

Diallel crossing in *Pinus cembra* : IV. Age trends in genetic parameters and genetic gain for growth and branching traits

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Abstract. This paper reports results from a complete 10 x 10 diallel carried out in a natural population of Swiss stone pine (*Pinus cembra* L.) from the southern Carpathian Mountains. At age six, after nursery testing, the material was field planted on one site, using a completely randomized block design with 100 families, four replicates and 15 tree row-plots per replication, spaced 2.5 x 2.5m. Total and annual height growth, root collar diameter, number of branches per whorl and survival were assessed at successive ages between ages eight and 14 after seed. In addition, several traits that were assessed during the nursery test were used in correlation and some other analyses. Plot means of the measured traits were analyzed using the general least-squares method by means of the computer DIALL programme prepared by Schaffer and Usanis (1969). Across the field testing periods, significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) differences occurred in total height growth and root collar diameter for general and specific combining ability as well for maternal-interaction effects. These results suggest that the traits are controlled by nuclear (additive and non-additive) and by nuclear x extra-nuclear gene interactions. In an ascendant trend, the additive variance, as a percent of the total genetic variance, ranged from 35% at age eight to 66% at age 14 for total height growth, while that for root collar diameter trend varied less between 16% and 34%. In a descendant trend, the dominance ratios $\sigma^2_{SCA} / \sigma^2_{GCA}$ for total height growth ranged from 0.9 at age eight to 0.3 at age 14, suggesting that the additive variance should be used in the breeding programme. Parents with significant general combining effects for all but one trait were found. For total height growth, the narrow-sense family mean heritability estimates varied in an ascendant trend between 0.45 and 0.65 while the narrow-sense individual tree heritability varied irregularly from year to year between 0.31 and 0.37. By selecting the best 20 families and the best 20% of individuals within families, a genetic gain in total height growth of 9.7% and 10.9%, respectively, could be achieved at age 14. The improvement of growth and branching by using both family and individual selections could be applied. The very high age-age and trait-trait genetic correlations suggest that both early and indirect selection could be applied effectively.

Keywords: *Pinus cembra*, diallel crossing, additive variance, dominance ratio, genetic effect, genetic correlation, heritability, early selection, indirect selection, genetic gain.

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Introduction

Swiss stone pine occurs at high elevations in the Alps and the Carpathian Mountains. It is closely related to *Pinus sibirica*, from which it is separated by a 1500-mile gap (Critchfield & Little 1966). As a glacier relict it occurs in the Southern Romanian but also in the Northern Carpathians range (Georgescu & Ioanescu-Barlad 1932). It is a pioneer species for the subalpine zone which ascends high in the single tree zone above the timber line (Holzer 1975), that because of the human impact receded by about 150 to 250 m elevation (Holtmeyer 1994). The species should be used in reforestation of the subalpine zone in order to raise the timberline to its former limit where it is important for: (a) slowing watersheds, avalanche and torrent damming and in reducing the effects of flash floods (Holzer 1958; Holzer 1975); (b) increasing the wind break and wind throw resistance of spruce-cembra mixed stands (Blada 1996); (c) its high genetic resistance to blister-rust caused by *Cronartium ribicola* J.C. Fisch ex Rabenh. (Bingham 1972; Hoff et al. 1980; Blada 1994); (d) its dense reddish-brown wood which is highly valued for paneling and traditional furniture and handicrafts (Contini & Lavello 1982).

The literature concerning the species genetics and breeding is not too rich. The first breeding work with Swiss stone pine was made in Austria where the height growth in open pollination progenies showed clinal variation. When progenies were grown in production forests from below the timberline, growth was positively correlated to elevation and on the contrary, above the timberline this correlation was negative (Holzer 1994).

Reliable data about genetic variation and genetic parameters estimation for elaboration an appropriate tree improvement programme were missing. For this reason, a genetic improvement programme was launched (Blada 1990). So far, a few results were achieved and published. At age six, in a nursery test, highly significant differences between provenances for total height, height increment and root collar diameter were noticed. According to the Duncan (1955) multiple range test, major gaps separate provenances in their natural range,

suggesting that in both the Alps and Carpathians, genetically distinct populations could be found. The pattern of distribution seemed to be a discontinuous one (Blada 1997). A genetic test with 136 Swiss stone pine half-sib families assessed at age six in the nursery (Blada 2003), showed that: (i) highly significant differences among families were detected for growth and branching traits; (ii) very high narrow-sense family heritabilities were estimated for total height (0.968), root collar diameter (0.938) and total number of branches (0.966); (iii) genetic correlations among growth traits were high or very high, ranging between 0.804 and 0.969; (iv) by selecting the best 30 to 45 families, genetic gains in total height growth and root collar diameter between 28.8% and 23.4% and between 18.8% and 15.3%, respectively, could be achieved.

The present 10 x 10 full diallel field trial with Swiss stone pine which is the subject of this article, was first evaluated in the nursery at age six (Blada 1999) and the main results were: (i) between ages two and six, the G.C.A. and S.C.A. variances for height and root collar diameter growth increased from 2 to 25% and from 15 to 27%, respectively; (ii) narrow-sense heritability estimates at both family and individual level for total height growth progressively increased with age from 0.065 to 0.453 and from 0.021 to 0.366, respectively; (iii) two out of 10 parents were detected as good general combiners for height growth; (iv) moderate to high positive genetic correlations among growth traits were found throughout the testing period; (v) if selected the best families and the best individuals within families, a variable genetic gain for total height growth between 5.5% and 10.6% and between 11.2 and 16.5%, respectively, could be achieved at age six.

The present paper provides information about genetic and non-genetic parameters of growth and branching traits useful in breeding Swiss stone pine originating in the Gemenele natural population located in the Southern Carpathians. This study was based not only on the present field test between ages eight and 14 after seed, but partially, on the nursery test, as well (Blada 1999). The nursery and field tests

were put together in order to have a clear picture on age trends in genetic parameters across the whole living period of the material.

Materials and methods

Initial material and mating design

The 10 Swiss stone pine parent trees used in this study were selected at random from the Gemelele natural population located at about 1800 m elevation in the Retezat Massif in the Southern Carpathians. However, in order to have enough female strobili for pollination, reproductive fertility was taken into account in parent selection. To avoid relatedness, the distance between selected trees was at least 100 m.

A 10 x 10 full-diallel mating design, according to Griffing's (1956) Method 1, was carried out. Controlled pollination took place by mid July, 1989, while the seed was collected by the end of September, 1990. Details about flower isolation, pollen processing, controlled pollination, cone collection, seed processing and sowing, and nursery testing procedures and results were presented in an earlier article (Blada, 1999).

Field trial

At age six, after nursery testing, one field trial was laid out in the Muncel zone located at about 1650 m elevation, 45° 16' north latitude and 24° 31' east longitude in the Cibinului Mountains (Southern Carpathians). The 100 families (90 from out-crossing and 10 selfs) were planted out in a randomized complete block design with four replicates, 15 trees per replicate in row plots, and 2.5 x 2.5m spacing (figure 1).

Measurements

Total and annual height growth, root collar diameter and total branches per whorl at successive ages, and survival at age (A) eight after planting and 14 after seed were recorded (table 1). Being a very slow-growing species, the Swiss stone pine has been taken into consideration firstly for its ecological characteris-

tics and secondly for its growth. Therefore, total height growth and the number of branches per whorl are the major traits to be improved, because: (i) faster growing trees have the ability to more quickly colonize the area; (ii) a larger number of branches per whorl per tree gives rise to a denser crown which has a higher capacity for snow and rain water retention; such an increase in precipitation retention may significantly contribute to preventing avalanche initiation, soil erosion and flooding downstream (Blada 2007).

Out of 15 trees planted per plot, only the first 10 survival trees per row plot were measured and their plot mean was included in the ANOVA. Due to the very high survival, all replications have had at least 10 alive trees to be assessed.

Statistical analysis

Although initially a full diallel mating design according to Griffing's (1956) Method 1 was used, the combining ability analysis was made according to Method 3 Model II, where one set of F1's and reciprocals but not the selfs were included. However, the selfs were included in the material grown in the experiment so that comparisons of outcrossed families (hybrids) with selfs could be made in other types of analyses. The mathematical model for analysis taken from Wilcox (1976) is a combination of Hayman (1954) and Griffing's (1956) models, as:

$$x_{kij} = u + g_i + g_j + s_{ji} + m_i + n_{ij} + e_{kij} \quad (1)$$

where x_{kij} = the value of the k^{th} progeny from the cross between i^{th} female and j^{th} male; u = the general mean; g_i and g_j = the general combining ability effects for the i^{th} and j^{th} parents, respectively; m_i = the maternal effect of the i^{th} parent; s_{ij} = the specific combining ability effect for the cross between the i^{th} and j^{th} parents so that $n_{ij} = n_{ji}$; n_{ij} = the interaction effect between the i^{th} and j^{th} parents, such that $r_{ij} = -r_{ji}$ (= reciprocal effect not accounted for by maternal or paternal effects); e_{kij} = the random error.

The general least squares analysis (Schaffer & Usanis 1969) based upon plot means was used in order to estimate the genetic and

environment variances. This analysis was based upon the random model assuming that

the parents were random samples from a panmictic population. This assumption makes possible estimates of the additive and non-additive genetic variance of the parent population. The model of analysis of variance, expected mean squares and formulas for estimating the variance components are presented in table 2.



Figure 1 Diallel trial at age eight after planting (14 after seed) laid out in the Cibirului Mts. at about 1650m elevation

Table 1 Measured traits

Traits	Units	Symbol
During the nursery test (Age 1 to 6)*		
100 seed weight	g	100 SW
Cotyledon number	No.	CN
Total height growth	cm	H.2 - H.6
Annual height growth	cm	h.4 - h.6
Root collar diameter	mm	RCD.4 - RCD.6
During the field test (Age 8 to 14 after seed)		
Total height growth	cm	H.8 - H.14
Annual height growth	cm	h.10 - h.14
Root collar diameter	mm	RCD.8 - RCD.12
Branches per whorl	No.	BW.13 - BW.14
Survival	%	SV.14

The standard errors (SE) of the variance component estimates were calculated according to the formula given by Anderson & Bancroft (1952).

The component of additive variance (σ^2_{GCA}) was used to estimate the variance in general combining ability among all of the parents in this experiment and was used as an estimator of $1/4\sigma^2_A$. It was assumed that all epistatic components of genetic variance were insignificantly small. With the same assumption, the component σ^2_{SCA} , the estimated variance in specific combining ability, was an estimator of $1/4\sigma^2_D$. Therefore, an estimate of the additive genetic variance is $4\sigma^2_{GCA}$ and an estimate of the dominance genetic variance is $4\sigma^2_{SCA}$ (Kriebel et al. 1972; Becker 1984).

To estimate the effectiveness of selection for early traits, three types of heritabilities were calculated.

Table 2 Analysis of variance of modified full diallel, random effects model, in a randomized complete block layout in one environment. (Wilcox, 1976).

Source	Df	MS	E (MS)	F-test
Rep.	k-1	MS_{Rep}	$\sigma^2_w/n + \sigma^2_p + p(p-1)\sigma^2_{Rep}$	
GCA	p-1	MS_{GCA}	$\sigma^2_w/n + \sigma^2_p + 2k\sigma^2_{SCA} + 2k(p-2)\sigma^2_{GCA}$	
SCA	$p(p-3)/2$	MS_{SCA}	$\sigma^2_w/n + \sigma^2_p + 2k\sigma^2_{SCA}$	
Rec.	$p(p-1)/2$	MS_{Rec}	$\sigma^2_w/n + \sigma^2_p + 2k\sigma^2_{Rec}$	
•Mat.	p-1	MS_{Mat}	$\sigma^2_w/n + \sigma^2_p + 2k\sigma^2_{Rec} + 2kp\sigma^2_{Mat}$	
•Mat-Interaction	$(p-1)(p-2)/2$	$MS_{Mat-Int}$	$\sigma^2_w/n + \sigma^2_p + 2k\sigma^2_{Rec} + 2K\sigma^2_{Mat-Int}$	
Error	$(k-1)(p^2-p-1)$	MS_E	$\sigma^2_w/n + \sigma^2_p$	
Within plot	$kp(p-1)(n-1)$	MS_w	σ^2_w	

Legend:
 $\sigma^2_w = MS_w$; $\sigma^2_c = MS_E$; $\sigma^2_p = \text{plot error} = \sigma^2_c - \sigma^2_w/n$;
 $\sigma^2_{Rec} = (MS_{Rec} - MS_E)/2k$; $\sigma^2_{Mat} = (MS_{Mat} - MS_{Mat-Int})/2kp$;
 $\sigma^2_{Mat-Int} = (MS_{Mat-Int} - MS_E)/2k$; $\sigma^2_{SCA} = (MS_{SCA} - MS_E)/2k$;
 $\sigma^2_{GCA} = (MS_{GCA} - MS_{SCA})/2k(p-2)$; $MS_{Rep} = (MS_{Rep} - MS_E)/2k$
 p = parents; n = seedlings per plot; k = replications.

The first heritability is the one commonly used for estimating the ratio of additive plus non-additive to total variance, which is appropriate for estimating gain from selection among full-sib families when they are vegetatively propagated. This is a broad-sense family mean heritability (h^2_1) and it is estimated by:

$$h^2_1 = (2\sigma^2_{GCA} + \sigma^2_{SCA}) / \sigma^2_{Ph1} = (2\sigma^2_{GCA} + \sigma^2_{SCA}) / (2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Mat-Int} + \sigma^2_e / k) \quad (2)$$

where: σ^2_{GCA} , σ^2_{SCA} , σ^2_{Mat} , $\sigma^2_{Mat-Int}$, σ^2_e , σ^2_{Ph1} = general, specific, maternal, maternal-interaction, error and phenotypic variances, respectively and k = number of blocks = 4.

According to Falconer (1981), the genetic gain (G_1) was estimated by:

$$\Delta G_1 = i_1 h^2_1 \sigma_{Ph1} \quad (3)$$

where: i_1 = the selection intensity taken from Becker (1984); σ_{Ph1} = the family mean phenotypic standard deviation.

The second heritability is the one commonly used for estimating the ratio of additive to total phenotypic variance, which is appropriate for estimating gain from selection among full-sib families when they are sexually propagated. This is narrow-sense family mean heritability (h^2_2) and it is estimated by:

$$h^2_2 = (2\sigma^2_{GCA}) / \sigma^2_{Ph1} = (2\sigma^2_{GCA}) / (2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Mat-Int} + \sigma^2_e / k) \quad (4)$$

and genetic gain (ΔG_2) from half-sib family selection is estimated by:

$$\Delta G_2 = i_1 h^2_2 \sigma_{Ph1} \quad (5)$$

The third heritability is the one commonly used for estimating the ratio of additive genetic to total phenotypic variance, which is appropriate for estimating gain from mass selection among randomly placed trees within plot. This narrow-sense individual heritability (h^2_3) was estimated by:

$$h^2_3 = (4\sigma^2_{GCA}) / \sigma^2_{Ph2} = (4\sigma^2_{GCA}) / (2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Mat-Int} + \sigma^2_p + \sigma^2_w) \quad (6)$$

where: tree values; σ^2_w = within plot variance; σ^2_p = plot error variance = $\sigma^2_e - \sigma^2_w / n$; n = seedlings per plot = 10.

The mass selection gain (ΔG_3) was estimated by:

$$\Delta G_3 = i_2 h^2_3 \sigma_{Ph2} \quad (7)$$

where: i_2 = the selection intensity for individual tree selection within family; σ_{Ph2} = phenotypic standard deviation which it refers to individual. If the best GCA combiners are to be selected and intermated, i_1 should be doubled (Kriebel et al. 1972) to give the expected

genetic gain (ΔG_4), such as:

$$\Delta G_4 = 2i_1 h^2_2 \sigma_{Ph2} \quad (8)$$

All genetic gains were expressed in comparison with the trial mean.

Genetic correlations (r_g) were calculated by the computer, i.e. all of the covariance components for each source of variance for each pair of traits/ages were computed by the same least squares diallel computer programme used to compute the variance components (Kriebel et al. 1972).

$$r_g = \sigma_{GCA(xy)} / (\mathcal{N} \sigma^2_{GCA(x)} \sigma^2_{GCA(y)}) \quad (9)$$

where: $\sigma_{GCA(xy)}$ is the additive covariance component between traits x and y and $\sigma^2_{GCA(x)}$ and $\sigma^2_{GCA(y)}$ are the variances due to GCA for traits x and y , respectively.

General combining ability (*g.c.a.*) effects of

each parental tree were calculated according to Griffing's (1956), Method 3, Model II.

Results

Genetic variation

The cross pollinated data from table 3 represent the mean female values over all males used in the mating design. At 14 years, the total

mean height growth was 120cm; the best female tree was 137cm while the worst one measured 105cm, i.e., a difference of about 30%. The mean annual growth in height was 19cm and the best female 23cm whereas the poorest one was 17cm, i.e., a difference of

Table 3 Parent performances at age 14 (after seed) except root collar diameter which was measured at age 12 (after seed)

Parent	Traits				
	H.14 (cm)	h.14 (cm)	RCD.12 (cm)	BW.14 (No.)	SV.14 (%)
2	120	20	31	5,7	99,8
3	110	18	30	5,9	99,3
45	105	17	30	5,5	99,1
50	122	20	30	5,7	99,0
205	111	17	30	5,6	99,7
206	125	20	30	6,2	99,8
209	120	20	31	6,9	96,7
X	137	23	34	7,6	99,8
Y	127	21	31	7,7	99,4
Z	124	20	31	7,1	98,6
Mean	120	19	31	6,4	99,1

about 35%. The richest parent in number of branches per whorl exceeded the poorest one by 40%. Mean survival was 99.1% and the difference between parent trees was insignificant. In comparison with the outcrossed families, the mean survival in selfed ones was as much as 85.3%. At age 12, the best performing tree in root collar diameter surpassed the poorest one by about 13%.

Comparisons of mean performance in total height growth and root collar diameter between control-cross-pollinated (CP) and control-self-pollinated (SP) progenies are displayed in figures 2 and 3. Throughout the life of the experiment, mean height growth and root collar diameter of outcrossed families exceeded the means of the selfed ones. Differences between the two categories of families were large. For example, at age 12, the mean outcrossed families exceeded selfed ones in total height and root collar diameter by 43% and 53%, respectively. The means of height and root collar diameter growth over time indicated that initially the self-pollinated offspring performed as well as outcrossed ones in both traits, but it is evident that the former drops behind the latter as trees become older. Because the selfed material tends towards inferiority with age, one may conclude that inbreeding depression is to be expected in Swiss stone pine and it should be taken into account.

The variation at individual level within tested population was very high. This significant variation was recorded in total height growth (figure 4) and in total number of branches per whorl or crown density (figure 5). It was proved that selection of faster growing trees and trees with a higher number of branches per whorl or a denser crown within tested population is possible. Consequently, the total height growth and the number of branches per whorl as major traits can be improved. The faster growing trees have the ability not only to produce more wood but to more quickly colonize the area, as well. Also, a larger number of branches per whorl per tree give rise to trees with a denser

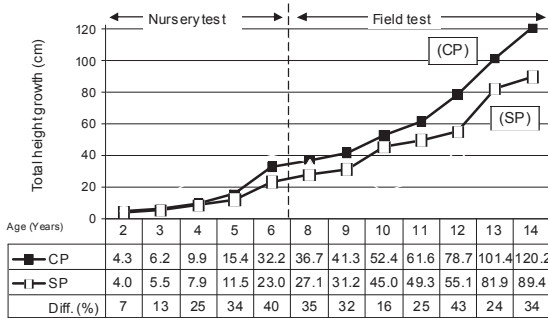


Figure 2 Age trend in total height growth (H) for mean control cross-pollinated (CP) and mean control self-pollinated (SP) progenies. Diff. (%) = difference between control and self-cross-pollination

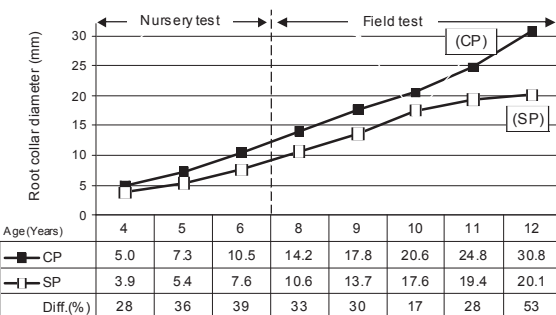


Figure 3 Age trend in root collar diameter (RCD) for mean control cross-pollinated (CP) and mean control self-pollinated (SP) progenies. Diff. (%) = difference between control and self-cross-pollination



Figure 4 Within different families individual variation in height growth; both trees are eight years of age after planting or 14 years after seed

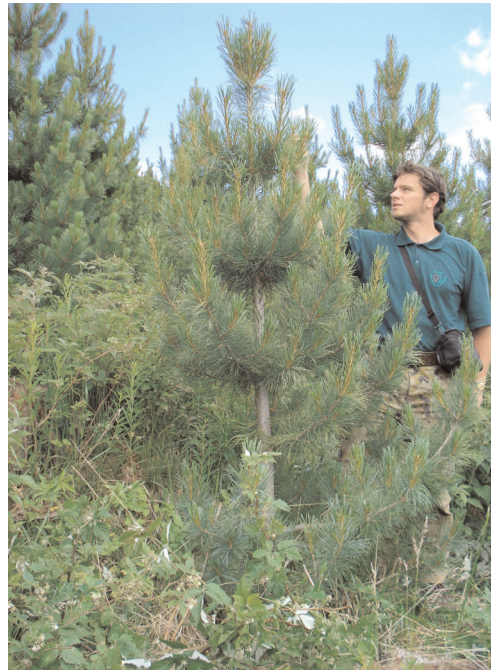


Figure 5 The crown density genetic variation: high retention capacity of both solid and liquid precipitations (left side) and very low retention capacity (right side)

crown; such trees have a higher capacity of retention of solid and liquid precipitation, i.e. they contribute to preventing avalanche initiation, soil erosion and flooding downstream. In order to make significantly higher genetic gains in these two traits, a breeding program with Swiss stone pine should take into account the best tested trees.

Variance components

The most important feature of this experiment was that the analysis of plot means from the 90 crosses showed significant ($p < 0.05$) and highly significant ($p < 0.01$; $p < 0.001$) variation in general (GCA) and specific (SCA) combining ability effects for total and annual height growth, root collar diameter and number of branches per whorl (table 4). This suggests that: (i) the traits are controlled by additive and non-additive genes, and (ii) selection within the basic population of good combiners to be used in further cycles of breeding might be effective.

The variance component estimates, standard errors and dominance ratios were listed in table 5. The proportion of σ^2_{GCA} for total height growth and root collar diameter expressed as a percentage of the total genetic variance increased strongly with age from 35% to 66% and from 16% to 34%, respectively. The σ^2_{GCA} for annual height growth showed a higher variation than the previous traits, i.e. between 61% and 91%, but it showed an irregular pattern. The σ^2_{SCA} for total height growth exhibited an irregular decreasing pattern trend from 32% at age eight to 17% at age 14. At age 14, the σ^2_{GCA} and σ^2_{SCA} for the number of branches per whorl contributed with 85% and 12%, respectively to the total genetic variance. For survival, only the specific combining ability variance component was highly significant suggesting that non-additive genetic variance is important in this population of Swiss stone pine.

A clearer development of the variances for total height growth and root collar diameter across both nursery and field testing periods was illustrated in

figure 6, where:

- the GCA variance tended to increase with age for both total height and root collar diameter; the largest GCA variance of this study was associated with total height growth at age 14;
- in general, the SCA and the maternal-interaction variances displayed a descending trend with age, which is more evident in total height growth;
- the maternal variance curves for total height growth displayed more or less a constant evolution across the testing period but for root collar diameter, after a decreasing trend between ages five and 11, by the end of the testing period, maternal variance displayed a slight ascending trend.

The $\sigma^2_{SCA} / \sigma^2_{GCA}$ ratios varied according to the trait and the age of the planted material (table 5). For total height growth, a continuous decreasing trend of the dominance ratios from 0.9 at age eight to 0.3 at age 14 was noticed. Also, for annual height growth and number of branches per whorl, the dominance ratios were in favor of additive variance but an irregular pattern of variation for the former trait was dis-

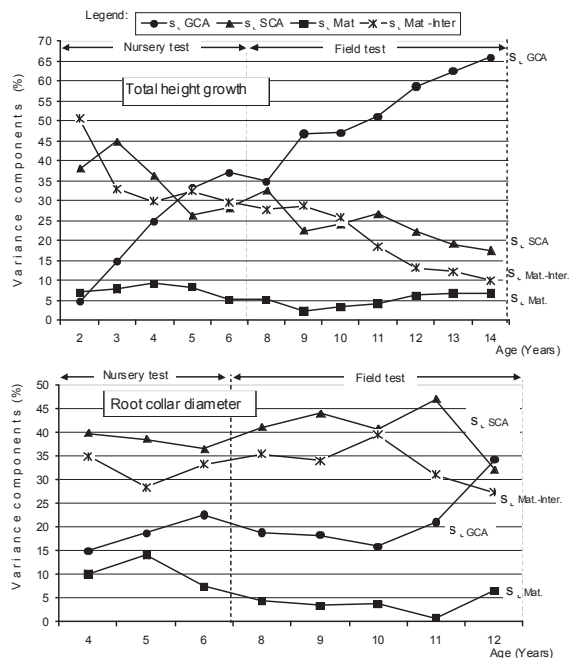


Figure 6 Age trend in GCA, SCA, Mat, Mat-interaction variance for total height growth (H) and root collar diameter (RCD)

Table 4 Analysis of variance of modified full diallel of the traits at different ages

Source of variation	Df.	Traits / Meansquares											
		H.8 (cm)	H.9 (cm)	H.10 (cm)	H.11 (cm)	H.12 (cm)	H.13 (cm)	H.14 (cm)	h.10 (cm)	h.11 (cm)	h.12 (cm)	h.14 (cm)	
Rep.	3	73.35	93.38	64.87	289.35	564.91	283.18	124.19	5.93	49.46	28.46		
GCA	9	304.80***	486.37***	831.23***	992.86***	1907.56***	2835.22***	4045.7***	61.20***	41.62***	147.34***		
SCA	35	40.68***	45.15***	82.19***	94.91***	150.89***	193.69***	253.86***	5.65*	4.14	7.35		
Rec.	45	46.00***	58.05***	98.14***	95.27***	164.33***	228.54***	296.12***	5.02	4.86	6.60		
•Mat.	9	85.25*	80.40	148.89	169.63*	351.78**	514.58**	683.34**	5.43	9.03	13.66		
•Mat-Inter.	36	36.18***	52.46***	85.45***	76.68***	117.46**	157.04**	199.32*	4.91	3.82	4.83		
Error	267	9.69	18.92	34.37	36.42	68.39	93.06	128.07	3.85	3.60	5.62		
Within plot	3240	26.68	48.81	84.34	117.50	185.98	340.15	401.69	11.34	13.70	18.93		

Table 4 (Continuation)

Source of variation	Df	Traits / Meansquares											
		h.13 (cm)	h.14 (cm)	RCD.8 (mm)	RCD.9 (mm)	RCD.10 (mm)	RCD.11 (mm)	RCD.12 (mm)	BW.13 (No.)	BW.14 (No.)	SV.14 (%)		
Rep.	3	37.05	22.53	10.26	20.05	25.68	96.05	32.10	2.02	5.06	77.56		
GCA	9	186.87***	110.24***	16.80**	24.97**	31.67**	38.56**	90.62***	29.80***	39.01***	69.79		
SCA	35	14.81***	11.06**	4.24***	7.70***	10.36***	11.15***	14.98***	1.62*	1.90*	81.24**		
Rec.	45	11.98***	10.06**	4.48***	7.33***	11.42***	8.84***	17.21***	1.38	1.60	53.11		
•Mat.	9	23.86*	20.23*	7.36	10.55	16.48	9.97	31.43	2.24	3.15	57.33		
•Mat-Inter.	36	9.01	7.52	3.76***	6.53***	10.16***	8.55***	13.66***	1.16	1.21	52.01		
Error	267	6.27	6.02	0.82	2.53	3.58	3.50	6.12	1.00	1.24	40.49		
Within plot	3240	23.08	15.13	2.70	7.94	11.21	17.28	28.26	4.75	3.85	--		

Table 5 Estimates of genetic environment (s^2_e), within plot (s^2_w) and plot error (s^2_p) variances, standard errors and dominance ratios Genetic variances as percent in brackets were calculated relative to the total genetic variance ($\Sigma\sigma^2_G$)

Components	Traits/ Estimates											
	H.8 (cm)	H.9 (cm)	H.10 (cm)	H.11 (cm)	H.12 (cm)	H.13 (cm)	H.14 (cm)	h.10 (cm)	h.11 (cm)	h.12 (cm)		
σ^2_{GCA}	4.127 (35) ±2.036	6.894 (47) ±3.245	11.704 (47) ±5.546	14.030 (51) ±6.624	27.448 (59) ±12.721	41.274 (62) ±18.903	59.247 (66) ±26.970	0.868 (70) ±0.408	0.586 (79) ±0.278	2.187 (91) ±0.982		
σ^2_{SCA}	3.874 (32) ±1.187	3.279 (22) ±1.328	5.978 (24) ±2.417	7.312 (27) ±2.786	10.313 (22) ±4.447	12.579 (19) ±5.718	15.723 (17) ±7.506	0.225 (18) ±0.169	0.067 (9) ±0.126	0.216 (9) ±0.222		
σ^2_{Mat}	0.613 (5) ±0.466	0.349 (2) ±0.454	0.793 (3) ±0.831	1.162 (4) ±0.930	2.929 (6) ±1.905	4.469 (7) ±2.779	6.050 (7) ±3.687	0.006 (1) ±0.032	0.065 (9) ±0.049	0.110 (5) ±0.074		
$\sigma^2_{Mar-int}$	3.312 (28) ±1.043	4.193 (28) ±1.518	6.386 (26) ±2.478	5.032 (18) ±2.234	6.135 (13) ±3.448	7.997 (12) ±4.614	8.906 (10) ±5.880	0.133 (11) ±0.147	0.027 (4) ±0.116	-0.099 (-4) ±0.151		
$\Sigma\sigma^2_G$	11.926	14.716	24.861	27.536	46.825	93.059	89.927	1.232	0.745	2.415		
σ^2_e	9.685	18.916	34.366	36.419	68.386	93.059	128.069	3.852	3.601	5.622		
σ^2_w	±0.835	±1.631	±2.963	±3.140	±5.897	±8.024	±11.043	±0.332	±0.310	±0.485		
σ^2_p	26.680	48.812	84.344	117.504	185.980	340.152	401.693	11.335	13.703	18.935		
σ^2_p	7.017	14.035	25.932	24.669	49.788	59.044	87.900	2.719	2.230	3.728		
$\sigma^2_{SCA}/\sigma^2_{GCA}$	0.9	0.5	0.5	0.5	0.4	0.3	0.3	0.3	0.1	0.1		

Table 5 (Continuation)

Components	Traits / Estimates																				
	h.13 (cm)	h.14 (cm)	RCD.8 (mm)	RCD.9 (mm)	RCD.10 (mm)	RCD.11 (mm)	RCD.12 (mm)	BW.13 (No.)	BW.14 (No.)	SV.14 (No.) ¹⁾	h.13 (cm)	h.14 (cm)	RCD.8 (mm)	RCD.9 (mm)	RCD.10 (mm)	RCD.11 (mm)	RCD.12 (mm)	BW.13 (No.)	BW.14 (No.)	SV.14 (No.) ¹⁾	
σ^2_{GCA}	2.688 (63)	1.550 (61)	0.196 (19)	0.270 (18)	0.333 (16)	0.428 (21)	1.182 (34)	0.440 (80)	0.580 (85)	0.000 (0)	±1.246	±0.736	±0.113	±0.169	±0.214	±0.260	±0.606	±0.199	±0.260	±0.000	±0.000
σ^2_{SCA}	1.068 (25)	0.630 (25)	0.427 (41)	0.647 (44)	0.847 (41)	0.957 (47)	1.107 (32)	0.077 (14)	0.082 (12)	5.093 (77)	±0.436	±0.328	±0.123	±0.226	±0.304	±0.326	±0.440	±0.048	±0.057	±2.401	±0.000
σ^2_{Mat}	0.186 (4)	0.159 (6)	0.045 (4)	0.050 (3)	0.079 (4)	0.018 (1)	0.222 (6)	0.013 (2)	0.024 (4)	0.069 (1)	±0.130	±0.110	±0.041	±0.059	±0.093	±0.059	±0.172	±0.012	±0.017	±0.341	±0.000
$\sigma^2_{Mat-Int}$	0.342 (8)	0.188 (7)	0.368 (35)	0.500 (34)	0.822 (39)	0.632 (31)	0.942 (27)	0.020 (4)	-0.004 (-1)	1.439 (22)	±0.267	±0.225	±0.108	±0.189	±0.294	±0.248	±0.397	±0.035	±0.037	±1.554	±0.000
$\Sigma\sigma^2_G$	4.284	2.526	1.037	1.467	2.081	2.035	3.453	0.551	0.682	6.601	4.284	2.526	1.037	1.467	2.081	2.035	3.453	0.551	0.682	6.601	±0.000
σ^2_e	6.268	6.021	0.819	2.532	3.583	3.496	6.123	1.000	1.240	40.492	±0.540	±0.519	±0.071	±0.218	±0.309	±0.301	±0.528	±0.086	±0.107	±3.491	±0.000
σ^2_W	23.078	15.129	2.696	7.937	11.210	17.281	28.262	4.746	3.853	0.000	23.078	15.129	2.696	7.937	11.210	17.281	28.262	4.746	3.853	0.000	±0.000
σ^2_p	3.960	4.508	0.550	1.738	2.462	1.768	3.297	0.526	0.855	0.000	3.960	4.508	0.550	1.738	2.462	1.768	3.297	0.526	0.855	0.000	±0.000
$\sigma^2_{SCA}/\sigma^2_{GCA}$	0.4	0.4	2.2	2.4	2.5	2.2	0.9	0.2	0.1	0.0	0.4	0.4	2.2	2.4	2.5	2.2	0.9	0.2	0.1	0.0	±0.0

1) Negative variance estimates were considered zero and their standard errors were not calculated

played. With one exception at age 12, the dominance ratios for root collar diameter were in favor of non-additive variance and the ratios varied from 2.2 to 2.5. Therefore, as evidenced by the dominance ratios, additive variance was a more important source of variation for height growth and branching and less important, but still usable, for root collar diameter. Consequently, the height growth and branching breeding strategy can employ additive variation, as considerable progress under direct selection is possible. On the other hand, because the dominance ratio for root collar diameter at age 12 was not consistent with the previous ratios, a definitive conclusion can not yet be reached.

Maternal effects were not significant for root collar diameter but significant ($p < 0.05$) or highly significant ($p < 0.01$; $p < 0.001$) in the last years of testing for total and annual height growth (table 4). Quantitatively, the amount of maternal variance for total height growth progressively increased from 2% at ages nine to 7% at age 14 while it varied irregularly between 1% and 9% for the other tested traits (table 5).

Across the testing period, the maternal-interaction effects were significant ($p < 0.05$) or highly significant ($p < 0.01$; $p < 0.001$) for total height growth and root collar diameter data, but insignificant for annual growth, number of branches per whorl and survival (table 4).

This suggests that the first two traits were controlled by nuclear x extra nuclear gene interactions while the other traits were not. For total height growth, and root collar diameter the maternal-interaction variance component estimates gradually declined from 28% to 10% and from 35% to 27%, respectively (table 5).

In general, GCA, SCA, maternal and maternal-interaction variance components were associated with standard errors smaller than the estimates themselves in all but 15 cases, thus making heritability estimates fairly reliable (table 5).

The variance analysis proved that although Swiss stone pine is an extremely slow-growing species, it does possess high genetic variation in tested traits. The present results have demonstrated that there is enough genetic variation to be used in an improvement pro-

gramme.

Heritability

The heritability estimates are listed in table 6. Broad-sense family heritability, for total and annual height growth and root collar diameter ranged from 0.65 to 0.74, from 0.56 to 0.76 and from 0.46 to 0.57, respectively. Narrow-sense family heritability estimates for the same three traits ranged from 0.45 to 0.65, from 0.53 to 0.73 and from 0.20 to 0.38, respectively. For total height growth the largest narrow-sense heritabilities on a family basis were recorded at the last age of measurement, i.e. at age 14. Narrow-sense individual heritability estimates for total and annual height growth and root collar diameter ranged from 0.31 to 0.37, from 0.14 to 0.32 and from 0.08 to 0.18, respectively.

Evolution of the three heritability estimates (h_1^2 , h_2^2 , h_3^2) for total height growth and root collar diameter was illustrated in figure 7 where an increased trend can be seen during the nursery test. But after planting, a slightly decreased trend occurred and towards the end of the field test again an increased one was noticed for both traits. Decreasing heritability during the early years shortly after planting is similar to that found in *Pinus contorta* Dougl. (Ying et al. 1989; Xie & Ying 1996) and seems to be a common phenomenon with conifers, e.g. *Pseudotsuga menziesii* (Mirb.) Frnaco (Johnson et al. 1997).

The above results indicate that heritability estimates are high enough to ensure genetic progress in improving Swiss stone pine growth and branching traits.

General combining ability

General combining ability effects (*g.c.a.*) calculated for each parent tree were listed in table 7. Both positive and negative significant ($p < 0.05$), and highly significant ($p < 0.01$; $p < 0.001$) effects were found in all traits. At all but one consecutive ages, the parent X exhibited the largest significant ($p < 0.05$) or highly significant ($p < 0.01$; $p < 0.001$) positive *g.c.a.* effects for total and annual height growth, root collar diameter and branches per whorl. The tree Z is the second in the rank; its *g.c.a.* effects were highly significant ($p < 0.01$;

Table 6 Estimates of phenotypic variances (σ^2_{Ph1} ; σ^2_{Ph2}), phenotypic standard deviations (σ_{Ph1} ; σ_{Ph2}) and heritabilities (h^2_1 ; h^2_2 ; h^2_3)

Parameters	Traits / Estimates									
	H.8 (cm)	H.9 (cm)	H.10 (cm)	H.11 (cm)	H.12 (cm)	H.13 (cm)	H.14 (cm)	h.10 (cm)	h.11 (cm)	h.12 (cm)
Mean	32.2	41.3	52.4	61.6	78.7	101.4	120.2	13.1	12.7	19.8
σ^2_{Ph1}	18.47	26.34	45.16	50.67	91.37	130.86	181.19	3.06	2.23	6.01
σ^2_{Ph2}	49.75	84.46	146.84	183.74	310.04	506.79	638.77	16.15	17.26	27.27
σ_{Ph1}	4.30	5.13	6.72	7.12	9.56	11.44	13.46	1.75	1.49	2.45
σ_{Ph2}	7.05	9.19	12.12	13.56	17.61	22.51	25.27	4.02	4.15	5.22
h^2_1	0.66	0.65	0.65	0.70	0.71	0.73	0.74	0.64	0.56	0.76
h^2_2	0.45	0.52	0.52	0.55	0.60	0.63	0.65	0.57	0.53	0.73
h^2_3	0.33	0.33	0.32	0.31	0.35	0.33	0.37	0.21	0.14	0.32

Table 6 (Continuation)

Parameters	Traits / Estimates									
	h.13 (cm)	h.14 (cm)	RCD.8 (mm)	RCD.9 (mm)	RCD.10 (mm)	RCD.11 (mm)	RCD.12 (mm)	BW.13 (No.)	BW.14 (No.)	SV.14 (%)
Mean	24.9	19.5	14.2	17.8	20.6	24.8	30.8	6.1	6.4	99.1
σ^2_{Ph1}	8.54	5.58	1.44	2.37	3.31	3.34	6.17	1.24	1.57	16.37
σ^2_{Ph2}	34.01	23.71	4.48	11.41	16.09	21.51	36.19	6.26	5.97	46.74
σ_{Ph1}	2.92	2.36	1.20	1.54	1.82	1.83	2.48	1.11	1.25	4.05
σ_{Ph2}	5.83	4.87	2.12	3.38	4.01	4.64	6.02	2.50	2.44	6.84
h^2_1	0.75	0.67	0.57	0.50	0.46	0.54	0.56	0.77	0.79	0.29
h^2_2	0.63	0.56	0.27	0.23	0.20	0.26	0.38	0.71	0.74	0.00
h^2_3	0.32	0.26	0.18	0.09	0.08	0.08	0.13	0.28	0.39	-

Legend:

$\sigma^2_{Ph1} = 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Mat-Int} + \sigma^2_e / k$; k = replications; n = seedlings / plot=10

$\sigma^2_{Ph2} = 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat} + \sigma^2_{Mat-Int} + \sigma^2_p + \sigma^2_w$; $\sigma^2_p = \sigma^2_e - \sigma^2_w / n$;

$h^2_1 = (2\sigma^2_{GCA} + \sigma^2_{SCA}) / \sigma^2_{Ph1}$; $h^2_2 = 2\sigma^2_{GCA} / \sigma^2_{Ph1}$; $h^2_3 = 4\sigma^2_{GCA} / \sigma^2_{Ph2}$

h^2_1, h^2_2, h^2_3 = broad-sense family mean, narrow-sense family mean and narrow sense individual heritability, respectively

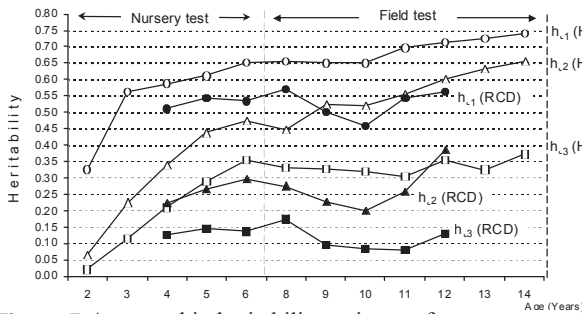


Figure 7 Age trend in heritability estimates for total height growth (H) and root collar diameter (RCD)

$p < 0.001$) in all cases for total height growth and branching per whorl, and in most cases for annual height growth. No significant effects were found in root collar diameter. Consequently, the X and Z parent trees should be promoted for further breeding work because of their high positive *g.c.a.* effects and high breeding value for both total height growth and number of branches per whorl, as major traits to be improved. If the stress will ever be placed only on branching improvement, then the parents Y and 209 that showed highly significant effects for this trait could also be taken into

Table 7 Estimates of general combining ability effects (g.c.a.)

Parent	H.8 (cm)	H.9 (cm)	H.10 (cm)	H.11 (cm)	H.12 (cm)	H.13 (cm)	H.14 (cm)	h.10 (cm)	h.11 (cm)	h.12 (cm)
2	-0.947	-1.938 *	-2.336 *	-1.645	-1.997	-1.356	-2.002	-0.387	-0.053	-0.093
3	-1.564 **	-1.974 *	-2.534 *	-3.562 ***	-5.210 ***	-5.700 ***	-6.508 **	-0.706 *	-0.492	-0.742
45	-3.829 ***	-4.605 ***	-6.196 ***	-6.713 ***	-9.108 ***	-11.141 ***	-13.175 ***	-1.573 ***	-1.356 ***	-2.377 ***
50	0.689	0.487	0.888	1.475	1.429	1.851	1.710	0.670	0.160	-0.152
205	0.389	1.088	0.514	0.056	-1.200	-2.246	-3.859	-0.694 *	-0.209	-1.229
206	1.457 **	2.026 **	3.340 **	2.870 **	3.275 *	3.344 *	3.843	1.112 **	0.060	0.123
209	-1.050	-0.903	-0.770	-0.880	-0.511	-1.818	-0.413	-0.072	-0.255	0.288
X	3.124 ***	3.434 ***	4.107 ***	5.027 ***	7.960 ***	9.792 ***	12.612 ***	0.742 *	1.416 ***	2.593 ***
Y	0.251	-0.256	-0.501	-0.279	1.000	1.264	1.974	-0.065	0.107	0.269
Z	1.480 **	2.642 ***	3.489 ***	3.650 ***	4.363 **	6.010 ***	5.818 **	0.974 **	0.621	1.318 **
S.E.(g _i - g _j)	0.550	0.769	1.036	1.067	1.462	1.705	2.001	0.347	0.335	0.419
LSD 5 %	1.078	1.507	2.031	2.091	2.865	3.342	3.921	0.680	0.657	0.822
LSD 1 %	1.419	1.984	2.674	2.752	3.772	4.400	5.161	0.895	0.865	1.081
LSD 0.1 %	1.810	2.529	3.409	3.510	4.810	5.610	6.582	1.142	1.104	1.379

Table 7 (Continuation)

Parent	h.13 (cm)	h.14 (cm)	RCD.8 (mm)	RCD.9 (mm)	RCD.10 (mm)	RCD.11 (mm)	RCD.12 (mm)	BW.13 (No.)	BW.14 (No.)	SV.14 (%)
2	0.199	0.238	-0.415**	-0.600*	-0.503	-0.267	-0.756	-0.296	-0.693***	0.821
3	-0.745	-0.698	0.034	0.109	-0.010	-0.327	-0.793	-0.560**	-0.299	0.282
45	-3.059***	-2.129***	-0.369*	-0.390	-0.471	-0.379	-1.246**	-0.980***	-0.891***	-0.217
50	0.656	0.114	-0.402*	-0.583*	-0.802*	-0.767*	-0.612	-0.247	-0.390*	0.935
205	-1.640***	-1.168**	0.451**	0.460	0.551	0.337	0.437	-0.622***	-0.690***	-0.174
206	0.301	0.277	-0.126	-0.135	-0.298	-0.432	-0.215	0.432*	-0.062	-0.244
209	0.023	0.191	-0.134***	-0.014	0.163	0.379	0.482	0.611***	0.582**	-0.201
X	2.434***	2.259***	1.009	1.175***	1.314***	1.654***	2.455***	0.458**	0.787***	0.679
Y	0.905*	0.739	-0.288	-0.399	-0.329	-0.395	-0.333	0.543**	0.905***	0.424
Z	0.926*	0.178	0.242	0.377	0.384	0.198	0.581	0.661***	0.751***	-2.304*
S.E.(g _i - g _j)	0.443	0.434	0.160	0.281	0.335	0.331	0.437	0.177	0.197	1.125
LSD 5%	0.867	0.850	0.314	0.551	0.656	0.648	0.857	0.347	0.386	2.205
LSD 1%	1.142	1.119	0.413	0.726	0.863	0.853	1.129	0.456	0.508	2.902
LSD 0.1%	1.456	1.427	0.526	0.925	1.101	1.087	1.439	0.582	0.648	3.701

LSD = least significant g.c.a. difference.

*p < 0.05; **p < 0.01; ***p < 0.001 = significant and highly significant g.c.a. effects

account (table 7; figure 8). In contrast, parent trees 3 and 45 were the worst, showing highly significant negative g.c.a. effects for all traits. These two and all another parent trees that have not showed significant effects, should be discarded.

If two out of 10 randomly selected parent trees exhibited significant positive g.c.a. effects for height growth and number of branches per whorl, then by extrapolation it may be assumed that 20% of trees within the base natural population might be selected as good combiners. This high occurrence of good g.c.a. trees in the native population suggests that selection of individuals for both seed orchard establishment and for later generation population development is possible. Therefore, selection and testing new candidates in order to detect enough number of good combiners should be continued.

The phenotypic expression of the parent general combining ability effects on height growth was illustrated in the figure 9.

Age-age correlations for the same trait

Age-age additive genetic correlations across

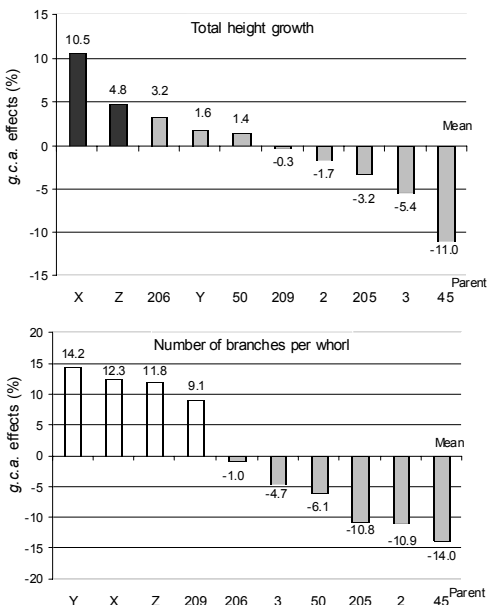


Figure 8 General combining ability effects (%) for total height and number of branches per whorl at age 14

both nursery and field test were moderate to very high for total and annual height growth, and root collar diameter ranging from 0.64 to 0.99, from 0.70 to 0.97 and from 0.81 to 0.99, respectively (table 8 above diagonal line within rectangle). This indicates that early selection for growth traits may be efficient. Age-age additive genetic correlation for total height growth and for root collar diameter rose from 0.85 at age two to 0.95 at age six and from 0.87 at age four to 0.93 at age eight and then leveled off across the field test (figure 10). Consequently, a generally high age-age genetic correlation for height growth indicates that if the goal is to improve 14-year height, early selection can be considered at age six. Lambeth (1980) in *Pinaceae* and Lambeth et al. (1983) in *Pinus taeda* reported that adequate estimates of rotation age performance can be obtained at much earlier ages. Thus, most selection is currently done between the ages of five and ten years.

Trait-trait genetic correlations

Table 8 presents the trait-trait additive genetic correlations for successive ages, as follows:

- a moderate to strong genetic correlation of height growth (both annual and total) with root collar diameter and number of branches per



Figure 9 The full-sib family from the right side belongs to the best general combiner parent while the other one belongs to an average general combiner parent

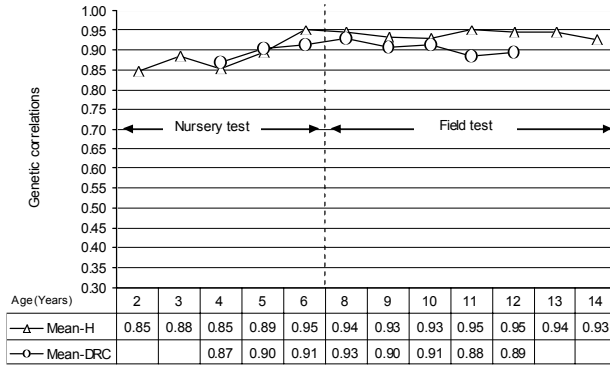


Figure 10 Evolution of age-age genetic correlations for total height growth and root collar diameter

whorl;

- a low to moderate genetic correlateon between root collar diameter and number of branches per whorl;

- a moderate genetic correlation between cotyledon number and root collar diameter at successive ages, whereas phenotypic correlations were statistically insignificant; this surprising result requires further confirmation.

Moderate to very high genetic correlations among growth traits and number of branches per whorl suggest that selection for one trait will cause a simultaneous improvement of the other. Consequently, these strong positive genetic correlations imply genetic gain in any of these traits even if selection is practiced on only one easily measurable trait, such as diameter or number of branches per whorl.

At all ages, without exception, highly significant ($p < 0.01$; $p < 0.001$) trait-trait phenotypic correlations among total and annual height growth and root collar diameter and number of branches per whorl were found. Also, highly significant ($p < 0.01$; $p < 0.001$) trait-trait phenotypic correlations were found between 100 SW and most of the successive total height growths and all of the successive root collar diameters. No significant phenotypic correlations were found between cotyledon number and any height growth and branches per whorl traits.

Selection and genetic gain

Generally, in a breeding programme selection is based upon the principle that genetic value

of selected families or individuals will be better than the average value of individuals in the population as a whole (Zobel and Talbert 1984).

The present study considers selection of both families, individual trees within families and progeny tested parent trees within base (initial) population where the best parents are selected according to their g.c.a. effects.

Four types of genetic gain that could be achieved at either family or individual level were estimated (table 9). The following genetic progress that could be achieved in total height growth was estimated at age 14:

- if the best 20, 30 or 40 out of 90 tested full-sib families were selected and vegetatively propagated, a genetic gain (ΔG_1) of 11.0%, 9.0%, or 7.3%, respectively could be expected; at the same intensity of selection if propagation takes place sexually, the gains (ΔG_2) that could be reached are 9.7%, 7.9% or 6.5%, respectively;

- if the best 10%, 15% or 20% individuals within the best families were selected, a genetic gain (ΔG_3) of 13.7%, 12.0%, or 10.9%, respectively, could be achieved.

- much greater genetic progress could be made if the best 20, 30 or 40 general combiners of, for instance, 100 progeny tested parents were selected; if such tested parents would be planted in a seed orchard, a genetic gain (ΔG_4) of 25.3%, 20.3% or 16.8%, respectively, could be obtained if the improved material were used in operational planting programmes. These high gains are in line with Carson (1986) who con-

Table 9 Expected genetic gain (ΔG %) if selecting the best families (ΔG_1 ; ΔG_2), the best individuals within family (ΔG_3) and the best g.c.a. combiners (ΔG_4)

Traits	$\Delta G_1 = i_1 h^2_1 \sigma_{ph1}$			$\Delta G_2 = i_1 h^2_2 \sigma_{ph1}$			$\Delta G_3 = i_2 h^2_3 \sigma_{ph2}$			$\Delta G_4 = 2i_1 h^2_2 \sigma_{ph1}$		
	Selection intensity / Gain estimates (%)											
	20	30	40	20	30	40	10 %	15 %	20 %	20	30	40
H.14	11.0	9.0	7.3	9.7	7.9	6.5	13.7	12.0	10.9	25.3	20.3	16.8
h.14	10.8	8.8	7.2	8.9	7.3	5.9	11.5	10.1	9.2	23.3	18.7	15.5
RCD.12	6.0	4.9	4.0	4.1	3.3	2.7	4.5	3.9	3.6	10.7	8.6	7.1
BW.14	20.6	16.8	13.7	19.2	15.7	12.8	26.1	23.0	20.8	50.2	40.2	33.3

ΔG_1 and ΔG_2 = genetic gain if the best 20, 30, 40 families are selected out of 90.

ΔG_3 = gain from mass selection if the best 10%, 15%, 20% of individuals are selected within family.

ΔG_4 = gain if the best 20, 30, and 40 out of 100 parents, are selected.

cluded, based on a study of *Pinus radiata*, that production of improved seed through crossing among the best general combiners is both an efficient and an effective strategy for optimizing gains from control-pollinated seed orchards.

The genetic gains that could be obtained in annual height growth were slightly smaller than those obtained for total height growth.

The greatest genetic gain could be obtained in number of branches per whorl, ranging from: 20.6% to 13.7% (ΔG_1); 19.2% to 12.8% (ΔG_2); 26.1% to 20.8% (ΔG_3) and 50.2% to 33.3% (ΔG_4), respectively.

The above mentioned gains underestimate the gain that might be obtained because the parental selections were random samples with regard to any of the tested traits. For this reason the estimated gains relate to the initial panmictic population mean, and not what might be possible to achieve in a selection program.

The estimated gains for growth and branching at age 14 may be good predictors of later performance. These gains can be multiplied for substantial returns in large planting programs. The gains in all tested traits from selection based on high g.c.a. parents (middle parent value) produced higher genetic gains than selection based on tested full-sib families. Therefore, establishing seed orchards after full-sib progeny testing would be recommendable.

Figure 11 displays the trend of the four genetic gain estimates over time. The curve shapes of both total height growth and root collar diameter displayed a relatively similar par-

allel trend for the four types (ΔG_1 , ΔG_2 , ΔG_3 and ΔG_4) of gains. They increased from age two to age six and then after a slight decrease they increased again. However, after age 12, the total height growth curves displayed a fairly stable trend. The curves suggest that in this Swiss stone pine population no additional significant genetic gain can be achieved in both total height growth and root collar diameter by selecting later than age six. These results suggest that selection may be done relatively early, by age six, after the nursery test and these results were in line with age-age additive genetic correlations.

Discussion

GCA and SCA variances

The purpose of this study was to evaluate genetic parameters on which the Swiss stone pine breeding programme should be based. The obtained results from both nursery and field tests showed that the amount of σ^2_{GCA} for total height growth progressively increased from age two to age 14. The additive variance for total height increased as trees became older, rapidly up to age six, then more gradually up to age 14 while the σ^2_{SCA} gradually decreased since age three (fig. 3). These results indicate that the additive variance should be employed in the breeding programme for the height growth improvement. Unfortunately, no other studies dealing with genetic parameter estimation

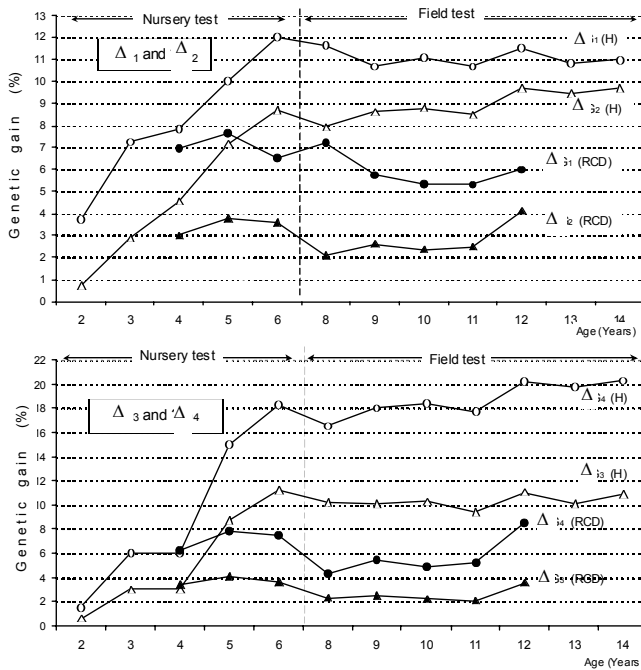


Figure 11 Age trend in expected genetic gain for total height growth (H) and root collar diameter (RCD) if selecting the best 20 out of 90 families (ΔG_1 , ΔG_2), the best 20% of individuals with family (ΔG_3) and the best 20% g.c.a. combiners (ΔG_4)

were found in Swiss stone pine species to compare with these results. An increase with age of additive variance for growth traits was also reported in *P. radiata* (King et al. 1998), in *Pinus pinaster* AIT. (Kusnandar et al. 1998) and in *Pinus taeda* L. (Gwaze et al. 2001; Xiang et al. 2003a; Xiang et al. 2003b). Other authors reported that both GCA and SCA were important sources of variation for growth traits in *Pinus taeda* (Foster & Bridgwater 1986), in *Pinus pinaster* and *P. radiata* (Cotterill et al. 1987) and in *Pseudotsuga menziesii* (Mirb.) Franco (El-Kassaby & Park 1993). The non-additive variance was often found to be less important than additive genetic variance for growth traits in *Pinus taeda* (Ballochi et al. 1993; Mckeand & Bridgwater 1986; Foster 1986; Li et al. 1996; XIANG et al. 2003a). Conversely, Samuel (1991) in *Picea sitchensis* (Bong.) Carr found that dominance variance accounted for a greater proportion of variation.

Maternal variance

Though in general significant across the field testing period, the maternal variances for total height growth were generally low. Similar estimates were obtained in the nursery test for all three growth traits (Blada 1999), suggesting that their importance could be neglected. Figure 3 showed that between ages three and five, the maternal variance curves displayed a slight ascending trend for both total height and root collar diameter growth, and then tended to decline and again to increase. In a previous study (Blada 1992), highly significant maternal gene effects in blister-rust resistance, diameter, basal area and volume growth rate were found in *Pinus strobus* L. at age nine. Conversely, various studies (Hough 1952; Sshell 1960; Green 1971, Barnes & Schweppen-hauser 1978; Bramlett et al., 1983) have shown that fast germinating and large seeds yield seedlings that initially grow more

vigorously than those from smaller seeds but this initial difference may decrease and even disappear after several months, or after a few years. Si-milarly, maternal effects are most often consi-dered of little importance in tree improvement and Barnes (1973) has shown that these effects are indeed negligible in most traits studied in *Pinus patula* Schiede & Deppe.

Heritability

The increasing time trend of narrow-sense family heritabilities for total height growth in the field test (figure 7) was consistent with that obtained in the nursery test where the estimates progressively increased with age from 0.06 at age two to 0.45 at age six (Blada 1999). This great consistency can be explained by the soil homogeneity in both nursery and field test, and perhaps because the same technical team assessed the trials across the whole testing period. Conversely, in two studies with *Pinus pinaster* Ait., the time trend of the narrow sense heritabilities at family level for tree height were very constant over time (Danjon 1994; Kusnandar et al. 1998).

As expected, the narrow-sense individual heritability estimates in the field test were smaller than those calculated on a family basis for all growth traits (table 6). Across the nursery test, a progressive clear ascendant time trend of heritability was detected for total height growth (Blada 1999), but in the field test, after some variation, a slightly increased

trend towards the end of age 14 was displayed (fig. 7). An increasing trend over time of narrow-sense heritability estimates for growth traits was also found in three *Pinus taeda* test regions (Xiang et al. 2003a). However, the age trend of heritability varies according to the species. So, in *Pinus tecunumanii* and *P. chiapensis* the heritability of height decreased with age (Vasquez & Dvorak 1996) but this is in contrast to other studies of pines in which heritability increased with age, for example in *Pinus pinaster* (Costa & Durel 1996) and in *Pinus taeda* (Xiang et al. 2003a).

In conclusion, the heritability estimates of Swiss stone pine are high or very high indicating that a substantial genetic gain can be achieved.

Implications for Breeding Strategy

The results presented indicate that annual and total height growth, root collar diameter and number of branches per whorl of Swiss stone pine are all under a high level of genetic control. Therefore, this species offers good opportunities for the further genetic improvement of all traits investigated. Reliable data on the amount of additive variance have already indicated the likely achievements from the programme of good *g.c.a.* combiner selections combined with clonal and seedling orchards for developing improved seed to be used in operational planting programmes. It is now evident that further substantial gain can be anticipated from the use of breeding

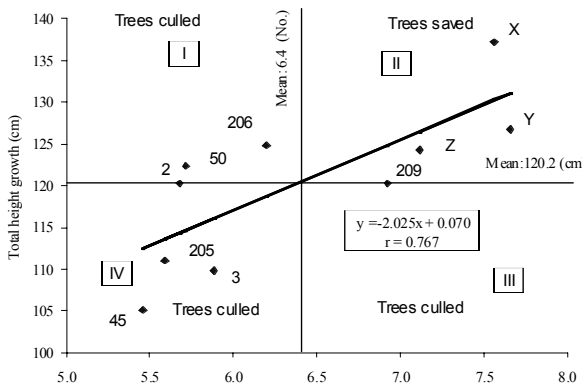


Figure 12 Regression between total height growth and number of branches per whorl of the parents at age

techniques that exploit GCA variance. Based on this test, only two parents (i.e. X and Z) exhibited high positive *g.c.a.* effects (table 7; figure 12) and high breeding value for both total height growth and number of branches per whorl, as major traits to be improved. Therefore, the testing and selection of new *g.c.a.* combiners originating in the natural base population should continue. The immediate main task consists in production and testing of more crosses in order to (i) detect enough good general combiners to be planted in seed orchards; (ii) selecting the best full-sib families and individuals within families to be used in both the seed orchards' development and in planting operations. The obtained results indicated that about 20% of trees within the base population could be found and selected as good combiners. Assuming that 20 or 30 or 40 parents with good general combining ability will be used for developing seed orchards and the improved seed used in operational planting programmes, a substantial genetic gain in height growth and number of branches per whorl could be made (table 9). However, in operational tree improvement programmes, the major objectives of progeny testing are parental evolution and the production of a base population for advanced generation selection (Mckinley 1983).

The additive variance for growth traits' improvement was also used in other conifers, (Cotterill et al. 1987; Samuel 1991; Dieters et al. 1995; Dieters, 1996; Gwaze et al. 2001; Xiang et al. 2003a; Jansson, G. & Li 2004).

Independent culling is a method of multitrait selection that involves setting minimum values for each trait of interest and individuals must meet these minimum criteria if they are to be retained (Zobel & Talbert 1984). Regression between total height growth and number of branches per whorl shows that parents X and Z fulfilled those minimum criteria for both height growth and number of branches per whorl to be used in tandem selection. If only the branching was to be considered, then the parents Y and 209 that showed highly significant effects for this trait could also be taken into account for breeding (table 7; figure 12).

Because the SCA variance was much lower than the GCA variance and because it is much more difficult to capture, and also because it

becomes less important at later ages, for the moment it will not be used in the programme.

Conclusions

A high genetic variation was found in number of branches per whorl and growth traits, indicating that selection within Swiss stone pine could be applied effectively.

General combining ability variances of the two main traits were much higher than specific combining ability ones, suggesting that the breeding programme should be based on additive variance.

The highly significant variation in general combining ability effects for growth and branching traits found in two of ten trees tested, suggested that enough good combiners to be used for both current planting programmes and for advanced breeding populations could be selected within the parent population.

Narrow-sense heritabilities at both family and individual tree level progressively increased with age for growth traits, indicating that the breeding programme could be successful.

The strong age-age genetic correlations at the additive level for branching and growth traits clearly suggest that early selection may be efficient.

The high trait-trait genetic correlations between height growth and number of branches per whorl suggest that indirect selection may be applied.

The trends of heritabilities and age-age correlations indicate that optimum selection age could be as early as six for height growth.

The genetic parameter estimates obtained in this study should help to make selection decisions for a better development of the current breeding programme.

High genetic gain in branching and growth traits could be obtained if the improved material is used in operational planting programmes.

This paper, together with the previously published one (Blada 1999), define the first quantitative genetic characterization of *Pinus cembra* and therefore makes a significant contribution to the literature.

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Rezumat. Blada I., Popescu F., 2008. Încrușări dialele la *Pinus cembra*: IV Tendința parametrilor genetici în funcție de vârstă și câștigul genetic pentru caracterele de creștere și ramificație *Ann. For. Res.* 51:93-116

Această comunicare prezintă rezultatele unei încrușări complet dialele de tipul 10 x 10 efectuate într-o populație de zămbru (*Pinus cembra* L.) din Carpații sudici.

La vârsta de șase ani, după testul de pepinieră, materialul a fost plantat în teren, într-o singură stațiune, folosind dispozitivul blocurilor complet randomizate compus din 100 familii, patru repetiții și 15 puiți pe repetiție la distanța de 2.5 x 2.5 m.

Creșterea totală și anuală în înălțime, diametrul la colet, numărul ramurilor pe verticil și supraviețuirii au fost caracterele evaluate la vârste succesive cuprinse între opt și 14 ani considerând și anul însămănțării. În plus, anumite

caractere care au fost măsurate în testul de pepinieră au fost utilizate în calculul corelațiilor și alte analize.

Mediile parcelor unitare (repetiții) a caracterelor măsurate au fost analizate statistic folosind Programul DIALL elaborat de Schaffer și Usanis (1969).

Pe parcursul perioadei de testare din teren au fost puse în evidență diferențe semnificative ($p < 0.05$) și foarte semnificative ($p < 0.01$; $p < 0.001$) la creșterea totală în înălțime și diametrul la colet în privința capacității generale și specifice de combinare precum și pentru interacțiunile efectelor materne.

Aceste rezultate sugerează că respectivele caractere sunt controlate de gene nucleare (aditive și neaditive) precum și de interacțiunile genelor nucleare x extranucleare.

Într-o alură ascendentă, varianța aditivă, exprimată în procente din varianța genetică totală, variază între 35% la vârsta de opt ani și 66% la vârsta de 14 ani pentru creșterea totală în înălțime în timp ce varianța diametrului la colet are un interval de variație mai mic, adică între 16% și 34%. Într-o alură descendentă, raportul de dominanță $\sigma^2_{CSC}/\sigma^2_{CGC}$ pentru creșterea totală în înălțime a variat între 0.9 la vârsta de opt ani și 0.3 la cea de 14, sugerând că varianța aditivă ar trebui utilizată în programul de ameliorare.

Cu o singură excepție, pentru toate caracterele au fost identificați părinți cu efecte semnificative pentru capacitatea generală de combinare.

Pentru creșterea totală în înălțime, valorile eredității în sens restrâns la nivel de familie au variat într-o alură ascendentă între 0.45 și 0.65 în timp ce valorile eredității în sens restrâns la nivel de individ a oscilat de la an la an într-o manieră neregulată între valorile 0.31 și 0.37.

La vârsta de 14 ani, selectând cele mai performante 20 familii și cei mai performanți 20% indivizi în interiorul familiilor, este posibilă realizarea unui câștig genetic la creșterea totală în înălțime de 9.7% și respectiv 10.9%.

Ameliorarea creșterii și a numărului de ramuri utilizând atât selecția la nivel de familie cât și la nivel de individ, ar putea fi aplicată.

Existența corelațiilor genetice vârstă-vârstă și caracter-caracter sugerează că atât selecția timpurie cât și cea indirectă pot fi aplicate cu succes.

Cuvinte cheie: *Pinus cembra*, încrucișare dialelă, varianța aditivă, raportul de dominanță, efecte genetice, corelații genetice, eritabilitatea, selecția timpurie, selecția indirectă, câștigul genetic.

(Tradus de I. Blada)