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A comparison of different methods to estimate species proportions by area in mixed stands

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Abstract

Aim of the study: This paper presents the most appropriate ways to estimate the species proportions by area in mixed stands of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) by comparing stand level and individual tree level approaches. It also investigates whether different ways of describing species proportions by area can result in different judgments on the over- or under-yielding of species in mixtures.

Area of the study: Three triplets of pure and mixed stands of Norway spruce and European beech in three locations in the northeast of Austria are investigated. The three locations differ considerably in slope, bedrock and soil type as well as in site index.

Material and methods: In all 9 plots the coordinates of all trees, their dbh, height, height to the crown base and five year increment were measured. The potentially available areas of individual trees are calculated by Voronoi- diagrams and potential densities are estimated from the comparable pure stands, yield tables, and published equations for maximum basal area and Reineke's maximum density line.

Main results: The species proportions estimated by the individual tree approach with leaf area as growth characteristic gave the best fit with the stand approach with the most appropriate, regional maximum basal area equations. By using various definitions of species proportions, in the worst case the mixing effects on individual species can be seriously over- or underestimated while the mixing effects on the total increment is only negligibly affected.

Research highlights:

— Measures of species proportions by area are needed for comparing growth per hectare of a species in a mixed stand with that of the same species in a pure stand.

— Species proportions at the stand level are based on estimates of the species' potential densities, either in terms of maximum basal area or of maximum stand density index.

— Species proportions at the tree level are derived from the area potentially available (APA) to the individual trees, based on the coordinates of trees in the stands, and on their growth characteristics, such as crown projection area or leaf area.

— For the examples of Norway spruce - European beech stands, the species proportions derived according to the individual tree approach using leaf area as growth characteristics fits best with the stand approach using the most appropriate maximum basal area equations

Key words: *Picea abies*; *Fagus sylvatica;* mixture proportion; growth efficiency; mixing effect.

Introduction

In central Europe, the conversion of forests dominated by broadleaves into mostly even-aged pure conifer forests started as early as in the 16th century (Johann *et al.*, 2014). At first the elimination of broadleaves was the result of unintentionally heavy exploitation for charcoal and the use of the timber in the mining industry. Later the expectation of higher yields and the ease of artificially regenerating even-aged pure conifer forests after clear-cuts led to a landscape with uniform and relatively young forests, dominated by conifers, mainly Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) (Johann *et al.*, 2014). At the end of the 19th century silviculture textbooks (*e.g.* Gayer, 1886, Gayer, 1889, Köstler, 1950)

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Abbreviations used: APA (area potentially available).

proposed that, due to ecological reasons this kind of forest management should be changed in favor of a close-to-nature forestry, based on the emulation of the local natural forest types.

According to Führer (1990), in the ecological debate of the 1980s, a silviculture based on the potential natural forest type was expected to reduce stresses on the forest ecosystem. Nowadays "the increasing interest in mixed forests is a reflection of an increasing complexity of societal demands upon forest ecosystems. Such demands include greater resistance and resilience to environmental hazards, an increasing demand for employment and business opportunities and recreational values, and a more diverse portfolio of environmental services" (Bravo-Oviedo *et al.*, 2014).

When forest management places greater emphasis upon mixed species forests, changes in species proportions and in productivity resulting from mixture effects have to be monitored.

Therefore, the determination of mixture proportions by area plays an essential role:

i. For investigating changes in tree species proportions, the mixture proportions of successive surveys have to be determined in the same way. Using basal area or volume as a reference could lead to incorrect interpretations because of species-specific differences in growth rate. This is the reason why the area occupied by each species should be used.

ii. For evaluating the species productivity in mixed species stands and especially for comparing this with productivity in pure stands, the increment of each species has to be related to the area which it occupies. For detecting overyielding, a hypothetical mixed stand is defined by weighting the growth found in pure stands of the component species by the proportion of the respective species in the observed mixed stand. The species in this hypothetical mixed stand do not exhibit any mixing effect. If the growth of the observed mixed stand exceeds the growth of this hypothetical mixed stand, the effect is called overyielding (Pretzsch and Schütze, 2009). While transgressive overyielding, *i.e.* the growth of the mixed stand exceeding the growth of a pure stand of the best growing species in the mixture, does not need the calculation of the species proportions, overyielding does.

Several methods of estimating mixture proportions are in use (Bravo-Oviedo *et al.*, 2014). However, they are rarely compared to each other. The validity and plausibility of the respective definitions are scarcely discussed. Moreover, they have never been compared with the species proportions which would result from the areas potentially available (APA) at individual tree level.

The most common method for reporting species proportions in the course of stand description is a visual estimate of crown cover - which suffers from low accuracy and poor reliability.

A more reliable approach would employ stem number, basal area or volume. Proportioning of area by stem number, however, is not meaningful because it does not consider any measure of tree size. Thus, it would only be reliable if all species in the mixture were the same size. The problem in using basal area or volume proportions is the assumption that every species at a site has potentially the same volume growth.

There are three options to determine proportions of species in a reliable and reasonable way:

i. Mixture proportion can be applied with reference to differences in potential stand density for each species. Basal area could serve as a meaningful measure of stand density.

ii. The second approach is to switch to the individual tree level. Crown projection or leaf area of every single tree can be applied to calculate proportions. A better way would be to use APA at tree level, thus taking into account the spatial distribution of the trees.

iii. The approach of Weber (1891, cit. Keller, 1995) assumes that different tree species produce the same dry mass on the same site. Therefore, different volume growth on the same site is caused only by differences in species-specific wood density.

In this study the authors investigated mixing proportions in stands of Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.), which is the most common mixture in Austria. The data were collected at three different sites and used to calculate the species proportions according to all the methods described above and also to compare the individual tree approaches with the stand - level approaches. Furthermore, the authors described the impact of the different definitions on the comparison of volume and biomass growth efficiency between pure and mixed stands.

Material and methods

Study areas

The study areas were located in the northeast of Austria. Two were investigated in 2011, one near the Lower

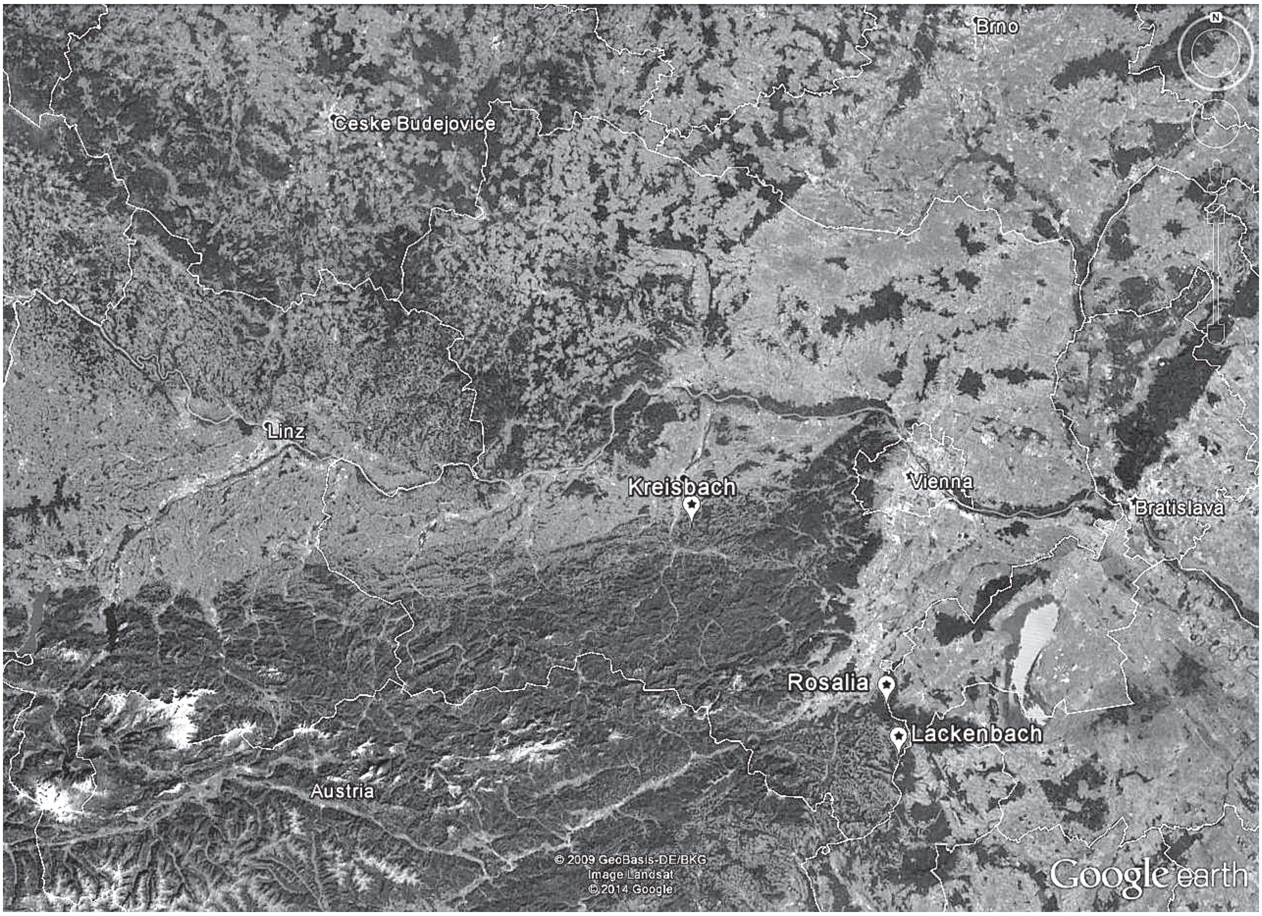

Figure 1. Location of the study areas (Google Earth, 2014).

Austria/Burgenland border at the University Forest Rosalia (47°42'22.21"N, 16°17'31.99"E) and the other one at the Pauliberg, near Lackenbach (47°35'42.40"N, 16°19'50.31"E). Another one was reinvestigated in 2013 in Lower Austria, near Kreisbach (48°5'49.69"N, 15°39'49.72"E) (Fig. 1). Due to a thinning in Kreisbach in 2011, only the previously investigated period from 1998 to 2003 is taken into account.

In each study area one stand triplet was established, with each one consisting of a mixed species stand of Norway spruce and European beech and two adjacent pure stands, spruce and beech, respectively. In Lackenbach and Kreisbach, there were only 10 to 20 meters between the three respective stands, whereas in Rosalia some hundred meters were required to get nearly comparable site conditions. Although the stands of each triplet were on similar soils, there was considerable site variation between the three locations (Table 1). Investigated plot size ranged from an average of 0.60 ha in Lackenbach and Rosalia to around 0.45 ha in Kreisbach.

Stand age of all triplets was nearly similar, around 71 to 79 years. According to the yield tables used (Norway spruce: "Fichte-Bruck" for Lackenbach and Rosalia and "Fichte-Bayern" for Kreisbach; European beech: "Buche Braunschweig" in Marschall (1975) for all study areas), all 9 stands were fully stocked.

All sample trees in all stands (spruce and beech) were measured for coordinates, diameter at breast height (1.30 m) and total height. For calculating volume increment in the locations Lackenbach and Rosalia, all trees were cored with an increment borer providing information on at least the last 15 years´ growth. The increment of 5 years (2006 to 2010) was measured in the laboratory to the nearest 1/100 mm. An adequate number of trees were also cored for verifying the stand age. In Kreisbach the measurements in 1998 and 2003, assessed with a diameter tape, were used for increment calculations.

Crown diameters were determined by measuring projected crown border in the mixed species stands and by calculation according to Pretzsch *et al.* (2002) in the

Table 1. Site characteristics of the three locations where pure and mixed stands of Norway spruce and European beech were compared

		Lackenbach	Rosalia	Kreisbach
Elevation [m a.s.l.]		570	450-630	480
Aspect		W	SW	N
Slope [%]		38-46	27-44	18
Slope position		Middle slope	Middle slope	Lower slope
Bedrock acc. to Gabler and Schadauer (2008)		Dystric silicate material	Dystric to eutric silicate material	Flysch
Soil type		Dystric cambisol	Dystric cambisol	Stagnic Gleysol
Mean annual temperature [°C]		8.3	6.5	8.4
Mean annual precipitation [mm]		679	796	850
Stand age [a]		79	77	71
mai_{100} [$m^3 \cdot ha^{-1} \cdot a^{-1}$]	Spruce	6.7	8.5	13.8
	Beech	4.6	7.2	9.9
Site index [m]	Spruce	24.4	27.2	30.1
	Beech	21.3	26.4	29.8

Growth characteristics are the mean annual increment (**mai_{100}**) and the site index with reference age of 100 years, as estimated from the yield tables by Marschall (1975).

pure stands. Coordinates and crown radii were measured with the FieldMap®-Equipment (IFER, 2008).

Volume increment and dry biomass increment

Volume increment was calculated from the diameter increment measured from the cores, with the application of the height increment equations of Nachtmann (2006). Form factor was calculated according to Pollanschütz (1974) and for diameters at breast height between 5 and 10 cm according to Schieler (1988). The latter had been developed in a way that both approaches give the same form factor at a diameter of 10 cm.

For calculating dry biomass increment, the current annual volume increment of each species was multiplied by its oven-dry density: 427 kg · m^{-3} for spruce and 650 kg · m^{-3} for beech (FHP, 2006).

Determination of mixture proportion

Calculation of mixture proportion by area equal to proportion by crown projection area, leaf area, APA and mass

Mixture proportion m_{sp} can be calculated by the ratio of a growing size X of the tree species *sp,* divided by the sum of this growing size at the stand.

$$m_{sp} = \frac{x_{sp}}{\sum_{sp=1}^{n} x_{sp}} \quad [1]$$

For calculating the growing size, crown projection area, leaf area, APA and dry matter were used in this study.

Crown projection area and leaf area

Crown projection area was determined as the horizontal circular area, calculated from the square mean of the measured crown radii in the mixed stands.

Leaf area was estimated via crown surface area for spruce and beech in mixed stands according to Gspaltl and Sterba (2011).

Area potentially available for each tree

Area potentially available was calculated by weighted Voronoi-diagrams. In this method the whole stand area is divided into small pixels. Every pixel is assigned to the tree for which

$$T = \frac{E_i^2}{w_i^2} \quad [2]$$

is at minimum (E_i is the distance from the pixel to the i^{th} tree, w_i is a growth parameter of the i^{th} tree),

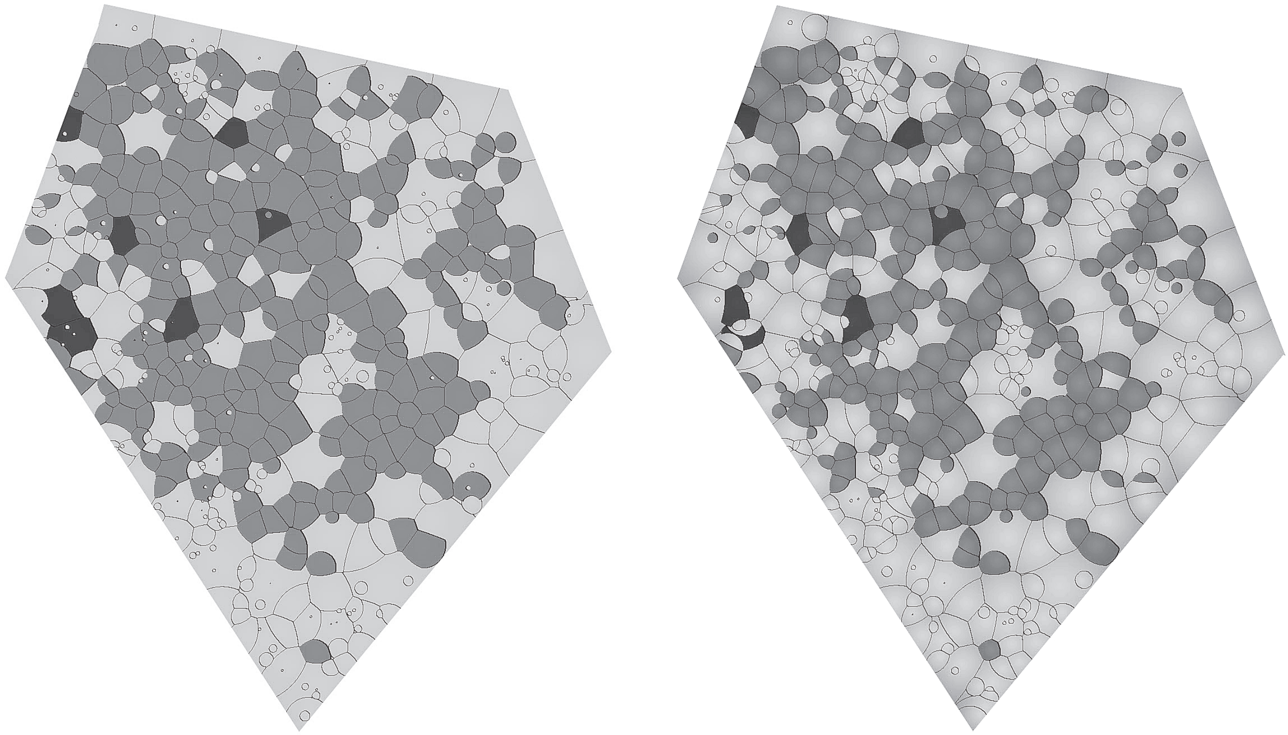

Figure 2. Area potentially available (APA) for each tree of the mixed stand in Rosalia. The Voronoi-diagrams are weighted by crown projection area (left) and by leaf area (right). Beech is colored bright, spruce is dark, black are a few small other conifers.

according to Römisch (1995). Hence, the pixel is assigned to the nearest tree at a given growth parameter and also to the tree with the highest growth parameter at a given distance. As growth parameters, crown projection area and leaf area were used (Fig. 2).

Determination of mixture proportion by dry matter

Weber (1891, cit. Keller, 1995) postulated that proportion of tree species could be determined by proportion of dry matter of a species in relation to the sum of dry matter of the stand. If basal area is used as a measure of stand density instead of volume, basal area (BA_{sp}) has to be modified by the basic density ($d_{v\,sp}$) to get mass per unit area (ma_{sp}), *sp* again for the tree species:

$$ma_{sp} = BA_{sp} * d_{v_{sp}}^{2/3} \quad [3]$$

Proportion by area is then calculated as proportion of mass per area of the species divided by the sum of mass per area of the stand. However, this assumes that all species produce the same amount of dry matter.

Keller (1995) used different basic densities for spruce (392 kg · m^{-3}) and beech (585 kg · m^{-3}), resulting in different multipliers for mass per area (53.56 kg$^{2/3}$ · m^{-2} for spruce and 69.95 kg$^{2/3}$ · m^{-2} for beech).

Determination of mixture proportion by using potential stand density in pure stands

Dividing the observed stand basal area of one species in the mixed stand (BA_{sp}) by the potential stand basal area in the respective pure stand ($BA_{pot\,sp}$) results in the area of a stand in hectare, which exhibits exactly this potential basal area (fully stocked) BA_{sp}. The ratio of this stand area of potential density and the sum of these stand areas over all species would be the mixture proportion of this species m_{sp}.

$$m_{sp} = \frac{BA_{sp} / BA_{pot_{sp}}}{\sum_{sp=1}^{n} BA_{sp} / BA_{pot_{sp}}} \quad [4]$$

In Equation [4] *sp* is the respective species and *n* is the number of tree species in the stand.

Such a calculation of proportion by area is plausible and logical. However, the potential basal area has to

Table 2. Determination of potential basal area (BA_{pot}) in Equation [4]. The basal area of the source and the respective coefficients are according to the key references

Method	**Equation**	**Key references**
Yield table	$BA_{pot} = BA_{yield\ table}$	Marschall (1975)
Competition-Density-Rule	$BA_{pot} = BA_{\max} = \frac{\pi}{160000 * a_0 * b_0} * h_{dom}^{-(a_1+b_1)}$	Sterba (1983) Schnedl (2003) Döbbeler (2004)
Stand Density Index	$BA_{pot} = BA_{\max} = \frac{\pi}{4} * e^a * dg^{2+b}$	Pretzsch and Biber (2005)
Adjacent pure stands	$BA_{pot} = BA_{obs,pure}$	

The abbreviations are: basal area of the respective yield table ($BA_{yield\ table}$), maximum basal area (BA_{max}), dominant height (h_{dom}), diameter of the tree of the mean basal area (*dg*), observed basal area of the adjacent or comparable pure stand ($BA_{obs,pure}$) and the estimated coefficients of the respective reference (a_0, b_0, a_1, b_1, *a and b*).

be known. In this study several approximations for the potential basal area were used (see Table 2).

Following von Laer (cit. Prodan, 1959), potential basal area should be taken from yield tables. Current yield tables do not represent potential stand basal area but rather values for a special silvicultural stand treatment- often different for each tree species. Due to this tendency, the maximum stand density was applied in this paper because the maximum value is untouched by any concept of an optimal stand treatment.

Such potential stand densities can be derived from the modified Competition-Density-rule (Sterba, 1983 and Sterba, 1987) or by the relation between stem number and mean diameter of the stand at maximum density, according to Reineke (1933).

Maximum basal area was calculated for both approaches. For the first approach, estimates were taken from the data of the Austrian National Forest Inventory for the coefficients a_0 to b_1 derived by Sterba (1983) for spruce and by Schnedl (2003) for beech, while Döbbeler (2004) determined estimates for both species for different regions in Germany.

For the second approach, the estimates for coefficients *a* and *b* were used, according to Pretzsch and Biber's (2005) investigation of long-term thinning experiments from A-grade plots (only removal of dead and dying trees).

The adjacent or comparable pure stands of this study can be used for comparisons with the maximum basal areas estimated from larger data, and can also serve as reasonable estimates of potential density for tree species in pure stands.

Definitions of growth efficiency

There are two ways of comparing the efficiency in mixed species stands (Fig. 3).

First, the observed mixed stand can be disaggregated into two pure stands of the respective species by dividing the observed growth of the species by its proportion

$$EFF_{sp} = growth\_obs_{sp} / m_{sp} \quad [8]$$

with EFF_{sp}, the efficiency of the species *sp*, $growth\_obs_{sp}$ the observed growth (in terms of volume or biomass increment) of this species, and m_{sp} the proportion of this species. This efficiency is then compared with the growth in the observed pure stand.

Second, a hypothetical mixed stand can be created by multiplying the growth of the pure stands by the respective species proportions, and adding them.

$$Growth\_hyp_{mix} = \sum_{sp=1}^{2} Growth\_obs, pure_{sp} * m_{sp} \quad [9]$$

with $Growth\_hyp_{mix}$ the hypothetical growth of the mixed stand, $Growth\_obs,pure_{sp}$ the observed growth of species *sp* in the pure stand and m_{sp} again the proportion of the species *sp*.

This hypothetical mixed stand is then compared with the observed growth of the mixed stand.

These comparisons can be done by building the ratio either (1) between the efficiency of the mixed stand´s species and the respective growth in the observed pure stands, resulting in the relative efficiency of the species $EFFrel_{sp}$

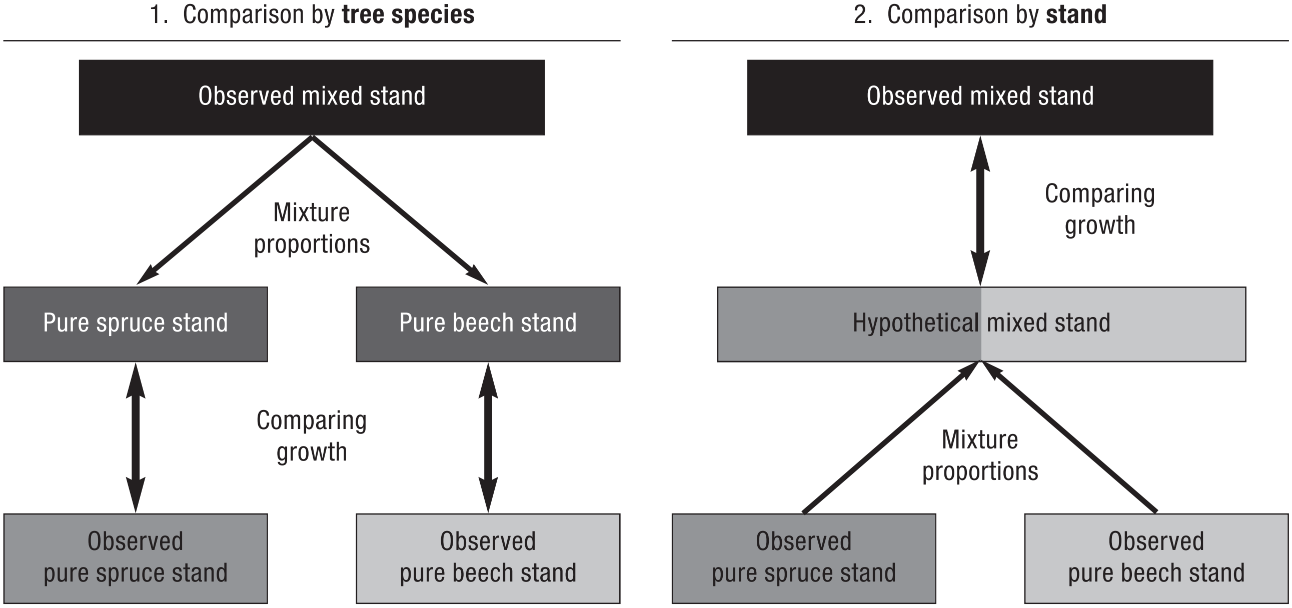

Figure 3. Methods for comparing growth efficiency of mixed and pure stands. On the left side, the growth of a single tree species is compared; on the right side the growth of the whole mixed stand is compared.

$$EFFrel_{sp} = 100 * \frac{EFF_{sp}}{Growth\_obs, pure_{sp}} \quad [10]$$

or (2) between the observed growth in the mixed stand and the respective hypothetical growth, resulting in the relative efficiency of the mixed stand $EFFrel_{mix}$

$$EFFrel_{mix} = 100 * \frac{Growth\_obs_{mix}}{Growth\_hyp_{mix}} \quad [11]$$

If there is no mixing effect at all, these relative efficiencies are 100%.

Results

Comparison of mixture proportion calculated at individual tree level

There are considerable differences in the species proportions depending on whether the area is weighted according to crown cover or by leaf area (Fig. 2, Table 3).

Taking into account that a spruce tree carries several ages of needles, it exhibits approximately twice the leaf area per unit of crown projection area in comparison to beech. Thus, beech needs twice the crown projection area of a spruce for the same leaf area.

Comparison of mixture proportion calculated at stand level

Table 3 also shows the results of the stand level approach.

Only the maximum basal area estimates which are higher than those observed in the adjacent pure stands (**bold** in Table 3) are suitable estimates in this study. Those estimations of basal area which are below the values observed in pure stands cannot be adequate estimations of the real potential - such values are written in brackets.

In Fig. 4 the estimations of mixture proportion at stand level are compared with the individual tree methods using APA.

Observation of increment for the calculation of growth efficiency

Stand volume increment, measured from the increment cores and the two diameter measurements in 1998 and 2003 (Kreisbach), is presented in Table 4 and Fig. 5. Increment in terms of dry biomass (lower rows

Table 3. Estimates of mixture proportions [%] of spruce and beech using four different approaches based on the individual tree approach, and nine different approaches based on the stand approach. Minima and maxima are shown in the last two rows

		Lackenbach		Rosalia		Kreisbach 2003	
		Spruce	**Beech**	**Spruce**	**Beech**	**Spruce**	**Beech**
Individual tree approach	Area potentially available weighted by leaf area	63.4	36.6	61.3	38.7	66.6	33.4
	Proportion by leaf area	64.4	35.6	59.3	40.7	66.0	34.0
	Area potentially available weighted by crown projection area	55.0	45.0	47.1	52.9	44.1	55.9
	Proportion by crown projection area	47.4	52.6	37.0	63.0	35.1	64.9
Stand approach	Adjacent pure stands	61.7	38.3	51.5	48.5	70.1	29.9
	Yield tables	(62.9)[1]	(37.1)	(59.0)	(41.0)	(69.7)	(30.3)
	Döbbeler "Southeast"	**56.3**[2]	**43.7**	**51.9**	**48.1**	**64.1**	**35.9**
	Döbbeler "East"	**59.6**	**40.4**	**55.4**	**44.6**	**67.3**	**32.7**
	Döbbeler "Northwest"	**61.9**	**38.1**	**58.0**	**42.0**	**69.8**	**30.2**
	Döbbeler "Southwest"	**65.7**	**34.3**	(63.3)	**36.7**	(69.9)	**30.1**
	Sterba /Schnedl	**63.8**	**36.2**	**60.7**	**39.3**	**68.3**	**31.7**
	Pretzsch and Biber	**58.7**	**41.3**	**54.2**	**45.8**	**65.7**	**34.3**
	Keller	62.6	37.4	59.4	40.6	71.3	28.7
	Minimum	47.4	34.3	37.0	36.7	35.1	28.7
	Maximum	65.7	52.6	63.3	63.0	71.3	64.9

[1] Values for which the maximum basal area is not as high as the observed basal area in the adjacent pure stands are in brackets.
[2] Bold characters indicate the maximum basal area being higher or nearly the same as the observed basal area in the adjacent pure stands.

in Table 4, right columns in Fig. 5) was also calculated separately for each tree species and summed up for the mixed stand.

With these values of increment, growth efficiencies (increment per unit area) can be calculated. For the comparison of mixed and pure stands, the relative efficiencies are shown in Table 5.

To determine the influence of using different methods for estimation of mixture proportion, efficiencies were calculated for the definition which resulted in the lowest proportion of spruce (47.4% in Lackenbach, 37.0% in Rosalia and 35.1% in Kreisbach) and for the one resulting in the highest proportion of spruce (65.7% in Lackenbach, 63.3% in Rosalia and 71.3% in Kreisbach) in order to investigate the sensitivity of efficiency statements (Table 5).

Discussion

Comparison of the methods at stand level and individual tree level

In general, the individual tree approach with the estimates using leaf area is a better match with all the stand level methods than those using crown projection area (Fig. 4, Table 3).

There are two reasons why using leaf area is the more reliable approach. On the one hand, the physiological effect of leaf area on tree productivity is more meaningful than the one by crown cover. On the other hand, as shown in Table 3, calculating mixture proportion by using leaf area directly or APA weighted by leaf area is more consistent than the approaches with crown

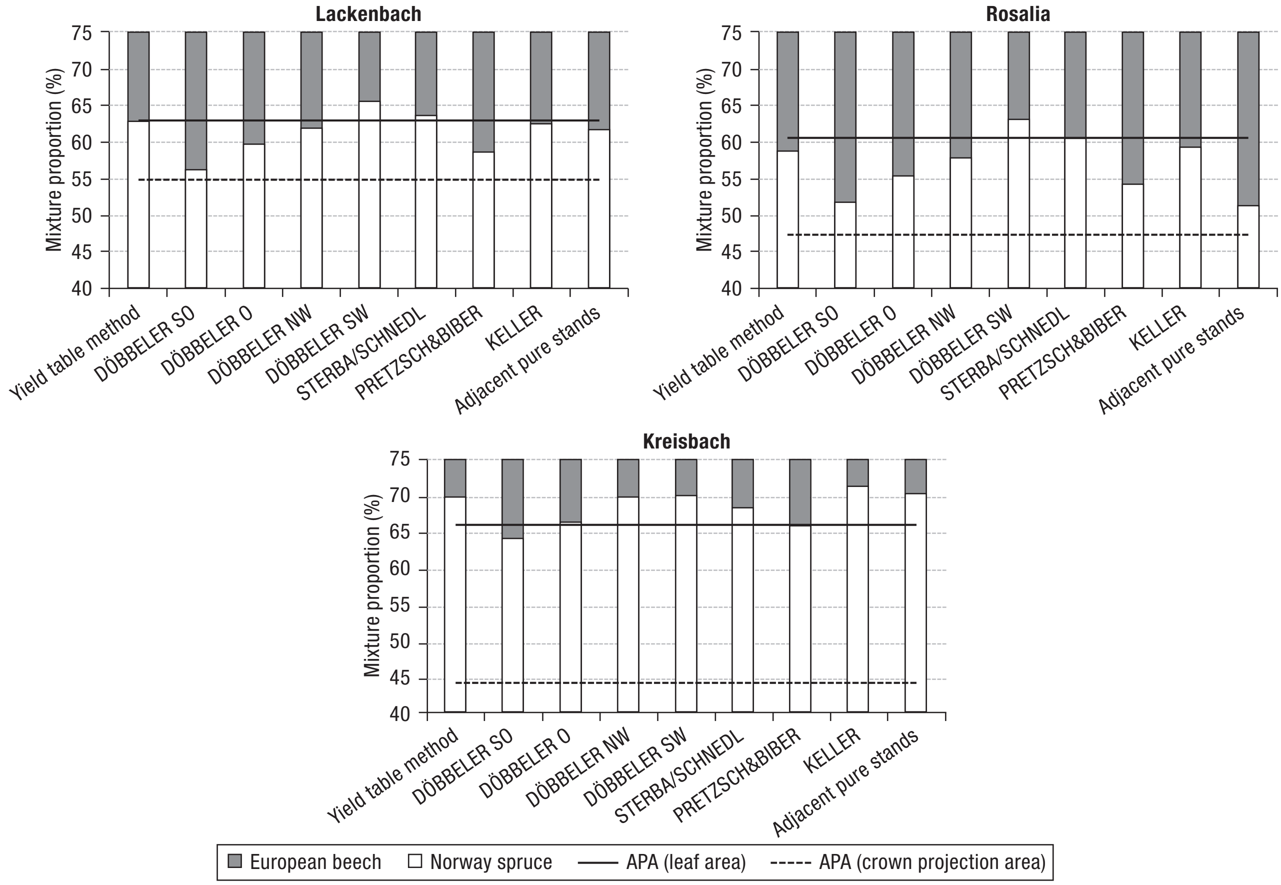

Figure 4. Comparison of the methods to estimate proportions of spruce and beech in mixed stands (*APA [leaf area]*, area potentially available weighted by leaf area; *APA [crown projection area]*, area potentially available weighted by crown projection area).

projection area. The differences between the proportions with and without considering the spatial distribution are much smaller for leaf area than for crown projection area.

The estimation of proportion by area using adjacent pure stands as potentials generally matches very well to the proportions estimated by APA weighted by leaf area (Fig. 4). This could be observed in both triplets of Lackenbach and Kreisbach. In Rosalia however, this was not the case. This might be caused by the fact that the pure stand of spruce in that triplet was grown on a more fertile silicate rock and the variability of several other site factors was higher in this triplet (Table 1), leading to a higher potential of spruce and consequently to a lower proportion by area of spruce.

Estimates from the potentials as well as those according to Keller (1995) show values between or near the two estimates of APA. Most of them are

Table 4. Observed current annual volume increment (**CAIv**) [$m^3 \cdot ha^{-1} \cdot a^{-1}$] and current annual increment of dry biomass (**CAIm**) [$t \cdot ha^{-1} \cdot a^{-1}$] of spruce and beech at the three stand triplets

		Spruce - pure stand	Beech - pure stand	Spruce in mixed stand	Beech in mixed stand	Spruce + beech mixed stand
CAIv	Lackenbach	15.4	6.8	7.3	3.3	10.6
	Rosalia	17.9	11.2	7.0	3.9	10.9
	Kreisbach	23.7	14.0	14.0	5.2	19.2
CAIm	Lackenbach	6.6	4.4	3.1	2.1	5.2
	Rosalia	7.7	7.3	3.0	2.5	5.5
	Kreisbach	10.1	9.1	6.0	3.4	9.4

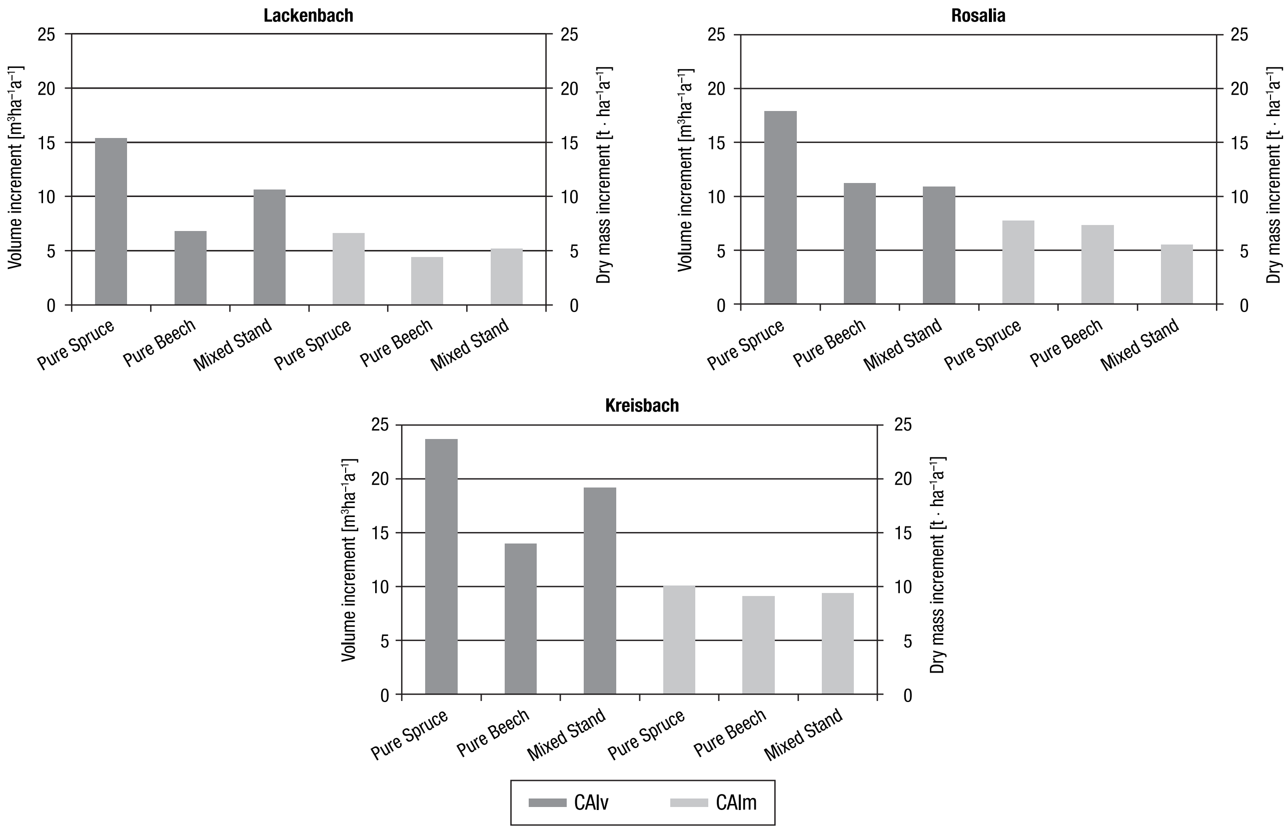

Figure 5. Volume increment (**CAIv**) and dry mass increment (**CAIm**) of the two pure stands and of the mixed stand of each site. Transgressive overyielding is not detectable since the mixed stands do not exceed the better pure stands growth.

Table 5. Relative efficiencies of the mixed stand of spruce and beech [%] in relation to the adjacent pure stands and to a hypothetical mixed stand with assumed mixture proportion (Minimum and Maximum of mixture proportion according to Table 3, and the stated best estimation of mixture proportion). For each the difference between relative volume efficiency and relative dry mass efficiency is shown. Values over 100 percent indicate overyielding of the mixed stand

		Highest spruce proportion		**Smallest spruce proportion**		**Proportions by area potentially available (APA) weighted by leaf area**	
		Volume	**Dry mass**	**Volume**	**Dry mass**	**Volume**	**Dry mass**
Lackenbach	Spruce[1]	72	72	100	100	75	75
	Beech[1]	140	140	92	92	131	131
	Mixture[2]	85	90	97	96	87	91
Rosalia	Spruce[1]	62	62	106	106	64	64
	Beech[1]	94	94	55	55	90	90
	Mixture[2]	71	73	80	74	71	73
Kreisbach	Spruce[1]	83	83	168	168	89	89
	Beech[1]	129	129	57	57	111	111
	Mixture[2]	92	95	110	99	94	96

[1] Relative efficiency of a tree species is calculated by dividing the species growth in the mixed stand per hectare (converted to hectare by mixture proportion) by observed growth in the respective pure stand.
[2] Relating the observed growth of the mixed stand to the growth of a hypothetical mixed stand (growth of all species in pure stands multiplied by their mixture proportion) results in the relative efficiency of the mixed stand.

near the APA weighted by leaf area, especially in Kreisbach.

Estimates using yield tables are also in good accordance with the proportions estimated by APA weighted by leaf area. Due to the fact that the basal areas of the used yield tables do not seem to be appropriate estimates for the potential stand density because the basal area is lower than in the adjacent pure stands, this method has to be dropped. The same result occurs when estimating mixture proportions according to Döbbeler (2004) for Rosalia and Kreisbach using coefficients of the German region "Southwest". The potential basal areas of spruce in Rosalia and Kreisbach also seem to be higher than estimated by this method.

The standard deviations of the estimates of mixture proportion by the stand approach (Table 3) are extremely low: ±2.8% in Lackenbach, ±4.1% in Rosalia and ±2.3% in Kreisbach. This accuracy seems sufficient for forest management.

As measured by APA, there are several methods giving good estimates of mixture proportion. Through the application of Keller 's (1995) approach, the fewest deviations from APA weighted by leaf area are demonstrated. Calculations of potential basal area according to Sterba (1983) and Schnedl (2003) are the most appropriate, and result in the most accurate estimates.

Growth efficiency of the different species

Comparison of volume increment is shown in Table 4. In Lackenbach and Kreisbach the increment of the mixed stand ranges between the border values drawn by the pure stands. In Rosalia it is even less than the weaker growing pure stand of beech.

Evidence of "transgressive overyielding", defined according to Pretzsch & Schütze (2009), is not detectable at any of the three mixed species stands, whether measured in volume or in tons of dry biomass (Table 4). Fig. 5 indicates that growth in mixed stands never exceeds the growth of pure spruce, which is the better growing species on each site.

Since growth efficiency was defined in this paper as increment per area occupied by a species, it is possible to compare the efficiencies of a species in pure and mixed stands. Needless to say, the result depends on the estimation of mixture proportion (see the different columns in Table 5 for relative efficiency in terms of volume and for dry mass). Using the definitions resulting in the highest spruce proportions leads to the interpretation that spruce in all three mixed stands grows worse than in the respective pure stand (72%, 62% and 83%), while beech grows nearly equally well in Rosalia (94%) and much better in Lackenbach & Kreisbach (140% and 129%, respectively).

Both species together grow worse in the observed mixed stand than in the respective hypothetical mixed stands, assuming no mixing effect (85%, 71% and 92% in terms of volume growth), meaning that the better growth of beech cannot fully compensate for the poorer growth of spruce.

The definitions where spruce has the smallest proportion lead to different results. Spruce grows equally well as in the pure stands in Lackenbach and Rosalia and grows much better in Kreisbach. Beech grows nearly equally well as in the respective pure stand in Lackenbach but much worse on the other two locations. The entire mixed stand by this definition grows about equally well in Lackenbach and Kreisbach. Here the better growth of spruce may compensate for the poorer growth of beech, while in Rosalia, the total growth of the mixed stand is clearly below the growth of the hypothetical mixed stand.

Bearing in mind that the interpretations above depend mainly on the different definitions of the species proportions, the same data could lead to partly contradictory statements on the mixing effects.

Recalling that the probably best definition of species proportions in these types of mixtures is the one by APA, weighted by leaf area, the last two columns in Table 5 give the most plausible interpretation, *i.e.* spruce grows worse than in the pure stands, whereas beech grows better in Lackenbach and Kreisbach but worse in Rosalia. Generally, the mixed stands in these three examples grow worse or at most nearly as well as the pure stand, assuming no or only compensating mixing effects.

Although there is no transgressive overyielding evident in this study, it might occur in other studies, depending on the mixture proportions and on the method of estimating them. With mixture proportions of around 50%, the comparisons of growth do not result in transgressive overyielding. It might occur, however if the stands were compared with more diverse proportions of the species in the mixed stand. A lower proportion of beech would maybe lead to transgressive overyielding (*e.g.* Río & Sterba, 2009, Condés *et al.*, 2013 or Sterba *et al.*, 2014).

Conclusions

A comparison of species growth in mixed stands can be drawn in two different ways, (1) comparing the observed species growth, related to its proportion in the mixed stand with the growth in the reference pure stand, and (2) comparing the observed growth of all species together in the mixed stand with the growth of a hypothetical mixed stand, on the assumption of no or only compensating mixture effects. Both approaches depend heavily on the definition of species proportions. It is equally true for any statement on overyielding.

Among the possible ways of defining species proportions, the most plausible ones are those using APA of trees, weighted by leaf area, and those taking into account the potential density in pure stands. These two approaches proved to be the best-fitting in the present study.

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