

GENOTYPIC CORRELATIONS BETWEEN EARLY CONE-SET AND HEIGHT GROWTH IN *PICEA ABIES* CLONAL TRIALS

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ABSTRACT

Trees are often selected for breeding and mass propagation on the basis of their height or height growth. This could affect genetic gain and diversity in the breeding populations, if there are strong genetic correlations between growth and reproductive traits. It could also affect the generative mass propagation of the selected materials. Therefore, we studied genotypic correlations between cone-set, height, and height growth before and after flowering in two series of *Picea abies* clonal trials. Broad sense heritability values derived for cone-set ranged from 0.29 to 0.57, and were two to three times higher than those for growth traits. The genotypic correlations between cone-set and height were weak and not statistically significant. Genotypic correlations between cone-set and height increment were also weak and non-significant. However, strong genotypic correlations (0.67–1.00) in cone-set were found between trials at sites where conditions and vegetative growth differed markedly, indicating a low G×E interaction for flower initiation. The results show that the differences in fecundity between clones are under strong genetic control. The weak and non-significant genotypic correlations found between early cone-set and growth traits imply that selection for growth traits should not affect fecundity in *Picea abies*.

Key words: *Picea abies*, heritability, breeding population, ontogenetic ageing, genetic correlation, cone setting

INTRODUCTION

In forest tree breeding the proportions of energy resources allocated to growth and reproduction, and the genetic regulation of growth and flowering/seed production are of considerable interest. Genetic correlations between growth and reproduction are of interest both in breeding programmes and in selecting material for mass propagation of improved reforestation material. Reproductive organs are strong competitors for the nutrient resources within a plant (LINDER & TROENG 1981). Seed cones develop at the same time as the vegetative apices of the next year's shoots are being formed, but after the main growth of the current years shoots. As a consequence one can therefore assume that a reduced number of stem units will be initiated in the apices, resulting in a reduced height growth the following year. In breeding programmes with species that have a very long juvenile phase, like *Picea abies* (L.) Karst., the breeder may be forced to make selections from clones that start to flower at a relatively early stage, ignoring others that will flower later, in order to avoid excessive delays. However, if there are strong negative genetic correlations between growth and reproductive traits this could affect both genetic gain and diversity. The main characteristic often used when

selecting plus trees is superior growth (volume or height). In such cases, if there are negative genetic correlations between growth and reproductive traits, seed production in the orchard will be reduced and the cost of producing improved seed will be increased. There would also be ecological effects, influencing (for instance) the ability of the species to reproduce naturally, and to serve as a food source for animals that feed on seeds.

Negative phenotypic relationships between reproductive and growth traits have been reported for many species (see CHALUPKA *et al.* 1975, TEICH 1975, and HEYBROCK & VISSER 1976 for examples). However, identifying these relationships does not necessarily give any information about how these are genetically linked to each other.

Both positive and negative genetic relationships between flowering and growth traits have been reported. In *Pinus taeda* SCHMITLING (1981) found a negative relationship between growth and flowering, and concluded that it had a genetic basis. BYRAM *et al.* (1986) found no relationship between the seed production of clones in a *Pinus taeda* seed orchard and their performance in progeny tests, while in *Pseudotsuga menziesii* a negative genetic correlation has been found between cone production and diameter increment in a

seed orchard (EL-KASSABY & BARCLAY 1992). In contrast, positive correlations between the production of female strobili and height have been found in *Picea glauca*, which strengthened as the trees aged from eight to 15 years (NIENSTAEDT 1985).

In *Picea abies* the female strobili are formed in the terminal apices of the branches, and in years when flowering is abundant there are few positions left in the crown for formation of either vegetative or generative organs. Therefore, some years must elapse before another abundant female flowering can take place. Weather conditions also have a strong influence on flower initiation in *Picea abies*. For abundant flowering the weather conditions must be favourable, and the vegetative status of the trees must be appropriate, i.e. they must have many potential shoot apices (ERIKSSON *et al.* 1973). In central Sweden *Picea abies* flowers in spring, normally during May, and fertilization takes place at the end of June. Seed development and maturation proceeds during summer and early fall, and cones are ready to be collected in the middle of October.

In many breeding programmes the principal aim is to improve the productivity of the species in terms of stem volume per unit area over a full rotation. Today, clonal and progeny tests are commonly established with a single-tree plot design. Selection of superior trees is normally based on height growth or height increment after only a small proportion of the rotation. Negative genetic relationships between flowering/cone-set and growth traits may cause the ranking of the clones to change, depending on whether or not the progenies or clones in the trials have flowered. However, the genetic correlations between height and height increment in young single-tree plots and volume per unit area in old multiple-tree plots of *Pinus sylvestris* are strong (JANSSON *et al.* 1998).

In 1995, an extremely abundant flowering occurred in young field trials of *Picea abies*, presenting an

opportunity to investigate potential relationships between cone-set and growth capacity. The objectives of the study prompted by this opportunity were to estimate the genotypic correlations between height growth characters and cone-set in young clonal field trials of *Picea abies*, and the genotypic correlations in cone-set across several locations.

MATERIALS AND METHODS

Field trials and materials

Data were collected in two series of clonally replicated field tests of *Picea abies*. The experiments were established with single-tree plots in a randomised block design at all sites. Key characteristics of the test sites are presented in Table 1. The number of clones analysed at each test site is given in Table 6.

Series 1 consisted of bare-root, 2nd and 3rd cycle cuttings that were two years old when planted. Age from seed when planted in the field trials varies between 8 to 11 years. The seedlings used as donor plants originated from open-pollinated seeds collected from Slovakian provenances, and is a subset of the material described by BENTZER *et al.* (1988). The number of cuttings measured per clone varied between one and seven, with a mean of 4.7.

Series 2 consisted of containerised 1st cycle cuttings that were three years old when planted. Age from seed when planted was six years. The cuttings originated from Belorussian provenances, and the number of cuttings measured per clone varied between one and six, with a mean of 5.0.

Data collection

The trials in Series 1 were measured in 1995 and 1997, 14 and 16 growing seasons after planting, respectively.

Table 1. Location and characteristics of the test sites.

	Latitude (° ' N)	Altitude (m.a.s.l.)	Heat sum (+5 °C) ¹	Year of planting	Land type	Site class
Series 1						
SO4	58° 37'	100	1300	1982	Forest	G28
SO5	59° 00'	40	1327	1982	Forest	G28
SO7	59° 38'	80	1255	1982	Forest	G29
SO8	59° 38'	45	1285	1982	Agricultural	G26
S13	61° 09'	255	1017	1982	Forest	G24
Series 2						
S1151	59° 50'	225	1122	1990	Forest	G30
S1152	59° 43'	140	1200	1990	Forest	G27

¹) Calculated using formula in MORÉN and PERTTU (1994)

In 1995 the total height, the 1992-1995 increment, and growth disturbances (e.g. frost injuries, leader shift etc.) were assessed. In 1997, the height increments for 1996 and 1997 were measured. In 1995 the number of cones on each ramet was recorded, in three classes (no cones, 1-5 cones, and more than five cones). No cone was set in the trials before 1995, nor in either 1996 or 1997.

The trials in Series 2 were measured in 1995 and 1998, six and nine growing seasons after planting, respectively. In 1995, the total height, the 1994-1995 increment, and growth disturbances were assessed. In 1998 the annual height increment for 1996-1998 was measured. In 1995 the number of cones on each ramet was recorded in three classes (no cones, 1-5 cones, and more than five cones). No cone set occurred in the trials before 1995 or in the period 1996-1998.

Daily mean temperatures and daily precipitation for the year of flower initiation were collected from climate stations of the Swedish Meteorological and Hydrological Institute (SMHI) located closest to the field trials. The distance between the field trials and the nearest climate station varied between 7 and 44 kilometres. Heat sums, derived by summing degree-days with a threshold of +5 °C (SARVAS 1967), were calculated for the whole growing season and for July (Table 2), the month when buds normally differentiate in *Picea abies* (LONGMAN 1989). Corresponding values based on 30-year average values were used for comparison (Table 2).

The weather during 1994, the year of flower initiation, was warmer than normal at all sites of the field trials (Table 2). The accumulated heat sum for the whole growing season was 8 % to 20 % higher than normal, but the annual precipitation was close to normal

at all sites. The weather in July, the normal time of flower initiation in *Picea abies*, was substantially warmer and drier than usual. The heat sum was 28% to 47% higher than normal and precipitation was 30 % or less than normal at all but one of the sites.

Statistical analysis

The cone-set variables CONE6 and CONE14 (Table 3) were transformed into normal scores to meet the requirements for normal distributions (GIANOLA & NORTON 1981).

Within-trial results were calculated using the LSMLMW and MIXMDL program package (HARVEY 1990), using the following mixed linear model:

$$y_{ij} = \mu + b_i + c_j + d x_{ij} + e_{ij} \quad [1]$$

where y_{ij} is the dependent variable, e.g. cone-set of tree ij , μ the overall mean, b_i the fixed effect of block i ($i = 1, \dots, m$), c_j the random effect of clone j ($j = 1, \dots, n$), $N(0, \sigma_c^2)$, d the regression coefficient, x_{ij} the height of tree ij used as a covariable (not included in calculations where HT-variables are the dependent variables), and e_{ij} is the residual ($N(0, \sigma_e^2)$). Height used as covariate was included in the calculations of heritability and genotypic correlations except for the height variables (HT6 & HT14).

Genotypic parameters were interpreted as $\sigma_G^2 = \sigma_c^2$ and $\sigma_E^2 = \sigma_e^2$ where σ_G^2 is the genotypic variance, and σ_E^2 is the environmental variance. The broad sense heritability was estimated as $H^2 = \sigma_G^2 / (\sigma_G^2 + \sigma_E^2)$. Genotypic (r_G) and environmental (r_E) correlations between traits in the same trial were estimated as

Table 2. Heat sum and precipitation data measured at the climate stations closest to the field trials. Flowering was induced in 1994.

	Heat-sum, whole growing season		Heat sum, July		Precipitation, whole growing season		Precipitation, July	
	30-year average (degree-days)	% of 30-year average for 1994	30-year average (degree-days)	% of 30-year average for 1994	30-year average (mm)	% of 30-year average for 1994	30-year average (mm)	% of 30-year average for 1994
Series 1								
SO4	1385	114	347	139	516	95	66	11
SO5	1278	115	344	135	634	100	70	9
SO7	1317	120	344	140	635	108	62	6
SO8	1413	110	360	128	629	105	79	64
S13	1133	116	326	135	627	91	73	30
Series 2								
S1151	1333	108	347	137	627	118	79	16
S1152	1100	118	313	147	679	99	79	28

$r_G = \sigma_{G_1, G_2} / (\sigma_{G_1} \sigma_{G_2})$ and $r_E = \sigma_{E_1, E_2} / (\sigma_{E_1} \sigma_{E_2})$ where σ_{G_1, G_2} is the genotypic covariance and σ_{E_1, E_2} is the environmental covariance between trait 1 and trait 2.

Genotypic correlations among the trials were calculated using the ASREML program (GILMOUR *et al.* 1999), applying the following mixed linear model expressed in matrix format:

$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{c} + \mathbf{e}$, where: $\mathbf{y} = (\mathbf{y}'_1, \mathbf{y}'_2)'$ represents the vector of phenotypic observations for trials 1 and 2; $\mathbf{X} = \mathbf{X}_1 \oplus \mathbf{X}_2$ and $\mathbf{Z} = \mathbf{Z}_1 \oplus \mathbf{Z}_2$ are known incidence matrices for fixed and random effects, respectively; $\mathbf{b} = (\mathbf{b}'_1, \mathbf{b}'_2)'$ and $\mathbf{c} = (\mathbf{c}'_1, \mathbf{c}'_2)'$ are vectors of unknown block means and random clone effects, respectively; \mathbf{e} is the vector of random residuals; $'$ is the transpose operation and \oplus is the direct sum operation.

The expected value and variance of the model equation terms are:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} \sim \begin{bmatrix} \mathbf{X}\mathbf{b} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{V} & \mathbf{Z}\mathbf{G} & \mathbf{R} \\ \mathbf{G}\mathbf{Z}' & \mathbf{G} & \mathbf{0} \\ \mathbf{R} & \mathbf{0} & \mathbf{R} \end{bmatrix}$$

where $\mathbf{V} = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R}$ and \mathbf{R} is the residual variance-

covariance matrix, $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{I}_N$ is the genotype variance-covariance matrix,

$$\mathbf{G}_0 = \begin{bmatrix} \sigma_{G_1}^2 & \sigma_{G_1, G_2} \\ \sigma_{G_1, G_2} & \sigma_{G_2}^2 \end{bmatrix} = \begin{bmatrix} \sigma_{C_1}^2 & \sigma_{C_1, C_2} \\ \sigma_{C_1, C_2} & \sigma_{C_2}^2 \end{bmatrix}$$

\mathbf{I}_N is an identity matrix equal to the total number of clones, and \otimes is the direct product operation.

In some cases when the variance-covariance matrix was not positive definite constraints were imposed on the (co)variance components to keep the additive genotypic correlations within the range -1 to +1 (GILMOUR *et al.* 1999). The estimated genotypic correlation was divided by its approximate standard error provided by the ASREML program based on Taylor series expansion. This statistic was compared to the *t*-distribution to get an approximate test if the genotypic correlation differs from zero.

RESULTS

In Series 1, the average height and increment in four of

Table 3. Description of measured variables.

Abbreviation	Description
Series 1	
CONE 14	Number of cones per ramet recorded in three classes in 1995, 14 years after trial establishment. Transformed to normal score values.
HT10, HT14	Total height 10 and 14 years after field trial establishment, (cm).
INC11-14	Height increment, years 11 to 14 (cm×year ⁻¹).
INC15, INC16	Height increment, years 15 and 16 respectively, (cm).
Series 2	
CONE6	Number of cones per ramet recorded in three classes in 1995, six years after trial establishment. Transformed to normal score values.
HT4, HT6	Total height, four and six years after field trial establishment, (cm).
INC5-6	Height increment, years 5 to 6, (cm×year ⁻¹).
INC7, INC8, INC9	Height increment, years 7, 8 and 9 respectively, (cm).

Table 4. Estimates of broad-sense heritability (H^2) for cone, height and increment variables in the Series 1 trials, and means for height growth variables. Standard errors for H^2 for all traits were between 0.04–0.05.

Test site No.	CONE14		HT14		INC11-14		INC15		INC16	
	H^2	Mean (cm)	H^2	Mean (cm)	H^2	Mean (cm)	H^2	Mean (cm)	H^2	
SO4	0.37	425	0.14	48.0	0.12	56.8	0.13	56.2	0.12	
SO5	0.38	405	0.10	49.4	0.09	64.5	0.15	71.2	0.06	
SO7	0.44	393	0.22	42.9	0.20	56.6	0.16	48.8	0.08	
SO8	0.55	338	0.35	40.7	0.36	54.1	0.30	65.1	0.28	
S13	0.37	222	0.11	13.4	0.19	15.7	0.14	17.9	0.13	

Table 5. Estimates of broad-sense heritability (H^2) for cone, height and increment variables in the Series 2 trials, and means for height growth variables. Standard errors for H^2 for all traits were around 0.02.

Test site No.	CONE6		HT6		INC5-6		INC7		INC8		INC9	
	H^2	Mean (cm)	H^2	Mean (cm)	H^2	Mean (cm)	H^2	Mean (cm)	H^2	Mean (cm)	H^2	
S1151	0.14	168	0.13	37.7	0.13	50.4	0.09	45.6	0.08	50.4	0.08	
S1152	0.24	130	0.15	24.0	0.05	48.6	0.07	45.8	0.05	46.0	0.07	

Table 6. Number of clones and proportion of ramets and clones with cones for the trials in Series 1 and 2.

Test site No.	No. of clones	Percent clones with cones	No. observations	Percent ramets with cones in each scoring class ¹
Series 1				
S04	112	52.7	499	75.1; 10.4; 14.4
S05	111	45.9	405	79.0; 10.6; 10.4
S07	112	71.4	525	62.8; 14.3; 22.9
S08	112	74.1	533	49.0; 12.6; 38.4
S13	112	56.2	671	78.8; 14.5; 6.7
Series 2				
S1151	481	14.3	2523	96.2; 2.7; 1.1
S1152	482	16.8	2348	94.7; 2.8; 2.5

¹ Cone-set on each ramet scored in one of three classes: no cones, 1-5 cones and >5 cones.

the trials were of similar magnitude (Table 4). In the fifth, most northerly trial (S13), the height in 1995 (HT14) and height increment, both before and after cone-set in 1995, were lower than in the other trials. The trials in Series 2, which had had only six growing seasons after planting averaged about 1.5 m in height in 1995 (Table 5).

The percentages of clones and ramets with flowers are given in Table 6. In Series 1 there were 102 clones (91%) that had at least one ramet with cones in at least one of the five trials. Twenty-seven clones (24%) had ramets with cones in all five trials. Comparing the trials in pairs, the number of clones that had at least one ramet with cones in one of the trials varied between 68 to 100. The number of clones that had ramets with cones in both trials ranged from 41 to 63. In Series 2 there were 111 clones (23%) that had at least one ramet with cones in at least one of the trials. 39 (8%) of the clones had ramets with cones in both trials.

In Series 1 the mean broad-sense heritability for the cone-set trait (CONE14) was about 0.4, two to three times higher than that for the growth traits (Table 4). Trial S08 gave heritability estimates for growth characters that were higher than in the other trials. The trials in Series 2 had lower heritabilities than the Series 1 trials for both cone-set and growth characters (Table 5).

In both series, the genotypic correlations between cone-set (CONE14 and CONE6) and the height increment variables were generally weak and not significant in most trials, both before and after cone-set in 1995 (Figures 1 and 2). The genotypic correlations between CONE14 and HT14 in Series 1, and between CONE6 and HT6 in Series 2, were also weak and not significant in most trials (data not presented). Only trials S08 and S1151 showed positive and significant correlations ($p < 0.05$) of 0.52 and 0.22, respectively. The environmental correlations between CONE14 and HT14, and CONE6 and HT6 in Series 1 and 2 respectively, were positive and in the range of 0.08 to 0.51 for all trials, indicating that the largest trees within each clone had the highest number of cones (data not presented).

Estimates of genotypic correlations for CONE14 between trials in Series 1 are all statistically significant and range between 0.67 and 1.00 (Table 7). For HT14 the correlations in Series 1 were in the range of 0.47 and 1.00, and all but one were statistically significant (Table 7).

The genotypic correlations between the two trials in Series 2 were 0.99 and 0.67 for CONE6 and HT6, respectively. Both correlations were significant ($p < 0.001$).

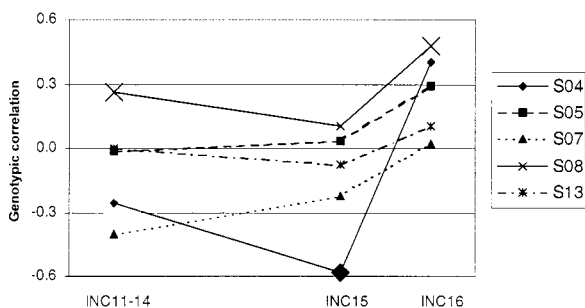


Figure 1. Genotypic correlations between cone-set (CONE14) and height increment variables within each trial in Series 1. INC11–14 is the height increment during the growing seasons 1992–95, i.e. the four years up to and including the flowering year. INC15 and INC16 are the height increments recorded in the first and second years after flowering, respectively. Significant correlations ($p < 0.05$) are marked with double-size data points.

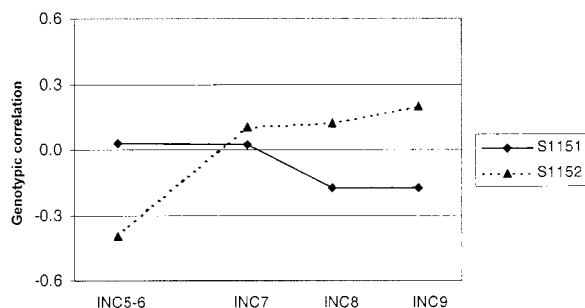


Figure 2. Genotypic correlations between cone-set (CONE6) and height increment variables within each trial in Series 2. INC5–6 is the height increment during the growing seasons 1994–95, i.e. the flowering year and the year before. INC7, INC8 and INC9 are the height increments in the first, second and third year after flowering, respectively.

Table 7. Estimated genotypic correlations (r_c) for cone-set (CONE14) and height (HT14) between individual trials in Series 1. Significant correlations ($p < 0.05$) are underlined and highly significant correlations ($p < 0.001$) are in extra bold type.

CONE 14	S05	S07	S08	S13
S04	1.00	0.77	0.67	0.87
S05		0.95	0.70	0.82
S07			0.73	0.71
S08				0.67
HT14	S05	S07	S08	S13
S04	0.47	0.63	0.71	0.63
S05		1.00	<u>0.47</u>	0.99
S07			0.50	0.68
S08				0.54

DISCUSSION

There are large differences in site conditions between the trials in Series 1, which are reflected in the tree height in S04 (4.2 metres) being almost double that in S13 (2.2 metres; see Table 4). There is a difference of almost 300 degree-days in annual heat sum between these two trials (Table 1), since the average temperatures during the growing season at the sites differ by about 1.5 °C, and the growing season in trial S04 is almost a month longer. Despite these differences in mean height between the two trials, the clones had a strikingly similar response to the favourable conditions for flower induction in 1994. This indicates that the clones had become ontogenetically old enough to start to flower on all sites in Series 1.

A number of clones were flowering in Series 2 at the beginning of the 6th growing season after the trials were established. This must be considered precocious flowering, indicating that the conditions during 1994 must have been extremely good for initiating flowers in the area where the trials were located.

Broad-sense heritabilities for height (HT14) and INC variables were higher in trial S08 than in the other trials of Series 1. In this trial frost injuries were recorded in 1995 with a broad-sense heritability of 0.18, and there was a fairly high frequency of ramicorns, which are also indicative of frost. HANNERZ *et al.* (1999) found that heritability for height is overestimated at sites with frost problems.

The heritabilities for cone-set (CONE14) varied between 0.37–0.55 in the trials in Series 1, which agree well with heritability estimates for flowering and cone-set traits in other conifer species (SCHMIDLING 1981, NIENSTEDT 1985, BYRAM *et al.* 1986, MATZIRIS 1997, HAN *et al.* 1999, HANNERZ *et al.* 2001).

The proportion of clones that were flowering was much lower in the young material in Series 2 than in the older material in Series 1. Thus, the lower broad sense heritability estimates found for flowering in Series 2 were consistent with expectations. Our results are also in accordance with most of the few reports on the heritability of precocious flowering that have been published previously. SCHMIDLING (1981) found a broad-sense heritability of 0.13 for precocious flowering and 0.61 for mature flowering in *Pinus taeda*. BYRAM *et al.* (1986) found lower broad-sense heritability for cone production in a young compared to an older seed orchard in *Pinus taeda*. In contrast, in *Eucalyptus* species flowering precocity is reported to be highly heritable (CHAMBERS *et al.* 1997, WILTSHIRE *et al.* 1998).

The genotypic correlations between cone-set and height (CONE14 & CONE6 and HT14 & HT6) were

weak and not significant in five out of seven trials in Series 1 and 2. These results are consistent with reports concerning other conifers (ZHOU *et al.* 1999, HANNERZ *et al.* 2001). One of the trials to give a significant correlation in our study was trial S08, which is situated at a site where frost had influenced both height and heritability for height. Thus, the correlation in this trial could be considered a correlation between “ability to withstand frost” and cone-set. This indicates that trees grown above the frost zone flowered most abundantly.

Even if most of the genotypic correlations between cone-set and the height increment variables (i.e. the CONE and INC variables) were weak and not statistically significant (Figures 1 and 2), a slight trend can be seen, especially in Series 1. There was a tendency for the genotypic correlation to decrease the year after flowering (INC15), and for it to be restored again in the second year after flowering (INC16) (Figure 1). For breeding, this lack of genotypic correlation implies that selecting for height or height increment should not cause any changes in the flowering capacity of the selected part of the population. Similarly, flowering in a clonal test before assessment should not seriously influence the ranking of clones for height or height increment. If the breeder is forced to select for height growth traits solely from among the flowering clones, the genetic gain in the growth traits would be expected to decrease, but only because of a reduction in selection intensity.

Genotypic correlations between cone-set (CONE14) in the different trials were all strong and significant. This implies that the G×E interactions involved in flower initiation were weak in the geographic range of our trials this particular year. G×E interactions in cone-set may be larger in years when the climatic factors affecting flower initiation differ more among sites, but this remains to be verified. In *Pinus contorta* HANNERZ *et al.* (2001) found positive and significant genetic correlations (0.53–0.78) between flowering in different years at a single site, indicating that the rank changes between clones in flowering are small within the usual range of weather conditions. MATZIRIS (1997) found a strong year-to-year correlation for clonal averages for cone production in *Pinus halepensis*.

Genotypic correlations between height (HT14) in the different trials moderate to were strong and significant at all but one trial. This shows that the G×E interactions affecting height growth traits of the *Picea abies* clones studied here were moderate to weak. Moderate to weak G×E interactions in height between test sites in a wide range of site locations have previously been found in *Picea abies* (KARLSSON 2000).

CONCLUSIONS

High broad-sense heritability for cone-set was found, implying that there are differences in fecundity between clones, and that it is under strong genetic control.

The genotypic relationship between cone-set and height or height increment in *Picea abies* is weak and negligible. This indicates that selection for these growth traits will not influence cone-set capacity. Similarly, selection for early flowering will probably not affect these growth traits. To confirm whether this is a general trend, further studies are needed.

The strong genotypic correlations in cone-set (CONE14) between trials indicate that the same clones respond to favourable conditions for flower initiation, regardless of the site conditions for vegetative growth, i.e. the G×E interaction is weak for flower initiation.

The moderate to strong genotypic correlations in height (HT14) found between trials indicate that *Picea abies* is a species with quite low G×E interaction and fairly high stability in its height growth performance, i.e. no serious changes in the rank of clones occurs among localities even when there are large differences in site conditions for height growth.

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