3 Diversity and Productivity in Forests: Evidence from Long-Term Experimental Plots

H. Pretzsch

3.1 Introduction: The Mixed Stands Issue – A Central European Perspective

At the beginning of regular forest management and systematic forestry sciences the primary objective was sustainable timber production. The sustainability principle, originally conceived by von Carlowitz (1713), served both Hartig (1791, 1804) and von Cotta (1828) as the basis from which they proceeded to develop methods for the sustainable management of forest enterprises. The main focus at the time was the sustainable production of timber. Attention was also called to diversity, protective, and recreational functions, inter alia, by von Hagen (1867), but none of these elements were included in the rules and regulations on sustainable planning. There was a widespread belief that, in the wake of sustainable timber production, all other forest functions would be automatically fulfilled. It was not until Dieterich's forest-functions theory was publicized (1957) that forests began to be discussed as habitats and recreational areas, with functions such as the protection of climate, soil, and water. Today, there is international consensus that the multiple function of forests includes protection of forest resources, health and vitality of forest ecosystems, production of wood and other forest products, biological diversity, and protective and socioeconomic functions (MCPFE 2000). The sustainability of biodiversity is becoming an imperative, similar to the sustainability of timber production in the past. Yet, what is the relationship between biodiversity and productivity? In the following we shall concentrate on how tree species' diversity and forest productivity are interrelated, a question of particular relevance to forestry practice.

   Hartig, considered the forefather of forestry science, commented on the mixed stands issue as follows (Hartig 1791, p. 134): "...the mixing of deciduous and coniferous species is not advantageous, as the coniferous trees generally tend to supplant deciduous ones and because one type of tree impedes the growth of the other; so that no mixed deciduous and coniferous forests

should be established with intent" (translation by the author = t. by a.). Concerned about serious production losses in mixed stands, Hartig (1804, p. 40) recommended: "All mixed stands with coniferous and deciduous species should be converted into pure stands of the constituent species, as soon as circumstances permit" (t. by a.). This was contradicted by von Cotta (1828, p. 115): "Endeavours to establish pure stands everywhere is based on an old and highly detrimental prejudice.... Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also, a wider range of timber will be available everywhere to satisfy different demands..." (t. by a.). This opinion was supported by Gayer (1886, p. 31): "The mixed forest does not only produce more, but also more valuable commercial timber than that grown in pure stands" (t. by a.). Statements by Möller (1922, pp. 41–42) are even more optimistic: "...if we design stands of shade-intolerant and shade-tolerant tree species, ...the potential for timber production is raised even more; the reason being that it is now possible to go considerably farther in the stratification of age classes than in the design of pure stands with only a single layer" (t. by a.). Wiedemann, a professional yield scientist, dampens the optimism voiced by the above silviculturists (Wiedemann 1951, p. 341) saying "...even in silviculture, room must be given to hard facts next to emotions" (t. by a.). It was not until data was evaluated from long-term experiments, under observation in many European countries since the founding of the Forestry Research Stations in 1870 to 1880, that a clearer picture was conveyed of the productivity in pure and mixed stands that differentiated between species and sites.

First evaluations of long-term experimental plots put a damper on hopes for increased yield through mixture. The reason for this was their revelation of far greater productivity in monocultures of Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) on many sites in temperate and boreal zones than in any mixture (Schwappach 1912; Wiedemann 1949; Assmann 1970; Schober 1975). Whenever the primary objective is to maximize dry biomass production, then in many places there is no alternative to pure stands of these species. Similar advantages of monospecific stands were noted for *Pinus* species in Mediterranean and for *Eucalyptus* as well as *Albizia* species in subtropical and tropical climate zones (Weck 1955; Kelty 1992).

By contrast, in grassland ecosystems, most studies found evidence for a logarithmic rise in productivity with increasing numbers of species (e.g., Hector et al. 1999; Loreau et al. 2001), as also reported for North American forests (Caspersen and Pacala 2001). According to these authors, production gains are most obvious when monocultures and two-species mixtures are compared. In this chapter, we therefore concentrate on pure stands and mixed stands composed of two species. Such two-species mixtures, especially those mixed by groups, are predominant in mixed forests (Bartelink and Olsthoorn

1999) and have been scientifically studied more intensively than any others (Kelty 1992).

I summarize some results from mixed-stand experimental plots in my network of permanent plots, and outcomes of other mixed-stand experiments reported in the literature in order to quantify the extent of increased or reduced productivity in mixed stands and to identify corresponding causes. Going beyond the studies of Cannell et al. (1992), Kelty (1992), and Olsthoorn et al. (1999), I present the following new aspects: first, suitable approaches and measures for productivity comparisons will be introduced; second, benchmarks for productivity increases or decreases for commercially important tree species in temperate and boreal zones will be derived. Then I will explore the relationships between productivity in pure and mixed stands as a function of species and site conditions. The decisive factor is to include stand management and risk in the yield comparison.

The chapter incorporates results of the long-term experimental network, surveyed by the Chair of Forest Yield Science of the Technical University of Munich. This network involves experiments in pure and mixed stands that are unique as far as observation time, sampling volume, and spectrum of silvicultural treatment methods are concerned (Pretzsch 2002, pp. 133–138).

3.2 Theoretical Considerations

3.2.1 Ecological Niche, Site–Growth Relationships

Considerations on the productivity $p_{1,2}$ of a mixed stand composed of two species usually refer to the productivity p_1 or p_2 of corresponding pure stands on the same site. Given species interaction without synergistic effects on growth the productivity $p_{1,2}$ of a mixed stand is represented as pure stand's growth weighted with the mixture proportions m_1 and m_2, i.e., $p_{1,2}=m_1\,p_1+m_2\,p_2$. The crucial factors for results from mixtures are the ecological niches of the species and their compatibilities, since this is what determines productivity on any given site. Beneficial effects from species interactions that enhance yield of a mixed stand are of particular interest in this context. The chances for an enhancement of biomass production by mixture depend on the relationship between p_1 and p_2 and on potential beneficial mixture effects.

The relationships will be explained using two model examples composed of species occupying similar and different ecological niches (Fig. 3.1a, b). The unimodal dose–response curves represent the different niches inasmuch as they reflect the dependence of productivity on growth conditions typical of the species. For simplicity's sake growth conditions on this graph are plotted
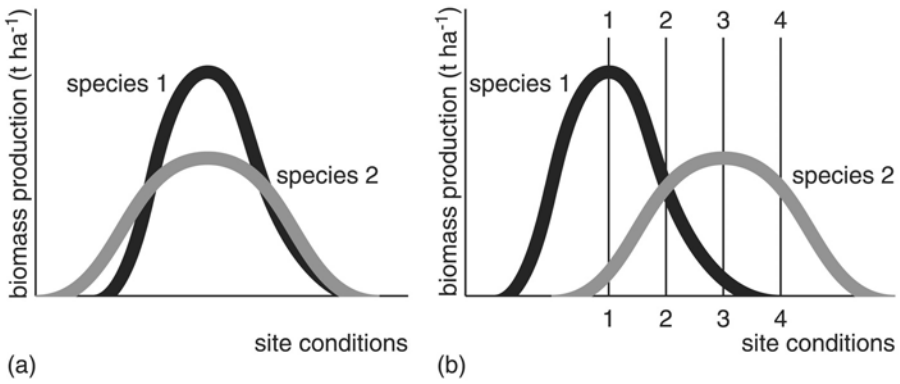
Fig. 3.1a, b. Dry biomass production of various tree species in relation to site conditions. **a** Productivity of two tree species with similar ecological amplitude but different levels of production. **b** Productivity of two tree species with different ecological amplitudes. *Numbers 1* to *4* below the abscissa represent different site conditions to which species 1 and 2 show different growth responses (cf. Fig. 3.2)

using one dimension only and are composed of the n-dimensional vector of environmental factors (e.g., temperature, pH of the soil, storm–snow load) and availability of resources (e.g., irradiation, water, nutrient supply, atmospheric carbon dioxide, etc.).

In the first case (Fig. 3.1a), the tree species 1 and 2 occupy similar ecological niches, but they differ clearly in growth yield on the given site. Productivities p_1 and p_2 for the superior and inferior tree species, respectively, vary to the extent that in these instances the addition of the inferior tree species will usually cause a reduction in stand productivity. Examples of this are the superiority of Douglas fir (*Pseudotsuga menziesii*) over Scots pine (*Pinus sylvestris*) or of red oak (*Quercus rubra*) over common oak (*Quercus petraea*) through a wide range in ecological amplitude for these species. Both examples compare an indigenous with a foreign species; corresponding examples for two indigenous species can be hardly found.

Relationships become more complicated if the species in the mixture occupy distinctly different niches (Fig. 3.1b). Let us assume species 1 and 2 are mixed in stands on four different sites (site conditions 1 to 4). Depending on site conditions yield relationships will consequently vary considerably. On site 1, optimal for species 1, the addition of species 2, inferior on this site, will become a burden. On site 2, well suited to both species, productivity is in balance. On site 3, optimal for species 2, the inferior species 1 will have a slowing-down effect on growth. Examples from practice demonstrating this kind of inferiority are a mix of common beech (*Fagus sylvatica*) and common oak (*Quercus petraea*) stands on fresh calcareous sites, or of Norway spruce (*Picea abies*) and common beech (*Fagus sylvatica*) stands on acidic, cool, and moist
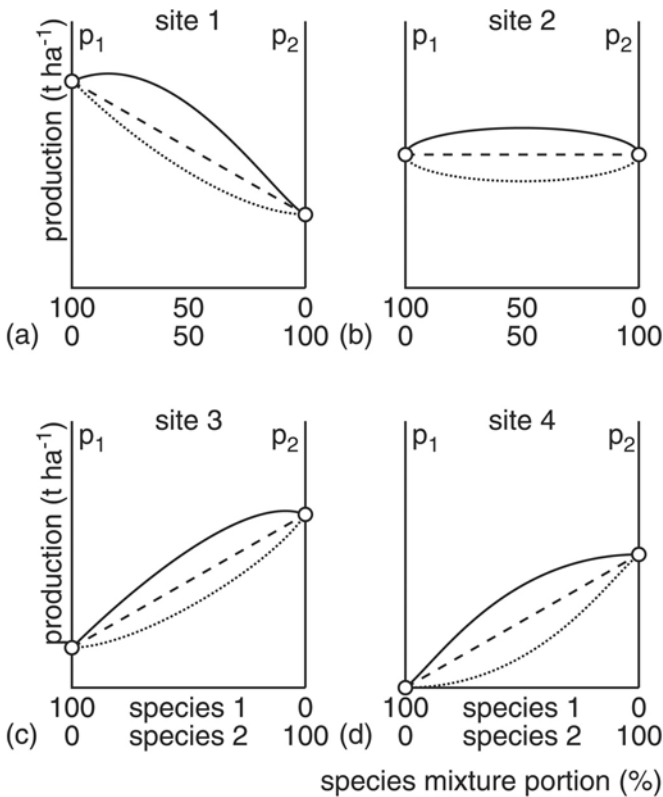
Fig. 3.2a–d. Dry biomass production for two species in pure and mixed stands under different site conditions 1 to 4 (cf. Fig. 3.1). Dry biomass productivities p_1 and p_2 of species 1 and 2 are shown for pure stands (*left* and *right ordinate*, respectively). The *connecting lines* show expected values for productivity $p_{1,2}$ in the mixture for different mixture proportions. The *linear connecting lines* (*dashed*) represent no interaction effects between species 1 and 2, the *continuous* and *dotted lines* reflect positive and negative effects from the species mixture, respectively

sites. In the first case, it is common oak, and in the second common beech that can only be sustained by silvicultural treatment. On site 4 species 1 will disappear sooner or later, while species 2 will achieve good productivity. Figure 3.2a–d depicts productivities p_1 and p_2 of species 1 and 2, respectively, on sites 1 to 4. The right-hand and left-hand ordinates plot productivities for species 1 and 2 in pure stands, the abscissa the mixture proportion. For sites 1 to 4 the resultant relationships are $p_1>p_2$, $p_1=p_2$, $p_1<p_2$, and $p_1<p_2$ with $p_1=0$, respectively. The example explains why the site-related productivity relationships diverge and serves to warn against generalizing results obtained from a limited spectrum of site conditions. If the mixed species don't interact at all or if mixture effects on growth cancel each other, productivity $p_{1,2}$ in the mixed

stand will lie on the straight reference line between p_1 and p_2 (dashed lines). In this case, an increase in the mixture portion would be reflected in a proportional increase of $p_{1,2}$.

3.2.2 Quantification of Effects from Species Interactions

If growth deviates positively or negatively from this straight reference line (convex and concave curves in Fig. 3.2, respectively), this is indicative of species interaction that will either increase or reduce productivity. Of special interest are positive deviations and their causes. Kelty (1992) distinguishes between "competitive reduction" (i.e., two or more species have reduced competition in mixture compared to pure stands, and they use the resources more efficiently) and "facilitation" (i.e., in mixture one species affects positively the growth of another species).

Misunderstandings frequently arise from the fact that *relative* superiority of productivity is frequently confused with *absolute* superiority. We adapt the term "overyielding" from agricultural science and population biology, and define relative and absolute superiority of mixed stands over the monoculture "non-transgressive" and "transgressive" overyielding, respectively (Hector et al. 2002).

Productivity superiority of the mixture versus the pure stand is *relative* if species 1 and 2 of the mixture together produce more than each constituent species on comparable pure stands of identical size, such that $p_{1,2} > m_1 p_1 + m_2 p_2$ (= non-transgressive overyielding). The percent relative superiority or inferiority in productivity is calculated from $\Delta p_{rel} = [p_{1,2}/(m_1 p_1 + m_2 p_2) - 1] \cdot 100$, where p_1 and p_2 equal productivity of species 1 and 2 in the pure stand, respectively, $p_{1,2}$ that of the two species in mixture, m_1 and m_2 are the proportions of species 1 and 2 in the mixed stand, calculated for instance from the proportions of dry biomass for both species (w_1 and w_2) in the mixed stand: $m_1 = w_1/(w_1 + w_2)$ and $m_2 = w_2/(w_1 + w_2)$, respectively. In Fig. 3.2 the solid convex (as seen from below) lines represent beneficial interaction effects, while the dotted concave lines stand for negative interaction effects through mixture. Which of the component species is favored or suppressed can be determined by analogy. Growth of species p_1 measured in the pure stand is compared with that in the mixture $p_{1,(2)}$. If, as in the case of the European larch and Norway spruce mixture (cf. Fig. 3.6 c), the result is $p_{1,(2)} > m_1 p_1$ and $p_{(1),2} > m_2 p_2$, this would indicate favorable mixture effects from which both tree species benefit.

We use the term *absolute* superiority of the mixed stand over the pure stand (transgressive overyielding) where $p_{1,2} > \max (p_1, p_2)$. We are dealing with absolute inferiority where $p_{1,2} < \min (p_1, p_2)$. Stand production thus lies above or below that for pure stands for species 1 and 2. For absolute superiority and inferiority we therefore use the expressions $\Delta p_{abs} = [p_{1,2}/\max(p_1, p_2) - 1] \cdot 100$ and $\Delta p_{abs} = [p_{1,2}/\min(p_1, p_2) - 1] \cdot 100$, respectively. For a better understanding of

these relationships, we shall return one more time to our model example. If the convex, solid lines in Fig. 3.2 exceed p_1 as well as p_2, this would indicate a case of absolute superiority. On site 2 this is true for all mixture proportions and for sites 1 and 3 whenever mixture proportions approach that of the more productive pure stand.

3.2.3 Yield Gains Through Risk Distribution

If one species in a mixture is more sensitive to disturbances, the more robust species may then, on account of its better adaptation, profit from the weakening or mortality of the inferior species. Assuming, e.g., a shift in environmental factors and resource availability with unfavorable effects on species 1 (Fig. 3.3, arrow 1→3), a significant decrease in production in pure stands would be the result. However, if a second species is added to the stand that is better adapted to the new growth conditions, this would enable that species to have a stabilizing effect on growth. Species 2 would then make better use of available resources and consequently improve its productivity and space sequestration. The same would happen if one species would disappear completely because of biotic calamities or natural mortality. In this case, the remaining species in the mixture would be able to recover the loss in production through accelerated growth, as suggested by the so-called insurance hypothesis (Yachi and Loreau 1999). This buffering by the remaining species would improve with the regularity of its distribution over the stand area. In both cases, the advantage of mixtures lies in risk distribution as a consequence of silvicultural diversification.
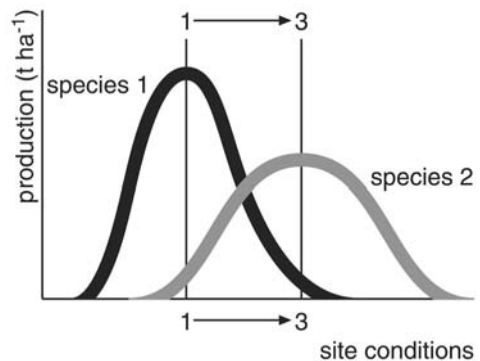

Fig. 3.3. Dry biomass production for species 1 and 2 (*black* and *grey lines*, respectively) in relation to site conditions. The shift in site conditions from 1 to 3 (*arrows*) results in a considerable increment loss for species 1. If species 1 and 2 are mixed, species 2 is capable of compensating for a loss in biomass production

3.3 Empirical Considerations

In order to keep the following empirical considerations as sound and valid as possible, they are based on findings in long-term experimental plots and avoid less reliable inventory data. For yield comparisons, only rarely are data on dry biomass available; information is usually confined to stem volume, which is considered to be of greater relevance in forestry practice. However, the yield comparisons below are mainly based on total dry biomass production (t ha^{-1}), since interspecific differences in wood density have to be eliminated in order to get meaningful results (Assmann 1970). Volume data were converted into dry biomass using specific wood densities reported by Trendelenburg and Mayer-Wegelin (1955) and Knigge and Schulz (1966). Specific wood densities for the individual species are as follows: common beech (*Fagus sylvatica*) 0.554 t m^{-3}, Norway spruce (*Picea abies*) 0.377, Scots pine (*Pinus sylvestris*) 0.431, common oak (*Quercus petraea*) 0.561, Douglas fir (*Pseudotsuga menziesii*) 0.412, European larch (*Larix decidua*) 0.487, common maple (*Acer pseudoplatanus*) 0.522, and common ash (*Fraxinus excelsior*) 0.564 t m^{-3}.

3.3.1 Productivity in Mixtures

Among the dominant tree species of a growth region, usually some are superior in total growth to all others, e.g., *Pinus pinaster* on the Iberian Peninsula, *Picea sitchensis* in Atlantic Western Europe. In central Europe, Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) are often superior in productivity. There is hardly any reduction in this preeminence, which is related to stem volume, if the biomass from branches, leaves, and roots as well as fruit is included (Assmann 1970). On many sites Norway spruce and Douglas fir therefore have the role of species 1 in the mixture constellation shown in Fig. 3.1a.

Figure 3.4 shows the hierarchy of *important* tree species in terms of total dry biomass production for ages 50 (Fig. 3.4a) and 100 (Fig. 3.4b) in pure stands. For the purpose of comparison, the volume yields (m^3 ha^{-1}) shown on conventional yield tables for the best and poorest sites were converted into dry biomass production (t ha^{-1}). Up to age 50 Douglas fir and Norway spruce yield two to four times as much as other commercial tree species, if grown in monocultures. At 100 years of age Douglas fir and Norway spruce are still the most productive species, although the difference from the other species has become smaller. Common beech and silver fir (*Abies alba*), at age 50 among the lower and intermediate third, have caught up considerably at age 100. Conversely, early culminating species such as Scots pine lose their superior positions. The change in productivity hierarchy between the
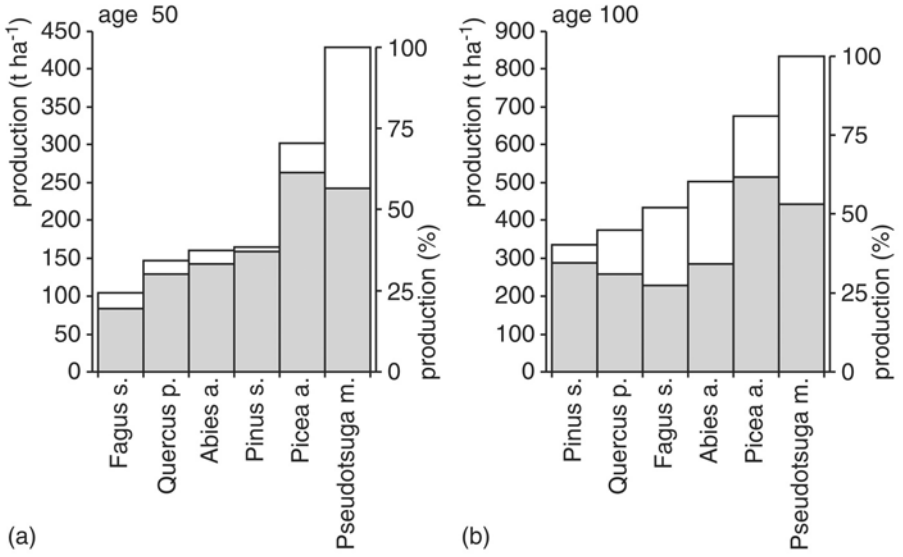
Fig. 3.4. Total yield in stem dry biomass production for selected commercial tree species at age 50 and 100 years (**a** and **b**, respectively). Production for best (total *bar* height) and most unfavorable yield classes (*gray bars*) are shown, calculated from yield tables for common beech (*Fagus sylvatica*; Schober 1967), common oak (*Quercus petraea*; Jüttner 1955), silver fir (*Abies alba*; Hausser 1956), Scots pine (*Pinus sylvestris*; Wiedemann 1948), Norway spruce (*Picea abies*; Assmann and Franz 1963), and Douglas fir (*Pseudotsuga menziesii*; Bergel 1985)

ages 50 to 100 underscores the effect of age on the results of yield comparisons.

Given the higher productivity in Norway spruce and Douglas fir stands, the admixture of other species usually causes production losses, since losses through the substitution of superior species by inferior species cannot be compensated for by the beneficial interactions between species in mixture. Let us assume the dry biomass production of Norway spruce in a pure stand comes to 800 and that of common beech to 480t ha^{-1} on a specific site. Let us further assume that 50 % common beech are added to the Norway spruce stand and that neutral interactions between the species prevail. This would reduce the production in the pure Norway spruce stand to $p_{1,2} = 0.5 \times 800$ t ha^{-1} + 0.5×480 t ha^{-1} = 640t ha^{-1}, i.e., to 80 % of the pure Norway spruce stand, a loss of 20 %. In the case of overyielding, the beneficial interactions from the mixture would have to compensate for this deficit. However, there are no examples of a mutual facilitation of Norway spruce and common beech to this extent. This implies that almost any admixture to the more productive pure Norway spruce stand would lower yield. The great superiority of pure Norway spruce and Douglas fir stands explains the outstanding progress

of their cultivation in the past. Still, in view of the objective to achieve multi-criteria sustainability outlined above, the unilateral and short-term optimization of productivity is increasingly coming under criticism.

3.3.2 Dependence of Yield on Site Conditions

Our model example shows how greatly the yield relationship between two tree species with different ecological niches may vary from site to site (Fig. 3.2a–d). Contradictory results involving identical species mixtures are better understood through the inclusion of site conditions. I elucidate the influence of site conditions on yield relationships between pure and mixed stands using the most important and best studied mixture in Europe, i.e., Norway spruce/common beech. For this mixture a unique database involving 9 experimental areas with 33 experimental plots under permanent observation is available, with data going back to the beginning of the last century. Most of the experiments have been surveyed by the Chair of Forest Yield Science of the Technical University of Munich. Due to the unique length of time involved, growth and yield of Norway spruce and common beech in pure and mixed stands have been the subject of several investigations (e.g., Kennel 1965; Assmann 1970; Pretzsch 1992, 2003). Here, I report on only the relationship between site condition and growth. The site spectrum ranges from calcareous, warm, and dry sites in central and northern Germany, with a natural dominance of common beech, to acidic, cool sites with heavy precipitation in southern Bavaria, typical for natural Norway spruce stands. The experiments involve plots in pure and mixed stands with different mixture proportions. As the stands all have been established by natural regeneration the species are not exactly even in age. Nevertheless, apart from minor site-dependent variations in height growth the stands are mono-layered. From the start of the experiments, both pure and mixed plots have been subjected to moderate thinning from above, i.e., the closed canopy was maintained. The common beech component ranges from 30–50 %. Reference age for the results is 100 years.

At this age stem dry biomass stock ranges from 500–1,300 t ha^{-1} and 400–1,100 ha^{-1} for Norway spruce and common beech in pure stands, respectively. In mixtures the stock values lie between those for the pure stand plots of the constituent species. Depending on whether the site has favorable or unfavorable effects on either Norway spruce or common beech, these values will approach those in the pure spruce or beech stand. The same is true for total dry biomass production, for which data exist from the entire long observation period. Figure 3.5 represents total volume growth from mixed stands in relation to that from pure Norway spruce stands (100 % line) on adjacent sites with equal site conditions. The experiments are ranked such that those optimal for growth of Norway spruce sites are plotted on the left-hand side of the
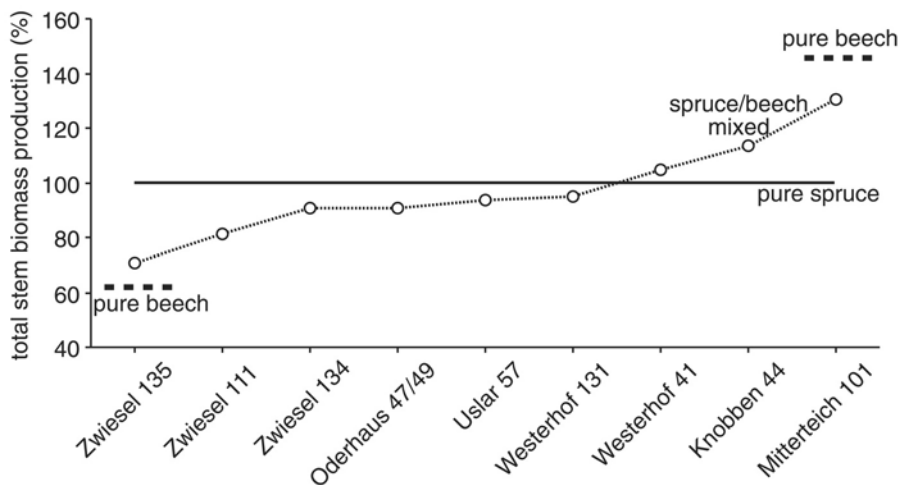
Fig. 3.5. Total stem biomass production of pure Norway spruce stands (*100% line*) and Norway spruce/common beech mixed stands in dependence on site conditions on long-term experimental plots at age 100. Since replications are not available for those long-term experiments, standard errors for the observations are lacking. See text for details

graph. From left to right, growth conditions for Norway spruce decrease while those for common beech improve. Mixture results on sites with optimal growth conditions for common beech are shown at far right. The yield for common beech, also related to the pure Norway spruce stand, is plotted for experiments "Zwiesel 135" and "Mitterteich 101," which mark the lower and upper yield spectra, respectively, for common beech (broken line). As can be seen, the admixture of common beech on typical Norway spruce sites reduces productivity to 70 % of the pure Norway spruce stand. On sites with optimal growth conditions for common beech, the inclusion of common beech to Norway spruce leads to a production increase of up to 130 % of pure Norway spruce. In the first case, the replacement of Norway spruce by common beech decreases yield, whereas in the second every admixture of common beech achieves a gain over productivity in the pure Norway spruce stand. The effects from species interactions Δp_{rel} between Norway spruce and common beech range between +10 and –20 %. In all available studies, however, the mixed stand of Norway spruce and common beech occupies a position between the corresponding pure stands, as far as productivity is concerned.

In a study by Jensen (1983), too, pure stands form the walls of the corridor, so to speak, in which the mixtures are positioned. Along a west–east transect through Jutland/Denmark he gives a model example of site-condition effects on the growth relationship between Norway spruce and silver fir. In the coastal dune belt, silver fir is superior to Norway spruce, the adjacent

Riss–glacial landscape leads to equivalent growth in silver fir and Norway spruce, whereas on the old inland moraines of the Würm glacial period silver fir is inferior to Norway spruce in dry biomass production. The decisive factor for the inland superiority of Norway spruce is its adaptability to low water supplies on acidic sites. By contrast, silver fir profits from better water availability and the more favorable nutrient supply in the coastal region. Even here, the evident beneficial effects from species interaction in mixtures are not sufficiently powerful to cause transgressive overyielding.

Yield limitations for mixtures composed of shade-tolerant trees such as Norway spruce/common beech and Norway spruce/silver fir are not transferable to mixtures consisting of shade-intolerant and shade-tolerant trees. Frivold and Kolström (1999) studied silver birch (*Betula pendula*), Scots pine, and Norway spruce growth in Finland, Sweden, and Norway. They emphasize that the potential superiority or inferiority of these species in mixtures is related to site conditions. Depending on site conditions, the effects of species interaction may be unfavorable, neutral, or beneficial, and in the latter case even lead to overyielding of mixed stands over the more productive pure stands. In southern and central Finland, Scots pine/silver birch mixtures surpass pure Scots pine and pure silver birch stands by 10 and 14 %, respectively (Mielikäinen 1980). For Norway spruce/silver birch mixtures a 10 to 15 % increase in production may occur compared with corresponding pure stands of these species, depending on the site (Mielikäinen 1985). In the oceanic regions of Norway and Sweden silver birch loses some of its increment capacity compared with coniferous species. There, Scots pine/silver birch mixtures do not achieve greater yield than the pure stands while Norway spruce/silver birch mixtures show a beneficial effect from mixtures only during the juvenile growth period (Frivold and Frank 2002).

3.3.3 Typical Mixture Effects on Yield

The examples shown in Fig. 3.6 illustrating antagonistic, neutral, and beneficial effects from species interaction (Fig. 3.6a–c) represent the frame for the mixture effects in a replacement series experiment from two-species mixtures to be expected in temperate and boreal zones (see Sect. 3.2.1 for theoretical background).

The Norway spruce/common beech experimental area "Freising 813" (Fig. 3.6a) represents negative effects from species interaction in mixtures (recognizable in the U shape of the connecting line of the total yield). With a proportion of 40 to 50 % common beech, total productivity decreases by about 30 % compared with expected values given neutral effects in mixture. The reaction of $p_{1,(2)}$ and $p_{(1),2}$ reveal that Norway spruce's productivity increases in proportion to the Norway spruce portion in the mixture, while that of common beech increases sub-proportionally. Common beech can
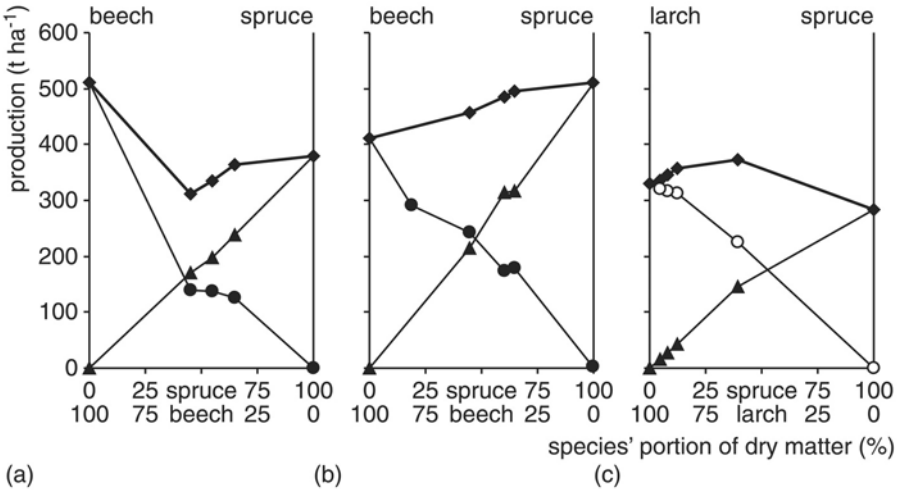
Fig. 3.6a–c. Typical response pattern of dry biomass production in two-species mixtures. Mixtures of Norway spruce and common beech in flat land areas with unfavorable mixture effects (**a**), Norway spruce and common beech in submontane areas with neutral effects (**b**), and European larch and Norway spruce in subalpine areas with beneficial mixture reactions (**c**). The dry biomass production from pure stands of common beech or European larch are plotted on the *left-hand ordinates*, while that for pure Norway spruce stands is plotted on the *right-hand ordinates*. The *upper connecting lines* (accentuated by *rhombuses*) represent total productivity $p_{1,2}$ of the mixed stands. The productivity for each mixture species $p_{1,(2)}$ and $p_{(1),2}$ is shown (*triangles* and *circles*, respectively). Data for are from **a** Pretzsch et al. (1998), **b** Pretzsch (1992), and **c** Zöhrer (1969)

thus be identified as the losing species that reduces the mixed stand's increment.

The Norway spruce/common beech experimental area "Zwiesel 111" (Fig. 3.6b) represents neutral effects from species interaction. On all plots of this experimental area, total dry biomass production increases in proportion to the portion of the constituent species in the mixture. Thus, total productivities of mixtures are between those of pure-stand plots. Accordingly, productivity gains are solely attributable to common beech being replaced by Norway spruce, which grows faster on this site, and not to beneficial interactions between the two species.

In both mixed Norway spruce/common beech stands (Fig. 3.6a, b) Norway spruce productivity (triangles) increases in proportion to its portion in the mixture. The reaction of common beech (circles), though, is negative or neutral. In the former case, beech is inferior to the more productive Norway spruce. In the latter case, a balance of competition is achieved. Wiedemann (1942, 1943, 1951) was already able to differentiate between the two reaction types. In northern Germany, Norway spruce/common beech mixtures with highly productive beech, approximately the same dry biomass as correspond-

ing pure stands are achieved. For common beech of moderate growth the mixed stand biomass production is about 19 % less than in pure common beech stands on identical sites. Kennel (1965) studied mixtures of Norway spruce and common beech in the Bavarian alpine foothills, the Bavarian Forest, and the Harz in Lower Saxony, as did Burger (1941) in Switzerland, with similar results. We note that in mixtures composed of two shade-tolerant species, dry biomass production in mixed stands never significantly exceeds that of comparable pure stands, and is often considerably lower.

On the other hand, beneficial effects from species interaction with over-yielding are often achieved in mixtures of shade-intolerant and shade-tolerant trees. Zöhrer (1969) provided evidence that the biomass production of European larch/Norway spruce mixtures in the Salzburger Land is superior to that of pure stands on identical sites (Fig. 3.6 c). With increase in the Norway spruce portion, total yield rises over-proportionately, reaches a peak at 40 %, and then declines to the value of the pure Norway spruce stand. The position of the resultant data above the connecting line between the dry biomass production of both pure stands is indicative of the beneficial effects of species' interactions in the mixture. The European larch/Norway spruce mixture therefore surpasses the pure Norway spruce stand by 22–28 % and the pure European larch stand by 2–13 %. For mixed stands, composed of shade-intolerant and shade-tolerant species such as common oak/common beech, Scots pine/Norway spruce and Scots pine/common beech, Bonnemann (1939) and Wiedemann (1943, 1951) found similar beneficial effects from species interactions after 50 years of observation. For long-term Scots pine/common beech experimental areas in the Dübener Heide, Dittmar et al. (1986) noted beneficial interaction effects compared with the pure stand of 7–25 %, depending on the age and structure of the mixture. Burger (1941) and Wimmenauer (1941) found the same strong superiority in European larch/common beech mixtures.

A considerably higher superiority of 50 % is claimed by DeBell et al. (1989) for mixtures of *Eucalyptus saligna* and the leguminous and nitrogen-fixing tree species *Albizia falcataria* in Hawaii. Other examples are summarized by Kelty (1992). Compared with these yield relationships in the subtropics, mixture effects of about ±30 % for commercial tree species in temperate and boreal zones appear rather moderate.

3.3.4 Disturbances and Silvicultural Treatment

The greater the niche variations among the constituent species of a mixed stand, the more elastic will be its response in the face of disturbances (Sect. 3.2.3). An example of this are the annual increment values from the Norway spruce/common beech experimental area "Schongau 814" in the period 1960–1995 (Fig. 3.7). In contrast to the component common beech,
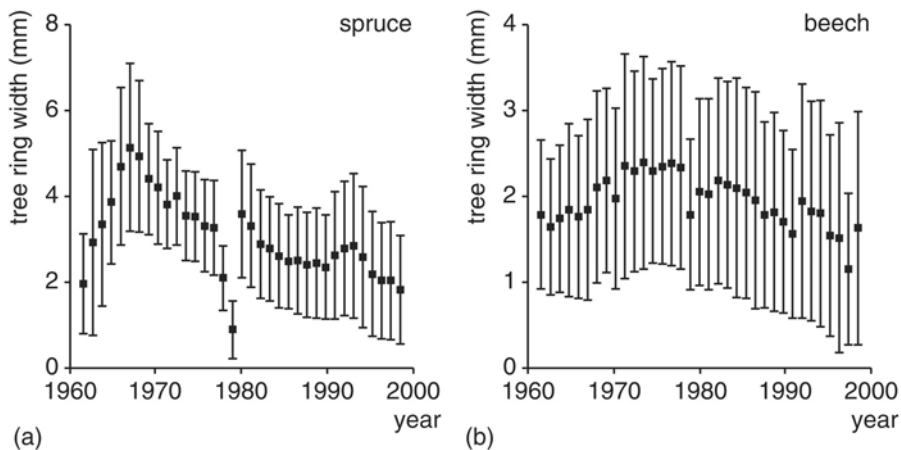
Fig. 3.7. Mean ± standard deviation of annual ring width for Norway spruce (**a**) and common beech (**b**) on the mixed stand experimental area Schongau 814 (n=193 for Norway spruce and n=87 for common beech). On that site Norway spruce shows much more sensitive reactions to the drought of the year 1976 than common beech

Norway spruce reacted to the drought of the year 1976 with a strong decrease in increment. In pure Norway spruce stands this would cause serious production losses. In Norway spruce/common beech mixtures, disturbances of this kind can be mitigated by compensatory growth of common beech (Fig. 3.3), as suggested by the "insurance hypothesis" (Yachi and Loreau 1999; Pretzsch 2003). Unfortunately, yield comparisons between pure and mixed stands usually refer to more or less undisturbed stands. Affected plots are abandoned after calamities or unplanned use and only undisturbed plots are kept under continuous observation. Statements about inferiority or superiority derived from these experiments therefore also apply merely to "normal" circumstances. If response patterns after disturbances were also considered yield comparisons would become more realistic. In the following, the example of Norway spruce and common beech will serve to illustrate that pure stands composed of these species respond in radically different ways to disturbances in the form of thinnings from mixed stands.

The ensuing analysis of thinning–growth relationships in pure stands is based on 19 thinning experiments with 26 Norway spruce and 30 common beech plots located in Bavaria and Lower Saxony. The oldest plots have been under regular observation since 1870–1880. With few exceptions they are composed of three plots each that are identical in site and age but were consistently managed according to the specifications for A, B, and C grade (slight, moderate, and heavy thinning from below) and thus cover a wide spectrum of stand densities (Pretzsch 2002, 2003). The analysis of density–growth relationships in mixed stands relies on data from a total of 23 experimental areas

with Norway spruce/common beech mixtures in south Germany involving a total of 78 plots under observation since 1954. With a basal area spectrum ranging from 20–80 m² ha⁻¹ at age of about 100, densities tend to vary even more here than in the pure stands. Removals from thinnings, remaining stand response, and hence total growth are quantifiable based on data from up to 20 routine inventories of removed, remaining, and total stand biomass.

Figure 3.8 represents the stem dry biomass yield for pure Norway spruce and common beech stands and mixed Norway spruce/common beech stands (Fig. 3.8a–c) on plots subjected to various grades of thinning in comparison with the untreated plots at age 100. If we first consider the response pattern in pure stands (Fig. 3.8a, b), it appears remarkable that dry biomass production in the transition from A grade to B grade rises by 5 to 10 % in either case. In the transition from B grade to C grade, we note a decrease in total growth. In common beech stands total growth yield for C grade is even higher than for A grade. After 130 years of experimental research we are therefore able to state for Norway spruce and common beech a significant increase ($p<0.05$) in growth from A grade to B grade and for Norway spruce a significant decrease ($p<0.05$) in growth in the transition from B grade to C grade. The relationship between density and growth hence represents an optimum curve. Any approach to maximum stand density is concomitant with growth reductions of 5 to 10 %. By contrast, the biomass production in Norway spruce/common
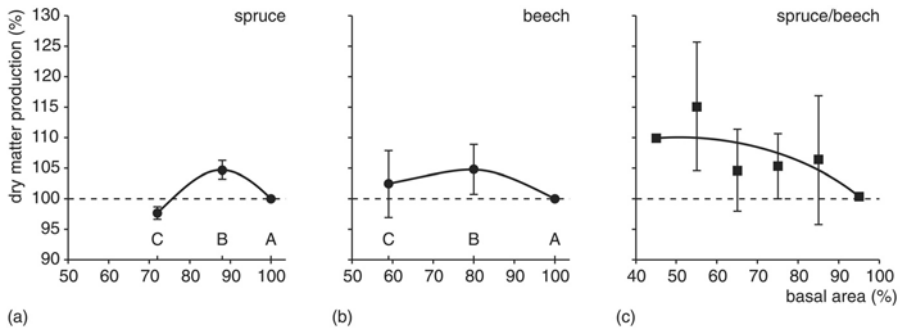

Fig. 3.8a–c. Density–growth relationships in pure and mixed stands from Norway spruce and common beech at age 100. *A*, *B*, and *C* grade, respectively, refers to slight, moderate, and heavy thinning from below in the pure stands. In the mixed stands, the experimental design included untreated plots, slight, moderate, strong, and accretion thinning. Means±SE. As the production of the untreated plots with maximal density were used as reference for the thinned plots and set to 100 %, they have no standard error. **a** Results from 9 Norway spruce thinning experiments with 26 plots, consistently slight, moderate, and heavy thinning since 1870. **b** Results from 10 common beech thinning experiments with 30 plots, consistently subjected to slight, moderate, and heavy thinning from below since 1870. **c** Results from 23 mixed stand experiments with 78 plots under observation since 1954. Dry biomass production in heavily thinned mixed stands is depicted without standard error, since replications were lacking

beech mixtures (Fig. 3.8 c) achieves similar values over a wide range of densities. Their is no significant reduction ($p>0.05$) of biomass production even when stand density is reduced to 50 %. In comparison with corresponding pure stands, Norway spruce/common beech mixtures are able to compensate for disturbances caused by thinnings through accelerated growth in the remaining stand.

The cause for this response pattern is the space sequestration by dominant Norway spruce and dominant but also subdominant common beech. This leads to an increase, from pure to mixed stands, in the total crown shading area and also in the frequency of multiple crown shading. In mixed stands removals from or losses in the upper crown layer can be compensated for by stronger growth in the lower layer. This buffer effect through a vertical stratification of the canopy becomes particularly effective with increasing age. In the mixed stand the remaining trees are able to close any gaps that may form by mortality, to slow down age-related breakup of the crown layer and to have a stabilizing effect on stand biomass production.

3.4 Discussion and Conclusions

Lack of data during the founding period of forestry sciences led to statements on yield relationships between pure and mixed stands that were based on faith rather than knowledge (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 utilization 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 consequent effects from species interactions may be negative, with a reduction in productivity up to 30 %.

There is special potential for increased productivity in mixtures of about equally productive species on a given site which complement each other in the spatial-temporal utilization of space, leading to a reduction of competition (Kelty 1992). This can be achieved by joint growing space occupation with shade-intolerant species (e.g., European larch, Scots pine), semi-shade-tolerant species (e.g., Norway spruce, Douglas fir) and shade-tolerant trees (e.g., common beech, silver fir). This kind of stratification using species of different shade tolerance will allow light transmitted through the upper canopy to be used by the layers underneath. Gains in productivity are also achieved in tree mixtures where the temporal courses in seasonal growth

period and in the aging process complement one another. Let us assume growth of species 1 in a two-species mixture culminates early and then declines rapidly. The decrease in total increment can then be made up for by addition of species 2, the development of which is anti-cyclic to that of the other. Assmann (1970) shows that species-specific periodicity is reflected in different time scales. Species which culminate early in the season also exhibit the same characteristic as regards lifespan. Mixtures of species with anti-cyclic seasonal growth characteristics also often complement one another in the aging process.

Temporal and spatial resource use complementarity, e.g., in Norway spruce/common beech mixtures, may also occur in combined form. In spring, before the leafing of common beech, more intense light can penetrate the stand and curtail the winter dormancy of Norway spruce, thus prolonging its seasonal growth period which, per se, is longer than that of common beech (Schober 1950/1951). From this kind of "job-sharing," e.g., Norway spruce and common beech, mixtures may draw advantages in resource utilization (Mitscherlich 1952). Beneficial interaction effects will be stronger the closer and more intensive the mixing of Norway spruce and common beech (Ellenberg et al. 1986).

Systematic yield gains by up to 30 and 50 % for grasslands and natural forest ecosystems in the transition from pure stands to two-species mixtures (Hector et al. 1999; Caspersen and Pacala 2001; Loreau et al. 2001; Pfisterer and Schmid 2002) can be transferred to managed forests only to a very limited extent. Presumably, in boreal and temperate forests niche differentiation is comparatively low due to species reduction in the course of the ice ages and due to the much slower evolutionary and co-evolutionary processes of long-lived trees. This may be a reason why increased efficiency in resource use and productivity of mixed stands compared with pure stands is much lower in long-lived woody ecosystems than in short-lived herbaceous stands. Many of the European forest stands are "artifacts" designed with very productive species such as Norway spruce and Douglas fir cultivated outside their natural habitats. Often, genetic variation in these species no longer reflects natural selection but a choice controlled by mankind's commercial criteria. These forests are therefore not designed for optimum niche utilization by the mixture species. Niche overlapping and risks may occur that are reflected in unfavorable effects from species interactions in the mixture.

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. Let us assume a pure Norway spruce stand on a site in the Bavarian alpine foothills with good water supply and acidic soil, where Norway spruce growth far surpasses that of common beech, but to which common beech is added to raise stand biodiversity and aesthetic value. As a consequence the replacement of Norway spruce by the slower-growing common

beech under undisturbed development causes considerable yield loss because of opportunity costs. However, if the greater elasticity against disturbances is included in the calculation, opportunity costs may be considerably lower. This has been shown in simulation studies on the effect of climate change on the growth of pure and mixed Norway spruce and common beech stands in Germany (Pretzsch and Dursky 2002). Assuming temperatures within the growth period rise by 2 °C for the above site, precipitation in the vegetation period drops by 10 %, and the growing season is prolonged by 10 days, a decrease would occur in Norway spruce productivity on that particular site by over 10 %. The substitution of 30 % of the Norway spruce by common beech, which is better adapted to the assumed changing climate conditions, could compensate for the climate-related increment losses in Norway spruce. In view of the increasing disturbances to which our forest ecosystems are being subjected through chemical emissions and climate change, the chances for advantages being realized through this kind of risk distribution by species mixture will probably rise in the future (Lindner and Cramer 2002).

Variations in stand density, too, are more easily compensated for in mixed stands. This property of mixed stands keeps their growth rate stable under lack of treatment and maximum density as well as under density reductions due to silvicultural treatment or calamity. In pure stands an optimum relationship exists between density and growth. 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. The broad saddle in the resultant curve looks similar to the much discussed curve by Langsaeter (1941, p. 173; Fig. 3.3). In contrast to the pure stands under study, the approach to maximum density causes merely a slight and statistically insignificant decrease in growth. This important relationship is schematically represented in Fig. 3.9. The mixture (black) is compared with two pure stands (grey lines). The first case (upper line) assumes the production superiority of pure stands versus mixtures at average density. Whenever density is reduced due to some kind of disturbance, pure stands will respond with considerable increment loss and become inferior. By contrast, growth in the mixed stand remains stable over a wide range of densities. Even though mixed stands may be inferior under "stable" conditions they may develop superiority on account of their greater resilience in the face of perturbation or non-treatment. 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., lack of treatment or unplanned disruption of stand canopy, the stand becomes even more inferior.

In short, the productivity relationship between pure and mixed stands under "normal" conditions may shift considerably once risks are included (Pretzsch 2003). The decisive factor here, in essence, is the probability of the occurrence of disturbances and damage. The temporarily dazzling productiv-
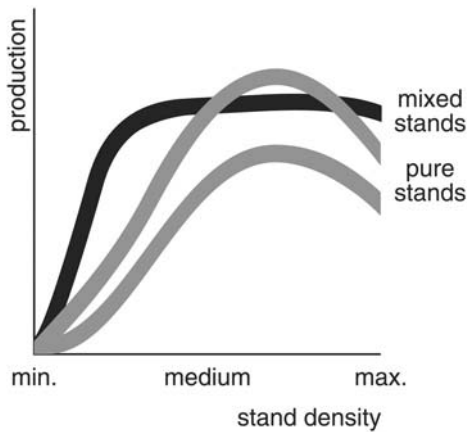
Fig. 3.9. Schematic representation of relationships between stand density and biomass production in pure and mixed stands. The overlapping of different response patterns for Norway spruce and common beech leads to a considerably wider plateau in the density–growth relationship of mixed stands than for corresponding pure stands. This reflects the greater growth resilience in mixed stands (*black line*) as compared with that in pure stands (*grey lines*)

ity superiority of artificial pure stands is often reversed and turns into inferiority if risks are included in the calculation (Pretzsch und Dursky 2002). Thus, while Norway spruce is overwhelmingly superior to common beech on many sites under normal conditions, storm damage in Norway spruce stands is four times as high as in common beech stands (von Lüpke and Spellmann 1999). To a considerable extent mixtures can overcome this kind of perturbation, equivalent to an abrupt reduction in stand density from medium to lower levels, without greater growth reductions. Of course, the above relationships between species number and biomass production do not alone justify decisions in favor of pure or mixed stand establishment or a certain stocking density. The outcome of such decisions may be quite different, depending on frame conditions and specific objectives of forest management – for instance if the major aim is quantity (e.g., pulp, fuelwood, C storage), quality (e.g., structural wood or veneer), or safety and risk prevention (stabilization 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 important forest functions (cf. MCPFE 2000) are fulfilled in addition, then the above yield relationships may become primary in controlling the decisions.

In comparison with annual systems, the lifespan of forests is longer by two orders of magnitude and the danger from risks consequently much greater. In addition, cyclic disturbances through silvicultural treatment 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 close mixture of tree species. The desired diversification could also be achieved by plot mosaics of pure stands of different species. Through this kind of species separation even likely unfavorable effects from species interactions and

greater efforts required to facilitate inferior species in mixtures could be avoided. However, the above-mentioned beneficial interactions in mixtures, which may raise the productivity of commercial tree species in temperate and boreal zones up to 30 % under "stable" conditions, as well as the higher resilience and superior productivity of mixed stands under disturbances, require a close spatial association of the mixed species.

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