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Increment and Yield in Mixed Stands with Norway Spruce in Southern Sweden

Magnus Lindén

Swedish University of Agricultural Sciences

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Abstract

The productivity of mixed stands with Norway spruce is a matter of increasing importance in Swedish forestry. Non-wood factors, such as biodiversity issues, and the vast abundance of mixed stands, demonstrate a need for silvicultural methods that incorporate several tree species at the stand scale in the long-term. Until recently, such methods have been little studied, due to the predominant use of monospecific stand types in practical forestry as well as in research. The work underlying this thesis was designed to contribute to our knowledge of mixed stands. Through both experimental and modelling approaches, increment and yield in mixtures with Norway spruce and Scots pine or birch or oak were studied. It was found that wood decay in Norway spruce caused by butt rot can be reduced using certain types of mixed stands, and that such stands usually have similar volume increment to the more productive monocultures on sites similar to those in this thesis. An experiment with long-term mixtures using spontaneously regenerated birch in spruce regeneration areas has been initiated and the mixtures appear to be easy to manage according to a first evaluation. Productivity and economic performance of oak stands using spruce admixtures were evaluated, and indications of some beneficial effects (especially economic) were detected. The practice of retaining large deciduous trees in spruce stands for enhancing biodiversity was analysed. The results suggest that to minimise growth reductions in the spruce crop, retained green trees should be clustered rather than spread out. Mixtures consisting of two tree species are suggested to generally display a compensatory growth pattern between tree species, in which one is usually favoured at the expense of the other. Growth in the individual tree species may be very different from its corresponding growth in monoculture, whereas total productivity appears to be more similar to the mean yield of the two corresponding monocultures. Variability in stem size in mixed stands, which can be explained by differences in the growth parameters of the associated tree species, tended to increase for parameters such as height distribution and diameter distribution in the total population, whereas for the individual tree species, a more clustered distribution was noted in some of the studied mixtures.

Keywords: *Betula spp.*, butt rot, compensatory growth, competition model, diameter, height, *Heterobasidion annosum*, increment, layering, logistic regression, mixed stand, mixture, Norway spruce, *Picea abies*, *Pinus sylvestris*, *Quercus robur*, stem distribution, volume, yield.

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Men strunt är strunt och snus är snus,
om ock i gyllene dosor,
och rosor i ett sprucket krus
är ändå alltid rosor.

Gustaf Fröding

Contents

Appendix

Papers I-V

This thesis is based on the following papers, which will be referred to by their respective Roman numerals:

I. Lindén, M. and Vollbrecht, G., 2002. Sensitivity of *Picea abies* to butt rot in pure stands and in mixed stands with *Pinus sylvestris* in southern Sweden. Silva Fennica 36:767-778.

II. Lindén, M. and Agestam, E., 2002. Increment and yield in mixed and monoculture stands of *Pinus sylvestris* and *Picea abies* based on an experiment in southern Sweden. (In press, Scandinavian Journal of Forest Research)

III. Lindén, M. 2002. Increment in a recently established experiment with single-storied intimate mixtures of *Picea abies* and *Betula spp.* in southern Sweden. (Manuscript)

IV. Lindén, M. and Ekö, PM. 2002. Increment and economic performance in a mixed forest with *Quercus robur* and *Picea abies* compared to monocultures. (Manuscript)

V. Lindén, M. and Örlander, G. 2002. The effect of retaining large deciduous trees on the 25-year increment in planted understorey of *Picea abies*. (Manuscript)

Introduction

Wood production is generally the main reason for conducting forestry operations in Sweden. However, in recent years other considerations have come to play an increasingly important role in Swedish forestry. Increased concerns for biodiversity, water quality, nutrient sustainability and carbon cycling have added to the factors to be taken into account in forestry, alongside more traditional considerations of productivity, forest health and social values (Helsinki Conference 1994). Mixed stands are often considered appropriate to take these considerations into account (*e.g.* Seitschek 1991, Gardiner 1999). International agreements (the Helsinki Conference 1994), Swedish society (Swedish Cabinet Office 2001) and Swedish non-governmental forest certification organisations (FSC 1998, PEFC 1999), all promote the use of enhanced levels, or stipulate minimum levels, of mixed forests. This work investigates some consequences for increment and yield of using mixed stands instead of monocultures.

Development of mixed stands

The most widely used definition of a mixed stand in Sweden is a forest stand where at least two tree species are present, none of which account for more than 70 percent of the basal area (Anon. 1999). Recent data show that mixed stands in Sweden cover approximately 24 percent of the forestland according to this definition (NFI 2002). In contrast, the most common stand types, monocultures of Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.), collectively cover 70 percent. In the middle of the former century the proportion of mixed stands was greater, but since the beginning of the 1980s the proportion has remained fairly constant (Table 1). Including stands where the admixture is less than 30 percent, but more than 5 percent, mixtures cover approximately 45 percent of the forestland (Statistical yearbook of forestry 2001). Comparison with other countries is difficult since definitions and access to recent data vary significantly, but generally this figure appears to be neither particularly large nor particularly small (Bartelink & Olsthoorn 1999). For example, in the United Kingdom the proportion of mixed stands is considerably lower, whereas in Germany, where the definition of a mixed stand requires an admixture of at least ten percent, mixtures account for 50% of the forestland (Polley 1994). In Norway, where definitions are similar to those used in Sweden, the extent is slightly greater (28%, Bartelink & Olsthoorn 1999). The most common type of mixed stand in Sweden are mixtures with Scots pine and Norway spruce (16% of the total). Mixed coniferous-deciduous stands are most common in young stands. Figures for mixed deciduous stands are lacking, but they are significantly lower than 6%, which is the total extent of deciduous forests (Table 1).

Table 1. Extent of mixed stands as percentages of the forest area in Sweden. P.sylv and P.abies, forest land where at least 70% of the basal area is Pinus sylvestris and Picea abies respectively; Mix. conif., mixed coniferous forest with atleast 70% conifers; Mix. conif.-decid., Mix. conif.-decid., mixtures with 40-60% deciduous trees; Deciduous, atleast 70% deciduous tree. Data from National Forest Inventory: years 1938-1977 (Agestam 1985), years 1984-1999 (NFI 2002)

Period (yr.)	*P.sylv.*	*P.abies*	Mix. conif.	Mix. conif.-decid.	Deciduous
1938-1952	23	24	15	32	6
1953-1962	24	21	20	31	4
1968-1972	32	28	22	14	4
1973-1977	37	31	18	9	5
1984-1988	41	31	16	7	5
1989-1993	42	30	16	7	5
1994-1999	42	28	16	8	6

In 1993, a new forestry act was passed in Sweden (Anon. 1994). The new act, like the former (Anon. 1988), regulates regeneration by setting minimum levels of seedling density and quality. However, in the former act spontaneously regenerated deciduous trees were generally not allowed to be included in the regeneration in coniferous stands other than in special cases, *e.g.* on sites with extreme soil moisture conditions. In the new act, all tree seedlings of acceptable quality can be included, irrespective of their species. Consequently, all individuals of acceptable quality may be included in the future stand. Since birch (*Betula pubescens* Ehrh. and *B. pendula* Roth.), especially, regenerates spontaneously and abundantly in forest regeneration areas on many sites (Fries 1985), and the birch seedlings are often competitive in the new stand (Folkesson & Bärring 1982), numerous ways of regulating species composition have emerged. In many cases, exploiting spontaneous regeneration is probably a more cost-effective approach compared to man-made establishment of deciduous trees. Since birch wood is more valuable today than it was just a few decades ago, utilising spontaneously regenerated birch offers an interesting option in forest management.

Limited knowledge

Although mixed stands are common, and the occurrence of mixtures is tending to increase, at least in young stands (SUS 2001), forestry practices still focus on the use of one main tree species, usually Norway spruce or

Scots pine. Although Swedish forestry has taken some steps to increase the use of spontaneously occurring species mixtures, additional tree species in conifer stands are generally included on a more temporary basis or in small proportions (Karlsson *et al.* 1997, Anon. 2000, Anon. 2001). Since monocultures have been exploited and researched for centuries they are well understood systems where prognosis of wood production using different management programmes can be made on firm grounds (see, for instance, Söderberg 1986). In contrast, our knowledge of using mixed stands for wood production is relatively poor. Any major deviation from the well-known systems may be subject to great risks before our knowledge of management and yield in mixed stands has increased substantially. Therefore, there is an urgent need to increase our understanding of the processes and management of mixed stands. In recent decades, research efforts focused on mixed stands have increased internationally (Zing 1999), but still, data on the growth and yield of mixed stands are scarce (Bartelink & Olsthoorn 1999).

Mixtures of tree species generally result in more heterogeneous stand structures (Oliver & Larson 1990) and more yield assortments compared to monocultures (Utschig 1999), which may complicate management (Savill *et al.* 1997) and logging operations (Warkotsch 1999). Any attempt to study increment and yield in mixtures with many different tree species before even the simplest of mixtures is properly understood may prove difficult. Therefore this work focuses on mixtures of two tree species; Norway spruce and one additional tree species (Scots pine, birch or oak).

Aspects of sustainability

In Sweden, and various other places, efforts have been made to adjust forest management in order to improve its effect on biodiversity values. Given the large number of species involved and the limited state of knowledge of their habitat requirements, management based on species requirements may be very difficult (Franklin 1994). The identification of forest structures and forest composition of the past, when human influence was weak, may be a more effective way to define forest features required for the maintenance and enhancement of species biodiversity values (Hunter *et al.* 1988). According to several central-European forestry researchers (*e.g.* Schütz 1999) natural stands are generally composed of relatively unmixed stands, dominated by a few very competitive tree species, and virgin forests generally show regular structures, at least during the essential part of their development. Rackham (1992) argues that most natural forests in Europe consist of mixtures of tree species. In southern Sweden the former landscape contained an abundance of many of the naturally occurring tree species, and it was dominated by hardwoods.

These stands have been replaced by more uniform coniferous forests dominated by Norway spruce (Björse & Bradshaw 1998, Lindbladh *et al.* 2000). Studies of plant macro-fossils have indicated that the pre-agricultural forest composition consisted of an intimate mixture of tree species (Hannon *et al.* 2000, Hannon 2002).

The effects of forestry operations on soil water quality in soil and run-off in Sweden have been discussed in several reports recently (*e.g.* Anon. 2002). Results from studies on the quality of the soil water (*e.g.* Örlander 1998) and the quality of the run-off from forests to forest streams (Arheimer 1993) show the potential impact silvicultural decisions may have on the water quality in streams. The finding that different tree species influence soil water conditions in different ways (Brown & Iles 1991, Bergkvist & Folkesson 1995) suggests that mixed stands may have a different influence on water quality compared to monocultures.

Mixed stands may also differ from monoculture stands in their impact on nutrient sustainability. For example, in a study by (Brandtberg *et al.* 2000) it was found that the concentration of base cations was greater in mixed stands with Norway spruce and birch than in spruce monocultures. The availability of base cations has been calculated to be a potentially limiting factor for the growth of Norway spruce in Sweden (Sverdrup *et al.* 2002). Mixed stands with oak and Norway spruce have been argued to have greater nutrient sustainability compared to spruce monocultures (Thelin *et al.* 2002).

Strategies for growing mixed stands

Mixed stands may be grown using different silvicultural systems, such as cultivating even-aged systems with the removal of a final harvest after each rotation, or multi-cohort stands with selective cuttings. In principle, both of these methods are probably valid from a biological point of view. Depending on the role of forestry in the society being considered, *e.g.* the balance between the demand for pulpwood and wood production efficiency on the one hand, and non-wood considerations on the other, either of these systems may be considered more appropriate than the other for wide-spread use. In Sweden, even-aged systems, with or without a two-storeyed phase, has been the most widely used system for a long time, and will probably continue to be (Gemmel & Remröd 1991). Multi-cohort stands, which were associated with a detrimental exploitation of Swedish forests in the past, have often been considered less suitable for efficient and sustainable wood production (*e.g.* Andrén 1985). Hence, important elements of future forestry in Sweden will be the silviculture of mixed stands using modifications of the even-aged systems. The work underlying this thesis focused on such modifications of the even-aged systems to grow mixed stands. Multicohort stands were not specifically studied.

Objectives

The concept of mixed stands is based on defining what they are not, since a mixed stand is anything but a pure stand. Irrespective of which definition of mixed stands is used, they comprise innumerable possible combinations of tree species and stand types. Hence, any attempt to overview mixed stands will be incomplete. The overall objective of the work described in this thesis was to investigate some possibilities to improve forest health, maintain or increase productivity and avoid a need for an increased need of tending when using mixtures with Norway spruce and one other tree species instead of pure stands of economically important tree species in southern Sweden. The thesis explores aspects of increment and yield: especially diameter, height, basal area and volume. The specific objectives of the various studies the thesis is based upon were as follows:

To evaluate the effect on the incidence of butt-rot of including an admixture of a semi-resistant tree species, Scots pine, in forest stands with a sensitive tree species, Norway spruce (Paper I).

To investigate the effects of using mixed stands with Scots pine and Norway spruce, instead of monocultures, on increment and yield on sites with medium fertility (Paper II).

To start evaluating the possibilities of growing long-term mixtures of deciduous trees and Norway spruce to test the hypothesis that two tree species with different growth parameters can both be managed to reach maturity in terms of timber production with sustained yield and without causing serious damage to the trees. A field experiment was therefore established and early results from this experiment have been presented (Paper III).

To evaluate yield and financial aspects of admixing a fast-growing tree species, Norway spruce, in slow-growing but valuable pedunculate oak (*Quercus robur* L.) stands to test the hypothesis that yield and economic returns can be improved using such mixtures instead of pure oak stands. A further objective was to compare the outcome of the mixture with spruce monocultures (Paper IV).

To investigate the effect on spruce increment of the practice of retaining large deciduous trees in spruce stands to quantify a hypothesised growth reduction in Norway spruce that may follow from such practices (Paper V).

Increment and yield

Comparing mixed stands with monocultures

The main concern of this work was to investigate increment and yield in mixed stands with Norway spruce compared to monocultures. Mixtures can be compared with monocultures in several possible ways, and the choice of method will affect the conclusions (Assmann 1970, Trenbath 1974). Tree species can be compared individually or collectively. Furthermore, comparison of the total volume yield in mixtures with monocultures may be based on at least any of the following parameters: the mean yield of the corresponding monocultures, the yield of the more productive of the monocultures or the yield of the less productive of the monocultures. The mean monoculture yield may be appropriate if the desired proportion of the tree species used is more or less fixed and we only need to determine where the trees should be grown. The more productive monoculture may be suitable if the tree species of interest mainly are important in terms of volume production and the value per volume unit does not convey significantly different value from the other. Using the least productive of the monocultures as the reference may be apt in situations where the least productive of the monocultures is a desired tree species.

Aspects of competition

The general hypothesis that yield is likely to be higher in mixtures compared to the expected yield, *i.e.* mean monoculture yield, is based on ecological niche theory, which suggests that stratification of foliage and roots in time or space of tree species with differing properties is likely to reduce competition in mixed stands compared to monocultures (Auclair 1983, Kelty 1992).

Differences between pure and mixed stands may involve differences in the potential uptake of nutrients from the soil, according to studies of the amount and extension of tree root systems. In mixed stands with Sitka spruce and Scots pine, the vertical distribution of fine roots was observed by McKay and Malcolm (1988) to be greater than in monocultures of Sitka spruce, whereas the total root mass was greater in the spruce monoculture. A reduction in the amount of fine roots has been found for Norway spruce in mixtures with birch compared to pure spruce stands (Brandtberg *et al.* 2000). In mixed stands with Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and common beech (*Fagus sylvatica* L.), Henricks and Bianchi (1995) found that the root density of deeper soil layers was greater than in either of the monocultures. In mixtures of Norway spruce and common beech the spruce rooted more shallowly, but the beech rooted more deeply compared to their corresponding monocultures (Roth & Binkley 2001). Utilisation of greater soil depth may be an indicator of access to a greater pool of nutrients in mixed stands. However, since the concentration of roots in the upper soil layer, where the access to nutrients is generally greatest, was lower in the mixture and the root mass was also lower in the mixtures, the results of the work cited above do not necessarily imply that the mixtures have access to more nutrients. According to Roth and Binkley (2001) the most common situation is that mixtures display intermediate values in terms of root distribution and nutrient supply compared to the corresponding monocultures.

Light is utilised and transmitted differently by different tree species due to differences in their specific crown and leaf properties (Terborgh 1985, Canham 1994). Hence, mixing tree species implies that the light regime will be different compared to conditions in the corresponding monoculture stands. Theoretically, competition for light may decrease as a result of a stratification in height with shade intolerant tree species in the upper strata and shade-tolerant in lower strata, which may allow a more efficient utilisation of the site's potential productivity (Assmann 1970, Auclair 1983). However, combinations of crown structures might on the other hand lead to heavy physical competition for space. In some cases such competition may cause severe damage to one of the tree species, leading to growth reductions or even mortality (Kagis 1952, Cayford 1957). Such damage is probably more common in mixed stands, since tree species differ in their physical properties, *e.g.* branch stiffness.

Spatio-temporal stratification of foliage or roots may reduce competition in some types of mixtures, whereas in other mixtures of species it may increase competition. Generally, according to Trenbath (1974) the most common situation in mixtures of agricultural crops is that the total yield lies somewhere between the yields of the more productive and less productive of the corresponding monocultures. However, the yield per individual of either species is rarely equal in the mixture compared to the respective monoculture, suggesting that competitive mechanisms favouring or disfavouring increment affect the mixture that do not occur in the monoculture. According to Auclair (1983), who reviewed forest stand mixtures, the mixture yields lie somewhere between the corresponding monoculture yields in most cases, but comparisons are often difficult to make since many studies use yield tables as a basis for comparison with the mixture. There is often a lack of appropriate control monoculture plots.

Mixed stands differentiate in height growth more than monocultures because tree species differ in their growth parameters (Oliver & Larson 1990). According to Pretzsch (1995) the increment is generally lower when the spatial stand composition is irregular compared to more regular distributions. Norway spruce can be characterised as a shade-tolerant, late-successional species in comparison with Scots pine and birch, the other two major tree species in Swedish forests, which are characterised as shade-intolerant or pioneer species. Lundqvist (1989) found that the mean annual increment using selective cuttings in multi-cohort Norway spruce stands was similar to the volume increment derived from site index estimations for pure even-aged stands. In some stands studied the volume increment was lower with the selection system, which appeared to be due to density effects. It has been well established that increment is positively correlated with stand density (*e.g.* Pettersson 1993, Savill *et al.* 1997). According to Elfving (1990) the volume production in Norway spruce selection forest is generally lower than in even-aged Norway spruce forest. However, under ideal conditions, *i.e.* on fertile soils and with appropriate management practices, selection forests may yield more, due to the loss in growth that occurs during the regeneration phase of the even-aged forests. Scots pine volume production is lower in layered stands compared to single-storied stands, but a two-storied stand with a shade-intolerant species in the upper storey and a shade-tolerant species in the lower storey will yield more than a single-storied monoculture of either species (Auclair 1983, Elfving 1990). according to the same author. Hence, it appears that utilising shade-intolerant and shade-tolerant properties of different tree species may be an effective means of obtaining high volume yield. This may also be an important element to consider when seeking to explain growth patterns in more single-storied mixtures, since tree species rarely have exactly the same increment.

Volume

Spruce and Scots pine mixtures are usually grown on sites where both the spruce and the pine are considered to grow well, and most previous studies have been done under such conditions, *i.e.* on sites of medium fertility. In an experiment with mixtures of Norway spruce and Scots pine, Jonsson (2001) found that the total volume yield up to mid-rotation was greater than the mean yield of the monocultures. According to growth models for Swedish forests, the differences in total volume increment in mixed stands and the mean increment of corresponding monocultures are generally small (Agestam 1985, Ekö 1985). Growth models presented by Pukkala *et al.* (1994) suggest that 10-year volume increment at mid-rotation will be a few percent greater in mixed stands compared to the highest yielding monoculture. In addition, the 35-year volume increment from mid-rotation will be greater when the proportion of pine is gradually reduced by thinnings compared to when the proportions are maintained at a constant level. Poleno (1981) reported that to maximise volume increment the proportion of Scots pine in mixed stands should be gradually reduced from 40-50 years of age.

Compared to the monoculture with the greatest volume yield, Scots pine, Brown (1992) found an 18 percent greater increment in the mixture on experimental plots studied up to 30 years of age. In an experiment by Jonsson (2001) the volume increment of the studied mixture was lower compared to that of the most productive monoculture, which was pine. Wiedemann (1943) observed a greater volume increment in mixed stands compared to pure pine stands and slightly smaller increment compared to pure spruce stands. Agestam (1985) found small differences in total volume increment between the mixtures and the more productive monoculture (spruce) on medium fertility sites. According to Ekö (1985) the volume increment was generally slightly greater in the more productive monoculture (pine where the site index was low, and spruce where the site index was high) compared to the mixtures.

The conflicting results of these studies remain partly unexplained, but it is noteworthy that Brown's study (1992), which found the greatest relative increment for mixtures in terms of volume, was performed in an oceanic climate, whereas the other studies were located in sites with a more continental climate. Furthermore, the mixture in Brown's study was established as group mixtures, whereas in the other studies reported the mixtures were more or less intimate mixtures. Hence the results of previous investigations generally indicate that the yield of mixtures with Scots pine and Norway spruce differ only little from the mean monoculture yield but these indications are to a large extent based on survey material since experiments are rare. A long-term experiment with such mixtures is reported in study II.

Using data from temporary plots, Frivold (1982) studied growth patterns in mixtures of Norway spruce and birch, and found that the total volume in mixed stands was lower compared to pure spruce stands, and close to that of pure birch stands. Based on calculated growth models from temporary plots, Mielikäinen (1985) reported that with an admixture of silver birch (*Betula pendula* Roth.) the total volume increment was increased by a few percent, whereas admixture with downy birch (*B. pubescens* Ehrh.) caused a reduction in total volume increment compared to pure stands of Norway spruce. Agestam (1985) reported a decrease in total volume yield of a few percent in mixtures on moderately fertile sites compared to pure spruce stands. The decrease was greater in stands with a high proportion of birch (50%) compared to stands with a lower proportion (25%). According to Ekö (1985), the total volume yield was smaller in mixed stands compared to pure spruce stands, and the difference increased with longer rotations. In stands with various proportions of birch (5-70%, according to basal area) spruce growth was positively correlated with the proportion of birch (Jögiste 2000). Frivold and Frank (2002) found a 55 percent greater yield in mixtures during early stand development (birch top height < 17m) and similar yields in later stages of stand development compared to pure spruce stands.

In shelterwood mixtures, *i.e.* birch shelter and spruce understorey, the total volume yield has usually been found to be greater in the mixture compared to spruce monocultures during the shelterwood period (see, for instance, Tham 1988, Norokorpi 1994). This has been confirmed in several experimental studies in recent years. According to Mård (1996) the five-year total volume increment following pre-commercial thinning was greater on plots where the shelter was retained compared to plots released from the shelter. In a later study based on the same experimental plots, the total volume increment was still greater on plots where the shelter had been retained compared to those where the shelter had been removed (Johansson 2001). Comparing plots with spruce planted under shelter with plots planted with no shelter up to first thinning, the total mean annual increment in the shelterwood mixtures was on average 24 percent greater compared to pure spruce stands (Klang & Ekö 1999). The increment of Norway spruce under birch shelter was similar to spruce stands released from the shelter during a ten-year period following the removal of the shelter according to Johansson (2001). However, other studies with longer shelterwood periods have reported volume increments to be lower in Norway spruce growing under birch shelter than in the absence of shelterwood (Klang & Ekö 1999, Bergqvist 1999).

It appears that the total volume increment in shelterwood mixtures is greater compared to the fastest growing monoculture (spruce), at least during the shelterwood phase, mainly because of the wood production contributed by the shelter. What happens in the long run is still largely unknown, since the experiments established to study long-term yield in shelterwood mixtures have not yet reached one rotation. The effect of the shelter on Norway spruce growth is influenced by the length of the shelterwood period and the density of the shelter. The growth patterns of the shelterwood mixtures may be used to give insight into expected effects on spruce growth from green tree retention which is studied in Paper V. In the mixtures lacking a clearly two-storied structure the results are not consistent, but the total volume yield generally appears to be more similar to that of the more productive monoculture, spruce. Interestingly, the results indicate that the volume yield of the mixture is more competitive during early stand development, whereas the growth during later stand development is less competitive than in the spruce monoculture. Prolonged rotations appear to decrease the relative productivity of the mixture. Both the species of birch used and the proportion of spruce may be important factors affecting the yield. However, the single-storied mixtures have been less thoroughly studied in experiments and, hence, conclusions based on the literature do not have firm foundations. A long-term experiment with such mixtures has been established as part of this thesis (Paper III).

Growing mixtures of oak and spruce has often been discussed in the literature as a promising means to enhance early volume yield, and thus improve the financial returns of oak stands (*e.g.* Scaffalittzky de Muckadell 1959). Relatively little experimental work has been performed on this type of mixture. However, in mixtures with spruce and oak up to 30 years old Brown (1992) reported that the total volume yield was 2.6 times higher than that of the oak monoculture, 1.1 times higher than the mean monoculture yield and 0.7 times higher than the spruce monoculture yield. In an earlier investigation by Vanselow (1937), the difference in total volume yield between mixtures and oak monocultures up to 60 years of age was similar to that found in the study by Brown. The production and economic performance of mixtures with Norway spruce and pedunculate oak is studied in Paper IV.

Diameter

Diameter increment during 14 yr. in young Norway spruce was greater in mixtures with Scots pine and larch compared to pure stands (Melzer *et al.* 1979). Jonsson (1962) generally found the diameter increment in Norway spruce to be positively correlated with the proportion of pine in the stand. In an experiment with mixed plantations up to 30 years of age, Yanai (1992) reported that the diameter increment of Norway spruce was lower in mixtures with pine compared to pure stands, whereas the diameter increment in pine was greater in the mixture compared to when planted alone. Poleno (1981) found that diameter growth of pine was generally positively correlated to the proportion of Norway spruce admixture in stands of various ages. According to Pukkala *et al.* (1994), the diameter growth in pine at mid-rotation was favoured by an admixture of spruce. Jonsson (1962) found the diameter growth of pine increased with an increasing admixture of Norway spruce in the stand. Hence, pine diameter growth has generally been found to be favoured by spruce admixtures in young and middle aged stands. The effect on spruce diameter growth of pine admixtures is less clear from the literature.

In a study by Bergqvist (1999) the mean diameter of Norway spruce was smaller under birch shelter than in the absence of shelter. In a study by Klang and Ekö (1999) the diameter of spruce tended to be reduced by a birch shelter. Following release from the birch shelter the spruce displayed greater diameter growth compared to the spruce with retained shelter (Mård 1996). Diameter growth in Norway spruce was greater with a 25%

admixture of birch compared to greater or smaller admixtures (Mielikäinen 1985). In a study of spruce mixed with birch, where the mean spruce height was 70 percent of the mean birch height, Frivold (1982) found the diameter of the spruce and birch to be positively correlated to the degree of birch admixture, since the spruce growing with a greater proportion of birch was older than the spruce growing with a small proportion of birch. This illustrates the importance of investigating the age structure in mixtures (Paper III).

Generally, the diameter increment of associated tree species in mixed stands is different from that of the corresponding monoculture, but the effect varies, probably because of differences in the tree species involved, the stand type used, cuttings and site conditions. Birch shelter appears to decrease spruce diameter growth, but the effect in more single-storeyed stands is less evident. Birch diameter growth has been poorly studied in mixtures with spruce. According to Oliver and Larson (1990) tree species that emerge into the upper strata generally have greater diameter increment compared to trees in lower strata. Hence, in mixtures where tree species differentiate in height, the diameter increment of the dominating tree species will probably be greater than in the corresponding monoculture (Paper II).

Height

In even-aged 30-year old mixtures of Norway spruce and Scots pine, spruce top height was greater in the mixture compared to spruce monocultures (Brown 1992). At mid-rotation, Jonsson (2001) found no differences in spruce top height between the mixture and monocultures he was studying, and similar results were found by Hägglund (1975) up to one rotation. Pine top height was unaffected by the mixture in Brown's study (1992) and in Jonssons study (2001), but in harvest age stands, pine top height was found to be favoured by admixture (Jonsson 1962, Hägglund 1975). In mixtures with Norway spruce and oak the top height of both tree species was similar to that in pure stands (Brown 1992). Mielikäinen (1985) found birch top height development to exceed that of Norway spruce up to approximately 40 years of age, after which the difference decreased. Development of the top height in mixtures with Norway spruce is discussed in Papers II and III, respectively.

Height increment in Norway spruce under an overstorey has been found to be lower than in spruce with no overstorey (Assmann 1970). Skoklefald (1989) also found spruce height increment during the first 20 years of stand development to be reduced by an overstorey. However, in a report by Braathe (1988) the ten-year height increment of spruce after pre-commercial thinning was greater on plots where a birch shelter was retained compared to plots where all the birch was removed. According to a growth model for mixtures with Norway spruce and birch, height growth in Norway spruce is increased following release from birch shelter, and released trees attain equal height to unsheltered spruce after a number of years (Tham 1988). Five-year height growth of dominant and co-dominant spruce individuals following release from a birch shelter was greater compared to when the shelter was retained in a study by Mård (1996). In other tree classes, height growth was similar in the treatments. In young stands of planted spruce and naturally regenerated birch, the height growth in Norway spruce was similar on plots where dominant and co-dominant birches had been removed compared to when all birch was left in the stand (Mosandl & Küssner 1999). According to Bergqvist (1999) mean annual spruce height growth up to 56 years of age was similar with and without birch shelter establishment shelter, whereas Klang and Ekö (1999) found the mean height growth in spruce up to 33 years of age to be reduced by a birch shelter. The conflicting results of these last two studies are probably explained by the length of the shelterwood period and by differences in shelterwood density, which averaged 1200 st./ha in the study by Klang and Ekö (1999) compared to 450 st./ha in the study by Bergqvist (1999). Hence, unless the shelterwood period is short and the shelter is very sparse, spruce height growth is probably reduced under birch shelter, largely because of reductions in the growth of dominant and co-dominant spruce individuals.

In mixtures with several stories the growing conditions are probably different from those in single-storied stands. The height increment of the lower storey is generally reduced, at least for some time. Another important factor is the density of the stand. In single-storied monoculture stands of Norway spruce and Scots pine examined by Pettersson (1992) the height increment was greater in dense stands compared to sparsely stocked stands. In single-storied mixtures, the 14-year height increment of young Norway spruce was greater in mixtures with *Pinus* and *Larix* compared to pure stands (Melzer *et al.* 1979). The mixed stands were denser than the monoculture in the cited study. In even-aged mixtures with Norway spruce and beech, height growth of the Norway spruce was similar to that in pure stands studied by Lüpke and Spellmann (1999). Thus, a mixtures where there is growth space to allow and increased density compared to pure stands without any significant stratification into layers the height growth will probably be increased compared to the monocultures.

There are few reports concerning birch height growth in the literature, but it is probably an important factor to study when attempting to grow long-term mixtures, since large-scale height differentiation between the tree species may make the retention of the species mixtures problematic (see Paper III). Birch generally has greater initial height growth compared to spruce, and the reverse may be expected during later stages of stand development (*cf.* Mielikäinen 1985).

Stem form

It is difficult to establish a generally applicable definition of the stem form of trees it varies greatly between individual trees (Larson 1963). However for practical purposes the stem form is commonly estimated as the relationship between height and diameter of a tree and, hence, it depends on its relative growth in diameter and height. The stem form influences the wood value since increases in stem taper increase losses during sawing. Stem form also influences the stability of the tree since trees with increased stem taper are more resistant to wind throw (Valinger *et al.* 1993). Competitive interactions that influence diameter growth and height growth of a tree species in different directions (or degree) will lead to changes in the stem form. Spruce trees under a birch shelter have generally been found to grow more slender compared to spruce trees released from shelter (Braathe 1988, Mård 1996, Bergqvist 1999). Johansson (2001) found the stem taper of suppressed and co-dominant Norway spruce individuals to be smaller in even-aged mixtures with birch, whereas the dominant spruces had greater stem taper in the mixtures compared to the monocultures he examined. In spruce-beech mixtures, where the spruce component was dominant over the beech, the height increment in spruce was similar in mixtures compared to monocultures, but the stem taper was greater in the mixture (Lüpke & Spellmann 1999). In the beech component the stem taper was smaller in the mixture. Dominant trees generally have greater stem taper compared to co-dominant or suppressed trees (Larson 1963). Following pre-commercial thinning in mixed stands of Scots pine and various deciduous trees, the stem taper in pine was smaller on plots with a high density compared to lower density plots after 12 years growth in a study by Karlsson *et al.* (2002). In conclusion, stem form (which is influenced by structure and density of a forest stand) will probably display greater variability in mixed stands as a whole compared to monocultures. In mixtures of tree species that tend to differentiate into different cohorts, the tree species will probably develop a different stem form compared to their corresponding monocultures. Such differences are investigated in Paper II.

Forest health

Damage caused by pathogenic organisms, insects, wind and snow causes great economic losses to forestry every year. Mixed stands are often promoted as being more resistant to damage (see, for instance Seitshek 1989). Forest stands composed of several tree species with differing susceptibility to damaging agents will in most cases react differently to stress compared to pure stands. However, resistance may be either increased or decreased (Heybroek 1980). For example, the probability of insect attack by the spruce budworm in North America was decreased in mixtures with deciduous trees compared to spruce monocultures in a study by MacLean (1996). The fungus *Melampsora pinitorqua*, which attacks newly developed shoots of Scots pine, is generally dependent on the presence of aspen for the fulfilment of its life cycle (Anon. 1995, Savill *et al.* 1997), which has led to the widely-held belief that damage is greater in mixed stands of aspen and Scots pine than in pure pine stands. Another example of admixture increasing resistance can be found in the greater resistance to wind damage expected in mixtures of one vulnerable and one resistant tree species, compared to a monoculture of the vulnerable tree species (see, for instance, Auclair 1983). However, mixtures of Norway spruce and oak were more heavily damaged by wind compared to spruce monocultures, which were believed to be more sensitive, in an investigation by Bilde-Jörgensen (2001). Hence it is not clear that mixed stands in general are more resistant to damaging agents compared to monocultures.

Butt rot in Norway spruce is a matter of great concern since it often causes serious economic losses to spruce stands. Despite intensive research efforts butt rot continues to be one of the most serious problems affecting Norway spruce stands. Spread of butt rot caused by the most important butt rot-causing fungus, *Heterodasidion annosum*, can be restricted with silvicultural measures (Vollbrecht & Agestam 1995). Concentration of thinnings and final cuttings in the winter time (Brandtberg *et al.* 1996), stump treatment to prevent spore infection (Kuhlmann *et al.* 1976) and choice of relatively resistant tree species (Petersen 1989) are all measures that can be taken to decrease the spread of butt rot. Several authors suggested early that the admixture of a second tree species would decrease the incidence of butt rot in Norway spruce (Gayer 1886, Zimmermann 1908, König 1926), but others have argued that levels of butt rot are likely to be similar or higher in mixed stands (Falck 1930, Kangas 1952, Kató 1967, Werner 1971). Several features of mixed stands could make them more or less susceptible to butt rot: Since different tree species differ in their susceptibility to butt rot, a mixture of tree species will have different amounts of susceptible wood exposed to infection as a result of operations such as thinning in comparison to a monoculture. The mixture will also have different spacing between susceptible individuals if a tree species that is more or less resistant is introduced, which may influence the rate of spread of the fungus below ground (Heybroek 1980). The abundance of damaging agents may increase (Werner 1973), but so may the frequency of antagonistic fungi, which may reduce the spread of butt rot (Johansson & Marklund 1980, Fedorov and Poleschuk 1981).

Scots pine is attacked by *H. annosum* (Rishbeth 1951, Rennerfelt 1952), but on most sites in Sweden Scots pine generally exhibits low levels of butt rot caused by this fungus (Rennerfelt 1946, Vollbrecht *et al.* 1995). Rennerfelt (1946) found the frequency of Norway spruce trees with butt rot to be lower in mixed stands with Scots pine compared to pure Norway spruce stands. Bruchwald (1984) found that the total incidence of butt rot was lower in mixtures, and that the difference between mixtures and monocultures was greater in old stands compared to young stands. According to Rymer-Dudzinska (1986), the incidence of butt rot in Norway spruce was lower in mixtures with Scots pine. However, the incidence of spruce butt rot in such mixtures was similar to that in spruce monocultures in a study by Siepmann (1984). Piri *et al.* (1990) found a positive correlation between the proportion of Norway spruce and the incidence of butt rot in the spruce trees. These results indicate that spruce butt rot may be decreased by an admixture of Scots pine.

In Norway spruce mixed with beech the frequency of trees with butt rot has been found to be similar to that in spruce monocultures, but the proportion of butt rot caused by *Heterobasidion annosum* was lower in the mixture compared to the monocultures (Werner 1973, Siepmann 1984). Other fungi, mainly *Armillaria* spp., were more important in the mixture. Piri *et al.* (1990) found a slight decrease in the incidence of butt rot in Norway spruce in mixtures with deciduous trees, mainly birch, compared to pure stands. In stands examined by Peace (1938), Norway spruce in mixtures with deciduous trees was more heavily rotted than in pure stands or mixtures with other conifers. The differing results from different types of mixtures may be partly explained by differences in the tree species used, indicating that admixture of deciduous trees generally does not decrease the incidence of butt rot.

The consensus in the literature cited in this section (*e.g.* Heybroek 1980) suggests that an admixture of a more resistant tree species, *e.g.* Scots pine, with a less resistant tree species, *e.g.* Norway spruce, will decrease the incidence of butt rot compared to monocultures of the less resistant tree species. However, the silvicultural measures taken are generally not fully described in the cited studies. Since silvicultural measures have been found to strongly influence the development of butt rot, in many cases it is difficult to conclude that the obtained effects of mixed stands are generally valid. In contrast to the addition of a more resistant tree species, the admixture of a tree species with similar or lower resistance will probably not have a positive effect (*cf.* Peace 1938) on the incidence of butt rot. The potential for increasing resistance to butt rot using mixed stands was studied in the work described in Paper I.

Summary of the papers

Paper I

To estimate the potential of using mixed stands to restrict the development of butt rot in Norway spruce a study was performed in which the development of butt rot was compared in pure Norway spruce stands and stands with various degrees of admixture of Scots pine. The data consisted of repeated measurements from permanent experimental plots in southern Sweden. Previous measurements taken in the stands were known and well described, as was the previous land use. Altogether, 100 pure spruce plots and 22 mixed stand plots were used. Using a logistic equation calculated from the resulting data, butt rot frequency in Norway spruce was predicted for cases with 0, 25, 50 and 75 percent Scots pine admixtures, according to basal area.

The butt rot frequency in pine was consistently very low on the plots (<1.5%) and, consequently, the total frequency of butt rot was much lower in the mixed stands compared to the monoculture. The study also revealed that in the mixed stands the proportion of spruce trees with butt rot was lower than in pure Norway spruce stands. The difference could not be explained by differences in site, silviculture or windthrow since these factors were accounted for in the study. The most probable explanations for the reduction in butt rot was that less spruce wood was exposed in thinnings and the spread of the fungus below ground was reduced, due to the greater resistance of Scots pine to infection. The most significant effect of an admixture of Scots pine on butt rot development in Norway spruce was found when the Scots pine admixture was 50%. The findings in this study show that admixture of Scots pine may provide an effective means to reduce the frequency of butt rot in Norway spruce in southern Sweden.

Paper II

The use of mixtures of Norway spruce and Scots pine has a long tradition in Sweden and such mixtures cover approximately 16% of the country's forestland. The mixtures are considered easy to manage. The increment in such mixtures has not been studied intensively in experiments, but growth simulators indicate that the volume increment is similar to that in pure stands on many sites. Experimental growth data collected over twenty years were used to estimate volume increment and yield in mixed and monoculture stands with Scots pine and Norway spruce on sites of medium fertility for southern Sweden. The materials examined in the experiment were a mixture of 50 percent spruce and pine (by stem number) and pure pine and spruce stands. Measurements were taken every fifth year during the time period studied.

Differences in total volume increment were generally small between the different types of stands, indicating that there is little to be gained in terms of total volume increment from using mixed stands with Norway spruce and Scots pine instead of monocultures on sites with medium fertility. During the course of the observation period the volume increment was greater in the mixture and the spruce monoculture compared to the pine monoculture, supporting expectations that the growth of the spruce would tend to increase due to differences in the growth rhythms of the tree species. Since the volume increment of pine per unit area was higher in the mixture compared to the monoculture, the results indicate that retaining some Norway spruce in Scots pine stands is likely to increase the total volume increment. The diameter growth of the Scots pine was greater in the mixture compared to the monoculture, resulting in 1.2 cm greater mean diameter in the mixture at the end of the observation period. This is explained by the smaller increment of the spruce component, implying that the competition from the spruce was less intensive compared to the competition from the pine. The pine stems developed greater stem taper in the mixture than in the monoculture, which was explained by their relative size compared to the spruce component. There was no layering on the plots, but the Scots pine trees were slightly taller and thicker than the spruce. Diameter distributions of the total tree population as well as those of the Scots pine and Norway spruce were similar on the plots at the start of the experiment. However, at the end of the observation period the pine diameters in the mixture were significantly more clustered round the mean compared to the pine monoculture (coefficients of variation; 0.16 and 0.26, respectively). The diameter distribution of the total tree population in the mixture tended to be less tightly clustered round the mean than in the monocultures.

Paper III

Many deciduous tree species are difficult to establish in southern Sweden due to factors such as browsing by wild animals. Birch is a tree species that produces economically valuable wood and regenerates spontaneously on many sites. It is, therefore, an attractive tree species to use to increase the amount of deciduous trees in Swedish forests. Previous investigations of birch and spruce mixtures in Sweden have focused on two-storied stands with birch shelter. In those studies the total volume increment has generally been found to be higher in the mixtures compared to spruce monocultures, provided they are properly managed. To retain the birch in the stand for a prolonged period it may be necessary to create single-storied mixtures. Such mixtures have not been studied much under experimental conditions. Thus, our knowledge of the increment and yield of such mixtures is poor. The studies that have been performed have been mainly based on surveys, and have indicated that the volume increment is similar or lower in the mixtures compared to spruce monocultures.

A field experiment was established in a 16-year old planted Norway spruce stand with abundant, spontaneously regenerated silver birch. The purpose of the study was to investigate the increment and development in long-term, single-storied mixtures compared to spruce monocultures and to obtain knowledge relevant to the management of such mixtures. Three treatments were randomly applied to nine plots divided into three blocks and, hence, there were three replicates of each treatment. The treatments were: spruce monoculture, and spruce with 20% birch and 50% birch admixtures by stem number. The treatments were applied in such a way as to minimise the height difference between the birch and the spruce. The experiment was re-measured after four growing seasons when the age structure of the birches was also studied.

The birches in the stand were established during a ten-year period, starting four years before and ending six years after the spruce was planted. Height differentiation, which occurred prior to the treatment of the stand, could not be eradicated completely by pre-commercial thinning. Height growth and development of dominant height between 1998 and 2002 was similar in the spruce and birch on the mixed plots, indicating that the height differentiation had stopped. Spruce height growth and development of the top height was similar in the treatments. This was also true for birch. Diameter growth in spruce was also similar in the treatments. In birch, the diameter growth was greater in the 20% admixture compared to the 50% admixture. This was probably due to the total initial density and the initial density of birch being lower in the 20% birch treatment. Total basal area growth was greatest in the 20% admixture, due to enhanced spruce growth in this treatment. The height distribution of the total tree population was more clustered (*i.e.* the tree heights had a lower coefficient of variation) in the spruce monoculture compared to the mixtures. Crown damage to the tops of Norway spruce trees was higher in the mixtures. Severely damaged spruce trees had lower height increment compared to undamaged trees. The amount of damage changed from year to year, indicating that crown damage to spruce associated with whipping by the birch was not persistent, so it is unlikely to seriously affect the value of future harvests in the mixed stands.

Paper IV

Oak forests in Sweden are mainly found in the southern part of the country. Compared to the dominating tree species used in forestry, the silviculture of oak is characterised by long rotations and low volume increments. The valuable harvest from oak stands occurs at the end of the rotation, which is typically 120-150 years. During the first half of stand development, net values from thinnings and other silvicultural measures are usually negative. Introducing spruce into oak stands has been suggested as a means to increase early incomes and to increase the volume increment. In this study, stand data from a mixed forest stand with oak and spruce were used in combination with growth simulators to evaluate the outcome in terms of increment and economic performance against monocultures of oak and spruce. Using the increment parameters obtained from the stand, and corresponding parameters generated by the growth simulators, the yield parameters of the mixture were evaluated against those of the monocultures. Using current market prices and five different scenarios, the economic outcomes derived by deducting costs for tending the stands from the income from wood sales were calculated. The tested scenarios were: exclusion of state subsidies for oak silviculture, price increases for oak wood, discounts for oak tending, reduction of risks in Norway spruce due to hazards such as butt rot, windthrow or insect attack, and a control scenario with current conditions. The figures obtained on incomes and payments over time were analysed using land values, cashflow and accumulated net values.

Mean annual increment, MAI, at mid-rotation was greater in the mixture compared to the oak monoculture, but at one rotation the difference was smaller, because the spruce had to be removed from the stand to prevent it from inhibiting the growth of the oaks. The spruce volume increment was almost as great in the mixture (90%) as in the monoculture during the time spruce was retained in the stand. The diameter increment in oak was lower in the mixed stand compared to the monoculture. In previous work, the proportion of spruce was recommended to be smaller than in this study, especially in young stands, to maximise the oak increment. The land value of the mixture was higher compared to the oak monoculture at low interest rates, owing to early returns from spruce thinnings in the mixture. At the highest interest rate used (4%) land values were similar in the mixture and the oak monoculture. The greatest land values were obtained with the spruce monoculture, irrespective of which scenarios were compared. The oak monoculture was particularly sensitive to changes in timber prices or subsidies at low interest rates. The mixture was the most stable stand type with respect to changes in economic conditions.

Paper V

In recent years retaining overstorey trees after harvest has become a common recommendation and practice in Swedish forestry. The retained trees are left to grow, eventually die and break down from natural causes. The retention of old trees is considered to enhance biodiversity values. However, the effects on increment and yield of this practice are largely unknown. Therefore a field study was established in a 25-year old, unthinned Norway spruce plantation on a fertile site in southern Sweden with large retained deciduous trees. The overstorey consisted mainly of pedunculate oak, European aspen (*Populus tremula* L.) and Norway maple (*Acer plataniodes* L.) with a mean height of 22 m and an average density of 6.1 m^2 per hectare. The experimental design consisted of a grid of 3-m radius spruce sample plots where growth parameters were recorded. The size and diameter growth of the overstorey trees was measured, as well as their position in relation to the spruce plots.

The effect of overstorey retention is likely to vary over time. For young seedlings it is recognised that an overstorey may improve establishment and early growth by improving the growing conditions for the seedlings on sites liable to adverse conditions, such as early summer frosts. When the seedling establishment has been secured, competition from the overstorey trees becomes more important. Retention of overstorey trees for the enhancement of biodiversity may very well prove to have beneficial effects on the regeneration, but unlike shelterwoods the overstorey is not removed when the regeneration is secured. Consequently, overstorey retention is expected to reduce growth in the new stand. Thus, it is important to know the magnitude of such a growth reduction in order to estimate the price we pay for taking these measures to enhance biodiversity values.

The increment on the spruce plots with a dense overstorey of retained trees was significantly lower compared to plots with little or no overstorey. Previous results from similar types of long-term overstorey retention studies support these findings, as well as studies on the effect of long-term shelter on understorey spruce growth. Investigations into the effect of retention trees on Douglas fir in North America have been performed in stands of various ages, and their results suggest that such growth losses are persistent. A distance-dependent competition model was used to predict the influence of retaining various low densities of overstorey trees on the spruce growth. Five different densities were used: 0, 5, 10, 15 and 20 deciduous trees per hectare. The results indicate that retention of even a few large deciduous trees per hectare reduces basal area, height and diameter growth in the spruce understorey. In fact, the greatest reduction per retention tree was found at low densities, whereas the difference between 15 and 20 trees per hectare was small. Hence, a clustered distribution of retention trees is probably more effective than a dispersed distribution. Total productivity of the forest may not be affected if the growth of the overstorey is similar to the growth reduction in the understorey. In this experiment the growth of the spruce with no overstorey was greater than the growth of the understorey plus overstorey.

Discussion and conclusions

Volume increment and yield quality

Height differentiation may cause silvicultural complications. Unless it is appropriately regulated, height differentiation in mixtures of tree species with different growth parameters, such as Norway spruce-Scots pine mixtures and Norway spruce-birch mixtures may have detrimental implications for both the volume yield and the quality of the yield. Compared to monocultures, optimisation of increment and yield in mixtures requires one more factor to be regulated compared to monocultures, namely species composition.

To maximise volume increment, the most suitable species proportions in mixtures is likely to vary during stand development due to differences in the growth rhythms of the different species. This was indicated in the pine mixture (Paper II), where the growth increase in the mixture was greater than in the pine monoculture, although the pine monoculture had the greatest mean annual increment. In this case the proportion of spruce should probably be gradually increased to maximise the total volume increment in the stand. This hypothesis is corroborated by previous studies of mixtures with Scots pine and Norway spruce (Poleno 1981, Pukkala *et al.* 1994). In the birch mixture (Paper III) the study period was too short to draw any firm conclusions, but combined with findings from previous studies where shelterwood mixtures generally out-yield single-storied mixtures, the results suggest that this is also valid for birch mixtures, *i.e.* the proportion of spruce should be increased in older stands. In the retention tree mixture (Paper V) the total volume yield was lower than in spruce monocultures, but in this case adjustments of the species composition would probably not compensate for the growth losses, and it would not be possible to change the basic structure in this respect unless the overstorey was removed.

The effect of physical competition on the quality of the yield was evident in the oak mixture (Paper IV), where complete removal of the spruce was enforced at mid-rotation so as not to jeopardise the development of the oaks. Damage to Norway spruce caused by the mixtures was generally minor or insignificant in this thesis. Crown damage to spruce over-topped by other tree species that under extreme conditions (*i.e.* a dense overstorey of trembling aspen) has previously been reported to cause persistent growth reductions or even mortality (Kagis 1952, Cayford 1957) occurred in the birch mixtures in Paper III, as well as in previous studies (Frivold 1982, Mielikäinen 1985). However, the damage was not generally so extensive or persistent for it to be likely to have any significant effect on yield quality. In the pine mixture (Paper II) no differences in the technical quality of either tree species were found between the mixture and the monocultures. In the first study (Paper I) pine admixture had a positive effect on the quality of the yield by reducing wood decay in spruce caused by butt rot, which is consistent with the principles for interactions between resistant and susceptible trees in mixed stands (Heybroek 1980).

The volume or basal area increment of individual tree species was generally higher in one of the species, at the expense of the other in the mixtures, and the growth of the favoured tree species was stimulated by increased proportions of the dominated species. This conclusion was supported in all studies where the increment was examined (Papers II-V). In the study reported in Paper II, the increment in Scots pine was increased in the mixture compared to the monocultures, whereas growth of the spruce appeared to be decreased for a long time. Similar results were found by Jonsson (2001). The birch growth (Paper III), although only studied over a short period, tended to be enhanced by an increased abundance of Norway spruce, whereas spruce growth was greater with a relatively small proportion of birch (*cf.* Frivold & Frank 2002). In oak mixtures (Paper IV) spruce growth was almost as great in the mixture as in monocultures during the spruce rotation (90%), in spite of the presence of oak, whereas the growth in oak tended to be lower in the mixture compared to oak monocultures. In the retention tree mixture (Paper V) spruce growth had a strong tendency to be reduced by the retention trees, corroborating the findings of previous workers (*e.g.* Acker *et al.* 1998). A proposed model for increment interactions and compensatory growth in single- or two-storied mixtures with two tree species is illustrated in Figure 1.

Diameter, height and stem form

A similar pattern, of one tree species growing faster at the expense of the other, was also valid for the diameter growth (Fig. 1). In the pine mixture (Paper II) the Scots pine had greater diameter growth compared to the pine

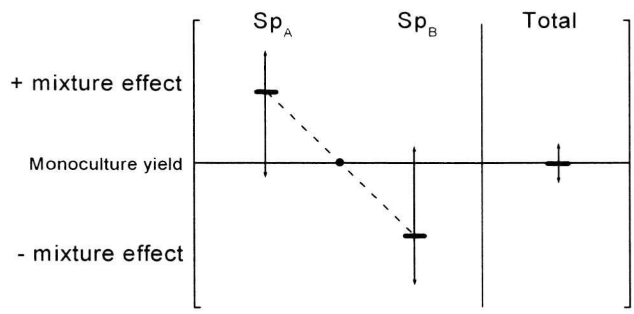

Figure 1. Proposed model of productivity interactions in mixed stands. A positive mixture effect on one of the tree species (Sp_A) is generally associated with a negative mixture effect on the other species (Sp_B), and a change in the level of either species will generally result in a change in the opposite direction for the other species. The association between species productivity (dashed line) may assume a different shape and slope as a result of silvicultural measures, *e.g.* thinnings and choice of tree species. Note that the total increment of a given stand type varies considerably less than that of the individual tree species.

monocultures. This was also found by Jonsson (1962) and Pukkala *et al.* (1994). The spruce diameter growth tended to be smaller in the mixture than in monoculture. Birch diameter growth (Paper III) was greater on plots with a greater proportion of spruce compared to plots with a smaller proportion, whereas spruce diameter growth did not differ significantly between the treatments. Oak (Paper IV) appeared to have greater diameter increment in pure stands compared to mixtures with spruce. Large overstorey trees decreased the diameter growth in spruce (Paper V).

In contrast to the diameter growth, height growth in individual tree species was not significantly different in the mixtures compared to the monocultures (Papers II and III). This may be explained by height growth generally being less affected by competition than diameter growth (Caldwell 1987). The differences in height growth between the tree species in the mixtures of Papers II and III were relatively small, indicating that height differentiation was not problematic for the management of these mixtures. The stem taper in the tree species that was dominant in the mixture was greater than when the same species was growing in monocultures (Paper II). Stem taper was not studied specifically in the birch mixture (Paper III), but since the diameter growth in birch was greater in the 20% compared to the 50% birch admixture, the stem birches were probably more slender on the plots where there was more birch. In accordance with the stem taper results presented in Paper II, the crown base of pine was lower in the mixture compared to the monoculture.

Yield assortments

A greater size stratification in mixtures compared to monocultures may be considered to be of particular importance since the mixtures contain an additional source of variation in the yield assortments, *i.e.* different tree species. The number of tree species, diameter distribution and stem form are important factors influencing the composition of the harvest. The diameter distribution of individual tree species was more clustered in the pine mixture (Paper II), but in the birch mixture (Paper III) no such tendency could be detected, at least at the time of measurement. However, the total diameter distribution generally tended to be wider in the mixtures compared to the monocultures, implying there was greater stratification of log dimensions of harvested volumes in mixtures compared to monocultures. This was also found by Utschig (1999), who compared monospecific spruce stands with mixtures of several tree species. In the oak mixture (Paper IV), size stratification between the tree species was detected, but since the spruce was mainly harvested during the spruce rotation the difference between these mixtures and the monocultures in yield assortments per cutting was considered to be small.

Silvicultural possibilities and limitations

The need for silvicultural measures to control stand structure is probably greater in mixed stands than in even-aged monocultures, since they have a stronger tendency to form layered stands. The need for such measures will probably increase with a more pronounced difference in growth between tree species, and/or increases in the number of tree species. In the oak mixture (Paper IV) silviculture up to mid-rotation was particularly intensive, even in comparison with typical silviculture of oak monocultures (which is considered an intensive form of silviculture). However, using appropriate tree species and types of mixture the amount of additional measures needed in mixtures can probably be reduced to similar levels to those deployed in monocultures in many cases. This may be achieved with spruce and pine mixtures (Paper II), for instance, and to some extent with spruce and birch mixtures (Paper III) and retention tree mixtures (Paper V).

Scots pine and Norway spruce

Butt rot is the most serious disease in terms of economic losses to established stands of Norway spruce in southern Sweden. The results reported in Paper I reveal that admixture with a second, more resistant tree species, Scots pine, may reduce the proportion of Norway spruce trees with butt rot. Since extremely few Scots pine suffered from butt rot, the total proportion of butt rot was also reduced in the study. These findings are supported by previous studies. The greatest relative effect of a Scots pine admixture was seen at 50 percent admixture. It is shown in Paper II that mixtures of Norway spruce and Scots pine do not imply any significant reduction in total volume increment compared to pure stands on sites of medium fertility in southern Sweden. Previous research supports these findings. Furthermore, there is extensive practical experience from Scots pine mixtures in forestry, and the mixture is generally considered easy to manage. Therefore, mixed stands of Norway spruce and Scots pine are recommended for practical use to restrict butt rot in Norway spruce, while sustaining total volume increment. However, since the mechanisms responsible for the decreased incidence of butt rot in mixed stands have not been fully investigated, the recommendations should be treated with caution, and only applied to conditions similar to those in the study before further investigations are made.

Birch and Norway spruce

Use of long-term mixtures with birch and spruce where both tree species are grown to fully utilise their economic potential has been proposed as a possible way to increase the long-term admixture of deciduous trees in spruce stands (and amounts of deciduous trees in general) while sustaining volume yield and value. An experiment with such mixtures has been initiated and first results indicate that damage and associated with the mixture is not a serious problem. Field experiments with single-storied mixtures of birch and spruce have not been studied much before this work was initiated. More work remains to be done before final conclusions can be drawn regarding the increment and yield in such mixtures. Survey material and growth models indicate that the total volume yield may be similar to that obtained in spruce monocultures. On the other hand, stratified mixtures with regeneration of Norway spruce under a birch shelter have been studied intensively in recent years (*cf.* page **13**) and there is also considerable practical experience on the use of this system. Provided it is well managed, the total volume increment is generally greater than in spruce monocultures. Adoption of shelterwood mixtures in practical forestry therefore implies no great risk in this respect. To maintain long-term mixtures using the shelterwood system, a theoretically possible solution may be to retain a proportion of the shelterwood in the future stand.

Oak and Norway spruce

An addition of Norway spruce to oak stands improves their economic returns by increasing early net incomes from them. The volume increment is increased compared to oak monocultures, although not as much as may be expected from the high initial increment of Norway spruce, since it is difficult to retain Norway spruce in oak stands longer than up to mid-rotation of the oak without hampering the oak's development. If the alternative is a pure Norway spruce stand, oak mixtures cannot be recommended judging from the perspective of volume production. However, the increased robustness and more stable economic performance of such mixtures under changing conditions still make their use an interesting option compared to the oak monoculture. The mixture required intensive tending during the first half of the oak rotation to regulate the competition from the spruce, which may be problematic in some cases since delayed measures will probably have serious detrimental effects on the main oak crop. However the overall difference in silvicultural intensity is probably small. Management of the mixture was a balance between the desire to increase the productivity of oak stands by incorporating Norway spruce in as large proportions as was considered possible and for as long a time period as possible on the one hand, and the desire to avoid competition that would hamper the growth and vitality of the oaks. To deal with the latter previous work have suggested the proportion of spruce to be smaller compared to this study which may be a successful strategy unless hazards such as windthrow is associated with such measures.

Retention tree mixtures

The retention tree mixtures pose different conditions for wood production compared top the other mixtures studied in this thesis, since the retention trees are not accessible for wood production and hence the total productivity of the stands may be considered to be less important for wood production compared to their effect on the understorey productivity. Present recommendations for retaining large live eternity trees in forest stands influence the new conifer stand. Results of this work indicate that retaining large deciduous trees as opposed to clearcutting causes substantial growth losses to understorey Norway spruce, Whether the benefit gained from enhancement of biodiversity values from green tree retention exceed the value of the growth losses remain an unanswered question at this stage. However the results of Paper V indicate that to minimise the growth reductions to understorey spruce green tree retention should be concentrated in certain areas rather than spread out.

Concluding remarks

Increment and yield vary greatly between different types of mixed stands, so each type of mixed stand should be evaluated separately according to its own merits. Although the work underlying this thesis was restricted to two-species mixtures with regular structures there were great differences between the different types of stands studied in terms of structure, silviculture, growth and health. These differences emphasise the point that generalised judgements of any property of mixed stands should be made with even more care than for monocultures. Some of the most important factors influencing the results when comparing the increment and yield of mixed stands with monocultures are the tree species used, the structure of the mixture, the species proportions, the duration of the species mixture, damage that may occur, site properties and the choice of reference stand. Any serious attempt to evaluate a mixture against monocultures should consider most of the abovementioned factors. This thesis reveal some important properties of mixed stands with Norway spruce. For example, the total volume yield using an admixture of Scots pine may be maintained at a similar level to that obtained in the more productive monoculture. Certain types of mixed stands require more intensive silviculture to be successful, e.g. mixtures with oak, whereas other types, *e.g.* mixtures with Scots pine are easily manageable. It has also been shown that there are possibilities reducing wood decay in Norway spruce by using mixtures with a more resistant tree species, Scots pine.

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