborhood, as general allometric exponents for mixed stands were not yet available. Note that the latter exponents α were derived on A-grade and unthinned plots of long-term experiments in South Germany that are located in the same area as the age series of this study. They deviate from the species-overarching exponent of -1.605 , as proposed by Reineke (1933), are species-specific and representative for South Germany. The resulting local density index SDI was distant-dependent and easy to interpret. To standardize the density we applied the equivalence factors by Pretzsch and Biber (2016). These factors for the main tree species assemblages are shown in Supplementary Table 2.

Edge correction: 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 (Radtke and Burkhardt 1998, Pommerening and Stoyan 2006, Pretzsch, 2009). We use the plot SON 814/2 at the survey in autumn 2011 for visualization of this method in Supplementary Figure 4. Using the toroidal shift, we extended the same mixing patterns and distances between trees in all eight directions and avoided any overestimation of density, as it could result from other techniques (Radtke and Burkhardt, 1998).

Mixing proportions: The trees sampled in the circle were also used to calculate local mixing proportions. The mixing proportions $mportion_1 \dots mportion_n$ should reflect the area proportions of two or more species in the observed mixed stands (Pretzsch and del Río, 2020; Dirnberger et al., 2017). Tree number, basal area, or volume proportions are only appropriate for this purpose if the mixed species have similar growing

classes of increasing local SDI values from SDI = 0–100, 100–200, ..., 1800–2000 trees per hectare. For each SDI-class we used the 10% fastest growing trees and calculated the mean and standard error of their stem diameter growth. In this way we could find out whether the best growing trees in the mixed group grow better than in the monospecific group. The species-specific id-SDI relationships were visualized for each mixture in total but also for each ages series separately. Any exceedance of the tree growth in mixed neighborhood above the respective growth in monospecific neighborhood provided evidence for facilitation.

The detailed statistical analysis of facilitation by inter-specific neighborhood was also based on the 10% fastest growing trees on each plot and in each group (mono and mixed). By using only the respective 10% fastest growing trees, we addressed the potential growth. In this way we eliminated growth reductions by genetically determined low growth, crown size and shape effects (e.g., crown transparency and leaf losses), detrimental silvicultural treatment in the longer past (e.g., narrow spacing, abrupt and strong competition release), or abiotic (e.g., drought, frost) and biotic (e.g., bark beetle, fungal infestation) damages. This approach is suitable for addressing whether ceteris paribus the potential tree growth rates in inter-specific neighborhood can exceed those in intra-specific conditions indicating facilitation (H I).

The following mixed linear model revealed the mean effect of inter-versus intra-specific neighborhood after elimination of all relevant co-determining effects (see last paragraph of this section for a comprehensive explanation of the notation and assumptions used for testing H I, II, and III):

$$\ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(d_{ik}) + a_3 \times \ln(cr_{ik}) + a_4 \times \ln(SDI_{ik}) + a_5 \times \ln(SI_{ik}) + b_i + \varepsilon_{ik} \quad (2)$$

area requirements (Pretzsch et al., 2017). Tree species can vary per se in the growing area requirement and maximum stand density in fully stocked stands (de Prado et al., 2020). For example, a European beech with a stem diameter of 25 cm may require approximately double the growing space as a Norway spruce of the same diameter. This means, the density in terms of trees per hectare is only half of that of Norway spruce. To calculate the unbiased area-related mixing proportions, we again applied the equivalence factors shown in Supplementary Table 2.

Grouping of trees growing in mixed versus monospecific environment: For further exploration of co-determining variables on the mixing effects we introduced the binary variable mfactor that indicated the respective species assemblage. Circles with an admixture smaller than 10% of another species based on the SDI were classified as monospecific (mfactor = 0). Circles with an admixture of more than 10% were classified as mixed (mfactor = 1).

2.4. Statistical models for hypotheses testing

2.4.1 Inter-specific neighborhood can facilitate tree growth (H I): For scrutiny whether maximum stem diameter growth rates, at parity of competition, can be increased in inter-specific compared with intra-specific neighborhood we used the individual trees' annual stem diam-

Eq. (2) represented the full model if all variables would be included. Depending on the respective species-specific relationships it was simplified. We eliminated those variables that were not significant (i.e., $p > 0.05$) and did not lower the AIC value.

The model Eq. (2) with mfactor being the binary 0/1 variable addressed the effect of monospecific (mfactor = 0) or mixed stand condition (mfactor = 1). The back transformed version, e.g., $y = e^{a_0} \times e^{a_1 \times mfactor}$ showed that the dummy variable mfactor results in $e^0 = 1$ in case of monoculture and e^{a_1} in case of mixed stands. This means that e^{a_1} directly reveals any multiplicative effects of mixing on the dependent variables. Suppose $a_1 = 0.25$, the mixing effect on the target variable would be $e^{0.25} = 1.284$ and the effect size would be 28.4%. This helps to easily interpret the biological meaning of the respective coefficients of mfactor in model 2.

2.4.2. Tree species mixing reduces the competition and the competition reduction increases with the mixing proportion (H II)

For testing this hypothesis model 3 was formulated as follows

$$\ln(id) = a_0 + a_1 \times \ln(d_{ik}) + a_2 \times \ln(age_{ik}) + a_3 \times \ln(SDI_{ik}) + a_4 \times \ln(mportion_{ik}) + a_5 \times \ln(SDI_{ik}) \times \ln(mportion_{ik}) + b_i + \varepsilon_{ik} \quad (3)$$

eter growth, the local competition SDI, and the mixing proportions within the respective circles (Fig. 3b). The data was grouped in trees from monospecific and mixed circles. We then sorted the trees into

This model was fitted for each species using the whole dataset, i.e., using all data including the 10% fastest growing trees.

2.4.3 Facilitation and competition reduction are modulated by site

conditions (H III): The plots of the mixture of Norway spruce and European beech and of sessile oak and European beech covered a sufficiently wide range of site conditions for analyzing any interaction between mixing and site index on growth. We first analyzed the interaction between mixing and site index on the growth of the 10% fastest growing trees by model 4.

$$\ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(SI_{ik}) + a_3 \times mfactor_i \times \ln(SI_{ik}) + b_i + \varepsilon_{ik} \quad (4)$$

Using the same model, we further analyzed the interaction between mixing and site index based on the full dataset for the mixtures of

Norway spruce and European beech and of sessile oak and European beech.

“For testing H I-H III we applied linear mixed models”. The dependent variable was the mean annual stem diameter growth, id . The independent variables were individual tree diameter, d , tree age, local SDI, the binary variable $mfactor$ (0/1 for mono/mixed), mixing proportion, $mportion$, and site index, SI . In all equations, the indexes i and k represented the k^{th} observation of the i^{th} tree. The fixed effects were covered by the parameters a_0 - a_n . With the random effect $b_i \sim N(0, \tau^2)$ we cover the correlation between the single observations on tree level. In preliminary model formulations we also worked with random effects

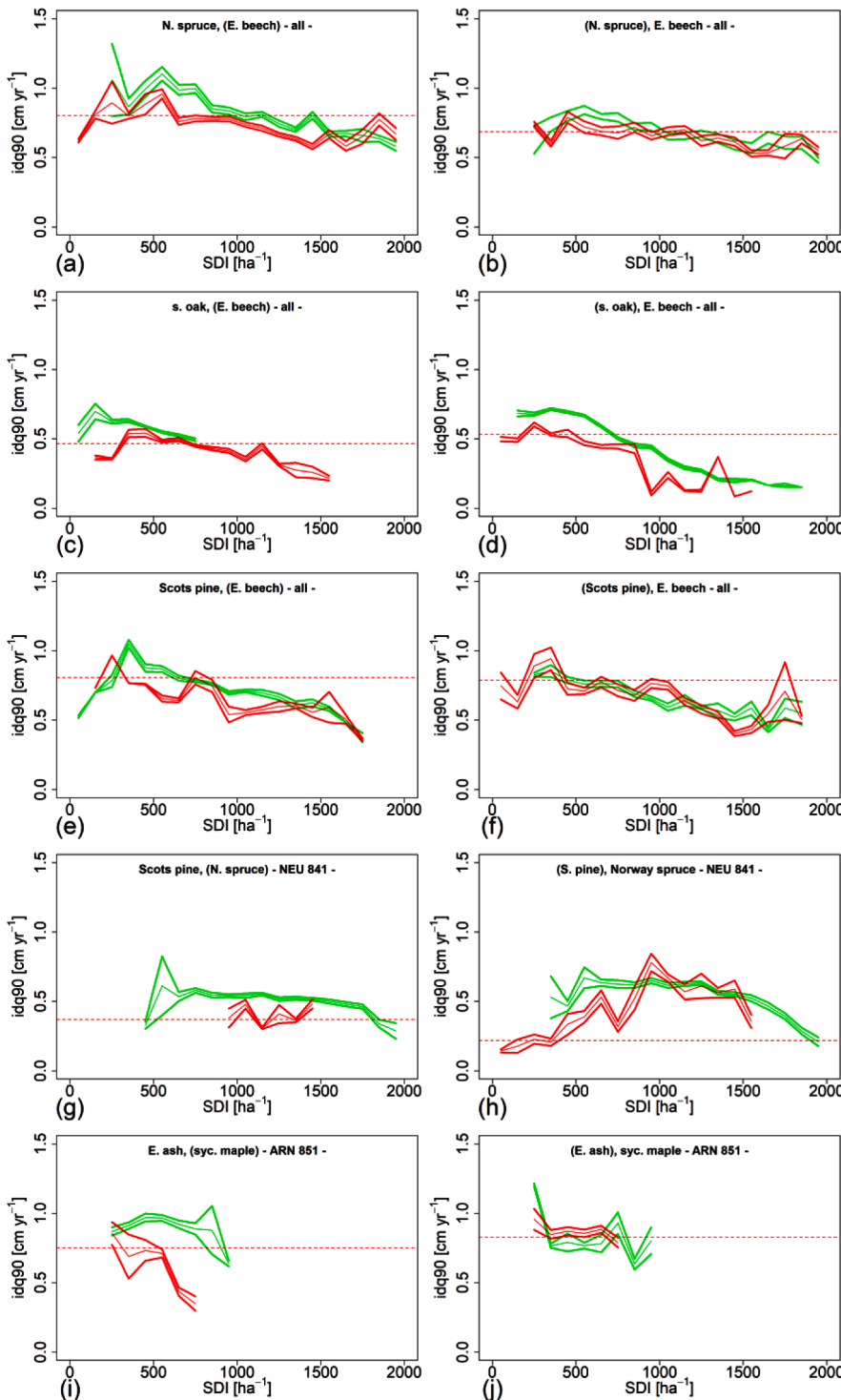


Fig. 4. Annual stem diameter growth (mean±se) of the 10% fastest growing trees plotted over local SDI in mixed (green) compared with monospecific stands (red). The broken horizontal line reflects the mean growth rate of the 10% fastest growing trees in monospecific neighborhood under sparsely stocked conditions (SDI = 250–500 ha⁻¹) as reference. For the graphs we pooled all trees of the respective species combinations. (a and b) Norway spruce and European beech (FRE 813, SON 814, NOR 811), (c and d) sessile oak and European beech (KEH 804, ROT 801, SWE 803), (e and f) Scots pine and European beech (GEI 832, AMB 833), (g and h) Scots pine and Norway spruce (NEU 841), (i and j) European ash and syc. maple (ARN 851). For separate evaluation of each of the 10 age series of this study see Supplement Figs. 1–3.

Table 4

Statistical characteristics of models 2.1–2.8 for testing H I. The equation numbers refer to the models introduced in section 2.5 *Statistical models for hypotheses testing*. For reasons of space the table reports only the fixed effect variables of the respective models. The factor e^{a_1} (in bold letters) reflects the ratio between the potential growth in inter- versus intra-specific environment. For further variable explanation see Table 2. *Model 2.1* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d) + a_3 \times \ln(cr) + a_5 \times \ln(SI)$, *Model 2.2* $\ln(id) = a_0 + a_1 \times mfactor + a_3 \times \ln(cr) + a_4 \times \ln(SDI) + a_5 \times \ln(SI)$, *Model 2.3* $\ln(id) = a_0 + a_1 \times mfactor + a_3 \times \ln(cr) + a_5 \times \ln(SI)$, *Model 2.4* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d) + a_4 \times \ln(SDI) + a_5 \times \ln(SI)$, *Model 2.5* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d)$, *Model 2.6* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d) + a_3 \times \ln(cr)$, *Model 2.7* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d) + a_3 \times \ln(cr) + a_4 \times \ln(SDI) + a_5 \times \ln(SI)$, *Model 2.8* $\ln(id) = a_0 + a_1 \times mfactor + a_2 \times \ln(d) + a_5 \times \ln(SI)$.

Group	Model	n	a_0	std(a_0)	p-value	a_1	Factor e^{a_1}	std(a_1)	p-value	a_2	std(a_2)	p-value	a_3	std(a_3)	p-value
N. sp., (E. be.)	2.1	134	-3.55	1.26	0.006	0.13	1.14	0.05	0.004	-0.47	0.06	<0.001	0.28	0.11	0.011
(N. sp.), E. be.	2.2	135	-3.71	1.15	0.002	0.32	1.38	0.11	0.003			<0.001	0.36	0.14	0.012
s. oak, (E. be.)	2.3	106	-3.67	0.64	<0.001	0.13	1.14	0.05	0.006			<0.001	0.20	0.08	0.013
(s. oak), E. be.	2.4	247	-2.27	0.46	<0.001	0.49	1.63	0.07	<0.001	0.35	0.06	<0.001			
S. pine, (E. be.)	2.3	119	-2.85	0.91	0.002	0.49	1.63	0.10	<0.001	0.28	0.11	0.011	0.57	0.16	<0.001
(S. pine), E. be.	2.5	82	-1.72	0.15	<0.001	0.53	1.69	0.08	<0.001	0.27	0.05	<0.001			
S. pine, (N. sp.)	2.6	62	0.32	0.18	0.070	0.38	1.47	0.10	<0.001	-0.40	0.06	<0.001	0.21	0.11	0.050
(S. pine), N. sp.	2.7	74	-5.93	0.65	<0.001	0.56	1.74	0.22	0.013	0.81	0.06	<0.001	0.61	0.11	<0.001
E. ash, (syc. Maple)	2.4	73	-13.04	1.28	<0.001	0.33	1.39	0.08	<0.001	-0.21	0.10	0.043			
(E. ash), syc. maple	2.8	97	-8.27	1.26	<0.001	0.58	1.78	0.11	<0.001	-0.14	0.05	0.009			

on plot level, i.e., one additional nesting level. As this caused confounding effects with the fixed effect, we constrained ourselves to the simpler random effect structure of Eqs. (2)–(4). With ε_{ik} we denote the independently and identically distributed errors ($\varepsilon_{ik} \sim N(0, \sigma^2)$).

For all calculations we used the statistical software R 3.6.3 (R Core Team, 2019); for fitting the mixed linear models explained above, we in particular used the libraries nlme (Pinheiro et al., 2018) and lme4 (Bates et al., 2015).

3. Results

3.1. Overview of the tree and stand characteristics

The mixtures were represented by young to old stands with an age range of 15–238 years (Supplementary Table 3). The mean diameter ranged from 7.8 to 51.5 cm. The standing volume was the highest (1774 $m^3 ha^{-1}$) in mature stands of Norway spruce and European beech. The annual stem volume growth was the highest (36.2 $m^3 ha^{-1} yr^{-1}$) in the stands with Norway spruce and European beech and Scots pine and European beech. For further information see Supplementary Table 3.

The models could be based on $n = 1112$ –6233 observations per

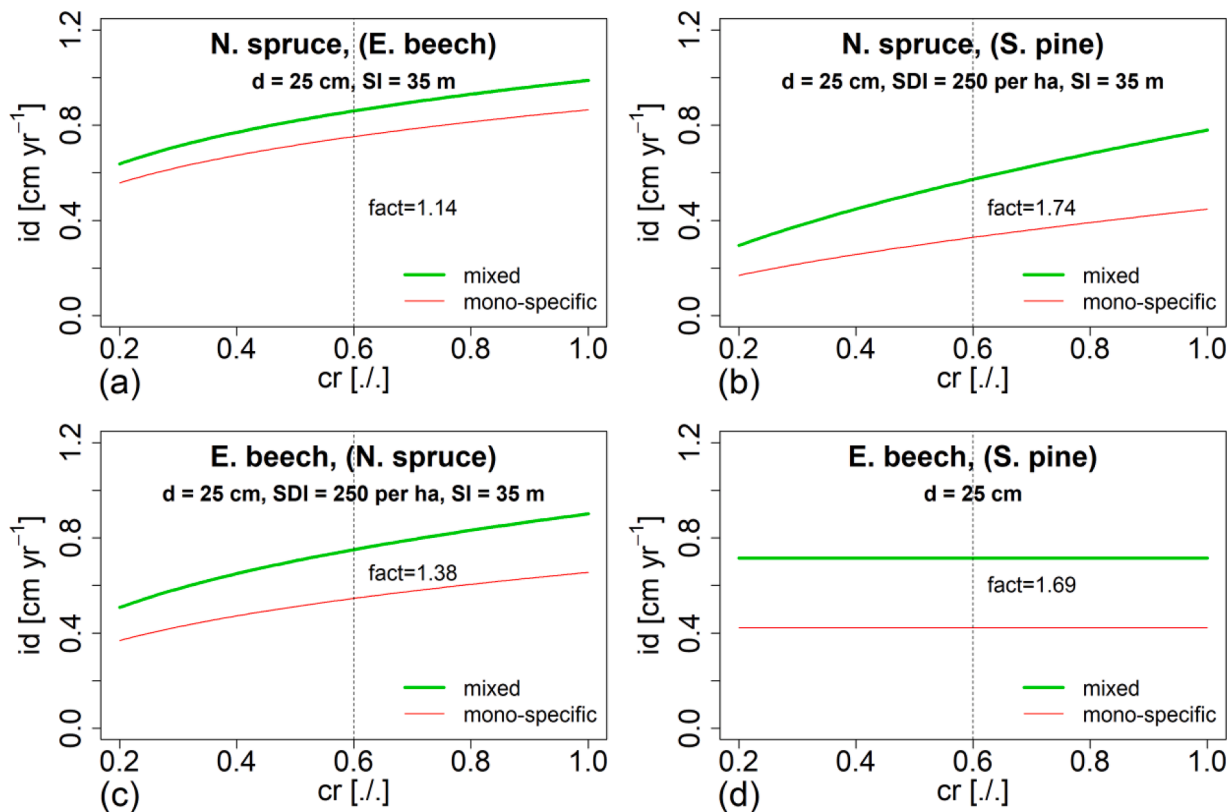


Fig. 5. Potential stem diameter growth in mixed- compared with monospecific neighborhood plotted over crown ratio. The inscribed factors reflect the relative growth superiority of mixed- versus monospecific conditions (see regression results in Table 4). (a and b) Norway spruce in mixture with European and Scots pine, respectively. (c and d) European beech in mixture with Norway spruce and Scots pine, respectively.

species and species combination (Supplementary Table 4). The annual stem diameter growth rates ranged from 0.01 to 1.48 cm yr⁻¹, and the diameters from 9.28 to 103.40 cm. The crown diameters ranged from 0.18 to 15.58 m and the crown ratios from 0.05 to 0.94 m/m. The data covered low local competition of SDI = 2.64 but also very dense stand parts with SDI = 4487.49 trees per hectare. Compared to the usually reported stand related SDI values of 500–2000 trees per hectare (Pretzsch, 2019; Sterba, 1981) the local SDI's can become low as well as very high as they refer to the local density within the search radius *sr*. The site index related to the quadratic mean height at age 100 and based on the yield tables quoted in the section *Descriptive data evaluation*. The SI ranged between 20 - 43 m at age 100. The mixing proportions cover the whole range between monospecific conditions of one to the other species. Especially the wide range of diameters, local densities, mixing proportions, and site indices made the data suitable for testing of H I-H III. For further information see Supplementary Table 4.

3.2. Facilitation and increase of potential growth rate in inter- versus intraspecific environment (H I)

Fig. 4 shows that the annual stem diameter growth of the 10% fastest growing trees in inter-specific neighborhood (green) can significantly exceed the growth rates under monospecific conditions at parity of stand density. The horizontal broken lines indicate the growth rate of the 10% fastest growing trees in monospecific neighborhood for trees with competition of SDI = 250–500 trees. In mixed stands (green curves) the growth rates exceed this level by up to 40%. The finding that the potential growth is superior in mixed environment provides evidence of inter-specific net facilitation. In seven out of 10 cases this net facilitation occurs mainly under low competition. For detailed information about the stem diameters of the 10% fastest growing trees see Supplementary Table 5.

For Fig. 4 we pooled all trees of all chronosequences of the same species assemblage. For separate visualization of each of the ten chronosequences of this study see Supplement Figs. 1–3. In summary 8 out of 10 species assemblages provided evidence of net facilitation and increased potential growth rates in mixed compared with monospecific environment.

For further statistical analysis of any facilitation effects by inter-specific neighborhood on the potential growth rate of trees we used again the fastest 10% of trees without and with interspecific neighborhood. Table 4 reflects that in all 10 cases the growth in the inter-specific group was significantly higher than in the intra-specific group at least at the level *p* < 0.05. The superiority ranged between a plus of 14% in case of Norway spruce in European beech or sessile oak in European beech. The superiority amounted to plus 74 and 78% in case of Norway spruce when growing in Scots pine or sycamore maple growing mixed with European ash. In most cases the crown ratio had an additional positive influence. In some cases also the other considered variables such as *d*, SDI, and SI had an additional effect. This covariance analyses of the

Table 5

Statistical characteristics of models 3 used for analyzing the effect of mixing on the stem diameter growth (H II). For reasons of space the table reports only the fixed effect variables of the respective models. For variable explanation see Table 2. $Model\ 3\ \ln(id) = a_0 + a_1 \times \ln(d) + a_2 \times \ln(age) + a_3 \times \ln(SDI) + a_4 \times \ln(mportion) + a_5 \times \ln(SDI) \times \ln(mportion)$.

Group	n	a ₀	std (a ₀)	p-value	a ₁	std (a ₁)	p-value	a ₂	std (a ₂)	p-value	a ₃	std (a ₃)	p-value
N. sp., (E. be.)	11,017	0.78	0.18	<0.001	1.47	0.03	<0.001	-1.35	0.04	<0.001	-0.21	0.02	<0.001
(N. sp.), E. be.	6549	-0.06	0.25	0.81	1.46	0.03	<0.001	-1.09	0.04	<0.001	-0.25	0.03	<0.001
s. oak, (E. be.)	7945	-1.73	0.25	<0.001	1.90	0.03	<0.001	-1.17	0.04	<0.001	-0.15	0.0376	<0.001
(s. oak), E. be.	19,650	-0.69	0.12	<0.001	1.27	0.02	<0.001	-0.84	0.02	<0.001	-0.23	0.01	<0.001
S. pine, (E. be.)	6051	0.12	0.224	0.58	1.15	0.05	<0.001	-0.71	0.04	<0.001	-0.35	0.03	<0.001
(S. pine), E. be.	4233	-1.62	0.21	<0.001	1.47	0.04	<0.001	-0.49	0.03	<0.001	-0.34	0.0378	<0.001
S. pine, (N. sp.)	3910	-0.81	0.85	0.34	1.66	0.05	<0.001	-1.24	0.05	<0.001	-0.20	0.12	0.080
(S. pine), N. sp.	6232	-1.84	0.22	<0.001	1.97	0.03	<0.001	-1.02	0.03	<0.001	-0.24	0.0353	<0.001
E. ash, (syc. Maple)	1112	-0.91	0.37	< 0.014	1.31	0.05	<0.001	-1.12	0.07	<0.001	0.01	0.0602	0.996
(E. ash), syc. maple	2032	-2.60	0.35	<0.001	1.66	0.05	<0.001	-0.80	0.06	<0.001	-0.11	0.05	0.018

potential stem diameter growth in inter- versus intra-specific neighborhood (factor *m*) based on model 2. The model included the covariables stem diameter, crown ratio, local SDI, and site index in case that they were significant at least at the level *p* < 0.05 and that they increased the AIC criteria of the regression compared with the basic model (*id* = *f* (factor)). This variable selection resulted in the model variants 2.1–2.8 presented in Table 4.

Fig. 5 visualizes the results for four selected tree species combinations where the potential growth was 14–78% higher in mixed-compared with monospecific neighborhood (factor = 1.14–1.78). In three out of the shown four cases the crown ratio had an additional positive effect on the growth rate. Fig. 5 corroborates that any benefit of mixing depends on both the species identify of the basis species and the neighbors. Fig. 5, a and b show that the potential growth rate of Norway spruce benefitted moderately when mixed with European beech (14%) but much stronger when mixed with Scots pine (74%). Fig. 5, c and d show a plus of 38% for European beech when mixed with Norway spruce and a plus of 69% when mixed with Scots pine. Note that the mentioned superiorities refer to growth rates of the 10% best growing trees in both groups (mixed versus mono) after elimination of any additional effects of *d*, *cr*, SDI, SI. Thus the 14–78% plus reflects mainly the effect of facilitation of the different neighboring tree species in low density environment and at parity of other modulating factors such as *d*, SI. This means that competition and density effects were as far as possible eliminated by only selecting the fastest growing trees per plot and group and by elimination of any other size or density related group differences.

Group	a ₄	std (a ₄)	p-value	a ₅	std (a ₅)	p-value
N. sp., (E. be.)				1.38	0.36	< 0.001
(N. sp.), E. be.	-0.12	0.05	0.049	1.12	0.33	< 0.001
s. oak, (E. be.)				0.91	0.19	< 0.001
(s. oak), E. be.	-0.18	0.06	0.001	0.36	0.08	< 0.001
S. pine, (E. be.)				0.47	0.23	0.041
(S. pine), E. be.						
S. pine, (N. sp.)						
(S. pine), N. sp.	-0.22	0.08	0.007	1.04	0.14	< 0.001
E. ash, (syc. Maple)				3.71	0.42	< 0.001
(E. ash), syc. maple				2.26	0.39	< 0.001

3.3. Density dependent competition reduction (H II)

When testing H II based on model 3 we found in nine out of ten cases an increase of stem diameter growth with increasing admixture proportion (Table 5). For Norway spruce when mixed with European beech we found a neutral effect of admixture; there was no significant facilitation. In most species assemblages both tree species benefitted from the mixture (see, e.g., Fig. 6, c and d). In the mixture of Norway spruce and European beech only the latter benefitted (Fig. 6, a and b). There were no cases where one species benefitted at the expense of the other species, i.e., that an increase of one was coupled with a loss of the other. In all

mixtures the growth of European beech strongly benefitted from living in mixture (Fig. 6, b, d, f). In most of the cases the benefit of growing in mixture was present under low density but even increased with local stand density from SDI = 500–2500 trees per hectare.

Group	a_4	std (a_4)	p -value	a_5	std (a_5)	p -value
N. sp., (E. be.)	-0.13	0.58	0.82	0.02	0.08	0.840
(N. sp.), E. be.	-1.59	0.60	0.008	0.29	0.09	<
						0.001
s. oak, (E. be.)	-1.73	0.50	<	0.29	0.08	<
			0.001			0.001
(s. oak), E. be.	-0.66	0.19	<	0.21	0.03	<
			0.001			0.001
S. pine, (E. be.)	-0.59	0.48	0.22	0.10	0.08	0.200
(S. pine), E. be.	-1.15	0.60	< 0.05	0.27	0.09	0.002
S. pine, (N. sp.)	-6.41	1.99	<	0.98	0.28	<
			0.001			0.001
(S. pine), N. sp.	1.01	0.54	0.062	-0.11	0.08	0.160
E. ash, (syc. maple)	1.74	0.83	<	-0.23	0.14	0.091
			0.037			
(E. ash), syc. maple	0.35	1.44	0.81	0.11	0.23	0.630

3.4. Inter-specific facilitation and competition depending on site conditions (H III)

Any dependency of inter-specific facilitation on site conditions was first tested for the collective of the 10% fastest growing trees per group and plot by model 4. Any dependencies of the mixing effects on the site conditions were analyzed only for the mixtures of Norway spruce/European beech and sessile oak/European beech. For the other species the range of the site conditions was too narrow for analogous analyses.

We found a significantly positive effect of inter-specific neighborhood on growth, however, this on average positive effect remained constant along the whole site gradient. In none of the cases there was a significant interaction between site conditions and mixing effect (see coefficients a_3 in Table 6). Fig. 7 visualizes that in both mixtures the fastest growing trees benefitted from living in mixture. However, the benefit did not change along the site gradient (SI = 20–40 m mean height at age 100) covered by this study.

An analogous analysis based on model 4 was done based on the whole dataset in order to reveal any modulation of the competition reduction by site quality. For the competition reduction we found a tendency of increase with site quality that was close to significant for the mixture of Norway spruce and European beech (see Table 7 and Fig. 8). For European beech when growing in association with oak we found a significant ($p = 0.002$) increase of competition reduction with increasing site quality cases (see last row in Table 7 and Fig. 7d). In summary in all cases diameter growth was higher in mixed compared with monospecific stands, in case of beech in oak the superiority increased slightly with improving site quality.

4. Discussion

4.1. A consolidated view of facilitation and competition effects on growth

Analyzing, understanding, modeling, and prognosticating monocultures often entails a thorough consideration of the effects of competition between neighboring plants (Larocque et al., 2013; Nambiar and Sands, 1993), but hardly of the facilitation or reduction of competition by neighbors (Maestre et al., 2009; Bruno et al., 2003; Vandermeer, 1992). The results of this study provide evidence that the assumption of maximum growth under solitary conditions and of an exponential growth reduction through increased competition and density (as shown in Fig. 1) is an over-simplification. In particular, we show that tree growth can be increased beyond solitary growth (by 14–78%) through

an inter-specific neighborhood under moderate density (Fig. 5 and Table 4).

We analyzed the feedback *spatial stand structure* → *facilitation and competition* → *tree growth* and its dependency on site conditions (e.g., site index) and silvicultural interventions (e.g., stand density, mixing proportion) (Fig. 9). By modeling the effects of different stand characteristic on individual tree growth we showed that tree growth can be promoted or reduced (facilitation versus competition) by intra- and interspecific neighborhood. Models 1–3 showed for different species combinations how the facilitation and competition is modulated by site conditions and stand density.

Our results suggest that the growth-competition relationship is unimodal, as represent by the bold curve in Fig. 10a. Facilitation and competition act simultaneously (Pretzsch, 2017; Vandermeer, 1992). They are difficult to disentangle, and the measured growth reaction represents the net effect of the interaction between facilitation and competition (thin and broken lines, respectively, in Fig. 10a). In Fig. 10a the tree growth in solitary conditions is used as a reference (1.0-line) and indicates that the trajectory of the measured growth may result from the interplay between facilitation and competition. This pattern may apply even in some monospecific populations, especially under harsh conditions (Callaway and Walker 1997, Canham et al., 1994, 2004). We also found that an inter-specific neighborhood can increase the facilitation, and reduce the competition, so that the net effect on growth becomes more positive (see Fig. 10b, vertical and horizontal arrows).

Fig. 10b indicates the shift of the tree growth-density relationship due to a facilitation (e.g., tapping of nutrients in deep soil layers which are favorable for species 1) or a reduction in competition (e.g., by spatial or temporal niche complementarity). Further, the inter-specific neighborhood may cause a widening of the density range with net facilitation (horizontal arrow). This may cause a narrowing of the range where net competition has the upper hand. Figs. 4 and 5 showed such a facilitation of trees in mixed stands. In several cases trees with moderate density grew even faster in an inter-specific neighborhood than trees with low competition in monospecific stands.

Fig. 10a shows that net facilitation may dominate at low densities, and that net competition may predominate in denser stands. The reason may be, that around widely spaced trees, the negative effect of competition on growth may be still low enough to be compensated or even overcompensated for by the positive effect of facilitation. When stand density further increases, the growth reduction cannot be balanced out as easily by facilitation and may cause net competition. Although not easy to detect and to disentangle from competition, facilitation may also play a role in closed forest stands with high stand density.

The study further showed that facilitation and competition reduction may depend on environmental conditions (Gonzales de Andres et al., 2018). They may become stronger in high quality sites. This means that the stand density range with a net facilitation effect and an increase of tree growth is extended towards higher stand densities (see horizontal arrow in Fig. 10c). Finally, this study showed a strong facilitation and competition reduction through inter-specific conditions. However, this facilitation was site-invariant (Fig. 7, Table 6). The competition reduction increased only slightly with improving site quality (Fig. 6, Table 7).

4.2. Causes of facilitation and reduction of competition in an inter-specific neighborhood

Comparing the 10% fastest growing trees in a mixed- versus monospecific neighborhood (Fig. 5, Table 4) showed a 14–78% increase in growth in mixed stands. This result remained consistent across different neighboring tree species in low density environments and at parity of other modulating factors, such as d and SI. The finding that stem diameter was not always significant in the models may be attributed to the fact that other tree dimensions such as crown ratio or age overtopped d in correlation with growth. The finding that the 10% fastest growing trees of several species were superior means that they had a higher

growth rate when surrounded with other species, than when growing widely spaced and open. We furthermore found a competition reduction of 16% on average (ranging from -1% - +36%) calculated for a local SDI value of 1000 ha⁻¹, quadratic mean diameter of 25 cm, stand age of 30 years, and a mixing proportion of 50:50 for each pair of species (Fig. 5, Table 5).

How can a higher growth in inter-specific mixtures compared to growth without neighbors be explained, i.e., how is it possible that the positive effect of a neighbors is higher than the negative effect? What may be the main causes underlying the demonstrated competition reduction under high density conditions? The measured net effects of density and distance of neighboring trees on tree growth allowed us the following speculations about the potential mechanisms underpinning the revealed mixing effects.

Norway spruce and European beech: Many studies showed that the negative effects of soil compaction (Wiedemann, 1923), acidification (Pallant and Rihac, 1990), and nutrient depletion (Kaarakka et al., 2014) through Norway spruce monocultures can be mitigated by many species admixtures, and especially by European beech (Rothe and Binkley, 2001; Rothe, 1997; Wiedemann, 1942). The latter can facilitate the growing conditions of Norway spruce by increasing the temperature (especially in early spring) by improving litter decomposition, and nutrient cycling and turnover (Pretzsch et al., 2020, 2010; Goisser et al., 2016; Rothe et al. 2002, 2003). Furthermore, beech can benefit from Norway spruce through its higher leaf area, resulting in higher eutrophic deposition filtering (Alveteg et al., 1998; Cannell et al., 1998; van Dijk and Roelofs, 1988). An advantage and competition reductions for both species may be their crown shape complementarity, i.e., the ▲-shaped

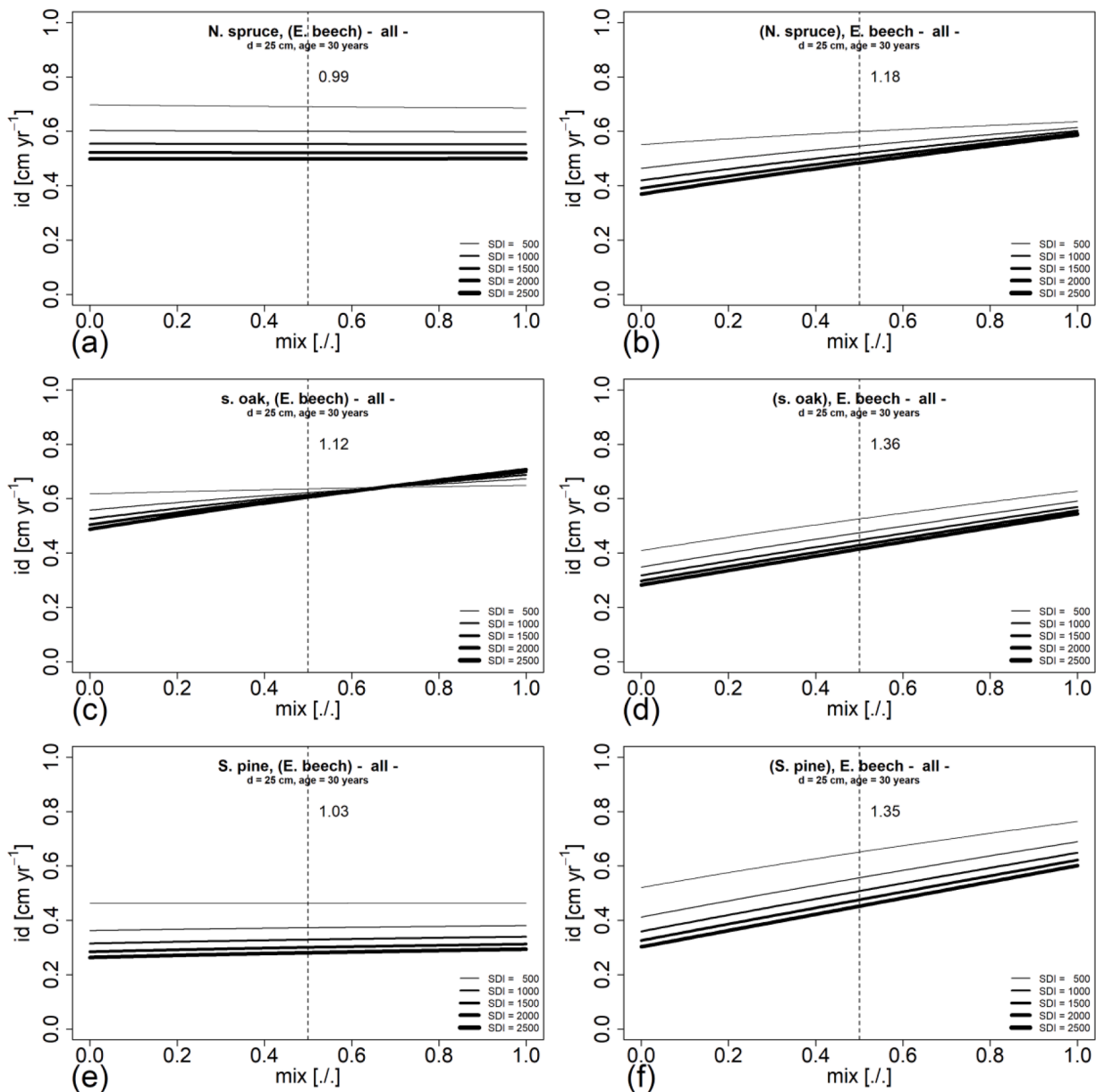


Fig. 6. a (see Fig. 6b for continuation) Effect of the admixture proportion, mportion, of a second tree species on the stem diameter growth for different local stand densities SDI = 500–2500. The graphs are based on model 3, and the respective parameters are shown in Table 5. The stem diameter was set to $d = 25$ cm and the age to 30 years. (a-f) The relationships were visualized separately for the two component tree species (left and right, respectively). 6b (continuation of Fig. 6a) Effect of the admixture proportion, mportion, of a second tree species on the stem diameter growth for different local stand densities SDI = 500–2500. The graphs are based on model 3 and the parameters shown in Table 5. The stem diameter was set to $d = 25$ cm and age to 30 years. (g-j) The relationships were visualized separately for the two component tree species (left and right, respectively).

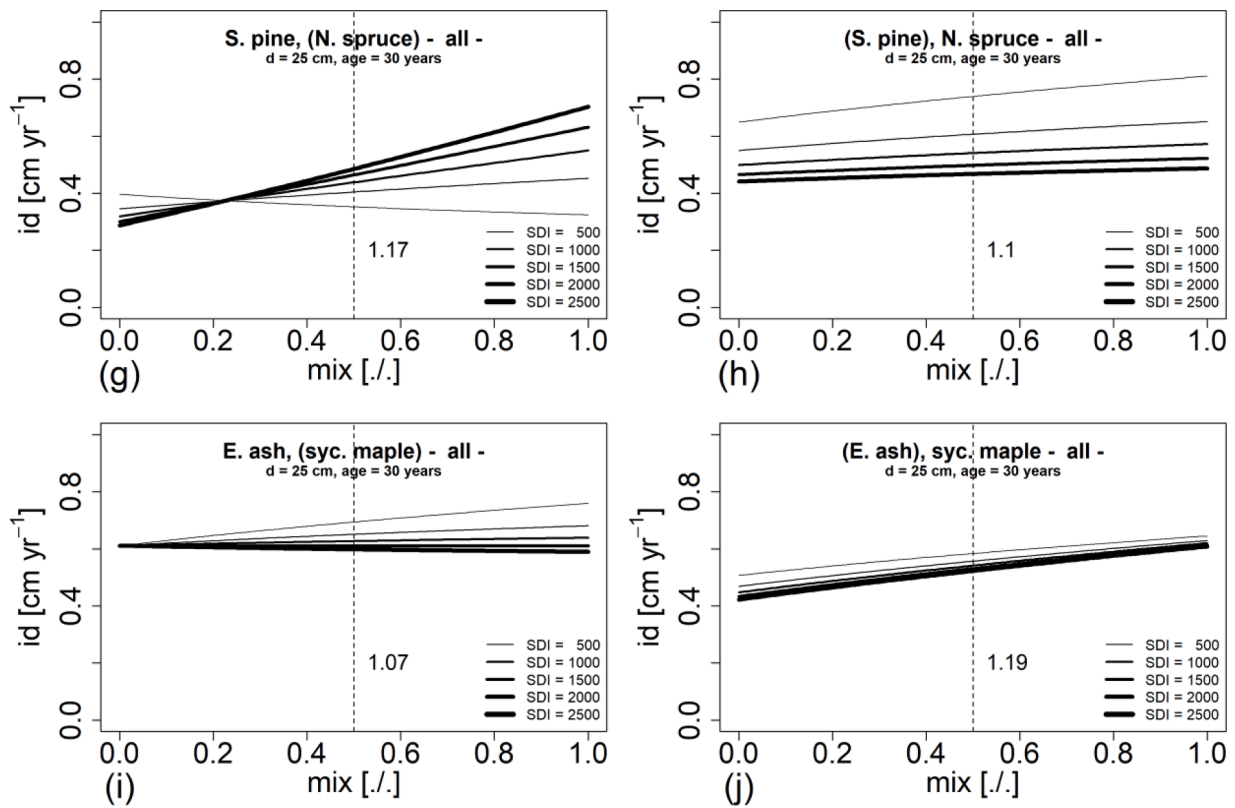


Fig. 6. (continued).

Norway spruce (bottom heavy) versus ▼-shaped European beech (top heavy) crowns enable a higher canopy packing density (Barbeito et al., 2017; Jucker et al., 2015; Pretzsch, 2014). Complementarity in shape may, across all mixtures, reduce mechanical abrasion and crown shyness (Hajek et al., 2015; Fish et al., 2006; Meng et al., 2006). It may also cause higher canopy packing density, stand density (Thurm and Pretzsch, 2021), and stand leaf area (Pretzsch and Schütze, 2021; Peng et al., 2017). In this way complementarity in shape may result in overyielding (Williams et al., 2017). In addition, physiological asynchrony of tree species may be beneficial for their growth (Pretzsch, 2005; Rötzer et al., 2017; Schober, 1950/51). For instance, Norway spruce may benefit of a reduced competition for water in early spring when European beech is still leafless and lives from the reserves of the previous year. During this period, photosynthesis and growth of spruce may further profit from higher temperatures and light supply until beech sprouts in April/May.

Sessile oak and European beech: In mixture with oak, beech may be facilitated by hydraulic lift. This has been observed in particular on dry sites with deeply extending root systems, which release water at night into surface-near soil horizons of low water potential (Caldwell et al., 1998; Prieto et al., 2012). Sessile oak may benefit from beech by the improvement of soil activity, decomposition, and nutrient turnover (Jonard et al., 2008). Competition reduction may promote European

beech when admixed to all species that are less shade tolerant (e.g., oak). European beech benefits in such cases by increasing lateral crown expansion or often simply by penetrating crowns of neighbor trees that are less shade tolerant (Metz et al., 2020; Bayer et al., 2013; Ellenberg and Leuschner, 2010).

Scots pine and European beech: Especially on poor sites, Scots pine can be facilitated by the substantial nutrient input from European beech-induced litter translocation and the improved decomposition and turnover of the mixed litter (Yeste et al. 2021). This can improve the water storage and have a particularly positive effect on the mineral nutrient supply. European beech can have a beneficial effect on pine, primarily through stimulation of the bio-element turnover, and by improving the nutrition of pine. In comparison to pine, beech litter has a higher Ca, Mg and K content, as well as a lower C/N ratio (Augusto et al., 2002). Moreover, activity of soil fauna and microflora is higher in beech than in conifer stands, resulting in a higher litter decomposition rate (Augusto et al., 2002; Wiedemann, 1942), reduced acidity, and a better humus type (Block et al., 1997).

Scots pine and Norway spruce: Both species complement each other in light ecology, crown and root shape, and in behavior under drought (Ruiz-Peinado et al., 2021; Wellhausen et al., 2017). Competition reduction may result from the fact that pine is light demanding, round-crowned, deep-rooted, and less drought sensitive, whereas spruce

Table 6

Statistical characteristics of Models 4 for analyzing H III based on the growth of the fastest growing trees. The equation numbers refer to the models introduced in Section 2.5. For reasons of space the table reports only the fixed effect variables of the respective models. For variable explanation see Table 2. $\ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(SI_{ik}) + a_3 \times mfactor_i \times \ln(SI_{ik})$.

Group	n	a_0	std (a_0)	p-value	a_1	std (a_1)	p-value	a_2	std (a_2)	p-value	a_3	std (a_3)	p-value
N. sp., (E. be.)	134	3.40	2.06	0.101	-0.02	3.026	0.995	0.80	0.58	0.167	0.02	0.86	0.978
(N. sp.), E. be.	135	1.95	4.38	0.675	-6.82	4.54	0.135	-0.87	1.31	0.509	2.12	1.36	0.121
s. oak, (E. be.)	106	-3.98	1.71	0.022	-0.87	1.79	0.627	0.98	0.52	0.064	0.28	0.55	0.616
(s. oak), E. be.	247	-2.07	0.48	<0.001	1.11	0.55	0.046	0.25	0.15	0.109	-0.11	0.18	0.510

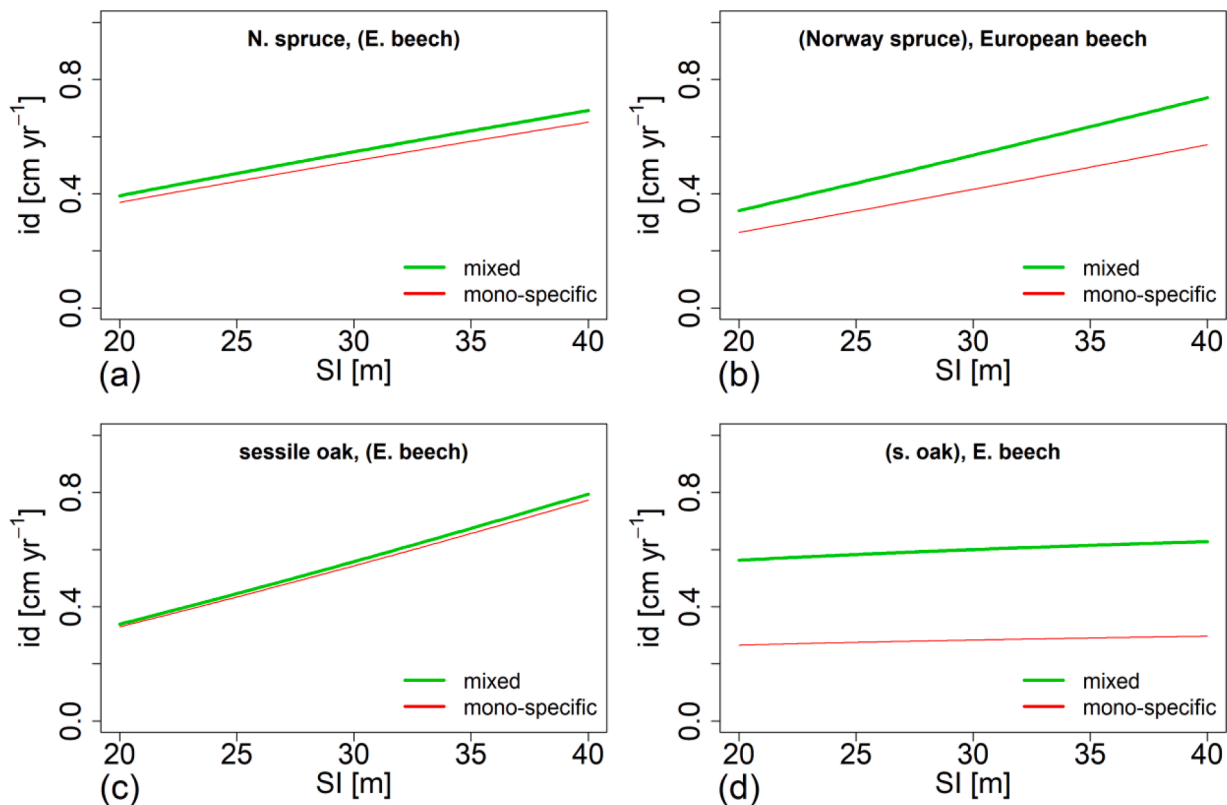


Fig. 7. Effect of site conditions in terms of site index (SI = 20–40 m at age 100) on the facilitation of stem diameter growth of the 10% fastest growing trees in both groups on each plot. The parallel lines indicate a site-invariant facilitation for both species and species assemblages. Results based on Model 4, see Table 6.

Table 7

Statistical characteristics of Models 4 for analyzing H III based on the growth of all trees. The equation numbers refer to the models introduced in Section 2.5. For reasons of space the table reports only the fixed effect variables of the respective models. For variable explanation see Table 2. $\ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(SI_{ik}) + a_3 \times mfactor_i \times \ln(SI_{ik})$.

Group	n	a ₀	std (a ₀)	p-value	a ₁	std (a ₁)	p-value	a ₂	std (a ₂)	p-value	a ₃	std (a ₃)	p-value
N. sp., (E. be.)	11,017	-5.00	0.39	< 0.001	-0.62	0.47	0.194	1.08	0.11	< 0.001	0.18	0.13	0.173
(N. sp.), E. be.	6549	-2.05	0.40	< 0.001	-0.74	0.46	0.111	0.23	0.12	0.046	0.23	0.14	0.101
s. oak, (E. be.)	7945	3.72	0.50	< 0.001	-0.20	0.51	0.701	0.72	0.15	< 0.001	0.07	0.16	0.662
(s. oak), E. be.	19,650	1.24	0.12	< 0.001	-0.39	0.13	0.003	-0.05	0.04	< 0.195	0.13	0.04	0.002

is shade-tolerant, slim-crowned, shallow-rooted, and strongly isohydric (Table 1 in Drössler et al., 2018, p.3).

European ash and sycamore maple: This species combination creates high biodiversity in the soil, high nutrient turnover, and a suppression of other competing species (e.g., European beech) in its stand (Ellenberg and Leuchner, 2010, pp. 297–303, Frech, 2006). These effects may facilitate both component species in such mixtures.

This brief literature review of the most likely mixing effects within the five analyzed species combinations suggests a differentiation between (i) density invariant, far-range effects, such as far reaching root systems, mycorrhiza (Nickel et al., 2018) and other root-associated microbial networks (Steidinger et al., 2019). To this category of effects also belong the slowing-down of wind speed, avoidance of storm-breakage, shading and avoidance of sunburn, provision of barriers against spread of insects, suppression of forest floor vegetation and competing weeds, and protection against snow slides or browsing by different neighboring tree species. A second category of effects may be (ii) density-driven close-range mixing effects, such as mechanical abrasion, crown shyness, and pre-emption of water and light by neighbors of a different tree species.

Our results show that density invariant/far-range effects may cause facilitation and growth increase at low stand density. Low density conditions are often created in contemporary forest management through edges, strong thinning, opening for natural regeneration, or by natural disturbances. They generate the potential of considerable facilitation of tree growth. This may not raise the stand-related productivity above the level of closed stands, but can reduce the losses brought about by density reduction. This is in line with the finding by Thurm and Pretzsch (2021) that the stand density-productivity relationship has a broader plateau in mixed compared with monospecific stands. In mixed stands the plateau of the stand density-productivity relationship may reach further into both the low-density and also high-density range.

The percentage of diameter growth increase caused by reduction of competition (16% on average, ranging from -1% to +36%) is in line with the magnitude of overyielding reported for the respective mixtures in fully stocked stands (see introduction). This indicates that the overyielding in fully stocked stands may be driven mainly by close-range effects. It may result from competition reduction and increased density, resulting in an advantageous productivity. This is in line with Thurm and Pretzsch (2021), who recently showed that density can be raised by

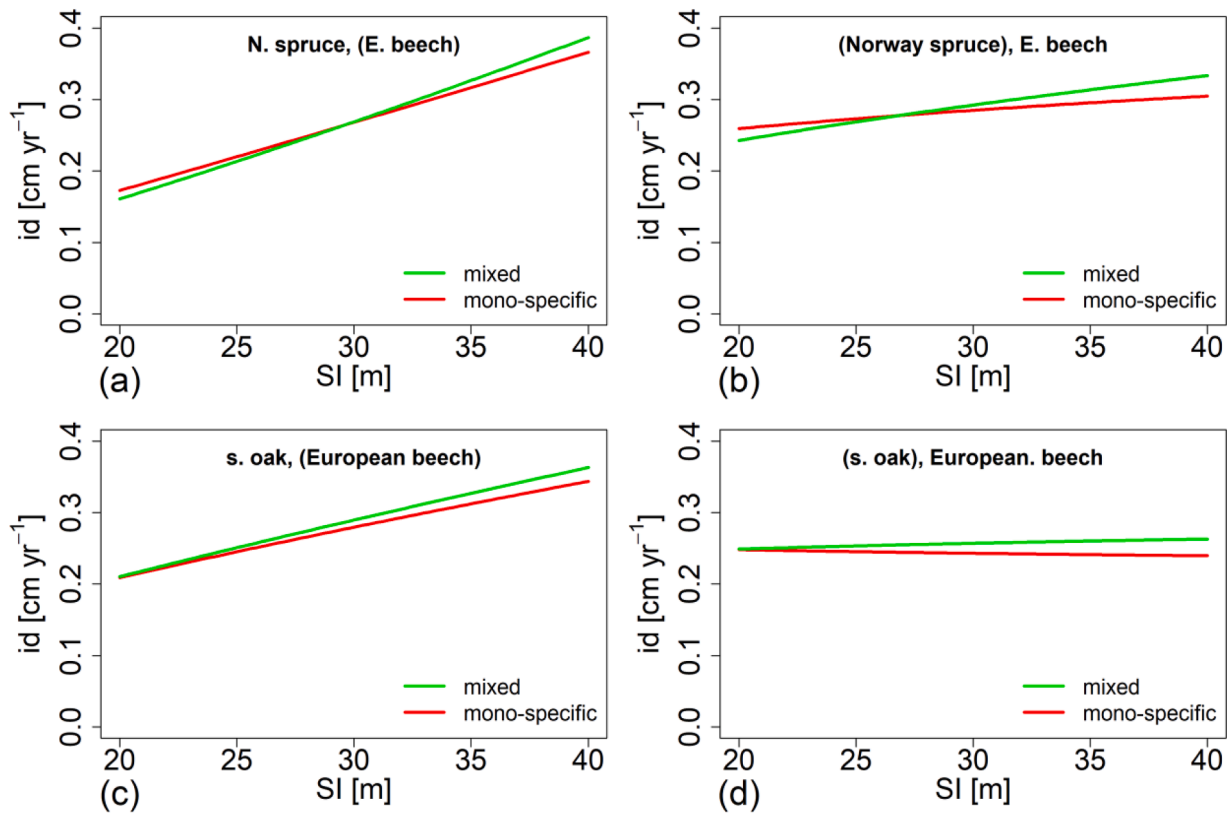


Fig. 8. Modulation of the competition reduction by tree species mixing shown for site index levels SI = 20...40 (d, age, and SDI kept at a constant level). The results are based on model 4 and visualized for (a) Norway spruce when mixed with European beech, (b) European beech when mixed with Norway spruce, (c) sessile oak when mixed with European beech, and (d) European beech mixed with sessile oak.

tree species mixing, and that overyielding in mixed stands can peak at maximum density.

4.3. Consequences of the facilitation and competition reduction for individual tree modeling

The potential-modifier approach for individual tree growth modeling splits the prediction of the size growth (e.g., stem diameter growth) into two components (Pretzsch et al., 2019; Weiskittel et al., 2016). The first

is the estimation of the potential tree growth rate, i.e., the expected growth without competition that mainly depends on the tree and site characteristics. The second component is the modifier that reduces the potential growth rate depending on the competition and density in the tree's neighborhood.

Our results suggest that in contrast to the common assumptions made in many individual tree models, the tree stem growth may not peak under monospecific open-grown conditions, but rather in mixed-species environments and at moderate stand density. Thus, the potential-

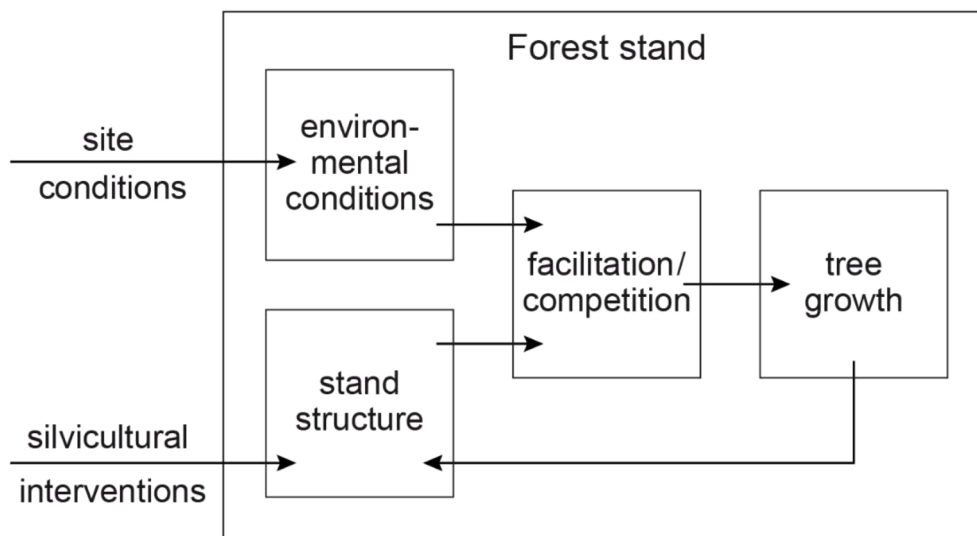


Fig. 9. The models 1–3 of this study analyze the feedback *spatial stand structure* → *facilitation and competition* → *tree growth* and its modulation by site conditions and stand density.

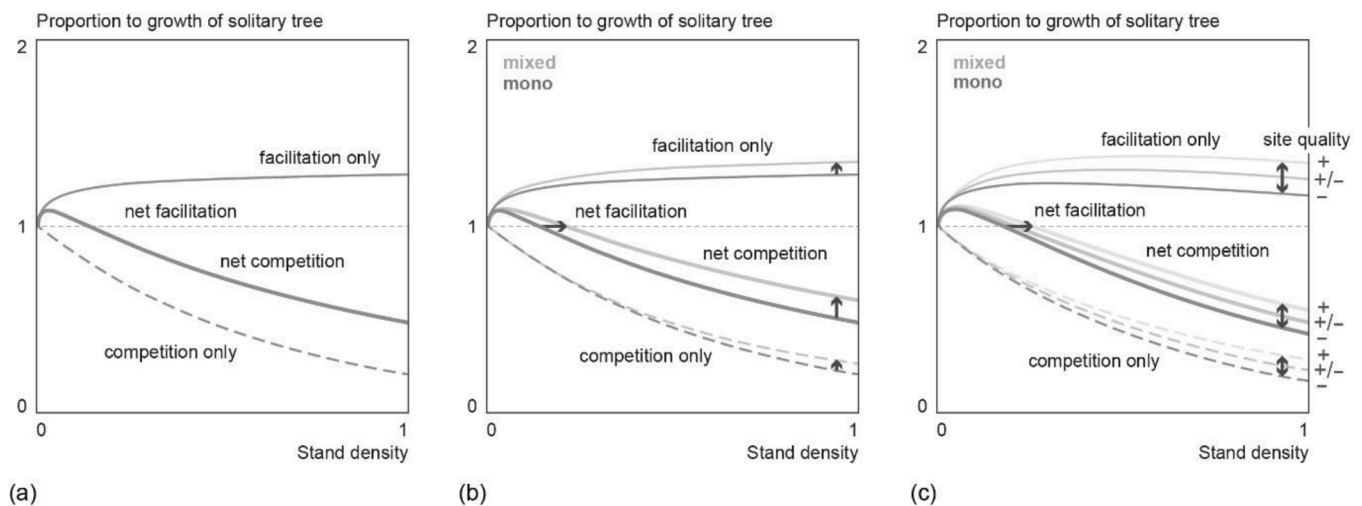


Fig. 10. Hypothesized modulation of potential tree growth (1.0-line) through facilitation and competition in (a) monocultures, (b) additional modulation in mixed-species stands, and (c) additional modulation through site conditions (modified after Pretzsch, 2017, pp. 280–281). (a) The balance between competition only and facilitation only in intra-specific neighborhood may result in net facilitation at low stand density, and net competition at high stand density, as shown in Fig. 10. (b) Widening of the range of net facilitation (horizontal arrow pointing right) caused by additional inter-specific facilitation and competition reduction caused by species mixing. (c) Facilitation and competition reduction may further depend on environmental conditions.

modifier function may not exponentially decrease, but rather grow unimodal with modifier values above 1.0 at moderate density in mixtures. In contrast to the declining modifier function shown in Fig. 1, the modifier function in mixed stands may be bell shaped, as shown in Fig. 10. Further research considering other tree species, species combinations, site conditions, and stand structures is required to substantiate these assumptions.

Relevant for modeling are the mostly positive interactions between mixing proportion and local competition that we found in this study. Positive interactions between tree species were also found by Rebola-Lichtenberg et al., (2021), Cavard et al., (2011) or Forrester et al., (2011). However, our results indicate that the competition reduction through an inter-specific neighborhood is even stronger in denser stands. We also found a slight positive interaction effect of site index and mixing proportion on growth of European beech when mixed with sessile oak (Fig. 8). This suggests that the competition reduction may be stronger on high-quality sites. Certainly, site index is a vague proxy marker of site quality. Analyses based on environmental factors and resource supply will provide further insight into the relationships between environmental conditions and competition reduction. Accordingly, the potential-modifier models should modify the potential growth rate to the expected rate depending on, among others, crown characteristics and competition index (Burkhardt and Tomé, 2012, p. 314–315), but also stand age, and site variables.

Presently used models largely neglect the revealed mixing effects on stem diameter growth. However, silvicultural guidelines and forest management are often derived from, or supported by, management models (Hilmers et al., 2020; Mason et al., 2018; Hanewinkel and Pretzsch, 2000). The presented findings may aid the further development of individual tree models.

4.4. Consequences of the results for forest management

This study aimed to answer several of the ten highest-ranked questions regarding mixed-forests that Coll et al., (2018, Table 1) identified by interviewing 168 managers from European countries. Specifically, the study addressed which species combinations are beneficial (question #4), how the productivity of mixtures differs from that in monospecific stands (#5), and which positive and negative effects mixtures can have (#6 and #7).

This study substantiated that, at parity of tree size and stand density,

trees in the most common species combinations in Central Europe grew faster than in monospecific stands in the considered time period 1991–2016. This superior wood production of trees in mixed stands adds to their well-known advantages in biodiversity (Dieler et al., 2017; Felton et al., 2010), stability (Hilmers et al., 2020; Knoke et al., 2008), and recreation (Edwards et al., 2012; Pukkala et al., 1988) services. In forest management, facilitation effects are, so far, specifically used in terms of nurse crop against frost damage (Pommerening and Murphy, 2004), and in the admixture of atmospheric nitrogen fixing tree species, such as *Alnus*, *Robinia*, or *Acacia* (Binkley, 2003; Carl et al., 2018; Forrester et al., 2006). It is also well known that trees growing in group structures in the alpine zone compete for light but their neighbours also protect them against snow and wind, so that they frequently benefit from being associated and grow more than solitary trees. Forest management makes use of such a permanent 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).

The results of this study quantified the facilitation in inter-specific neighborhood. It showed that facilitation can improve tree growth in common mixed species forests in both widely spaced stands by far-range facilitation effects and in dense stands by near-distant competition reduction effects. Both effects are relevant for silviculture. Facilitation, even at low density conditions, enable the production of large and long-lived forest products with lower expenses in terms of stand stock and mass productivity at the stand level. This means an advantageous growth at low-density, as commonly observed in selective or future crop tree thinning systems for individual tree size growth acceleration (Schober, 1988a and b; Abetz, 1975; Schädelin, 1942). Competition reduction enables an increase in stand density, mass production, and climate change mitigation through higher carbon storage. The competition reduction observed here enables the maximization of mass production at high density stand management in mixed stands (Zeller et al., 2021; de Prado et al., 2020; Pretzsch, 2020, 2022, Assmann, 1970).

Silvicultural management mainly entails the modification of spatial design and interference into stand structure. The distinction between (i) *density invariant, far-range effects* and (ii) *density-driven close-range operating mechanisms* may be a step forward for future spatially explicit tree and stand modeling approaches and experiments, as well as for a more goal-oriented silvicultural design and stand establishment. Thus, silvicultural measures are suitable for the regulation of density-driven close-range mixing effects.

Both facilitation and competition reduction can result in higher growth per unit area, and be exploited by low or high stand density, respectively. The reported effects apply to all analyzed species and sites. To implement these findings, they should be integrated into silvicultural guidelines for mixed species stands, as claimed by Coll et al., (2018) and proposed by Mason et al., (2018) and Pretzsch and Zenner (2017).

CRedit authorship contribution statement

Hans Pretzsch: Conceptualization, Data curation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The author declares that he has no conflict of interest.

Acknowledgements

Thanks are due to Brian D. Fath for inviting me to this contribution to the Jorgensen Reviews and Research series of the journal Ecological Modelling and for pre-reviewing this manuscript before submission. This publication is part of the CARE4C project that has received funding from the European Union's HORIZON 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 778322. The author also thanks the German Science Foundation (Deutsche Forschungsgesellschaft) for funding the projects "Structure and dynamics of mixed-species stands of Scots pine and European beech compared with monospecific stands; analysis along an ecological gradient through Europe" (# DFG PR 292/15–1). I also thank Peter Biber for reviewing the statistical approach, Charlotte Marie Pretzsch for the English language revision, and the three anonymous reviewers for their constructive criticism.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2021.109812](https://doi.org/10.1016/j.ecolmodel.2021.109812).

References

- Abetz P. (1975) Entscheidungshilfen für die Durchforstung von Fichtenbeständen (Durchforstungshilfe Fi 1975). Merkbl Forstl Versuchs- u Forschungsanst Bad-Württ 13, Freiburg, 9 p.
- Alveteg, M., Walse, C., Warfvinge, P., 1998. Reconstructing historic atmospheric deposition and nutrient uptake from present day values using MADEP. *Water Air Soil Pollut.* 104 (3), 269–283.
- Assmann, E., 1970. *The Principles of Forest Yield Study*. Pergamon Press, Oxford, New York, p. 506 p.
- Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. *Ann. For. Sci.* 59 (3), 233–253.
- Barbeito, I., Dassot, M., Bayer, D., et al., 2017. Terrestrial laser scanning revealed differences in the crown structure of *Fagus sylvatica* in mixed vs. pure European forests. *For. Ecol. Manage.* 405, 381–390. <https://doi.org/10.1016/j.foreco.2017.09.043>.
- Bayer, D., Seifert, S., Pretzsch, H., 2013. Structural crown properties of Norway spruce and European beech in mixed versus pure stands revealed by terrestrial laser scanning. *Trees* 27 (4), 1035–1047.
- Biging, G.S., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* 41 (2), 360–377.
- Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. *Can. J. For. Res.* 33 (11), 2274–2279.
- Binkley, D., 1984. Importance of size—Density relationships in mixed stands of douglas-fir and red alder. *For. Ecol. Manage.* 9 (2), 81–85.
- Blanco, J.A., de Andrés, E.G., San Emeterio, L., Lo, Y.H., 2015. Modelling mixed forest stands: methodological challenges and approaches. *Developments in Environmental Modelling*. Elsevier, pp. 189–215. Vol. 27.
- Block, J., Roeder, A., Schüler, G., 1997. Waldbodenrestauration durch Aktivierung ökosystemarer Nährstoffkreisläufe. *AFZ-DerWald* 1, 29–33.
- Botkin, D.B., Janak, J.F., & Wallis, J.R. (1972). Some ecological consequences of a computer model of forest growth. *J. Ecol.*, 849–872.
- Bravo, F., Fabrika, M., Ammer, C., Barreiro, S., Bielak, K., Coll, L., Bravo-Oviedo, A., 2019. Modelling approaches for mixed forests dynamics prognosis. Research gaps and opportunities. *For. Syst.* 28 (1), eR002.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol. (Amst.)* 18 (3), 119–125.
- Burkhardt, H.E., Tomé, M., 2012. *Modeling Forest Trees and Stands*. Springer Science & Business Media.
- Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113 (2), 151–161.
- Cannell, M.G.R., Thornley, J.H.M., Mobbs, D.C., Friend, A.D., 1998. UK conifer forests may be growing faster in response to increased N deposition, atmospheric CO₂ and temperature. *Forestry* 71 (4), 277–296.
- Carl, C., Biber, P., Veste, M., Landgraf, D., Pretzsch, H., 2018. Key drivers of competition and growth partitioning among *Robinia pseudoacacia* L. trees. *For. Ecol. Manage.* 430, 86–93.
- Cavard, X., Bergeron, Y., Chen, H.Y., Paré, D., Laganière, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. *Oikos* 120 (11), 1683–1695.
- Chamagne, J., Tanadini, M., Frank, D., Matula, R., Paine, C.T., Philipson, C.D., Hector, A., 2017. Forest diversity promotes individual tree growth in central European forest stands. *J. Appl. Ecol.* 54 (1), 71–79.
- Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manage.* 186 (1–3), 297–310.
- Coll, L., Ameztegui, A., Collet, C., Löf, M., Mason, B., Pach, M., Ponette, Q., 2018. Knowledge gaps about mixed forests: what do European forest managers want to know and what answers can science provide? *For. Ecol. Manage.* 407, 106–115.
- del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Bravo-Oviedo, A., 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *Eur. J. For. Res.* 135 (1), 23–49.
- del Río, M., Pretzsch, H., Ruiz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bravo-Oviedo, A., 2017. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*-*Fagus sylvatica* mixtures across Europe. *J. Ecol.* 105 (4), 1032–1043.
- de Prado, D.R., San Martín, R., Bravo, F., de Aza, C.H., 2020. Potential climatic influence on maximum stand carrying capacity for 15 Mediterranean coniferous and broadleaf species. *For. Ecol. Manage.* 460, 117824.
- Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T., Pretzsch, H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *Eur. J. For. Res.* 136 (4), 739–766.
- Drössler, L., Agestam, E., Bielak, K., Dudzinska, M., Koricheva, J., Liziniwicz, M., Wellhausen, K., 2018. Over- and underyielding in time and space in experiments with mixed stands of scots pine and Norway spruce. *Forests* 9 (8), 495.
- Edwards, D.M., Jay, M., Jensen, F.S., Lucas, B., Marzano, M., Montagné, C., Weiss, G., 2012. Public preferences across Europe for different forest stand types as sites for recreation. *Ecol. Soc.* 17 (1).
- Ek A.R., Monserud R.A. (1974) Trials with program FOREST: growth and reproduction simulation for mixed species even- or uneven-aged forest stands. In: Fries J (ed.): *Growth Models For Tree and Stand simulation*. Royal College of Forestry, Stockholm, Sweden, Res Notes 30, pp 56–73 (379 p).
- Ellenberg, H., Leuschner, C., 2010. *Vegetation Mitteleuropas mit den Alpen. ökologischer, Dynamischer Und Historischer Sicht* (Vol. 8104). Utb.
- Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *For. Ecol. Manage.* 260 (6), 939–947.
- Fish, H., Liefers, V.J., Silins, U., Hall, R.J., 2006. Crown shyness in lodgepole pine stands of varying stand height, density, and site index in the upper foothills of Alberta. *Can. J. For. Res.* 36 (9), 2104–2111. <https://doi.org/10.1139/x06-107>.
- Forrester, D.I., Vanclay, J.K., Forrester, R.I., 2011. The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop. *Oecologia* 166 (1), 265–272.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292.
- Forrester, D.I., 2017. *Ecological and physiological processes in mixed versus monospecific stands*. Mixed-Species Forests. Springer, Berlin, Heidelberg, pp. 73–115.
- Forrester, D.I., Bausch, J., Cowie, A.L., Vanclay, J.K., 2006. Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. *For. Ecol. Manage.* 233 (2–3), 211–230.
- Franz, F., Bachler, J., Deckelmann, B., Kennel, E., Kennel, R., Schmidt, A., Wotschikowsky, U., 1973. Bayerische Waldinventur 1970/71, Inventurabschnitt I: großrauminventur Aufnahme- und Auswertungsverfahren. Forstl. Forschungsber. München. 11, 143.
- Frech, A., 2006. *Walddynamik in Mischwäldern des Nationalparks Hainich* (Doctoral Dissertation. Niedersächsische Staats- und Universitätsbibliothek Göttingen).
- Goisser, M., Geppert, U., Rötzer, T., Paya, A., Huber, A., Kerner, R., Bauerle, T., Pretzsch, H., Pritsch, K., Häberle, K.H., Matyssek, R., Grams, T.E.E., 2016. Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*? *For. Ecol. Manage.* 375, 268–278.
- Gonzalez de Andres, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.H., Sangüesa-Barreda, G., Castillo, F.J., 2018. Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* 106 (1), 59–75.
- Grams, T.E., Hesse, B.D., Gebhardt, T., Weikl, F., Rötzer, T., Kovacs, B., Pritsch, K., 2021. The Kroof experiment: realization and efficacy of a recurrent drought experiment plus recovery in a beech/spruce forest. *Ecosphere* 12 (3), e03399.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Modell.* 115 (2–3), 129–148.

- Hajek, P., Seidel, D., Leuschner, C., 2015. Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest. *For. Ecol. Manage.* 348, 108–116. <https://doi.org/10.1016/j.foreco.2015.03.019>.
- Hanewinkel, M., Pretzsch, H., 2000. Modelling the conversion from even-aged to uneven-aged stands of Norway spruce (*Picea abies* L. Karst.) with a distance-dependent growth simulator. *For. Ecol. Manage.* 134 (1–3), 55–70.
- Hasenauer, H., 1997. Dimensional relationships of open-grown trees in Austria. *For. Ecol. Manage.* 96 (3), 197–206.
- Hasenauer, H., Kindermann, G., Steinmetz, P., 2006. The tree growth model MOSES 3.0. Sustainable Forest Management. Springer, Berlin, Heidelberg, pp. 64–70.
- Hilmers, T., Biber, P., Knoke, T., Pretzsch, H., 2020. Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. *Eur. J. For. Res.* 139 (4), 567–584.
- Jonard, M., Andre, F., Ponette, Q., 2008. Tree species mediated effects on leaf litter dynamics in pure and mixed stands of oak and beech. *Can. J. For. Res.* 38 (3), 528–538.
- Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct. Ecol.* 29 (8), 1078–1086. <https://doi.org/10.1111/1365-2435.12428>.
- Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecol. Lett.* 17 (12), 1560–1569.
- Jüttner, O., 1955. Eichen-ertragstafeln. In: Schober, R (Ed.), (1971) Ertragstafeln der Wichtigsten Baumarten. JD Sauerländer's Verlag, Frankfurt am Main, pp. 12–25, 134–138.
- Kaarakka, L., Tamminen, P., Saarsalmi, A., Kukkola, M., Helmsaari, H.S., Burton, A.J., 2014. Effects of repeated whole-tree harvesting on soil properties and tree growth in a Norway spruce (*Picea abies* (L.) Karst.) stand. *For. Ecol. Manage.* 313, 180–187.
- Kelty, M.J., 1992. Comparative productivity of monoculture and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), *The Ecology and Silviculture of Mixed-Species Forests* vol. 40. Springer, Dordrecht, pp. 125–141. https://doi.org/10.1007/978-94-015-8052-6_8.
- Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *Eur. J. For. Res.* 127 (2), 89–101.
- Larocque, G.R., Luckaj, N., Adhikary, S.N., Groot, A., Bell, F.W., Sharma, M., 2013. Competition theory—Science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. *Environ. Rev.* 21 (2), 71–84.
- Ledermann, Thomas (2004) PROGNAUS – ein Waldwachstumsmodell zur Fortschreibung von Inventurdaten, 2004. Bundesforschungs- und Ausbildungszentrum für Wald, Naturgefahren Und Landschaft (BFW), Vienna, Austria.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97 (2), 199–205.
- Mason, W.L., Löf, M., Pach, M., Spathelf, P., 2018. The development of silvicultural guidelines for creating mixed forests. *Dynamics, Silviculture and Management of Mixed Forests*. Springer, Cham, pp. 255–270.
- Meng, S.X., Rudnicki, M., Lieffers, V.J., DE, Reid, Silins, U., 2006. Preventing crown collisions increases the crown cover and leaf area of maturing lodgepole pine. *J. Ecol.* 94 (3), 681–686. <https://doi.org/10.1111/j.1365-2745.2006.01121.x>.
- Mette, T., Albrecht, A., Ammer, C., Biber, P., Kohnle, U., Pretzsch, H., 2009. Evaluation of the forest growth simulator SILVA on dominant trees in mature mixed Silver fir–Norway spruce stands in South-West Germany. *Ecol. Modell.* 220 (13–14), 1670–1680.
- Metz, J., Annighöfer, P., Westekemper, K., Schall, P., Schulze, E.D., Ammer, C., 2020. Less is more: effects of competition reduction and facilitation on intra-annual (basal area) growth of mature European beech. *Trees* 34 (1), 17–36.
- Moore, A.D., 1989. On the maximum growth equation used in forest gap simulation models. *Ecol. Modell.* 45 (1), 63–67.
- Nagel, J., Spellmann, H., Pretzsch, H., 2012. Zum Informationspotenzial langfristiger forstlicher Versuchsflächen und periodischer Waldinventuren für die waldwachstumkundliche Forschung. *Allg. Forst Jagdzeitung* 183 (5/6), 111–116, 183.
- Nagel, J., Duda, H., Hansen, J., 2006. Forest Simulator BWINPro7. *Forst. Holz.* 61, 427–442.
- Nagel, J., 1986. Wachstumsmodell Für Bergahorn in Schleswig-Holstein. Dissertation Universität Göttingen, Göttingen, Germany.
- Nambiar, E.S., Sands, R., 1993. Competition for water and nutrients in forests. *Can. J. For. Res.* 23 (10), 1955–1968.
- Nickel, U.T., Weikl, F., Kerner, R., Schäfer, C., Kallenbach, C., Munch, J.C., Pritsch, K., 2018. Quantitative losses vs. qualitative stability of ectomycorrhizal community responses to 3 years of experimental summer drought in a beech–spruce forest. *Glob. Change Biol.* 24 (2), e560–e576.
- Pallant, E., Riha, S.J., 1990. Surface soil acidification under red pine and Norway spruce. *Soil Sci. Soc. Am. J.* 54 (4), 1124–1130.
- Peng, S., Schmid, B., Haase, J., Niklaus, P.A., 2017. Leaf area increased with species richness in young experimental stands of subtropical trees. *J. Plant Ecol.* 10 (1), 128–135. <https://doi.org/10.1093/jpe/rtw016>.
- Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77 (1), 27–44.
- Pretzsch, H., 2022. Mixing degree, stand density, and water supply can increase the overyielding of mixed versus monospecific stands in Central Europe. *For. Ecol. Manage.* 503, 119741 <https://doi.org/10.1016/j.foreco.2021.119741>.
- Pretzsch, H., 2020. Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning. *For. Ecol. Manage.* 460, 117879.
- Pretzsch, H., Grams, T., Häberle, K.H., Pritsch, K., Bauerle, T., Rötzer, T., 2020. Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. *Trees* 34 (4), 957–970.
- Pretzsch, H., del Río, M., 2020. Density regulation of mixed and mono-specific forest stands as a continuum: a new concept based on species-specific coefficients for density equivalence and density modification. *Forestry* 93 (1), 1–15. <https://doi.org/10.1093/forestry/cpz069>.
- Pretzsch, H., Zenner, E.K., 2017. Toward managing mixed-species stands: from parameterization to prescription. *For. Ecosyst.* 4 (1), 1–17. <https://doi.org/10.1186/s40663-017-0105-z>.
- Pretzsch, H., 2002a. Application and evaluation of the growth simulator SILVA 2.2 for forest stands, forest estates and large regions. *Forstwiss. Centralblatt* 121, 28–51.
- Pretzsch, H., 2002b. Grundlagen Der Waldwachstumsforschung. Blackwell, Berlin, Vienna.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared to monocultures. *For. Ecol. Manage.* 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>.
- Pretzsch, H., 2017. Individual tree structure and growth in mixed compared with monospecific stands. *Mixed-Species Forests*. Springer, Berlin, Heidelberg, pp. 271–336.
- Pretzsch, H., 2019. The effect of tree crown allometry on community dynamics in mixed-species stands versus monocultures. A review and perspectives for modeling and silvicultural regulation. *Forests* 10 (9), 810.
- Pretzsch, H., Schütze, G., 2021. Tree species mixing can increase stand productivity, density, and growth efficiency and attenuate the tradeoff between density and growth throughout the whole rotation. *Ann. Bot.* 128 (6), 767–786. <https://doi.org/10.1093/aob/mcab077>.
- Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* 67 (7), 712. S. 1–12.
- Pretzsch, H., Biber, P., Durský, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Manage.* 162 (1), 3–21.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015a. Representation of species mixing in forest growth models. A review and perspective. *Ecol. Modell.* 313, 276–292.
- Pretzsch, H., del Río, M., Ammer, Ch., Avdagic, A., Barbeite, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015b. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 134 (5), 927–947.
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013a. Productivity of mixed versus pure stands of oak (*Quercus pretraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.* 132 (2), 263–280.
- Pretzsch, H., Schütze, G., Uhl, E., 2013b. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant. Biol.* 15 (3), 483–495.
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T.H., Seifert, S.T., 2008. Models for forest ecosystem management: a European perspective. *Ann. Bot.* 101 (8), 1065–1087.
- Pretzsch, H., 2005. Diversity and productivity in forests. In: Scherer-Lorenzen, M., Körner, C., Schulze, E-D (Eds.), *Forest Diversity and function*. *Ecol. Studies* 176. Springer-Verlag, Berlin, pp. 41–64.
- Prieto, I., Armas, C., Pugnaire, F.I., 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytol.* 193 (4), 830–841.
- Pukkala, T., Kellomäki, S., Mustonen, E., 1988a. Prediction of the amenity of a tree stand. *Scand. J. For. Res.* 3 (1–4), 533–544.
- R Core Team, 2019. R: a Language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rebola-Lichtenberg, J., Streit, J., Schall, P., Ammer, C., Seidel, D., 2021. From facilitation to competition: the effect of black locust (*Robinia pseudoacacia* L.) on the growth performance of four poplar-hybrids (*Populus* spp.) in mixed short rotation coppice. *New For.* 52 (4), 639–656.
- Reventlow, D.O.J., Nord-Larsen, T., Biber, P., Hilmers, T., Pretzsch, H., 2021. Simulating conversion of even-aged Norway spruce into uneven-aged mixed forest: effects of different scenarios on production, economy and heterogeneity. *Eur. J. For. Res.* 1–23. <https://doi.org/10.1007/s10342-021-01381-0>.
- Rötzer, T., Biber, P., Moser, A., Schäfer, C., Pretzsch, H., 2017. Stem and root diameter growth of European beech and Norway spruce under extreme drought. *For. Ecol. Manage.* 406, 184–195.
- Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. *Can. J. For. Res.* 31 (11), 1855–1870.
- Rothe, A., Kreutzer, K., Küchenhoff, H., 2002. Influence of tree species composition on soil and soil solution properties in two mixed spruce-beech stands with contrasting history in Southern Germany. *Plant. Soil.* 240 (1), 47–56.
- Rothe, A., Ewald, J., Hibbs, D.E., 2003. Do admixed broadleaves improve foliar nutrient status of conifer tree crops? *For. Ecol. Manage.* 172 (2–3), 327–338.

- Rothe A. (1997) Einfluß des Baumartenanteils auf Durchwurzelung, Wasserhaushalt, Stoffhaushalt Und Zuwachsleistung eines Fichten-Buchen-Mischbestandes am Standort Höglwald. For. Forsch. München 163, 174 p.
- Ruiz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., del Río, M., 2021. Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe. For. Ecol. Manage. 482, 118834.
- Saha, S., Kuehne, C., Kohnle, U., Brang, P., Ehring, A., Geisel, J., Leder, B., Muth, M., Petersen, R., Peter, J., Ruhm, W., Bauhus, J., 2012. Growth and quality of young oaks (*Quercus robur* and *Quercus petraea*) grown in cluster plantings in central Europe: a weighted meta-analysis. For. Ecol. Manage. 283, 106–118.
- Schädelin, W., 1942. Die Auslesedurchforstung als Erziehungsbetrieb höchster Wertleistung, 3rd edn. Verlag Paul Haupt, Bern, Leipzig, p. 147. p.
- Schober, R., 1988a. Von der Niederdurchforstung zu Auslesedurchforstungen im Herschenden. AFJZ 159 (9/10), 208–213.
- Schober, R., 1988b. Von Zukunfts- und Elitebäumen. AFJZ 159 (11/12), 239–249.
- Schober, R., 1967. Buchen-Ertragstafel für mäßige und starke Durchforstung. In: Schober, R (Ed.), (1972) Die Rotbuche 1971. Schr Forstl Fak Univ Göttingen u Niedersächs Forstl Versuchsanst 43/44. JD Sauerländer's Verlag, Frankfurt am Main, p. 333 p.
- Schober, R., 1975. Ertragstafeln Wichtiger Baumarten. JD Sauerländer's Verlag, Frankfurt am Main.
- Schober, R., 1950. Zum jahreszeitlichen Ablauf des sekundären Dickenwachstums. Allgem. For.- Jagdz. 122, 81–96.
- Shugart, H.H., 1984. A theory of forest dynamics. The Ecological Implications of Forest Succession Models. Springer-Verlag, New York, Berlin, Heidelberg, Tokyo, p. 278 p.
- Shugart, H.H., West, D.C., 1981. Long-term dynamics of forest ecosystems: computer simulation models, which allow for numerous seedlings and the long lives of large trees, predict how forests will respond to different management techniques. Am. Sci. 69 (6), 647–652.
- Steidinger, B.S., Crowther, T.W., Liang, J., Van Nuland, M.E., Werner, G.D., Reich, P.B., Peay, K.G., 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. Nature 569 (7756), 404–408.
- Sterba, H., Monserud, R.A., 1997. Applicability of the forest stand growth simulator prognas for the Austrian part of the Bohemian Massif. Ecol. Modell. 98, 23–34. [https://doi.org/10.1016/S0304-3800\(96\)01934-5](https://doi.org/10.1016/S0304-3800(96)01934-5).
- Strobel G.W. (1995) Rottenstruktur und Konkurrenz im subalpinen Fichtenwald, PhD ETH Zürich Nr. 11292, p. 162 + references.
- Thurm, E.A., Pretzsch, H., 2021. Growth-density relationship in mixed stands—results from long-term experimental plots. For. Ecol. Manage. 483, 118909 <https://doi.org/10.1016/j.foreco.2020.118909>.
- Thurm, E.A., Pretzsch, H., 2016. Improved productivity and modified tree morphology of mixed versus pure stands of European beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) with increasing precipitation and age. Ann. For. Sci. 73 (4), 1047–1061. <https://doi.org/10.1007/s13595-016-0588-8>.
- van Dijk, H.F., Roelofs, J.G., 1988. Effects of excessive ammonium deposition on the nutritional status and condition of pine needles. Physiol. Plant. 73 (4), 494–501.
- Vandermeer, J.H., 1992. The Ecology of Intercropping. Cambridge University Press.
- Volquards, G., 1958. Die Esche in Schleswig-Holstein. Dissertation Universität Göttingen, Hann, Münden, Germany.
- von Felten, S., Schmid, B., 2008. Complementarity among species in horizontal versus vertical rooting space. J. Plant Ecol. 1 (1), 33–41.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. John Wiley & Sons.
- Weiskittel, A., Kuehne, C., McTague, J.P., Oppenheimer, M., 2016. Development and evaluation of an individual tree growth and yield model for the mixed species forest of the Adirondacks Region of New York, USA. For. Ecosyst. 3 (1), 1–17.
- Wellhausen, K., Heym, M., Pretzsch, H., 2017. Mischbestände aus Kiefer (*Pinus sylvestris* L.) und Fichte (*Picea abies* (KARST.) L.): ökologie, Ertrag und waldbauliche Behandlung. Allgem. For.- Jagdz. 188 (1/2), 3–34.
- Wiedemann, E., 1936. Die Fichte 1936. /42. Verlag M & H Schaper, Hannover, p. 248. p.
- Wiedemann, E., 1943. Kiefern-Ertragstafel für mäßige Durchforstung, starke Durchforstung und Lichtung. Wiedemann E (1948) Die Kiefer 1948. Verlag M & H Schaper, Hannover, p. 337 p.
- Wiedemann, E., 1942. Der gleichaltrige Fichten-Buchen-Mischbestand. Mitt. Forstwirtsch. Forstwiss, 13, 1–88.
- Wiedemann, E., 1923. Zuwachsrückgang und Wuchsstockungen der Fichte in den mittleren und unteren Höhenlagen der sächsischen Staatsforsten. Kommissionsverlag W Laux, Tharandt, p. 181 p.
- Wikström, P., Edenius, L., Elfving, B., Eriksson, L.O., Lämås, T., Sonesson, J., Öhman, K., Wallerman, J., Waller, C., Klintebäck, F., 2011. The Heureka forestry decision support system: an overview. Math. Comput. For. Nat. Sci. 3, 87–94.
- Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. 1 (4), 1–7. <https://doi.org/10.1038/s41559-016-0063>.
- Yeste, A., Blanco, J.A., Imbert, J.B., Zozaya-Vela, H., Elizalde-Arbilla, M., 2021. *Pinus sylvestris* L. and *Fagus sylvatica* L. effects on soil and root properties and their interactions in a mixed forest on the Southwestern Pyrenees. For. Ecol. Manage. 481, 118726.
- Zeller, L., Caicoya, A.T., Pretzsch, H., 2021. The effect of silvicultural management on the trade-off between stand structural heterogeneity and productivity over time. Eur. J. For. Res. 140 (3), 615–634.