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Variation in Nutrient Utilization and Juvenile Growth in Open-pollinated Families of *Picea sitchensis* (Bong.) Carr. Grown in a Phytotron and Correlations with Field Performance

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Abstract

The purpose of this study was to estimate genetic variation in nitrogen (N) and phosphorus (P) utilization (= amount of biomass produced per unit nutrient in the needles), and growth traits in seedlings from 27 open-pollinated families of *P. sitchensis*. Further, the purpose was to estimate juvenile – mature correlations between these traits and breast height diameter in field trials. The seedlings were grown for two growth periods in climate chambers. There were two treatments: free access and restricted access to nutrients. The nutrient treatment in restricted access was chosen to result in a growth of approximately one third of the growth in the free access treatment. Height, shoot, root and needle dry weights, as well as amount of N and P in the needles and N and P utilization were assessed. There was a strong treatment effect of nutrients on all height and above-ground biomass traits. They were statistically different at the 1 % level. There was a significant family effect for N and P utilization and for all other traits studied under restricted access to nutrients. On the contrary, no significant family effects were noted for nitrogen and phosphorus utilization under free access to nutrients, this may be attributed to luxury consumption of nutrients. The precision of the family variance estimates and heritabilities were slightly higher in restricted access than in the free access treatment. The family x nutrient interaction was significant for most of the traits studied, which resulted in non-significance for most of the family effects in the joint analyses of data from the two treatments. Selection of families that responded strongly to a high availability of nutrients could be useful at regeneration of sites with high soil fertilities. The family mean correlations between juvenile traits and breast height diameter in field were all weak ($R^2 \le 0.2$).

Key words: Nutrient utilization, *Picea sitchensis*, genetic correlations, growth chamber.

Introduction

Sitka spruce (*Picea sitchensis*) is economically the most important conifer tree species in Ireland where it accounts for about 60 % of the current forest estate and about 65 % of current afforestation (Anonymous, 1996). It has been included in Irish tree breeding since 1960 (O'Driscoll, 1977). Future breeding will benefit from a deeper genetic-physiological understanding of variation in growth.

Nutrients, and particularly phosphorus and nitrogen, are often lacking under Irish forest conditions. In Ireland it is almost standard practice to apply phosphate to sites prior to planting and during the growth of the crop, but current concerns about nutrient run-off have lead to more regulated applications. There are several reports on conifers indicating genetic variation in response to different nutrient levels (e.g. Roberds *et al.*, 1976; Nambiar 1984, Li *et al.*, 1991; Jonsson *et al.*, 1997). Therefore, it is of interest to study genetic variation in the Irish breeding population of *P. sitchensis* with respect to growth at different availability of nitrogen and phosphorus.

There is some confusion as regards the terminology of nutrient efficiency. We use this term to cover uptake of nutrients,

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their utilization once the nutrients are inside the plant, and their translocation within the plant. *Nutrient utilization* is defined as total plant dry matter produced per amount of nutrient in the needles. Each nutrient element such as phosphorus and nitrogen has its own utilization. In this connection it ought to be pointed out that mycorrhizae, which play a great role in the supply of nutrients to conifers are expected to play a much larger role in uptake of nutrients than in their utilization.

Significant family x nutrient treatment interaction was observed in several studies. JONSSON *et al.*, (1997) reported larger family x nitrogen treatment variance components than family components in a study of nitrogen utilization in seedlings of *Pinus sylvestris*. Significant family x nutrient interaction was reported for many traits in *Picea mariana* (MULLIN, 1985) and *P. abies* (MARI *et al.*, in press a and b), JONSSON *et al.*, in press). We hypothesize that there is a similar variation in *P. sitchensis* too. To test this hypothesis, it is necessary to expose families to different levels of nutrient availability. It may be possible to identify families, which perform well under low nutrient availability, as well as families that respond strongly at high levels of nutrients also in *P. sitchensis*. Finally, it is of interest to identify families, which perform well independently of nutrient availability.

The long rotation time in forest trees is a constraint to tree breeding. Our group has carried out several attempts to develop early selection methods that predict future performance (JONSSON, 2000). Many of these attempts failed (ABRAITIS *et al.*, 1998, JANSSON *et al.*, 1998; DANUSEVICIUS *et al.*, 1999; SONESSON *et al.*, 2002), but some were successful (ERIKSSON *et al.*, 1993; JONSSON *et al.*, 2000). The two successful studies were inspired by experiments which suggested that cultivation under growth limiting environmental factors was useful for early testing (CANNELL *et al.*, 1978; WAXLER and VAN BUIJTENEN, 1981). Seedlings were exposed to different levels of nitrogen since nitrogen is limiting growth in many Swedish conifer forests (ERIKSSON *et al.*, 1993) or to different spacings (JONSSON *et al.*, 2000) to simulate different light conditions.

The first objective of this study was to estimate in a first step genetic variation in nutrient utilization and juvenile growth in open-pollinated families of *P. sitchensis*. In a second step, we used juvenile-mature correlations between these traits and breast height diameter of the same families in the field as a tool to explore the potential of early testing.

Material and Methods

Material and experimental design

Open-pollinated offsprings from phenotypically selected plus trees growing in above average yield class commercial stands of *Picea sitchensis* were studied. Progeny tests were planted in four locations through Ireland, one of which was planted on an abandoned farmland at 200 m asl as 3-year old seedlings in 1988. At planting 250 kg ha^{-1} of ground mineral phosphate was applied. At age 14 from seed, the breast height diameter was measured in one of the four trials. Each family mean was based on measurements of 50 trees. The field trial design was made of 5 completely randomised blocks with 10-tree row plots.

In the phytotron experiment, the originally planned experimental design comprised 30 families x 24 blocks x 2 treatments x 1 seedling =1440 seedlings. However, due to poor seed germination, only 27 families could be used in the restricted access treatment and 17 in the free access treatment (see details of nutrient treatment below). This gave an average of 20 and 22 seedlings per family and per treatment in the restricted and free access treatments, respectively and a total number of 918 seedlings. This means that all places in the originally planned 24 blocks were not filled with plants included in the experiment.

Cultivation in the climate chamber

The seedlings were cultivated for two growth periods (49 weeks) in growth chambers. The material was sown directly into tubes of 26 mm diameter and 80 cm^3 volume, filled with mineral wool and pre-weighed after drying to constant weight. The tubes had bottom drainage and were placed in metal racks that were in turn placed in plastic boxes with bottom drainage. The number of seedlings per box was 120. There was one nutrient treatment per box. The boxes were randomised in the growth chamber.

Table 1. – Photo- and thermoperiodic conditions during the two growth periods of cultivation. Night length was prolonged with 1h per week during weeks 16–24 and 35–40.

	Week no.	Night length (h)	Day temperature °C	Night temperature °C	Duration of day temperature(h)
First growth period					
Germination and growth	1-15	6	20	15	15
Growth cessation	16-17	7,8	20	10	14
	18-21	9-12	20	10	8
	22-24	13-15	15	5	8
Resting stage	25-26	16	15	5	8
Breaking of dormancy	27	16	10	5	8
	28	24	2	2	0
	29	16	10	5	8
Second growth period					
Growth	30-34	6	20	15	15
Growth cessation	35-36	7,8	20	10	14
	37-40	9-12	20	10	8
Resting stage	41-42	16	20	10	8
	43-44	16	15	5	8
	45	16	10	5	8
Harvest	46-49	16	5	5	-

The photo- and thermoperiodic conditions during the two growth periods are shown in *Table 1*. The gradually prolonged nights (1h per week) together with decreasing temperatures induced growth cessation and a resting stage. As light source, 250 W day-light lamps providing light of 300 µmol m^{-2} s^{-1} within the spectrum range 400–700 nm were used. Relative air humidity was kept at 75 percent.

Nutrient treatment

After pre-cultivation of plants for six weeks with free access to nutrients, two nutrient treatments were applied; one set of seedlings was given free access and the other restricted access to nutrients. Free access treatment consisted of irrigation with a balanced nutrient solution that contained 100 mg N per litre and with ammonium and nitrate ions in proportion 2:3. Macroelement proportions by weight were 100N: 84K: 20P: 6Ca: 8Mg and 8S. Microelements were also added (for details see INGESTAD and LUND, 1986).

Within the restricted access, seedlings were fertilized according to the principles of INGESTAD (1979) – the nutrient supply increased with increasing size and needs of seedlings, i. e. the daily dose varied over time during the growth period. The dose curves were calculated based on earlier experience of growth curves of *Picea abies*. The accumulated amount of N given during the growth period was expected to result in one third of the biomass in the free access treatment, which amounted to 4 mg N per plant during the 1st growth period and 15mg N per plant during the 2nd growth period.

Every second day during the periods of active growth, the substrate was saturated with deionized water for 30 minutes. After one hour of drainage, 2 ml of nutrient solution with N amount according to a modified version of the dose curve presented by JONSSON *et al.*, (1997) were pipetted into individual tubes. An auto-pipette with a side feed connected to a cylinder containing nutrient solution was employed for this purpose.

Traits assessed in the growth chamber

Traits assessed and abbreviations of their names are given in *Table 2*. Height measurements were made at the end of the first and second growth periods. Shoot dry weight was determined after drying at 70°C for 40 hours in an oven. Root weight was determined by subtracting the initial dry weight of the tube and mineral wool from the final dry weight of the tube and mineral wool with the root. This method was employed due to practical difficulties in disentangling roots from mineral wool. The needles were analyzed for the concentration of nitrogen and phosphorus present in a sub sample (about 500 mg DW), which was mineralised in H_2SO_4 and H_2O_2 (8 h for 3 days at 250°C). After dilution, the N and P contents were determined using a Latchet flow injection auto-analyser as described by KALTRA and MAYNARD (1991).

N or P amount in the needles was estimated by multiplying the N or P concentration (mg g^{-1}) in the needles by the needle dry weight (g). N or P utilization was estimated by dividing the total plant dry weight (g) by the amount of N or P in the needles (mg). Before calculation of N utilization, a correction for „structural" or inactive N, i. e. the N required for growth to occur (cf ÅGREN, 1985; INGESTAD and KÄHR, 1985; INGESTAD and ÅGREN, 1988) was done by subtracting 4 mg g^{-1} from the concentration of N in the needles.

Statistical analysis

Estimation of variance components and genetic effects was based on the restricted maximum likelihood (REML) method and mixed model equations (MME), using the "Proc mixed" procedure in the SAS software (SAS, 1997). MME gives estimates of the best linear unbiased predictors (BLUP) of the random effects. For the joint analysis, the variables were transformed logarithmically prior to analyses to obtain a normal distribution of the residuals and homogeneity of the variances. The following linear models were used to process the individual treatments separately and to perform a joint analysis of individual treatments.

Separate:

$$y_{ij} = \mu + \beta_i + f_j + e_{ij} \qquad \text{model 1}$$

Joint:

$$y_{ijk} = \mu + \theta_k + \beta_i(\theta)_k + f_j + (f\theta)_{jk} + e_{ijk} \qquad \text{model 2}$$

where:

y_{ij} and y_{ijk} = values of single observation

μ = grand mean

β_i = fixed effect of block i

$\beta_i(\theta)_k$ = fixed effect of block i within nutrient treatment k

θ_k = fixed effect of nutrient treatment k

f_j = random effect of family j

$(f\theta)_{jk}$ = random interaction effect of family j and nutrient treatment k

e_{ij} and e_{ijk} = random error terms

Mean family seed weight was first used as a covariate in the above models to adjust for maternal effects, but was removed when it was found not significant in any of the estimates. Estimation of variance and covariance components for the estimation of genetic correlations between traits within the same treatment was based on the following mixed model:

$$\mathbf{y}_i = \mathbf{X}_i\boldsymbol{\beta}_i + \mathbf{Z}_i\mathbf{u}_i + \mathbf{e}_i$$

where:

i pertains to restricted or free access treatment, respectively

$\mathbf{y}_i$ is the vector of individual seedling observations for trait i

$\mathbf{X}_i$ is the incidence matrix connecting the observations to the fixed block effects

$\boldsymbol{\beta}_i$ is the vector of fixed block effects within treatments

$\mathbf{Z}_i$ is the incidence matrix connecting the observations to the random family effects

$\mathbf{u}_i$ is the vector of random family effects

$\mathbf{e}_i$ is the vector of random residuals.

For two traits this can be summarised as $\mathbf{y'} = (\mathbf{y_1'}, \mathbf{y_2'})$, $\boldsymbol{\beta}' = (\boldsymbol{\beta}_1', \boldsymbol{\beta}_2')$, $\mathbf{u'} = (\mathbf{u_1'}, \mathbf{u_2'})$, $\mathbf{e'} = (\mathbf{e_1'}, \mathbf{e_2'})$, $\mathbf{X'} = (\mathbf{X_1'}, \mathbf{X_2'})$, and $\mathbf{Z'} = (\mathbf{Z_1'}, \mathbf{Z_2'})$. The random effects are assumed to have a bivariate normal distribution (*BND*). Means and variances of these effects are

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} \sim BND \left(\begin{bmatrix} \mathbf{Xb} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{V} & \mathbf{ZG} & \mathbf{R} \\ \mathbf{GZ'} & \mathbf{G} & \mathbf{0} \\ \mathbf{R} & \mathbf{0} & \mathbf{R} \end{bmatrix} \right)$$

where $\mathbf{V = ZGZ'+R}$, and **R** is the residual variance-covariance matrix, and **G** is the parent variance-covariance matrix. The variances and covariances were estimated from the same data using the average information algorithm (GILMOUR *et al.*, 1995) implemented in the ASREML-program (GILMOUR *et al.*, 1998).

Genetic parameters

The families were considered as true half-sibs and additive genetic variance ($\hat{\sigma}_A^2$), coefficient of variation in percent ($\hat{CV}_A$), heritability ($\hat{h}^2$) and genetic correlation ($\hat{r}_{A_{XY}}$) were calculated as:

$$\hat{\sigma}^2_A = 4\hat{\sigma}^2_f$$

$$C\hat{V}_A = \frac{\hat{\sigma}_A}{\bar{x}}100$$

$$\hat{h}^2 = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_A + \hat{\sigma}^2_E}$$

$$\hat{r}_{A_{xy}} = \frac{\hat{\sigma}_{A_{xy}}}{\hat{\sigma}_{A_x}\hat{\sigma}_{A_y}}$$

where:

$\bar{x}$ = trait mean value
$\hat{\sigma}^2_f$ = family variance estimate
$\hat{\sigma}^2_E$ = environmental variance estimate = $\hat{\sigma}^2_e - 3\hat{\sigma}^2_f$
$\hat{\sigma}^2_e$ = estimate of error variance component
$\hat{\sigma}_{A_{xy}}$ = estimate of additive genetic covariance between trait x and y
$\hat{\sigma}_{A_x}$ = estimate of additive standard deviation of trait x
$\hat{\sigma}_{A_y}$ = estimate of additive standard deviation of trait y

Standard errors of the estimates are calculated by ASREML, using a standard Taylor series approximation (GILMOUR *et al.*, 1998).

Stability analyses of individual families

To estimate the contribution of each of the families to the interaction sum of squares, the ecovalence value (WRICKE, 1962) was calculated for each family. The ecovalence value is the interaction sum of squares for each family expressed in percent of the total interaction sum of squares. The ecovalence analyses were carried out on all the traits that showed significant effect of interaction. Families that contributed significantly to family x treatment interaction were determined by a stepwise removal of families from a joint analysis of the two treatments together, in a decreasing order beginning with the family with the highest ecovalence. For the estimation of ecovalences family was considered as a fixed effect in model 1.

Juvenile-mature family mean correlations

Juvenile-mature family mean correlations were run between all traits studied in the phytotron and breast height diameter in the field.

Results

The mean values for most traits were significantly higher in free access treatment than in the restricted access treatment (*Table 2*). Nitrogen utilization had an average value of 0.63 and 0.39 g mg^{-1} in the restricted access and free access treatment, respectively (*Fig. 1, Table 2*).

In the separate ANOVAs (model 1) of data from the treatment with restricted access, family effects were significant for all traits with large variance components and coefficients of additive variation (*Table 2*). In the free access treatment, traits with significant family effects were fewer and the level of significance was mostly lower.

In the joint ANOVA (model 2, *Table 3*), which comprised the 17 families common to both treatments, most traits showed a significant family x treatment interaction. Five of the fourteen traits had large family x treatment interaction variance components exceeding 15%. The performance of the six most extreme families with respect to interaction for TDW is illustrated in *Fig. 2* with their percentage ecovalence values.

The genetic correlations between traits in the restricted access treatment did not show any general pattern (*Table 4*). Genetic correlations between traits in the two treatments are not indicated since the standard errors were invariably larger than the estimates.

The family mean correlations between juvenile traits and breast height diameter in field were all weak and no more than 20% of the variation in field breast height diameter could be explained by variation in juvenile traits for any of the traits.

Discussion

Previous tests of this experimental approach with a related species, *Picea abies*, were successful (JONSSON et al., in press), however, several problems were encountered with *Picea sitchensis*. There was an abnormal growth pattern during the second growth period in the free access treatment with a plant elongation of 39 mm only compared to 56 mm in the restricted access treatment. Since the plants in the restricted nutrient treatment grew under stress, it is likely that they responded rapidly to night prolongation with growth cessation, while the plants in the free nutrient access responded slowly to night prolongation. Moreover, *Picea sitchensis* is a maritime coastal species with relatively long chilling requirement (140 days at

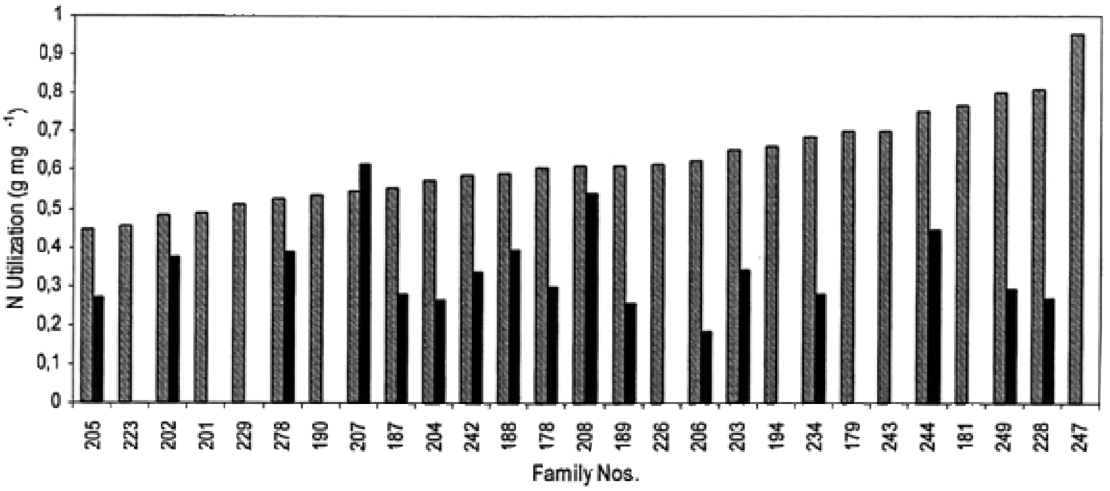

Figure 1. – Nitrogen utilization in 27 open-pollinated families of *P. sitchensis* with restricted access treatment (shaded) and 17 families with free access treatment (black).

Table 2. – Separate ANOVA, model 1. Trait names, abbreviations and units. Trait mean values, percent family variance ± standard error, coefficient of additive variance and heritabilities with standard errors. Level of significance of family effects is denoted by: * = 0.05>P≥0.01, ** = 0.01>P≥0.001. For each trait, means with different letters are statistically different at the 1 % level.

Trait, abbreviation, units	Restricted access				Free access			
	Mean	$\hat{\sigma}_f^2$	$\hat{CV}_A$	$\hat{h}^2$	Mean	$\hat{\sigma}_f^2$	$\hat{CV}_A$	$\hat{h}^2$
Height, 1st growth period H_1, mm	50.5^b	32.3±10.6**	28.88	1.29±0.29	111.7^a	17.3±7.6*	21.42	0.69±0.25
Height, 2nd growth period H_2, mm	106.5^b	9.5±4.4*	11.87	0.38±0.15	151.0^a	7.8±4.3^{ns}	16.91	0.31±0.16
Height increment, H_2-H_1 HINC, mm	56.0^a	11.9±4.5**	22.41	0.47±0.17	39.3^b	7.8±4.2^{ns}	59.60	0.31±0.16
Shoot dry weight SDW, g	1.23^b	22.1±7.3**	15.14	0.89±0.24	2.97^a	25.2±10.2*	35.28	1.01±0.31
Root dry weight RDW, g	0.83^b	20.8±7.3**	28.97	0.83±0.23	1.31^a	15.1±6.8*	36.15	0.60±0.24
Root shoot ratio RSR, -	0.68^a	17.4±6.4**	-	-	0.45^b	1.7±2.2^{ns}	-	-
Total dry weight TDW , g	2.07^b	22.3±7.5**	17.81	0.89±0.24	4.28^a	24.8±10.0*	35.11	0.99±0.31
Needle dry weight NDW, g	0.44^b	16.8±6.0**	22.39	0.67±0.21	0.87^a	16.3±7.1*	53.81	0.65±0.24
N concentration in needles NCONC, mg g^{-1}	12.70^b	15.0±5.4**	17.35	0.60±0.19	27.1^a	11.6±5.5*	8.08	0.47±0.20
P concentration in needles PCONC, mg g^{-1}	2.16^b	20.0±6.8**	18.59	0.80±0.23	3.3^a	10.4±5.1*	10.71	0.42±0.19
N amount in needles NAMT, mg	5.4^b	18.2±6.5**	18.35	0.73±0.22	23.6^a	16.5±7.2*	53.67	0.66±0.24
P amount in needles PAMT, mg	0.93^b	19.4±7.0**	18.88	0.77±0.23	2.8^a	17.1±7.4*	55.26	0.69±0.25
N utilization NU, g mg^{-1}	0.63^a	16.8±6.0**	34.60	0.67±0.21	0.39^b	1.6±2.1^{ns}	67.84	0.06±0.00
P utilization PU, g mg^{-1}	2.38^a	21.8±7.4**	29.22	0.87±0.24	2.54^a	1.2±2.0^{ns}	45.41	0.05±0.00

or below 5°C [CANNELL and SMITH, 1983]) to prevent too early a bud break in mild, costal conditions in the spring. Therefore, it can be speculated that while the chilling requirement of the plants in the restricted access treatment was at least partially satisfied, the chilling requirement in the free access plants was not. As a result, plants in the free access treatment failed to break their apical buds and grow normally when suitable growing conditions returned, resulting in arrested height growth for the second growth period.

Within treatment variation

Treatment with restricted access to nutrients. The large estimates of heritability (0.38–0.89, excluding first year height) and coefficients of additive variance in this treatment agree with our earlier studies of *P. abies* (JONSSON *et al.*, in press, MARI *et al.*, in press (b), and SONESSON *et al.*, 2002) and *Pinus sylvestris* (JONSSON *et al.*, 1997, SONESSON and ERIKSSON, 2000) under controlled conditions. The heritability for first year height exceeding the allowed value of 1.0 may be attributed to maternal seed weight effects. As seen from *Table 2*, the precision of the estimates was satisfactory. The high CV_A estimates (12–35 %) indicate that there are good long-term prospects for improvement of all traits with restricted access.

The mean values for growth traits were mostly slightly lower than in the corresponding study in *Picea abies* (MARI *et al.*, in

Table 3. – Joint ANOVA, model 2. Percent family variance and family x treatment interaction variance ± standard error. Level of significance of family and interaction effects are denoted by: * = 0.05>P≥0.01, ** = 0.01>P≥0.001. The numbers of families that contribute significantly to family x treatment interaction are indicated. Families in the restricted access treatment that were not represented in the free access treatment were removed from the data prior to the joint analyses.

Trait	$\hat{\sigma}_f^2$	$\hat{\sigma}_{ft}^2$	*No. of Families*
H_1	3.0±5.9ns	16.9±7.2**	5
H_2	0	8.4±3.1**	2
HINC	2.7±3.3ns	6.2±3.6*	1
SDW	5.4±7.3ns	20.2±8.3**	6
RDW	6.6±5.1ns	8.9±4.5*	3
RSR	4.2±3.1ns	3.0±2.7ns	-
TDW	6.5±7.2ns	18.5±7.7**	6
NDW	3.7±5.0ns	12.6±5.6*	5
NCONC	1.0±4.3ns	12.3±5.7*	1
PCONC	14.8±6.21**	2.0±1.8ns	-
NAMT	0.59±5.01ns	16.0±6.9*	4
PAMT	1.3±5.2ns	16.0±6.9*	4
NU	0	1.9±1.6ns	-
PU	0.2±0.9ns	0	-

Table 4. – Additive genetic correlations ± standard error. Correlations between traits within the restricted access treatment = normal style. Correlations between traits within the free access treatment = bold style. Correlations are indicated only in cases where the family variance has a significant effect in both traits in the separate analysis.

	H_1	H2	HINC	NDW	SDW	RDW	TDW	RSR	NCONC	PCONC	NAMT	PAMT	NU	PU
H_1	-	-	-	**0.52±0.24**	**0.78±0.12**	**0.91±0.08**	**0.84±0.10**	-	**0.08±0.32**	**-0.39±0.29**	**0.49±0.24**	**0.43±0.26**	-	-
H_2	0.58±0.17	-	-	**0.55±0.23**	**0.47±0.26**	**0.33±0.32**	**0.43±0.28**	-	**-0.33±0.33**	**-0.13±0.36**	**0.43±0.27**	**0.52±0.26**	-	-
HINC	-0.54±0.19	0.36±0.24	-	**0.08±0.34**	**-0.28±0.31**	**-0.59±0.24**	**-0.39±0.29**	-	**-0.44±0.30**	**0.24±0.36**	**0.03±0.34**	**0.14±0.33**	-	-
NDW	-0.19±0.23	-0.14±0.27	0.03±0.26	-	**0.93±0.06**	**0.71±0.18**	**0.88±0.09**	-	**0.14±0.32**	**-0.45±0.27**	**0.99±0.01**	**0.98±0.01**	-	-
SDW	0.34±0.21	0.07±0.26	-0.31±0.24	0.73±0.11	-	**0.93±0.06**	**0.99±0.00**	-	**0.18±0.30**	**-0.44±0.26**	**0.92±0.06**	**0.88±0.08**	-	-
RDW	0.92±0.05	0.44±0.23	-0.60±0.18	-0.05±0.25	0.50±0.18	-	**0.97±0.03**	-	**0.34±0.29**	**-0.43±0.29**	**0.73±0.18**	**0.65±0.20**	-	-
TDW	0.78±0.10	0.31±0.24	-0.54±0.19	0.33±0.22	0.83±0.08	0.90±0.04	-	-	**0.23±0.30**	**-0.45±0.26**	**0.88±0.09**	**0.82±0.11**	-	-
RSR	0.89±0.07	0.50±0.23	-0.49±0.20	-0.50±0.20	0.00±0.25	0.87±0.06	0.57±0.17	-	-	-	-	-	-	-
NCONC	-0.50±0.19	-0.08±0.28	0.48±0.22	-0.60±0.16	-0.89±0.05	-0.70±0.13	-0.90±0.05	-0.29±0.24	-	**-0.21±0.35**	**0.30±0.30**	**0.13±0.32**	-	-
PCONC	-0.58±0.16	-0.31±0.25	0.32±0.24	-0.60±0.16	-0.82±0.08	-0.63±0.15	-0.82±0.08	-0.24±0.24	0.89±0.05	-	**-0.46±0.27**	**-0.26±0.31**	-	-
NAMT	-0.65±0.14	-0.26±0.26	0.45±0.21	0.75±0.11	0.19±0.23	-0.57±0.17	-0.28±0.23	-0.79±0.10	0.06±0.25	-0.02±0.25	-	**0.97±0.02**	-	-
PAMT	-0.71±0.13	-0.45±0.23	0.33±0.23	0.75±0.11	0.24±0.23	-0.54±0.18	-0.23±0.23	-0.78±0.11	-0.03±0.25	0.07±0.24	0.92±0.04	-	-	-
NU	0.83±0.09	0.13±0.28	-0.77±0.13	-0.19±0.25	0.40±0.21	0.88±0.06	0.77±0.10	0.78±0.11	-0.62±0.16	-0.47±0.20	-0.76±0.12	-0.99±0.00	-	-
PU	0.88±0.07	0.31±0.26	-0.66±0.16	-0.40±0.21	0.20±0.23	0.80±0.09	0.61±0.15	0.81±0.09	-0.38±0.22	-0.38±0.21	-0.86±0.08	-0.99±0.00	0.93±0.04	-

press b). Needle dry weight was much lower and as a consequence of this the total dry weight was also much lower in *Picea sitchensis*. The amounts of nitrogen and phosphorus were also much lower in *P. sitchensis* than in *P. abies*.

Treatment with free access to nutrients. For some traits such as final height and height increment, a comparison with all data from the related study in *Picea abies* is less meaningful owing to the abnormal growth pattern. However, the total dry weights may be compared. The dry weight in *Picea sitchensis* was somewhat higher than in *P. abies*. Apart from high CV_As, the genetic parameters were somewhat lower and the precision of the estimates was also lower in this treatment, an obvious consequence of the lower number of families in this treatment, 17 compared to 27. These results contrast with the results in a similar study of *P. abies* (MARI *et al.*, in press b) and may partly be attributed to the previously described abnormal growth pattern in the free access treatment. Notably, nitrogen and phosphorus utilization did not show any genetic variation in this treatment and average N utilization was much lower than in the restricted access treatment. This agrees with previous studies (JONSSON *et al.*, 1997 and in press; MARI *et al.*, in press b). The lower N utilization might be attributed to luxury

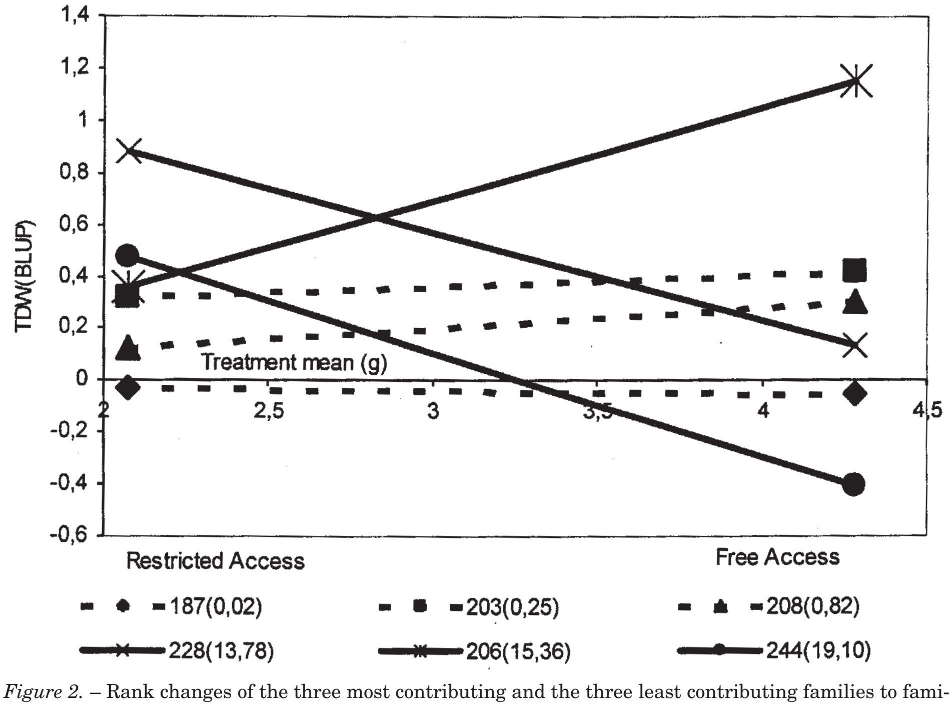

Figure 2. – Rank changes of the three most contributing and the three least contributing families to family x treatment interaction for total dry weight. Their BLUP values are plotted against trait means. The corresponding ecovalence values are indicated in brackets. Families with high ecovalence estimates are connected with full lines while families with low ecovalence estimates are connected with dashed lines.

consumption of nitrogen, which in turn may have drastically reduced any genetic differences. Our results with significant family effects for most traits in the two treatments agree with other related studies with other conifer species (Bell *et al.*, 1979; Li *et al.*, 1991). No good explanation could be found for the generally higher $CV_A s$ despite lower precision of family estimates.

Joint analysis of treatments

Figure 2 illustrates contrasting performances of families in the two treatments. Family 203 was one of the few stable families with above average performance in the two treatments, which suggests that there are possibilities to select families that perform above average independent of nutrient availability. Families 228 and 244 performed well at restricted access but poorly at free access. Family 206 responded strongly positively to free access to nutrients suggesting that there are families that may be useful for high site fertilities should this holds for the full rotation.

The varying response of the families to free access of nutrient treatment resulted in significant family x treatment interaction for most traits in the joint analysis of these two contrasting treatments (*Table 3*). This in turn resulted in low family variance components and non-significant family effect for the majority of traits (*Table 3*). In spite of the strong family x treatment interaction for SDW and TDW, no more than six families contributed significantly to family x nutrient treatment interaction sum of squares. The large interaction variance component is in agreement with the similar observation in our previous study of *Picea abies* (Mari *et al.*, in press b) and results reported by Mullin (1985) for a *Picea mariana* study at three nitrogen fertilization levels. However, in another similar study with 15 open-pollinated families of *P. abies*, Jonsson *et al.*, (in press) found significant interaction only for nitrogen concentration and utilization.

Genetic correlations within treatments

In earlier, related studies (Mari *et al.*, in press b), Sonesson and Eriksson, 2000; Sonesson *et al.*, 2002) with juvenile material growing in growth chambers we observed strong genetic relationships between traits of similar type, such as height traits. This did not occur in the present study (*Table 4*). As regards the treatment with free access the abnormal growth pattern during the second growth period was probably responsible for the variable genetic correlations between height traits. The height increment could also account for weak relationships in the restricted access treatment, in which the plants did not show any obvious signs of abnormal growth but they still may have suffered to some extent from inadequate chilling during the short rest period. Root weight did not correlate strongly with needle or shoot dry weight in the restricted access treatment while its correlation with total dry weight was strong. The latter is partially due to an autocorrelation so a strong correlation is expected between these two traits. As expected, all biomass traits correlated strongly with each other in the free access treatment. The strong correlations between nitrogen and phosphorus amounts in the two treatments (0.92 and 0.97) may be attributed to the use of a balanced nutrient solution. The negative relationship between NAMT traits and PCONC under free access may be attributed to varying luxury consumption of nutrients among families.

In agreement with a similar study in *Picea abies* (Mari *et al.*, in press b) there was no significant relationship between nitrogen amount and total dry weight with restricted access. The obtained correlation between nitrogen utilization and total dry weight ($r=0.77$) may be expected when there is no relationship between nitrogen amount and total dry weight.

Juvenile-mature family mean correlations

The extremely weak juvenile-mature correlations were striking. In a parallel study with *Picea abies* we observed a higher number of significant correlations than expected for random reasons (Karlsson *et al.*, 2002). Jansson *et al.*, (1998) discussed several reasons for weak juvenile-mature correlations. It is impossible from our study to get any definite information on the possible reasons. However, it may be speculated that different sets of genes are active during different ontogenetic phases. Such an explanation is supported by the well-documented occurrence of free growth during the first few growth periods in contrast to the mainly predetermined growth in adult trees of *Picea* species (e.g. Kang *et al.*, 1994 and lit. cit.). During the evolution of *Picea sitchensis*, it is highly likely that different ambient conditions such as non-optimum temperature, water availability, and site fertility have constrained growth. As a consequence, individuals which are least constrained by limiting levels of growth-promoting factors will have the highest fitness. If such an assumption is correct it cannot be expected that nutrient utilization, which is just one of the traits related to site fertility, will show any strong juvenile – mature correlation. Combining different growth constraining factors rather than studying them separately must probably be done to develop strong J-M correlations. However, such studies will be very space and cost demanding.

In conclusion, there are good prospects for improving several traits by selection. The coefficients of additive variance were generally higher for the free access treatment than for the restricted access. For traits with significant family x treatment interaction only a few families contributed significantly to interaction sum of squares. Selection for family stability would thus be possible. The selection of families that respond strongly positively upon good availability of nutrients, would also be useful for afforestation of sites with high site fertilities. All weak juvenile-mature family mean correlations mean that none of the traits studied in this experiment is suitable for early selection.

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Variability in Drupe Characters and their Relationship on Seed Germination in Teak (*Tectona grandis* L.f.)

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Abstract

Seeds of teak (*Tectona grandis* L.f.) were collected from 30 sources covering India, Bangladesh and Laos and germination trials were conducted. Variability in drupe and germination characteristics was observed. Correlation studies carried out between drupe characters and seed filling percentage showed a positive correlation between drupe weight and seed filling percentage. The mesocarp weight and drupe/shell weight ratio were negatively correlated with germination percentage. A polynomial regression for prediction of germination percentage using drupe/shell weight ratio was established ($R^2 = 0.599$). Germination percentage was found to be correlated with percentage of two seeded drupes.

Key words: Seed source, Teak, *Tectona grandis*, Germination, Drupe characters, variability studies, correlation.

Introduction

One of the world's most valuable and widely planted tropical tree species is teak. It has a wide natural range, which covers India, Burma, Thailand, Laos, Malaysia and Indonesia. Teak has mostly been planted in tropical regions including Asia, Africa and Central America (Kadambi, 1972). Teak exhibits a great variability between provenances and land races in various quantitative and qualitative traits (Keiding *et al.,* 1986). Variation in drupe physical characteristics and germination behaviour was observed in seven provenances from the Kerala state of India (Jayasankar *et al.,* 1999).

Studies on variability in seed characters and germination behaviour of a species will help in identifying own seed lots for a planting program (Kertadikara and Prat, 1995). Germination behaviour of teak drupes was observed to be highly variable from source to source (Dasappa, 1990; Indira and Basha, 1999). Variation in teak drupe characters of different seed

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