

IMPROVEMENT OF *POPULUS TREMULA* × *P. TREMULOIDES* BY PHENOTYPIC SELECTION AND CLONAL TESTING

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ABSTRACT

Field tests, including 280 clones of hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) planted on 10 different sites in the southern part of Sweden, were evaluated after up to 16 years of growth in the field. Survival rates were generally high and under weak genetic control. Symptoms of canker damage varied in frequency across sites, affecting 1 to 19 % of the trees and, again, was mainly under weak genetic control. All growth traits were strongly influenced by genetic factors. Selection of the best 10 % of the genotypes with respect to height resulted in a 14 % gain, corresponding to an estimated total yield of up to 25 m³ stem wood ha⁻¹ yr⁻¹ on fertile sites in southern Sweden. Strong age × age correlations for growth traits were found, suggesting that the optimal time for clonal selection would be after 3 or 4 years of testing in the field. However, since it is essential to avoid selecting clones that are sensitive to canker, the final selection of clones for commercial use should not be made until the trees are 10–15 years old. Since there was a negative genetic correlation between growth and straightness, multiple trait selection is needed to optimise value production.

Keywords: *Populus tremula* L., *Populus tremuloides* Michx., genetic parameters, genetic gain, growth, stem quality, phenology, survival

INTRODUCTION

The hybrid resulting from crossing *Populus tremula* L. and *P. tremuloides* Michx., henceforth called hybrid aspen, is a species with high growth potential in northern Europe. Previous studies have shown that its mean annual increments can be higher than 15 m³ ha⁻¹ yr⁻¹ during a 30-year rotation period in the Nordic countries (JAKOBSEN 1976; ELFVING 1986). This should be compared to approximately 9 and 14 m³ ha⁻¹ yr⁻¹ for *Betula pendula* Roth (KARLSSON *et al.* 1997; FRIVOLD & MIELIKÄINEN 1991) and *Picea abies* (L.) Karst (ERIKSSON 1976), respectively, both of which are suitable alternatives for growth on fertile sites in southern Scandinavia. In addition, hybrid aspen's ability to regenerate from root suckers after final felling considerably reduces the cost of establishment in the following generation. These favourable characteristics, combined with hybrid's aspen excellent wood and fibre characters for producing high quality printing paper (DHAK *et al.* 1997; KARL 1988) indicate that hybrid aspen has substantial commercial potential.

In Sweden, the first hybrid crossings were made in 1939 and, due to the great interest in aspen shown by

the Swedish Match Company, a breeding project was initiated. Since the growth of the hybrids was superior to that of the parent species, the breeding program was concentrated on producing hybrid families that grew well (JOHNSON 1953). In the 1960's the match production was moved out of the country, and attempts to improve the hybrid ceased. However, in the 1980's, the search for alternative uses of surplus agricultural land aroused interest in hybrid aspen once again. Aiming to produce superior hybrid aspen commercial material, an improvement project was initiated at the Forestry Research Institute of Sweden (Skogforsk). Selecting plus-trees from the old field tests and from commercial stands was assumed to be the best way to produce material with desirable genetic qualities. A total of 280 plus-tree clones were selected, vegetatively propagated and established on 14 test sites in southern Sweden during the period 1986–1991.

The potential of hybrid aspen breeding has previously been demonstrated in both Europe and North America (see, for instance, JOHNSON 1953; MELCHIOR 1985; LI & WYCKOFF 1993; YU 2001). However, reliable estimations of genetic parameters are rare. Traits of commercial value such as vitality, growth, straightness, branching and different wood and fibre

Table 1. Basic information about the clonal test. Trials with the same series numbers include the same clones.

Trial No.	Series No.	Name, county	Latitude	Longitude	Altitude [m]	Year of establishment	Clones in test	Replication per clone	Spacing (square) [m]	Soil type	Field age when measured
1055	1	Bulstofta, M	56°00'	13°00'	75	1986	54	20	2	Clay, moraine	0, 1, 2, 3, 4, 5, 6, 9
1083	1	Ingelstad, G	56°43'	14°54'	150	1987	60	12	2.8	Fine sand, sediment	0, 2, 4, 8
1108	2	Lönntorp, M	55°57'	13°06'	80	1988	106	15	2.5	Clay, moraine	3, 4, 8, 12
1109	2	Braxstad, E	58°18'	15°20'	100	1988	107	15	2.5	Clay, moraine	3, 4, 8, 12
1157	3	Källstorp, M	55°57'	13°07'	95	1990	38	8	2.5	Clay, moraine	3, 8
1158	3	Kavlås, R	58°13'	13°52'	145	1990	38	8	2.5	Clay, moraine	3, 8
1161	4	Kavlås, R	58°13'	13°52'	145	1990	72	8	2.5	Clay, moraine	3, 8
1196	5	Trolleholm, M	55°55'	13°21'	95	1991	41	12	2	Clay, moraine	8
1197	5	Sofielund, M	55°58'	13°01'	75	1991	41	12	2.5	Clay, moraine	8
1198	6	Åttersta, D	59°08'	15°57'	60	1991	63	12	2.5	Fine sand, moraine	6, 9

traits should be considered when superior clones are to be selected. For each of these traits, information on genetic variation, heritability and genetic correlations between traits and sites is required for efficient clonal selection, breeding and prediction of genetic gains.

The objectives of this study were to estimate genetic parameters within and among sites related to survival, damage, growth and stem quality traits, and to predict genetic gains for growth based on clonal tests of hybrid aspen in southern Sweden after 8–12 years of growth in field.

MATERIALS AND METHODS

Material

The study was based on 280 hybrid aspen clones distributed amongst 10 of the 14 sites in southern Sweden in which trials were initiated between 1986 and 1991 (Table 1). Four sites were excluded from the study due to poor establishment as a result of problems caused by weeds or damage by voles (*Arvicola terrestris*). All 10 trials examined were established on former agricultural land, in a randomised block design using single-tree plots. Each clone was represented, in most cases, in two trials planted in the same year (Table 1), and the material in different trial series were genetically related, to varying degrees, since they included varying numbers of clones in common.

All clones were phenotypically selected from field tests and commercial stands of hybrid aspen established during the 1950's, 1960's and 1970's based on vitality, growth, stem straightness and branching characteristics. Since canker (caused by *Hypoxylon mammatum* and *Lecostoma niveum*) can be a serious problem, only trees without visible signs of canker were selected. Information about the parental origin of the selected clones was poor, but was registered if available. The *P. tremula* parents mostly originated from southern Sweden (latitudes 55.5°–60.0°) and Poland (latitudes 53°–54°). The *P. tremuloides* parents originated mainly from the American states and Canadian provinces around the Great Lakes of North America (Ontario, Michigan, Colorado, Wisconsin, New Hampshire, Minnesota, Quebec and New Brunswick) within the approximate latitudinal range of 45°–50°. All 280 clones were vegetatively propagated as herbaceous root sprout cuttings at the Skogforsk research station at Ekebo (55°57'N, 13°07'E, 80 m). The material was established in the form of one-year old container plants in all trials, apart from trial 1083, which was planted with two-year old plants.

The results are based on assessments of different

Table 2. Description of traits.

Trait	Abbreviation	Description
Height	H	Total height, (dm)
Diameter	D	Diameter at breast height, (cm)
Volume	V	Stem volume, as estimated by functions based on H and D (JOHANSSON 1953), (dm ³)
Straightness	Str	Scored above breast height in five classes (1 = very crooked ... 5 = straight).
Apical dominance	ApD	Problems with inconsistent main stems (lack of apical dominance) above breast height were scored in 5 classes (1 = serious problems, ..., 5 = no problems)
Branch thickness	BrT	Scored above breast height in 5 classes (1 = very thick ... 5 = weak branches).
Branch angle	BrA	Scored above breast height in 5 classes (1 = very acute ... 5 = right angle).
Branch number	BrN	Scored above breast height in 5 classes (1 = many ... 5 = few branches per running meter).
Survival	Surv	Scored as 0 = dead and 1 = alive
Canker and stem cracks	Cnk1	Observations of canker on stems (probably <i>Hypoxylon mammatum</i>) and branches (probably <i>Lecustoma niveum</i>) and observations of stem cracks (presumed to be related to canker) were carried out in an additional inventory in the summer of 2001. A 1–5 scale was used where 1=serious damage and 5 = no damage). Since the frequency of serious damage was low, the scale used in subsequent analyses was 0 = no damage and 1 = damage.
Canker	Cnk2	Observations of canker (probably <i>Hypoxylon mammatum</i> or <i>Lecustoma niveum</i>) on stems and branches in connection with assessments of growth for ages 1–12 years. The scale used in the analyses was 0 = no damage and 1 = damage.
Small poplar borer	Bor	Damage by <i>Saperda popoulnea</i> . Scored as 0 = no damage and 1 = damage
Vole	Vol	Damage by <i>Microtus agrestis</i> . Scored as 0 = no damage and 1 = damage

traits in inventories made during the years 1987–2001 (Tables 1 and 2). All observations refer to field ages prior to thinning, but those related to canker in the year 2001 and those from trial 1055, where a systematic (alternate diagonal rows of trees were removed), cleaning was carried out after five years of growth in the field. Field age is henceforth abbreviated to age.

Statistical analyses

The statistical analysis was based on individual tree observations according to the model:

$$y_{ijk} = \mu + b_i + c_j + e_{ijk} \quad [1]$$

where y_{ijk} = observation k, in block i for clone j, μ = trial mean, b_i = fixed effect of block i, c_j = random effect of clone j, $NID(0, \sigma_c^2)$ and e_{ijk} = random error term for observation ijk, $NID(0, \sigma_e^2)$. Pedigree informa-

tion was not included in the model since the information was incomplete. To test the influence on genetic parameters of the effects of selection site, s_n = fixed effect of site n, was for some trials included in the model. Survival, and all stem quality and damage traits deviated from normal distributions and were transformed to normal scores prior to analysis following GIANOLA and NORTON (1981).

The variances σ_c^2 and σ_e^2 were estimated for different traits according to the REML (Restricted Maximum Likelihood) method, as performed in ASREML software (GILMOUR *et al.* 1999). Genetic parameters were interpreted as $\sigma_G^2 = \sigma_c^2$ and $\sigma_E^2 = \sigma_e^2$, where σ_G^2 = the genotypic variance among clones and σ_E^2 = environmental variance. The individual-tree broad sense heritability (H^2) was calculated as

$$H^2 = \sigma_G^2 / \sigma_P^2 \quad [2]$$

where $\sigma_p^2 = \sigma_G^2 + \sigma_E^2$. The genotypic coefficient of variation (CV_G) was calculated as

$$CV_G = \sigma_G \cdot 100 / X \quad [3]$$

where X is the phenotypic mean. The following model, expressed in matrix notation, was used in the multivariate analysis of the clonal trials:

$$y_i = X_i b_i + Z_j c_j + e_i \quad [4]$$

where i pertains to traits 1 and 2 measured in the same trial, or, as in the $G \times E$ analysis, the same trait measured in two different trials, y is the vector of individual tree observations, b is the vector of fixed block effects, c is the vector of random clone effects and e is the vector of random residuals. X and Z are design matrices of the block effects and clone effects, respectively. The random effects are assumed to have a multivariate, normal distribution with expectation zero and may be summarized as $c' = (c'_1, c'_2)$ and $e' = (e'_1, e'_2)$. The variance-covariance matrix is assumed to be

$$Var \begin{bmatrix} c \\ e \end{bmatrix} = \begin{bmatrix} G \otimes I & 0 \\ 0 & R \otimes I \end{bmatrix} \quad [5]$$

where G is the matrix with the clonal variances and covariances, R is the matrix with the residual variances and covariances and I is an identity matrix. When traits are measured on different sites R is reduced to a diagonal matrix including the residual variances only. Finally, \otimes symbolises the direct product.

The genotypic correlation (r_G) between traits within sites and genotypic correlations between the same trait measured in two trials (r_{GE}) were estimated as

$$r_G = \sigma_{G_1 G_2} / \sigma_{G_1} \sigma_{G_2} \quad [6]$$

where $\sigma_{G_1 G_2}$ is the genotypic covariance between two traits. Standard errors of the parameter estimates (H^2 , r_G , r_{GE}) were calculated by first-order Taylor series approximations in the ASREML software.

Predicted genetic selection gain (ΔG) was estimated as

$$\Delta G = i_{n,N} \cdot CV_G \cdot (r_{GE})^{0.5} \cdot r_{ii} \quad [7]$$

where $i_{n,N}$ is the intensity of selection based upon selection of n from N tested clones. Values for $i_{n,N}$ were derived from BECKER (1984), r_{GE} is the genotype × environment correlation and r_{ii} is the estimated relation between the “true” and “predicted” clone values calculated as

$$r_{ii} = (H^2 \cdot k) / (1 + H^2 (k - 1)) \quad [8]$$

where k is the harmonic mean of the number of replications per clone. The values of CV_G , r_{GE} and r_{ii} for each trait were estimated means for all 10 trials at the age of 8 and 9 years.

Selection efficiency was analysed as the relative efficiency of indirect selection (CR_Y) of trait Y compared to that of direct selection (R_X) of the target trait, X , which in this case was set as volume at age 8 or 9 years, expressed as:

$$CR_Y / R_X = i_Y \cdot H_Y \cdot r_G / (i_X \cdot H_X) \quad [9]$$

and since i_X and i_Y were equal, the expression was simplified to

$$CR_Y / R_X = H_Y \cdot r_G / H_X \quad [10]$$

where H_Y and H_X = the square root of H^2 for the indirect selected trait Y and the direct selected trait X , respectively, and r_G = genetic correlation between traits X and Y (FALCONER & MACKAY 1996). Selection efficiency based on gain per year was expressed as

$$CR_Y / R_X = (H_Y \cdot r_G / T_Y) / (H_X / T_X) \quad [11]$$

where $T_X = 9$ and T_Y = test age for the indirectly selected trait.

Possible trends with age for H^2 , CV_G and r_G were tested by linear regression analyses using the model:

$$y_{ij} = a + b \cdot \ln(x_i) + e_{ij}$$

where y_{ij} = estimates of H^2 , CV_G and r_G at site i , a and b = regression coefficients, x_i = fix effect of logarithm of age at site i and e_{ij} = random error term for observation ij , NID $(0, \sigma_e^2)$. The significance level used for testing the null hypothesis of no difference between tested ages was 5 % (*i.e.* it was rejected if $p \leq 0.05$).

Table 3. Results for survival and damage in each trial. All traits were scored as 0 or 1. The means refer to the original data expressed in %, while the H^2 –estimations are based on nscore-transformed values. Note that field age only refers to the traits "Surv" and "Cnk1" and total plants, i.e. total number of planted plants, only refers to "Surv".

Trait		Trial									
		1055	1083	1108	1109	1157	1158	1161	1196	1197	1198
Surv	Field age	2	2	3	3	3	3	3	8	8	6
	Total plants	1073	677	1347	1325	268	275	532	492	490	728
	Mean %	95	99	85	91	86	96	97	97	80	97
	H^2	0.07		0.04	0.04	0.22				0.03	
	s.e. H^2	0.02		0.02	0.02	0.08				0.02	
Bor	Mean %	6	9	2	41	11	4	8			
	H^2	0.01			0.02	0.07	0.07	0.03			
	s.e. H^2	0.01			0.01	0.05	0.06	0.03			
Vole	Mean %	23		9	10	3					
	H^2	0.04		0.02	0.01						
	s.e. H^2	0.02		0.02	0.01						
Cnk1	Field age	16	15	14	14	12	12	12	11	11	11
	Mean %	19	11	10	17	6	1	4	5	5	6
	H^2	0.16	0.04	0.04	0.01	0.07		0.09	0.01	0.11	0.05
	s.e. H^2	0.06	0.04	0.02	0.01	0.08		0.05	0.03	0.04	0.03
Cnk2	Mean %	9	10	2	2	8	4	1			
	H^2	0.01	0.16	0.16	0.07						
	s.e. H^2	0.01	0.05	0.03	0.02						

RESULTS

Survival and damage

Mean values and genetic parameters for survival and damage observed in each of the trials are presented in Table 3. Survival was high in all trials except 1108, 1157 and 1197. The H^2 estimates were generally very low or too low to estimate except for trial 1157, which showed a moderate and significant H^2 value. The difference in mortality between the early assessments presented in Table 3 and later assessments (not presented) was very low (at most 4 %).

Damage at young ages by the small poplar borer (*Saperda populnea*) and vole (*Microtus agrestis*) were low (< 10 %), with some exceptions, and the corresponding estimations of H^2 were very low and not significant.

The incidence of canker and stem cracks (Cnk1) at ages 11–16 varied among the trials from 1 to 19 %. Trees in the older trials (≥ 14) tended to be damaged more than those in the younger ones. H^2 for these types of damage was generally very low and not statistically significant, except for trial 1055. Frequencies of canker damage observed during growth assessments (Cnk2)

were generally low (≤ 4 %) in all but three trials, where an incidence of around 10 % was found. Estimations of H^2 were low to modest. Genetic correlations between canker and growth traits at ages of 8 or 9 years were generally weak and not significant (not presented) except for D \times Cnk1 and V \times Cnk2 in trial 1055, which showed significant r_G values of -0.43 and -0.45 , respectively, and H \times Cnk2 in trial, 1109 where r_G was 0.30 and significant.

Growth

The H^2 estimates were high and significant for growth traits in all 10 trials, and the mean H^2 values across trials were around 0.38 for all three growth traits (Table 4). The CV_G for volume was on average 31 %, which was three and two times as high as for height and diameter, respectively. An analysis across sites and ages detected a weak, but statistically significant, tendency for H^2 to increase with increasing age for height ($b = 0.54$, $p = 0.0032$) and diameter ($b = 0.49$, $p = 0.0178$), while no significant trends were obtained for CV_G (Figures 1–4). However, when data for trial 1055 were analysed separately, a significant trend between CV_G and age for diameter ($b = -0.81$, $p = 0.0272$) was found.

Table 4. Mean values (Mean) based on individual observations, heritabilities (H^2) with standard errors (s.e.) and genetic coefficients of variation (CV_G) for three growth traits in the 10 hybrid aspen clonal tests after 8–9 years growth in the field.

Trial	Age	Trait											
		H				D				V			
		Mean dm	H^2	s.e.	CV_G %	Mean mm	H^2	s.e.	CV_G %	Mean dm ³	H^2	s.e.	CV_G %
1055	9	120	0.36	0.06	6.7	120	0.44	0.06	10.9	66.8	0.41	0.06	24.1
1083	8	95	0.33	0.05	7.4	96	0.36	0.05	11.3	35.4	0.36	0.05	24.9
1108	8	67	0.26	0.03	9.2	62	0.32	0.04	14.9	12.0	0.29	0.04	31.6
1109	8	44	0.23	0.03	12.1	33	0.25	0.04	17.6	3.2	0.26	0.04	31.9
1157	8	99	0.37	0.08	8.4	99	0.33	0.08	12.8	40.1	0.41	0.08	29.2
1158	8	95	0.49	0.07	12.6	84	0.51	0.07	16.5	28.8	0.52	0.07	37.5
1161	8	100	0.38	0.05	8.8	88	0.39	0.05	13.7	32.5	0.42	0.05	29.6
1196	8	98	0.63	0.06	15.4	79	0.62	0.06	23.0	27.4	0.59	0.06	42.7
1197	8	74	0.34	0.06	10.4	68	0.28	0.06	15.7	16.4	0.28	0.06	31.5
1198	9	119	0.43	0.05	9.3	97	0.34	0.05	13.1	45.6	0.39	0.05	28.8
Mean		91	0.38		10.0	83	0.38		15.0	30.8	0.39		31.2

Table 5. Genetic correlation estimates (r_{gE}) for growth and stem quality traits measured at two sites in four pairs of trials at a field age of 8–9 years.

Trial series	Trait							
	H	D	V	Str	ApD	BrT	BrA	BrN
1055 – 1083	0.65	0.82	0.80	0.56	0.92	0.96	0.80	0.79
1108 – 1109	0.88	0.87	0.88	0.61	0.44	0.88	0.87	0.93
1157 – 1158	0.86	0.84	0.84	0.98	0.70	0.84	0.96	0.91
1196 – 1197	0.91	0.91	0.93	0.75	0.91	0.77	0.59	0.55
Mean	0.82	0.86	0.86	0.73	0.74	0.86	0.80	0.79

Estimations of r_G between height and diameter, when assessed on the same occasion, averaged 0.81 and varied between 0.51 and 0.96 for ages from 3 to 12 years. These estimates were all significant within each trial (Figure 5). There were no significant age trends for these traits in the joint analyses across all sites and ages, but the data for trial 1055 when analysed separately showed a strong and significant trend ($b = -0.99$, $p = 0.0003$). The r_G values for the correlations between D and V at the same age were extremely strong, ranging from 0.95 to 0.99 for ages 3–12 years (not presented).

Age × age correlations, *i.e.* r_G values, between height at young ages and height at age 8 or 9 years, and the corresponding r_G values for diameter were all significant within each trial, varying between 0.54 to 0.96 for H and 0.84 to 0.98 for D (Figures 6–7). The age trends for these variables were also significant and strong ($b = 0.79$, $p = 0.0013$ and $b = 0.84$, $p = 0.0186$,

respectively). The r_G value for the relationship between height at different ages and the target trait, *i.e.* volume at ages 8–12 years, was on average 0.78 with no significant age trend (Figure 8). The corresponding r_G value for diameter was 0.94, and again there was no significant age trend (Figure 9).

The genetic correlations between the same trait measured in two trials were evaluated in pairs of parallel trials, *i.e.* 1055 – 1083, 1108 – 1109, 1157 – 1158 and 1196 – 1197. These correlations (r_{gE}) were strong for all traits (Table 5).

The estimated genetic gain at different selection intensities is illustrated for three growth traits in Figure 10. Selection of the best 10 % of the genotypes with respect to height, diameter and stem volume over bark, resulted in genetic gains of 14 %, 22 % and 45 %, respectively.

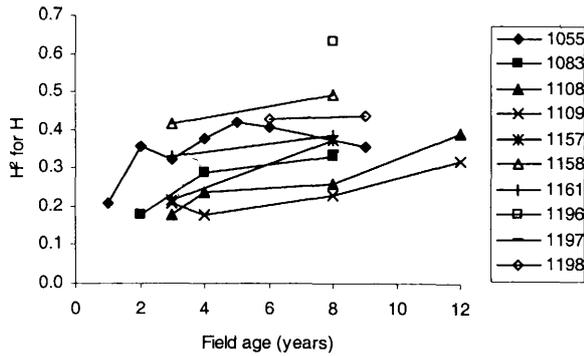


Figure 1. Broad-sense heritability for height over age for each trial.

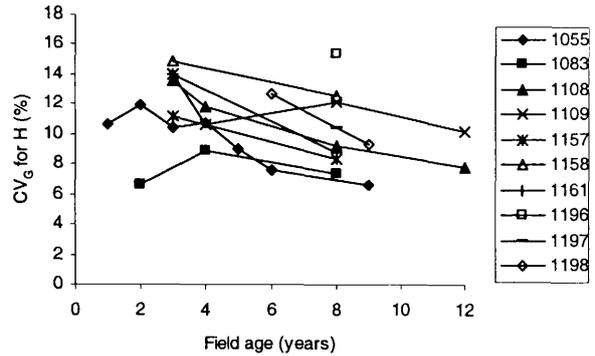


Figure 2. Genetic coefficient of variation for height over age for each trial.

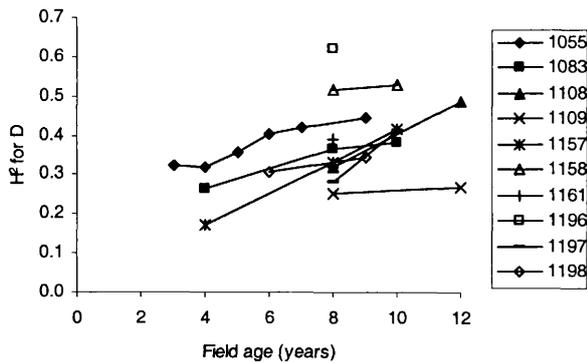


Figure 3. Broad-sense heritability for diameter over age for each trial.

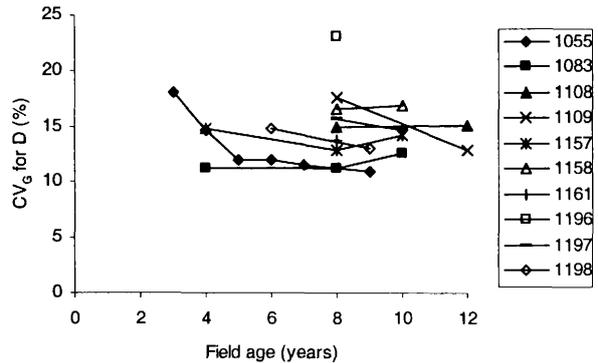


Figure 4. Genetic coefficient of variation for diameter over age for each trial.

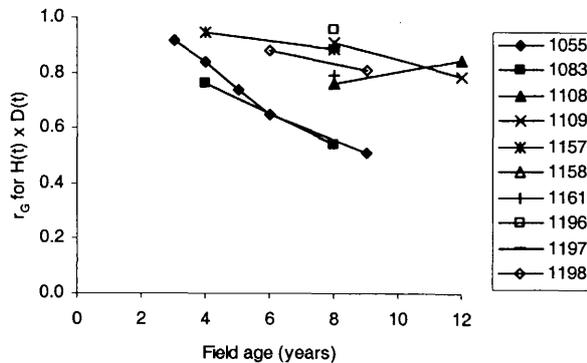


Figure 5. Genetic correlations over field age between height and diameter measured on the same occasion for each trial.

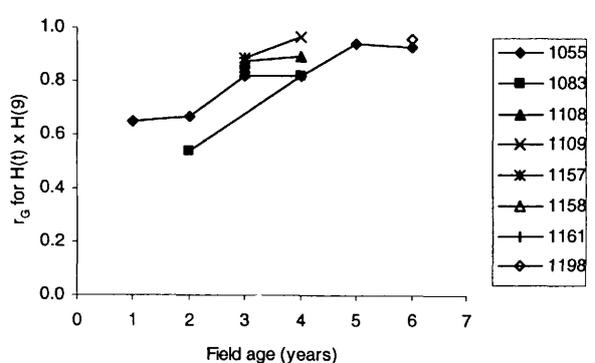


Figure 6. Genetic correlations between height at a specific field age and height at field age 9 years for trials where data was available.

Selection efficiency, *i.e.* the merit of early selection when compared to selection for volume at the age of 8 or 9 years, is presented in Figure 11. The H^2 values used to estimate selection efficiency at different ages were obtained from the regression of H^2 against the natural logarithm of age, based on data shown in figures 1 and 3 and corresponding data for volume (not presented), while the r_G values were kept unchanged over age (0.78 for H, 0.94 for D and 0.92 for V). The

“total” selection efficiency increased towards the target age, but rather weakly, especially for volume. On a per year basis there were strong tendencies for efficiency to decline with age. Selections based on volume at ages of 3 and 5 years were approximately 2.5 and 1.6 times as efficient per year, respectively, compared to selection at ages of 8 or 9 years.

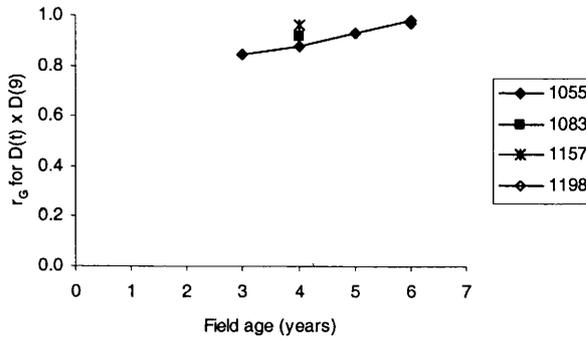


Figure 7. Genetic correlations between diameter at a specific field age and height at field age 9 years for trials where data was available.

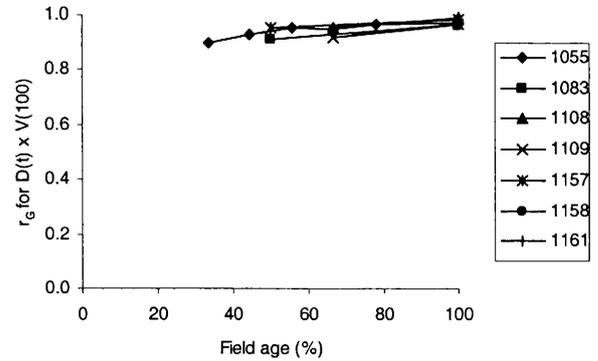


Figure 8. Genetic correlations between height at different field ages and volume at the target age which depending on trial varied between 8–12 years. Field age is expressed as the ratio between field age at a specific age and target age in %.

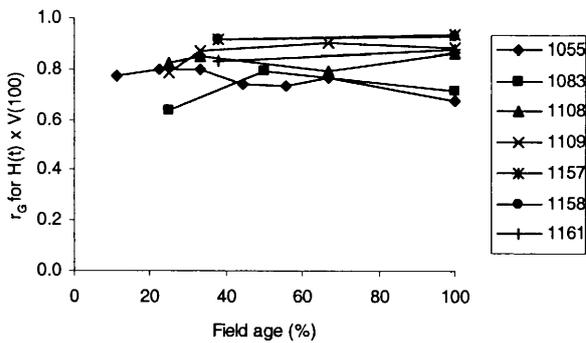


Figure 9. Genetic correlations between diameter at different field ages and volume at the target age which depending on trial varied between 8–12 years. Field age is expressed as the ratio between field age at a certain young age and target age in %.

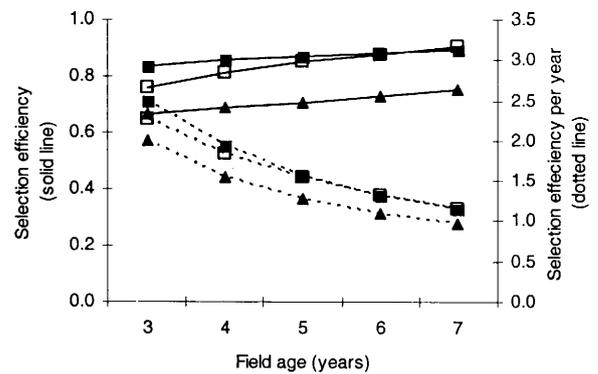


Figure 10. Predicted genetic gain after selection based on height (lower, solid line), diameter (middle, dotted line) and volume (top, solid, thick line) at a total population of 280 clones at field age 8–9 years.

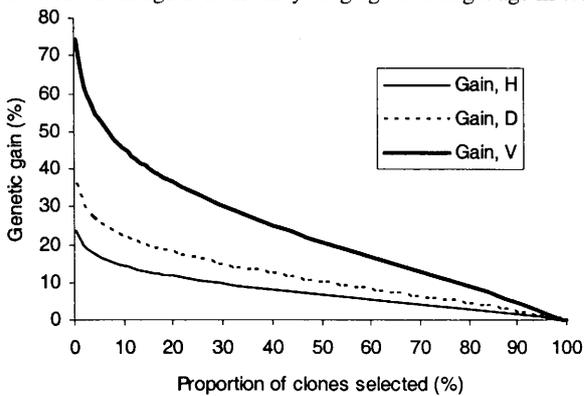


Figure 11. Selection efficiency, i.e. the merit of early selection based on height (triangles), diameter (white squares) and volume (black squares) when compared to selection for volume at the age of 8 or 9. Dotted lines refer to gain per year estimates (right y-axis) and solid lines refer to total gain estimates (left y-axis).

Stem quality

H^2 values of the stem quality traits were generally modest and significant for all traits and trials apart from ApD, where H^2 was low but still significant in nine out of 10 trials (Table 6). In some trials observations

Table 6. H^2 values for stem quality traits in all 10 trials based on observations at the field age of 8 years in all trials except for 1055 (nine years) and 1198 (six years).

	Trait				
	Str	ApD	BrT	BrA	BrN
Mean	0.21	0.10	0.20	0.27	0.29
Min	0.06	0.07	0.14	0.12	0.14
Max	0.35	0.17	0.24	0.36	0.44

regarding stem straightness have been recorded at different times, allowing genetic age × age correlations to be estimated. The r_G value for Str was 0.68 between the ages of 3 and 9 years in trial 1055, 0.78 and 0.86 between the ages 8 and 12 years in trials 1108 and 1109, respectively, and 1.00 between the ages of 4 and 8 years in trial 1109. All these estimates were significant.

Table 7. Genetic correlations (r_G) among stem quality traits in all 10 trials based on observations at field age of 8 years in all trials except for 1055 (9 years) and 1198 (6 years). The number of trials where r_G was significant ($P < 0.05$) is shown in the row “Sign”.

Traits		ApD	BrT	BrA	BrN
Str	Mean	0.64	0.49	-0.17	0.02
	Min	0.31	0.19	-0.47	-0.54
	Max	0.98	0.76	0.47	0.54
	Sign	7	7	4	5
ApD	Mean		0.61	0.24	0.27
	Min		0.33	-0.35	-0.15
	Max		0.84	0.66	0.54
	Sign		9	6	4
BrT	Mean			0.19	0.43
	Min			-0.59	0.06
	Max			0.95	0.82
	Sign			6	5
BrA	Mean				0.45
	Min				0.14
	Max				0.81
	Sign				6

Table 8. Genetic correlations between growth and stem quality traits in 10 hybrid aspen clonal tests after 6–9 years growth in the field. Significant ($P < 0.05$) r_G values are shown in bold.

Trial	Age	Trait									
		H					D				
		Str	ApD	BrT	BrA	BrN	Str	ApD	BrT	BrA	BrN
1055	9	-0.27	0.30	-0.17	0.48	0.35	-0.10	-0.14	-0.51	0.25	-0.31
1083	8	-0.31	0.14	-0.37	0.48	0.56	0.22	0.28	-0.52	0.31	-0.13
1108	8	-0.27	-0.34	0.11	0.21	0.30	-0.28	-0.52	-0.28	0.05	0.00
1109	8	0.22	0.14	0.25	0.17	0.40	0.25	-0.08	0.01	0.05	0.24
1157	8	-0.35	-0.67	-0.32	0.46	0.31	-0.39	-0.69	-0.37	0.25	-0.14
1158	8	-0.67	-0.48	-0.31	0.59	0.41	-0.65	-0.63	-0.45	0.42	0.01
1161	8	-0.05	0.20	-0.11	0.18	0.26	-0.28	-0.06	-0.47	-0.06	
1196	8	-0.65	-0.59	-0.74	-0.52	-0.40	-0.68	-0.67	-0.80	-0.60	-0.47
1197	8	-0.31	-0.35	-0.33	0.09	-0.04	-0.42	-0.45	-0.62	-0.17	-0.20
1198	9	-0.33	0.01	0.06	0.54	0.55	-0.33	-0.16	-0.21	0.52	0.27
Mean		-0.30	-0.16	-0.19	0.27	0.27	-0.27	-0.31	-0.42	0.10	-0.08

The r_G estimates among stem quality traits were modest to strong and positive for Str × ApD and ApD × BrT, and were also mostly significant within each trial (Table 7). Weak to modest and positive r_G values were found for Str × BrT, BrT × BrN and BrA × BrN, while the remaining correlations were weak and varied in sign

among the trials. The r_G values between growth and stem quality traits were mostly negative and weak to modest for H × Str, D × Str, D × ApD, H × BrT and D × BrT while H × BrA and H × BrN mostly showed positive and weak to modest correlations (Table 8).

DISCUSSION

Survival and damage

The survival was high (> 90 %) in seven out of 10 trials (Table 3). Initial mortality can be high in broad-leaved plantations if competing vegetation is poorly controlled during the first years of establishment, especially on former agricultural land. Dense vegetation increases competition for water, and makes environments more favourable for voles (FERM *et al.* 1994; MARINO & GROSS 1998). These general findings were consistent with our observations, and appeared to be the main reasons for the high mortality in trials 1108, 1157 and 1197 (Table 3). However, it should be noted that in trials where establishment was initially difficult, the growth rates of the trees recovered after some years. The survival of hybrid aspen was studied in Germany by MELCHIOR and SEITZ (1966), who found mortality to be independent of genotype after the first years of growth. This seems to be consistent with our results, since broad-sense heritabilities (H^2) were low in all but one trial (1157), which was seriously affected by two months without precipitation during the summer of 1992. Genetic differences in sensitivity to drought have been reported for other species (see for instance, SONESSON & ERIKSSON 2003; DUTKOWSKI 1995), which might explain the high heritability found in trial 1157. In another study (ILSTEDT & GULLBERG 1992, 1993) 16 % mortality at 14 years of age was reported from a hybrid aspen trial at Mykinge in southern Sweden. From ages 14 to 26 another third of the trees died, and this was explained as being due to disease (probably canker) and damage by moose. A significant family effect ($h^2 = 0.25$) was found for survival during this period. In our material, no evidence for mortality increasing with age was found, at least not up to 16 years of age. On the contrary, mortality after the first years of establishment was very low (< 4 %). In this context it should be mentioned that all 10 trials were fenced, reducing moose and roe deer damage to zero.

Stem canker (*Hypoxylon mammatum*) and branch canker (*Leucostoma niveum*) present serious threats to the poplar section *Leuce* to which hybrid aspen belongs. ILSTEDT and GULLBERG (1992, 1993) reported 25 % and 43 % frequencies of canker damage at the ages of 14 and 26 years, respectively, in the Mykinge trial. These infections are mainly associated with bark injuries, wounds by insects and 1–2 years old lateral branches (MANION 1975, ANDERSON *et al.* 1979). The phenotypic selection of the 280 clones included in our trials was mainly carried out in 20 to 40 year-old trials and stands, where the trees had been potentially exposed to canker throughout their time in the field. Since

only vital trees, i.e. trees without any visible sign of canker damage, were selected it was assumed that the selected material would be less sensitive to canker than hybrid aspen in general. As shown in Table 3, symptoms of canker or stem crack damage in this study were still quite high (10 to 19 %) in the four oldest trials, aged 14–16 years. The corresponding frequencies for medium to severe damage were much lower (4–7 %), although these figures are somewhat biased since the canker inventory was carried out in the year 2001, i.e. after all of the four oldest trials but 1109 had been thinned, and up to 40 % of the trees had been harvested. There were no reports of serious damage during these felling operations, but it is possible that trees with relatively low vitality, e.g. canker-infected trees were removed. It should be pointed out that no trees have been killed by canker in our trials, so far, in contrast to the figures presented by ILSTEDT and GULLBERG (see above) and to an estimated 2 % annual mortality for *P. tremuloides* in North America (ANDERSSON 1964; PITT *et al.* 2001). The risk of canker damage, and thus possibly mortality, increasing with age is hard to predict since contradictory findings related to interactions between stand age and canker damage have been reported (ANDERSON & ANDERSON 1968; MANION & GRIFFIN 1986; FALK *et al.* 1989). However, the oldest trials had the largest frequencies of canker, implying that infections may increase with age.

Observations in the field suggest there is no (ILSTEDT & GULLBERG 1992, 1993) to moderate (COPONY & BARNES 1974) genetic control of canker resistance. In the present study we found weak clonal influence on canker damage (Table 3) since H^2 estimates were low in all trials but 1055 (Cnk1), 1083 (Cnk2) and 1108 (Cnk2). A problem when evaluating canker damage, is that infection pressure varies amongst different sites and also probably over time, causing results to differ between different trials, even when the same clones are tested. Observations of canker damage will continue to be taken in the trials throughout the rotation, in order to check that the clones selected for commercial propagation remain vital and monitor the genetic influence.

There were no clear indications of any correlation between growth and incidence of canker. This is in accordance with findings by BRUCK and MANION (1980), ANDERSON and ANDERSON (1968) and PITT *et al.* (2001), who all found mortality due to *Hypoxylon* to be independent of tree size.

No dependence between site parameters and canker damage were found in our study. Results of previous studies concerning interactions between site and incidence of canker have often been inconsistent, and the genetic component has not been considered (AN-

DERSON & MARTIN 1981; ANDERSSON 1964; BRUCK and MANION 1980).

A number of studies have suggested that there are genetic differences in sensitivity to hares and voles (*e.g.* GILL 1992; HJÄLTEN & PALO 1992). In Finland for instance, tree breeders try to improve the resistance of *Betula pendula* to attacks by hares (*e.g.* ROUSI 1990). However, no significant differences in vole damage between different hybrid aspen clones were detected in our study (Table 3).

Finally, it should be mentioned that genetic differences are difficult to identify for traits related to rare conditions. This was generally true for all traits describing damage and survival, since the proportion of damaged and dead trees was mostly low.

Growth – Genetic parameters

All growth traits were under strong genetic control (Table 4), as indicated in other studies. Broad-sense heritabilities for height in *P. tremuloides* have been reported to be 0.52 (VAN BUIJTENEN *et al.* 1959), 0.45 (BARNES 1969), 0.33 and 0.69 (EINSPAHR *et al.* 1963; 1967). For diameter, H^2 -values of 0.14 (VAN BUIJTENEN *et al.* 1959), 0.29 (THOMAS *et al.* 1997), 0.36 (BARNES 1969) and 0.45 (EINSPAHR *et al.* 1967) can be found in the literature. For hybrid aspen H^2 -values of 0.60 for height and 0.51 for diameter were reported by YU and PULKKINEN (2003). In an 11-year old clonal study of *Betula pendula*, which is also a pioneer species, H^2 values for height, diameter and volume were all around 0.40 (STENER & HEDBERG 2003), which are consistent with our estimations. The corresponding CV_G -estimations from the study just cited were 6, 11 and 23 %, respectively, which are somewhat lower than those found here, but the relationships among the traits are of roughly the same magnitude.

We were unable to include any family terms in model [1], since the pedigree information was mostly missing. The genetic relationships that were present among the clones to some degree, though unknown, may have influenced the estimates of genetic variation, probably giving some upward bias. If so, the values for both H^2 and CV_G would have been slightly overestimated, even though they were still more or less consistent with the previous estimates mentioned above. Selection site (trial or stand number) was another variable that was considered to have possible effects on the results. The introduction of selection site into model [1] changed the estimates of H^2 and CV_G only marginally (not presented). The effects of family and selection site were thus considered to have introduced only minor bias to the results.

A weak but significant tendency for H^2 to increase with age was found in our study when all H^2 estimates were analysed jointly across sites and ages (Figures 1 and 3). A similar trend has been found by earlier investigators, *e.g.* JANSSON *et al.* (1998) for *Pinus silvestris*, which is a pioneer species like aspen, and LAMBETH and DILL (2001) claimed that H^2 increases more often than it decreases with age in conifers. It has been suggested that genotypic variances may be exaggerated by competition among trees (FOSTER 1989). All trials in the present study were of a single-tree plot design and, despite the fairly wide spacing, mostly of 2.5×2.5 m or more, they had most likely passed the age at which competition starts. Diameter growth appears to be more sensitive to competition than height growth (SAKAI & MUKAIDE 1967; MAGNUSSEN 1989). Although the increasing trends with age were similar for both height and diameter, it is likely that competition among trees caused estimates of H^2 to increase with age.

A valid and relevant time series of height and diameter observations can be analysed for trial 1055, since quite intensive assessments have been carried out here. From the data in figure 1 it can be seen that H^2 values for height increased considerably from year 1 to 2 (0.21 to 0.35) and then weakly, to 0.42 at 5 years of age, after which it decreased to 0.36 at 9 years. Diameter started with a H^2 value of 0.32 at ages 3 and 4, at age 6 it had risen to 0.40 and it increased further, to 0.42 and 0.44, at ages 7 and 9 years, respectively. These findings suggest that competition started at around 5 or 6 years of age, *i.e.* at a mean height of 5 to 7 m. This seems to be consistent with expectations, but cannot be statistically verified since no H^2 values between the years 1 to 9 were significant, except for year 1, at which stage they were probably still affected by *c*-effects, *e.g.* effects of vegetative propagation or nursery effects.

No significant trends were detected for CV_G when analysed across all sites and ages (Figures 2 and 4). However, the data for trial 1055 showed a significant reduction in CV_G over time, which is consistent with results from previous authors, *e.g.* HOULE (1992), showing a tendency for CV to decline as trait means increase.

Growth – Genetic correlations and selection efficiency

The mostly strong genetic correlations between height and diameter (Figure 5) indicates that the same set of genes regulates the two traits. In the analyses across all sites and ages no age trend was found. However, a negative trend with age was found when the true time series of trial 1055 was analysed separately. The most

probable explanation for this tendency is that competition increases as the stand matures, and has different effects on each trait (see above).

In both previous studies (LAMBETH 1980; LAMBETH & DILL 2001) as well as here (Figures 6 and 7), age-age correlations for growth traits have been found to decline with increasing difference in age. Successful early selection requires strong genetic correlations between the selection and the target age. In relation to the target age of 8 and 9 years, the mean genetic correlations at 4 years of age was as high as 0.92 for diameter and 0.87 for height. Similar correlations were obtained between diameter at 40–50 % of the target age and volume at target age, while the corresponding r_G values for height were somewhat lower (Figures 8 and 9). The very strong age × age correlations for diameter, and those between diameter and volume suggests that selection of superior clones for diameter at age 3 or 4 years (i.e. 30–50 % of the target age in Figure 9) should lead to more or less the same selection of superior clones as a selection based on volume at age 8 or 9 years. Diameter seems to be a better selection criterion than height for predicting volume at the target age due to its stronger genetic correlation with volume at all ages. Furthermore, diameter is easier to measure, and the measurements are more precise (especially in older trials), it is better correlated with wood density (STENER 1998) and its H^2 values are comparable to those of height. The most serious drawback associated with using diameter is that it is more adversely affected than height by competition, but this could be avoided, as indicated above, by early selection.

The effectiveness of early selection is also confirmed by the results of the selection intensity analysis (Figure 11). The absolute responses to early selection improved weakly towards the target age as a result of increasing age × age correlations, whereas the efficiency on a per year basis decreased strongly over time. Selection at age 3 years was approximately 2.5 times as efficient per year as compared to selection at 9 years. Earlier studies have also shown that the gains per unit time peak at an early phase of stand development (e.g. LAMBETH 1980). It should also be noted that economic considerations are likely to favour selection at an even younger age than analyses, like this one, where they are ignored (BALOCCHI 1990; NEWMAN & WILLIAMS 1991).

A significant genotype × environment interaction indicates that clones perform differently in various environments. Such interactions make testing and selection more complex and reduce genetic gain. The results from the four pairs of trials in the present study demonstrate that there are weak G × E interactions for both growth and stem quality traits, indicating that

clonal rankings are quite stable across sites (Table 5). In a study by Yu and PULKKINEN (2003) G×E for height and diameter at a total age of 4 years was evaluated for 25 clones planted on two agricultural and two forest sites. Significant differences were found between the trials on the different types of sites. The ranking of clones differed between sites, indicating that G×E interactions were present. However, the correlation between the two agricultural sites was quite strong (0.62 and 0.72). LI and WYCKOFF (1993) detected no important G×E environment interactions for aspen hybrid families over sites in the Lake States. These findings support our results and indicate that agricultural land in southern Sweden can be treated as a single test and utilization zone, at least for hybrid aspen. This will simplify future possible hybrid aspen breeding programmes. The results also suggest that few sites are needed for genetic tests.

Growth – Genetic gain

The results suggest that genetic gain would be 14, 22 and 45 % if the best 10 % of the genotypes in terms of height, diameter and volume, respectively, were selected from the 280 clones at the age of 8 or 9 years (Figure 10). This age corresponds to approximately 40 % of the rotation time for intensive hybrid aspen management in southern Sweden (RYTTER *et al.* 2002). Our gain estimations correspond quite well to those obtained in other studies. For instance, YU and PULKKINEN (2003) reported a genetic gain of 17 % for height growth increment during the third year from a selection of two out of 25 (8 %) hybrid aspen clones. RANDALL and COOPER (1973) reported a 9% genetic gain in height and 21 % for diameter after selecting four out of 32 (12.5 %) eastern cottonwood clones.

These gain estimates refer to the gains for individual trees, but a more relevant consideration is the gain per unit area, i.e. the increase in $\text{m}^3 \text{ha}^{-1}$. The annual mean production in the trials included in the present study was estimated by RYTTER *et al.* (2002) to be around $20 \text{ m}^3 \text{ha}^{-1} \text{yr}^{-1}$ for 20–25 year rotations. This is 20 % higher than the yield cited for the best site index class in the Danish normal yield table for hybrid aspen (JAKOBSEN 1976). However, since this is the only yield table available for hybrid aspen, at least to our knowledge, it was used to estimate the volume per hectare production at the age of 25 years. Realized gain was based on the predicted genetic gain for height (14 % gain at 10 % selection) since height has been suggested to be less affected than diameter by competition amongst trees (SAKAI & MUKAIDE 1967; MAGNUSSEN 1989). Estimations from the yield table indicated that a 14 % improvement in height at age 10 years would lead

to roughly a 25 % higher yield in $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ at the age of 25 years. The comparison assumes that the trees in our study will follow the same growth pattern as the Danish hybrids, that the relationship between height and diameter will not change over time, and that there will be a perfect correlation of 1.0 between height at the ages of 8–9 and 25 years. This is, of course, a very rough estimate, but it is supported by results related to *Pinus taeda*, for which a transformation factor of around two between individual height at age 6 years and unit per area gain at age 25 years has been reported (LI 1998). Thus, the results indicate that production of up to $25 \text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ should be possible on good sites after selecting the best 10 % of the clones.

Stem quality

Stem quality traits were mostly modestly genetically controlled and generally gave lower H^2 estimates than growth traits (Tables 4 and 6). The highest H^2 estimates were obtained for branch angle and number of branches. The latter was in accordance with results from the *Betula pendula* study by STENER and HEDENBERG (2003). The generally weak to modest correlations among stem quality traits (Table 7) suggest that traits are independently genetically controlled.

Stem straightness is one of the most important stem quality characters. Crooks are likely to be due to a shift of leaders, which can happen for various reasons, e.g. drought, frost or insect damage. Our results indicate that early selection is possible since there were strong correlations between stem traits at young and more mature ages. However, the genetic correlations between growth and stem straightness were mostly unfavourable (Table 8), indicating that selection of superior clones for growth tends to be less straightforward. Similarly unfavourable tendencies were found for apical dominance and branch thickness. It should be pointed out that the mean values for these traits did not indicate that utilising hybrid aspen for pulp wood would pose any problems, but if it was to be grown for high quality log production, multiple trait selection should be used in order to optimise growth and stem quality.

CONCLUSIONS

The results from this study allow us to draw the following conclusions. Many important traits for fibre production are strongly influenced by genetic factors and show substantial genetic variation. Genetic correlations among the same traits measured at different ages and sites are strong. Overall, these correlations provide

scope for powerful clone selection after early evaluation of clone tests at just one or a few sites.

If only growth is considered, early selection would be advisable. However, even though canker susceptibility seemed to be under weak genetic control generally, at some sites the genetic effects seemed to be more significant. Since it is essential to avoid clones that are sensitive to canker damage, and it might take 10–15 years for canker to develop fully, final selections of clones for commercial use should not be made until ages of 10–15 years, unless reliable, early artificial tests can be developed.

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