Characteristic	Proportion of trees correctly classified
	---- percent ----
bark texture	89
foliage resin gland occurrence	85
bark color	48
crown shape	29
bark texture and foliage resin gland occurrence	76

Table 1. — Analysis of homogeneity of frequency distributions for traits of Arizona cypress trees sampled in Alabama.

Source of Variation	Trait	Degrees of Freedom	Calculated chi-square value
Between varieties	bark color	4	24.37
	bark texture	2	89.41
	foliage resin gland occurrence	2	23.40
	crown shape	6	28.85
	foliage color	6	2.52
Among seed sources within var. *arizonica*	bark color	24	24.15
	bark texture	12	24.42
	foliage resin gland occurrence	12	14.83
	crown shape	36	25.33
	foliage color	36	31.73
Among seed sources within var. *glabra*	bark color	4	2.95
	bark texture	2	0.00
	foliage resin gland occurrence	2	.92
	crown shape	6	5.86
	foliage color	6	3.44

Bark texture and foliage resin gland occurrence were the only two characteristics which were satisfactory as classification variables, correctly classifying 89% and 85% of the trees, respectively. When used concurrently, they correctly classified 76% of the trees. Other single characteristics and combinations of characteristics were unsatisfactory as classifiers.

It can be concluded that trees of var. *arizonica* are identifiable by their furrowed bark and lack of resin glands on the foliage. Conversely, var. *glabra* trees will frequently have smooth bark and foliage dotted with resin glands.

Literature Cited

Goggans, J. F. and C. E. Posey: Variations in Seeds and Ovulate Cones of Some Species and Varieties of *Cupressus*. Auburn Univ. Agric. Exp. Sta. Circ. 180 (1968). — Greene, E. L.: New Western Plants. Bull Torrey Bot. Club 9: 62—65 (1882). — Kearney, T. H. and R. H. Peebles: *Cupressus*. p. 67 in Flowering Plants and Ferns of Arizona. U.S.D.A. Misc. Publ. 423 (1942). — Little, E. L.: Atlas of United States Trees. U.S.D.A. Forest Service, Misc. Publ. 1146 (1971). — Little, E. L.: Checklist of United States Trees. U.S.D.A. Forest Service, Hdbk. 541 (1979). — Posey, C. E. and J. F. Goggans: Observations on Species of Cypress Indigenous to the United States. Auburn Univ. Agric. Exp. Sta. Circ. 153 (1967). — Sargent, C. S.: Manual of North American Trees, Second edition. Houghton Mifflin Co., New York (1922). — Schoenike, R. E., R. H. Hord, R. E. Bullock, and R. D. Woody: Effects of variety and seed source on survival of Arizona Cypress planted in South Carolina. Tree Planters Notes 26 (1): 16—18 (1975). — Schoenike, R. E.: Assessment of gene resources in *Cupressus arizonica* in the United States. pp. 63—74 in Third World Consultation on Forest Tree Breeding. Sponsored by FAO and IUFRO. CSIRO Division of Forest Research, Canberra, Australia (1977). — Sudworth, C. B.: American Forests 16: 88 (1910). — Wolf, C. B. and W. E. Wagner: *Cupressus arizonica* pp. 97—116 and *Cupressus glabra* pp. 131—144 in The World Cypresses. El Aliso, Vol. 1. Rancho Santa Ana Botanic Gardens, Santa Ana, Calif. (1948).

Growth of intra- and interprovenance families of Picea abies (L.) Karst.

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Summary

Data on tree growth from five field trials of interprovenance hybrids and parent provenances of *Picea abies* in central Sweden are presented. They belong to three series of trials established in 1958, 1966 and 1974, respectively. The mating design is factorial in all series, but many families are missing.

In two trials the variance components for GCA for tree growth characters were 3-10 times larger than for SCA. In one case they were of similar size and in trial No. 2 the ratio between the components GCA:SCA varied between 1.4 and 5.2. In the fifth trial no estimate of GCA or SCA was made owing to too many missing values. Strong significance for GCA was noted in three of the trials, but strong significance for SCA was only obtained in the second trial. Good general combiners were revealed in all but one of the provenances tested. Our data provide little or no support for a concept of general superiority of interprovenance hybrids.

A graphic technique to illustrate the stability of a family at two or more test sites is presented in *Figs. 4* and *5* and families superior at two test sites were distinguished.

Outstanding performance of some individual families was noted. The largest gains will be obtained by producing commercial seed of selected families.

Key words: *Picea abies* (L.) Karst., provenance hybrids, general combining ability (GCA), specific combining ability (SCA), genotype × environment interaction.

Zusammenfassung

In fünf Feldversuchen mit Provenienzhybriden von *Picea abies* (L.) Karst. in Zentralschweden wurden Baumhöhen und Volumenzuwachsmessungen durchgeführt. Die Versuche gehören zu drei verschiedenen Serien, die 1958, 1966 und 1974 gepflanzt wurden. Das Kreuzungsschema ist in allen Serien faktoriell, wobei jedoch viele Familien fehlen.

In zwei der Versuche waren die Varianzkomponenten für allgemeine Kombinationseignung (GCA) 3—10 Mal

größer als für spezifische Kombinationseignung (SCA). In einem Fall waren sie gleich groß· Im zweiten Versuch variierte die Quote GCA:SCA zwischen 1,4 and 5,2. Im fünften Versuch fehlten so viele Familien, daß keine Schätzung durchgeführt wurde. Hohe Signifikanz für GCA wurde in drei Fällen erreicht. Hohe Signifikanz für SCA wurde nur im zweiten Versuch erlangt. Klone mit guter GCA fanden sich mit einer Ausnahme in allen Provenienzen. Diese Resultate stützen nicht eine allgemeine Überlegenheit von Provenienzhybriden.

Es wurde eine graphische Methode entwickelt, um die Stabilität der Familien in mehreren Feldversuchen zu illustrieren, (siehe *Fig. 4* und *5)*. Überlegenheit von denselben Familien kam in zwei Feldversuchen vor.

Unvergleichlich guter Zuwachs wurde für einzelne Familien erreicht. Bei familienweiser Produktion von Samen lassen sich die größten kommerziellen Gewinne erzielen.

1. Introduction

Following the last glaciation *Picea abies* migrated westwards from its refuge in the eastern part of Russia (cf. Schmidt-Vogt, 1977)· When the species reached the western part of the Soviet Union the migration continued both in southern and northern directions. This species came to Sweden via Finland following a northward migration, and then a southward migration within Sweden. This pattern may have given rise to two important conditions for the selective breeding of *Picea abies:*

1. A deficiency of growth promoting genes in southern and central Swedish populations, lost during the migration northwards.
2. A substantial genetic differentiation between Swedish and central European populations of *Picea abies.*

The loss of vigour is probably a consequence of earlier growth termination than needed in southern and central parts of the country. This is one of the reasons for the superiority in growth of exotic provenances of *Picea abies* in southern and central Sweden first reported by Langlet (1960). His results have later been confirmed in other provenance experiments (Engsjö *et al.*, 1978). Therefore, it is tempting to try to combine the good vigour of the central European provenances with the hardiness of the native Swedish provenances of *Picea abies.* In addition, there are reports from other species that crosses between different provenances may lead to a luxuriance of the hybrid offspring (Dengler, 1939; Johnsson, 1956). Both these possibilities were considered when experimentation with provenance hybridization in *Picea abies* started during the early fifties (cf. Nilsson, 1958). The belief in the benefits of provenance hybridization in *Picea abies* was so strong that the majority of Swedish seed orchards with this species were composed of clones of two widely separated provenances.

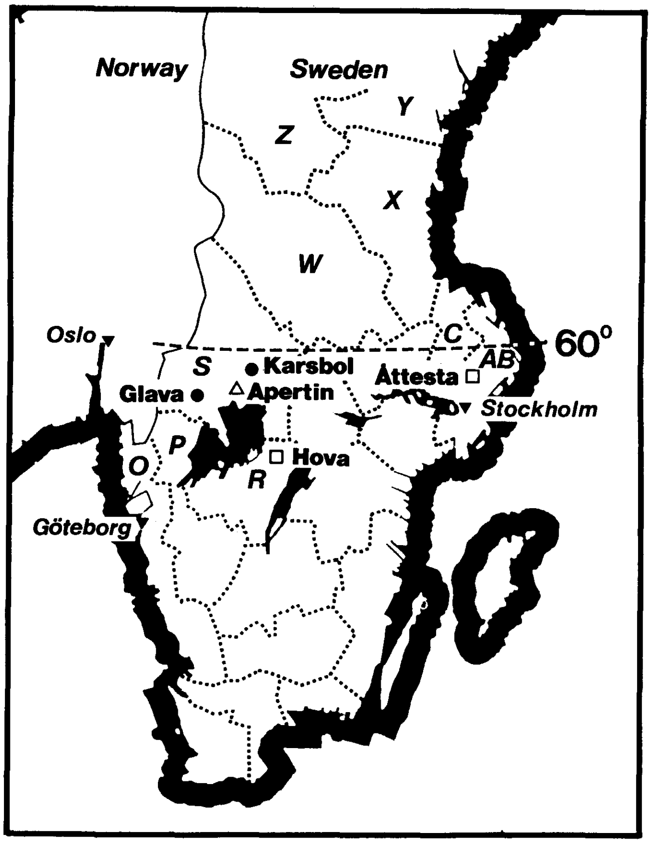

Fig. 1. — Location of the trials
● = 1955/1958 trials
△ = 1965/1966 trial
□ = 1971/1974 trials
Letters O—Z = location of Swedish parent trees.

Promising results of interprovenance hybridization were later on reported for *Picea abies* by Nilsson (1964, 1975), Ericsson (1975) and Blomqvist (1976).

The purpose of this paper is to present data and study the question of hybrid vigour in five field trials with interprovenance hybrids of *Picea abies* planted at different localities in central Sweden.

Table 1. — Geographic data of the test sites, plot size, replications, characters assessed and age at assessment.

Locality	Latitude	Longitude	Altitude	Plot size	Repl	Characteristics of the site	Traits studied	Age at assessment
Karsbol	59°37'	13°37'	80	4x8	4	farm land, clay	Height Diameter Stem volume Volume per ha	22 " " "
Glava	59°33'	12°36'	60	1x1	5-32 $\bar{x}$=20.0	farm land, fine soil	Height Diameter Stem volume	22 " "
Apertin	59°32'	13°21'	90	1x1	5-47 $\bar{x}$=31.6	farm land, fine soil	Height Diameter Stem volume	13 " "
Hova	58°47'	14°11'	120	1x1	20-31 $\bar{x}$=26.6	farm land, organic soil	Height	8
Attesta	59°39'	18°06'	25	1x1	9-24 $\bar{x}$=15.9	high productive, forest site	Height	8

Table 2. — Mating design of Karsbol (1) and Glava (2) trials planted 1958. S-clones originate from the western part of central Sweden. Eo-clones are selected plus trees in south Swedish stands of central European origin.

♀ \ ♂	S 3129	S 3366	Eo72	Eo73	Eo74	Eo75	Eo76	Eo77
S 3348	1;2	1;2	1;2	1;2	1;2	2	1;2	1;2
S 3366	1;2	-	1;2	1;2	-	1;2	-	-
S 3369	1;2	1;2	1;2	1;2	1;2	1;2	1;2	-
S 3353	1;2	2	1;2	1;2	1;2	1;2	1;2	1;2
S 3043	-	1;2	1;2	-	1;2	2	-	-
S 3044	1;2	1;2	1;2	1;2	-	1;2	-	-

2. Material and Methods

2.1 The trials

The experimental plantations included in the present investigation are listed in *Table 1*. All trials were established by Dr. Bo Nilsson. The location of the trials is shown in *Figure 1*. To illustrate the approximate origin of the clones the letters of their reference numbers are indicated on the map.

2.1.1. Karsbol and Glava

In *Table 2*, the families planted at Karsbol and Glava are given. Some of the clones of Swedish origin were so-called plus trees, others were ordinary trees or minus trees, the latter showing poor vigour in the stands. The mating design may be regarded as a factorial one with several families missing. However, estimates of general and specific combining ability variances (GCA and SCA) may be obtained. Two commercial control seedlots from local stands were planted at both sites. All seedlots were sown in a greenhouse in March 1955, and field planting was carried out during spring 1958 at a spacing of 1.5 × 1.5 m. At Karsbol thinnings were carried out in 1964 and in 1971 and at Glava in 1973.

The assessments were made in 1976 when the trees had reached an age of 22 years from seed. Results from Karsbol and Glava were presented by Nilsson (1964, 1975).

2.1.2. Apertin

In the trial at Apertin six clones from the western part of central Sweden and one clone of central European origin were crossed with 12 males selected in west Germany in a factorial design.

Twelve open pollinated families of Swedish and German parents were included in the Apertin trial as shown in *Table 3*.

The seeds were sown on gravel in a greenhouse during spring 1965 and the field trial was established during autumn 1966 at a spacing of 1.8 × 2.4 m.

The assessments at Apertin were made in 1977 at an age of 13 years from seed.

2.1.3. Hova and Åttesta

The families tested at Hova and Åttesta are shown in *Table 4*. The mating design may be regarded as a partial factorial one or as three separate factorial experiments between which there are no common families. The number of seeds was in many cases too low to allow field planting at two test sites. These two trials are the oldest ones containing hybrids between central Swedish clones and clones of eastern European origin. The males were selected in Danish provenance trials. They are not plus trees but may be regarded as representatives of their respective populations. The Swedish clones are plus trees of varying origin.

Open pollinated progenies from some of the males constitute controls in these trials and four open pollinated families from a central Swedish stand of central European origin were also included. The same commercial controls as planted at Karsbol were planted at Hova and Åttesta as well.

The seeds were sown in a greenhouse in 1971 and the field trials were established during spring 1974. The spacing was 2.3 × 2.3 m.

Heights were measured in 1978 at age 8 from seed.

The volumes of the trees were estimated depending on size by the formulae presented by Näslund (1941) and Andersson (1954).

2.2. Statistical methods

An analysis of variance was carried out to test the significance of GCA and SCA differences and to estimate variance components. Different linear models were used depending on the experimental design of the trials.

Table 3. — Mating design of Apertin trial — planted 1966. Family reference numbers are denoted.

CONTROL POLLINATED (FULL-SIB) FAMILIES

♀ \ ♂	Up 285	Up 286	Up 287	Up 288	Up 289	Up 290	Up 291	Up 292	Up 293	Up 294	Up 295	Up 199
S 3125	1	8	15	22	29	36	43	50	56	61	66	71
S 3357	2	9	16	23	30	37	44	51	-	-	-	-
S 3364	3	10	17	24	31	38	45	52	57	62	67	72
S 6231	4	11	18	25	32	39	46	53	58	63	68	73
S 6318	5	12	19	26	33	40	47	-	-	-	-	-
W 6007	6	13	20	27	34	41	48	54	59	64	69	-
Up 1	7	14	21	28	35	42	49	55	60	65	70	74

OPEN POLLINATED (HALF-SIB) FAMILIES:

S 3125	Open pollination in the clone archive at Grimstad.
S 3357	"
S 3364	"
S 6318	"
W 6007	"
Up 1	"
E 2002	" in the stand in which the tree is growing.
E 2003	" " "
E 2004	" " "
E 2007	" " "
S 3357	" " "
S 6318	" " "

S- and W-clones are of central Swedish origin.

E-clones are of central European origin.

Up-clones are of western German origin.

Table 4. — Mating design of Hova and Åttesta trials — planted 1974. Family reference numbers are denoted. Numbers written in italics indicate that those families are only represented at Hova.

Full-sib families:

	♀ \ ♂	Swedish O 2011 O 2012 O 2014	Swedish S 3355 S 3387 W 2026	Swedish Y 2014 Y 4000 Z 3005	4 6 8 Wiezenhof Latvian	1 2 3 Smolensk Russian	4 6 10 Rachovo Russian	2 5 8 Bialowitza Polish	6 7 9 Tatra Slovakian	2 6 7 Bihor Rumanian	O 1001 O 1005 O 1009 French
	O 2006	27	4	72	58	35	26	91	33	21	*101*
	O 2008	30	5	102	13	1	*17*	*69*	*88*	23	85
	P 2001	*68*	29	84	57	9	*44*	52	*65*	*54*	47
Swedish	W 2005	93	6	64	28	59	83	*77*	96	97	36
	W 2024	10	*2*		16	94	*100*	86	*15*	11	*50*
	W 2025	41	*34*	*7*		108	71	32	67	*73*	*82*
	Z 1001	62	70	*51*	92	42	98	56	22	104	46
	Z 3004	*43*	*95*		*89*	*76*	*80*	*74*	*31*	*99*	*12*
	Z 3007	24	*87*	*61*	63	81	14	90	103	*53*	49

OP families from:

Danish provenance trials.

03	Bialowitza	2
75	"	8
107	"	-
106	Smolensk	A
60	"	B
78	"	C
38	Wiezenhof	2
55	"	4
48	"	6
37	Tatra	6

A stand in central Sweden (Älvan, E county) of central European origin.

25 E 2002
19 E 2003
40 E 2004
39 E 2007

Two stands in S county (commercial controls).

20 Värmland 150 m above sea level
45 " 375 m " " "

The trials at Karsbol, Hova and Åttesta were laid out in randomized blocks (cf. *Table 1*). The Åttesta trial was not included in this type of analysis since the number of families missing was regarded as too high (cf. *Table 4*). The trials at Glava and Apertin have a completely randomized design (cf. *Table 1*). Two linear models were used; for Karsbol and Hova, model (1) and for Glava and Apertin, model (2):

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + b_k + e_{ijk} \quad (1)$$

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk} \quad (2)$$

where

μ = an effect common to all crosses and blocks
g_i = the GCA of parent i
s_{ij} = the SCA in the cross between parents i and j
b_k = the effect of block k
e_{ijk} = the error term

We assume that g_i, s_{ij} and e_{ijk} are independent random variables with means zero and variances σ_g, σ_s and σ_e respectively.

For Karsbol and Hova an analysis of variance for a two-way classification was carried out according to Matérn (1977).

For Glava and Apertin an analysis of variance with a one-way classification was made. Since the number of replicates are unequal an unweighted means analysis was used (Searle, 1971 p. 365—369).

Estimation of GCA for individual parents was carried out according to Henderson (1975) for Karsbol, Apertin and Hova.

3. Results and Discussion

3.1. *The relationship between GCA and SCA variance*

The relationship between the size of GCA and SCA variance is of crucial importance for the forest tree breeder. At present only the GCA variance can easily be exploited by establishment of conventional seed orchards.

The computation of GCA and SCA variance is, according to the formulae derived for their estimation, only strictly valid for randomly selected trees originating from the same Mendelian population.

None of these conditions were present in our study which involved pure and hybrid offspring from widely separated populations. Moreover, in most cases the trees selected constituted some of the best performing trees in their stands. The estimates of the GCA and SCA variances may therefore be of limited value if the breeding is confined within either of the provenances. This must be kept in mind when these variables are presented in our paper.

There is a need for trials with a systematic mating design which include a sufficient number of all three types of crosses within and between two provenances. Based on such trials it would be possible to compare GCA's estimated from *intra*-provenance crosses with the GCA's estimated from *inter*-provenance crosses. Such data would be very useful for most of the breeding zones for *Picea abies* in Scandinavia since interprovenance hybridization is thought to be one good means of improving vigour in *Picea abies*.

Until we have this knowledge, the estimates of GCA and SCA variances obtained in our study can with reliability only be utilized for a renewed hybridization between the provenances tested in our study. Another prerequisite for the reliability of the estimates is that the trees to be used in such a hybridization should be selected in the same way as they were in our study.

The data from the analyses carried out are summarized in *Table 5*. The F ratios for GCA were in most cases highly significant (except Glava, diameter and stem volume). The F ratios for SCA were non-significant or of lower significance than for GCA, with the exception of Glava. The deviation from the general pattern at Glava may be due to various reasons. Competition became more severe in this trial because thinnings were too late. Each family was also represented by varying numbers of plants which may have given rise to uneven effects of competition. According to Nilsson (pers. comm.) the border effects were strong in this trial which was planted without border rows. These factors may also have operated in combination. Accordingly, greater weight should be placed on the results from Karsbol than those from Glava. The variance components for the characters studied at Karsbol, Hova, and Apertin were several times higher for GCA than SCA, with one exception — tree height at Hova. Whether this could be attributed to a different sample of clones at Hova as compared to Karsbol and Apertin or to the uncertainties in the estimation of GCA and SCA at Hova can only be speculated about.

Table 5. — Mean squares, F ratios and variance components for trials at Karsbol, Glava, Apertin and Hova.

	GCA		SCA		F ratio		Variance components		
	D.f.	M.S.	D.f.	M.S.	GCA	SCA	GCA	SCA	error
KARSBOL									
Height, m	12	3.07	20	0.424	7.24***	1.18	0.14	0.02	0.36
Diameter, mm	12	267.1	20	63.66	4.20**	1.32	11.18	3.87	48.19
Stem volume, dm^3	12	150.4	20	29.89	5.03***	1.25	6.62	1.49	23.92
Volume per ha, m^3	12	1034.2	20	173.1	5.97***	1.12	47.31	4.66	154.43
GLAVA									
Height, m	12	0.724	20	0.196	3.70**	1.78*	0.42	0.08	2.03
Diameter, m m	12	186.9	20	85.19	2.19	3.07***	82.06	57.44	513.2
Stem volume, dm^3	12	199.1	20	89.38	2.23	3.19***	88.47	61.35	518.3
APERTIN									
Height, m	17	0.57	48	0.075	7.62***	1.47*	0.07	0.02	1.21
Diameter, mm	17	153.3	48	19.39	7.90***	1.58*	19.58	7.12	292.10
Stem volume, dm^3	17	19.84	48	2.16	9.17***	1.54*	2.58	0.76	33.33
HOVA									
Height, cm	35	1524.02	51	444.6	3.43***	2.42**	42.37	43.47	183.77

The previous reports from Karsbol and Apertin are somewhat ambiguous with respect to the relative size of GCA and SCA variance for height growth. NILSSON (1964) stressed that strong GCA was noted for height growth but stated that SCA may also be of importance. Later on NILSSON and ANDERSSON (1969) stated that "The hybrids show strong specific combining effects in relation to general combining effects". In his summary of interprovenance hybridization in *Picea abies* NILSSON (1975) focused attention on the exploitation of SCA in *Picea abies* breeding whereas nothing was mentioned about the exploitation of GCA. For bud-set and bud-flushing NILSSON (1964, 1969) reported that GCA was significant whereas SCA was non - significant. This finding agrees largely with the results reported by ERIKSSON *et al.* (1978).

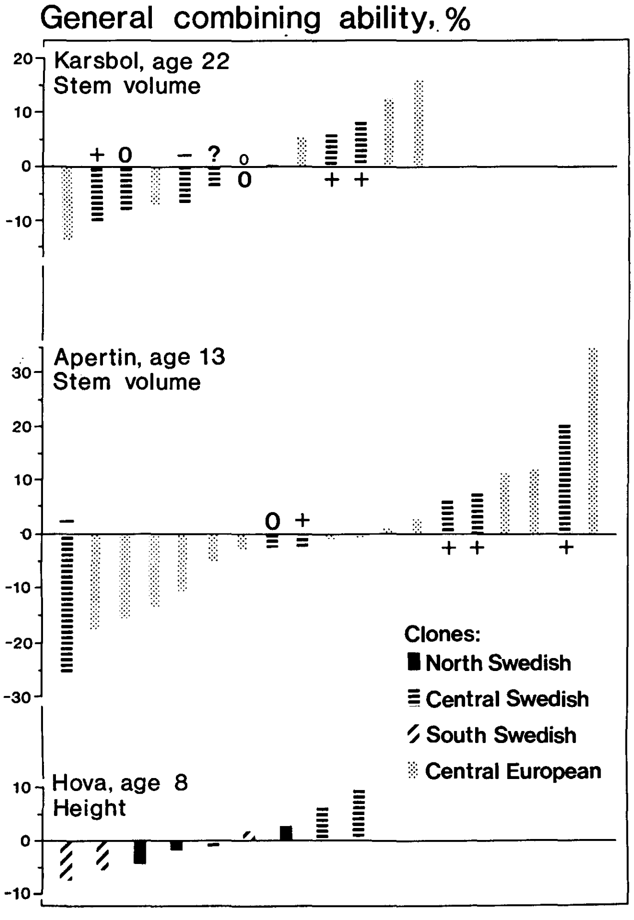

Fig. 2. — Parental GCA's in percentage units above and below experiment mean ($\hat{\mu}$). At Karsbol $\hat{\mu}$ = 25.7 dm^3. At Apertin $\hat{\mu}$ = 10.7 dm^3. At Hova $\hat{\mu}$ = 107 cm.
+ = plus tree, – = minus tree, O = intermediate, ? = unknown.

There is only one paper known to us, presenting data on the relative role of GCA and SCA following interprovenance hybridization in *Picea abies*. SKRØPPA (1979) reported that SCA variance was significantly larger than GCA variance in an eight year old trial consisting of interprovenance hybrids between Norwegian and German clones. The mating design was a 7 × 2 factorial one. On the other hand the GCA and SCA variances in two other factorials, 5 × 2 and 8 × 2 respectively, were of almost the same magnitude. In these cases all clones were of Norwegian origin. In another Norwegian investigation, both types of effects are found significant both for growth rhythm characteristics and height growth of families in diallel matings, each carried out within three separate stands (SKRØPPA, pers comm., 1981).

3.2 GCA of parents

The high significance for GCA variance noted at Karsbol, Apertin, and Hova called for an examination of the GCA of individual parents. In *Fig. 2*, in which the GCA of individual parents at Karsbol, Apertin, and Hova is shown, different screens are used to make it possible to distinguish parents of varying origins. An examination of these figures discloses that there are no apparent provenance differences between parental GCA values. The only clear tendency is the poor performance of the South Swedish parents at Hova. Good general combiners may be found in all origins except for the South Swedish one. These results stress the need for individual progeny test-

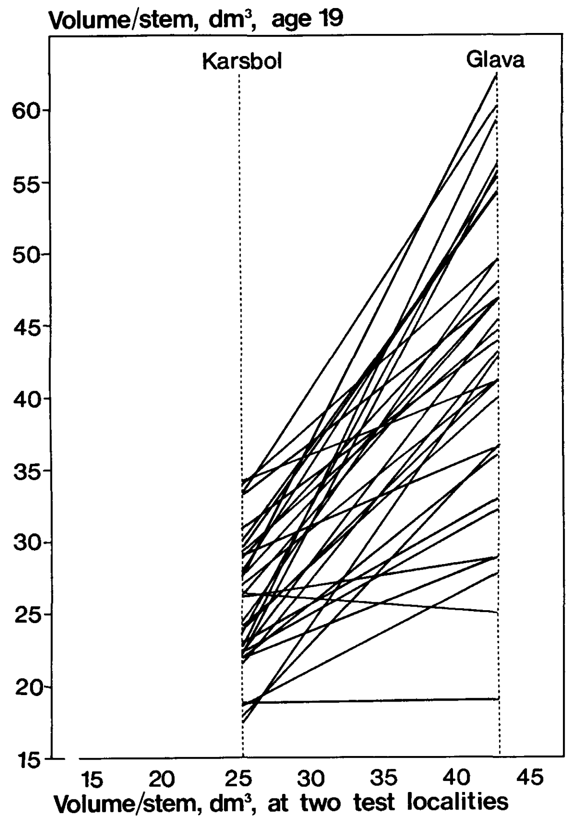

Fig. 3. — Mean volume/tree of the families at Karsbol and Glava.

ing of clones originating from different populations (see also Nilsson and Andersson, 1969).

3.3 Genotype × environment interaction

To get a graphical impression of the genotype × environment interaction, the results from Karsbol and Glava for stem volume were plotted in a diagram of the type used by Finlay and Wilkinson (1963). From this diagram (cf. *Fig. 3)* it is evident that some pronounced changes in ranking from Karsbol and Glava occurred.

A similar pattern was noted for the families tested at Hova and Åttesta. Using Tukey's test for non-additivity (Sokal and Rohlf, 1969, p. 378) the interaction was shown to be significant at the 0.1% level for Karsbol — Glava whereas it was non-significant for Hova — Åttesta.

For a proper selection of clones for future seed orchards it is necessary to cover the variability in site conditions when candidate clones are progeny tested. In his study on genotype × environment interaction, Owino (1977) found that the efficiency of selection of the best families was increased by 20% when three instead of one test site was used.

Different methods to estimate the genotype × environment interaction have been derived (Yates and Cochran, 1938; Wricke, 1962; Finlay and Wilkinson, 1963; Eberhart and Russel, 1966; Tai, 1971). In most of them a regression on the performance over sites is calculated. Many of the old Swedish progeny tests were only planted on one site or replicated at two or three test localities only. The small number of sites does not permit an estimate of stability by using regression analysis. We have tried to develop a simple method for the breeder to directly identify the most stable families in a diagram. By stable is meant that an entry shows the same relative performance on two or more test sites (cf. Eberhart and Russel, 1966).

When many families are illustrated in the Finlay-Wilkinson type of diagram it is difficult for the breeder to trace individual families, especially if three or more test sites are involved. Therefore, for such a situation we suggest that the differences between the results ("amplitude") at the two test sites are plotted against the mean value of the family at the two sites. In such diagrams *(Figs. 4* and *5),* the families of greatest interest for the breeder are easily indentified in the lower right corner of the diagram. The difference between progeny values at different test sites (amplitude) may be expressed in measurement units or in standard deviation units. We preferred to use the latter since it varied from one trial to the other. If it is assumed that the two sites are of equal importance for breeding in a certain zone, the families to the right of the diagonal axis in *Fig. 5* ought to be selected. A large average height or volume can only to a certain extent compensate for the drawback of a large amplitude.

The type of diagram shown in *Figs. 4* and *5* can be extended to experimental series comprising three or more

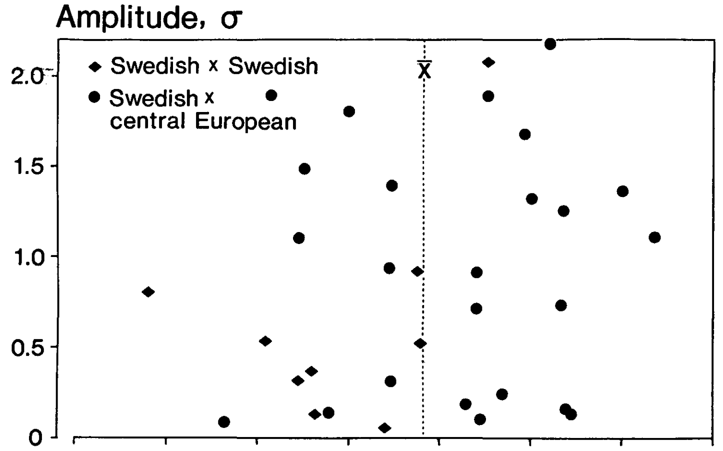

Fig. 4. — Amplitude (difference between sites) plotted against family means over test sites — Karsbol and Glava.

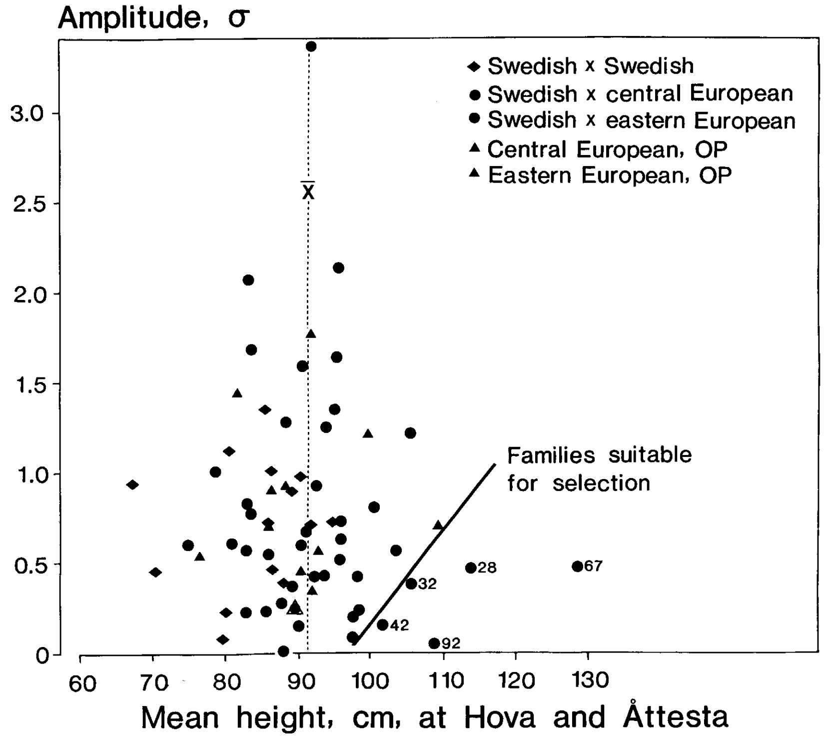

Fig. 5. — Amplitude (difference between sites) plotted against family means over test sites — Hova and Åttesta.

trials. For such series comprising e.g. four trials the mean amplitude for the differences trial 1 — trial 2, trial 2 — trial 3, trial 3 — trial 4 has to be plotted against the mean volume at all four trials. The numbers are given according to declining mean performance of the trial.

3.4 Realized gains

The gains obtained from different types of families are shown in *Fig. 6* with the standard deviation as the unit, which is analogous to the approach used by GIERTYCH (1976) for Norway spruce provenances. With assessments at different ages and for different characters, percentage gains will diminish with age whereas gains in standard deviation units may be expected to be more independent of age. Neither the commercial controls nor the open pollinated families were included in the calculation of the standard deviation and the gains shown in *Fig. 6* are gains in relation to the average of the artificially pollinated families.

The same two commercial controls were used for four of the five test sites illustrated in *Fig. 6.* Their mean values varied from −0.650 to −1.280. The presence of central Swedish × eastern European hybrids at Hova and Åttesta may have caused the slightly lower values of the commercial controls at these test sites. Eastern European provenances are the best growing provenances for this part of Sweden *(e.g.* LANGLET, 1960; KRUTZSCH, 1975).

Gains obtained following mating between the three best Swedish and three best central (or eastern) European clones identified on the basis of GCA (cf. *Fig. 2)* are shown in *Fig. 6.* At Karsbol five of the nine possible families were present while seven families were present at Glava. The mating design for the trials at Hova and Åttesta did not permit such an illustration. For these two trials the mean values for the hybrid families (Swedish × eastern European) including the three best Swedish parents are illustrated. The best Swedish × Swedish and Swedish × central/eastern European families are also illustrated in these figures.

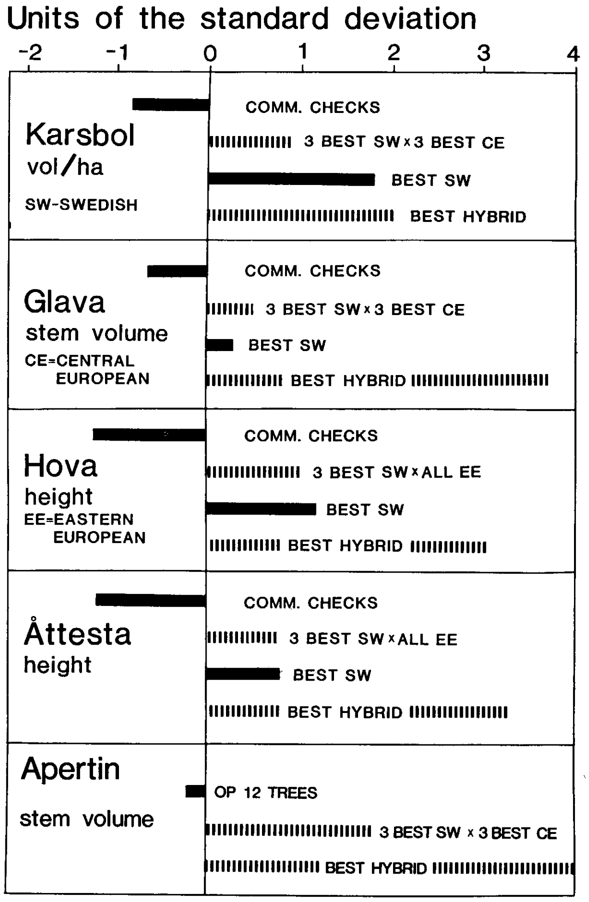

Fig. 6. — Deviations (in standard deviation units) from experiment mean for families or groups of families and commercial control means.

Except for Glava, where the differences between families were probably exaggerated by not thinning at the proper time, the 3 × 3 best families exceed the mean value by at least 0.95 standard deviation units. The difference between them and the mean value for the two commercial controls amounted to approximately two units of the standard deviation.

The biggest gains will be obtained by making use of the best full-sib families, which exceed the average by 2—4 units. This points to the potential gains that may be obtained by using two-clone seed orchards. A prerequisite would be that the families are superior at two or more test sites (cf. page) and that clones are fairly self-sterile.

At Karsbol, Glava, and Apertin none of the provenances or provenance combinations was superior to the others. In contrast to this, the analysis of variance on the data from Hova revealed a significant difference between the different types of mating included in this trial. This could probably be attributed to the good performance of the Swedish × eastern European families. At the nursery stage the interprovenance hybrids, later on tested at Apertin, outgrew the Swedish parental population, according to Nilsson (1975).

4. Concluding Remarks

Data in the present investigation give little or no support for a general superiority of interprovenance hybrids. Some families are superior while others are inferior. The reason for this is apparently that they are offspring of good or poor parents. A good parent thus contributes a growth promoting growth rhythm to its offspring.

Some genetic improvement from interprovenance hybridization at the population level may be obtained but the greatest progress will be obtained by crossing good general combining parents. Gains exceeding the family average by 4 standard deviation units may be obtained from some full-sib families. Such big gains suggest that commercial seed ought to be produced in biclonal seed orchards or by any other method that ensures the mass production of full-sib families.

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References

Andersson, S.-O.: Funktioner och tabeller för kubering av småträd. (Funktionen und Tabellen zur Kubierung kleiner Bäume.) Medd. Statens Skogsforskningsinst. **44** (12): 1—29 (1954). — Blomqvist, S.: Några erfarenheter av granprovenienshybrider. Granförädling, Bogesund 1976: 19—27 (1976). — Dengler, A.: I. Abhandlungen. Über die Entwicklung künstlicher Kiefernkreuzungen. Zch. f. Forst- und Jagdwesen **71**: 457—485 (1939). — Eberhart, S. A. and Russell, W. A.: Stability parameters for comparing varieties. Crop Science **6**: 36—40 (1966). — Engsjö, T., Persson, A., Eriksson, G., Kiellander, C. L., Lindgren, D. and Perttu, K.: Projekt 63310302 — Klimatzonkarta för gran. Forskningsverksamheten 1977. Department of Forest Genetics, Royal College of Forestry. Research Notes **26**: 5—16 (1978). — Ericsson, T.: Resultat från några försök med provenienskorsningar av gran. Föreningen för skogsträdsförädling, Institutet för skogsförbättring. Årsbok 1974: 149—159 (1975). — Eriksson, G., Ekberg, I., Dormling, I., Matérn, B. and Wettstein, D. von.: Inheritance of bud-set and bud-flushing in *Picea abies* (L.) Karst. Theor. Appl. Genet. **52**: 3—19 (1978). — Finlay, K. W. and Wilkinson, G. N.: The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. **14**: 742—754 (1963). — Giertych, M.: Summary results of the IUFRO 1938 Norway spruce (*Picea abies* (L.) Karst.) provenance experiment. Height growth. Silvae Genet. **25**: 154—164 (1976). — Henderson, C. R.: Best linear unbiased estimation and prediction under a selection model. Biometrics **31**: 423—447 (1975). — Johnsson, H.: Heterosiserscheinungen bei Hybriden zwischen Breitengradrassen von *Populus tremula*. Z. Forstgenet. Forstpflanzenzücht. **5** (5—6): 156—160 (1956). — Krutzsch, P.: Zwei Herkunftsversuche mit Fichte in Schweden (IUFRO 1938). Department of Forest Genetics, Royal College of Forestry. Research Notes **16**: 93 pp. (1975). — Langlet, O.: Mellaneuropeiska granprovenienser i svenskt skogsbruk. (Mitteleuropäische Fichte in Schweden, nach den Ergebnissen des internationalen Provenienzversuches von 1938). Kungl. Skogs- och Lantbruksakademiens Tidskrift **99** (5—6): 259—329 (1960). — Matérn, B.: Some aspects of the analysis of incomplete diallel experiments. Evaluation of mating designs. Department of Forest Genetics, Royal College of Forestry. Research Notes **23**: 37—59 (1977). — Näslund, M.: Funktioner och tabeller för kubering av stående träd. Medd. Statens Skogsforskningsinst. **32**: 56 pp. (1941). — Nilsson, B.: Studier av 3-åriga avkommor efter korsning svensk gran × kontinentgran. Föreningen för Växtförädling av Skogsträd, Årsberättelse 1957: 30—55 (1958). — Nilsson, B.: Intraspecific hybridization and heterosis within *Picea abies*. World consultation on forest genetics and tree improvement, 2b/6 FAO, Rome (1964). — Nilsson, B.: Försök med provenienshybrider av gran (*Picea abies* (L.) Karst.). Department of Forest Genetics, Royal College of Forestry. Research Notes **5**: 1—8 (1969). — Nilsson, B.: Recent results of interprovenance crosses in Sweden and the implications for breeding. Proc. 14th Meeting of the Can. Tree Improv. Ass. 1973, part 2: 3—14 (1975). — Nilsson, B. and Andersson, E.: Spruce and pine hybrid variations in Northern Europe. Department of Forest Genetics, Royal College of Forestry. Research Notes **6**: 1—10 (1969). — Owino, F.: Genotype × environment interaction and genotypic stability in loblolly pine. IV. Correlation studies. Silvae Genet. **26**: 176—179 (1977). — Schmidt-Vogt, H.: Die Fichte. Paul Parey, Hamburg and Berlin. 647 pp. (1977). — Searle, S. R.: Linear Models. John Wiley & Sons Inc., New York, London, Sydney, Tokyo. 532 pp. (1971). — Skrøppa, T.: Height growth and flushing of German × Norwegian provenance hybrids of Norway spruce (*Picea abies*). Proc. of the IUFRO joint meeting of working parties on Norway spruce provenances and Norway spruce breeding, Bucharest 1979: 468—471 (1979). — Sokal, R. R. and Rohlf, F. J.: Biometry. Freeman, San Francisco. 776 pp. (1969). — Tai, G. C. C.: Genotypic stability analysis and its application to potato regional trials. Crop Science **11**: 184—190 (1971). — Wricke, G.: Über eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen. Z. Pflanzenzücht. **47**: 92—96 (1962). — Yates, F. and Cochran, W. G.: The analysis of groups of experiments. J. Agric. Sci. **28**: 556—580 (1938).