The elasticity of growth in pure and mixed stands of Norway spruce (*Picea abies* [L.] Karst.) and common beech (*Fagus sylvatica* L.)

H. PRETZSCH

Technical University of Munich, Faculty of Forest Science and Resource Management,
Chair for Forest Yield Science, Munich, Germany

ABSTRACT: This study indicates that the growth of mixed stands with Norway spruce (*Picea abies* [L.] Karst.) and common beech (*Fagus sylvatica* L.) is more stable across a range of stand densities than it is in pure forests of the same species. Typical density-growth-relationships are derived from 42 long-term experimental areas with 134 plots in total, the oldest of them under survey since 1870. From these results it is apparent that in pure stands maximum growth can be obtained only at medium stand density, whereas in mixed stands growth is almost unchanged over a range of low, medium and high stand density. The finding that mixed stands may perform a superior growth to pure stands with either decreasing or increasing stand density has often been overlooked but is nevertheless of major practical importance.

Keywords: elasticity of growth; density-growth-relationship; risk spreading; diversity; productivity; pure and mixed stands

Lack of data during the founding period of Forestry Sciences lead to statements on yield relationships between pure and mixed stands that were based on faith rather than knowledge (COTTA 1828; HARTIG 1791; MÖLLER 1922; WIEDEMANN 1951). Today, thanks to long-term experiments, the vastly increased knowledge on two-species mixtures can be consolidated. Mixture effects may vary considerably depending on species mixture, site, silvicultural treatment and risks. Compared with pure stands resource utilisation can be improved by almost 30% by combining early and late successional species, ontogenetically early and late culminating species, shade-intolerant and shade-tolerant tree species. However, where ecological niches and functional characteristics are similar, species may compete for the same resources in crown and root systems. The consequence may be negative effects from species interaction and a reduction in productivity by 30% (CANNELL et al. 1992; CASPERSEN, PACALA 2001; KELTY 1992; PRETZSCH 2003).

Comparisons of growth in pure and mixed stands of Norway spruce and common beech were made by a number of authors (ASSMANN 1970; LÜPKE, SPELLMANN 1999; PETRI 1966; ROTHE 1997; WIEDEMANN 1942, 1951). All of these assessments are based on regularly and moderately thinned forests. Divergent conclusions, drawn with respect to growth and yield in pure versus mixed stands, are mainly due to site differences. In general, increasing water availability and decreasing base-saturation and temperature, increases the competitiveness of spruce relative to beech (KRAMER 1988; WIEDEMANN 1942; MOOSMAYER 1957). Differences of total stem volume production between pure and mixed stands reported for sites with medium moisture, temperature and base supply often diminish down to only a few percent, if the findings are expressed on a dry weight basis rather than on a stem volume basis.

This paper addresses an aspect of mixed forest research that is largely neglected in consequence of a severe lack of appropriate data. The focus of the paper is (i) on the elasticity of growth in pure stands of Norway spruce and common beech and (ii) on a comparison with the growth reaction in mixed stands. Over and above the comparison of the productivity of pure and mixed stands by CANNELL et al. (1992), KELTY (1992) or OLSTHOORN et al. (1999) this contribution presents the following new aspects: The better ability to buffer and compensate disturbances of the stand structure may cause a superior productivity of mixed stands compared with pure stands of Norway spruce and common beech.

MATERIAL AND METHODS

Database

For the analysis, long-term experimental plots were selected from pure and mixed stands of Norway spruce

Table 1. Database for the analysis of the density – growth relation in pure and mixed stands of Norway spruce *Picea abies* (L.) Karst. and common beech *Fagus sylvatica* L. The range of site conditions of spruce and beech is characterised by the top height in age 100

Species composition	Treatment	Experimental plots		Survey period first-current	Age span	h_{100}	
						spruce	beech
Spruce	light-heavy thin. f. below	9	26	1882–2000	32–143	31–39	
Beech	light-heavy thin. f. below	10	30	1870–2001	38–179		22–30
Spruce/beech	unthinned, moderate thin. f. above	20	60	1991–2000	36–155	32–43	25–40
Spruce/beech	light-heavy thin.f. above, mixture portion	3	18	1954–2001	57–121	36–41	26–36

and common beech, these being the dominant tree species in Germany that occupy 54% of the forested area (pure Norway spruce 28%, pure common beech 9% and Norway spruce/common beech 17%). The investigation is based on 42 long-term experimental areas with 134 plots in pure and mixed stands of Norway spruce and common beech in Germany. The oldest of these trials are maintained and remeasured since 1870 regularly by the Chair for Forest Yield Science, Munich University. Table 1 summarises species composition, silvicultural treatment, number of experiments and plots, survey period and age span. The spectrum of site conditions is characterised by the range of top height spruce and beech achieve in age 100.

The experimental areas of pure stands of spruce and beech (Table 1, row 1 and 2) included in this study are located in South and Central Germany (Bavaria, Saarland, Lower Saxony, North Rhine-Westphalia). These 9 experiments in spruce stands (26 plots) and 10 experiments in beech stands (30 plots) belong to the oldest thinning experiments in the world. Many of these experiments on thinning from below have been under regular observation ever since long-term growth and yield experiments were first established in the mid-19th century. With few exceptions these experimental plots are composed of three plots identical in site and age, which were consistently treated since the start of the experiments according to the thinning rules for grades A, B and C (VEREIN DEUTSCHER FORSTLICHER VERSUCHSANSTALTEN 1902).

The included experiments Sachsenried 02, Sachsenried 03, Denklingen 05, Ottobeuren 08, Sachsenried 67, Sachsenried 68, Eglharting 72, Eglharting 73 and Paderborn 697 in spruce stands (ASSMANN 1956, 1970; PRETZSCH 2002; RÖHLE 1994) and Kirchheimbolanden 11, Waldbrunn 14, Fabrikschleichach 15, Elmstein 20, Lohr 24, Mittelsinn 25, Rothenbuch 26, Hain 27, Haiger 333 and Saarforst 1606 in beech stands (FRANZ et al. 1993; LÜPKE, SPELLMANN 1999; PRETZSCH 2002; SCHOBER 1972) have been the subject of numerous evaluations. Out of the experiments established since 1870, about half have remained under observation to this day. Correspondingly, the age span thus covered by measurements is fairly long (cf. Table 1, age span). The top heights at age 100 show Norway spruce to grow on good to excellent sites (31 to 39 m) and common beech on average to good sites (22 to 30 m). The Stand Density Index (SDI; REINEKE 1933) of Norway spruce varies during the survey period between 664 and 1609, the SDI

of common beech between 250 and 1,183. Basal areas and remaining volume vary from between 23.9 to 89.5 m²/ha and 118 to 1,637 m³/ha for Norway spruce and from 13.0 to 48.3 m²/ha and 47.6 to 795 m³/ha for common beech.

The analyses of the density-growth relationships in mixed stands are based on the age series Freising 813, Schongau 814 and Nordhalben 811 with in all 60 plots (20 plots in pure stands of Norway spruce, 20 plots in pure stands of common beech and 20 in mixed stands of spruce and beech). The mixed stand plots (Table 1, row 3) represent different development phases and stand densities, from unthinned conditions to heavy thinning. They cover an age span of 36 to 155 years and represent an artificial time series of stand growth. Increment cores were taken for tracing back tree and stand growth. With top heights of 32–43 m in Norway spruce stands and 25–40 m in common beech stands the plots vary from medium to very good site conditions. For Norway spruce and common beech, respectively, the range of stand basal area varies from 37.8 to 93.9 m²/ha and from 18.6 to 60.6 m²/ha, the standing volume from 368 to 1,551 m³/ha and from 134 to 914 m³/ha and the periodical annual growth from 11.2 to 32.7 m³/ha/a and from 5.5 to 28.9 m³/ha/a.

A second dataset is provided by the long-term experimental areas Zwiesel 111, 134 and 135 in the Bavarian Forest (Table 1, row 4). They are amongst the very few mixed stand plots under observation where crown maps, stem charts etc. were taken for decades. Each covers a wide spectrum of intermingling proportions and includes structures ranging from individual to group mixtures. On all plots common beech is the tree species with the lowest height; its average height is surpassed by that of the Norway spruce by 5–10 m. Basal area, remaining volume and annual volume growth therefore differ widely in the current inventory: basal areas from 29.7 to 67.9 m²/ha, remaining volume 338 to 1,069 m³/ha stemwood and annual volume growth from 7.8 to 17.1 m³/ha/a. These experiments have already been the subject of publications, inter alia by KENNEL (1965), PRETZSCH (1992, 2003), PRETZSCH et al. (1998), and we shall therefore not repeat the basic results.

METHODS

On the plots up to 20 successive inventories were done in which the removed and residual trees were measured, making it possible to accurately quantify the volumes re-

moved during thinning, the response of the remaining stand and, consequently, the cumulative volume production of the plots. This calculation followed the DESER standard of the German Association of Forestry Research Institutions (JOHANN 1993; PRETZSCH 2002, p. 185). Volume of standing stock results from the sum of all individual trees, using form functions according to FRANZ et al. (1973) to calculate the volume. All data on stock refer to cubic metres standing stock with bark and diameters > 7 cms. A sound comparison between mixed stands varying in species portions must consider the specific wood density of the species and their different growing space requirements. The volume growth (m³/ha/a) was transformed to stem dry matter (t/ha/a) using wood density 0.39 and 0.56 t/m³ for Norway spruce and common beech, respectively (KENNEL 1965). Based on investigations on the experimental area Zwiesel 111, inter alia by ASSMANN (1970) and KENNEL (1965), for Norway spruce and common beech the conversion factors 0.7 and 1.44 respectively were found in order to calculate from their basal area portion the respective contribution to crown cover area and mixture proportion. Thus, basal area of common beech was increased by the factor 1.44 in order to make it comparable with Norway spruce and to consider the specific contribution of Norway spruce and common beech to total density in mixed stands. For the analysis of the density-growth relationship, the plots with the highest density were assumed to represent 100% and the other plots were compared to these.

The following variables are discussed in detail: (1) Cumulative volume (CV) = volume of remaining stand at a given age + volume of all thinnings and self-thinnings in the past, (2) Periodic annual increment (PAI) = average volume increment over a defined period, (3) Intermediate yield (IY) = volume of all thinnings and self-thinnings since establishment of the stand and (4) Relative intermediate yield (RIY) = percentage of cumulative volume that is removed by intermediate fellings (RIY = IY/CV . 100). All volume data are given in cubic meters for compact wood with bark per hectare. The fact that volume portions < 7.0 cm were ignored is of negligible significance for the results. The analysis of the density-growth relationship is mainly directed at the long-term effects of different densities and less at temporary growth reactions. For the analy-

sis of pure stands we therefore selected PAI in periods of 5–12 years as well as CV. Due to the shorter observation periods for mixed stands we chose, instead, only the PAI in periods of 5–16 years. As a measure of density we used midperiod basal area and the Stand Density Index SDI = N . $(25/d)^{-1.605}$ (SDI; REINEKE 1933), which quantifies stand density by using both, the stem number per hectare N and the quadratic mean diameter d.

RESULTS

Density-growth relationship in pure stands

For selected spruce and beech thinning trials Figs. 1 and 2 show the development of the density-growth relationship from the start of the experiment in the years 1870 to 1907 up to the very last survey. For spruce and beech two trials each were selected which (1) had been under observation for the longest possible time and (2) represent unfavourable and favourable site conditions (Sachsenried 02 and Hain 27; Eglharting 72 and Fabrikschleichach 15, resp.). The average periodic increments (PAI) for the A, B and C grades (Figs. 1 and 2: o, •, Δ) were recorded period by period. Values from the same survey were joined by lines to emphasize the shape of the density-growth relationship. In the face of the discussion that stand basal area is the density measure better known by forest practice, whereas SDI takes into account the allometric development stage of the stand and represents a biological more adequate measure of density (ZEIDE 2003; AVERY, BURKHART 2002) PAI was plotted over SDI. The unfilled circles at the right end of the growth-density lines represent the A grade plots. Following the pattern of this circles the end-period ages are added in the graph. In several cases the age values were shifted in parallel in order to keep the growth-density lines clearly arranged.

In most periods an optimum relationship between density and growth is apparent. The periodic annual increment (PAI) increases from the C to the B grade and then decreases in the transition to grade A. This response pattern is valid for about 90% of the surveyed periods. The curvature of the optimum curve is pronounced at the beginning of the survey, in the juvenile phase of the
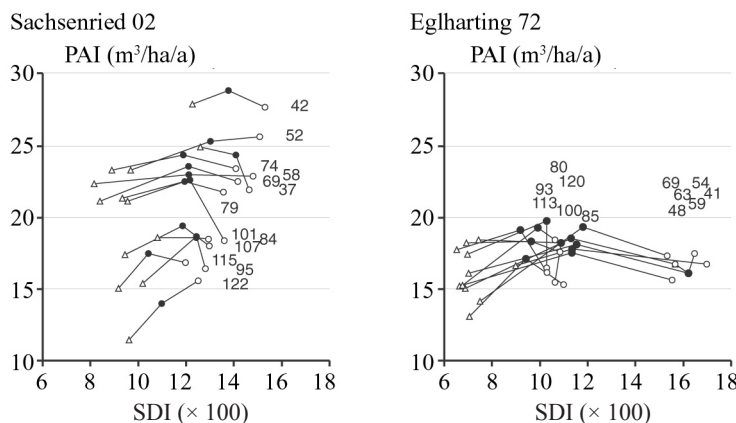

Fig. 1. Development of the density-growth relationship for the thinning trials Sachsenried 02 (left) and Eglharting 72 (right) since the start of the experiment in the years 1883 and 1907 respectively. The periodic annual increment (PAI) is plotted over the stand density index SDI. The unfilled circles at the right end of the growth-density lines represent the A grade plots. Following the pattern of this circles the endperiod ages are added in the graph

SDI = Stand Density Index according to REINEKE (1933)

Age = stand age at the end of the period
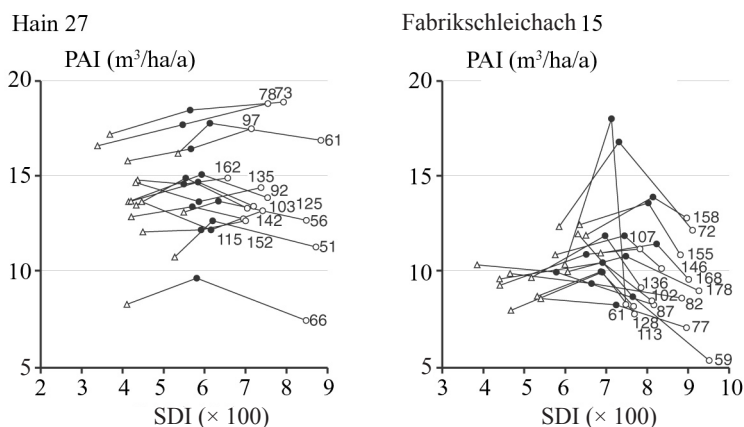
o, •, Δ = grades A, B and C, respectively

Fig. 2. Development of the density-growth relationship on thinning trials Hain 27 (left) and Fabrikschleichach (right) since the start of the experiment in the years 1870 and 1871, respectively. Shown is the periodic annual increment (PAI) over stand density index SDI. Explanations cf. Fig. 1

stand, becomes flatter in middle aged stands and smooth in mature stands. A shift to the left in the density lines is evident; SDI is at a maximum at about the time when height increment reaches its culmination point and then decreases due to the age-related gradual opening-up of the stand (ZEIDE 2003). The decrease of the SDI results from gaps in the crown layer, which occur sporadically with progressing stand development.

The experimental area Sachsenried 02 is representative of very good site conditions (mean height at age 100 = 35.4 m). In this trial the optimum curves show a pronounced bend and are seen to shift considerably in the course of stand development. The experimental area Eglharting 72 represents the response pattern of spruce on sites with a mean height of 30.5 m at age 100. The optimum curves are flatter and change less markedly with

age. For beech, site conditions have a different effect on the shape of the optimum curve: Optimum curves for the experimental area Hain 27 (mean height at age 100 = 31.8) with very good site conditions are distinctly flatter than those for Fabrikschleichach 15 (mean height at age 100 = 28.7) and tend to change more markedly and with greater regularity with progressive stand development.

Fig. 3 represents the cumulative volume for the entire range of B and C grade plots in relation to grade A (= 100% line). Again, the B and C grades are set in relation to the respective A grade for each experimental site so that absolute differences in level are eliminated and the relative growth responses with approaching maximum density are more obvious. For the B and C grade plots the respective basal areas are denoted in relation to the A grade. Separate evaluations were made for age 60 and
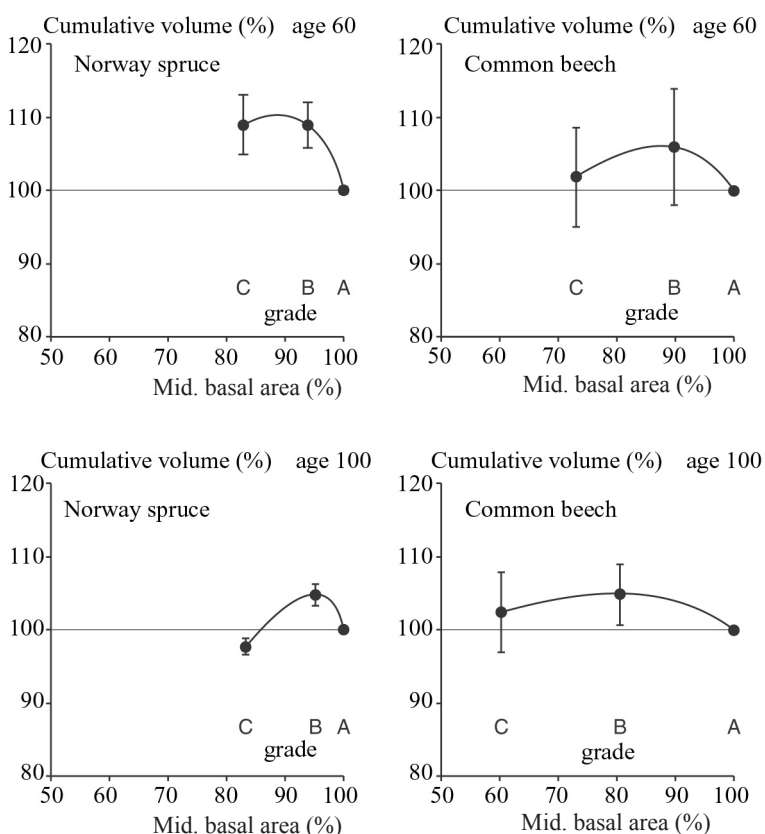

Fig. 3. Cumulative stem volume production (CV) on long-term experimental areas of Norway spruce and common beech (left and right, respectively) in relation to thinning for different age phases. Mean values and standard errors for cumulative volume for grades B and C and the corresponding midperiod stand basal areas are shown in relation to grade A (= 100% line)

100 years (Fig. 3, top and bottom, resp.). It is remarkable that in all cases cumulative volume rose by 5–10% with the transition from grade A to B. This increase is more pronounced at an intermediate rather than a more advanced age. The transition from grade B to C reveals a reduction in volume production. For the majority of experimental plots, volume production for the C grade is however still higher than for the A grade. The standard error bars show mainly significant differences between grades B and A (= 100% line). After 130 years' experimental research, we are therefore able to note a distinct increase in growth from grade A to B and a growth decline beyond grade B. Approaching maximum density, one can expect an average decrease in cumulative volume of 5–10%. Expressed in absolute figures this is equivalent to losses of 80 to 160 m^3/ha for Norway spruce and 30–60 m^3/ha for common beech stands at rotation age which are 100 and 130 years, respectively.

Density-growth relationship in mixed stands

Fig. 4 (left) shows the periodic annual volume increment plotted over the stand basal areas for the age range 60–100 years of the experimental areas Zwiesel 111, 134 and 135 (black triangles) and Freising 813, Schongau 814 and Nordhalben 811 (black rectangles). The stand basal areas in the mixed stands were adjusted and the dry mass calculated as described in the paragraph "Methods". The adjusted stand basal areas reach from 37 to 71 m^2/ha on the long term experimental plots Zwiesel 111, 134 and 135 and 38 to 85 m^2/ha on the areas Freising 813, Schongau 814 and Nordhalben 811. The values for dry mass increment in t/ha/a plotted versus the adjusted basal area of the stands in m^2/ha show considerable scattering and there appears to be no clear relationship between density and growth. Within this wide range of stand densities periodic annual dry mass increment lies mainly between 5 and 10 t/ha/a.

As for the even-aged analysis of the density-growth relationship, the plots with the highest density of the respective experiments were assumed to represent 100% and the other plots of the same experiments compared to these. This relative approach is done separately for each experimental area to eliminate absolute differences in growth between the experiments and to outline the relative growth

responses to density. Fig. 4 (right) is a summary of the results from both experimental areas and shows the PAI of dry mass in percent for stands of equal density, as defined by the following classes: < 50%, 50–59, 60–69, 70–79, 80–89 and 90–99%. The relationship between relative increments with corresponding standard errors and density is fundamentally different from the corresponding pattern in pure stands. Obviously, mixed stands are able to largely compensate for density reductions due to thinning by increased growth within the remaining stand. Within the observed density spectrum of 40–100%, increment does not decrease significantly despite a 60% reduction in stand density. It can also be observed that there is no significant decrease in growth when maximum density is approached, except perhaps a non-significant tendency towards a decline.

DISCUSSION

The sites, where Norway spruce and common beech are grown in pure and mixed stands in Germany range from alkali-rich, warm and dry sites in Central and Northern Germany favourable for beech; to acidic, cool sites with heavy precipitation in Southern Bavaria favourable for Norway spruce. For this reason the published results of comparisons between growth of pure and mixed stands depend very much on site conditions. WIEDEMANN (1942, 1951) found spruce-beech mixtures in Northern Germany where highly productive beech yield approximately the same dry biomass as corresponding pure stands. For beech of moderate growth he found that mixed stand biomass production is about 19% less than in pure beech stands on identical sites. KENNEL (1965) studied mixtures of spruce and beech in the Bavarian alpine foothills, the Bavarian Forest and the Harz in Lower Saxony as did BURGER (1941) in Switzerland, with similar results. Taking increment-neutral effects through species interaction as reference (100% = expected productivity of a mixed stand as a linear combination of pure stand growth p_1 and p_2 weighted with the mixture proportions m_1 and m_2, i.e. $p_{12} = m_1 \cdot p_1 + m_2 \cdot p_2$) the effects from species interactions between spruce and beech range between + 10 and – 20%. In all cases, however, the mixed stand occupies a position between the corresponding pure stands as far as productivity is concerned (PRETZSCH 2003).
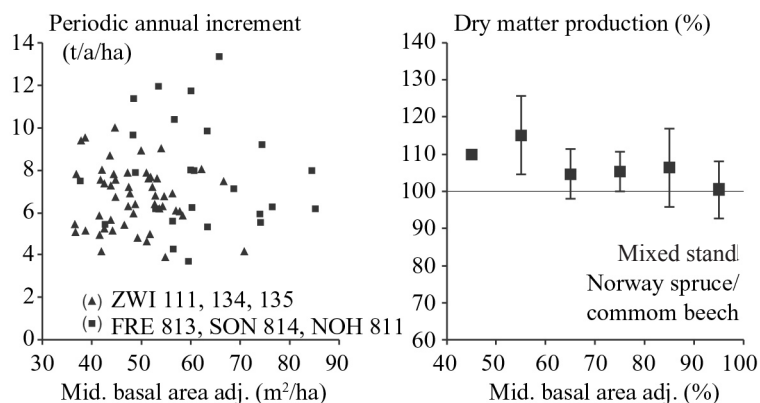

Fig. 4. Means and standard error of the periodic annual dry matter production (PAI) in relation to density for mixed spruce-beech stands Zwiesel 111, 134 and 135 and age series Freising 813, Schongau 814, Nordhalben 811. The dry matter production is represented in 10% steps for equal basal area densities in relation to unthinned plots (= 100% line)
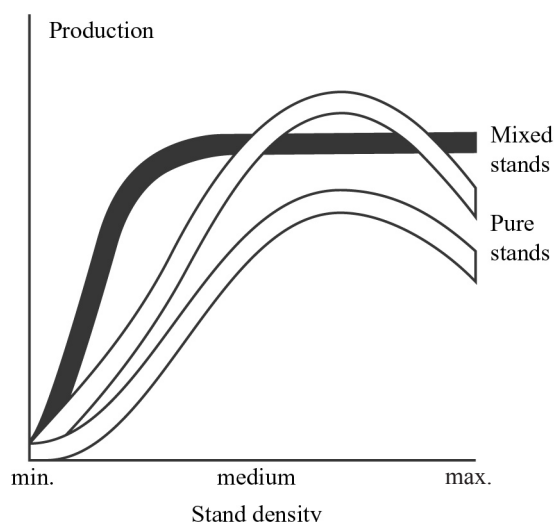
Fig. 5. Schematic representation of relationships between stand density and growth in pure and mixed stands. In mixed stands the density-growth relationship follows a saturation curve and an optimum curve in pure stands. This reflects the greater growth elasticity in mixed stands (black solid line) as compared with that in pure stands (white solid lines)

The results of this study shows that even though mixed stands may be inferior or equal in productivity under "normal" conditions they may develop superiority on account of their greater elasticity in the face of perturbation or non-treatment. In pure stands an optimum relationship exists between density and growth. For mixtures a saturation relationship was found to exist. This important relationship is schematically represented in Fig. 5. The mixture (dark solid line) is compared with two pure stands (white solid lines). The first case (upper line) assumes the production superiority of pure stands at average density versus mixture. Whenever density is reduced due to disturbances of some kind, pure stands will respond with considerable increment losses and become inferior. By contrast, growth in the mixed stand remains stable over a wide range of densities. In the second instance (lower line) the pure stand is less productive than the mixture, even under "normal" conditions. In this case, given positive or negative deviations from average density, e.g. on account of lack of treatment or

unplanned disruption of stand canopy, the stand becomes even more inferior.

Fifty years after ASSMANN's evaluation and a correspondingly longer observation period and with an even more comprehensive data material, the optimum relationship between stand density and growth can now be confirmed for Norway spruce and common beech in Central Europe and differentiated according to site conditions and tree species. The studied common beech stands behave according to the pattern described by ASSMANN (1970, pp. 232–233). The optimum curve is flatter on sites where there is sufficient water and nutrients and steeper where resources are scarce. The Norway spruce stands exhibit the opposite behaviour: on poor sites the optimum curve is flatter but steeper on favourable ones. This inverse behaviour in Norway spruce as compared to common beech is also reflected in all of 1,476 inventories of experimental areas which form the basis for the Norway spruce yield tables established by ASSMANN and FRANZ (1963, p. 25, Figs. 5 and 6). Here, good sites also show a steeper optimum curve, which is synonymous with greater growth losses with the approach to maximum density. There are less growth losses with approaching maximum density on poor sites. ASSMANN (1970) and MAR:MØLLER (1945) attribute the causes for growth losses with the approach to maximum density or for growth gains with decreasing density to the unfavourable relation between assimilation of carbon and respiration of trees subjected to competition.

The overlapping of different response patterns for Norway spruce and common beech leads to a considerably wider plateau in the density-growth relationship of mixed stands than for corresponding pure stands (Fig. 4). The broad saddle in the resultant curve looks similar to the much-discussed curve by LANGSAETER (1941, p. 173, Fig. 3). In contrast to the pure stands under study, the approach to maximum density causes merely a slight and statistically insignificant decrease in growth. The greater growth elasticity in mixed stands of Norway spruce and common beech is easily understood by taking a look at the complementary response patterns of Norway spruce and common beech to density and site conditions (Figs. 1 and 2). One tree species is able to compensate for potential losses in the other. MITSCHERLICH (1952) and PRETZSCH (1985) confirm that mixed stands of Norway spruce (*Pi-*
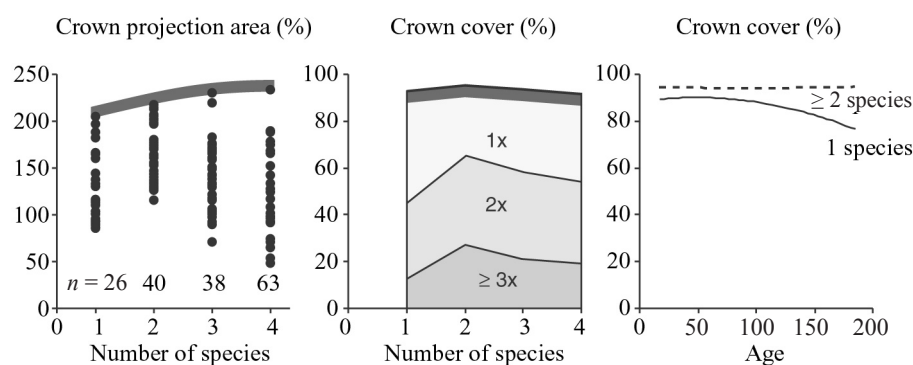

Fig. 6. Crown projection area and crown cover in dependence of species number and stand age. Left: Crown projection area increases with species number within the stand. Middle: Crown cover percent varies independently from species diversity between 90 and 95% but twice and threefold crown cover increases with diversity. Right: Crown projection area decreases with age in pure stands but remains stable if 2 or more species are mixed
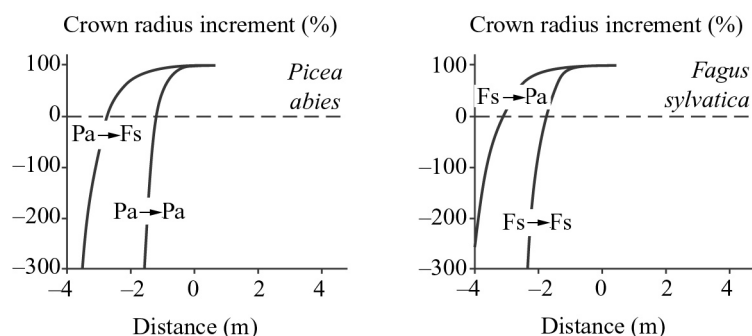
Fig. 7. Effect of distances between crowns on the relative crown radius increment for the species Norway spruce (*Picea abies* [L.] = Pa) and common beech (*Fagus sylvatica* L. = Fs) in pure and mixed stands. Left: Crown radius increment in spruce with spruce trees as next neighbours (Pa→Pa) and with beech trees as next neighbours (Pa→Fs). Right: Crown radius increment in beech with beech trees as next neighbours (Fs→Fs) and with spruce trees as next neighbours (Fs→Pa)

cea abies [L.] Karst.), silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.) are less sensitive to density variations.

From the experimental plots, which are under survey at the Chair of Forest Yield Science, Munich was taken a random sample of 167 plots to analyse their crown maps in respect to crown projection area and crown cover percent (PRETZSCH 2002, p. 221). As it is shown in Fig. 6 the maximum sum of crown coverage increases with increasing species diversity from 200% in monocultures to 240% in four-species stands (left, upper border line). However, the relation between covered and total ground area is mostly between 90 and 95 percent (middle). The twofold or multiple overlap occurs more often in mixed stands (middle). With increasing age, however, the covered ground area tends to decrease only in pure stands (right, solide line), whereas the multi-layer space sequestration in mixed stands ensures a stable coverage even if more and more trees are eliminated due to thinning or because of natural reasons (right, broken line). Besides higher ground coverage percentages, this also results in denser stands and higher growing stocks in old mixed stands compared to pure stands of the same age.

These findings at stand level are supported by analyses at individual tree level (PRETZSCH 2002, p. 287). Spruce and beech trees tend to interlock their crowns much more intensively in mixed than in pure stands. Fig. 7 demonstrates the relationship between distances between crowns and crown radius increment for the experimental areas Zwiesel 111, 134 and 135. The relative crown radius variations in relation to the distance of crowns from that of the nearest neighbour are plotted for both, spruce and beech. A 100 percent change of radius indicates that the tree shows the increment that is expected with no lateral crowding of the crown (potential crown radius increment). The response functions in Fig. 7 demonstrate the decrease in crown radius increment with increasing overlap of neighbouring crowns (from the zero value at the *x*-axis to the left). The different response curves represent different neighbourhood situations between Norway spruce (*Picea abies* L. = Pa) and common beech (*Fagus sylvatica* L. = Fs). From these curves it is apparent that much more overlap occurs in mixed stands (Pa→Fs and Fs→Pa) than in pure stands (Pa→Pa and Fs→Fs), and that the same overlap leads to much less decrease in growth. Hence it can be assumed

that space sequestration is much more effective in mixed stands (PETRI 1966).

CONCLUSION

The combination of several species is synonymous with a distribution of risks. As a rule mixed stands are more elastic in their response to changing site conditions and show greater resilience in the face of natural losses or calamities. The productivity relationship between pure and mixed stands under "normal" conditions may shift considerably once risks are included. The decisive factor here, in essence, is the probability of the occurrence of disturbances and damages. The temporarily dazzling productivity superiority of artificial pure stands is often reversed and turns into inferiority if disturbances are included in the calculation. Mixtures can get over interruptions and of the crown space by windthrow, storm damages or biotic calamities, equivalent to an abrupt reduction in stand density from medium to lower level, without greater losses in growth.
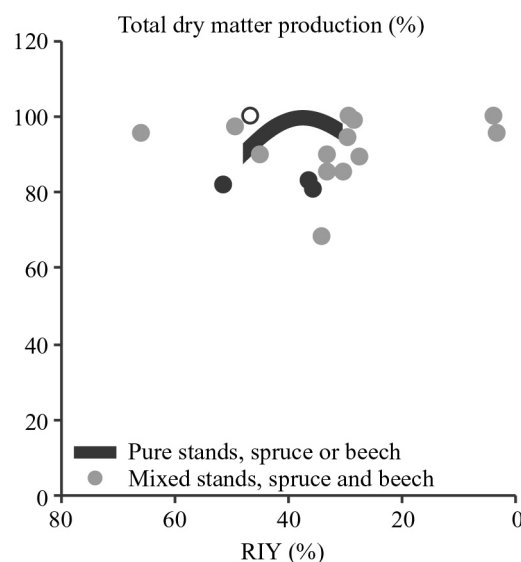

Fig. 8. Relationship between percentage of intermediate fellings (RIY) and the total stem dry matter production in pure stands (black optimum curve) and mixed stands of Norway spruce and common beech (points)

The higher elasticity of growth in mixed stands of spruce and beech is reflected by Fig. 8. It shows the relation between the percentage of intermediate fellings RIY and total stem matter production. Base are the survey results from the mixed plots ZWI 111, 134, 135 (dots) and the long-term plots in pure stands of spruce and beech (black line). The figure emphasises an important consequence for forest management. The total dry mass stem production of the investigated pure forests is expected to occur if approximately 40 percent of total yield are removed regularly from the stand by moderate thinning prior to final harvest or due to natural reasons. Total production is expected to decrease with both, higher or lower RIY than 40%. Actually, in the analysed pure stands RIY is found to be between 30 and 50 percent which is in close distance from the maximum. In contrast, RIY of the investigated mixed stands varies between 10 and 70 percent without any systematic effect on total dry mass stem production. This means that intensive thinning or disturbances that result in percentage of intermediate yield RIY = 50–70% can be compensated in mixed stands but not in pure stands by increasing growth of the remaining individuals. Also under discontinued silvicultural treatment or self-thinning (RIY = 10–30%) mixed stands are more stable in total dry matter production while pure stands show a significant decrease. The revealed feature represents an important immanent advantage of mixed stands of spruce and beech compared to pure forests.

Of course, the above relationships for dry biomass production alone do not justify decisions in favour of pure or mixed stand establishment or a certain stocking density. The outcome of such decisions could be quite different, depending on overall conditions and ultimate objectives, for example if the major aim were quantity (e.g. pulp, fuelwood, C-storage), quality (e.g. structural wood or veneer), or safety and risk prevention (stabilisation against storms or erosion control). However, if we recall that a suitable mixture may raise dry biomass production by up to 30% and, moreover, ensures that other forest functions are fulfilled, then the above yield relationships may become the key factor controlling the decisions.

In comparison with annual systems the lifespan of forests is two decimal powers longer and the danger from risks consequently much greater. Added to which cyclic disturbances through silvicultural treatment also take their toll. It is for this reason that the risk distribution in forests achieved in mixtures carries so much more weight than in short-lived ecosystems. Risk distribution through tree species diversity, however, need not necessarily imply a mixture of tree species. This is because the desired diversification could also be achieved by a mosaic of spatially separated pure stands of these species. Through this kind of species separation even likely unfavourable effects from species interaction and the greater efforts required to treat species mixtures could be avoided. The beneficial mixture effects of up to 30%, the greater elasticity against disturbances and savings in stand establishment costs in case of total loss of one species cannot be taken advantage of, though, unless species are closely mixed.

The consequences of the presented relation between density and growth in pure and mixed stands can be viewed best by examining windthrow damages, which are the most important disturbances of forest growth in Central Europe. In 1990, damages in southern Germany by means of heavy storms were 4–5 fold higher in spruce than in beech stands. Extensive research by LÜPKE and SPELLMANN (1999) showed that resistance against windthrow was not altered in stands were beech was accompanied with spruce. Thus, increased stability against this kind of damage is achieved only by the replacement of spruces by beeches, which usually have deeper root systems and less above ground resistance. No benefit for individual spruce trees could be derived from the mixture with beech. However, the ability to compensate growth losses from removed trees clearly increases with increasing admixture of beech. This demonstrates the faster feedback reaction between disturbance and growth increase, which is caused by a more even space sequestration and possibly also by the higher crown shape flexibility of beech. Windthrow damages reduce the stand density and activate the feedback loop 'stand structure → resource availability → growth → stand structure'. The reduction of standing volume by the disturbance means a shift of the stand density to the left in Figs. 5 and 8 with immediate negative effects on growth in pure stands and a buffered and slighter growth reaction in mixed stands.

SUMMARY

The focus is on the growth reaction pattern of pure and mixed stands of Norway spruce and common beech below or above medium stand density, caused e. g. by disturbances, heavy or postponed thinning. The analyses of the density-growth relationship in pure stands is based on 9 long-term thinning experiments in pure stands of Norway spruce, respectively 10 experiments in pure stands of common beech in Middle and South Germany. The investigation in mixed stands of Norway spruce and common beech are based on age series with 20 experiments and 60 plots located in South and East Bavaria. Furthermore 3 long-term experiments in the Bavarian Forest were included. The oldest of these experiments are maintained and remeasured since 1870 regularly by the Chair for Forest Yield Science, Munich University. Table 1 summarises species composition, silvicultural treatment, number of experiments and plots, survey period, age span and site class.

For selected spruce and beech thinning plots Figs. 1 and 2 show the development of the density-growth relationship from the start of the experiment in the years 1870 to 1907 up to the very last survey. In most periods an optimum relationship between density and growth is apparent. The periodic annual increment (PAI) increases from the C grade (heavy thinning) to the B grade (moderate thinning) and then decreases in the transition to grade A

(light thinning). This response patterns is valid for about 90% of the surveyed periods. Fig. 3 represents the cumulative volume for the entire range of B and C grade plots in relation to grade A (= 100% line). It is remarkable that in all cases cumulative volume rose by 5–10% with the transition from grade A to B. This increase is more pronounced at middle rather than at more advanced age. The transition from grade B to C reveals a reduction in volume production. For the majority of experimental plots, volume production for the C grade is however still higher than for the A grade. The relationship between density and growth therefore represents an optimum curve. For Norway spruce the optimum is more pronounced on good sites than on unfavourable ones, whereas the inverse situation for common beech is observed.

In mixed stands the relationship between density and increment is fundamentally different from the corresponding pattern in pure stands (Fig. 4). Obviously, mixed stands are able to largely compensate for density reductions due to thinning by increased growth within the remaining stand. Within the observed density spectrum of 40–100%, increment does not decrease significantly despite a 60% reduction in stand density. It can also be observed that there is no significant decrease in growth when maximum density is approached, except perhaps a non-significant tendency towards a decline (Fig. 5).

The greater elasticity of growth against a reduction in stand density can be attributed to the multi-layer stand structure in mixed stands. Spruce and beech trees tend to interlock their crowns much more intensively in mixed than in pure stands. As it is shown in Fig. 6 for 167 lightly to heavily thinned plots in general, the sum of crown coverage increases with increasing species diversity from 200% in single-species stands to 240% in four-species stands (left, upper border line). However, the relation between covered and total ground area is mostly between 90 and 95% (middle). The twofold or multiple overlap occurs more often in mixed stands (middle). With increasing age, however, the covered ground area tends to decrease only in pure stands, whereas mixed stands ensure a stable coverage even if more and more trees are eliminated due to thinning or because of natural reasons (right). Fig. 7 demonstrates the relationship between distances between crowns and crown radius increment for the long-term experiments in mixed stands. Any positive or negative deviations from average stand density, e.g. on account of lack of treatment or unplanned disruption of stand canopy, could be more easily buffered in mixed stands. Mixtures can recuperate from this kind of disturbance, equivalent to an abrupt reduction in stand density from medium to lower level, without significant growth losses. This greater growth elasticity is the cause of the plateau-shaped density-growth curve (Fig. 8). In comparison with annual systems the lifespan of forests is two magnitudes longer and the danger from risks consequently much greater than in short-lived ecosystems. It is for this reason that the greater elasticity of growth may become the key factor controlling silvicultural decisions.

References

ASSMANN E., 1953. Bestockungsdichte und Holzerzeugung. Forstw. Cbl., *72*: 69–101.

ASSMANN E., 1956. Natürlicher Bestockungsgrad und Zuwachs. Forstw. Cbl., *75*: 257–265.

ASSMANN E., 1970. The Principles of Forest Yield Study. Oxford, New York, Toronto, Sydney, Braunschweig, Pergamon Press Ltd.: 507.

ASSMANN E., FRANZ F., 1963. Vorläufige Fichten-Ertragstafel für Bayern. München, Institut für Ertragskunde der Forstl. Forschungsanst.: 104.

AVERY T.E., BURKHART H.E., 2002. Forest Measurements. Fifth edition. New York, McGraw-Hill: 456.

BURGER H., 1941. Beitrag zur Frage der reinen oder gemischten Bestände. Mitt. der Schweiz. Anst. F. d. Forstl. Versuchsw., *XXII*: 164–203.

CANNELL M.G.R., MALCOM D.C., ROBERTSON P.A., 1992. The Ecology of Mixed-Species Stands of Trees. Oxford, Blackwell Scientific Publications: 312.

CASPERSEN J.P., PACALA S.W., 2001. Successional diversity and forest ecosystem function. Ecol. Res., *16*: 895–903.

COTTA H., 1828. Anweisung zum Waldbau. Dresden, Leipzig, Arnoldische Buchhandlung: 413.

FOERSTER W., 1993. Der Buchen-Durchforstungsversuch Mittelsinn 025. Allg. Forstz., *48*: 268–270.

FRANZ F., BACHLER J., DECKELMANN B., KENNEL E., KENNEL R., SCHMIDT A., WOTSCHIKOWSKY U., 1973. Bayerische Waldinventur 1970/71. Inventurabschnitt I: Großrauminventur Aufnahme- und Auswertverfahren. München, Forstliche Forschungsberichte, *11*: 143.

FRANZ F., RÖHLE H., MEYER F., 1993. Wachstumsgang und Ertragsleistung der Buche. Allg. Forstz., *48*: 262–267.

HARTIG G.L., 1791. Anweisung zur Holzzucht für Förster. Marburg, Neue Akademische Buchhandlung: 144.

JOHANN K., 1993. DESER-Norm 1993. Normen der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten zur Aufbereitung von waldwachstumskundlichen Dauerversuchen. Tagungsbericht von der Jahrestagung 1993 der Sektion Ertragskunde im Deutschen Verband Forstlicher Forschungsanstalten in Unterreichenbach-Kapfenhardt: 96–104.

KELTY M.J., 1992. Comparative productivity of monocultures and mixed stands. In: KELTY M.J., LARSON B.C., OLIVER C.D. (eds.), The Ecology and Silviculture of Mixed-species Forests. Dordrecht, Kluwer Academic Publishers: 125–141.

KENNEL R., 1965. Untersuchungen über die Leistung von Fichte und Buche im Rein- und Mischbestand. Allg. Forst-Jagdztg, *136*: 149–161, 173–189.

KENNEL R., 1972. Die Buchendurchforstungsversuche in Bayern von 1870 bis 1970. Mit dem Modell einer Strukturertragstafel für die Buche. München, Forstliche Forschungsberichte, *7*: 264.

KRAMER H., 1988. Waldwachstumslehre. Hamburg, Berlin, Verlag Paul Parey: 374.

LANGSAETER A., 1941. Om tynning i enaldret gran- og furuskog Maddel. Det Norske Skogforoksvesen, *8*:131–216.

LÜPKE B. VON, SPELLMANN H., 1999. Aspects of stability, growth and natural regeneration in mixed Norway spruce-beech

stands as a basis of silvicultural decisions. In: OLSTHOORN A.F.M., BARTELINK H.H., GARDINER J.J., PRETZSCH H., HEKHUIS H.J., FRANC A. (eds.), Management of Mixed-species Forest: Silviculture and Economics. Wageningen, IBN Scientific Contributions, *15*: 245–267.

MAR:MØLLER C., 1945. Untersuchungen über Laubmenge, Stoffverlust und Stoffproduktion des Waldes. Kopenhagen, Kandrup und Wunsch: 287.

MITSCHERLICH G., 1952. Der Tannen-Fichten-(Buchen)-Plenterwald. Freiburg im Breisgau, Schriftenreihe der Badischen Forstlichen Versuchsanstalt, *8*: 1–42.

MÖLLER A., 1922. Der Dauerwaldgedanke. Sein Sinn und seine Bedeutung. Berlin, Verlag Julius Springer: 84.

MOOSMAYER H.U., 1957. Zur ertragskundlichen Auswertung der Standortsgliederung im Ostteil der Schwäbischen Alp. Mitt. Ver. Forstl. Standortskart., *4*: 52–60.

OLSTHOORN A.F.M., BARTELINK H.H., GARDINER J.J., PRETZSCH H., HEKHUIS H.J., FRANC A. (eds.), 1999. Management of Mixed-species Forest: Silviculture and Economics. Wageningen, IBN Scientific Contributions, *15*: 389.

PETRI H., 1966. Versuch einer standortgerechten, waldbaulichen und wirtschaftlichen Standraumregelung von Buchen-Fichten-Mischbeständen. Mitt. a. d. Landesforstverw. Rhld.-Pfalz, zugleich Mitt. a. d. Koblenz, *13*: 145.

PRETZSCH H., 1985. Die Fichten-Tannen-Buchen-Plenterwaldversuche in den ostbayerischen Forstämtern Freyung und Bodenmais. Forstarchiv, *56*: 3–9.

PRETZSCH H., 1992. Konzeption und Konstruktion von Wuchsmodellen für Rein- und Mischbestände. München, Forstl. Forschungsber., *115*: 358.

PRETZSCH H., 2002. Grundlagen der Waldwachstumsforschung. Blackwell: 414.

PRETZSCH H., 2003. Diversität und Produktivität von Wäldern. Allg. Forst- Jagdztg, *174*: 88–98.

PRETZSCH H., KAHN M., GROTE R., 1998. Die Fichten--Buchen-Mischbestände des Sonderforschungsbereiches „Wachstum oder Parasitenabwehr?“ im Kranzberger Forst. Forstw. Cbl., *117*: 241–257.

REINEKE L.H., 1933. Perfecting A Stand-Density Index for Even-Aged Forests. J. Agric. Res., *46*: 627–638.

RÖHLE H., 1994. Zum Wachstum der Fichte auf Hochleistungsstandorten in Südbayern. Ertragskundliche Auswertung langfristig beobachteter Versuchsreihen unter besonderer Berücksichtigung von Trendänderungen im Wuchsverhalten. [Habilitationsschrift.] Universität München, Forstwissenschaftliche Fakultät: 249.

ROTHE A., 1997. Einfluß des Baumartenanteils auf Durchwurzelung, Wasserhaushalt, Stoffhaushalt und Zuwachsleistung eines Fichten-Buchen-Mischbestandes am Standort Höglwald. München, Forstl. Forschungsber., *163*: 213.

SCHOBER R., 1972. Die Rotbuche 1971. Frankfurt a. Main, J.D. Sauerländer's Verlag, Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt 43/44: 333.

VEREIN DEUTSCHER FORSTLICHER VERSUCHSANSTALTEN, 1902. Beratungen der vom Vereine Deutscher Forstlicher Versuchsanstalten eingesetzten Kommission zur Feststellung des neuen Arbeitsplanes für Durchforstungs- und Lichtungsversuche. Allg. Forst- Jagdztg, *78*: 180–184.

WIEDEMANN E., 1942. Der gleichaltrige Fichten-Buchen--Mischbestand. Mitt. Forstwirtsch. u. Forstwiss, *13*: 88.

WIEDEMANN E., 1951. Ertragskundliche und waldbauliche Grundlagen der Forstwirtschaft. Frankfurt, J. D. Sauerländer's Verlag: 346.

ZEIDE B., 2003. Undisturbed stand density: A benchmark for damage assessment. Trees (in print).

Pružnost růstu v nesmíšených a smíšených porostech smrku ztepilého (*Picea abies* [L.] Karst.) a buku lesního (*Fagus sylvatica* L.)

H. PRETZSCH

Technická univerzita Mnichov, Fakulta lesnických věd a řízení zdrojů, Německá spolková republika

ABSTRAKT: Studie ukazuje, že růst smíšených porostů smrku ztepilého (*Picea abies* [L.] Karst.) a buku lesního (*Fagus sylvatica* L.) je vyrovnanější i při různé hustotě porostu, než je tomu v nesmíšených porostech příslušných druhů. Typické příklady vztahů mezi hustotou a růstem vycházejí ze 42 dlouhodobých pokusů na celkem 134 plochách, přičemž nejstarší je sledována již od roku 1870. Z výsledků je zřejmé, že v čistých porostech lze dosáhnout maximálního růstu pouze při střední hustotě porostu, zatímco ve smíšených porostech se růst při nízké, střední ani vysoké hustotě porostu téměř nemění. Poznatek, že smíšené porosty mohou vykazovat větší růst než čisté porosty bez ohledu na snížení či zvýšení hustoty porostu, se často přehlíží, ačkoliv má značný praktický význam.

Klíčová slova: pružnost růstu; vztah mezi hustotou a růstem; míra rizika; diverzita; produktivita; nesmíšené a smíšené porosty

Hlavní pozornost je věnována modelu reakcí růstu v nesmíšených a smíšených porostech smrku ztepilého a buku lesního při nižší či naopak vyšší hustotě porostu, způsobené např. nahodilými jevy, silným nebo pozdním výchovným zásahem. Analýzy vztahu mezi hustotou a růstem v nesmíšených porostech jsou založeny na devíti dlouhodobých probírkových pokusech v čistých smrkových porostech a 10 pokusech v čistých porostech buku lesního ve středním a jižním Německu. Výzkum smíšených porostů smrku ztepilého a buku lesního je založen na věkových řadách s 20 experimenty na 60 plochách v jižním a východním Bavorsku. Navíc byla zahrnuta i tři dlouhodobá šetření v Bavorském lese. Nejstarší z těchto pokusů se pravidelně provádějí a měří od roku 1870 na katedře nauky o produkci lesa Technické univerzity v Mnichově.

Tab. 1 shrnuje dřevinnou skladbu, pěstební zásahy, počet pokusů a ploch, sledované období, věkové rozpětí a bonitu stanoviště. Obr. 1 a 2 se týkají vybraných probírkových pokusů smrku a buku a ukazují vývoj vztahu hustota – růst od prvopočátku experimentu v letech 1870–1907 až k poslednímu šetření. Ve většině period existuje zřetelný vztah mezi hustotou a růstem. Průměrný periodický roční přírůst (PAI) se zvyšuje od stupně C (silná probírka) ke stupni B (mírná probírka) a pak se snižuje při přechodu ke stupni A (slabá probírka). Tento model platí pro zhruba 90 % sledovaných období. Obr. 3 představuje kumulativní objem pro celý rozsah ploch stupně B a C ve vztahu ke stupni A (= hranice 100 %). Je pozoruhodné, že ve všech případech stoupl kumulativní objem o 5–10 % při přechodu ze stupně A do B. Tento přírůst je zřetelnější ve středním spíše než ve vyšším věku porostu. Přechod od stupně B k C znamená snížení objemové produkce. Na většině pokusných ploch je však objemová produkce u stupně C vyšší než u stupně A. Vztah mezi hustotou a růstem tedy představuje optimální křivku. U smrku ztepilého je optimum výraznější na dobrých stanovištích než na stanovištích nevhodných, zatímco u buku je situace opačná.

Ve smíšených porostech je vztah mezi hustotou a přírůstem zásadně odlišný od příslušných modelů v nesmíšených porostech (obr. 4). Smíšené porosty jsou pochopitelně schopné do značné míry kompenzovat snížení hustoty probírkou zvýšeným růstem hlavního porostu. V rámci sledovaného spektra hustoty porostu od 40 do 100 % nepoklesl přírůst nijak významně, a to ani v případě 60% snížení hustoty porostu. Lze rovněž konstatovat, že růst významně neklesá ani tehdy, blíží-li se hustota maximu; pouze vykazuje nepatrnou tendenci k poklesu (obr. 5).

Větší pružnost růstu ve vztahu ke snížení hustoty porostu lze přisuzovat víceetážové porostní struktuře smíšených porostů. Koruny smrků a buků mají tendenci vzájemně prorůstat daleko intenzivněji ve smíšených než v nesmíšených porostech. Jak ukazuje obr. 6, který obecně znázorňuje 167 ploch se slabou až silnou probírkou, suma plošných průmětů korun se zvyšuje s rostoucí druhovou bohatostí od 200 % v jednodruhových porostech až k 240 % u čtyřdruhových porostů (vlevo, horní hranice). Nicméně poměr mezi korunami pokrytou a celkovou plochou porostu se většinou pohybuje mezi 90–95 % (uprostřed). Dvouetážový nebo víceetážový překryv se objevuje mnohem častěji ve smíšených porostech (uprostřed). Se vzrůstajícím věkem má však plocha porostu krytá korunami tendenci se snižovat pouze v čistých porostech, zatímco ve smíšených porostech se pokrytí nemění, přestože se stále zvyšuje množství odstraněných stromů probírkou nebo v důsledku přírodních faktorů (vpravo). Obr. 7 ukazuje vztah vzdálenosti mezi korunami a přírůstem průměru koruny v dlouhodobých experimentech prováděných ve smíšených porostech. Jakékoli kladné i záporné odchylky od průměrné hustoty porostu, způsobené např. nedostatečnou péčí nebo neplánovaným narušením porostního zápoje, se ve smíšených porostech snáze vyrovnají. Smíšené porosty snáze překonají takový zásah, jakým může být výrazný pokles hustoty porostu z průměrné na nižší úroveň bez významného snížení růstu. Díky této větší růstové pružnosti je křivka poměru hustoty a růstu vyrovnaná (obr. 8). Ve srovnání s ročními systémy je délka života lesů o dva řády vyšší a riziko je tedy mnohem větší než u krátkodobých ekosystémů. Právě z tohoto důvodu se větší pružnost růstu může stát klíčovým faktorem, který ovlivňuje pěstební rozhodování.

Corresponding author:

Prof. Dr. Hans Pretzsch, Chair for Forest Yield Science, Faculty of Forest Science and Resource Management, Technical University of Munich, Am Hochanger 13, D-85354 Freising, Germany
tel.: + 49 8161 714 710, fax: + 49 8161 714 721, e-mail: H.Pretzsch@lrz.tum.de