Table 6. — Absolute allelic frequencies in paternal contribution — SV: Serreyrede forest; PF: Plo-du-Four forest.

Mother-trees	MDH1		IDH1		
	100	120	84	100	116
SV1	120	31	8	153	11
SV2	59	23	7	63	12
SV3	60	7	3	60	6
SV4	14	12	0	21	7
SV5	21	4	3	18	4
SV6	16	6	1	18	2
SV7	16	8	1	23	0
SV8	21	8	0	25	4
SV9	16	9	1	17	7
SV10	20	11	0	31	0
Total T4	363	119	24	429	53

$\chi^2 = 21.51 \ (p<0.005)$ $\chi^2_{(1)}=14.55 \ (p<0.05)$

	MDH1		IDH1		
PF1	101	82	12	167	14
PF2	18	12	5	20	5
PF3	18	4	0	21	1
PF5	4	5	2	8	0
PF6	16	15	0	30	2
PF7	14	9	1	19	3
PF8	22	3	0	27	0
PF9	26	8	3	27	1
PF10	11	13	4	22	3
Total T5	230	138	27	341	29

$\chi^2 = 22.01 \ (p<0.01)$ $\chi^2_{(1)} = 8.91 \ \text{n.s.}$

$\chi^2_{(1)}$: Calculation was carried out grouping the two rarest alleles and excluding classes whose size was smaller than 4.

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Within- and Between-Population Variation in Growth of Pinus contorta var. latifolia: A Combined Study of Growth-Chamber and Field-Trial Experiments

By I. B.-J. Jiang[1]), A. Jonsson and G. Eriksson

Department of Forest Genetics,
Swedish University of Agricultural Sciences,
Box 7027, S-750 07 Uppsala, Sweden

Summary

Thirty-four plus trees of *Pinus contorta* var. *latifolia* were selected from four stands at the same latitude (60° N) in Yukon, Canada. Single-tree families from wind pollination were sown and grown in the growth chamber for four growth periods. Two levels of nutrient treatment (ordinary and stress) were applied from the second growth period and onwards. Plant height after each of the four growth periods, final stem diameters, green and oven-dry weights of the

¹) Current address: Department of Forest Science, University of Alberta, Edmonton Alberta T6G 2H1, Canada.

above-ground part, and frequencies of polycyclic plants were investigated. In analyses of variance, nutrient-treatment effects were significant in most traits. Seedlings from ordinary treatment had a much higher frequency of polycyclic shoots than those from stress treatment. The same families were also planted in a field trial in northern Sweden and plant height at age 6 was measured. Only 2% of the total variation in the field trial could be explained by the within-stand effect in contrast to 20% in the growth chamber. The relationships between results from the growth-chamber and field-trial studies, expressed as ordinary linear regressions and Pearsonian correlations, were weak. However, the plant biomass in the growth chamber showed significant correlations with plant height in the field trial.

Key words: Lodgepole pine, provenance, geographic variation, nutrient level, stress environment, contingency tables.

Zusammenfassung

Vierunddreißig Plusbäume von *Pinus contorta* var. *latifolia* wurden von vier Beständen von demselben Breitengrad, 60° N, in Yukon, Kanada, ausgewählt. Einzelbaumfamilien von Windbestäubung wurden in der Klimakammer ausgesät und wuchsen dort unter vier Wachstumsperioden. Es wurden zwei Stufen von Nährstoffbehandlungen (Normal und Streß) von der zweiten Wachstumsperiode an gewandt. Folgende Eigenschaften wurden untersucht: Pflanzenhöhe am Ende jeder der vier Wachstumsperioden, endgültige Stammdurchmesser, Frisch- und Ofentrockengewicht der oberirdischen Pflanzenteile und Frequenz von polyzyklischen Pflanzen. In den Varianzanalysen waren die Effekte durch die Nährstoffbehandlung für die meisten Eigenschaften signifikant. Die Sämlinge der Normalbehandlung zeigten eine höhere Frequenz von polyzyklischen Trieben als die Sämlinge der Streßbehandlung. Die gleichen Einzelbaumfamilien wurden auch in einem großen Feldversuch in Nordschweden gepflanzt und die Pflanzenhöhe im Alter von 6 Jahren wurde gemessen. Nur 2% der gesamten Variation im Feldversuch konnte durch Effekte innerhalb der Bestände erklärt werden, im Gegensatz zu 20% im Klimakammerversuch. Zwischen den Resultaten von der Klimakammer und dem Feldversuch gab es schwache Beziehungen, ausgedrückt als gewöhnliche lineare Regressionen und Pearson-Korrelationen. Doch waren die Korrelationen zwischen der Pflanzenbiomasse in der Klimakammer und der Pflanzenhöhe im Feldversuch signifikant.

Introduction

In recent years, *Pinus contorta* (lodgepole pine) has become a common reforestation species in northern Sweden. An intensive *Pinus contorta* improvement program is in progress in Sweden (ROSVALL, 1980). In nature, *Pinus contorta* forests exhibit considerable structural variability (FAHEY and KNIGHT, 1986). It has been well documented that the genetic variation in morphology and growth habit at the provenance level is large (for a review, see CRITCHFIELD, 1980; for recent works, see WHEELER and GURIES, 1982; LINDGREN, 1983; WHEELER and CRITCHFIELD, 1985; YING et al., 1985).

Three are reports of highly significant differences between provenances in annual rhythm (HAGNER, 1970); large between- and within-provenance differences in seed quality (HAGNER, 1980); extensive allozyme variation associated with geography (YEH et al., 1985); and variation in height and dry weight among families within populations considerably larger than that between populations in a greenhouse study (PERRY and LOTAN, 1978). FRIES (1986) and FRIES and LINDGREN (1986) reported that variation in single-tree families within populations was larger than that between populations in nine- and ten-year tree heights respectively whereas REHFELDT (1985) noted the reverse in six-year tree height. Relative proportions of variances reflect the range of sampling and relative sampling size (i.e. degrees of freedom) among sources of variation. For instance, the relative proportion of the genetic variation between and within populations is expected to vary from a range-wide provenance study to a study comprising a few adjacent provenances. For breeding, the relation of within- and between-population variation for stands from one climatic zone is of interest and has not to our knowledge been reported.

Pinus contorta has been subdivided into "coastal" and "interior", or more detailed sub-species (CRITCHFIELD, 1957; 1980). Most coastal sources did not survive and grow well in the harsh continental climate of northern Sweden. The present work was undertaken to study the genetic variation in growth performance of seedlings in the growth chamber and in a field trial. The seed lots used in the study originated from the same latitude, but from different natural stands of the northern Rocky Mountain-Intermountain source representative of seven degrees of longitudinal range. We have applied two nutrient treatments in the growth-chamber experiment to study the potential effects of genotype × environment interaction, and thus to study whether the two treatments differ in their predictive power.

LAMBETH et al. (1983) proposed that plant dry weight should be used as an early-testing character in *Pseudotsuga menziesii*. In the present study several traits were assessed to identify those suitable for predicting field performance.

The objectives of the research reported here are:
1) To investigate variation in juvenile growth in a growth chamber, of single-tree progenies selected from one latitude.

2) To investigate the genotype × nutrient-treatment interaction by applying two different levels of nutrient in the growth-chamber experiment.

3) To investigate the performance at early age of selected single-tree progenies in harsh environmental condition in nature.

4) To investigate the possibility of extrapolating from growth-chamber results to plants growing in the field.

In this paper, we shall lay emphasis upon the growth-

Table 1. — The four stands in the study.

Stand		No. of trees	Latitude	Longitude	Elevation (m)	Note
Simpson Lake	(SL)	9	60°50′	129°15′	775	
Canol Road	(CR)	9	60°40′	133°02′	850	
Champagne	(CP)	8	60°50′	136°32′	900	An isolated stand (2 hectares)
Whitehorse	(WS)	8	60°35′	134°45′	780	

Table 2. — Regimes in the growth chamber. The maximum and minimum values for each period are given.

Period	Night length	Day/Night temperature	Weeks
First Growth Period			
Sowing - transplantation	4 h	20°C	2
Growth - growth cessation	4 h	25/15°C	3
	gradual prolongation 4.5 - 16 h	25/10°C, 10/5°C (several noon peaks with 30°C)	16
Dormancy and dormancy breaking	16 - 24 h	10/5°C, 2°	5
Second to fourth growth periods			
Growth - growth cessation	gradual prolongation 2.5 - 16 h	20/10°C, 10/5°C (several noon peaks with 23°C)	18
Dormancy and dormancy breaking as above			

chamber experimental data, because more characters were investigated there than in the field trial.

Material and Methods

Seed Lots

The material studied came from the Swedish *Pinus contorta* selection project (BARTRAM, 1979). Open-pollinated seeds were collected from phenotypical plus-trees in various stands of *Pinus contorta* var. *latifolia* in Yukon, Canada. The plus trees were located at nearly the same latitude, but from a range of seven degrees in longitude. Detailed information about the stands studied is shown in *Table 1*.

The Growth Chamber Experiment

The study was carried out in the growth chamber of the phytotron at the Swedish Universiity of Agricultural Sciences in Stockholm, Sweden. The seeds were sown in a mixture of sand and vermiculite. After germination the seedlings were grown in boxes on mobile trolleys (wagons) of size 470 mm × 400 mm × 100 mm. The substrate was granulated mineral wool. A 25 mm layer of gravel at the bottom of the boxes served for drainage, a 15 mm layer of gravel at the top of the substrate kept the surface dry and free from algae.

Thirty-two plants from each of the 34 families were studied. They were grown in 38 boxes, each taking 30 plants (5 × 6) some of which served as filling. In each box, two adjacent plants belonged to the same family (two-tree plots).

Two nutrient treatments were applied in this study. During the first growth period all the plants were treated with a complete nutrient solution (INGESTAD, 1979) of low concentration (100 mg N/1). The proportions of N:K:P were 100:65:13. From the beginning of the second growth period one half of the plants received reduced amounts of nutrients and water (stress), the other half received the ordinary treatment (ordinary). Each box received one treatment only. For stressed plants, nutrient solution of a concentration lower than in the ordinary treatment was given only when the plants showed signs of wilting or the tensiometers in the boxes showed low values. Each box under stress treatment did not receive equal amounts of nutrient solution.

A systematic thinning was applied after the second growth period, leaving one plant of each pair (single-tree

plots) and reducing the plant number per family and treatment from 16 to 8 plants in eight different boxes.

The air humidity was kept at 75 per cent relative humidity. The light intensity at seedling level was 22,000 lux (70W.m², 270 nm to 695 nm).

The cultivation regime (*Table 2*) during the first growth period mimicked conditions in a nursery in northern Sweden while the cultivation regimes during the second to the fourth growth periods mimicked conditions at a field trial located about two degrees northwards of the nursery (see next section). Both night lengths and temperatures changed gradually during each growth period.

Traits evaluated in the growth-chamber experiment were: plant height at the end of four growth periods, number of plants with polycyclic annual shoots during the second, third, and fourth growth periods, stem diameter at basal and second-whorl levels at the end of the fourth growth period, and green and oven-dry weight of the above-ground biomass at the end of the fourth growth period.

Field Trial

A field trial of selected *Pinus contorta* material was established in 1981 at Mader, northern Sweden (Lat. 65°48', Long. 19°00', Alt. 490 m). It contains seed lots from 18 stands in Canada, among them the four stands studied in the growth-chamber experiment.

The 18 stands and four checker seed lots were randomized in each of the five blocks. Within each stand, individual seed trees were distributed at random in 10-tree row plots. According to the original design, 10 seedlings of each of the 12 seed trees in each of the 18 stands ought to be planted in each block. However, owing to the small size of the stand Champagne, only six trees were selected. Thus, each of the six seed trees from Champagne was represented by 20 sedlings in each block. In autumn 1986 the total plant height was assessed in the field trial. Four stands studied in our growth-chamber were sampled from the 18 stands for measurements. By the time of assessment in 1986, around 13% of the trees measured were dead. Seriously damaged trees were excluded from the statistical analysis.

Statistical Procedure

A computer package program from SAS (Statistical Analysis System) was used for the statistical analysis (SAS Institute, Inc., 1985). Two kinds of estimates of variance com-

ponents, Henderson's method III and the restricted maximum likelihood method, were applied in both growth-chamber and field-trial data sets. When no exact F-test was available for one or more factors in the design model, the pseudo-F test was applied (Hicks, 1973), which is an approximation to the F test.

1. Growth Chamber Experiment

For data taken from the first two growth periods, plot means were used as the unit for analysis. After thinning at the end of the second growth period, the experimental design became single-tree plots. Individual plants were therefore used as the unit for analysis.

Variances were not homogeneous between the two treatments in the growth chamber. Furthermore, variances were compared among stands within each treatment using Hartley's F(max) test of homogeneity of variance (Ott, 1977). In general, the standard deviations changed in proportion to the means. We therefore transformed the original data to natural logarithms to satisfy the assumption of equal variances for the analysis of variance (Scheffe, 1959).

For binomial data such as number of plants with polycyclic annual shoots (Lanner, 1976) Bernoulli trials were applied first to test the hypothesis of equal probabilities of equal frequencies of polycyclic plants between the two nutrient treatments (Larsen and Marx, 1981). The null hypothesis was rejected whenever the statistic

$$\frac{\dfrac{x}{n} - \dfrac{y}{m}}{\sqrt{\dfrac{\left(\dfrac{x+y}{n+m}\right)\left(1 - \dfrac{x+y}{n+m}\right)(n+m)}{nm}}} \quad \text{either} \quad \begin{cases} \leq -z_{\alpha/2} \\ \geq +z_{\alpha/2} \end{cases}$$

where x is the number of polycyclic plants in the ordinary treatment, y is the number of polycyclic plants in the stress treatment, and n and m are the total number of plants in the ordinary and stress treatments, respectively. Second, we also applied the log likelihood ratio test (Sokal and Rohlf, 1981) to analyze the three-way contingency table of the frequencies of polycyclic shoots of four stands under the two nutrient treatments. The analysis is to test whether the proportion of polycyclic plants is independent of the stand origin and nutrient treatment. Since our sample size is at least ten times the number of cells in the contingency table (Fienberg, 1977), the G-statistics have approximate Chi-square distributions.

$$G = 2 \Sigma \, (observed) \, \log_e \left(\frac{observed}{expected}\right)$$

We also took away one factor in the rows at a time to check the change of the G-statistic and probability. The G-values were then compared to find the potential impact, if any, of each stand.

Log-transformed data were analyzed according to the linear model:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_{k(j)} + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik(j)} + W_{l(i)} + e_{ijkl}$$

where

Y_{ijkl} = individual observation
μ = grand mean
α_i = nutrient-treatment effect, i = 1, 2.
β_j = stand effect, j = 1, 2, 3, 4.
$\gamma_{k(j)}$ = single-tree-family effect within each stand, k = 1, 2 .... 8 or 9.
$(\alpha\beta)_{ij}$ = interaction between nutrient treatment and stand
$(\alpha\gamma)_{ik(j)}$ = interaction between nutrient treatment and single-tree family
$W_{l(i)}$ = box (wagon) effect within each treatment, l = 1, 2, 3, ... 19.
e_{ijkl} = residual error

The nutrient effect was considered as fixed, and stands and families-within-stands as random effects. The estimation of variance components did not include nutrient-treatment effect. Structures of the expected mean squares of the design model are presented in *Table 3*.

Posterior-comparison procedures, Duncan's multiple-range test and Tukey's HSD were applied to compare means of the four stands.

Table 3. — Structure of the analysis of variance of data set in growth chamber.

Source	D.F.	Expected mean squares
Treatment	1	$\sigma^2_E + K_1 \cdot \sigma^2_{W(T)} + K_2 \cdot \sigma^2_{F(S) \times T} + K_3 \cdot \sigma^2_{S \times T} + K_4 \cdot \sigma^2_T$
Stand	3	$\sigma^2_E + K_5 \cdot \sigma^2_{F(S) \times T} + K_6 \cdot \sigma^2_{F(S)} + K_7 \cdot \sigma^2_{S \times T} + K_8 \cdot \sigma^2_S$
Stand × T	3	$\sigma^2_E + K_9 \cdot \sigma^2_{F(S) \times T} + K_{10} \cdot \sigma^2_{S \times T}$
Family (S)	30	$\sigma^2_E + K_{11} \cdot \sigma^2_{F(S) \times T} + K_{12} \cdot \sigma^2_{F(S)}$
Family (S) × T	30	$\sigma^2_E + K_{13} \cdot \sigma^2_{F(S) \times T}$
Wagon (T)	36	$\sigma^2_E + K_{14} \cdot \sigma^2_{W(T)}$
Error	431	σ^2_E

Note: The coefficients, K_i, are not constant integers owing to imbalance of the design. Error degree of freedom changes over time.

$$\text{Individual-tree heritability} = \frac{4 \; \sigma^2_{F(S)}}{\sigma^2_E + \sigma^2_{W(T)} + \sigma^2_{F(S) \cdot T} + \sigma^2_{F(S)} + \sigma^2_{S \cdot T} + \sigma^2_S}$$

Source	D.F.	Expected mean squares
Block	4	$\sigma^2_E + K_1 \cdot \sigma^2_{F(S) \times B} + K_2 \cdot \sigma^2_{S \times B} + K_3 \cdot \sigma^2_B$
Stand	3	$\sigma^2_E + K_4 \cdot \sigma^2_{F(S) \times B} + K_5 \cdot \sigma^2_{S \times B} + K_6 \cdot \sigma^2_{F(S)} + K_7 \cdot \sigma^2_S$
Family (S)	30	$\sigma^2_E + K_8 \cdot \sigma^2_{F(S) \times B} + K_9 \cdot \sigma^2_{F(S)}$
Stand × Block	12	$\sigma^2_E + K_{10} \cdot \sigma^2_{F(S) \times B} + K_{11} \cdot \sigma^2_{S \times B}$
Family (S) × Block	112	$\sigma^2_E + K_{12} \cdot \sigma^2_{F(S) \times B}$
Error	1412	σ^2_E

Note: The coefficients, K_j, are not integers owing to imbalanced data set.

$$\text{Individual-tree heritability} = \frac{4 \, \sigma^2_{F(S)}}{\sigma^2_E + \sigma^2_{F(S) \times B} + \sigma^2_{S \times B} + \sigma^2_{F(S)} + \sigma^2_S}$$

2. Field Trial

Analysis of variance was applied according to the linear model:

$$y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_{k(j)} + (\alpha \beta)_{ij} + (\alpha \gamma)_{ik(j)} + e_{ijk}$$

where

Y_{ijk} = individual observation
μ = grand mean
α_i = block effect, i = 1, 2, 3, 4, 5
β_j = stand effect, j = 1, 2, 3, 4.
$\gamma_{k(j)}$ = single-tree-family effect within each stand, k = 1, 2 .... 8 or 9.
$(\alpha \beta)_{ij}$ = interaction between block and stand
$(\alpha \gamma)_{ik(j)}$ = interaction between block and single-tree family
e_{ijkl} = residual error

In the above model, all the effects are considered as random effects. Structures of the expected mean squares of the design model are presented in *Table 4*. DUNCAN's multiple-range test and TUKEY's HSD were applied for posterior comparisons of means of the four stands.

Table 5. — Mean value, standard error of the means and coefficient of variation of traits measured at the end of the growth-chamber experiments.

Traits	Ordinary treatment		Stress treatment	
	Mean	C.V.	Mean	C.V.
Plant height (mm)				
1st-Growth Period	46.55 ± 1.02	35.94	46.76 ± 0.96	33.80
2nd-Growth Period	184.78 ± 3.05	27.01	154.14 ± 2.38	25.50
3rd-Growth Period	380.77 ± 5.60	24.11	249.21 ± 3.40	22.52
4th-Growth Period	563.31 ± 9.31	27.15	412.54 ± 5.16	20.64
Traits measured at the end of the experiment				
Green weight (g)	134.18 ± 5.82	71.28	78.77 ± 2.39	50.04
Oven-dry weight (g)	44.50 ± 1.99	73.33	25.36 ± 0.81	52.64
Stem diameter (mm) (Basal level)	12.46 ± 2.56	33.74	9.10 ± 1.37	24.82
Stem diameter (mm) (2nd-whorl level)	5.93 ± 1.28	34.96	4.99 ± 0.55	18.22

3. Relationships between Growth-chamber and Field-trial Data Sets

Ordinary linear regression analysis (GUNST and MASON, 1980) was applied to transpose growth-chamber results to the field trial. Single-tree-family means were used as units in the regression analysis. In the present study, only plant height in the field trial was available as response variable, while many characters investigated in the growth-chamber experiment were used separately as single-predictor variables. Pearsonian correlations were calculated to determine the degree of association found in the regression analysis. The significance of the difference between two values of correlation coefficient obtained from two treatments was tested by transforming correlation coefficients to the Z distribution (SOKAL and ROHLF, 1981).

4. Estimation of Heritabilities

Half-sib relationship is assumed in our experimental seed lots, which is a simplified assumption. This was extensively discussed by FRIES and LINDGREN (1986). Individual-tree narrow-sense heritabilities were calculated according to the formulae in *Tables 3* and *4*.

Results and Discussion

1. Growth Chamber Experiment

Nutrient-Treatment Effects

All growth characters were strongly affected by nutrient treatments (*Table 5*). Nutrient-treatment effects were statistically significant except for biomass characters (*Table 6*) although *Figure 1* demonstrates that the effect of nutrient treatment on green weight was pronounced. One reason for the non-significant results for nutrient-treatment effects on biomass traits might be that the statistical tests of treatment effect were based upon the pseudo-F test of which the error term was a linear combination of mean squares (HICKS, 1973). In our case, one of the mean squares was substracted in the linear combination, i.e. the coefficient was negative. GAYLOR and HOPPER (1969) cautioned against the use of the pseudo-F test under this condition. However, the low P-values for nutrient-treatment effects on green and dry weights (0.15 and 0.14, respectively) also indicated that there are nutrient-treatment effects.
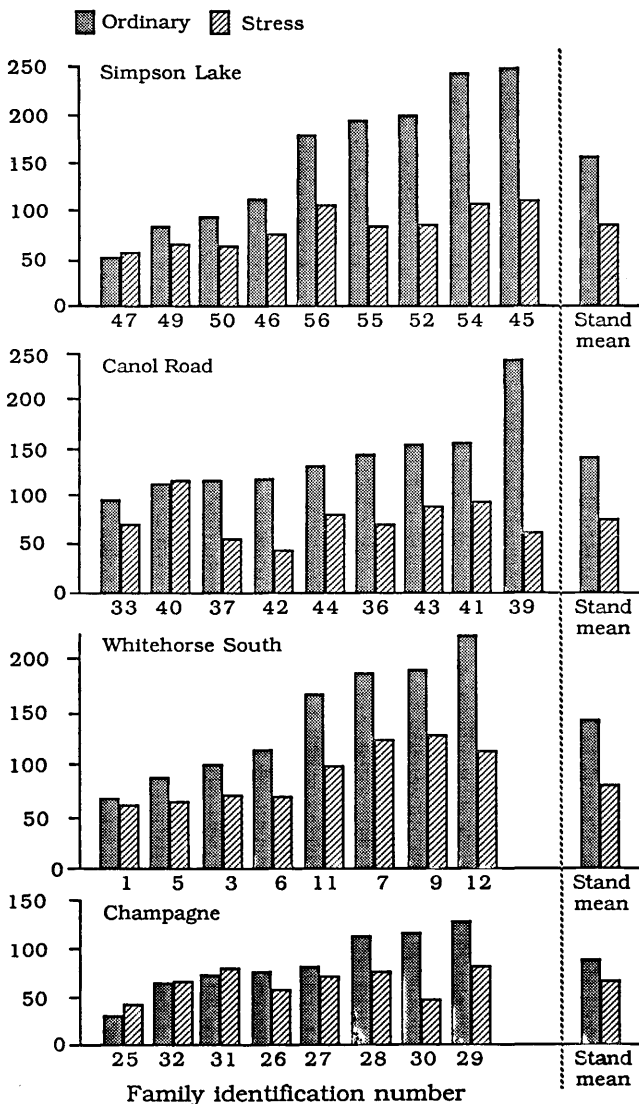
Figure 2 shows that the frequency of plants with polycyclic shoots was higher in the ordinary treatment than in

Table 6. — Mean squares and P-values from the analysis of variance of the growth-chamber experiment based on logarithmically transformed data.

Source		1st-GP			2nd-GP			3rd-GP		4th-GP	
	D.F.	Height M.S.	P-value	D.F.	Height M.S.	P-value	D.F.	Height M.S.	P-value	Height M.S.	P-value
Treatment	1	-	-	1	3.69	0.01	1	22.67	0.0001	11.72	0.01
Stand	3	0.19	0.69	3	0.53	0.25	3	0.78	0.10	0.97	0.08
Stand x T.	3	-	-	3	0.09	0.31	3	0.07	0.27	0.12	0.08
Family (S)	30	0.35	0.66	30	0.34	0.001	30	0.29	0.0001	0.29	0.0001
Family (S)xT.	30	-	-	30	0.08	0.30	30	0.05	0.39	0.05	0.50
Wagon (T)	36	0.16	0.30	36	0.08	0.19	36	0.07	0.07	0.05	0.58
Error	431	0.14		426			431	0.05		0.05	

Source	D.F.	Green weight M.S.	P-value	Oven-dry weight M.S.	P-value	Basal stem diameter M.S.	P-value	2nd-whorl stem diameter M.S.	P-value
Treatment	1	18.13	0.15	19.70	0.14	10.52	0.02	1.03	0.03
Stand	3	5.46	0.18	5.50	0.19	0.88	0.24	0.28	0.35
Stand x T.	3	1.26	0.11	1.23	0.14	0.23	0.10	0.03	0.96
Family (S)	30	2.11	0.0003	2.29	0.0003	0.42	0.0001	0.31	0.34
Family (S)xT.	30	0.57	0.23	0.63	0.23	0.10	0.36	0.27	0.02
Wagon (T)	36	0.21	0.999	0.26	0.995	0.06	0.94	0.25	0.04
Error	431			0.53		0.10		0.17	

Final biomass, above-ground green weight, g

■ Ordinary ▨ Stress

Family identification number

Figure 1. — Thirty-four family means of green weight in the growth-chamber study

the stress treatment during all growth periods. The significance of the treatment effect is evident from the log likelihood ratio test summarized in Table 7. Bernoulli trials showed high Z values for the three growth periods (10.616, 8.655, 5.761, respectively), which also confirms the effect of treatment.

Polycyclic shoots are usually found on fast-growing trees in nature (LANNER and VAN DEN BERG, 1975). This might be one reason for the low frequency of polycyclic plants from the stress treatment. In a study of four-year-old Pinus-contorta REHFELDT (1983) reported that 87% of seedlings grown at low elevation (750 m) produced polycyclic shoots, in contrast to none at high elevation (1,500 m). In REHFELDT's study the difference between seedlings grown at low and high elevation was large (113 cm vs. 26 cm in final height). In a nursery study of Pinus contorta (FRANKLIN and CALLAHAM, 1970) most seedlings were monocyclic in the first and second growing seasons. In the third to fifth growing seasons almost all seedlings produced polycyclic shoots. O'REILLY and OWENS (1985) reported that the average percent of polycyclic shoots increased to a maximum at the third year, then decreased in the fourth year in provenances from British Columbia and Yukon.

Between-stand Differences

Multiple comparison procedures (DUNCAN's multiple-range test and TUKEY's HSD) showed that stand Champagne was always significantly different from the other three stands even if there was no significant stand effect in the overall test of the analysis of variance (cf. MEAD and CURNOW, 1983). We therefore assume that there is a difference between stand Champagne and the three other stands. The reason for the difference between stand Champagne and others might be that it is small and isolated from the nearest neighboring stands of pine (BARTRAM, 1979). In a provenance study including 34 natural stands from southern Rocky Mountains, MOORE (1984) found

Table 7. — Log likelihood ratio test of the frequencies of polycyclic shoots.

Tests	D.F.	2nd-growth period		3rd-growth period		4th-growth period	
		G	Probability	G	Probability	G	Probability
1. Four stands and two treatments are included	7	136.98	0.00*	81.93	0.00*	42.10	0.00*W
2.1 Four stands in 'Stress' treatment	3	2.02	0.57	2.05	0.56	2.66	0.44W
a. Stand 'CP' is excluded	2	0.41	0.82W	0.05	0.97W	2.14	0.34W
b. Stand 'CR' is excluded	2	1.43	0.49	1.65	0.44	2.02	0.37W
c. Stand 'SL' is excluded	2	1.53	0.47	1.73	0.42		-N
d. Stand 'WS' is excluded	2	1.99	0.37	1.99	0.37	2.12	0.35W
2.2 Four stands in 'Ordinary' treatment	3	2.60	0.46	8.18	0.04*	0.15	0.99
a. Stand 'CP' is excluded	2	2.46	0.29	5.45	0.07*	0.10	0.95
b. Stand 'CR' is excluded	2	2.47	0.29	7.79	0.02*	0.10	0.95
c. Stand 'SL' is excluded	2	1.03	0.60	0.68	0.71	0.10	0.95
d. Stand 'WS' is excluded	2	0.98	0.61	8.04	0.02*	0.10	0.95

W: More than 50% of the cells have expected values less than 5. Chi-square may not be valid.
N: Not testable since none of the plants showed polycyclic shoots.
*: Significant at the 5% level.

clinal latitudinal effects of seed source on growth pattern, but no clear elevational effects. Our stands, however, originated from a northern area; the potential impact of elevational difference might be pronounced. RrHFELDT and WYKOFF (1981) and REHFELDT (1985) found in northern Rocky Mountains studies that elevation accounted for approximately three times as much variance in shoot elongation as geography. LINDGREN (1983) and FRIES (1986) stressed that there is a reduced growth of trees originating above 800 m from this part of Canada, which is in agreement with the inferior performance of the Champagne stand from 900 m. Thus, a combination of strong selection at this altitude and genetic drift might have broadened the difference between this stand and others.

Table 7 shows that stand differences in frequency of polycyclic shoots were significant only for ordinary treatment in the third growth period. In natural stands, polycylic shoots are common, but there is no obvious difference between coastal and interior localities (CRITCHFIELD, 1980). In a progeny-trial study including provenances from northern British Columbia and Yukon, FRIrs and LINDGREN (1986) found no significant difference between areas of origin. O'REILLY and OWENS (1985) found large differences between provenances. Their report did not mention whether or not this difference could be related to the origin of the provenances. Our data suggest that for the occurrence

of polycyclic shoots the environmental factor (nutrient regime) is much more important than the genetic factor (stand).

Within-stand Differences

Table 6 shows that family-within-stand effects are statistically significant for green and dry weights and plant height from the second growth period onward. This agrees with other observations on conifers (eg. ERIKSSON, 1982; FRIES and LINDGREN, 1986; JONSSON et al., 1986; FRIES, 1986).

The relative proportions of the variance components of four-year plant height in the growth chamber are shown in Figure 3. The figures were obtained by the restricted maximum likelihood method which gave almost identical estimates to those of HENDERSON's method III. The calculated individual tree heritability amounts to over 0.8 which is an extremely high value. For open-pollinated progeny tests such as ours, the common assumption that the seeds collected from a single tree have a half-sib relationship is usually invalid. Therefore, any uncounted error such as full-sibling, inbreeding, and maternal effects present in the within-stand term would be inflated by the multiplier term (eg. LOWE et al., 1982). Our stands originated from the same latitude, which means that the relative variance component of the stands is small. Furthermore, the growth chamber environment is quite homogeneous. These com-

Percentage of polycyclic plants
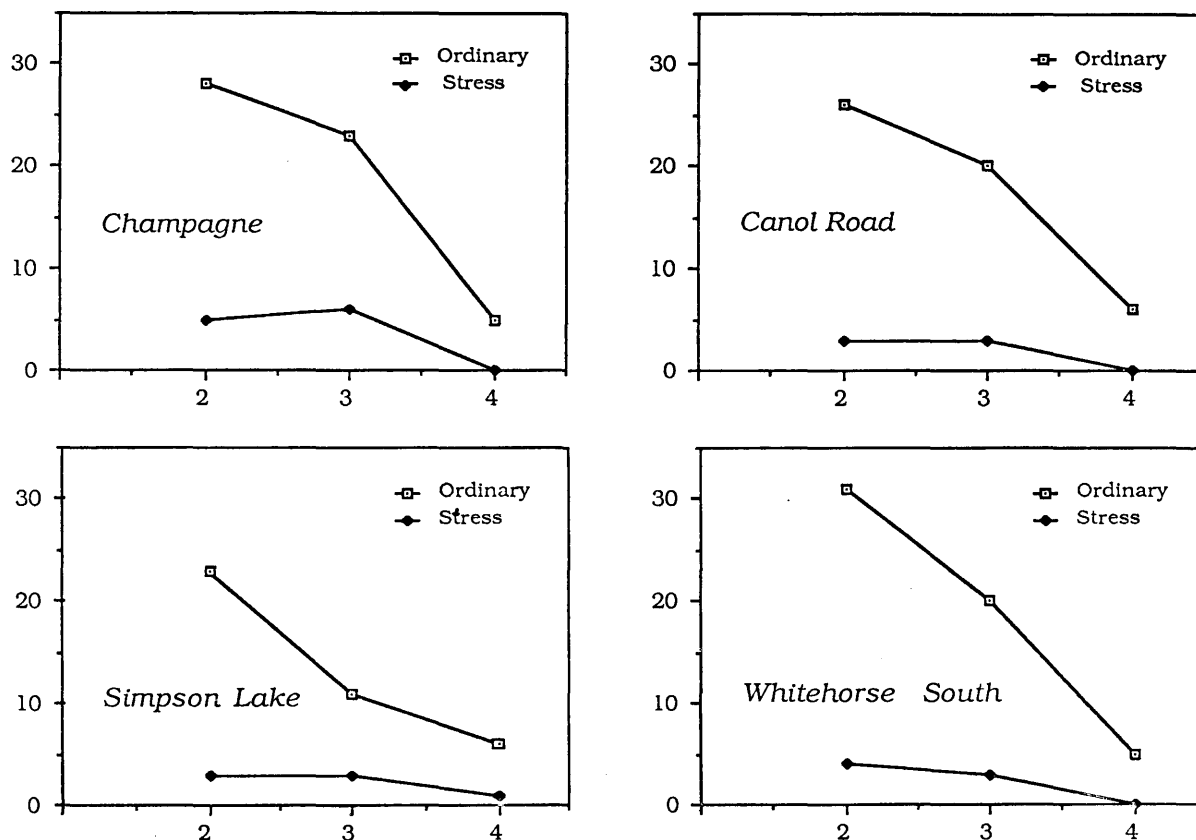
Growth periods in growth chamber

Figure 2. — Frequency of plants with polycyclic shoots during different growth periods in the growth chamber.

bined effects might explain the unusually high value for the heritability.

The log likelihood ratio test could not be run at the family level because most cells contain less than 5 observations of polycyclic plants. No conclusions could therefore be drawn about the family difference in the character although some families showed different growth patterns.

The variation patterns in natural populations is determined by the properties of the genetic system and the kind of environmental variation (STERN and ROCHE, 1974). For long-lived tree species, such as *Pinus contorta*, environment heterogeneous in time is usually taken as the explanation of the genetic variation within populations. But ENNOS (1983) argued that temporal variation in the direction of selection should not be taken as the sole explanation for maintenance of genetic variation. He further stressed that the demography, the mating system, and the amount of gene flow in natural populations are important factors for maintaining the genetic variation within populations.

Interaction

With one exception, i.e. the second-whorl stem diameter, the analysis of variance did not show any significant interaction either at the stand or at the family level (cf. *Table 6*). The lack of significant genotype $\times$ treatment interactions suggests that the genetic entries do not respond differently to nutrient levels.

2. Field Trial

Table 8 shows the results from the analysis of variance. There is clearly significant genetic variation of families within stands, which is in agreement with the results from the growth-chamber experiment, from which we also found larger variation within than among stands. The variance components for family effect, however, accounted for only two percent of the total variation (cf *Figure 3*).

The results from the field trial must be interpreted with caution since this trial has not yet passed the phase of establishment, which for pines in northern Sweden may last 20 years (cf EICHE and ANDERSSON, 1974).

Our analysis of the field trial is based upon a single-location data set. The estimate of additive genetic variance is therefore confounded with the genotype $\times$ environment interaction. In a study of 19 sites covering latitudes 56 to 67 throughout Sweden (IUFRO collections) LINDGREN et al. (1976) reported that there were no important provenance $\times$ site interactions in height growth after four growing seasons in field. After eight seasons a study of the same material showed that some provenances performed better in some sites than others (LINDGREN, 1983; 1984). The field trial in the present study is located in an extremely harsh area. In this area planting *Pinus contorta* is not allowed from the planting season 1988. The provenances used in this study might be too southern for the site. This could explain the low heritability in the field

trial. The significance and magnitude of potential genotype × environment interactions of our stands will be presented when data from more test sites are available.

3. Relationship between growth-chamber and field-trial performance

Table 9 shows the results from the linear regression analysis of the growth-chamber and field-trial data sets. Three main results are: 1) Among 16 P-values, seven are significant at or lower than the 5% level. Other P-values are also quite low, with one exceptional case which is higher than 0.5. This indicates a relationship between the growth-chamber and field-trial data sets. 2) Green, oven-dry weights, and basal stem diameter, show significant linear relationship with field-trial height. 3) Pairwise comparisons of the correlation coefficients between field and growth-chamber plant heights reveal that the ones from the ordinary treatment are always higher than the ones from the stress treatment. For other traits, the pattern is the opposite. This suggests that there are stress effects on the results. *Figure 4* shows the bi-variate plots for green weight in growth chamber and plant height in field trial.

It is worth pointing out that the coefficients of determination, R^2, of the linear regression model are in general quite low (from 0.013 to 0.238). The figures of the adjusted R^2, which always fall inside the confidence interval (HELLAND, 1987), are smaller and even negative in one case. The low coefficients of determination thus limit the conclusion that can be drawn from our regression analyses (GUNST and MASON, 1980). But in considering genetic gain from selection, the figures for the correlation coefficients presented in *Table 9* are of interest. The Pearsonian correlation coefficients were calculated on family means, which reflect an approximation of the true genetic correlations. The coefficients (0.37 to 0.49) imply a similar performance of the genetic entries in both growth-chamber and field conditions.

We have tested the difference between the two correlation coefficients for ordinary and stress treatments for the following traits: plant height at the end of the fourth growth period, green and oven-dry weights, and basal stem diameter. We could not reject the null hypothesis that there was no difference between the pair of correlation coefficients (P-values are 0.74, 0.67, 0.63, and 0.61, respectively). Thus, we have no evidence to differentiate the predictive power of the two nutrient treatments in growth-chamber experiment.

Final plant height in growth chamber
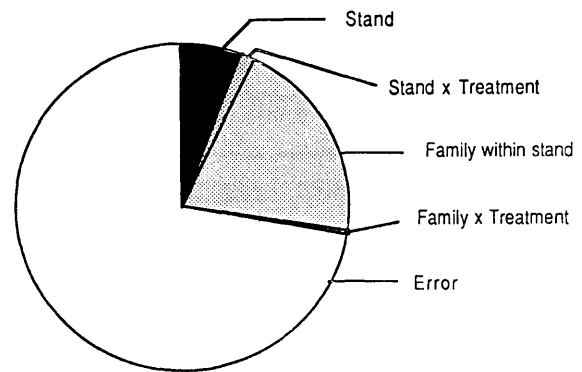
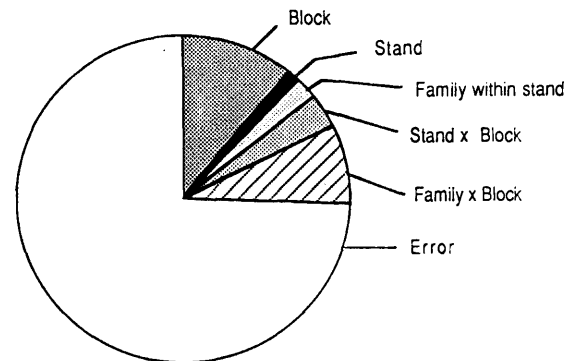### Plant height in field trial

Figure 3. — Variance component distribution (%) in growth chamber and field trial.

Conclusion

Our studies in both the growth chamber and the field trial show that the genetic variation within stands is larger than the variation between stands in the material from the same latitude. However, one of the stands studied, Champagne, is consistently ranked last and significantly different from the other three stands in our growth-chamber and field-trial studies. This might be due to the unique

Table 8. — Analysis of variance of tree height in the field trial.

Source	D.F.	Mean square	P-value	Variance component (%) Henderson's method III	Restricted maximum likelihood
Block	4	29274.44	–	11.0	11.2
Stand	3	7936.40	0.14	1.1	1.1
Family (Stand)	30	1992.44	0.04	2.0	2.3
Stand x Block	12	2980.84	0.009	2.9	3.2
Family (S) x Block	112	1252.69	0.0001	8.0	7.7
Error	1412	623.45		74.9	74.4

Note: "Family (S) × Block" includes plot error within blocks.

Table 9. — Linear relationships between growth-chamber traits and field-trial plant height.

(Field) Dependent variable	Total D. F.	(Growth chamber) Independent variable	Regression coefficient	P-value	Pearsonian correlation coefficient
Plant height	33	1st-GP height (O)	0.28 ± 0.16	0.096	0.29
"	33	" " (S)	0.14 ± 0.21	0.520	0.11
"	33	2nd-GP height (O)	0.10 ± 0.05	0.064	0.32
"	33	" " (S)	0.10 ± 0.07	0.154	0.25
"	33	3rd-GP height (O)	0.05 ± 0.02	0.051	0.34
"	33	" " (S)	0.08 ± 0.05	0.096	0.29
"	33	4th-GP height (O)	0.03 ± 0.01	0.032*	0.37
"	33	" " (S)	0.05 ± 0.03	0.097	0.29
"	33	Green-weight (O)	0.01 ± 0.002	0.021*	0.39
"	33	" " (S)	0.02 ± 0.006	0.004**	0.48
"	33	Oven-dry weight (O)	0.02 ± 0.01	0.024*	0.39
"	33	" " (S)	0.06 ± 0.02	0.004**	0.49
"	33	Stem diameter (O) (basal)	0.01 ± 0.006	0.044*	0.35
"	33	Stem diameter (S) (basal)	0.03 ± 0.01	0.006**	0.46
"	33	Stem diameter (O) (2nd-whorl)	0.01 ± 0.02	0.361	0.16
"	33	Stem diameter (S) (2nd-whorl)	0.04 ± 0.03	0.203	0.22

(O) = Ordinary treatment
(S) = Stress treatment
* = $p < 0.05$
** = $p < 0.01$

evolutionary history of the stand. Local differentiation between stands implies the need for the preservation of genetic variation between stands in breeding populations.

Among the characters evaluated in the growth-chamber experiment, the incidence of polycyclic shoots was found to be a trait influenced mainly by nutrient treatment. The lack of stand effects could be attributed to the climatically limited origin of the stands.

Plant height at the end of the fourth growth period, above-ground biomass, and basal stem diameter studied in the growth-chamber experiment showed significant but weak correlations with plant height in the field trial. The comparative results of the variance components estimation suggest that the growth-chamber environment is more able to differentiate among the genetic entries than the field trial. However, we need to wait for a longer time than just five years for reliable results from field trials to evaluate the relative efficiency of early testing in controlled environments.

Acknowledgements

Plant height in field trial, cm

Figure 4. — Bi-variate plot of green weight in growth chamber and plant height in field trial based on 34 family means.

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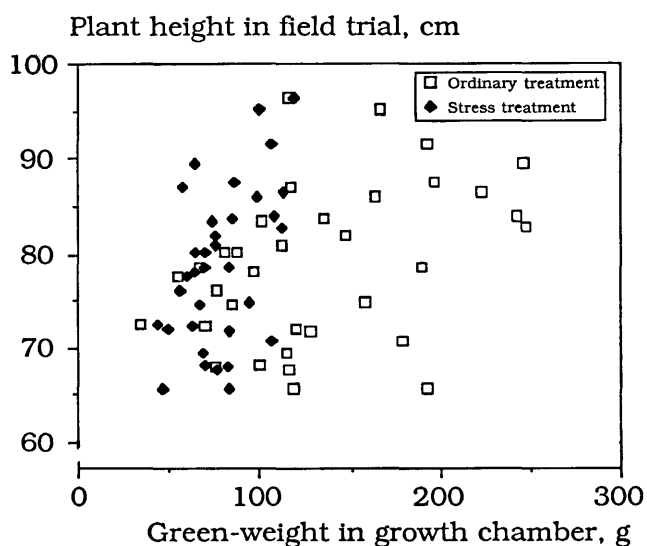
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