GENOTYPIC PARAMETERS AND CLONE × SITE INTERACTION IN CLONE TESTS OF NORWAY SPRUCE (*PICEA ABIES* (L.) KARST.)

Bo Karlsson & Karl-Anders Högberg

The Forestry Research Institute of Sweden, Ekebo, S–268 90 Svalöv, Sweden

Received June 5, 1997; accepted October 7, 1997

ABSTRACT

Genotypic parameters for growth and qualitative traits were estimated in an 11-year-old series of five field tests containing 311 cutting propagated clones selected from 5 different provenance groups. Significant differences among provenance groups and rather high broad sense heritabilities ($H^2 = 0.08 - 0.34$) for clones were found for growth traits. For most qualitative traits no significant differences were found between provenance groups, while heritabilities for such traits varied more than for growth traits. Significant clone × site interaction components of variation were found for most traits. Bud flush was the most stable trait over sites with a low interaction component of variance compared with the clone variance. Since height increment during the last 5 years showed higher interaction with site than total height, it is concluded that clone × site interaction may be increasing with age in Norway spruce and ought to be studied more carefully. Despite the significant interaction, the results are not considered to be a problem for efficient use of genetically improved material of Norway spruce in Sweden since the legislation requires rather large numbers of genetic entries for reforestation.

Key words: BLUP, clone test, cuttings, genetic gain, genotype × environment interaction, *Picea abies*.

INTRODUCTION

Clonal forestry with Norway spruce cuttings has been applied in several European countries in various scales (KLEINSCHMIT & SCHMIDT 1977, BENTZER 1993, KARLSSON 1993). Despite the obvious potential, cutting propagated plants have been used only in small amounts for reforestation in European countries. Different factors contribute to this hesitation shown by practical forestry, among them being concern that clone × site interaction might reduce the genetic gain achieved.

Information about variation and other genetic parameters is essential for carrying out efficient breeding activities (ZOBEL & TALBERT 1984), estimation of genetic gain and the application of clonal forestry.

For utilisation of genetically improved material it is important to be aware of possible genotype × environment (G × E) interaction and, if it exists, how to use the information in a favourable way. Several methods of detecting and analysing G × E interaction are available (SKRØPPA 1984, VAN EEUWIJK *et al.* 1996). Significant G × E interaction on clone level for Norway spruce has been reported by ST. CLAIR & KLEINSCHMIT (1986) and BENTZER *et al.*(1988). When clones are tested as mixtures, the interaction variance component tends to decrease (BENTZER *et al.* 1988, 1990, LUNDKVIST *et al.* 1992). The interaction seems to be difficult to utilise, except when it is caused by large well-defined climatic differences between sites.

In Sweden, two large clonal test programmes have been run since 1975. Hilleshög Forestry AB has tested more than 15 000 clones in field tests (Twetman pers. comm.), and another programme, run on contract by the former Institute for Forest Improvement, covers about 9 500 clones in field tests (KARLSSON 1993). The present study was carried out to study genetic parameters including G × E for growth and quality traits in a clone test series, planted out in order to select the best performing clones for vegetative mass propagation.

MATERIAL AND METHODS

In 1978, a total of 8 558 seedlings were selected in 12 different nurseries in southern Sweden. The selected seedlings originated from 39 different commercial seedling stocks, of which a majority were of east European origin. The provenances were grouped into 5 different provenance groups (Table 1). In the spring of 1978, new plants were obtained from the selected clones by cutting propagation. The rooted cuttings were transplanted as bare root plants in the following year. Growth cessation pattern was registered in September 1980 in three different classes: (1) Height growth terminated and bud set. (2) The growth has started again from the formed bud (Lammas shoot). (3) Height growth still continuing (free growth). In the spring of

Table 1. List of seedling stocks for the clone selection and the grouping in provenance groups. (w) indicates that the parent stands were of West European continental origin.

Provenance	Country	Group no.	No. of clones
Kosta	Sweden	1	11
Ö Blekinge	Sweden	1	16
Karsholm	Sweden (w)	2	15
Karsholm	Sweden (w)	2	2
Karsholm	Sweden (w)	2	12
Karsholm	Sweden (w)	2	1
Karsholm	Sweden (w)	2	6
Maglehem	Sweden (w)	2	5
Maglehem Seed orchard	Sweden (w)	2	2
Tunbyholm	Sweden (w)	2	7
Brosteni	Romania	3	5
Ilva Mica	Romania	3	16
Ilva Mica	Romania	3	8
Ilva Mica	Romania	3	19
"Romania"	Romania	3	11
Minsk	Belorussia	4	7
Minsk	Belorussia	4	25
Minsk	Belorussia	4	11
Minsk	Belorussia	4	10
Minsk	Belorussia	4	13
Minsk	Belorussia	4	2
Minsk	Belorussia	4	7
Vitebsk	Belorussia	4	24
Vitebsk	Belorussia	4	9
Breasa	Slovakia	5	11
"Tjeckoslovakien"	Czechoslovakia	5	13
Zakamenné	Slovakia	5	39
Zakamenné	Slovakia	5	1
Čierny Balog	Slovakia	5	2

1981, secondary cuttings were taken from fewer than 3 000 clones which remained after culling for low number of ramets/clone and plagiotropic growth. The cuttings were rooted in a greenhouse and transplanted as bare root plants the following year. In the autumn of 1983, the plants were lifted and divided into test series according to the number of ramets/clone. This study is based on 311 clones with more than 45 ramets/clone, which means that they were planted out in the spring of 1984 at 5 field sites with 9 replications/clone (Table 2) in a randomised block design. Culling for bad rooting or plagiotropic growth resulted in a total of 1 038 clones that were planted out in this and two other field test series. The selection effect is assumed to be insignificant for this study since no growth or quality traits were taken into consideration. Bud flush class according to KRUTZSCH (1975) was determined in 1984 on archive ramets and in the spring of 1986 on plants derived from cuttings taken from the field test plants before leaving the nursery.

In the spring of 1989, bud flush class (KRUTZSCH 1975) was registered in two of the trials, 977 Västra Ryd and 978 Knutstorp. In the autumn the same year, the first assessment was carried out in order to select clones for mass propagation of reforestation material. At that assessment, total height (H6) was measured and damage was recorded in all trials. In 1994, 11 years after planting, the trials were assessed for the second time. All traits measured in the trials are shown in

Table 2. Description of the test sites. Site index according to HÄGGLUND & LUNDMARK (1977). High site index indicate high productivity.

No.	Name	Ltitude	Longi-tude	Altitude	Site index
979	Hjuleberg	56o58'	12°44'	60	G34
976	Bölö	57°32'	15°36'	225	G26
977	Västra Ryd	57°44'	15°13'	270	G26
978	Knutstorp	56°01'	13°05'	110	G36
979	Årdala	59°01'	16°48'	40	G28

Table 3. Measured and calculated traits analysed in this report. Traits included in the analyses are indicated by X.

Trait	Abbreviation	Unit	Description	Trial no.				
				975	976	977	978	979
Bud break	BUD	0–8	Scored spring of 1989 according to KRUTZSCH (1975).			X	X	
Height 6	H6	cm	Height 6 years after planting.	X	X	X	X	X
Frost damage year 6	FR6	0–2	Scored frost damage 1989, where 0 is no damage and 2 is badly damaged.			X		
Survival[a]	SU	%	Survival rate from planting to assessment 1994.	X	X	X	X	X
Height11	H11	dm	Height 11 years after planting.	X	X	X	X	X
Increment	INC	cm	Height increment year 7–11.	X	X	X	X	X
Diameter	DIA	mm	Stem diameter at breast height.	X	X	X	X	X
Crookedness	CRO	1–5	Stem crookedness. Scored from 1–5, where 1 is straight and 5 is very crooked.	X	X		X	X
Number of branches	BRN	1–5	Number of branches in each whorl. Scored from 1–5, where 1 means few and 5 many branches.	X			X	X
Branch diameter [a]	BRD	1–5	Scored branch diameter, where 1 means relatively smaller and 5 means bigger branch diameter compared with stem diameter below whorl.	X			X	X
Branch length [a]	BRL	1–5	Scored branch length, where 1 means relatively short and 5 means long branches compared with leader length above whorl.	X			X	X
Branch distribution[a]	BRR	1–5	Scored vertical branch distribution in the whorl, where 1 means that all branches in the whorl are at the same level and 5 means that the whorl is spread along the stem.	X			X	X
Branch symmetry [a]	BRS	1–5	Scored branch symmetry around the stem, where 1 means good symmetric distribution and 5 means poor distribution.	X			X	X
Branch quality [a]	BRQ	1–5	Scored branch quality, where 1 means good branch quality and 5 means low quality.			X		
Branch angle [a]	BRA	1–5	Scored branch angle, where 1 is rather straight angle and 5 is a narrow angle.	X	X		X	X
Vertical branches [a]	VER		Number of whorls that contain vertical branches (ramicorns).	X	X	X	X	X
Frost damage year 11 [a]	FR11	0–4	Scored frost damage 1994, where 0 is no damage and 4 means severely damaged.			X		
Pilodyn value [a]	PIL	mm	Penetration measure at breast height with Pilodyn 6J.	X			X	

[a)] observed values were transformed to normal score values before analysis

distribution were transformed to normal score values (ERICSSON 1994) before analysis.

Analyses of variance and estimation of statistic and genotypic parameters for single trials were done using software by HARVEY (1990).

The model equation used for the analysis within field trials was:

$$Y_{ijkl} = \mu + B_i + P_j + c_{k(j)} + e_{ijkl}$$

where: Y_{ijkl} = Value of the *ijkl*th observation, μ = mean value of the population, B_i = fixed effect of block *i*, P_j = fixed effect of provenance group *j*, $c_{k(j)}$ = random effect of clone *k* in provenance group *j*, N(0, s^2_c), e_{ijkl} = random error term, N(0, s^2_e)

Genetic parameters were interpreted as:

$$\sigma^2_G = \sigma^2_c$$

$$\sigma^2_E = \sigma^2_e$$

where: σ^2_G = the genotypic variance, σ^2_E = the environmental variance.

Genotypic correlation estimates (r_g) between traits in the same trial was calculated as:

$$r_g = \sigma_{GG'} / \sigma_G \cdot \sigma_{G'}$$

where: $\sigma^2_{GG'}$ = the genotypic covariance between traits

The broad sense heritability, denoted H^2, on an individual ramet basis was calculated as the ratio between σ^2_G and $\sigma^2_G + \sigma^2_E$ (FALCONER 1960). Best linear unbiased predictors for clones (BLUP) were calculated using software by DANELL (1988). Correlations between trials were estimated as Pearson product moment correlations (SAS Institute Inc., Cary, NC, USA) between BLUP-values for the same traits in different trials.

REML variance estimates for the complete experiment series were computed by using the "Mixed" procedure in the SAS software (SAS Institute Inc., Cary, NC, USA).

The following model was assumed for the complete experiment series:

$$Y_{ijklm} = \mu + S_i + B_{j(i)} + P_k + c_{l(k)} + cs_{il(k)} + e_{ijklm}$$

where: Y_{ijklm} = value of the *ijklm*th observation, μ = mean value of the population, S_i = fixed effect of site *i*, $B_{j(i)}$ = fixed effect of block *j* in site i, P_k = fixed effect of provenance group *k*, $c_{l(k)}$ = random effect of clone *l* in provenance group *k*, N(0, σ^2_c), $cs_{il(k)}$ = random interaction effect of clone *l* and site *i* in provenance group *k*, $_N(0,\sigma^2_{cs})$, e_{ijklm} = random error term, N(0, σ^2_e)

Genetic parameters were interpreted as:

$$\sigma^2_G = \sigma^2_c$$

$$\sigma^2_{GE} = \sigma^2_{cs}$$

$$\sigma^2_E = \sigma^2_e$$

Broad sense heritabilities on an individual ramet basis over the experiment series were calculated as:

$$H^2 = \sigma^2_G / (\sigma^2_G + \sigma^2_{GE} + \sigma^2_E)$$

RESULTS AND DISCUSSION

Results for the five trials are presented in Table 4. Trials 975 and 978 showed the best height development with a mean height at 11 years (H11) above 5 metres, while trials 976 and 977 reached only about half of that height in the same time. Trial 977 was severely damaged by frost, which explains the low mean height of this trial.

After 11 years in field tests, survival (SU) varied between 84 and 95%. The variation among clone means was low in all trials with broad sense heritabilities never exceeding 0.03. Bud break (BUD) showed strong significance at provenance level and higher heritabilities than any other trait in this study, 0.78 and 0.66 respectively, which confirms the strong genetic influence on that trait found in other studies (NIENSTAEDT 1985, BIROT & NEPVEU 1979).

H^2 estimates for H11 varied between 0.12–0.34 with an average of 0.20, while the values for INC (height increment) and DIA, (diameter) were slightly lower in most trials. These estimates for growth traits agree well with other reports (ROULUND 1977, ROULUND *et al.* 1986, SHAW *et al.* 1988, BENTZER *et al.* 1989, LEPISTÖ 1993), and once again illustrates that use of clones is an efficient way of utilising genetic variation in Norway spruce. There were significant differences between provenance groups in all trials except 977. In three of the trials, provenance group 3 (Romania) performed the best, while group 1 (Sweden) was inferior in all trials. Crookedness (CRO) showed rather high H^2 (0.19–0.26), but lacked significant differences on provenance level. High H^2-values (0.23–0.35) were obtained for branch angle (BRA), but, as for CRO, there were no significant differences on provenance level. Among branch traits, the number of branches (BRN) had the same H^2 (0.20) in all three trials. Also branch diameter (BRD) had high heritabilities, while branch length (BRL) showed considerably lower heritability values. Moderate H^2-values were attained

Table 4. Mean values, probabilities from F-test in the analysis of variance and broad sense heritabilities (H^2) for analysed traits in different trials. PROV = provenance group, ns = p > 0.05.

Trial		SU	H6	BUD	FR6	H11	INC	DIA	CRO	BRN
975	Mean	95.0	235	–	–	52.1	286	60.6	2.69	2.98
	Prob (PROV)	0.0041	0.0000	–	–	0.0000	0.0000	0.0000	ns	ns
	Prob (CLONE)	0.0000	0.0000	–	–	0.0000	0.0000	0.0000	0.0000	0.0000
	H^2	0.01	0.31	–	–	0.34	0.31	0.31	0.20	0.20
976	Mean	95.1	150	–	–	25.9	109	27.4	2.72	–
	Prob (PROV)	0.0088	0.0013	–	–	0.0003	0.0002	0.0000	ns	–
	Prob (CLONE)	ns	0.0000	–	–	0.0000	0.0000	0.0000	0.0000	–
	H^2	0.01	0.14	–	–	0.12	0.08	0.10	0.21	–
977	Mean	84.2	134	2.79	0.74	25.5	120	24.7	–	–
	Prob (PROV)	ns	ns	0.0000	0.0000	ns	0.0422	ns	–	–
	Prob (CLONE)	ns	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	–	–
	H^2	0.00	0.17	0.78	0.19	0.20	0.19	0.18	–	–
978	Mean	88.3	193	4.46	–	53.5	342	58.5	2.81	2.91
	Prob (PROV)	ns	0.0112	0.0000	–	0.0008	0.0020	0.0000	ns	ns
	Prob (CLONE)	ns	0.0000	0.0000	–	0.0000	0.0000	0.0000	0.0000	0.0000
	H^2	0.01	0.11	0.67	–	0.14	0.15	0.11	0.26	0.20
979	Mean	90.5	158	–	–	39.1	233	40.8	2.71	3.00
	Prob (PROV)	ns	0.0002	–	–	0.0003	0.0016	0.0000	ns	ns
	Prob (CLONE)	0.0018	0.0000	–	–	0.0000	0.0000	0.0000	0.0000	0.0000
	H^2	0.03	0.15	–	–	0.18	0.17	0.17	0.19	0.20

		BRD	BRL	BRR	BRS	BRQ	BRA	VER	FR11	PIL
975	Mean	3.10	3.06	3.03	3.06	–	3.00	0.08	–	18.8
	Prob (PROV)	0.0000	0.0036	ns	ns	–	ns	ns	–	0.0070
	Prob (CLONE)	0.0000	0.0000	0.0000	0.0000	–	0.0000	0.0000	–	0.0000
	H^2	0.19	0.06	0.16	0.13	–	0.35	0.05	–	0.36
976	Mean	–	–	–	–	2.83	3.06	0.13	–	–
	Prob (PROV)	–	–	–	–	0.0000	ns	ns	–	–
	Prob (CLONE)	–	–	–	–	0.0000	0.0000	0.0000	–	–
	H^2	–	–	–	–	0.12	0.23	0.06	–	–
977	Mean	–	–	–	–	–	–	0.22	1.35	–
	Prob (PROV)	–	–	–	–	–	–	0.0009	0.0000	–
	Prob (CLONE)	–	–	–	–	–	–	0.0000	0.0000	–
	H^2	–	–	–	–	–	–	0.20	0.30	–
978	Mean	3.07	3.03	3.07	3.04	–	2.98	0.10	–	19.1
	Prob (PROV)	0.0000	ns	ns	ns	–	ns	ns	–	0.0006
	Prob (CLONE)	0.0000	0.0000	0.0000	0.0000	–	0.0000	0.0000	–	0.0000
	H^2	0.18	0.08	0.14	0.16	–	0.30	0.05	–	0.26
979	Mean	3.14	3.02	2.96	3.04	–	3.00	0.06	–	–
	Prob (PROV)	0.0000	ns	ns	ns	–	ns	ns	–	–
	Prob (CLONE)	0.0000	0.0000	0.0000	0.0012	–	0.0000	0.0000	–	–
	H^2	0.13	0.08	0.14	0.04	–	0.34	0.09	–	–

Table 5. Arithmetic means of estimated intra-trial genotypic correlations. The number of trials behind each estimate is given below. For PIL, the correlation estimates are based on BLUP-values in each trial.

	H6	H11	INC	DIA	CRO	BRN	BRD	BRL	BRR	BRS	BRA	VER	BUD	FR6
H11	0.92 5	.	.	.	.	.	.	.	.	.	.	.	.	.
INC	0.76 5	0.95 5	.	.	.	.	.	.	.	.	.	.	.	.
DIA	0.89 5	0.89 5	0.80 5	.	.	.	.	.	.	.	.	.	.	.
CRO	0.09 4	−0.02 4	−0.09 4	−0.08 4	.	.	.	.	.	.	.	.	.	.
BRN	−0.08 3	−0.12 3	−0.13 3	0.11 3	−0.35 3	.	.	.	.	.	.	.	.	.
BRD	0.07 3	0.00 3	−0.05 3	0.08 3	0.26 3	−0.25 3	.	.	.	.	.	.	.	.
BRL	0.11 2	0.00 2	−0.08 2	0.00 2	0.17 2	−0.36 2	0.46 2	.	.	.	.	.	.	.
BRR	0.13 3	0.15 3	0.15 3	0.23 3	0.00 3	0.44 3	−0.16 3	−0.14 3	.	.	.	.	.	.
BRS	−0.03 3	−0.11 3	−0.16 3	−0.24 3	0.58 3	−0.49 3	0.14 3	0.10 3	0.08 3	.	.	.	..	.
BRA	−0.30 4	−0.31 4	−0.27 4	−0.16 4	−0.26 4	0.44 3	0.09 3	0.01 3	0.32 3	−0.14 3	.	.	.	.
VER	−0.15 5	−0.22 5	−0.25 5	−0.17 5	0.25 4	−0.12 3	−0.05 3	−0.03 3	0.06 3	0.34 3	0.08 4	.	.	.
PIL	0.37 2	0.42 2	0.39 2	0.53 2	−0.09 2	0.06 2	0.05 2	0.03 2	0.17 2	−0.13 2	−0.04 2	−0.04 2	−0.10 1	.
BRQ	0.24 1	0.17 1	0.07 1	0.30 1	0.17 1	.	.	.	..	.	0.44 1	0.17 1	.	.
BUD	−0.15 2	−0.16 2	−0.16 2	−0.17 2	0.27 1	−0.10 1	0.22 1	0.10 1	−0.24 1	0.20 1	−0.09 1	0.60 2	.	.
FR6	−0.80 1	−0.79 1	−0.72 1	−0.82 1	.	.	.	.	.	.	.	0.82 1	0.71 1	.
FR11	−0.66 1	−0.75 1	−0.76 1	−0.73 1	.	.	.	.	.	.	.	0.80 1	0.80 1	0.85 1

for BRR (vertical branch distribution) (0.14–0.16), while H^2 for BRS (branch symmetry) was lower and more variable (0.04–0.13). VER (vertical branches) showed low H^2 (0.05–0.09), except for trial 977 (H^2 = 0.20). Heritability estimates for crookedness, vertical branches, branch angle, number of branches, branch diameter and branch quality traits correspond well with HÖGBERG (1990). Of all branch quality traits measured, only BRD showed significant differences between provenances. Group 2 (Swedish provenances of west continental origin) had considerably larger BRD than other groups. High H^2–values (0.36 and 0.26, respec-

tively) were obtained for pilodyn measurements (PIL) which also varied considerably among provenances. The relatively high heritabilities in our study correspond well with findings in other reports (LEWARK 1982, YANCHUK & KISS 1993). It may be discussed whether PIL is a good estimate of wood density, but YANCHUK & KISS (1993) report significant correlation estimates between specific gravity and pilodyn penetration for interior spruce in British Columbia.

Genotypic correlations within trials

Genotypic correlation estimates (Table 5) between H6 and H11 were high in all trials (r_g = 0.86–0.96). Correlations between INC and H6 were lower (r_g = 0.64–0.89), which might indicate a decreasing trend. ISIK *et al.* (1995) reported correlation estimates between height at 5 years and diameter at 17 years of only 0.60 which means a considerable loss in genetic gain on mature height when selecting after early evaluation of a clone test. With a mean of genotypic correlation estimates of 0.89 between H6 and diameter at age 11 and 0.92 between H6 and H11, it seems likely that the correlations in our study assure a good selection gain, since Swedish clonal forestry regulations (ANON. 1994) allow selection for multiclonal varieties at age 6 after planting.

BUD correlated strongly negatively with H11 in trial 977 (r_g = –0.42), which was planted at a site with severe frost problems, but no significant correlation was obtained in trial 978 where frosts during the growing period are rare. The strongly significant correlation estimates between BUD and FR6 and FR11 in 977 (r_g = 0.71 and 0.80, respectively) were expected and confirm findings by LUNDKVIST (1987). CRO correlated significantly with H11 only in trial 975 (r_g = 0.37). Both BRL and BRD correlated weakly with both H11 and DIA, while stronger correlations were obtained for BRR and DIA. The correlation estimates between H11 and BRA were significant (r_g = –0.31 —0.27). PIL showed the strongest correlations with DIA (r_g = 0.42 and 0.63).

Correlations between trials

Correlation estimates among trials were generally strongly significant for growth traits, despite their rather low values (Table 6). This may be interpreted as a strong plasticity when Norway spruce is planted in different environments. INC showed the lowest estimates (0.29–0.54) and H11 the strongest (0.37 –0.61), which may indicate that the clone × site interaction increases with age. Comparable measures of correlation estimates between genotypic values are rare in the literature, but BENTZER *et al.* (1988) reported average height correlation estimates between 5 trials ranging between 0.59 and 0.71 in one field trial series and 0.82–0.99 in another. In general, the correlation estimates for qualitative traits were slightly higher than for quantitative traits (Table 7). The highest correlation

Table 6. Correlation estimates between BLUP-values for the same growth traits in different trials.

Trial	Trait	H6				H11				INC				DIA			
		975	976	977	978	975	976	977	978	975	976	977	978	975	976	977	978
H6	976	0.56															
	977	0.56	0.42														
	978	0.53	0.41	0.42													
	979	0.49	0.45	0.36	0.47												
H11	976					0.53											
	977					0.61	0.48										
	978					0.51	0.40	0.37									
	979					0.44	0.44	0.39	0.45								
INC	976									0.43							
	977									0.54	0.47						
	978									0.44	0.32	0.29					
	979									0.33	0.38	0.38	0.39				
DIA	976													0.53			
	977													0.58	0.44		
	978													0.45	0.37	0.36	
	979													0.46	0.47	0.39	0.47

Table 7. Correlation estimates between BLUP-values for the same trait in different trials. Branch traits, PIL and BUD.

		CRO			BRN		BRD		BRL		BRR	
		975	976	978	975	978	975	978	975	978	975	978
CRO	9769	0.47										
	7897	0.68	0.57									
	9	0.53	0.61	0.61								
BRN	9789				0.54							
	79				0.51	0.54						
BRD	9789						0.62					
	79						0.59	0.58				
BRL	9789								0.32			
	79								0.29	0.35		
BRR	9789										0.50	
	79										0.29	0.44

		BRS		BRA			VER				PIL	BUD
		975	978	975	976	978	975	976	977	978	975	977
BRS	9789	0.28										
	79	0.01	0.22									
BRA	9769			0.59								
	7897			0.71	0.58							
	9			0.77	0.66	0.73						
VER	9769						0.08					
	7797						0.27	0.05				
	8979						0.11	0.05	0.09			
							0.16	0.29	0.14	0.18		
PIL	978										0.66	
BUD	978											0.88

estimate (0.88) between trials was found for BUD. BRA showed strong correlations ranging between 0.58 and 0.77 while CRO varied between 0.47 and 0.68. BRN varied between 0.51–0.54 and for PIL a correlation of 0.66 was estimated.

Experiment series analysis

Large significant clone × site variance components were found for growth traits (Table 8). For H11 and DIA it reached about 50% of the clone variance. For the same characters, BENTZER *et al.* (1988) reported G × E variance components of 40 and 20% of the clone components, respectively. In another study, BENTZER *et al.* (1989) found a ratio below 20% up to 10 years height, while the clone × site component for diameter and volume at age 10 reached slightly above 50% of the clone component. ST. CLAIR and KLEINSCHMIT (1986) found highly significant clone × site interaction for 10-year height in a 7-site series with 40 clones. The interaction component was 40% of the clone component which was less than in our study. In another analysis of the same clone test series, ISIK *et al.* (1995) reported clone × site components below 35 % of the clone component in all traits from age 3 to age 17. INC had the largest interaction component with 8.2% of the random variance, while clone variance contributed with 10.7%. The fact that the interaction component is almost as large as the clone component may be a warning that interaction is increasing.

Most of the branch quality traits had rather small interaction components compared with the clone component. There were exceptions for branch symmetry and vertical branches , where the interaction compo-

Table 8. Variance components estimates, standard errors and broad sense heritability estimates from the full model analysis. % = percentage of the total random variation, s.e. = standard error.

Trait	Source of variation										
	Clone (provenance)				Clone × site				Error		
	σ^2_c	s. e.	P<	%	σ^2_{cs}	s. e.	P<	%	σ^2_e	s. e.	H^2
SURV	1911	798	0.0167	0.6	2265	1487	0.1278	0.8	296332	3793	0.01
H6	323	33	0.0001	12.8	14.5	16	0.0001	5.8	2050	28	0.13
H11	14.5	1.5	0.0001	13.3	7.9	0.8	0.0001	7.2	86.7	1.2	0.13
INC	481	53	0.0001	10.7	371	34	0.0001	8.2	3656	50	0.11
DIA	29.5	3.1	0.0001	11.6	17.3	1.8	0.0001	6.8	207.4	2.80	0.12
CRO	152931	14697	0.0001	18.4	31078	5257	0.0001	3.7	646020	9691	0.18
BRN	81365	8685	0.0001	15.8	20971	4202	0.0001	4.1	411207	7193	0.16
BRD	87999	9188	0.0001	15.0	11719	4249	0.0058	2.0	487379	8519	0.15
BRL	20671	3034	0.0001	6.0	4768	2648	0.0717	1.4	321002	5616	0.06
BRR	71820	8819	0.0001	10.4	29664	6031	0.0001	4.3	589021	10309	0.10
BRS	6980	1640	0.0001	3.3	10376	2009	0.0001	5.0	191353	3351	0.03
BRA	163540	14893	0.0001	26.5	26510	3727	0.0001	4.3	426829	6400	0.27
VER	7357	1629	0.0001	2.4	11163	2185	0.0001	3.7	284893	4268	0.02
PIL	1.51	0.16	0.0001	25.8	0.27	0.07	0.0001	4.7	4.05	0.09	0.26
BUD	1.00	0.09	0.0001	65.4	0.01	0.01	0.0001	6.5	0.43	0.01	0.65

nent was larger than the clone component. BRA, PIL and BUD had very low interaction components compared with the clone variance. LUNDKVIST (1987) reported significant clone × site interaction for bud flush stage but not for growth. The interaction component in his study was as large as the clone component, while bud break in our study, which is a comparable trait, was very stable over sites with an interaction component of only 10% of the clone variance. That was the lowest proportion found for any trait included in the study.

Frost is likely to be one of the causal factors of G × E since the lowest correlation estimate was found between 977 (Västra Ryd), which is the trial that was the most affected by summer frost, and 978 (Knutstorp), which has the best climatic conditions. Frost damage was concluded to be a factor causing G × E by LUNDKVIST *et al.* (1992). Furthermore, SHAW *et al.* (1988) showed a strong decrease of the interaction variance component when damaged cuttings were omitted.

No transformation was carried out in order to homogenize variation within sites, which may explain some of the interaction effects. Studying Tables 6 and 7 it does not appear that sites with similar variance have higher correlation estimates.

Latitude transfer causing G × E interaction should also be discussed. Between-trial correlation estimates for INC are rather low between trial 979 (Årdala), which is the northernmost trial, and the other trials. This indicates that the transfer for some clones, which perform well further south, becomes too long and increase the clone × site interaction. This series of trials was not intended to specifically study G × E interaction but rather to evaluate genotypic parameters for Norway spruce clones in south Sweden. Including G × E interaction in the analysis has clearly demonstrated that further studies of interaction effects are necessary. Forest tree breeding in Sweden has adopted the multiple population breeding strategy (NAMKOONG 1984, DANELL 1993, KARLSSON & ROSVALL 1993) and a thorough understanding of the reaction norms of different genotypes is needed in order to handle the different breeding populations properly. For Norway spruce, it is especially important to learn more about adaptive traits. It is of great importance to detect whether most genotypes are involved in interactions, since that would require revision of breeding zones (SKRØPPA 1984). If few clones were the main cause of the interaction, it would probably be very hard to utilise them due to the difficulties in predicting the site impact on these specific clones. However, with the limited possibilities to use less than 40 clones in a mix for reforestation, as regulated by the Swedish forestry act (ANON. 1994), a G × E interaction of the magnitude detected in our study will not cause practical problems other than a slight reduction of the expected genetic gain.

ACKNOWLEDGEMENTS

We are very grateful to Dr. Ph. Baradat and Dr. J. Kleinschmit for valuable comments on the manuscript.

REFERENCES

ANONYMUS. 1994: SKSFS 1994:4 Skogsstyrelsen Jönköping, 5 pp.

BENTZER, B. G. 1993: Strategies for Clonal Forestry with Norway Spruce. *In:* Clonal Forestry II Conservation and Application (eds. M. R. Ahuja, W. J. Libby). pp. 120–138. Springer-Verlag, Berlin. ISBN 3-540-55714-8.

BENTZER, B. G., FOSTER, G. S., HELLBERG, A. R. & PODZORSKI, A. C. 1988: Genotype × environment interaction in Norway spruce involving three levels of genetic control: seed source, clone mixture, and clone. *Can. J. For. Res.* **18**:1172–1181.

BENTZER, B. G., FOSTER, G. S., HELLBERG, A. R. & PODZORSKI, A. C. 1989: Trends in genetic and environmental parameters, genetic correlations, and response to indirect selection for 10-year volume in a Norway spruce clonal experiment. *Can. J. For. Res.* **19**:897–903.

BENTZER, B. G., FOSTER, G. S. & HELLBERG, A. R. 1990: Impact of clone mixture composition on stability of 7th-year mean height in a series of Norway spruce clone tests. *Can. J. For. Res.* **20**:757–763.

BIROT, Y. & NEPVEU, G. 1979: Varabilite clonale et liaisons ortet-ramets dans une population d'epicea. *Silvae Genetica* **28**:37–47.

DANELL, Ö. 1988: OWST-BLUP, a computer programme for univariate best linear unbiased prediction of genetic values in half-sib tests or clone tests with standard varieties included. The Institute for Forest Improvement, Uppsala, (Mimeographed): 6 pp . (User's guide in Swedish.)

DANELL, Ö. 1993: Breeding programmes in Sweden.1. General approach. Corrected reprint. *In:* Progeny testing and breeding strategies, Proceedings of the Nordic group of tree breeding, Edinburgh, Scotland, October 1993 (ed. S. J. Lee). pp 1–4. Forestry Commission.

VAN EEUWIJK, F. A., DENIS, J.-B. & KANG, M. S. 1996: Incorporating additional information on genotypes and environments in models for two-way genotype by environment tables. *In:* Genotype by environment interaction. (eds. M. S. Kang, H. G. Gauch Jr). CRC Press, Inc. ISBN 0-8493-4003-9.

ERICSSON, T. 1994: Lodgepole pine (*Pinus contorta* var. latifolia) breeding in Sweden – results and prospects based on early evaluations. Swedish University of Agricultural Sciences, Faculty of Forestry, Dept. of Forest Genetics and Plant Physiology, Umeå. Dissertation: 32 pp.

FALCONER, D. S. 1981: Introduction to Quantitative Genetics. London: Longman Group Limited.

HARVEY, W. R. 1990: User's guide for LSMLMW and MIXMDL PC-2 version, Ohio State University, (Mimeographed): 91 pp.

HÄGGLUND, B. & LUNDMARK, J-E. 1977: Skattning av höjdboniteten med ståndortsfaktorer. Tall och gran i Sverige. SHS, Department of Forest Ecology and Forest Soils, Research Notes 28, 240 pp. [in Swedish].

HÖGBERG, K-A. 1990: Effects of selection for quality in three clonal trials with Norway spruce cuttings. The Institute For Forest Improvement. Report No. 19: 17 pp. [In Swedish with English summary]. ISSN 0284-4230.

ISIK, K., KLEINSCHMIT, J. & SVOLBA, J. 1995: Survival, growth trends and genetic gains in 17-year old *Picea abies* clones at seven test sites. *Silvae Genetica* **44**:116–128.

KARLSSON, B. 1993. Twenty years of clonal forestry in Sweden. *In:* Norway spruce provenances and breeding. Proceedings of the IUFRO S2.2–11 symposium, Riga, Latvia 1993 (ed. V. Rone). pp 208–212.

KARLSSON, B. & ROSVALL, O. 1993: Breeding programmes in Sweden. 3. Norway spruce. *In:* Progeny testing and breeding strategies, Proceedings of the Nordic group of tree breeding, Edinburgh, Scotland, October 1993 (ed S. J. Lee). pp 16–21. Forestry Commission.

KLEINSCHMIT, J. & SCHMIDT, J. 1977: Experiences with *Picea abies* cutting propagation in Germany and problems connected with large scale application. *Silvae Genetica* **26**:197–203.

KRUTZSCH, P. 1975: Die Pflanzschulenergebnisse eines inventierenden Fichtenherkunftversuches. Department of Forest Genetics, Royal College of Forestry, Research notes 14: 64 pp. Stockholm.

LEWARK, S. 1982: Untersuchungen von Holzmerkmalen junger Fichten aus Stecklingsklonen. Univ. Göttingen. *Forstarchiv* **53**(1):14–21.

LEPISTÖ, M. 1993: Genetic variation, heritability and expected gain of height in *Picea abies* in 7 to 9-year-old clonal tests. *Scand. J. For. Res.* **8**:480–488.

LUNDKVIST, K. 1987: Earliness and growth performance in clones of *Picea abies* selected for late frost resistance. *Scand. J. For. Res.* **2**:31–43.

LUNDKVIST, K. ERIKSSON, G. & NORELL, L. 1992: Performance of clonal mixtures and single-clone plots in young *Picea abies* trials. *Scand. J. For. Res.* **7**:53–62.

NAMKOONG, G. 1984: Strategies for gene conservation in forest tree breeding. In Plant Gene Resources: A Conservation Imperative. (Eds. C.W. Yeatman, D. Kafton, and G. Wilkes). AAAS Selected Symposium 87. Westview Press, Boulder, CO.: 79–89

NIENSTAEDT, H. 1985: Inheritance and correlations of frost injury, growth, flowering and cone characteristics in white spruce, *Picea glauca* (Moench) Voss. *Can. J. For. Res.* **15**:498–504.

ROULUND, H. 1977: A comparison of seedlings and clonal cuttings of Norway spruce (*Picea abies* L. Karst). *Forest Tree Improvement* **10**:1–26.

ROULUND, H., WELLENDORF, H. & WERNER, M. 1986: A selection experiment for height growth with cuttings of *Picea abies* (L.) Karst. *Scand. J. For. Res.* **1**:293–302.

SHAW, D. V., HELLBERG, A. & FOSTER, G. S. 1988: The effect of damage on components of variance for fifth-year height in Norway spruce. *Silvae Genetica* **37**:19–22.

SKRØPPA, T. 1984: A critical evaluation of methods available to estimate the genotype environment interaction. *Studia Forestalia Suecica* **166**:3–14.

ST. CLAIR, J. B. & KLEINSCHMIT, J. 1986: Genotype-environment interaction and stability in ten-year height growth of Norway spruce clones (*Picea abies* Karst.). *Silvae Genetica* **35**:177–186.

TWETMAN, J. Managing director of Odlarna Tve AB, former Hilleshög Forestry AB.

YANCHUK, A. D. & KISS, G. K. 1992: Genetic variation in growth and wood specific gravity and its utility in the improvement of Interior spruce in British Columbia. *Silvae Genetica* **42**:177–186.

ZOBEL, B. & TALBERT, J. T. 1984: Applied Forest Tree Improvement. John Wiley & Sons, Inc., 505 pp. ISBN 0-471-09682-2.