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Volume yield to mid-rotation in pure and mixed sown stands of *Pinus sylvestris* and *Picea abies* in Sweden

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Abstract

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Volume yield to mid-rotation in pure and mixed sown stands of Scots pine and Norway spruce was investigated in an experiment in central Sweden. The 43-year-old stands were situated on a 7-ha site and were treated and inventoried at the time of establishment, then at intervals in the life of the stands, to give results at half-rotation age. The dynamics of the mixed stands implied a favourable ecological mixed-stand effect on the height growth of spruce in early development and before crown closure. Even at this stage, pines were taller than spruces, but height was not influenced by admixture with spruce. Pines continued to grow faster than spruces in both height and diameter, resulting in dense mixed stands with dominant pines and co-dominant or suppressed spruces. Diameter of pines was increased by weaker competition for nutrients, while weaker competition for light led to a lower height of dominant pines in mixed stands than in pure pine stands. The results indicate a slight etiolation effect of competition for light in the crown layer. Total volume yield was higher in mixed stands than the mean yield in pure stands of pine and spruce, mainly owing to the dominance of pine in mixed stands. However, it was lower in mixed stands than in pure pine stands. The growth dynamics to the present time indicates that, after a slow start, volume growth of spruce increases remarkably in pure stands and increases slightly in mixed stands, while volume growth of pine began early and is culminating.

Key words: boreal forests, mixed stand yield, pure stand yield, fertilisation, windthrow.

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Introduction

The mixed-forest concept includes a number of specific questions. A plan for an investigation of mixed forests, presented in 1905 by the German federation of forest research institutes, defined a number of problems in this field of study. According to the plan, the investigation had a threefold aim (Schwappach, 1909; Borgman, 1916):

(1) Comparison of the development of mixed stands with that of pure stands,
  (a) as regards the development of increment,
  (b) as regards volume yield, with particular attention to quality,
(2) Establishment of mixed stands on different sites and examination of the most suitable method of regeneration,
(3) The most economical treatment of mixed stands.

With respect to (1) above, the present investigation concerns only the volume yield and volume components. With respect to (2), the type of mixture, it is restricted to pure stands and to mixed stands of Scots pine and Norway spruce. With respect to the form of the mixture, the investigation is restricted to even-aged, single-storey stands with an individual mixture of the tree species concerned.

Jonsson (1962) presented an analysis of mixed stands of Scots pine and Norway spruce, based on non-experimental sample plots. As that study repeatedly argues, causal conclusions, drawn from non-experimental material regarding less clearly evident effects, are often unreliable. For an insight into causality, experiments are required.

Consequently, three major experiments involving pure and mixed stands of Scots pine and Norway spruce were set up in Sweden (Jonsson 1961, 1976; Holm *et al.*, 1984; Jonsson, 1999). The primary aim of the present study was to test the hypothesis whether mixed stands in a certain site quality range give a higher yield than pure stands (see Jonsson, 1962, Fig. 1, p. 9). The three experimental areas reflect different site quality ranges.

It should be borne in mind that the results from the present study are half-time results, since the stands have reached only half-rotation age.

Material & Methods

Situation, climate and site

The experiment is situated at Främlingshem, Sandviken municipality, Sweden (60°30′N, 16°54′E), on level ground *ca.* 70 m a.s.l. The nearest meteorological station is at Gävle, *ca.* 22 km NE of the experimental site, 33 m a.s.l. In the period 1951–1980, the mean annual temperature was 5.0 °C; the mean temperature in June, July and August was 14.5 °C, 16.0 °C and 15.0 °C, respectively (Eriksson, 1982). The mean annual precipitation for 1951–1980 was 596 mm, while mean precipitation for June, July and August was 43, 72 and 81 mm, respectively (uncorrected values). The mean annual precipitation, corrected for the location of the gauge, was 725 mm (Eriksson, 1983).

According to Odin *et al.* (1983), the length of the growing season at the site is *ca.* 185 days (threshold temperature 5 °C). On average, the growing season begins on 20 April and ends on 20 October. The temperature sum during the growing season, derived by summing the temperature of days with a mean temperature >5 °C, is *ca.* 1300 day-degrees.

According to the classification of Hägglund & Lundmark (1981), the average site index for the experiment, assessed from height curves, is T26.9 for pine and G24.6 for spruce (see Table 1 and Fig. 1), *i.e.* dominant height at age 100 years would be 26.9 m and 24.6 m, respectively.

Experimental design

The experiment was laid out in ten randomised blocks (numbered 0–9), each block including three 35 × 40 m parcels with 5 m borders. Thus, the experimental site comprised 6.75 ha in total. There were three treatments: a pure Scots pine (*Pinus sylvestris* L.) stand, a pure Norway spruce (*Picea abies* (L.) Karst.) stand, and a stand with Scots pine and Norway spruce in equal numbers. Treatments were randomly assigned to the parcels within each block. All stands were established by sowing on a clearfelled area.

In practice, parcels belonging to the same block were situated close together on as uniform an area as possible. Owing to wide variation within the extensive clearfelled area, the blocks were distributed throughout the area, to obtain uniform conditions for each block. Thus, the distance between the outermost blocks was four kilometres.

Terminology

In what follows, Scots pine stands are denoted PI, Norway spruce stands SP, and the mixed stands MI. The combination pi|PI denotes Scots pine trees in pine stands, pi|MI Scots pine trees in mixed stands, sp|SP Norway spruce trees in spruce stands, *etc.* A numeral after such a combination, *e.g.* pi|PI|26, denotes stand age.

Statistical significance is shown thus: *, ** and *** denote significance at the 5%, 1% and 0.1% ($p \leq 0.001$) levels, respectively.

Initial situation

The experiment was laid out in 1961 on an extensive, previously sown area. At that time, the plant stand was only five years old. The following measures had previously been implemented:

At the beginning of January 1954, a storm caused widespread windthrow in this part of Sweden (Werner & Årman, 1955). In the following years, the ravaged areas were cleared and restored. The fallen timber was harvested in 1954/55, and the clearfelled area, on which the experiment was laid out, was cleaned in 1955 and then burnt and sown. Blocks 0–7 were burnt and sown in 1956, and blocks 8–9 in 1957. Mixed seed of Scots pine and Norway spruce was sown in equal proportions on elongated scarified patches. A spacing of 1.7 × 1.7 m was aimed at. The seeds were from the same district and altitude as the experimental area, and were collected in 1953 (pine) and in 1955 (spruce).

Seeding resulted in a plant population of closely spaced, dense clusters of both pine and spruce.

Observations and measures in 1961 (stand age: 5 years)

On each parcel, 12 circular sample plots with radius 3 m ('circular plots' in what follows) were laid out in a systematic pattern. In all, the circular plots covered 24% of the area of each parcel. Before cleaning, the following properties were noted on each circular plot: The number of plant clusters was summed twice and recorded individually. First, if the tallest plant per cluster of pine was within the circular plot, the clusters were counted. Secondly, if the tallest plant per cluster was spruce, the same procedure was carried out. In the northernmost and southernmost clusters, (a) the number of pine and spruce plants was counted, (b) the height of the tallest pine and spruce was measured and (c) the length of the cluster was measured.

After this inventory, the various treatments (PI, SP, MI) were randomised on the three parcels within each block. In accordance with the experimental plan, the plant population on the parcels was transformed by cleaning in 1961, into pure Scots pine stands, pure Norway spruce stands and stands containing Scots pine and Norway spruce in equal numbers. The tallest plant per cluster of the desired tree species was retained. On some parcels, the number of plants after cleaning was so small, that some restocking of blanks was required.

Observations and measures in 1976 and early 1983 (stand ages: 20 and 26 years)

In 1976 and 1983, diameter and height of all trees on the 12 circular plots per parcel were measured. In 1976, height increment of the same trees during the latest five years was also measured. Cleaning/thinning was also carried out (Table 4 and Fig. 3).

A further windthrow

About 1988, a further minor windthrow occurred on some parcels. The fallen trees were harvested in a practical forestry operation, without our knowledge or involvement. Fortunately, the stumps were preserved, making it possible to reconstruct the windthrow.

Fertilisation

From August 1981 up to and including 1990, block 5 was treated with combined irrigation-fertilisation by the forestry company which owned the experimental area, as a concession to the company. A requirement was that all three parcels within the block should be fertilised equally. The total supply of plant nutrients during the period was 1160 kg N, 332 kg K, 100 kg P and 10.7 kg B ha^{-1} (Willén, 2001). The annual water supplied was 100 mm, distributed over 100 days.

Observations 1999-2000 (stand age: 43 years)

Between 1 October 1999 and 3 June 2000 (*i.e.* between the growing seasons), the following properties were observed:

(a) All living and dead trees were calipered on bark (o.b.) at breast height (BH, 1.3 m), and recorded individually. In all, 6041 trees were measured. (b) The tree species was also recorded individually, as well as the character of any damage and the cause of death.

Trees were sampled with a probability proportional to the square of diameter at breast height (DBH). In all, 1103 sample trees were measured. The following characters were measured: (a) DBH o.b., (b) height, (c) height to live crown base, and (d) bark thickness at BH.

On each parcel, four circular plots with radius 10 m were laid out contiguously. In what follows, they are denoted '10-m circular plots'. On each such plot, the two dominant trees (*i.e.* the two trees with the largest DBH) per tree species were chosen. The same properties were measured as for the sample trees. Thus, 2 × 4 dominant trees on each pure parcel and 2 × 2 × 4 on each mixed parcel were obtained (with some exceptions; see below).

The following observations were made in October 2000, to reconstruct the windthrow and the contemporary sanitation felling: (a) The tree species and diameter under bark (u.b.) of all relevant stumps – *i.e.* only stumps connected with the windthrow and felling – were recorded. (b) On some standing trees per parcel, tree species, DBH o.b., and diameter o.b. and bark thickness at stump height, were recorded.

Calculation of volume and height of calipered trees

Tree volume was determined for (a) each sample tree and (b) each calipered tree. First, tree volume was calculated for each sample tree by means of Brandel's volume functions (Brandel, 1990). A volume curve was then constructed, with tree volume as a function of tree diameter, according to the following model (Jonsson, 1978):

$$\ln \mathit{Volume} = \alpha + \beta_1 DBH + \beta_2 \ln DBH \quad (1)$$

Such a volume curve was made for each tree species and parcel stand. In total, 40 such curves were produced (unpublished).

In the same way, a height curve was made for each tree species and parcel stand. Forty such curves were produced (unpublished). In this case, the following model was used:

$$\ln \mathit{Height} = \alpha + \beta_1 DBH + \beta_2 DBH^2 \quad (2)$$

Volume and height were then estimated from the above functions, for each calipered tree. Diameter, height and volume were thus available for each calipered tree, as well as for each sample tree in the entire experiment.

The volume unit is m^3sk, *i.e.* forest cubic metres (whole stem including bark).

Reconstruction of the volume of stump-trees

Data from the stumps were used to reconstruct the original standing trees, by means of measurements from trees calipered at both BH and stump height (see above). For these trees, a regression function was estimated for each tree species for pine and mixed parcels, according to the following model:

$$\ln(DBH_{o.b.}) = \alpha + \beta_1(\text{stump diameter}_{u.b.}) + \beta_2 \ln(\text{stump diameter}_{u.b.}) \quad (3)$$

Since there were no stumps on spruce parcels, a corresponding function for spruce on such parcels was not required. Thus, three such functions were calculated (unpublished), and used to reconstruct the DBH o.b. for each stump.

From the sample trees, a height curve was calculated for each tree species and parcel of interest. The following model was used:

$$\ln \mathit{Height} = \alpha + \beta_1\ 1/DBH \quad (4)$$

Thirty such curves were produced (unpublished). This model gave 'stiffer' curves than the height curves described above. This was necessary to allow extrapolation for small stumps. From these curves, a height was estimated for each former tree, valid for 1999. To reduce tree height to the 1988 level, the estimated height was multiplied by 0.8.

Given an estimate of DBH o.b. and height for each former tree, its volume was calculated by means of Brandel's volume functions (Brandel, 1990). The total volume of the former trees was then calculated for each tree species and parcel.

Remarks on the analysis of variance tables

The number of hypotheses is large. The conceptual level of significance throughout is the single test. The reason for this is that the response variables differ between the tests; hence procedures for testing the level of significance for the multiple comparison at a higher level cannot be applied. For some tables, MANOVA could have been used (*e.g.* Table 10b), but this is barely justifiable. It is evident that the test outcomes in these cases may be highly correlated.

Results

Stand

Site index, height and diameter of dominant trees in 1999

The height and diameter of two dominant trees per tree species were measured on four 10-m circular plots per parcel in 1999, *i.e.* 2 × 4 trees on each pure parcel and 2 × 2 × 4 trees on each mixed parcel (above, p. 5). The dominant pine trees in pure and mixed stands were suitable for determining the pine site index for each 10-m circular plot. Thus there are four pine site indices for the stand on each such parcel. In the same way, the dominant spruce trees in pure spruce stands were used for determining four spruce site indices for each parcel. The dominant spruce trees in mixed stands were not suitable for use in this way.

A mean site index was determined for the stand on each parcel ('parcel SI'), and a mean height and diameter for eight dominant trees of the relevant tree species (Fig. 1), denoted 'parcel dominant height' and 'parcel dominant diameter'. However, because of the windthrow, and the subsequent sanitation felling, there were no useful dominant spruce trees in mixed stands of blocks 7–9.

There were significant (** and ***) differences between the two tree species in site index, mean height and mean diameter of the dominant trees (Table 1). Pine was always larger than spruce.

In the present study, whether or not there were differences between treatments and blocks for a tree species, the analysis of variance gave the results shown in Table 1b. With respect to parcel SI and parcel dominant height, there were significant (* and **) differences between blocks, indicating that there were differences in site quality within the experiment. The differences between treatments are not obvious (p = 0.092 and p = 0.087), but indicate that SI for pine may depend on the treatment applied. The parcel dominant diameters differed significantly between the treatments for both tree species; there were significant (*) block differences for spruce only.

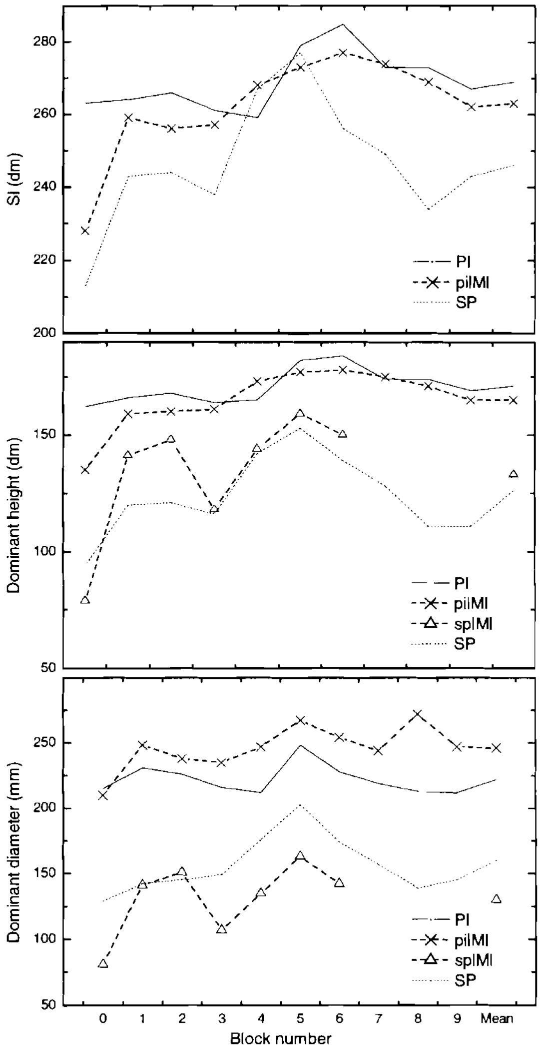

Fig. 1. Block means of parcel site indices, parcel dominant heights and parcel dominant diameters in 1999 (see Table 1).

Height of dominant trees in 1971 and 1976 and height increment 1972–1976

The measurements in 1976 were used for studying the effect of treatment on tree height development. For each 3-m circular plot, the mean

Table 1a. *Block means and standard deviations of parcel site indices, parcel dominant heights and parcel dominant diameters, based on 8 dominant trees per tree species and parcel stand (see Fig. 1). The standard deviation is shown within parentheses*

Treatment	Tree species	Statistics	Site index dm	Dominant height dm	Dominant diameter mm
PI	pi	Mean	269 (10)	171 (11)	222 (17)
MI	pi	Mean	263 (16)	165 (16)	246 (23)
MI	sp	Mean[a]	–	133 (28)	130 (30)
SP	sp	Mean	246 (20)	126 (21)	160 (27)

[a]Mean of blocks 0–6.

Table 1b. *p-values from the analysis of variance in a test of equality between variable levels for parcel SI and for parcel dominant heights and parcel dominant diameters*

Comparison	Variable	Source	p-value
Scots pine in monoculture vs. Norway spruce in monoculture	SI	Block	0.188
		Treatment	0.002**
	Parcel dominant height	Block	0.073
		Treatment	0.000***
	Parcel dominant diameter	Block	0.052
		Treatment	0.000***
Scots pine in monoculture vs. Scots pine in mixed stand	SI	Block	0.047*
		Treatment	0.092
	Parcel dominant height	Block	0.016*
		Treatment	0.087
	Parcel dominant diameter	Block	0.155
		Treatment	0.001***
Norway spruce in monoculture vs. Norway spruce in mixed stand	Parcel dominant height	Block	0.005**
		Treatment	0.190
	Parcel dominant diameter	Block	0.033*
		Treatment	0.013*

height in 1976 and mean height increment for the period 1972–1976 of the two tallest trees were calculated, for pure parcel stands. For mixed stands, however, these properties were obtained only for the tallest tree of each species. Dominant height, and dominant height increment per circular plot, were obtained, *i.e.* there were 12 such heights and height increments for each pure parcel stand and 2 × 12 for each mixed parcel stand. The mean of these values gave a parcel dominant height and a parcel dominant height increment for the tree species in question (Fig. 2).

For spruce (Table 2), the parcel dominant heights in 1976 and parcel dominant height increments in the period 1972–1976 were significantly (** and ***) higher in mixed stands than in pure stands. There were no such differences for pine, nor for parcel dominant heights for spruce in 1971.

Correlation between parcel dominant heights in 1976 and 1999

Regression analysis was used to study the correlation between parcel dominant heights in 1976 and 1999. For this purpose, the fertilised block 5 was excluded to avoid the effect of fertilisation. From the regression functions estimated (Table 3a), parcel dominant heights and site indices without fertilisation were reconstructed for block 5 in 1999, and residuals for block 5 were calculated. This revealed the effect of fertilisation on the development of dominant height in the three treatments. Fertilisation enhanced height development, especially in spruce (Table 3b).

Total volume yield up to and including 1999

The primary aim of this study was to test the hypothesis whether mixed stands in a certain site quality range give higher yields than pure

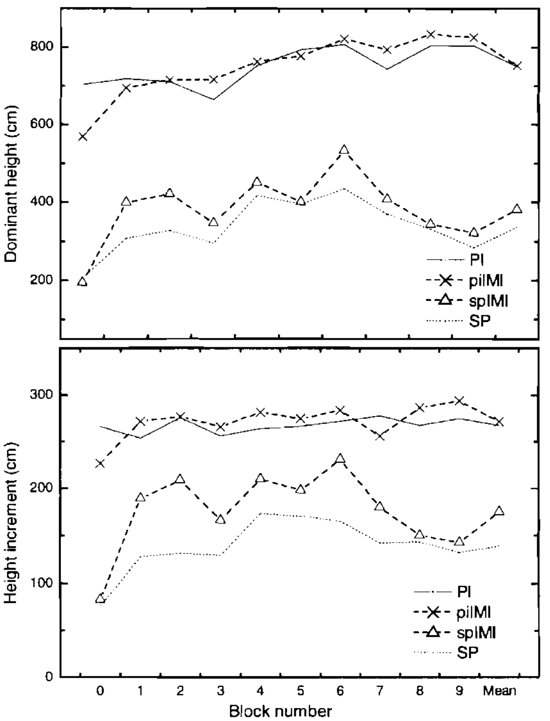

Fig. 2. Block means of parcel dominant heights in 1976 and parcel height increments 1972–76 of the dominant trees (see Table 2).

stands, *i.e.* larger total volume yields during a given period of growth.

Before cleaning in 1961, there were, on average, 48 000 plants ha^{-1} on the experimental area, distributed among the clusters. After cleaning, only 2873 plants ha^{-1}, on average, remained. The number of remaining plants or stems after cleaning or thinning during the life of the stands is shown in Table 4a and Fig. 3, as also is the number of stems removed by cleaning or thinning. The number of windthrows in 1988 (at stand age 32 years) is indirectly revealed by the low stem numbers in 1999 (at stand age 43 years), in pure pine stands and mixed stands in blocks 5–9. This is shown more clearly in Tables 4b,c. Total volume yield ha^{-1} (m^3sk), up to and including 1999, was estimated by adding to the growing stock in 1999, the wood removed by all thinnings and windthrows.

Of especial interest is a comparison between the block means for total yield in mixed stands, and the corresponding average yield in pure stands of pine and spruce, denoted (PI + SP)/2 (Fig. 4–7). As may be seen from Table 5a, the mean total volume yield in mixed stands in 1999 was 21% higher than the average yield in pure stands of pine and spruce, but 20% lower than that in pure pine stands, *i.e.* 244/201 and 244/304, respectively. The yield of pine in mixed stands was 41% higher than half the yield in pure pine stands; the yield of spruce in mixed stands was 39% below half the yield in pure spruce stands. Thus, in mixed stands pine trees were favoured and spruce trees disfavoured.

Evidently, total yield up to mid-rotation was higher in mixed stands, as compared with the average total yield in pure stands of pine and spruce. Notwithstanding this, the yields in pure pine stands were higher than those in mixed stands in the site quality range in question.

Windthrow in 1988

The windthrows in 1988 reduced tree numbers, but only in pine and mixed stands, and in particular, in blocks 5–9. No spruce parcel stand was affected. The windthrows were concentrated to blanks. They caused growth losses (*cf.* Tables 6a, 9a), as a result of the decreased production base and the empty areas. The loss of total volume yield in 1999 was 72% and 62% of the windthrow and sanitation volume in pine and mixed stands, respectively. The loss of mean annual increment

Table 2a. *Block means of parcel dominant heights in 1971 and in 1976 and parcel dominant increments 1972–1976 (see Fig. 2)*

Treatment	Tree species	Dominant height 1971 cm	Dominant height 1976 cm	Dominant height increment 1972–1976 cm
PI	pi	482	750	268
MI	pi	480	752	272
MI	sp	207	382	175
SP	sp	198	337	139

Table 2b. *p-values from the analysis of variance in a test of equality between variable levels for parcel dominant heights in 1971 and in 1976 and parcel dominant increments 1972–1976*

Comparison	Variable	Source	p-value
Scots pine in monoculture vs. Scots pine in mixed stands	Parcel dominant height 1971	Block	0.010*
		Treatment	0.813
	Parcel dominant height 1976	Block	0.010*
		Treatment	0.959
	Parcel dominant height increment 1972–1976	Block	0.381
		Treatment	0.498
Norway spruce in monoculture vs. Norway spruce in mixed stands	Parcel dominant height 1971	Block	0.000***
		Treatment	0.206
	Parcel dominant height 1976	Block	0.000***
		Treatment	0.005**
	Parcel dominant height increment 1972–96	Block	0.003**
		Treatment	0.001***

Table 3a. *Estimated regression functions for dominant heights without block 5. Dependent variable: parcel dominant height in 1999, dm*

	pi|PI		pi|MI		sp|SP	
Independent variable	β	p-value	β	p-value	β	p-value
Constant	98.62	0.007***	61.06	0.011*	53.37	0.000***
Parcel dominant height 1976, dm	0.95	0.031*	1.38	0.001***	2.02	0.000***
Standard deviation	5.11		5.75		4.56	
Multiple correlation coeff.	0.71		0.91		0.96	

Table 3b. *Parcel dominant heights and site indices in 1999 with and without fertilisation effect for block 5 and fertilisation residuals for the same block*

	Dominant heights of block 5 in 1999, dm			Site indices of block 5 in 1999, dm		
Tree species and treatment	With fertilisation effect (measured)	Without fertilisation effect (estimated)	Fertilisation effect (residuals)	With fertilisation effect (measured)	Without fertilisation effect (estimated)	Fertilisation effect (residuals)
pi|PI	182	174	8	279	273	6
pi|MI	177	168	9	273	266	7
sp|SP	153	133	20	277	252	25

during the period 1983–1999 was 4% and 5% of the windthrow and sanitation volume in pine and mixed stands, respectively.

Correlation between total volume yield and dominant height in 1999

The correlation between parcel total volume yield and parcel dominant height in 1999 was studied by regression analysis. The fertilised block 5 was excluded from the study, to avoid the fertilisation effect. From the estimated regression functions (Table 6a) and estimated dominant height (Table 3b), total volume yield without fertilisation was reconstructed for block 5 in 1999, and residuals for block 5 were calculated, giving the fertilisation effect on total volume yield for the three treatments. Fertilisation increased the total volume yield for spruce by 75% (Table 6b).

Mean annual volume increment

For each parcel stand, mean annual volume increment was calculated on the basis of the total volume yields for the periods between measurements, including fertilisation effects and growth losses caused by windthrow and sanitation felling. In Table 7, these increments are shown as block means, and analysed (see also Fig. 5).

Table 4a. *Block means and standard deviations (SD) of cleaned/thinned stem numbers and of standing stem numbers after cleaning/thinning at the measurement times (see Fig. 3)*

Treatment	Statistics	Cleaned/thinned stem number ha^{-1}				Standing stem number ha^{-1} Before	After cleaning/thinning			
		1976	1982	1988[a]	1999[b]	1961	1961	1976	1982	1999
PI	Mean	427	714	(444)	18	48 000	2797	2484	1663	1334
	SD	262	99	(237)	15	21 000	462	209	37	307
MI	Mean	442	750	(446)	37	52 000	2956	2523	1640	1235
	SD	329	136	(303)	35	22 000	491	225	56	343
SP	Mean	501	856	0	27	40 000	2865	2402	1645	1662
	SD	270	118	–	20	16 000	426	211	37	90
pi|MI	Mean	271	369	(258)	3	–	1412	1261	833	652
	SD	176	90	(151)	5	–	244	128	33	161
sp|MI	Mean	171	381	(188)	34	–	1544	1261	807	584
	SD	171	66	(169)	34	–	324	127	32	194

[a]Based on stump measurements.
[b]Natural thinning.

Table 4b. *Ratios between standing stem numbers in 1999 after windthrow/sanitation felling in 1988 and corresponding standing stem numbers after thinning in 1983*

Treatments	All blocks	Blocks 0–4	Blocks 5–9
PI	0.80	0.93	0.67
MI	0.75	0.94	0.57
SP	1.01	1.03	0.99

Table 4c. *Block means for volumes of windthrow/ sanitation fellings in 1988, based on stump measurements, m^{3}sk ha^{-1}*

Tree species| Treatment	All blocks	Blocks 0–4	Blocks 5–9
pi|PI	(33.3)	(17.6)	(49.0)
pi|MI	(30.4)	(14.1)	(46.6)
sp|MI	(4.8)	(1.3)	(8.2)
pi+sp|MI	(35.2)	(15.5)	(54.8)
sp|SP	0.0	0.0	0.0

Volume increment ratios

Block means of mean annual volume increment for mixed and spruce stands, respectively, were related to the corresponding increments for pine stands by the calculation of ratios (Table 8, Fig. 6). The relative increase in the increment of spruce stands during the final period (1983–1999) is noteworthy. The average increment ratio for the period was 0.49. A cautious extrapolation gave a ratio of *ca.* 0.7 during 1999, which implies that volume growth in spruce stands was increasing remarkably, and is promising.

Idealised total volume yield and volume increment in relation to site index

The windthrows in 1988 were concentrated to blanks, and caused a loss of growth (above, p. 8). From the regression functions (Tables 6a, 9a), an idealised total volume yield up to and including 1999 was estimated, and an idealised annual volume increment during the period 1983–1999, relative to the relevant dominant heights; *i.e.* yield and increment without a fertilisation effect and without growth losses caused by windthrow and sanitation felling. From other regression functions (unpublished), which gave the estimated correlation between parcel dominant height and site index for pine in mixed stands, the idealised total volume yield and idealised annual volume increment were calculated for the three treatments, in relation to site index for pine in mixed stands (Fig. 7).

Mean tree

Basal-area-weighted mean tree properties

Various mean tree properties were studied, either (a) for all calipered, undamaged trees or (b) for the sample trees. Diameter, height and volume for each calipered tree in the whole experiment were available (*cf.* p. 5). Thus it was possible to calculate basal-area-weighted means of these tree properties for each tree species and parcel stand.

Diameter, height and volume were also available for each sample tree. From these, a form factor for each tree was calculated. Because of

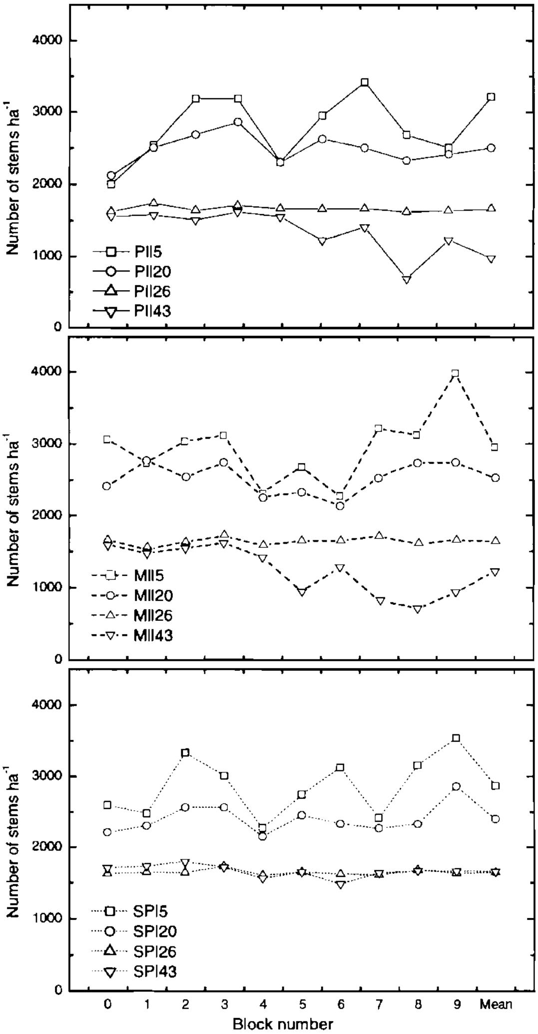

Fig. 3. Block means of stem number after cleaning/ thinning in 1961, 1976, 1982 and 1999; *i.e.* at stand ages: 5, 20, 26 and 43 years (see Table 4).

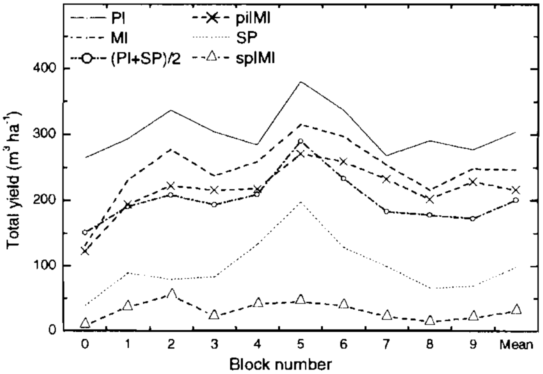

Fig. 4. Block means of total volume yields up to and including 1999 (see Table 5).

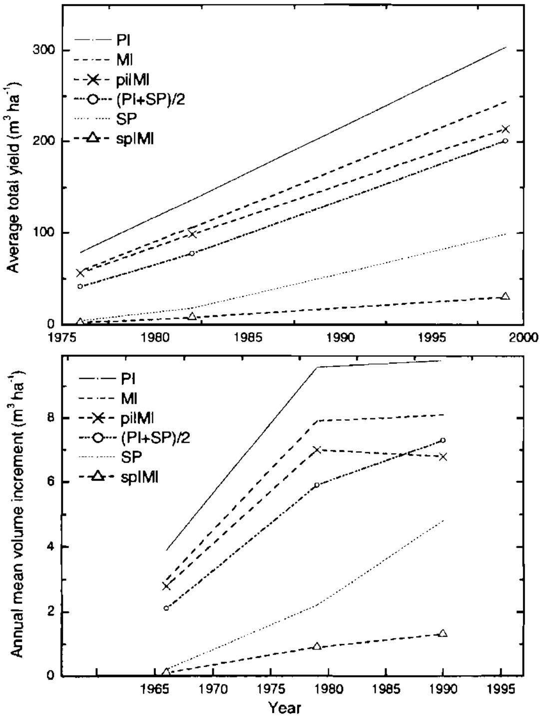

Fig. 5. Upper figure: Total volume yields on average for blocks (see Table 5). Lower figure: Mean annual volume increments on average for blocks during some growth periods (see Table 7).

the probability choice of the sample trees (above, p. 5), basal-area-weighted means of form factor, height to live crown base and bark thickness for tree species and parcel stands were readily obtained. To obtain the basal-area-weighted tree means for the entire experiment, the values for each species and parcel stand were weighted with the stand basal area for the appropriate species and parcel stand.

The results are shown in Table 10 and Fig. 8. In all respects, there were significant (***) differences between pine and spruce (not shown in table). There were also significant differences between treatments within species, with the exception (a) of tree height in both species, and (b) of volume and height to live crown base in spruce (notwithstanding this, see Fig. 8: live crown base in spruce).

Discussion & Conclusions

Mixed-stand dynamics

Up to a stand age of 15 years, and at a dominant tree height of *ca.* 5 m for pine and *ca.* 2 m for

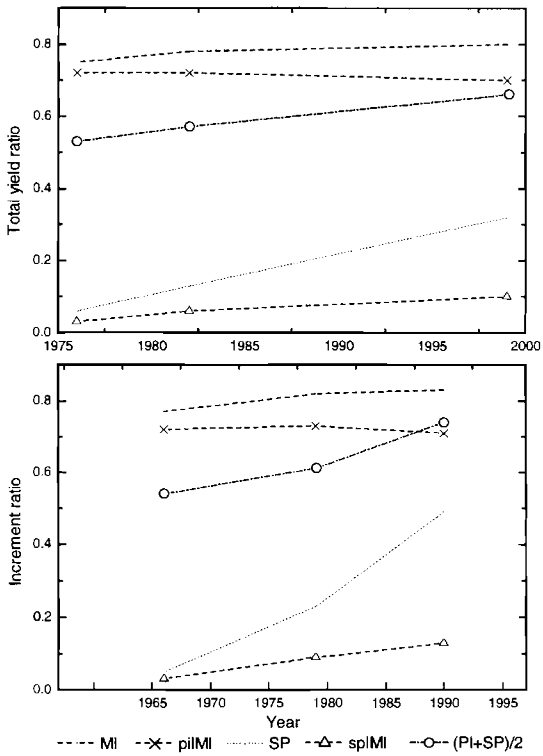

Fig. 6. Upper figure: Ratios between total volume yields at certain times for mixed and spruce stands, and the same for pine stands (see Table 8). Lower figure: Ratios between mean annual volume increments during certain growth periods for mixed and spruce stands, and the same for pine stands (see Table 8).

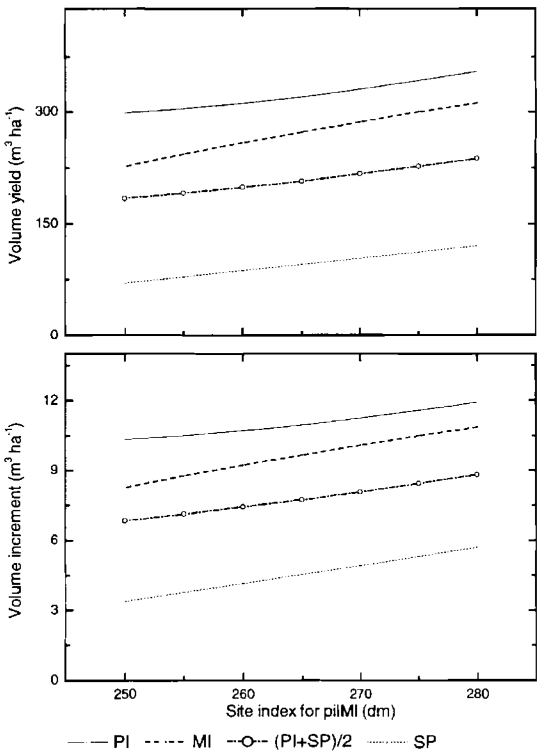

Fig. 7. Upper figure: Idealised total volume yields up to and including 1999, without the fertilisation effect and without growth loss by windthrow and sanitation felling. Lower figure: Idealised annual volume increments during 1983–1999, without the fertilisation effect and without growth loss caused by windthrow and sanitation felling.

spruce in mixed stands, there were no differences in dominant height, as compared to the species in pure stands (Table 2). During the next five years, however, the height increment of dominant spruce trees in mixed stands was significantly greater than that of spruce in pure stands. This resulted in a significantly greater dominant height for spruce in mixed stands (Table 2, Fig. 2). This was also found for single spruce trees in a similar experiment (Jonsson, 1999). No such difference was found for pine in the present experiment, nor in that just referred to (Jonsson, 1999). Thus, at the early stage of tree development, and before crown closure, there was a favourable, ecological mixed-stand effect on the height growth of spruce. It may reasonably be argued that the taller pines in mixed stands provided a better growth climate for the shorter, sheltered spruces.

However, the pines continued to grow faster in both height and diameter than did the spruces, which resulted in dense, mixed stands with pine trees as the dominant and spruce as the co-dominant or suppressed (Fig. 1, 8). In the crown layer of mixed stands, there was less competition for light than in the crown layer of pure pine stands, owing to the smaller number of dominant trees in mixed stands. Weaker competition for nutrients resulted in a larger DBH for pine trees (Tables 1, 10); weaker competition for light resulted in a lower height for dominant pine trees ($p=0.087$, Table 1) in mixed than in pure pine stands.

Cannell *et al.* (1984), in a study with *Pinus contorta* and *Picea sitchensis*, found that competition between trees was overwhelmingly one-sided, suggesting that light was the main environmental resource 'competed for'. *P. contorta* developed a greater ratio of height to radial growth than *P. sitchensis*, resulting in a noticeably etiolated appearance.

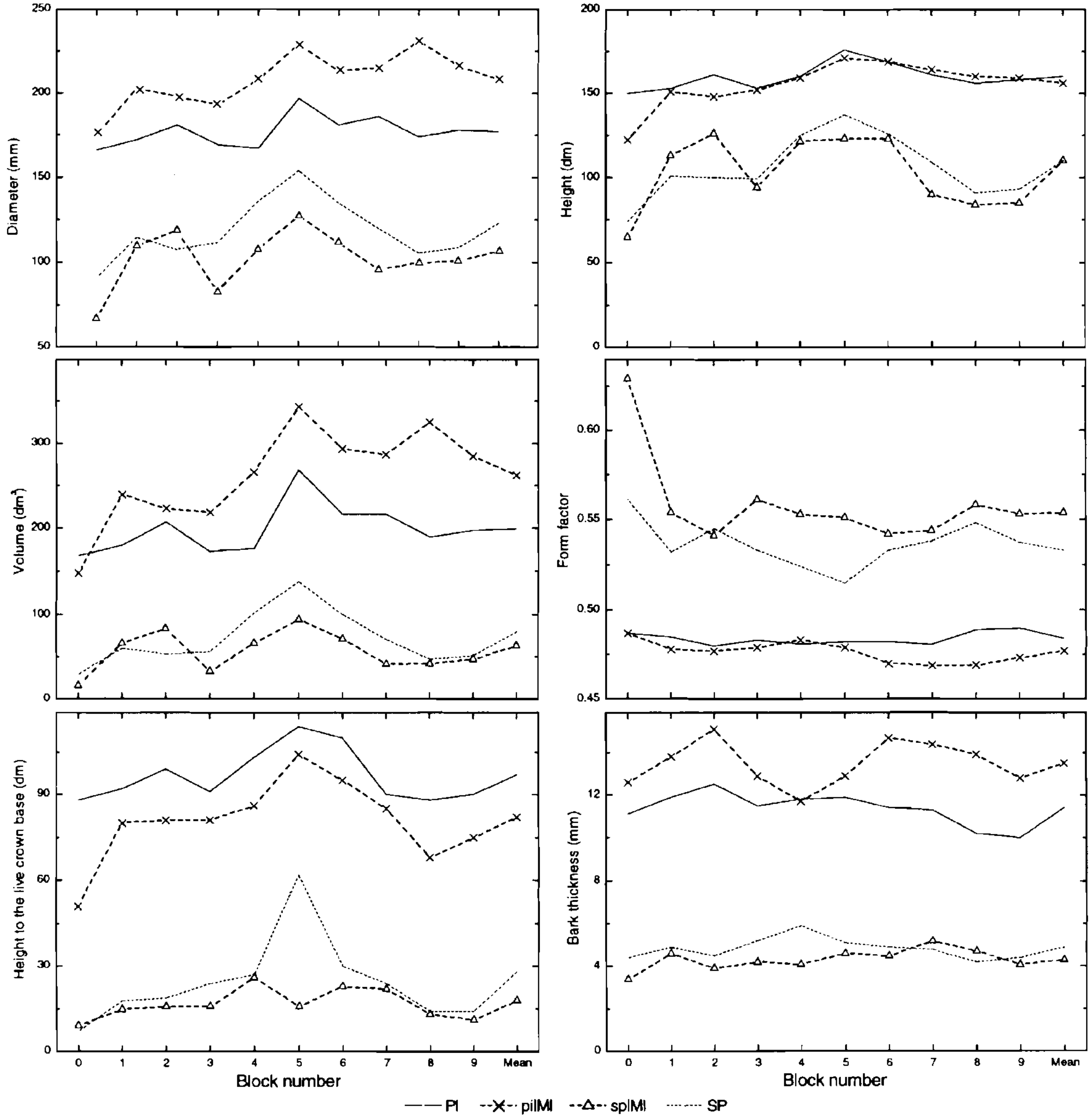

Fig. 8. Basal-area-weighted mean tree properties in 1999 (see Table 10).

On the whole, the results from the present experiment may show a mild etiolation effect, as a result of competition for light in the crown layer (*cf.* Björkman, 1945). Pines in pine stands with high crown density were tall and slender in comparison with pines in mixed stands, as is shown both by the diameter–height relationship in Tables 1, 10, and by the form factor in Table 10 and Fig. 8. Co-dominant or suppressed spruces in mixed stands were also tall and slender in comparison with spruces in pure stands, and had also a higher form factor, probably in consequence of the etiolation effect.

Although it was mild, the etiolation effect may have influenced the determination of site index in general. In the present experiment, site index for pine was 26.9 m, on average, in pine stands and 26.3 m in mixed stands; an analysis of variance test of equality gives the p-value 0.092.

However, preliminary results from Hägglund (1975) indicate that there is a positive mixture effect on the height development of pine in

Table 5a. *Total volume yields (m^3sk ha^{-1}) on average for blocks, and standard deviation (SD; see Fig. 5). (The figures include the fertilisation effect and the increment loss due to windthrow and sanitation felling.)*

Treatment	Tree species	Statistics	Year 1976	1982	1999
PI	pi	Mean	78.5	136.3	304
		SD	14.7	14.6	37
PI	pi/2[a]	Mean	39.2[b]	68.2[b]	152[b]
MI	pi + sp	Mean	58.6	105.9	244
		SD	15.6	24.3	49
MI	pi	Mean	56.2	98.2	214
		SD	15.3	22.2	38
MI	sp	Mean	2.3	7.7	30
		SD	1.1	5.1	15
SP	sp	Mean	4.4	17.7	98
		SD	2.1	7.2	45
SP	sp/2[a]	Mean	2.2[b]	8.8[b]	49[b]
PI + SP	(pi + sp)/2	Mean	41.5	77.1	201
		SD	8.1	9.8	38

[a]pi/2 and sp/2 denote total volume yield on 0.5 ha for pine and spruce, respectively, in pure stands.
[b]m^3sk $(0.5\ ha)^{-1}$.

Table 5b. *p-values from analysis of variance in a test of equality between variable levels for total volume yields at different times*

Comparison	Source	p-value 1976	1982	1999
Half of Scots pine in monoculture + half of Norway spruce in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.058	0.026*	0.001***
	Treatment	0.002**	0.000***	0.001***
Half of Scots pine in monoculture vs. Scots pine in mixture	Block	0.076	0.067	0.054
	Treatment	0.002**	0.000***	0.000***
Half of Norway spruce in monoculture vs. Norway spruce in mixture	Block	0.000***	0.003**	0.031*
	Treatment	0.602	0.229	0.008**
Scots pine in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.021*	0.005**	0.007**
	Treatment	0.001***	0.000***	0.000***
Scots pine in monoculture vs. Norway spruce in monoculture	Block	0.289	0.075	0.006**
	Treatment	0.000***	0.000***	0.000***
Norway spruce in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.374	0.143	0.002***
	Treatment	0.000***	0.000***	0.000***
Scots pine in monoculture vs. Scots pine in mixture	Block	0.027*	0.004**	0.015*
	Treatment	0.001***	0.000***	0.000***

Table 6a. *Estimated regression functions for total volume yield without block 5. Dependent variable: total volume yield in 1999, m^3sk ha^{-1}*

Independent variable	PI β	PI p-value	MI β	MI p-value	SP β	SP p-value
Constant	802	0.008**	803	0.001***	−152.8	0.000***
1/Parcel dominant pine height 1999, dm	−81893	0.055	−88775	0.005**	–	–
Parcel dominant spruce height 1999, dm	–	–	–	–	1.996	0.000***
Windthrow + sanitation felling 1988, m^3sk ha^{-1}	−0.719	0.066	−0.615	0.248	–	–
Standard deviation	20.5		25.7		4.9	
Multiple correlation coefficient	0.78		0.88		1.00	

Table 6b. *Total volume yields in 1999 with and without fertilisation effect for block 5 and fertilisation residuals for the same block*

Treatment	Total volume yield in 1999, m³sk ha⁻¹ With fertilisation effect (measured)	Without fertilisation effect (estimated)	Fertilisation effects Residuals	Residuals, %
PI	381	300	81	27
MI	315	235	80	34
SP	198	113	85	75

Table 7a. *Block means of mean annual volume increments (m^3sk ha^{-1}) during different periods, and corresponding standard deviations (SD; see Fig. 5). (The figures include the fertilisation effect and the increment loss due to windthrow and sanitation felling.)*

Treatment	Tree species	Statistics	Period 1957–1976	1977–1982	1983–1999
PI	pi	Mean	3.9	9.6	9.8
		SD	0.7	1.0	1.7
PI	pi/2[a]	Mean	2.0[b]	4.8[b]	4.9[b]
MI	pi + sp	Mean	3.0	7.9	8.1
		SD	0.8	1.9	1.9
MI	pi	Mean	2.8	7.0	6.8
		SD	0.8	1.4	1.4
MI	sp	Mean	0.1	0.9	1.3
		SD	0.1	0.7	0.7
SP	sp	Mean	0.2	2.2	4.7
		SD	0.1	0.9	2.3
SP	sp/2[a]	Mean	0.1[b]	1.1[b]	2.4[b]
PI + SP	(pi + sp)/2	Mean	2.1	5.9	7.3
		SD	0.4	0.6	1.9

[a]pi/2 and sp/2 denote mean annual volume increment on 0.5 ha for pine and spruce, respectively, in pure stands.
[b]m^3sk $(0.5\ ha)^{-1}$.

Table 7b. *p-values from analysis of variance in a test of equality between variable levels for mean annual volume increments during different periods*

Comparison	Source	p-value 1957–1976	1977–1982	1983–1999
Half of Scots pine in monoculture + half of Norway spruce in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.043*	0.230	0.000***
	Treatment	0.001***	0.006**	0.028*
Half of Scots pine in monoculture vs. Scots pine in mixture	Block	0.068	0.563	0.039*
	Treatment	0.002**	0.002*	0.000***
Half of Norway spruce in monoculture vs. Norway spruce in mixture	Block	0.011*	0.007**	0.048*
	Treatment	0.168	0.160	0.006**
Scots pine in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.025*	0.665	0.008**
	Treatment	0.001***	0.037*	0.004**
Scots pine in monoculture vs. Norway spruce in monoculture	Block	0.327	0.746	0.019*
	Treatment	0.000***	0.000***	0.000***
Norway spruce in monoculture vs. Scots pine + Norway spruce in mixture	Block	0.408	0.016*	0.001***
	Treatment	0.000***	0.000***	0.000***
Scots pine in monoculture vs. Scots pine in mixture	Block	0.027*	0.571	0.023*
	Treatment	0.001***	0.001***	0.000***

Table 8. *Block means of total volume yields and of mean annual volume increments in mixed and spruce stands in relation to these characters in pine stands (see Fig. 6). (The figures include the fertilisation effect and the increment loss due to windthrow and sanitation felling.)*

Treatment	Tree species	Total volume yield ratio Year			Mean annual volume increment ratio Period		
		1976	1982	1999	1957–1976	1977–1982	1983–1999
MI	pi+sp	0.75	0.78	0.80	0.76	0.82	0.83
MI	pi	0.72	0.72	0.70	0.72	0.73	0.71
MI	sp	0.03	0.06	0.10	0.03	0.09	0.13
SP	sp	0.06	0.13	0.32	0.05	0.23	0.49
(PI + SP)/2	pi+sp	0.53	0.57	0.66	0.54	0.61	0.74

Table 9a. *Estimated regression functions for annual volume increment during 1983–1999, excluding block 5. Dependent variable: annual volume increment during 1983–1999, $m^3sk\ ha^{-1}$*

Independent variable	PI β	PI p-value	MI β	MI p-value	SP β	SP p-value
Constant	24.48	0.058	25.74	0.008**	−6.935	0.000***
1/Parcel dominant pine height 1999, dm	−2300	0.232	−2692	0.037*	–	–
Parcel dominant spruce height 1999, dm	–	–	–	–	0.0923	0.000***
Windthrow+sanitation felling 1988, $m^3sk\ ha^{-1}$	−0.0444	0.033*	−0.0463	0.100	–	–
Standard deviation	1.032		1.271		0.291	
Multiple correlation coefficient	0.75		0.74		0.98	

Table 9b. *Mean annual volume increments during 1983–1999 with and without fertilisation effect for block 5 and fertilisation residuals for the same block*

Treatment	Mean annual volume increment, $m^3sk\ ha^{-1}$ With fertilisation effect (measured)	Without fertilisation effect (estimated)	Fertilisation effects Residuals	Residuals, %
PI	13.2	9.3	3.9	42
MI	11.6	6.7	4.9	73
SP	10.2	5.3	4.9	92

mixed stands of Scots pine and Norway spruce; no such effect was found for spruce. Mielikäinen (1985) shows that an admixture of birch (*Betula pendula* Roth. or *B. pubescens* Ehrh. or both) seems to have no effect on the dominant height of pine and spruce.

Windthrow

Some pure pine stands and mixed stands were windthrown in 1988, but no spruce stands. In a study of the 1954 windthrow in the province in question, Werner & Årman (1955) found that the risk for windthrow was related to the height of the stands (*cf.* also Persson, 1975). Werner and Årman found no windthrow damage in stands with height <10 m; the stands on spruce parcels in the present experiment were below this limit in 1988. The stands on pine and mixed parcels were in the height interval 10–15 m, where, according to Werner & Årman (1955), there was a slight risk of windthrow damage. Thus the difference in windthrow damage between treatments was probably a consequence of different stand heights.

Fertilisation

Fertilisation gave a positive growth response, particularly for spruce. The site index was increased by 2.5 m in the spruce stand of fertilised block 5, and annual volume increment was doubled during the period 1983–1999. In pine and mixed stands, the responses were relatively lower (Tables 3b, 6b and 9b). Tamm (1971), in an earlier experiment, found that pine responded much less vigorously than spruce to fertilisation with the same amount of ammonium nitrate (60 kg N ha^{-1}).

Volume

Up to stand middle age, pine was the stronger tree species, superior to spruce in height and volume growth. In mixed stands, the pines were dominant and the spruces co-dominant and suppressed. The total volume yield was higher in mixed stands than the average yield in pure stands of pine and spruce, which mainly depended on the dominance of pine in mixed stands. However, it was lower in mixed stands than in pure pine stands.

On approximately equivalent sites, Mielikäinen (1980) found a similar relationship between birch (*Betula pendula*) and Scots pine in mixed stands. Birch grew better in mixed stands than in pure birch stands, while pine grew less well in mixture with birch than in pine stands. However, the total volume yield was equal or insignificantly higher, in mixed stands of Scots pine and birch, than in pure pine stands during a rotation (at most 2% higher). Mielikäinen (1985) also studied the yield in

Table 10a. *Basal-area-weighted mean tree properties (see Fig. 8)*

Treatment	Tree species	Basal-area-weighted mean properties, based on calipered trees			Basal-area-weighted mean properties, based on sample trees		
		Diameter mm	Height dm	Volume dm^3sk	Form factor	Height to live crown base dm	Bark thickness mm
PI	pi	177	160	199	0.484	97	11.4
MI	pi	208	156	262	0.477	82	13.5
MI	sp	107	110	63	0.554	18	4.3
SP	sp	123	110	80	0.533	28	4.9

Table 10b. *p-values from analysis of variance in a test of equality between variable levels for basal-area-weighted mean tree properties*

Comparison	Properties (see Table 7a above)	Source	p-value
Scots pine in monoculture vs. Scots pine in mixture	Diameter	Block	0.044*
		Treatment	0.000***
	Height	Block	0.017*
		Treatment	0.201
	Volume	Block	0.034*
		Treatment	0.001***
	Form factor	Block	0.598
		Treatment	0.010**
	Height to live crown base	Block	0.004**
		Treatment	0.000***
	Bark thickness	Block	0.286
		Treatment	0.000***
Norway spruce in monoculture vs. Norway spruce in mixture	Diameter	Block	0.006**
		Treatment	0.004**
	Height	Block	0.002**
		Treatment	0.471
	Volume	Block	0.009**
		Treatment	0.068
	Form factor	Block	0.058
		Treatment	0.007**
	Height to live crown base	Block	0.237
		Treatment	0.137
	Bark thickness	Block	0.402
		Treatment	0.044*

mixed stands of Norway spruce and birch on the site quality range G24–G30. He found that mixed stands of spruce and *B. pendula* had a higher volume yield than pure spruce stands, by 2–5% during a rotation. On the other hand, an admixture of *B. pubescens* decreased volume yield by 1–5%.

Agestam's (1985) yield tables show no positive mixture effect on volume yield. They show that, on sites with a high site index, spruce stands had a higher yield than both pine stands and mixed stands of pine and spruce, and on sites with a low site index, pine stands had higher yield than both spruce stands and mixed stands. Agestam found rather that mixed stands produced slightly less than pure pine and spruce stands on such sites.

The results in the present study cannot be simply compared with the results just referred to, due to the fact that the rotation in the present experiment was incomplete. However, the growth dynamics up to the present time indicates that volume growth of spruce increases remarkably in pure stands, after a slow start, and increases slightly in mixed stands; while the volume growth of pine starts fast and culminates (Fig. 5, 6). Developments in the next half of the rotation should be interesting.

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