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Effect of species proportion definition on the evaluation of growth in pure *vs.* mixed stands

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Abstract

Aim of study: The aim of this paper is to compare differences in growth per hectare of species in pure and mixed stands as they result from different definitions of species proportions.

Area of study: We used the data of the Spanish National Forest Inventory for Scots pine and beech mixtures in the province of Navarra and for Scots pine and Pyrenean oak mixtures in the Central mountain range and the North Iberic mountain range.

Material and methods: Growth models were parameterized with the species growth related to its proportion as dependent variable, and dominant height, quadratic mean diameter, density, and species proportion as independent variables. As proportions we use once proportions by basal area or by stand density index and once these proportions considering the species specific maximum densities.

Main results: In the pine-beech mixtures, where the maximum densities do not differ very much between species, the mixing effects are very similar, independent of species proportion definitions. In the pine – oak mixture, where the maximum densities in terms of basal area are very different, the equations using the proportions calculated without reference to the maximum densities, result in a distinct overestimation of the mixing effects on growth.

Research highlights: When comparing growth per hectare of a species in a mixed stand with that of a pure stand, the species proportion must be described as a proportion by area considering the maximum density for the given species, wrong mixing effects could be introduced by inappropriate species proportion definitions.

Key words: mixing effects; proportion by area; Stand Density Index; overyielding; *Pinus sylvestris* L.; *Fagus sylvatica* L.; *Quercus pyrenaica* Wild.

Introduction

Growth in mixed species stands is a much discussed and recently much investigated issue (Forrester, 2014), especially under the aspect of changing climate conditions and changing societal demands on forests and forestry. Mixed forests might deal better than mono-specific forests with multifunctionality (Gamfeldt *et al.,* 2013), while providing a higher resilience against biotic and abiotic damages (Griess and Knoke, 2011; Pretzsch *et al.,* 2013). For managing mixed forests, a good understanding of how species interactions influence forest dynamics in terms of regeneration, growth, and mortality is essential.

Interspecific interactions occur at tree level but involve emergent effects at stand level, which are not directly derived from results at tree level (Perot and Picard, 2012). Many studies focussed on species interactions in terms of tree growth through the study of intra- and interspecific competition in mixed stands, but the net effect on stand growth is a key question when comparing growth and yield in pure and mixed stands. Negative and positive interactions between trees at stand level may result in underyielding, *i.e.,* species growth is lower in mixed than in pure stands, neutral yields, overyielding, or even transgressive overyielding, *i.e.,* growth in the mixed stand is greater than

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that of the most productive species in pure stand. When analysing the effect of interspecific interaction on stand growth in mixed species forests, the definition of species proportions plays an important role. Modelling growth of one species in a mixed stand has to consider that this species only occupies a portion of the stand's growing space. Consequently, to compare its growth with its corresponding growth in pure stands, it is necessary to correct the growth with the species proportion. Otherwise growth will be correlated with species proportions, a trivial effect that hampers analysis of interspecific competition.

Species proportions can be defined in many different ways, by crown cover, stem number, basal area, volume, or biomass; depending on the objective of the study (Bravo-Oviedo *et al.,* 2014). For a given mixed stand, the species proportion may differ considerably depending on species proportion definition, and, consequently, different net effects on stand growth were reported (Pretzsch, 2009). The most common way to define species proportion is by basal area (Légaré *et al.,* 2004; Perot and Picard, 2012; Groot *et al.,* 2014). However, for a given basal area (or volume), leaf area, living tree biomass, and growing space requirements differ, depending on species-specific crown allometry and wood density (Pretzsch, 2009). Thus, when comparing the growth per hectare of one species in the mixed stand with that of the same species in a pure stand, the proportion has to be a proportion by stand area, *i.e.,* relating the growth of the species in mixed stands to the growing space or area occupied by the respective species (Kennel, 1965). Using proportions by crown cover, by stem number, by basal area, by volume, or by biomass as proxies for the proportion by stand area requires a correction considering the potential or maximum growing space occupancy of each species. Without this correction, it would be assumed that all species in the mixed stand have the same potential on that site. However, only few recent studies consider that the species present in the mixed stand may have different potential or maximum stand density in the respective pure stand (Río and Sterba, 2009; Condés *et al.,* 2013).

Objectives

The objective of this paper is to compare differences in growth per hectare of species in pure and mixed stands using different definitions of species proportions, with and without correction by maximum stand density. We used two species mixtures for this study, one formed by two species with similar maximum stand densities, and the other by two species with greater differences. Two density indices, Reineke's stand density index and basal area, were used to calculate absolute and relative species proportions.

Theoretical considerations

According to von Laer [cit. (Prodan, 1959)], the area available for a species in a mixed stand or the species proportion by area can be defined as the ratio of the observed basal area per hectare and the potential (maximum) basal area per hectare for this species and site. Considering that basal area is a measure of density of spatial occupancy, this definition could be extended to other density indices, using their respective potential values. Two approaches are available to determine maximum stand densities: the maximum Stand Density Index proposed by Reineke (1933) and Assmann's concept of natural basal area, which is the basal area of even-aged, unthinned stands. Sterba (1987) showed how both concepts can be described by the Competition Density Rule, resulting in:

$$N_{max} = C \cdot D_g^E \text{ and } G_{max} = C' \cdot h_{dom}^{E t}$$

with C and E derived directly from maximum density plots, and C' and E' from the coefficients a_0 to b_1 determined from plots with varying dominant height and density. For the mathematical derivations, see Sterba (1987) and Río and Sterba (2009).

If the maximum stand density index (SDI_{max}) or maximum basal area (G_{max}) of each species are known, species proportion by area can be estimated using the respective relative stand densities by species (SDIR_i, A_i) and total relative stand densities (SDIR, A) as shown in Table 1.

The species proportion by area using the relative stand density index (P_{Ri}) can be related to species proportions by stand density index in absolute term (P_i) as follows:

$$P_{R_i} = \frac{\mathrm{SDI}R_i}{\mathrm{SDI}R} = \frac{\dfrac{\mathrm{SDI}_i}{\mathrm{SDI}_{max_i}}}{\dfrac{\mathrm{SDI}_i}{\mathrm{SDI}_{max_i}} + \dfrac{\mathrm{SDI}_j}{\mathrm{SDI}_{max_j}}} = \frac{1}{1 + \dfrac{\mathrm{SDI}_j}{\mathrm{SDI}_i} \cdot \dfrac{\mathrm{SDI}_{max_i}}{\mathrm{SDI}_{max_j}}}$$

Defining the ratio of the maximum densities of the species as $K = \dfrac{\mathrm{SDI}_{max_i}}{\mathrm{SDI}_{max_j}}$ and getting the ratio between

Table 1. Definitions of stand density and species proportion used in the growth models

	Stand density by species	**Total stand density** SD	**Species proportion** P_i
Stand density index	$SDI_i = N_i \left(\frac{25}{d_{g_i}} \right)^{E_i}$	$SDI_i + SDI_j$	$\frac{SDI_i}{SDI_i + SDI_j}$
Maximum stand density index	$SDIR_i = \frac{SDI_i}{C_i \cdot 25^{E_i}}$	$SDIS_i + SDIR_j$	$\frac{SDIR_i}{SDIR_i + SDIR_j}$
Basal area	$G_i = \frac{\pi}{4} Ni \cdot d_{g_i}^2$	$G_i + G_j$	$\frac{G_i}{G_i + G_j}$
Maximum basal area	$A_i = \frac{G_i}{C_i' \cdot {h_{dmi}}^{E_i^1}}$	$A_i + A_j$	$\frac{A_i}{A_i + A_j}$

SDI of both species from the definition of species proportions by stand density index in absolute terms results in

$$P_i = \frac{\mathrm{SDI}_i}{\mathrm{SDI}_i + \mathrm{SDI}_j} = \frac{1}{1 + \frac{\mathrm{SDI}_j}{\mathrm{SDI}_i}} \rightarrow \frac{\mathrm{SDI}_j}{\mathrm{SDI}_i} = \frac{1}{P_i} - 1$$

and

$$P_{Ri} = \frac{1}{1 + K\left(\frac{1}{P_i} - 1\right)} = \frac{P_i}{K + P_i(1-K)}$$

Both proportions become the same when the maximum stand density for both species are identical (K = 1). The greater the differences between the two maximum densities (K), the higher the differences between the species proportions in relative terms and in absolute terms (Fig. 1).

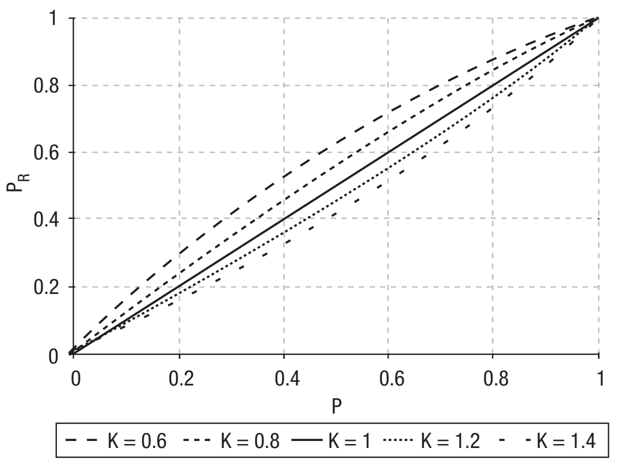

Figure 1. Relationship between species proportions by absolute densities (P) and by relative densities (P_R), depending on the ratio between the two maximum densities (K). (Calculated for SDI_{max} = 1,200).

In the same way, the stand density index in relative terms (SDI*R*) and in absolute terms (SDI) can be related through K and P_i as follows:

$$P_{Ri} = \frac{\mathrm{SDI}R_i}{\mathrm{SDI}R} \rightarrow$$

$$\rightarrow \mathrm{SDI}R = \frac{\mathrm{SDI}R_i}{P_{R_i}} = \frac{\frac{\mathrm{SDI}_i}{\mathrm{SDI}_{max_i}}}{P_{R_i}} = \frac{\mathrm{SDI}_t \cdot [K + P_i(1-K)]}{\mathrm{SDI}_{max_i} \cdot P_i}$$

as $P_i = \frac{\mathrm{SDI}_i}{\mathrm{SDI}} \rightarrow \mathrm{SDI}_i = P_i \cdot \mathrm{SDI}$

$$\mathrm{SDI}R = \frac{\mathrm{SDI} \cdot [K + P_i(1-K)]}{\mathrm{SDI}_{max_i}}$$

It is important to note that the relation between relative and absolute stand density index is not constant for a given K, but varies according the absolute species proportion (more variation with increasing differences among maximum densities, Fig. 2). This variation of relative density with the species proportion in absolute terms highlights the difficulty to express stand density (growing stocks) and maximum densities in mixed stands.

These relationships are similar for species proportions calculated by basal area instead of SDI. Note, however, that in this case, K is not a constant, because the development of the maximum basal area over dominant height may be different, indicated by differing E_i and E'_i in Reineke's maximum density line and the G_{max} relationship, respectively.

The relations between absolute and relative species proportions and stand densities have the consequence that growth effects in mixed stands depend on the definition of species proportion and density index.

We illustrate this effect with a theoretical example of two species with different maximum stand densi-

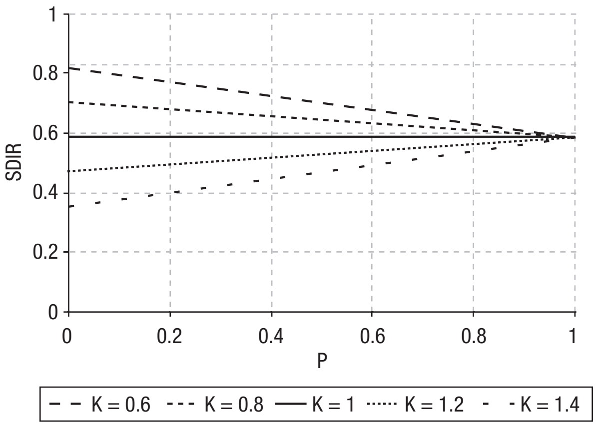

Figure 2. Relationship between the ratio of stand density index and maximum SDI (SDIR) and species proportions by absolute densities (P) depending on the ratio between the two potential densities (K). (Calculated for SDI = 700 and SDI_{max} = 1,200).

ties, SDI_{max1} = 1,200 trees/ha and SDI_{max2} = 800 trees/ha, which gives a value of K = 1.5. Assuming volume growth of 20 and 10 m^3 ha^{-1} $year^{-1}$ for the two species in pure stands, respectively, and no mixing effect on volume growth when defining species proportion by area (P_{Ri}), volume growth of species 1 and species 2 in mixed stands will be proportional to the species proportion. However, if these growth values are shown over species proportions in absolute terms (P_i) using the relationship between P_i and P_{Ri}, there is a negative effect of mixing on volume growth of species 1 (Fig. 3a). For species 2, the effect is opposite, giving a slight positive mixing effect, while for the total stand growth, underyielding can be observed. This means that different species proportion definitions can introduce effects of growth that are similar to over- and underyielding observed in mixed stands. In Fig. 3b, the example is repeated, keeping K constant, but exchanging the pure stand growth between species. In this example, the total stand growth indicates overyielding when using absolute species proportions, due to the overyielding of the more productive species 2.

Data

We used the data of the Spanish National Forest Inventory (SNFI) for two different mixtures. Scots pine (*Pinus sylvestris* L.) and beech (*Fagus silvatica* L.) mixtures were from the third and fourth SNFI in the province of Navarra. Scots pine and Pyrenean oak (*Quercus pyrenaica* Willd.) mixtures were from second and third SNFI in the Central mountain range and the North Iberic mountain range. Both data sets were used previously by Condés *et al.* (2013) and Río & Sterba (2009) to analyse mixture effects. Their re-use is based on the fact that Scots pine and Pyrenean oak have very different potential densities while Scots pine and beech do not differ much. For an overall description of the data, see Tables 2 and 3.

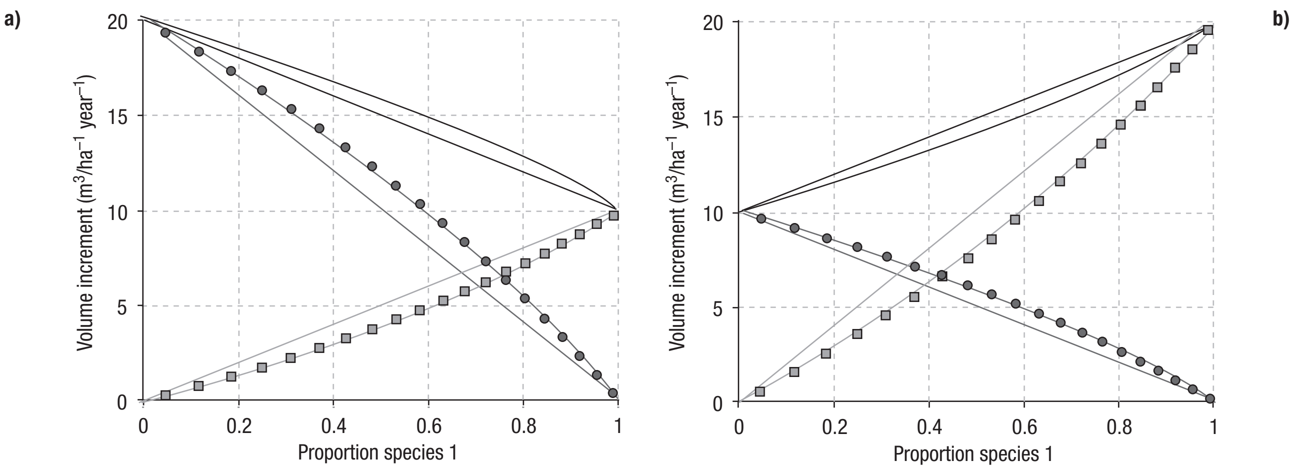

Figure 3. Influence of species proportion definitions on stand growth in a mixture of two species with different maximum densities, SDI_{max1} = 1,200 and SDI_{max2} = 800. Broken lines show the growth of species 1 (squares), species 2 (circles) and the total stand (black), without mixing effect over species proportion using species specific maximum densities (P_{Ri}); solid lines show the same growth over species proportion in absolute terms (P_i); a) volume growth in pure stand of species 1 and 2 are 20 and 10 $m^3 \cdot ha^{-1} \cdot year^{-1}$, respectively; b) volume growth in pure stand of species 1 and 2 are 10 and 20 $m^3 \cdot ha^{-1} \cdot year^{-1}$, respectively.

Table 2. Summary statistics for data of the SNFI for the study of the pine-beech mixtures. h_{dom} is the dominant height (m), *i.e.,* the mean height of the 100 largest trees per ha, d_g is the quadratic mean diameter (cm), N is the stem number per ha, G is the basal area [m^2/ha], SDI is Reineke's Stand density index (stem/ha) and IV the current annual increment of the last ten years [$m^3/(ha \cdot year)$]

	Pure Pine				**Pine-beech mixture**				**Pure beech**			
N° of plots	**174**				**69**				**452**			
	Min	**Mean**	**Std**	**Max**	**Min**	**Mean**	**Std**	**Max**	**Min**	**Mean**	**Std**	**Max**
h_{dom} (m)	3.8	13.3	4.8	27.8	8.7	19.4	4.8	30.3	6.0	21.6	5.0	36.9
Pine	3.8	13.3	4.8	27.8	8.3	18.8	5.0	30.2				
Beech					6.5	15.4	4.8	29.0	6.0	21.6	5.0	36.9
d_g (cm)	7.6	22.0	6.0	45.0	12.2	25.8	10.8	78.7	8.7	32.6	13.5	98.0
Pine	7.6	22.0	6.0	45.0	12.6	30.1	9.5	56.4				
Beech					7.7	26.3	21.5	114.8	8.7	32.6	13.5	98.0
N/ha	14	624	441	2,582	41	877	586	2,987	5	494	430	3,140
Pine	14	624	441	2,582	5	426	424	2,394				
Beech					5	451	572	2,769	5	494	430	3,140
G (m^2/ha)	0.50	22.76	15.27	82.70	12.74	34.40	13.38	77.52	0.82	26.82	10.69	60.31
Pine	0.50	22.76	15.27	82.70	0.70	22.27	17.55	73.14				
Beech					0.44	12.13	11.56	44.40	0.82	26.82	10.69	60.31
%G pine					0.02	0.61	0.34	0.99				
%G beech					0.01	0.39	0.34	0.98				
SDI	12	475	309	1,583	239	695	260	1,468	16	527	214	1,153
Pine	12	475	309	1,583	15	442	341	1,359				
Beech					10	254	243	1,003	16	527	214	1,153
%SDI pine					0.01	0.60	0.34	0.99				
%SDI beech					0.01	0.40	0.34	0.99				
IV	0.06	4.16	2.66	12.89	0.77	5.95	2.72	17.37	0.10	3.49	1.77	12.49
Pine	0.06	4.16	2.66	12.89	0.11	3.63	2.64	9.62				
Beech					0.01	2.32	2.49	16.87	0.10	3.49	1.77	12.49

Methods

Maximum stand density and species proportion definitions

The coefficients for calculating maximum density in terms of SDI_{max} and maximum basal area are taken from Río and Sterba (2009) and Condés *et al.* (2013) respectively (Table 4). The definitions of the four species proportions are presented in Table 1.

Potential densities

For the beech-pine and pine-oak mixture, we took the parameters of the maximum density line from the previously published studies (Río and Sterba, 2009; Condés *et al.,* 2013). All the coefficients are given in Table 4.

A comparison of the resulting maximum density lines for stem number and basal area are presented in Fig. 4. From all four diagrams it can be seen that the differences between the maximum densities of the two respective species are higher in the pine-oak mixture than in the pine-beech mixture.

The fact that the big differences in the maximum densities in the pine-oak mixture do not appear so clearly in the maximum SDI than in the maximum basal areas comes from the very different slopes of the maximum stem number - diameter lines in this mixture. While the reference d_g in this line for the SDI_{max} is 25 cm, the differences in the maximum stem numbers will depend very much on the chosen reference mean diameter. When the slopes of these lines are similar, like in the pine-beech mixture, the ratio between the maximum stem number is rather independent of the chosen reference mean diameter (Fig. 5).

Table 3. Summary statistics of data of the SNFI for the study of the pine-oak mixture. For description of the variables see Table 2

	Pure Pine				**Pine-oak mixture**				**Pure oak**			
N° of plots	**310**				**81**				**215**			
	Min	**Mean**	**Std**	**Min**	**Mean**	**Std**	**Min**	**Mean**	**Std**	**Min**	**Mean**	**Std**
h_{dom} (m)	5.0	13.7	4.7	27.8	4.3	10.1	3.6	18.1	4.8	9.5	2.5	17.4
Pine	5.0	13.7	4.7	27.8	4.0	10.3	4.2	19.3				
Oak					4.0	8.6	2.7	15.8	4.8	9.5	2.5	17.4
d_g (cm)	9.9	23.5	8.8	47.1	9.4	17.0	9.2	65.3	8.5	16.2	7.9	51.8
Pine	9.9	23.5	8.8	47.1	8.9	20.1	11.6	65.8				
Oak					7.5	15.3	10.1	64.9	8.5	16.2	7.9	51.8
N/ha	129	1,026	676	3,547	71	1,182	825	3,813	79	931	721	3,675
Pine	129	1,026	676	3,547	36	687	580	2,916				
Oak					25	496	454	1,974	79	931	721	3,675
G (m^2/ha)	14.92	33.13	11.97	67.93	3.96	19.97	10.01	46.12	3.77	13.37	7.34	40.17
Pine	14.92	33.13	11.97	67.93	1.85	13.73	8.19	38.77				
Oak					0.49	6.23	5.15	23.62	3.77	13.37	7.34	40.17
%G pine					0.23	0.68	0.20	0.98				
%G oak					0.02	0.32	0.20	0.77				
SDI	360	691	233	1,339	103	481	240	1,232	108	381	207	1,124
Pine	360	691	233	1,339	46	300	175	842				
Oak					14	181	145	637	108	381	207	1,124
%SDI pine					0.20	0.63	0.20	0.96				
%SDI oak					0.04	0.37	0.20	0.80				
IV	0.21	9.20	4.84	26.42	0.79	7.13	4.76	21.32	0.06	2.41	1.54	8.45
Pine	0.21	9.20	4.84	26.42	0.44	5.81	4.19	19.39				
Oak					0.00	1.32	1.20	4.88	0.06	2.41	1.54	8.45

Growth models

Growth efficiencies of the species were defined as the growth of the species corrected for its proportion, *i.e.,* the ratio $\frac{IV_i}{P_i}$, with *i* indicating the species, IV_i its volume increment, and P_i its proportion. The dependent variables were the dominant height, h_{dom}, the mean diameter, d_g, a density measure, and the species proportion. As density measures we used the SDI or the relative SDI*R* where the species proportions were by SDI_i or $SDIR_i$, respectively, and the absolute basal

Table 4. Coefficients for Reineke's maximum density lines and the G_{max} relationships by species and mixture type. Reg. 1 refers to the Central mountain range and Reg. 2 to the North-Iberic mountain range

Mixture	**Species**	**C**	**E**	SDI_{max}	**C'**	**E'**
Pine-beech	*Pinus sylvestris*	362,559	–1.750	1,297	31.65	0.2155
	Fagus sylvatica	330,087	–1.789	1,042	32.49	0.1468
Pine-oak	*Pinus sylvestris* Natural	403,840	–1.750	1,445	36.82	0.2061
	Pinus sylvestris Plantation				16.17	0.2347
	Quercus pyrenaica Reg. 1	196,512	–1.605	1,121	13.13	0.3988
	Quercus pyrenaica Reg. 2				16.46	0.3543

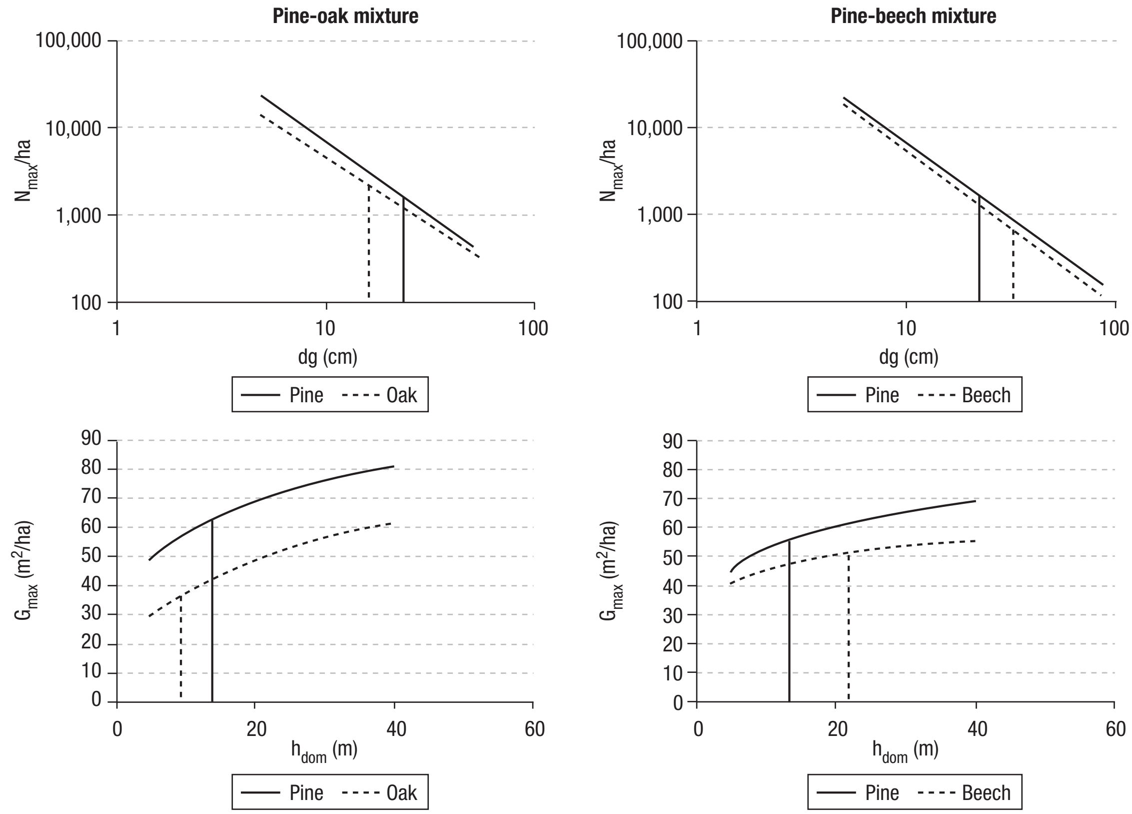

Figure 4. Maximum density models for stem number and basal area by species and mixture type. The vertical lines depict the respective values for the average quadratic mean diameter (d_g) and the average dominant height (h_{dom}) respectively observed in data sets (Tables 2 and 3).

area G or relative basal area A where the species proportion were by basal area or relative basal area, respectively (Table 1).

Growth efficiencies of the species were modelled with the following model, which accounted for heteroscedasticity by logarithmic transformations of the dependent and independent variables:

$$\log\left(\frac{IV_i}{P_i}\right) = a_0 + a_1 \log(h_{dom_i}) + a_2 \log(d_{g_i}) + \\ + a_3 \log(SD) + a_4 \log(P_i)$$

where IV_i is the current annual volume increment of species i, h_{dom_i} its dominant height, d_{g_i} its quadratic mean diameter, SD is the total stand density, and P_i the proportion of this species.

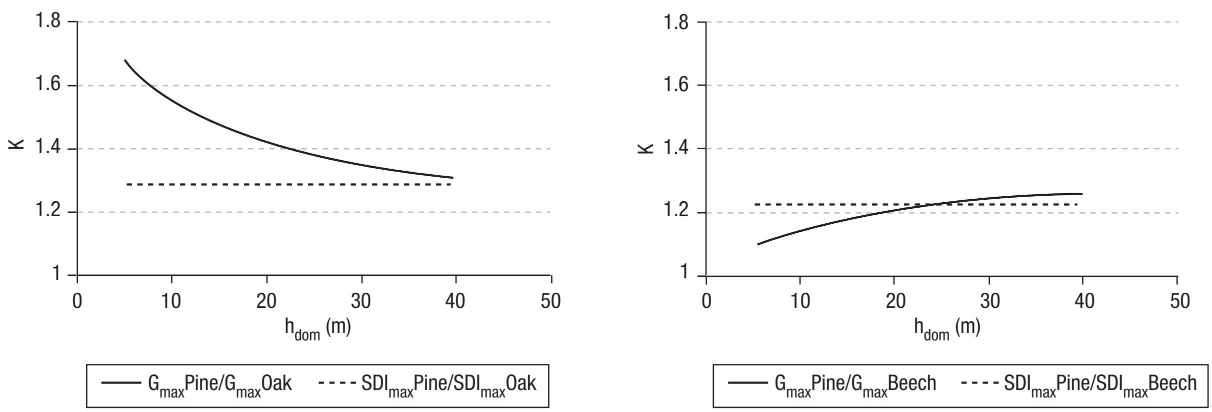

Figure 5. The ratios K between the species specific maximum SDI or the maximum basal area in the two mixture types.

Four different versions of this model were used, depending on the definition of stand density and species proportion (see Table 1). It should be noted that in previous analyses with the same data (Río & Sterba, 2009; Condes *et al.*, 2013), models were slightly different, including also interactions. The emphasis in the current analysis is on comparing the effect of species proportion variables across mixture types, and therefore models were simplified.

Mixing effects

With these models "hypothetical replacement series experiments" according to Kelty (1992) can be calculated. In this simulation, the "reference growth" (IV_{iREF}) is assumed to be unaffected by any mixture, *i.e.,* growth of the species is proportional to its species proportion. Using a general notation for all four species proportion definitions as

$$\frac{IV_i}{P_i} = f(h_{dom_i}, d_{g_i}, SD, P_i)$$

the reference growth is

$$IV_{i_{REF}} = f(h_{dom_i}, d_{g_i}, SD, P_i = 1) \cdot P_i$$

The mixing effect for the species i is then

$$MixEff_i = f(h_{dom_i}, d_{g_i}, SD, P_i) \cdot P_i - IV_{i_{REF}}$$

in m3 ha^{-1} yr^{-1}; and the relative mixing effect is

$$R\ MixEff_i = \frac{MixEff_i}{IV_{i_{REF}}}$$

If this mixing effect is greater than 0 and the relative mixing effect greater than 1, the effect is called overyielding, and underyielding otherwise. If the growth of the mixed stand is even better than the growth of the better growing pure stand, this effect is called transgressive overyielding.

Results

Growth models

Parameter estimates and the adjusted R^2s of the multiple linear regression models for the growth efficiencies are given in Tables 5 and 6. Except for the intercept in some cases and the parameter corresponding to dominant height in the pine models of the pine-oak mixture, all coefficients were significant with at least $\alpha = 0.05$ and exhibited the expected signs. Growth

Table 5. Parameter estimates and adjusted R^2 for the growth model in pine–beech mixture. For P_i and SD definitions see Table 1

sp	SD	a_0	a_1	a_2	a_3	a_4	R^2
Pine	SDI	–2.2747	0.6756	–0.2674	0.4367	–0.1464	0.629
	SDIR	0.8219	0.6952	–0.2742	0.4310	–0.1726	0.648
	G	–0.1938	1.0573	–0.7613	0.3650	–0.2355	0.653
	A	1.0506	1.1388	–0.7576	0.3648	–0.2582	0.668
Beech	SDI	–1.9969	0.5700	–0.5529	0.5284	–0.2639	0.424
	SDIR	1.6712	0.5691	–0.5509	0.5299	–0.2489	0.397
	G	0.5927	0.4741	–0.7761	0.5381	–0.2855	0.499
	A	2.4633	0.5595	–0.7829	0.5300	–0.2891	0.474

Table 6. Parameter estimates and adjusted R^2 for the growth model in pine–oak mixture. For P_i and SD definitions see Table 1

sp	SD	a_0	a_1	a_2	a_3	a_4	R^2
Pine	SDI	–0.2318	—	–0.8962	0.7755	–0.3125	0.391
	SDIR	5.4101	—	–0.8964	0.7733	–0.2958	0.399
	G	2.7242	—	–1.0896	0.7768	–0.3313	0.387
	A	5.5583	—	–0.9574	0.8364	–0.2770	0.398
Oak	SDI	–2.1088	1.1766	–0.5482	0.2728	–0.2758	0.169
	SDIR	–0.1981	1.1786	–0.5480	0.2767	–0.2243	0.156
	G	–0.7898	1.1890	–0.6862	0.2520	–0.3222	0.201
	A	–0.1275	1.2990	–0.6849	0.2643	–0.2228	0.165

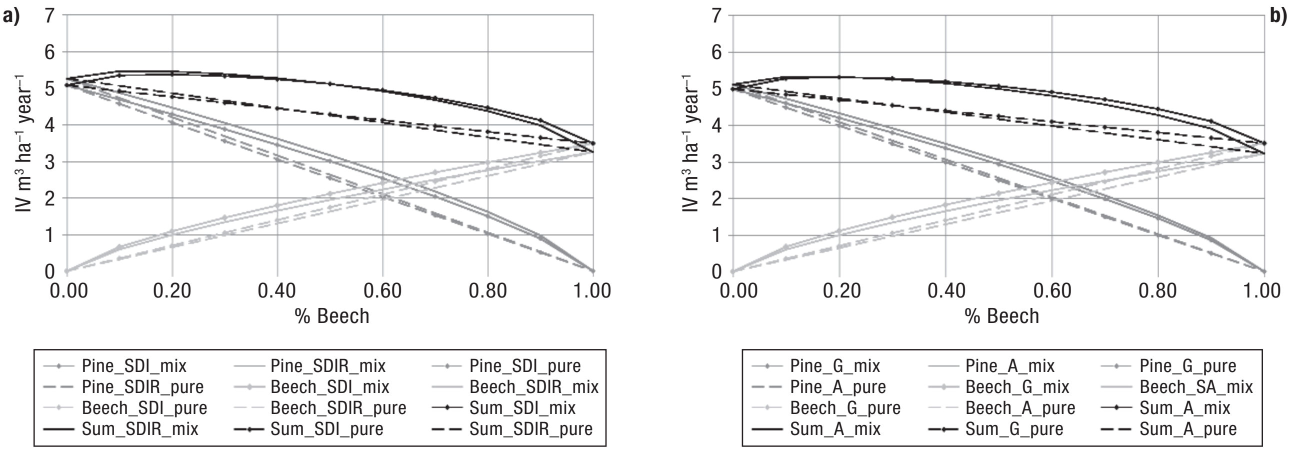

Figure 6. The hypothetical replacement series experiment for the pine-beech mixture. Comparison between growth for absolute proportions and proportions using species specific maximum densities in a) stand density index (SDI and SDIR, respectively) and b) basal area (G and A respectively). The dashed lines are the hypothetical growth if the growth efficiencies of the species were the same in the pure and in the mixed stands. The solid lines are the growth given by the fitted models. (Pine: $h_{dom} = 18.8$ m, $d_g = 30.1$ cm; Beech: $h_{dom} = 15.4$ m, $d_g = 26.3$ cm; SDI = 695.5; SDIR = 0.58, G m^2/ha = 34.4; A = 0.61).

efficiency increased with h_{dom} and decreased with d_g. Furthermore, growth efficiency increased with density and decreased with increasing species proportion. The latter relationship indicates for all species, all models, and both mixtures, that the growth efficiency was increasing with decreasing proportion of the respective species in the stand, thus indicating that in these stands interspecific competition is less intense than intraspecific competition. The smaller variation in most variables in the pine-oak mixtures resulted in lower R^2s in all respective models.

In order to illustrate the influence of species mixture on growth, the average observed values of independent variables (h_{dom}, d_g, and density measure) of the respective mixture (Tables 2 and 3) were inserted into the equations, and a hypothetical replacement series calculated for varying species proportions according to Kelty (1992) (Figs. 6 and 7).

In both mixtures, pine was the species growing better. In the pine-beech mixture, independently of the definition of the species proportions, both species grew better in the mixture, thus exhibited a clear overyielding. For both species together, transgressive overyielding was observed for pine proportion above 60%.

In the pine-oak mixture, overyielding of oak was very small. Overyielding was smaller when the pro-

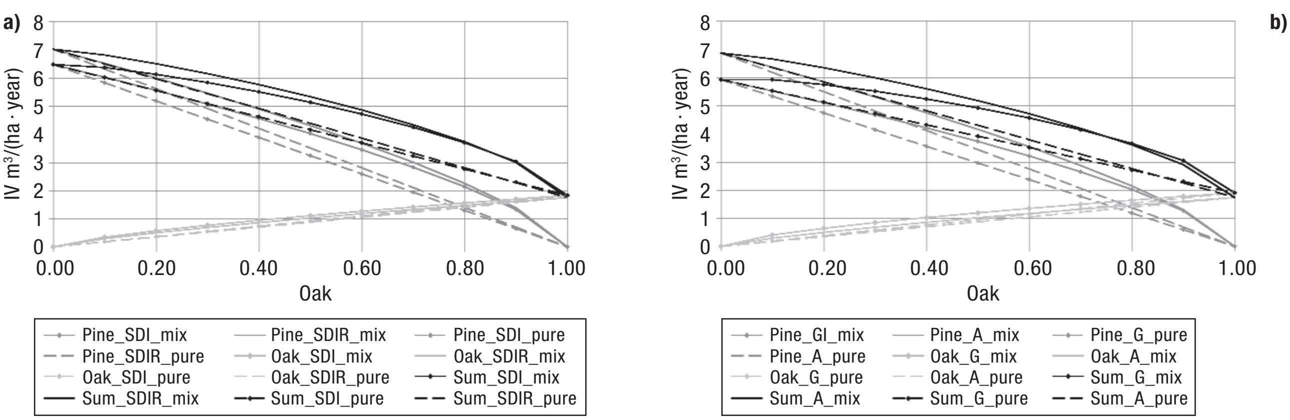

Figure 7. The hypothetical replacement series experiment for the pine-oak mixture. Comparison between growth for absolute proportions and proportions using species specific maximum densities in a) stand density index (SDI and SDIR, respectively) and b) basal area (G and A respectively). The dashed lines are the hypothetical growth if the growth efficiencies of the species were the same in the pure and in the mixed stands and the solid lines are the growth given by the fitted models. (Pine: $h_{dom} = 10.3$ m, $d_g = 20.1$ cm; Oak: $h_{dom} = 8.6$ m, $d_g = 15.3$ cm; SDI = 481.4; SDIR = 0.37; G = 20.0 m^2/ha; A = 0.40).

portions were relative to maximum densities by SDI or basal area. Overyielding of pine was somewhat higher, and there was a clear overyielding of both species together, however no transgressive overyielding at all, meaning that all mixtures grew less than the respective pure pine stands.

In order to allow comparisons between mixtures and species, the relative mixture effects are shown in Fig. 8. Relative overyielding was higher in the pine-oak mixture than in the pine-beech mixture. In all mixtures, the relative overyielding of the species decreased with their decreasing proportion. The relative overyielding of both species had a more distinct peak in the pine-oak mixture at a pine proportion of about 20%.

The relative overyielding effects in the pine-beech mixture were practically the same, independent of the definition of the species proportion, while in the pine-oak mixture there were larger differences in the overyielding effects between species proportion definitions. Generally, as could be seen already in Fig. 8, the overyielding effects in pine were bigger than in oak. For both species in the pine-oak mixture, however, there were clear differences in the overyielding effects, depending on the definition of species proportion. De-

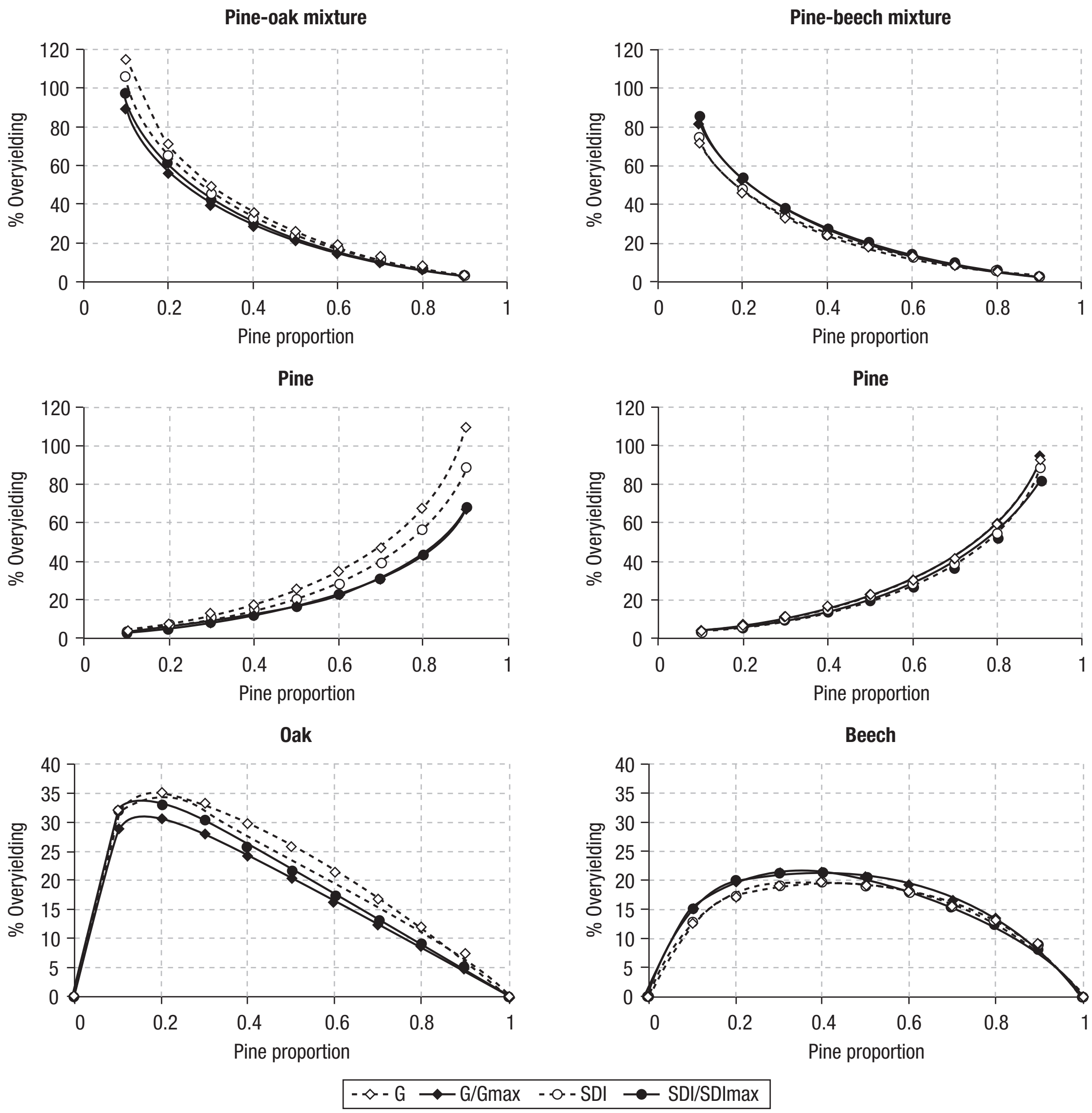

Figure 8. Relative mixture effect by species and for total stand in the two mixture types, depending on the definition of the species proportion. G is basal area in m²/ha, SDI stand density index in stem/ha, and G_{max} and SDI_{max} the potential basal area and stand density index respectively.

fining the proportions by relating them to the potential densities, they appeared smaller, and they were smaller when using the SDI in comparison with the basal area proportions.

Discussion

The objective of this paper was to compare growth in pure and mixed stands using different definitions of species proportions. If the maximum density of the species on a given site differs much, it is important to refer the observed density to the maximum density, because otherwise the relative density would differ by species and growth cannot be compared anymore to pure stands of the same density. Therefore, the earliest suggestion to define species proportions by area referred to the volume or basal area of yield tables (von Laer, cit (Prodan, 1959)). This approach, however, is only appropriate if the yield tables describe the maximum density. If there are triplets of unthinned stands available (Pretzsch, 2009; Pretzsch & Schütze, 2009), or at least with comparable densities (Pretzsch *et al,,* 2010), the neighbouring pure stands as well as the mixed stand may well be assumed to grow at maximum density and might be comparable. When using inventory data, the maximum density of pure stands has to be found in a different way.

As shown by Sterba (1987), Río & Sterba (2009) and Condés *et al.* (2013) maximum SDI and maximum basal area, both of them expressing the potential growth of the species, can be determined from inventory data by parameterising the Competition Density Rule.

In our growth models site quality is not explicitly described as site index due to the lack of age information in the SNFI. Dominant height can be understood as a proxy for site quality (compare Condés *et al.,* 2013), and mean diameter as a proxy for age (Pretzsch, 2005). All models describe the increase of growth with site quality in the expected way. The positive effect of stand density on growth did not contain an optimum, however, it exhibited the expected increase with a decreasing rate, indicated by parameters lower than one. It should however be noted that the comparisons in hypothetical replacement series experiments (Kelty, 1992) compare the growth of mixed stands with that of pure stands of the same dominant height, mean diameter and density. For interpreting the coefficients of the respective equations for growth efficiency the approximation of dominant height for site quality and mean diameter for age will be justified. Assuming that as long as density is in the equation too, its effect on mean diameter is considered. If however, density and/or dominant height growth are themselves affected by mixture, the choice of pure stands to which the mixtures should be compared is not obvious and needs further attention. These interactions would however be the same for all definitions of species proportions. For the average values of dominant height, density, and mean diameter observed in the data, the mixing effects (Figs. 6 and 7) were similar to those shown by Río & Sterba (2009) and Condés *et al.* (2013). In the pine-beech mixture, some overyielding was evident for both species, and for the whole mixture some transgressive overyielding was observed if the proportion of pine exceeds 60%. In the pine-oak mixture, there was only a minor overyielding of oak, and no transgressive overyielding for the total mixture. These general mixing effects were of the same direction in all four models, independently of species proportion definitions.

However, for the main objective of this work, the relative overyielding as depicted in Fig. 8 is most important. In the pine-beech mixture this relative overyielding, be it by species or for the whole mixture, was very similar for all definitions of species proportions. This was to be expected, because the potential densities of the two species did not differ by much. Nevertheless, a slightly lower overyielding was found when employing absolute species proportions. It is important to note the use of a common species proportion axis for all models in Fig. 8 irrespective differences in the definitions of the species proportions, which makes the comparison of the results difficult.

In the pine-oak mixture the maximum density of the two species differs more, especially when calculated by basal area (Fig. 5). Consequently, the overyielding of oak is much higher when the species proportions by basal area were calculated without referring to the maximum density of the species. Since the potential density of oak is much lower than that of pine, a given basal area of oak would represent a much higher relative density of oak compared with pine, causing a large difference between absolute and relative species proportions. As the difference between maximum basal areas of both species for the given mean dominant heights (Fig. 4) was much higher than between maximum stand density indices, the effect of using absolute or relative species proportions is also higher for basal area definitions (Fig. 8).

Groot *et al*. (2014) also found that different site occupancy measures lead to different relationships of them with species proportion by basal area, reflecting the difficulty to express properly growing space occupancy in mixed stands. These authors suggested the use of measures associated to light resource, but this kind of variables are often lacking in forest inventories. Among the two density measures used in this study, the maximum density index does not vary with age and site index, and thus not with mean diameter and dominant height. Therefore equations for the maximum basal area depending on dominant height seem to be a better option to define site occupancy. According to the theoretical considerations (Fig. 3), the growth effects introduced by using absolute species proportion instead of relative species proportions should be opposite for the two species. However, the figures based on fitted models and mean observed stand characteristics show the expected effect for oak but not for pine, where overyielding was also slightly higher for absolute than for relative proportions. This might be caused by other sources of variability not included in the models, since for the pine-oak mixture the variability explained by fitted models was low (Table 6). Moreover, interactions not included in the models could also change the mixing effects, as reported in Condés *et al.* (2013) for the pine-beech mixture. Another complication for the interpretation of the observed differences between the four models is that not only the species proportion variable is different, but also the density variable.

In any case, our findings indicate that the species proportion definition matters when comparing growth in pure and mixed stands. The selection of a species proportion definition that considers the different potential densities between species might be more advisable since it provides a better estimate of the growing space occupied by each species. This may be particularly important when the analysis is done based on forest inventory data, in which some factors influencing growth are not well described and direct comparison among pure and mixed species plots are not possible. However, growth effects introduced by species proportion definitions might also affect the interpretation in studies based on empirical data from triplets. If mixed plots grow better than the pure plots in the triplets, transgressive overyielding can always be confirmed (Pretzsch, 2009). However, for simple under- or overyielding, growth effects might be influenced by species proportion definitions. Therefore, when large differences in species potential densities are observed, relative species proportions might provide more reliable mixing effects, affecting the net total mixing effect as well as the relative importance of under-/overyielding by species.

Conclusions

Depending on the purpose of a study, very different definitions of species proportions in mixed forest stands may be used. When studying the space use efficiency of species, comparing growth in pure and mixed species stands, the definition of the proportions need to consider the potential density of the species. Otherwise, mixing effects that do not exist could be pretended or the other way around. Among the concepts describing potential density the maximum stand density index and the maximum basal area have well developed theories and can be estimated from large inventory data sets.

The attributed mixing effects introduced by the use of an inadequate species proportion definition mislead the interpretation of growth comparisons between mixed and pure stands. This involves a possible mistake in the net effect for the stand, *i.e.,* the magnitude of under/over-yielding, but also by species, misinterpreting the importance of the mixing effect for each species.

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