Variation of Quality and Predicted Economic Returns between European beech (*Fagus sylvatica* L.) Provenances

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Abstract

Height growth, volume per ha, bole length, stem straightness, spiral grain visible on the surface of stems, frequencies and height of forks were measured in 18 experimental plots with a total of seven European beech (*Fagus sylvatica* L.) provenances. The age in the plots varied between 61 and 65 years. The plots were located at three sites in Denmark. Economic returns for the coming 40-year-period were predicted for the seven provenances.

Stem straightness, spiral grain, bole length and cumulated economic returns for the future 40-year-period varied significantly between provenances. The variation in predicted economic returns was mainly due to two Swiss provenances Sihlwald (CH) and Adlisberg (CH) with cumulated predicted economic returns 11% and 10% above average, and a German provenance Rügen with cumulated economic returns 15% below average. The ranking in economic returns was largely in agreement with the ranking of provenances concerning stem straightness, bole length and frequency of severe visible spiral grain. Sihlwald and Adlisberg were characterised by a higher frequency of trees with straight stems, below-average spiral grain and trees with longer boles. Rügen (G) was characterised by frequently sinuous stems and below-average bole length.

Key words: Stem straightness, spiral grain, bole length, genetic variation.

Introduction

European Beech covers 16% (80000 ha) of the forest area in Denmark (Danmarks statistik 2002), predominantly on soils of clayey and sandy moraines. The wood of beech is highly valued and used for e.g. furniture, veneer and plywood. The large area with beech means that the species is economically important for Danish forestry.

Provenances of European beech (*Fagus sylvatica* L.) have been imported from the Carpathians, The Netherlands, Belgium, Sweden, and Switzerland to Denmark since the end of the 19th century (BARNER, 1958) because of frequent poor seed production in Danish stands and to achieve better growth and stem straightness compared with Danish provenances.

Experiences from field tests with the imported provenances show that the Sihlwald and the Adlisberg provenance from Switzerland have superior stem straightness and growth, but larger frequencies of forked trees compared to Danish provenances. Usually, West-Carpathian provenances from Slovakia and Hungary have superior stem straightness, but also large frequencies of trees with forks compared to Danish provenances while provenances from The Netherlands are similar to the Danish provenances (OPPERMANN, 1930; PLOUGHELD, 1933; HOLM, 1939; TULSTRUP, 1950; OKSBJERG, 1951; BANG, 1968; GØHRN, 1972; LARSEN, 1985).

Beech in Denmark, however, is increasingly naturally regenerated for ecological and economical reasons (Ministry of environment, 2002; HOLTEN-ANDERSEN, 1987; TARP et al., 2000), and natural regeneration is promoted and implemented in the Danish National Forest program (Ministry of environment, 2002). These facts, along with better opportunities to store beech seed (POULSEN, 1993) reduce the interest of importing beech seed.

Nevertheless, material from some of the superior provenances might still be used for afforestation and the old tests with different European beech provenances provide an opportunity to estimate the repeatability of growth and quality traits in old material and to examine how the economic returns are influenced by the choice of provenances with a wide range of quality. Knowledge, which is important when decisions are made concerning choice of provenance for afforestation and whether it is economically feasible to replace a provenance of poor quality with a provenance of high quality. An economic estimation of economic returns helps also to judge the importance of improving the quality in existing stands using selective thinning, or at least avoiding a negative selective thinning before natural regeneration.

The importance of provenances for economic returns has not been investigated yet to our knowledge. This initiated this study of the repeatability of growth, quality and economic returns of seven European beech provenances. The study was mainly examining the predicted economic returns in the last 40-year period before rotation age where the quality of beech logs is of major economic importance.

Material and Methods

Trees were sampled in 18 plots with the following provenances: Sihlwald and Adlisberg from Switzerland (CH), Forêt de Soignes from Belgium (B), Middachten Allé from The Netherlands (NL), Sölvesborg from Sweden (S), Rügen, FA Werder, Stubnitz from Germany (G) and Kokošovce, Sigord forest district, Tal Štiavnica (Alt. 550–650 m) from the West Carpathian mountains of Slovakia (SL). Sixteen of the plots were placed in two field tests (B80, B90) located in the forests Søllerup Indelukke and Horse Skov, and two plots were placed close to each other in the forest Grønholt (*Table 1, 2* and *Fig. 1*).

The two field tests B80 and B90 contained the same provenance samples from Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G), (TULSTRUP, 1950). Provenance samples from the forest Forêt des Soignes (B) and Sölvesborg (S) in the two field tests and in the forest Grønholt might be from different areas of the two forests. Furthermore, the provenance sample of Sihlwald (CH) represented in the forest Grønholt Hegn might originate from a different stand- or area within the forests Sihlwald (CH) than the Sihlwald (CH) samples in B80 and B90.

Results and conclusions were the same in almost all cases using all material, or restricting the material to the plots repli-

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cating the same seed samples of Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G). The latter results are consequently only shown and discussed when different from results and conclusions using the whole material.

The provenances are of course not representative for the countries they come from, but represent probably the wide span in quality, which can be found between beech provenances throughout Europe. The average number of trees sampled in each plot was 29 and with a minimum of 21 and a maximum of 43 trees. Age of plots ranged between 61 and 65 years (*Table 1*). The field tests are similar in climate (*Table 2*) and the soil is on all sites clayey moraine.

The frequency of trees with forks, average stem straightness scores and mean heights at age 21–26 was evaluated by GØHRN (1972).

Measured traits

Diameter at breast height and tree height was measured for all trees in the plots in the forests Søllerup Indelukke and Grønholt Hegn. In the forest Horse Skov, the height of 23 trees was measured within each plot. Heights of the remaining trees were estimated from height-diameter models elaborated for each plot using the data from the 23 measured trees and the non-linear model (NÄSLUND, 1937; JOHANNSEN, 1999)

$$h = \left(\frac{d}{c_1 + c_2 d} \right)^3 + 1.3 \qquad (1)$$

where d is the diameter at breast height (cm), h is the total tree height (m) and c_1 and c_2 are arbitrary constants. The heights were estimated using the procedure NLIN in SAS® and applying the Marquardt method (SAS Institute Inc., 1989). The constant c_1 and c_2 was constrained above 0.00001 to avoid negative relationships between diameters and heights. Total volumes of the individual trees were estimated using a model developed for beech in Denmark (MADSEN, 1987).

The bole length was defined as length from the ground to the first living branch belonging to the crown ignoring the influence of epicormic branches.

Trees with straight boles in two vertical planes at right angles to each other, (directions North-South and East-West)

Table 1. – Material for the study.

Forest/site and position	Trial or forest department	Provenance	Country of origin	Plot no.	Age of plot	Area of plot (ha)	No. of sampled trees	Stems per ha	D_g (cm)	H_g (m)
Søllerup Indelukke (55°25' N 12°07' E)	B80	Sölvesborg	Sweden	1	65	0.091	30	330	34	25
		Forêt de Soignes	Belgium	2	62	0.148	43	290	34	25
		Forêt de Soignes	Belgium	3	64	0.124	32	258	34	26
		Middachten Allé	The Netherlands	4	63	0.116	35	302	35	26
		Sihlwald	Switzerland	5	62	0.123	32	261	35	27
		Adlisberg	Switzerland	6	62	0.105	31	294	34	26
		Rügen, Forstamt Werder (alt. 60 m)	Germany	7	62	0.072	23	320	34	23
		Kokošovce Forest District, Sigord department, Tal Štiavnica (alt. 550-650 m)	Slovakia	8	62	0.096	30	312	34	25
Horse Skov (55°02' N 10°34' E)	B90	Sölvesborg	Sweden	9	64	0.143	27	189	38	26
		Forêt de Soignes	Belgium	10	63	0.117	21	180	36	27
		Forêt de Soignes	Belgium	11	63	0.140	26	186	37	27
		Middachten Allé	The Netherlands	12	62	0.103	20	195	37	24
		Sihlwald	Switzerland	13	61	0.167	33	197	39	29
		Adlisberg	Switzerland	14	61	0.174	32	184	38	29
		Rügen, Forstamt Werder (alt. 60 m)	Germany	15	61	0.169	31	184	38	28
		Kokošovce Forest District, Sigord department, Tal Štiavnica (alt. 550-650 m)	Slovakia	16	61	0.165	35	213	37	25
Grønholt Hegn (55°56' N 12°23' E)	242	Sihlwald	Switzerland	17	62	0.122	21	173	40	28
		Forêt de Soignes	Belgium	18	62	0.169	30	178	39	29

Table 2. – Climate data (1961–1990). Temperatures are from weather stations nearest to the forests (LAURSEN et al., 1999; CAPPELEN and JENSEN, 2001). Figures for the precipitation at the Danish sites are estimated from FRICH et al. (1997). [1] Weather station Værløse. [2] Weather station Keldsnor Fyr (from LAURSEN et al., 1999). Climate data for the provenances in mountain regions may have quite different climate than observed at nearest weather station.

Forest/site	Mean annual monthly tempe-rature (°C)	Average Max temp. July	Average Min. temp. July	Mean annual precipi-tation (mm)	Mean summer precipi-tation (mm)	Average date of last frost	Soil	Weather station	Alti-tude (m.a.s.)
Søllerup Indelukke	7.7	21	12	600	175	25. April[1]	Clayey	Vivede overdrev	20
Horse Skov	8.2	20	13	600	150	26. March[2]	moraine	Rudkøbing	10
Grønholt Hegn	7.7	21	12	650	175	25. April		Værløse	17
Sölvesborg	-	22	13	578	195	-	-	Kristians-stad	6
Forêt de Soignes	-	23	12	785	211	-	-	Uccle	100
Middachten Allé	-	23	13	693	199	-	-	Gemert	16
Sihlwald	-	25	14	1089	389	-	-	Zürich	556
Adlisberg	-	25	14	1089	389	-	-	Zürich	556
Rügen, Forstamt Werder (alt. 60 m)	-	22	13	630	210	-	-	Rostock	20
Kokošovce Forest District, Sigord department, Tal Štiavnica (alt. 550-650 m)	-	26	13	649	206	-	-	Bratislava	153

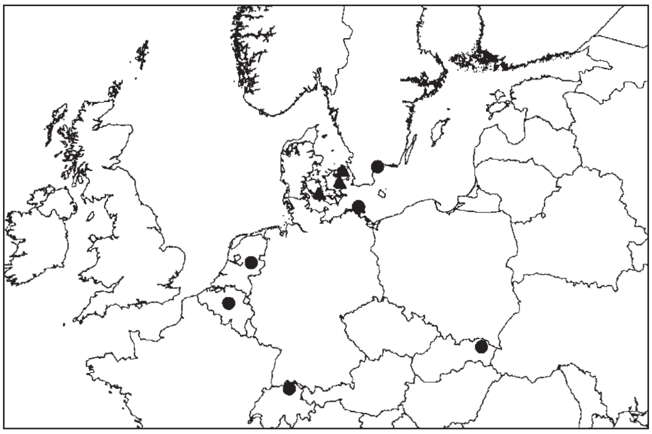

Figure 1. – Location of sites (▲) and origin (●) of provenances represented in the material.

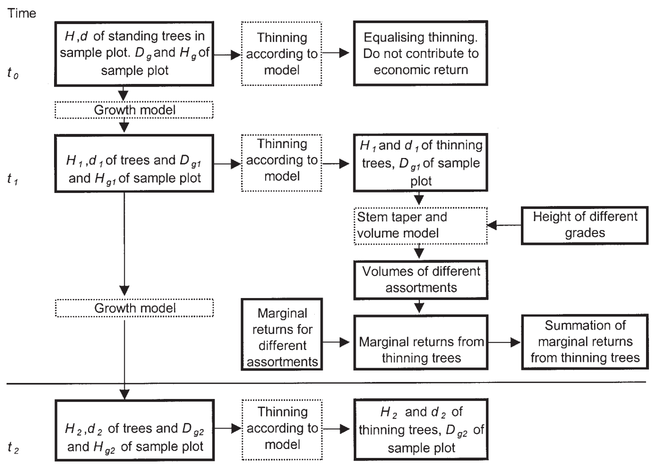

Figure 2. – The chart outlines the input and output of models applied to predict the marginal returns from assumed thinning trees at time t_1 in a plot. The step from t_1 to t_2 was repeated until t_{40} where all remaining trees were assumed felled. The marginal returns from harvested trees at $t_1 \ldots t_{40}$ were summed and divided by the area of the plot to obtain an economic return per ha. *H* and *d* are the height and diameter of individual trees in the plot. D_g is the diameter equal to the average basal area of the plot divided by the number of trees in the plot and H_g is the corresponding height.

obtained stem straightness scores of one. Trees with sinuous boles in one of the two vertical planes obtained the score two and trees with sinuous boles in both vertical planes obtained the score 3.

A tree was considered to fork if it was dividing into two branches beneath $^3/_4$ of the total tree height, if the diameter of the smallest branch was greater than 50% of the largest fork branch and if the branches and their sub-branches were part of the crown.

Spiral grain visible on the standing trees was registered when the grain deviation from the stem axis was more than 5 cm per meter according to the Danish grading rules (Statens Forstlige Forsøgsvæsen, 1990). Frequencies of trees with this severe spiral grain were calculated for each plot.

Prediction of economic returns

Economic returns were predicted for the coming 40-year period. The predictions involved for each plot a development of a thinning plan, a growth model to predict diameter and height of individual trees 40 years ahead, and a model to predict the volume and mid-diameter of logs and fuel wood from assumed harvested trees over the 40-year-period. The prediction of economic returns required information about the grade of the logs, marginal returns for these grades depending on the diameter of the logs and marginal returns for fuel wood (*Figure 2*). Provenances did not prove significantly different for growth (*Table 6* and *7*). Thus, only quality differences between the provenances determined the economic returns.

The impact of economic returns per ha in the 40-year period on land expectation value per ha were predicted for each plot according to FAUSTMANN (1849) (e.g. KUULUVAINEN and TAHVONEN, 1999) as

$$EV_r = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\sum_{k=1}^{l_j} \hat{v}_{ijk} MR_k (1+r)^{-(i+a_1)}}{A(1-(1+r)^{-a_2})} \quad (2)$$

where EV_r is the contribution to the land expectation value from the 40-year period before rotation age for a plot (DKK/ha) with discounting rate r, $\hat{v}_{ijk}$ is the volume (m^3) of an assortment $k=1 \ldots l_j$ between two height levels of the tree $j=1 \ldots n$ harvested at time $i=1 \ldots m$ from age a_1 of the plot and where l_j is specific to each tree j, MR_k is the marginal return (DKK/m^3) of the assortment k, and A is the area (ha) of the plot, r rate of return, and a_2 is the assumed rotation age that equals $a_2=a_1+m$, though assumed to be 100 for all plots to remove some of the dependency of age in the discounting. The discounting rates were 2%, 4% and 7%. These equal real rates since the real timber prices and felling costs were assumed unaltered over the 40-year-period and in coming generations. The model assumes that the economic returns of the provenances are the same before the 40-year-period. This is discussed further in the discussion section, but was accepted since most of the wood before age 60 years is sold as fuel wood or as floor logs, and because the provenances did not prove different regarding growth.

The sum of economic returns for the period of 40 years, and limited to one rotation (EV_0) was predicted as

$$EV_0 = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\sum_{k=1}^{l_j} \hat{v}_{ijk} MR_k}{A} \quad (3)$$

A similar procedure was used to predict economic returns for a shorter period of 30 years to investigate if the comparative predicted deviations of provenances for this shorter period resembled the comparative deviations using a 40-year period.

Grading

Boles of all trees in the plots were graded according to the commercial grading rules for flooring and veneer logs (Junckers Industrier A/S, 1998), logs for ice cream sticks (Pallisgaard A/S, 1994) and ordinary saw mill logs (Statens Forstlige Forsøgsvæsen, 1990). Thus, a bole was divided into different sections from the ground and upward according to the grade. Furthermore, the grades of the boles 10, 20, and 30 years ahead were estimated as well and this grading was assumed valid until end of rotation. The estimation of grades assumed a diameter growth of approximately 7 centimeters per 10 year in every plot and that branch scars were overgrown.

Marginal returns for different assortments

Sales prices for flooring logs and veneer logs equalled the recommended prices in the spring 1998 from Junckers Industrier A/S (1998). Sales prices for flooring logs given in DKK/ton were converted to DKK/m^3 assuming that 1 m^3 equals 1.15 ton (Junckers A/S, 1994). Sales prices of logs for ice cream sticks equalled the recommended prices in spring 1994 (Pallisgaard A/S, 1994) prolonged to 1997. This prolongation assumed an increase as found for veneer logs in the same period (Juncker A/S 1994, 1998). Sales prices for ordinary saw mill logs equalled the recommended prices given by the Danish Forest Association in 1997 (Dansk Skovforening, 1997). Approximate fuel wood selling prices were close to the prices given in Danish forest economy tables (Dansk Skovforening, 1995) for fuel wood processed and transported by the buyers themselves, which is common practice in Danish forestry. The sales prices were graduated according to dimensions according to our knowledge from Danish forestry. Felling and transportation costs for different assortments of logs were estimated as 1995 costs given in Danish forest economic tables (Dansk Skovforening, 1995). These were prolonged to equal the 1997 costs using the net retail index in Denmark for the period 1995-1997 (Danmarks Statistik, 1997). The 1997-prices were used since they reflected the prices for different qualities of beech over the last 10 years and without influence of temporary demands for specific qualities.

Marginal returns for assortments (DKK/m^3), which depend on grades and mid-diameters of boles, were estimated based on

Table 3. – Marginal returns (DKK/m^3) for different assortments of beech logs and fuel wood. Selling prices depend on the grade (A, B, and C) and the mid-diameter of the log. The demands to grade A, B, and C for veneer (Junckers Industrier A/S, 1998) and ice cream sticks (Pallisgaard A/S, 1994) are more extensive compared with the demands to A, B, C for saw mill logs (Statens Forstlige Forsøgsvæsen, 1990). Felling and transportation costs for the assortments are shown in the brackets. Fuel wood was assumed sold to buyers who process and transport the fuel wood themselves.

Veneer logs	>60 cm	50-59 cm			
A for export	2330 (70)	1930 (70)			
Veneer logs	>50 cm	40-49 cm	30-39 cm		
A	1465 (70)	1315 (70)	810 (70)		
B	885 (70)	705 (70)	600 (70)		
C	350 (70)	310 (70)	(70)		
Saw mill logs	>50 cm	40-49 cm	30-39 cm	30-34 cm	25-29 cm
A	1390 (70)	1250 (70)	770 (70)	655 (70)	609 (81)
B	840 (70)	670 (70)	570 (70)	525 (70)	484 (81)
C	290 (70)	280 (70)	280 (70)	280 (70)	244 (81)
Logs for ice cream sticks			30-39 cm	30-34 cm	25-29
A			917 (70)	697 (70)	536 (81)
B			752 (70)	615 (70)	467 (81)
Fuel wood	>10 cm	7-10 cm	5-10 cm	<5 cm	
	200 (0)	175 (0)	150 (0)	125 (0)	
Flooring logs	>70 cm	<70 cm			
	216 (79)	230 (98)			

the above figures as selling prices minus felling and transportation costs (*Table 3*). The predictions assumed that the real value of the marginal returns for the assortments was unaltered over the 40-year-period.

Thinning plans

Hypothetical thinning plans were worked out for the plots. These assumed an equalising thinning to achieve the same stem number per ha in plots at same site. In priority, the smallest trees were assumed harvested first and then the trees of poor quality. Additionally, the thinning plans aimed at creating an equal distribution of trees in the plots and the plans assumed subsequently that trees growing beyond a diameter of 50 cm in the middle of the bole were harvested successively. Finally, it was assumed that the remaining trees were felled at the end of the 40-year period (*Fig. 3*).

Economic returns from the equalising thinning were excluded from the estimations of economic returns from the provenances to improve the comparisons. Nevertheless, the stem number per ha in the start of the 40-year period was examined as covariant since the equalising thinning was not fully satisfying.

Growth model

Analyses of variance did not reveal certain provenance differences in growth (*Table 6* and *7*) and height classes of Henriksen and Bryndum (1996) were consequently assumed the same for plots within same site (*Table 4*). The height class and thus assumed volume increment per ha for a site was calculated as the mean height class of plots within the site. The height class of a plot was estimated from the relation between age and the height of the mean tree (Hg_0) at t_0 in the plot.

The steps in the growth models elaborated for each plot to predict the height and diameter of thinning trees at time t_1 based on information at t_0 are summarized below. These steps were repeated until t_{40}; i.e. height and diameter of thinning trees at a certain time n (t_n) were predicted based on data from t_{n-1}.

1. Estimation of the height for the mean tree (Hg_0) with a diameter corresponding to the average basal area of the plot (Dg_0) at t_0 using the non-linear height-diameter model (1) above. Dg_0 was estimated as $\sqrt{4g_0/\pi n_0}$ where g_0 is the basal area of the plot and n_0 is the number of trees within the plot at t_0.

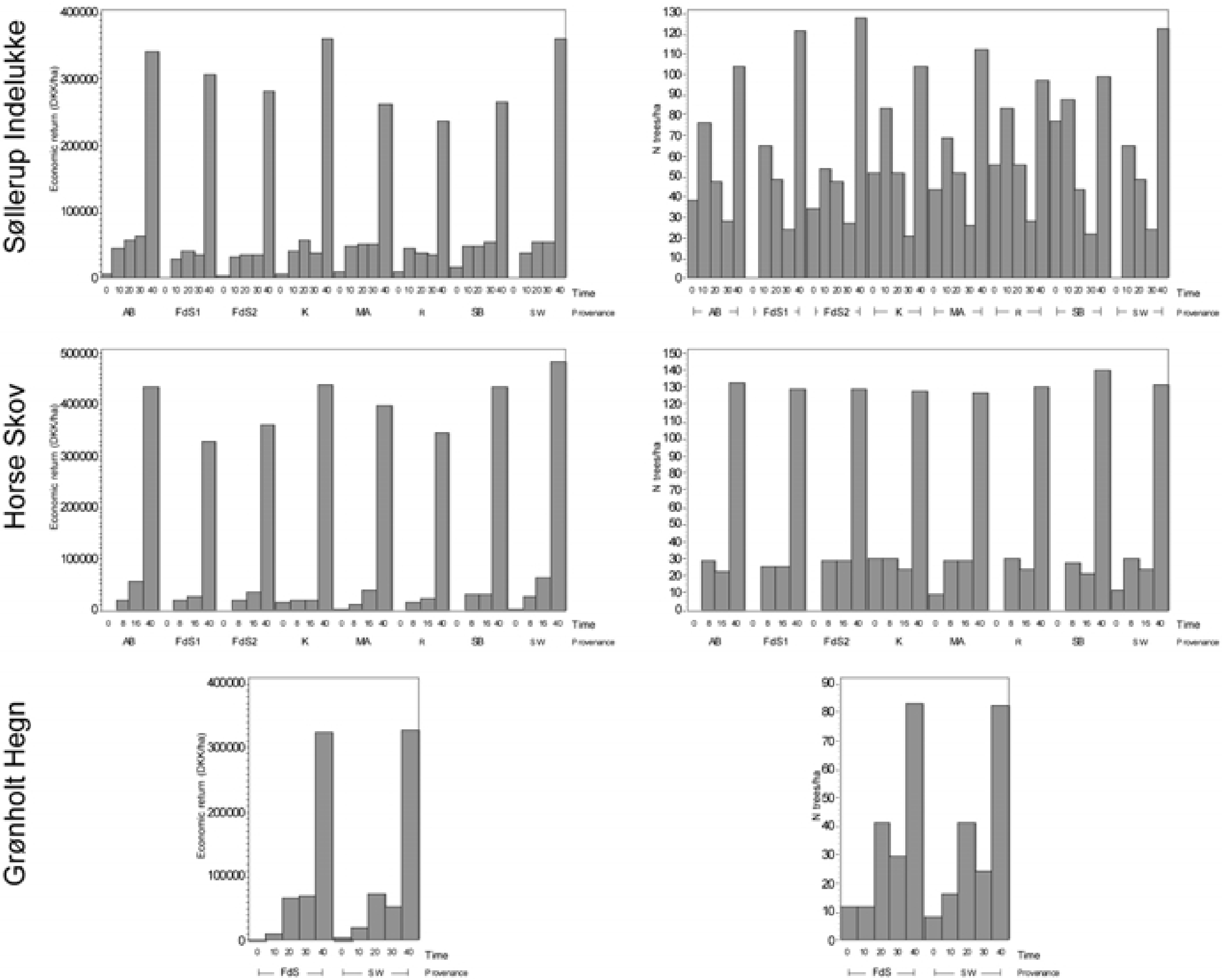

Figure 3. – Number of trees assumed felled in a 40-year period in the different sample plots and estimated marginal returns (DKK/ha) from the felling. All trees are assumed felled after a 40-year period. Marginal returns at time zero were not included in the overall predictions of marginal returns from the plots. Provenance abbreviations: Adlisberg (AB), FdS1 (Forêt des Soignes, first plot), FdS2 (Forêt des Soignes, second plot), K (Kokošovce), Midachten Allé (MA), Rügen (R), Sölvesborg (SB) and SW (Sihlwald).

Table 4. – Assumed volume and height increments at the sites corresponding to the assumed height classes of HENRIKSEN and BRYNDUM (1996).

Height class	Age year	Yealy height increment m	Volume increment m3/ha	Yearly volume increment m3/ha/year
32	60-70	0.26	162.4	16.2
32	70-80	0.22	155.1	15.5
32	80-90	0.19	148.5	14.9
32	90-100	0.15	140.4	14.0
33	60-70	0.25	168.6	16.9
33	70-80	0.22	161.4	16.1
33	80-90	0.19	154.7	15.5
33	90-100	0.16	146.7	14.7
34	60-70	0.24	174.9	17.5
34	70-80	0.22	167.6	16.8
34	80-90	0.19	161.0	16.1
34	90-100	0.16	152.9	15.3

2. Prediction of height (Hg_1) and volume (Vg_1) of the mean tree at t_1 using tabulated height- and volume increments by HENRIKSEN and BRYNDUM (1996) for the given height class of the plot (*Table 4*). Thus, $H_{g1} = H_{g0} + \delta H_{g01}$ and $V_{g1} = V_{g01} + \delta V_{g01}$, where δH_{g01} and δV_{g01} are height and volume increments from t_0 to t_1 according to the tabulated values by HENRIKSEN and BRYNDUM (1996). The age of all plots was assumed the same (62 years) to avoid the influence of different ages on the results. The tabulated values of HENRIKSEN and BRYNDUM (1996) were extrapolated two years to cover the age between 62 and 102 years.

3. The mean tree diameter at t_1 (D_{g1}) was then derived in an iterative process solving the volume model of MADSEN (1987) with respect to D_{g1} using V_{g1} and H_{g1} from step 2.

4. Prediction of individual tree heights ((h_1) at t_1. These were assumed to equal the height (h_0) at t_0 plus the mean height increment from t_0 to t_1, i.e. $h_1 = h_0 + \delta H_{g01}$. This approach was preferred over estimations from diameter-height regressions elaborated for each plot, which in the end were expected to give crude extrapolations.

5. A preliminary prediction of individual tree diameters at t_1 considering the position of the tree in the plot using the model:

$$d_1 - d_0 = \beta_1(D_{g1} - D_{g0}) + \beta_2(d_0 - D_{g0}) + \beta_3(D_{g1} - D_{g0})(d_0 - D_{g0}) \quad (4)$$

where d_1 is the diameter at t_1 of an individual tree, β_i, i = 1..3 are regression coefficients, and d_0 is the individual tree diameter at t_0. The model was elaborated to distribute the growth of a plot to the individual trees of the plot taking their diameters compared to the average diameter in the plot in consideration. Three thinning- and production experiments with beech in Denmark were used as material to derive parameters for model (4), (*Table 5*). The material is described in more detail by MADSEN (1987) p. 203. Diameter measurements from at least every 10th year were available within plots of the experiments. A preliminary study included as a start also the squared elements of the above variables. However, the adjusted R^2 proved best for model (4) with a value of 0.95.

6. Prediction of preliminary volumes for individual trees at t_1 from d_1, h_1, D_{g1} above and using the volume model for beech from MADSEN (1987).

7. Iterative adjustments of the preliminary diameters d_1 to achieve that the sum of volume increments for the individual trees equalled the assumed volume increment of the plot δV_{01}. These diameter adjustments were the same for all the trees in the plots.

Stem volume and taper model

Compatible stem volume- and taper equations were developed to estimate volumes and mid-diameters for sections of tree boles with different grades based on data from 2058 beeches from 42 stands (STOLTZE, 2000). This modeling followed the procedure used for other tree species in Denmark (MADSEN, 1985b; MADSEN and HEUSÉRR, 1993; TARP-JOHANSEN et al., 1997).

The total volume models including branches for beech (MADSEN, 1987) were combined with the stem volume equation to estimate residual firewood volumes of different dimensions.

Analysis of variance and estimation of genetic values

Plot means were calculated for tree heights, height of forks in percent of total tree heights, length of boles, bole percentage of total tree heights, and stem straightness scores and used for the analyses of variance. Furthermore, volumes per ha and percentages of trees within plots with severe spiral grain, percentages of trees with straight stems within plots and the estimated economic returns were used for the analyses of variance.

The mixed model applied to the data was

$$Y_{ijk} = \mu + S_i + p_j + \beta_1 X1_{ijk} + \beta_2 X2_{ijk} + \beta_3 X3_{ijk} + e_{ijk} \quad (5)$$

where Y_{ijk} is the mean of plot k with for provenance j at site i, μ is the general mean. S_i is the fixed effect of site i, p_j is the ran-

Table 5. – Thinning experiment material used to estimate parameters for model (4). D_{g0} is the diameter of a mean tree in the plot at t_0, d_0 is the individual tree diameter at t_0. D_{g1} is the diameter of the mean tree at t_1. Parameter estimates for the explanatory variables 1 and 2 were significant (P-value of 0.0001 and 0.0005, respectively), while the P-value of variable 3 was 0.0644). R^2 was 0.95.

Forest district	Forest	Experiment	Period with diameter observations	Number of thinning regimes	Number of trees in sample plots
København	Jægersborg Hegn	Q	51-121	1	24
Bregentved	Totterup	DP	52-74	3	9, 93,19
Odsherred	Grønnehave	K	58-120	1	24

	Explanatory variables: 1: D_{g1} - D_{g0}	2: d_0 - D_{g0}	3: (D_{g1} - D_{g0})(d_0 - Dg_0)
Parameter estimate	1.0000	0.0404	0.6401
Std. err of estimate	0.0076	0.0116	0.3457

Table 6. – Results from the analyses of variance. Analyses of variance are applied on cumulated future economic returns with an assumed rotation age of 30 and 40 years.

Trait	Source	DF	SS	MS	F-value	Pr>F
Height	Site	2	12	5.9	3.6	0.0716
	Provenance	6	13	2.2	1.3	0.3410
	Error	9	2	1.6		
Diameter	Site	2	5.94E-03	2.97E-03	86.5	<.0001
	Provenance	6	4.39E-04	7.31E-05	2.1	0.1481
	Error	9	3.09E-04	3.43E-05		
Volume per ha	Site	2	23577	11789	17.4	0.0008
	Provenance	6	6296	1049	1.6	0.2655
	Error	9	6086	676		
Percentage of straight trees	Site	2	1926	963	20.9	0.0004
	Provenance	6	1743	291	6.3	**0.0076**
	Error	9	415	46		
Straightness score	Site	2	0.5	0.26	11.3	0.0035
	Provenance	6	0.6	0.10	4.1	**0.0292**
	Error	9	0.2	0.02		
Bole percentage	Site	2	946	472.88	106.1	<.0001
	Provenance	6	58	9.63	2.2	0.1438
	Error	9	40	4.46		
Bole length	Site	2	55	27.31	102.5	<.0001
	Provenance	6	5	0.85	3.2	0.0585
	Error	9	2	0.27		
Percentage of forks	Site	2	831	415.42	1.7	0.2454
	Provenance	6	731	121.90	0.5	0.8053
	Error	9	2267	251.92		
Height of fork	Site	2	14	7.2	14.5	0.0050
	Provenance	6	7	1.2	2.5	0.1476
	Stem no. (site)	3	17	5.7	11.5	**0.0067**
	Error	6	3	0.5		
Frequency of severe spiral grain	Site	2	154	77	5.7	0.0257
	Provenance	6	344	57	4.2	**0.0272**
	Error	9	123	14		
Cumulated future economic return (40)	Site	2	1.69E+09	8.47E+08	0.6	0.5600
	Provenance	6	4.42E+10	7.37E+09	5.4	**0.0127**
	Error	9	1.23E+10	1.37E+09		
Cumulated future economic returns (30)	Site	2	2.71E+09	1.35E+09	2.2	0.1649
	Provenance	6	2.49E+10	4.15E+09	6.8	**0.0059**
	Error	9	5.49E+09	6.10E+08		

dom effect of provenance j with $E\sum_{j=1}^{n} p_j = 0$, $\mathrm{Var}(p_j) = \sigma^2_P$ where n is the number of provenances. $X1_{ijk}$ is the age of plot k with provenance j at site i, and β_1 is the corresponding regression coefficient. $X2_{ijk}$ is the number of stems per ha in plot k with provenance j at site i and β_2 is the corresponding regression coefficient. $X3_{ijk}$ is the diameter corresponding to the mean basal areas of plot k with provenance j at site i and β_3 is the corresponding regression coefficient. e_{ijk} is the residual/error with $E\sum_{i=1}^{s}\sum_{j=1}^{n}\sum_{k=1}^{m} e_{ijk} = 0$, $\mathrm{Var}(e_{ijk}) = \sigma^2_e$, where m is the number of plots within site i with provenance j. The error is assumed $N(0, \sigma^2_e)$ and observations independent.

Successive F-tests removed non-significant covariates. Effects with the lowest degree of significance were removed first. The mean tree diameter (D_g) was only used as covariate in models concerning bole percentage of total height, stem straightness, forks and spiral grain instead of stems per ha. Thus, D_g was assumed to reflect thinning plan differences over a longer period better than age and the present number of stems per ha. However, D_g was not used as explanatory variable in the cases of height growth, length of boles, volume per ha and economic returns to avoid confounding with provenance growth differences since D_g is a part of the growth.

The analyses of variance were made using the procedure GLM in SAS® (SAS Institute Inc., 1989). Normal distribution of residuals was tested using the Shapiro-Wilk tests in the procedure UNIVARIATE in SAS® (SAS Institute Inc., 1989). Residuals were plotted as function of predicted values to check for variance homogeneity (RUDEMO and SKOVGÅRD, 1984; CHATTERJEE and PRICE, 1991). Provenance deviations from the mean were predicted using the procedure MIXED in SAS® (SAS Institute Inc., 1989).

Table 7. – Results from the analyses of variance. Analyses of variance are applied on cumulated future economic returns with an assumed rotation age of 30 and 40 years. The material was restricted to replications of the same seed samples from Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G).

Trait	Source	DF	SS	MS	F-value	Pr>F
Height	Site	1	6.3	6.3	2.1	0.2181
	Provenance	4	14.7	3.7	1.2	0.4190
	Error	4	11.8	2.9		
Diameter	Site	1	2.61E-03	2.61E-03	346.8	**<.0001**
	Provenance	4	2.02E-04	5.06E-05	6.7	**0.0461**
	Error	4	3.01E-05	7.53E-06		
Volume per ha	Site	1	13290	13290	17.3	**0.0142**
	Provenance	4	908	227	0.3	0.8680
	Error	4	3080	770		
Percentage of straight trees	Site	1	749	749	63.2	**0.0014**
	Provenance	4	1235	309	26.0	**0.0040**
	Error	4	47.5	12		
Straightness score	Site	1	0.16	0.16	38.2	**0.0035**
	Provenance	4	0.38	0.09	22.0	**0.0055**
	Error	4	0.02	0.00		
Bole percentage	Site	1	518	518	61.4	**0.0014**
	Provenance	4	55	14	1.6	0.3248
	Error	4	34	8		
Bole length	Site	1	25.5	25.5	117.3	**0.0004**
	Provenance	4	5.7	1.4	6.5	**0.0487**
	Error	4	0.2	0.22		
Percentage of forks	Site	1	10	10	0.04	0.8541
	Provenance	4	311	78	0.30	0.8645
	Error	4	1036	259		
Height of fork	Site	1	0.02	0.02	0.00	0.9486
	Provenance	4	11.33	2.83	0.72	0.6211
	Error	4	15.74	3.94		
Frequency of severe spiral grain	Site	1	27	27	1.1	0.3471
	Provenance	4	173	43	1.8	0.2874
	Error	4	95	24		
Cumulated future economic return (40)	Site	1	8.36E+08	8.36E+08	1.5	0.2898
	Provenance	4	3.68E+10	9.19E+09	16.3	**0.0096**
	Error	4	2.25E+09	5.63E+08		
Cumulated future economic returns (30)	Site	1	1.40E+09	1.40E+09	3.6	**0.1305**
	Provenance	4	2.06E+10	5.14E+09	13.3	**0.0141**
	Error	4	1.55E+09	3.88E+08		

21 to 26-year-old data

An analysis of variance with a linear model similar to linear model (5) was applied to the plot mean values for stem straightness scores, heights and frequencies of trees with forks given in GØHRN (1972).

Results

Parameter estimates for the model giving the preliminary diameter predictions are given in table 5. Residuals were reasonable homogenous for the tests, though some heteroscadicity appeared for test Q (not shown). Nevertheless, the model was found acceptable for a comparison of the provenances.

Results, restricting the material to the plots replicating the same seed samples of Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G) are only mentioned when they were different from results and conclusions using the whole material.

Single traits

The mean bole length was 10.1 metres and the bole percentage of total height 39% across all sites using the whole materi-

Table 8. – Predicted provenance deviations. Mean percentage of straight stems across sites was 30%. Mean percentage of stems with severe visible spiral grain was 8% in the plots across the three sites. Mean bole length was 10.2 metres for the whole material and 9.8 metres for the restricted material (*).

	Percen-tage of straight stems		Percen-tage of straight stems*		Stem straight-ness score		Stem straight-ness score*		Percentage of stems with severe spiral grain		Bole length		Bole length*		Diameter*		
Mean	30%		32%		1.9		1.9		8%		10.1 m		9.8 m		35 cm		
Predicted deviation from mean of provenance	%	Std. err. (%)	%	Std. err. (%)	Score	Std. err.	Score	Std. err.	%	Std. err. (%)	m	Std. err. (m)	m	Std. err. (m)	cm	%	Std. err. (cm)
Adlisberg (CH)	3.3	5.5	1.6	5.9	-0.04	0.10	0.00	0.10	-3.3	2.7	0.4	0.3	0.5	0.4	-0.2	-0.6	0.3
Forêt des Soignes (B)	-5.7	4.8	-	-	0.14	0.09	-	-	-1.9	2.3	0.0	0.3	-	-			
Kokošovce (SL)	4.4	5.5	2.9	5.9	-0.10	0.10	-0.08	0.10	2.3	2.7	0.3	0.3	0.3	0.4	-0.2	-0.6	0.3
Middachten Allé (NL)	2.5	5.5	0.7	5.9	-0.05	0.10	-0.02	0.10	-4.6	2.7	-0.2	0.3	-0.2	0.4	-0.2	-0.7	0.3
Rügen (G)	-14.2	5.5	-19.1	5.9	0.21	0.10	0.33	0.10	3.2	2.7	-0.9	0.3	-1.1	0.4	-0.1	-0.2	0.3
Sihlwald (CH)	14.2	5.2	14.0	5.9	-0.21	0.10	-0.23	0.10	-2.0	2.6	0.3	0.3	0.6	0.4	0.8	2.1	0.3
Sölvesborg (S)	-4.5	5.5	-	-	0.04	0.10	-	-	6.2	2.7	0.1	0.3	-	-	-	-	-

* Include only material with replications of the same seed samples from Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL).

al. Effects of sites were significant. Differences between provenances were close to significant concerning bole length using the whole material (*Table 6*).

Differences were significant when restricting the material to the provenances Adlisberg (CH), Kokošovce (SL), Sihlwald (CH), Middachten Allé (NL) and Rügen (G) replicated by the same seed samples (*Table 7*). Thus, trees from the provenances Adlisberg (CH), Kokošovce (SL), Sihlwald (CH) had longer boles and trees from the provenance Middachten Allé (NL) and Rügen (G) shorter boles (*Table 8*).

The mean percentage of trees with straight stems (score 1) in the plots was 30% across the sites and using the whole material. Stem straightness scores and the percentage of straight trees were significantly different between provenances and between sites (*Table 6* and *7*). The percentage of trees with straight stems was 14% (predicted value) higher for Sihlwald (CH) and 14% (predicted value) lower for the provenance Rügen (G) (*Table 8*). These estimates were significantly different from the overall mean of all provenances with P-values of 0.0206 and 0.0247, respectively. Kokošovce (SL) and Adlisberg (CH) were also above average (*Table 8*). Results were very similar restricting the material to the provenances Adlisberg (CH), Kokošovce (SL), Sihlwald (CH), Middachten Allé (NL) and Rügen (G) replicated by the same seed samples (*Table 8*).

The mean percentage of stems with severe visible spiral grain in the plots was 8% across sites using the whole material. Sites and provenance effects proved significant (*Table 6*), but predicted deviations from the mean were small, e.g. the percentage of trees with severe visible spiral grain was 6% (predicted value) higher for Sölvesborg (S) and 4.6% (predicted value) lower for Middachten Allé (*Table 8*).

None of the provenance samples of Adlisberg (CH), Sihlwald (CH), Middachten Allé (NL), Kokošovce (SL) or Rügen (G) were significantly different when the material was restricted to encompass plots replicating the same seed samples of these provenances (*Table 7*). Thus, the predicted deviation of Middachten Allé above is questionable.

The mean plot height across sites was 26.2 meters, mean plot DBH was 36 cm, and mean volume per ha was 382 m^3/ha. Site effects were significantly different for volume and diameter and provenance effects were not significant using the whole material (*Table 6*). Similar results were obtained restricting the material to provenance samples originating from the same stand / sample trees with DBH as an exception. Provenances proved significantly different in DBH (*Table 7*) with a slightly higher (2%) average DBH in the two plots with Sihlwald (CH), (*Table 8*).

The mean plot percentage of forks was 45% and mean plot height of forks was 12 metres. Neither sites nor provenances influenced the percentage of forks or height of forks significantly (*Table 6* and *7*).

Economic returns

The overall mean cumulated predicted economic returns for the coming 40-year period was 451,925 DKK/ha across the three sites using the whole material. The overall mean was 467,892 DKK/ha when the material was restricted to encompass plots replicating the same seed samples of Adlisberg (CH), Sihlwald (CH), Middachten Allé (NL), Kokošovce (SL) or Rügen (G).

Provenances were significantly different from each other (*Table 6* and *7*) with Sihlwald (CH) and Adlisberg (CH) showing the highest cumulated predicted economic returns and provenance and Rügen (G) showing poorest cumulated economic return (*Table 9*). Deviations in cumulated economic returns over the 40-year-period from the mean were respectively 11, 10, and –19% for Sihlwald (CH), Adlisberg (CH), and Rügen (D). Almost similar results were obtained examining the influence on land expectation values using discount rates of 2, 4 and 7% (*Table 9*). Absolute predicted deviations ranged from 8900 DDK/ha (Sihlwald) to –9200 DKK/ha (Rügen) for a discount rate of 2% (*Table 9*). Absolute predicted deviations were small using discount rates of 4% and 7% simply stressing that improvements of the quality are of low value when the discount rates exceed 2% (*Table 9*).

The results changed in favour of the provenance Sihlwald (CH) when the material was restricted to include only replications of the same seed samples of Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G), (*Table 9*).

This change in predicted economic returns for Sihlwald (CH) was explained by a good appearance of Forêt des Soignes (B) compared with Sihlwald (CH) in the Forest Grønholt. This contrasted the plots with Forêt des Soignes (B) at the two other sites (*Fig. 3*). The good appearance of Forêt des Soignes(B) in the Forest Grønholt Hegn was mainly explained by long boles

Table 9. – Predicted provenance deviations from the overall mean in cumulated future economic returns over a 40-year-period ("0% scenario"). Furthermore, provenance deviations in land expectation value due to different economic returns from the 40-year period.

	Cumulated economic returns for 40-year-period			Cumulated economic returns for 40-year-period*			Influence on expectation value. Discount rate 2%			Influence on expectation value. Discount rate 2%*			Influence on expectation value. Discount rate 4%			Influence on expectation value. Discount rate 7%		
Mean	451925 DKK/ha			467892 DKK/ha			70849 DKK/ha			74468 DKK/ha			9771 DKK/ha			709 DKK/ha		
Predicted deviation from mean of provenance	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)
Adlisberg (CH)	43545	10	6	39770	8	7	7831	11	7	7456	10	7	1231	13	7	98	14	9
Forêt des Soignes (B)	-40019	-9	5	-	-	-	-6838	-10	6	-	-	-	-1089	-11	6	-93	-13	8
Kokošovce (SL)	25487	6	6	17941	4	7	3273	5	7	1987	3	7	357	4	7	12	2	9
Middachten Allé (NL)	-17391	-4	6	-33894	-7	7	-2905	-4	7	-5425	-7	7	-397	-4	7	-28	-4	9
Rügen (G)	-65559	-15	6	-92123	-20	7	-9207	-13	7	-12987	-17	7	-1142	-12	7	-65	-9	9
Sihlwald (CH)	50702	11	6	68307	15	7	8942	13	6	12224	16	7	1366	14	7	110	15	8
Sölvesborg (S)	3236	1	6	-	-	-	-1096	-2	7	-3255	-4	7	-325	-3	7	-34	-5	9

* Include only material with replications of the same seed samples from Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G).

Table 10. – Predicted provenance deviations from the overall mean of cumulated economic returns from harvested trees over a 30-year-period and harvest of all remaining trees at the end of the 30-year-period. Furthermore, provenance deviations in land expectation value due to different economic returns from the 30-year period.

	Cumulated economic returns for 30-year-period			Cumulated economic returns for 30-year-period*			Influence on expectation value. Discount rate 2%			Influence on expectation value. Discount rate 4%			Influence on expectation value. Discount rate 7%		
Mean	366134 DKK/ha			375979 DKK/ha			69003 DKK/ha			10639 DKK/ha			879 DKK/ha		
Predicted deviation from mean of provenance	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)	DKK/ha	(%)	Std. err. (%)
Adlisberg (CH)	39454	11	6	35759	10	7	7881	11	6	1329	12	7	121	14	2
Forêt des Soignes (B)	-30005	-8	5	-	-	-	-5906	-9	5	-1053	-10	6	-105	-12	-1
Kokošovce (SL)	15483	4	6	8847	2	7	2484	4	6	384	4	7	29	3	0
Middachten Allé (NL)	-13549	-4	6	-23723	-6	7	-2833	-4	6	-454	-4	7	-40	-5	-1
Rügen (G)	-53080	-14	6	-68131	-18	7	-8480	-12	6	-1162	-11	7	-78	-9	-1
Sihlwald (CH)	38081	10	5	47248	13	7	7949	12	6	1358	13	7	128	15	2
Sölvesborg (S)	3616	1	6	-	-	-	-1095	-2	6	-402	-4	7	-55	-6	-1

* Include only material with replications of the same seed samples from Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G).

(13.8 meters in contrast to 13 meters for Sihlwald (CH)) and optimistic quality-grade predictions despite a lower frequency of trees with straight stems; 30% of score 1, 43% of score 2 and 27% of score 3. The frequency in the Sihlwald (CH) plot was 53% of score 1, 33% of score 2, and 14% of score 3.

Comparative provenance deviations in cumulated economic returns were almost similar using a 30-year period instead of a 40-year period (*Table 9*), but the mean cumulated economic return for the 30-year period was off course lower (366,100 DKK/ha). The influence on land expectation values using the 30-year period were also similar to the results obtained using the 40-year period both concerning comparative and absolute deviations (*Table 9*).

The ranking of Sihlwald (CH) and Rügen (CH) as superior and inferior, respectively, was closely related to stem straightness. Adlisberg (CH) had also above-average stem straightness, above-average bole length and tended to have a low frequency of trees with severe spiral grain explaining the comparatively high economic returns for this provenance. Kokošovce (SL) was also above average in economic returns, but possibly not as much as Adlisberg (CH) because of a larger frequency of trees with visible severe spiral grain.

Marginal returns for remaining trees after thinning as function of their predicted diameter at breast height showed that the differences between provenances were small for diameters below 25–30 cm but increasing with increasing diameter (*Fig. 4*). Simply, because most of the wood is sold as fuel-wood or low-price logs, if diameters at breast height are below 30 centimeters (*Table 3*). Thus, differences in land expectation values because of the last 40-year period were to a large extent reflecting differences in land expectation values for a whole rotation.

Discussion

Stem straightness

The high frequency of straight stems in the Sihlwald and Kokošovce provenance correspond with previous observations in Denmark (PLOUGHELD, 1933; OKSBJERG, 1951; BANG, 1968; GØHRN, 1972), and more recent studies comprising Sihlwald (LARSEN, 1985) and a Slovakian provenance (MADSEN, 1995). The superiority of the Sihlwald provenance concerning stem straightness was also found in tests including a variety of Swiss provenances in Switzerland (BURGER, 1948) and in comparison with six German provenances (HOFFMANN, 1961). A genetic influence on stem straightness has further been shown from small progeny tests by BURGER (1933). The good performance of Sölvesborg (S) found by LARSEN (1985) was not recognised in this material. This might be a coincidence because of the small number of replications in this study, or it might be due to different seed samples from the Forest Sölvesborg.

A significant provenance variation in stem straightness has also been found in experiments with provenances from Northern Germany, where high elevation provenances showed the best stem form (KLEINSCHMIT, 1985; KLEINSCHMIT and SVOLBA, 1995; KLEINSCHMIT and SVOLBA, 1996). MADSEN (1985a) found no significant differences in a 24-25-year-old progeny test replicated at six sites with progeny from 27 approved Danish stands.

In conclusion, results from this and other studies suggest a genetic control of stem straightness, though the possibilities of adjusting for site differences are necessary when selecting provenances.

Significant (P-value of 0.0358) provenance differences in stem straightness scores were also present in the material of GØHRN (1972). The correlation coefficient was 0.87 (P-value of 0.0117) between provenance stem straightness score estimates in the material of GØHRN (1972) and the similar estimates in this study.

Spiral grain

The presence of severe visible spiral grain in European beech is a good indication of severe spiral grain in the outer rings (BIROT et al., 1980; TESSIER DU CROS et al., 1980) and severe spiral grain at one height level indicates severe spiral grain in the whole tree. Thus, correlation coefficients in a 100-year-old material of beech between height levels of 1, 5, and 9 metres were above 0.84 (BIROT et al., 1980)

The small frequency of severe visible spiral grain in the provenance Middachten Allé (NL), contradicts results from a previous investigation of trees at age 55-58 in the trial B80 showing the largest grain angles in trees from this provenance (BERGSTEDT, 1996). The discrepancy is probably coincidental as supported by the lack of significant differences between provenances when restricting the material to replications of the same seed samples of Adlisberg (CH), Sihlwald (CH), Kokošovce (SL), Middachten Allé (NL) and Rügen (G). The visual detection of spiral grain is further imprecise. Thus, five out of eight trees with spiral grain exceeding an angle of six degrees were not detected using this method in a 100-year-old beech material (TESSIER DU CROS et al., 1980). Nevertheless, this uncertainty of methodology the relative small frequency of trees with severe grain angles in Forêt des Soignes (B), Sihlwald (CH) and high frequency in Rügen (G) agrees with the findings of BERGSTEDT (1996).

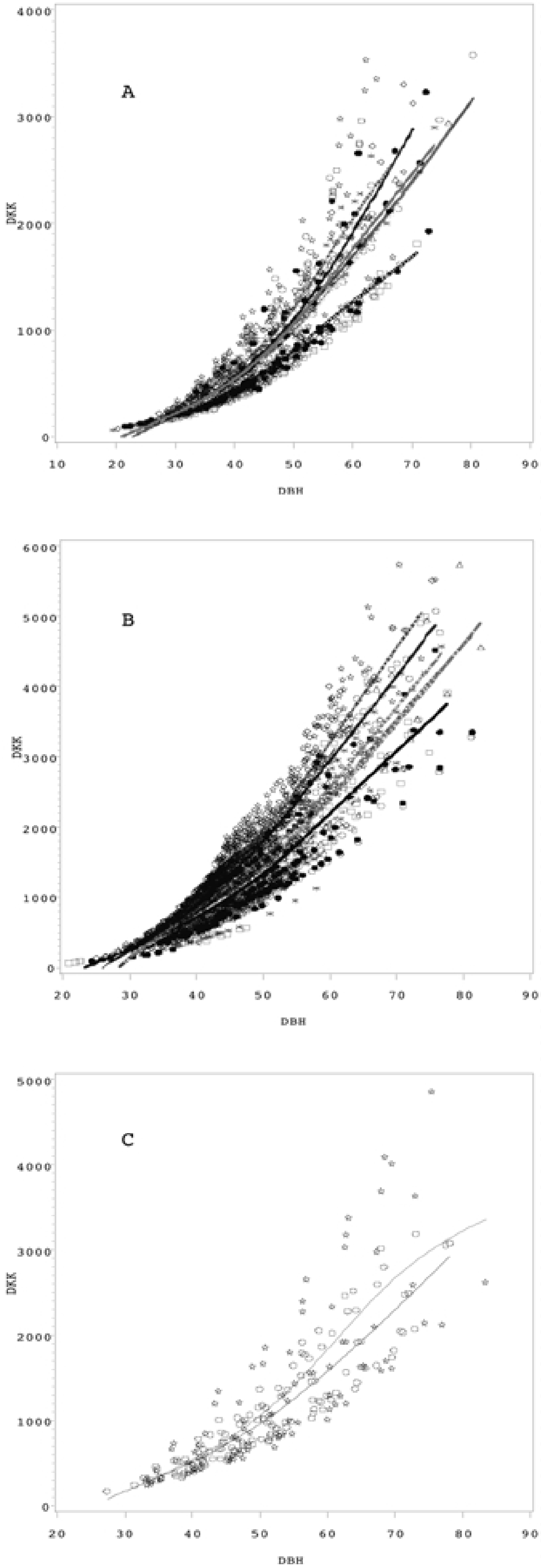

Figure 4. – Development in predicted marginal returns for single trees (DKK) as function of DBH for individual trees remaining after thinning. Marginal returns are based on the estimation of quality grades for trees at present, i.e. at age 61–65 years. Provenances: Adlisberg (◊), Forêt des Soignes (O), Kokošovce (△), Middachten Allé (•), Rügen (□), Sihlwald(*), Sölvesborg (⁎). A: Søllerup Indelukke. B: Horse Skov. C: Grønholt Hegn.

Genetic variation of spiral grain in European beech has also been found at the individual tree level (KRAHL-URBAN. 1962; TESSIER DU CROS et al., 1980). (TESSIER DU CROS et al., 1980) estimate a moderate narrow-sense heritability of 0.66 in a progeny test and they find a good agreement between grain angles of mother-trees and their progeny. KRAHL-URBAN (1953) finds groups of trees within stands with grain angles in a specific directions indicating a genetic influence from a specific mother-tree. Spiral grain is increasing with age in European beech limiting the possibilities for early selection (TESSIER DU CROS et al., 1980; RICHTER, 1999).

Height and diameter growth, volume per ha, forks

The few replications of the provenances might explain the non-significant differences between provenances in height and diameter growth, volume per ha and frequencies of forks. The significance between provenances in DBH when restricting the material to provenance samples originating from the same stand / sample trees was uncertain due to the small degrees of freedom for the test, low significance and lack of significance for height and volume (*Table 7*).

Provenance differences in growth have been found in other provenance tests with European beech provenances (e.g. PAULE, 1982; LARSEN, 1985; MADSEN, 1985a; MADSEN, 1994; KLEINSCHMIT and SVOLBA, 1995). One study found above-average height at age 20 years for Sihlwald (CH) compared with another Swiss provenance, a Danish provenance and four German provenances and two Swedish provenances, among these Sölvesborg (S), (LARSEN, 1985). Sölvesborg (S) had below-average height, but the significant height differences were not recognised for diameter growth (LARSEN, 1985).

Selective thinning removing trees with forks might have influenced the non-significant differences between provenances for this trait. Earlier investigations show that Sihlwald (CH) and especially provenances from the Carpathians have a large number of forks compared with Danish material (OPPERMAN, 1930; PLOUGHELD, 1933; HOLM, 1939; OKSBJERG, 1951; GØHRN, 1972). Sihlwald (CH) had also a larger frequency of forks compared with other Swiss provenances (BURGER, 1948). These observations are supported by two studies with statistical approaches concerning Sihlwald (CH), (LARSEN, 1985) and Czech provenances (WORREL, 1992). Other studies suggest that the provenance ranking over several environments might be variable (TEISSIER DU CROS and THIEBAUT, 1988; VERNIER and TESSIER DU CROS, 1996).

Economic returns of provenances

The ranking of Sihlwald (CH), Adlisberg (CH) and Rügen (G) as superior and inferior, respectively, was closely related to stem straightness, occurrence of spiral grain and length of boles. These provenance samples represent possibly some of the best and some of the poorest provenance material in Europe, but it should again be noticed that none of the provenances in this study are representative for the countries or regions they originally come from.

Occurrence of severe spiral grain might increase and we did not have the possibility to account for growth stress and formation of red heartwood.

Economic returns were possibly overestimated for Sihlwald (CH) known to have a large frequency of trees with forks (LARSEN, 1985). This might increase the risk of red heartwood formation, though this is uncertain (BORNER, 2002), storm damage and split of stems connected with felling (HUSSENDÖRFER et al., 1996). There is also some uncertainty whether the frequency of trees with growth stresses is extraordinary high for this provenance (BERGSTEDT, 1996). However, Sihlwald (CH) might have a better growth, though it has not been clearly proved yet (LARSEN, 1985).

The economic returns from the Kokošovce (SL) provenance might also be reduced because of larger frequencies of forks and a tendency, though not significantly in this study, to have high frequencies of trees with severe spiral grain.

Studies show early bud burst of East European and Swiss provenances compared with Atlantic provenances (TULSTRUP, 1950; GØHRN, 1972; MADSEN, 1995; WÜHLISCH et al., 1995; LIESEBACH et al., 1999) and generally early bud burst and early growth cessation with decreasing latitude and increasing longitude (WÜHLISCH et al., 1995; CHMURA and ROZKOWSKI, 2002). This limits the use of these provenances for sites with late frost.

Parameters likely to influence the prediction of economic returns were the prediction of quality grades 10–30 years ahead and the unknown thinning intensity in the plots before the start of this evaluation. Furthermore, it cannot be excluded that thinning plans adapted to different discount rates and rotation ages might change the relations between provenances marginally.

Nevertheless, the uncertainty in grading was possibly the same for all provenances. Stem straightness, which is an important trait for the quality grades, was also, not surprisingly, consistent over time as shown by the high correlation of stem straightness scores of this study with stem straightness scores of GØHRN (1972).

The results seemed further reasonable insensitive to changes in the assumptions concerning rotation ages, though it cannot be rejected that rotation ages adjusted specifically to each plot might change the comparative relations between the provenances marginally. Actually, we did try to predict future economic returns for a 50-year-period and to find the optimal rotation ages for the different plots for a discount rate of 2%, but found only marginally differences from the results using fixed rotation ages (not shown). Different thinning schedules before the evaluation have possibly not disturbed the economic comparisons between provenances considerably. Thus, the variation between plots within sites appeared to be small judged on stem number per ha and D_g (*Table 1*) and thinning schedules for plots in the two ordinary provenance field tests (B80, B90) have been the same as far as possible. The assumed equalising thinning reduced further a possible bias from earlier different thinning in the plots.

The growth model was simple with several assumptions, but the likelihood that this influenced the ranking and variation between provenances considerably seemed small since height and volume increments were the same for all plots within same sites.

Economic returns from the period before this evaluation were unknown, but the plots of marginal returns for single trees as function of their diameter at breast height suggested that differences in economic returns between provenances were small before the 40-year prediction period.

Conclusively, the predicted variation between provenances in economic returns for the future 40-year-period seemed reasonably certain and reflected possibly differences in land expectation values as well. This stresses the importance of choosing the right provenance for afforestation or reforestation to improve future economic returns. The genetic variation in stem straightness and spiral grain offers possibly also a good opportunity to improve future economic returns significantly by means of selective thinning in existing stands.

The difference between the best and the poorest provenance in land expectation value of 18000 DKK/ha for a discount rate of 2%, however, do not suggest that it is justifiable to replace a poor provenance with an superior provenance if a cyclic regime in beech with natural regeneration is an option. The difference is simply too large between minimum net present values of beech in cyclic regimes and expectation values of planted beech, mainly due to differences in establishment costs (HOLTEN-ANDERSEN, 1986; HOLTEN-ANDERSEN, 1987). This conclusion is even more relevant for discount rates of 4% and 7% where the advantage of using a high-quality provenance is negligible.

Conclusion

Provenance variation in stem straightness, occurrence of spiral grain and length of boles play a significant role for the economic returns, emphasising the importance of using the appropriate provenances for afforestation. The variation between provenances, even beside the variation due to the two provenances Sihlwald (CH) and Rügen (G), indicates also that it is economically reasonable to improve existing beech stands by means of selective thinning and to secure seed trees of high quality for the regeneration.

Nevertheless, the predicted economic returns did not show that it is economically feasible to replace even a very poor provenance like Rügen (G) with an economically superior provenance such as Sihlwald (CH) if natural regeneration is an option. An introduction of a new provenance requires also that the provenance is adapted to climate. Thus, a provenance such as Sihlwald (CH) with comparatively early bud burst is not recommendable for sites with late spring frost.

A wide use of a provenance requires also more knowledge about the wood quality of the provenance e.g. growth tensions, which might reduce the economic returns significantly.

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Insecticidal Activity and Transgene Expression Stability of Transgenic Hybrid Poplar Clone 741 Carrying two Insect-Resistant Genes

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Abstract

The insecticidal activity and the influence of transgenic hybrid poplar clone 741 carrying a Bacillus thuringensis gene (Bt*Cry1Ac*) and the arrowhead proteinase inhibitor gene (*API*) on the growth and development of different defoliating insects were tested during two years. The transgene expression stability during this period was documented.

Bioassays of transgenic poplar clone 741 on the larvae of Gypsy moth [*Lymantria dispar* (Linnaeus)], Scarce Chocolate-tip [*Clostera anachoreta* (Fabricius)] and other defoliating insects were carried out annually. The results showed that three transgenic subclones tested had a high resistance against these insects, but the insecticidal activity was different between years and with different insect species. Transgenic expression was generally stable during the 4 years. The insecticidal activity on the first larvae stage was obvious and decreased gradually with the development of the larvae (instar stage). Growth and development of the surviving larvae was seriously inhibited and delayed and in some cases could not even complete their development. Nevertheless feeding of transgenic poplar leaves could not kill the pests entirely. Proper planting strategies are necessary in order to prolong and optimize their resistance against the pests.

Key words: transgenic hybrid poplar clone 741, Bt*Cry1Ac* and *API* genes, insecticidal activity, transgenic expression stability, insect resistance.

Introduction

Inserting foreign DNA and into plants expressing insect-resistance is a new way to accelerate plant breeding. The development of transgenic insect-resistant plants provides a quick and safe approach to pest management. Some articles reported that the transformation of insect-resistant genes into poplars (*Populus nigra, P. euramericana, P. tomentosa P. tremula* x *P. tremuloides* and *P. alba* x *P. grandidentata*), larch (*Larix gmelinii*), spruce (*Picea asperata*) and Formosan sweetgum (*Liquidambar formosana*) (YU, 2000; XIE, 1999; ZHU, 1997; WU *et al.,* 1999). MCCOWAN *et al.* (1991) obtained regenerated plants (*Populus alba* x *Populus grandidentata*) with resistance to Gypsy moth (*L. dispar* (L)) and Tent caterpillar (*Malacosoma neustria testacea* [Motschulsky]). TIAN *et al.* (1993) transferred the 35S-Ω-Bt-Nos gene into black poplar (*Populus nigra*) with the binary vector Agrobacterium tumefaciens LBA4404. WANG *et al.* (1997) transferred the 35S-Ω-Bt-Nos gene into hybrid poplar (*Populus euramericana*) mediated by a binary vector