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RETROSPECTIVE STUDIES ON NITROGEN RESPONSE OF *PINUS SYLVESTRIS* L.

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ABSTRACT

Previously published data on juvenile growth and nitrogen efficiency components from 21 *Pinus sylvestris* L. OP families from clones in a central Swedish seed orchard were genetically correlated with growth traits at ages 13–17 from four field trials with progenies from the same clones. Tree height was measured at both ages in all four trials while breast height diameter was measured in one trial only at age 13. The J–M correlations were estimated separately for each of the four field trials and separately for the two nitrogen (N) treatments in the growth chamber. The total number of genetic correlations calculated was 576. The number of significant and positive correlations was highest for the low N treatment. The field trial with the poorest growth had the lowest number of strong correlations followed by the trial planted on a more fertile site than *Pinus sylvestris* normally occupies. Height after two growth periods, above ground biomass traits, and nitrogen utilization (= amount of dry matter produced per content of nitrogen in the needles) had the strongest positive correlations with field growth traits.

Key words: *Pinus sylvestris*, juvenile – mature genetic correlations, nitrogen efficiency.

INTRODUCTION

In order to supply constantly increasing human demands for wood for various purposes, measures must be taken to improve the amount of wood production. Tree breeding is one sustainable method that may alleviate the expected shortage of wood and therefore ought to be given priority. To cope with future environmental changes and increased human demands breeding programs must be flexible. To meet these demands NAMKOONG *et al.* (1980) developed the Multiple Population Breeding System. One great obstacle to breeding of boreal conifer species is their long generation times. Therefore, several attempts to develop early tests have been carried out (cf ERIKSSON *et al.* 1993). The correlations between juvenile and adult performance varied considerably in the studies carried out (ERIKSSON *et al.* 1993). There may be several reasons for this, one being that the field material was young. Another reason might be that there is a genotype x environment interaction that overrides the possibility of obtaining strong juvenile – mature (J–M) correlations. Most studies at the juvenile stage were carried out under favourable growth conditions whereas the adult relatives were growing under limiting conditions in the field. There was some support for the hypothesis that imitation of field conditions would give stronger J–M correlations (*eg.* CANNELL *et al.* 1978, WAXLER & VAN BUIJTENEN 1981, DEWALD *et al.* 1992). The results of our group contrasted with these findings by giving the strongest correlations at the highest nitrogen concentrations (ERIKSSON *et al.* 1993).

Nitrogen is frequently the limiting factor for tree growth in pine forests in Sweden (TAMM 1991). One approach to carry out early evaluation would be to mimic the limited availability of nitrogen in the field by adding nitrogen in limited amounts to the substrate. The efficiency with which a nutrient element is used by a genetic entry is frequently referred to as nutrient efficiency of that element. Several components of nitrogen efficiency might be distinguished. INGESTAD (1979) has developed the concept of *nitrogen productivity*, which is an estimate of the dry matter produced per internal nitrogen content and per day. *Nitrogen utilization* is dry matter produced per nitrogen content in the needles. Another component that is not studied in the present investigation is *nitrogen acquisition capacity* which is defined as the amount of nutrient taken up by a genetic entry under defined non-optimal conditions in relation to uptake under conditions of free access to nutrients.

N productivity can only be estimated properly by destructive sampling during cultivation and is thus unsuitable for genetic tests in which many families and many seedlings per family have to be tested. Therefore, a simplified N productivity (designated as preliminary N productivity) was estimated (JONSSON *et al.* 1997). N utilization is another trait that might be examined with respect to its predictive power for field growth traits. The results referred to above (ERIKSSON *et al.* 1993) did not consider N productivity and N utilization.

A series of field trials that have the individual trials located at a broad span of nitrogen availabilities would be useful for an analysis of J–M correlations with nitrogen growth components such as those discussed above. Such a series of progeny trials was established in 1981 in two climatic zones in central Sweden; in each zone one site has a low site index (SI) and the other a high.

The purpose of this investigation was to estimate J–M genetic correlations between two nitrogen efficiency components, preliminary N productivity from JONSSON *et al.* (1997) and N utilization, as well as juvenile growth traits in young siblings and field growth traits of their older sibling trees. Individual correlations with data from four field trials with varying site indices were carried out.

MATERIAL AND METHODS

Material

A complete 12 x 12 factorial mating design between 24 plus trees of Swedish and Finnish *Pinus sylvestris* provenances with their origin in the range of latitude 57°43' – 61°44' and altitude 35–220 m was accomplished in a seed orchard in central Sweden. The progenies were planted in two different climatic zones and in each zone, one fertile and one less fertile test site was selected. The parents are numbered 1–24, with 1–12 acting as females and 13–24 as males in the field trial. From 21 of the 24 clones open-pollinated progenies were included in the growth chamber study.

Field trials

Paper pots were used for seed sowing in the spring of 1980 and 4 field trials were established during spring 1981. A completely randomized single-tree plot design in four blocks with 10 trees per family was used for field establishment with a spacing of 1.7 × 1.7 m. Two of the trials were located at latitude 59° and two at 61.5°. At each locality the two trials differed with respect to N availability. The difference was especially pronounced at the southern locality. The trials were designated SLSI south-low-site-index-trial, SHSI south-high-site-index-trial, NLSI north-low-site-index-trial, NHSI north-high-site-index-trial. Finally, the trials were fenced to avoid game damage.

Two blocks per trial were assessed which means that at most 12 × 20 trees per parental tree were measured. When selecting the trees for analysis, suppressed trees were excluded. The nine traits included in our calculations are listed in Table 1.

Stem volume was computed according to equation 1 by BRANDEL (1990):

$$V=10^{-1.35369}\cdot D^{1.85469}\cdot(D+20)^{0.01896}\cdot H96^{2.04781}\cdot(H96-1.3)^{-1.00739} \quad [1]$$

in which D is breast height diameter at age 17 and $H96$ is tree height at age 17.

Growth chambers

The cultivation technique, the assessments, and the traits studied have been described elsewhere (JONSSON *et al.* 1997). Therefore, we only give the essence of the growth chamber experiment in which the survival was excellent (> 98 %). Open pollinated offsprings from 21 of the 24 parents of the factorial mating were cultivated for two growth periods in a growth chamber with two nitrogen treatments, one with free access of nitrogen, and the other with regular additions of nutrients to permit estimates of N productivity according to the technique developed by INGESTAD (1979). The N productivity was based on dry matter growth during the second growth period. Furthermore, it was assumed that there was a close relationship between height and dry matter growth. At the termination of the experiment dry matter was determined separately for needles, stem + branches, and roots of each plant. The N concentration in needles of individual plants was also determined. Plant height was continuously recorded during periods of active elongation. The 12 growth chamber traits used for estimates of J–M genetic correlations are shown in Table 6. Altogether 576 J–M genetic correlations were calculated.

Statistics

The field and growth chamber data vectors corresponding to a pair of traits are denoted by y and z, respectively. The orders of the vectors are $n_y \times 1$ and $n_z \times 1$. The linear models are expressed by matrices according to:

$$y = X_y\beta_y + G_y g_y + e_y$$

$$z = X_z\beta_z + G_z g_z + e_z$$

Table 1. Traits assessed or calculated in the four field trials included in the present study.

Field traits assessed	South		North	
	high SI	low SI	high SI	low SI
Age 17				
Tree height	x	x	x	x
Breast height diameter	x	x	x	x
Stem volume	x	x	x	x
Height increment 13–17	x	x	x	x
Breast height diameter increment 13–17	x			
Stem volume increment 13–17	x			
Age 13				
Tree height	x	x	x	x
Breast height diameter	x			
Stem volume	x			

where $\mathbf{X}_y$ and $\mathbf{X}_z$ are the design matrices for the fixed components β_y and β_z containing intercepts, block and truck effects. The vector $\mathbf{g}_y$ of genetic effects is of size 24 × 1 corresponding to the 12 females and 12 males. This implies that the design matrix $\mathbf{G}_y$ has two elements per row equal to 1 and the others equal to 0. For the growth chamber data, the additive genetic effects are contained in the vector $\mathbf{g}_z$. The elements of $\mathbf{G}_z$ are 0 or 1 corresponding to parent. In order to simplify calculation, the size of $\mathbf{g}_z$ is the same as of $\mathbf{g}_y$. The artificial effects of the three parents that do not exist in the growth chamber are eliminated by zeros in $\mathbf{G}_z$.

The genetic correlation ρ is defined as the correlation of $g_y(i)$ and $g_z(i)$ corresponding to the effects of parent i. In other respects, effects are assumed to be statistically independent. Assuming normal distributions for the random effects, the joint model is written:

$$\begin{pmatrix} y \\ z \end{pmatrix} \sim N\left(\begin{bmatrix} X_y & \beta_y \\ X_z & \beta_z \end{bmatrix}, \begin{bmatrix} \sigma_g^2 G_y \acute{G}_y + \sigma_e^2 I_y & \rho\sigma_g\tau_g G_y \acute{G}_y \\ \rho\sigma_g\tau_g G_z \acute{G}_z & \tau_g^2 G_z \acute{G}_z + \tau_e^2 I_z \end{bmatrix}\right)$$

where σ^2_g, τ^2_g and σ^2_e, τ^2_e denote the variances of the parent effects and the residual errors.

Using the REML (Restricted Maximum Likelihood) technique, see *eg.* SEARLE *et al.* (1992), the data are first transformed according to $y_R = K'_y y$ and $z_R = K'_z z$ such that the expectations of y_R and z_R are zero, *i. e.* $K'_y X_y = 0$ and $K'_z X_z = 0$. The likelihood principle is then used for transformed data leading to equations that needed to be solved by iterations. The numerical computations are performed by the SAS (1989) procedure IML (Interactive Matrix Language). In order to avoid numerical instability caused by different order of variation, the SAS (1990) procedure Standard was used before the calculation of the correlation. The values of the variance components are affected by this rescaling of data but the correlation ρ is not. Using the asymptotic covariance matrix of the estimates of variance and covariance components, the standard error of a ρ estimate was obtained by series expansions (delta technique) of the same type as in BULMER (1980, Ch. 6). This standard error was used for the Fisher z-transform, *i. e.* the inverse hyperbolic tangent function, which was applied to test the hypothesis H_0: $\rho = 0$.

RESULTS

The genetic parameters of the juvenile traits were presented elsewhere (JONSSON *et al.* 1997) with heritabilities varying in the range 0.2–0.4. The field data will be presented in a separate paper. The heritabilities of the field traits based on separate ANOVAS for each site did not exceed 0.20 and were in many cases even lower than 0.10. The genotype × test site interaction was of minor importance. Family mean values for two traits that correlated strongly and poorly with stem volume at the NLSI-trial is presented in Table 2 to illustrate the span in variance of original data.

Not all 576 J–M genetic correlations will be shown. Rather, we have illustrated the main trends in Tables 3–4 with the sites listed according to increasing growth with the smallest trees at the SLSI-trial. Since the number of entries was as low as 21 we have also illustrated the number of correlations > 0.7 and < –0.7 (Table 3). The reason for choosing ± 0.7 is that the ratio between the conditional and the unconditional variances becomes $1–0.7^2 = 0.51$. Such an increase in precision may be useful in breeding. The number of strong and positive relationships is considerably higher

Table 2. Family mean values for dry weight of needles and shoot/root ratio as the juvenile traits and stem volume at the north-low-site-index-trial as the adult trait.

Family No.	Stem volume, m^3	Needle dry weight, g.	Shoot/root ratio
1	0.37	3.18	1.42
2	0.34	2.94	2.44
3	0.36	3.21	1.37
4	0.32	2.99	1.33
5	0.38	3.20	1.49
6	0.41	3.33	1.45
7	0.40	3.37	1.95
8	0.35	2.96	1.51
9	0.40	3.22	1.52
10	0.35	2.95	1.31
11	0.35	2.79	1.16
12	0.37	3.19	1.32
13	0.37	2.87	1.36
14	0.35	3.21	1.64
15	0.36	2.90	1.40
16	0.36	3.25	1.45
17	0.37	3.42	1.45
18	0.37	3.43	1.26
19	0.38	3.21	1.35
20	0.38	3.23	1.32
21	0.36	3.24	1.40

Table 3. Number of significant and non-significant genetic correlations between field growth data in four trials with juvenile trait data from two N treatments in growth chamber.

Field trial	Low-N treatment in growth chamber			High-N treatment in growth chamber		
	Significant correlations		non-significant correlations	Significant correlations		non-significant correlations
	0	–		0	–	
South low site index	1	2	57	2	2	56
North low site index	2	2	56	0	0	60
North high site index	10	4	46	0	0	60
South high site index	3	0	105	0	0	108

for the low-N treatment than for the high-N treatment (Tables 3–4). Moreover, the number of significant relationships was largest for the northern trial with high site index (Table 3). At the two southern test sites the J–M correlations were frequently weak or even negative with the weakest relationships at the trial with a low site index.

From Table 5 it may be seen that the significant correlations at the SLSI-trial differed from the other trials with respect to juvenile traits. Moreover, for N utilization and N concentration the significances had opposite signs compared to the two northern sites. The other significant correlations from this trial comprised traits that for the other three trials mostly had weak relationships with field data.

Among the field traits, height increment had generally weaker correlations with juvenile traits than the other field traits. Sixteen of the 17 strong and positive correlations at the NLSI-trial comprised either breast height diameter or stem volume. Correlations with height at age 13 contributed mostly to the strong negative correlations at the SLSI-trial, four and seven for the low-N and high-N treatments, respectively.

The standard errors of the correlation coefficients were large as seen from Table 6, in which the two sites that differed mostly with respect to the strength of the J–M correlations for stem volume at age 17 as field trait are illustrated.

Table 4. Number of strong, positive and negative (> 0.7 and < - 0.7, respectively) genetic correlations between field growth data in four trials with juvenile trait data from two N treatments in growth chamber.

Field trial	Low-N treatment in growth chamber			High-N treatment in growth chamber		
	Significant correlations		non-significant correlations	Significant correlations		non-significant correlations
	>0.7	<-0.7		>0.7	<-0.7	
South low site index	2	4	54	3	8	49
North low site index	17	1	42	6	1	53
North high site index	4	2	54	0	0	60
South high site index	0	0	108	0	0	108

Table 5. The distribution of significant juvenile - mature genetic correlations among individual juvenile traits to different test sites. SLSI, NLSI, NHSI, and SHSI stand for southern low-site index, northern low-site index, northern high-site index, and southern high-site index.

Juvenile trait	No. of significant correlations low-N treatment							No. of significant correlations high-N treatment	
	positive				negative			positive	negative
	SLSI	NLSI	NHSI	SHSI	SLSI	NLSI	NHSI	SLSI	SLSI
Total dry weight			2						
Above ground dry weight			2						
Needle dry weight			4						
Root dry weight					1				
Shoot/root ratio	1								
Height GP2				3					
Basal diameter					1				
N utilization		2	2						2
N concentration						2	4	2	

Table 6. Genetic correlations ± standard errors for 12 juvenile traits with stem volume at age 17 in two field trials. The data refer to the low-N treatment in growth chamber.

Juvenile trait	Stem volume, age 17	
	South-low-SI	North-high-SI
Total dry weight	0.01±0.35	0.62±0.25*
Above ground dry weight	0.01±0.35	0.73±0.20**
Stem dry weight	–0.06±0.35	0.43±0.27
Needle dry weight	0.05±0.35	0.82±0.18***
Root dry weight	0.00±0.35	0.44±0.27
Shoot/root ratio	0.06±0.38	0.06±0.32
Height GP1	0.18±0.34	0.32±0.28
Height GP2	0.17±0.36	0.47±0.30
Basal diameter	–0.12±0.34	0.20±0.29
N productivity	–0.56±0.34	0.29±0.36
N utilization	–0.69±0.30	0.67±0.24*
N concentration	0.73±0.28	–0.82±0.18***

*, **, *** – significant at 5 %, 1 % and 0.1 % level, respectively

DISCUSSION

The low heritabilities of the field traits mean that the possibilities of obtaining significant J–M correlations will be limited. Moreover, the low number of families included do not contribute to a strong precision in the estimates (cf Table 6 and NAMKOONG *et al.* 1988). In spite of this there were more significant correlations for traits from the low-N treatment when correlated with field data from the two northern sites than could be attributed to chance only.

Juvenile treatment and correlations. The data in the present study lend some support to the hypothesis that mimicking of field conditions would improve the strength of the J–M correlations. This is especially evident if the number of strong correlations is added to those that showed significance (Tables 3–4). Since our growth chamber experiment was carried out in the unique way introduced by INGESTAD (1979) there are no exact counterparts to our study. Therefore, comparisons, even with traits that are common to many studies, may suffer from that difference. Our results are in agreement with data presented by DEWALD *et al.* (1992) who noted that in their trace-N treatment the four *Pinus elliottii* families ranked in the same way as in the field whereas this was not the case in treatments above a concentration of 10 mg N/litre. LI and colleagues have studied J–M family mean correlations in *Pinus taeda* seedlings growing under different nitrogen treatments. LI *et al.* (1991) observed the strongest correlation in the low-N treatment while in another study the opposite situation occurred when N fertilization was combined with irrigation (LI *et al.* 1992). In a previous study of a similar type of J–M genetic correlations (ERIKSSON *et al.* 1993) the weakest correlations were obtained for the lowest concentration of nitrogen. However, in that case we did not add the nutrients in the way required for estimates of nitrogen productivity. At the lowest concentration in that study the plants showed a retarded growth, which might explain the difference between the present investigation and the previous since the plants did not show any sign of starvation in the present investigation. Their biomass was approximately half of the biomass produced in plants growing under free access of nitrogen while the percentage in the study by ERIKSSON *et al.* (1993) was mostly less than a third of that at free access of nitrogen. JIANG (1988) presented J–M genetic correlations for a subset of the families included in the present experiment. He did not find any difference in proportion of significant relationships for the two N treatments (10 and 100 mg N·litre^{-1}). His material comprised other juvenile traits since his experiment lasted for four growth periods in a growth chamber and the age in the field was only 6 years.

Age of field traits. In the present investigation we found the strongest correlations with data from the two northern sites which had trees intermediate with respect to size. In the report on J–M genetic correlations by ERIKSSON *et al.* (1993) the correlations gradually became stronger with age which means that the strongest correlations were obtained with the largest trees. In that study the really strong correlations were obtained at slightly higher ages, 23–28 years. For the low-N treatment most of the positive significant correlations (4 of 6) as well as most strong but non-significant correlations (16 of 17) were noted with stem volume and breast height diameter at age 17. The absence of consistency among the J–M correlations at the SLSI-trial gives some support to the indication that the correlation increases with age. However, the low number of strong correlations at the SHSI-trial contradicts this. Moreover, the field trait heritabilities were highest at this high-site-index-trial which should be advantageous for strong J–M relationship unless the conditions are such that different sets of genes are active in growth chamber grown material and in field grown material. This trial is unique since it has a fertility beyond what is common for natural occurrence of *Pinus sylvestris*. It might be speculated that such a fertile *Picea abies* site is not useful for progeny testing of *Pinus sylvestris*. The number of significant J–M correlations was much higher at the NHSI-trial (Table 3). The survival was lower in the low-site-index-trial that gave rise to several openings which in turn might give rise to more environmental influence on the tree growth masking the genetic effects and thus lowering the precision of the estimates (compare Tables 3 and 4).

Juvenile trait and correlations. The data in Table 5 suggest that N utilization and needle dry weight, height after GP2, are good predictors of field growth. Needle dry weight is an important part of the two other biomass components which showed positive, significant relationships with field data. These three traits had additionally 2–3 strong, positive, but non-significant correlations each, which strengthens their position as the best predictors among the traits studied in our experiment. This deviates only slightly from the observation by ERIKSSON *et al.* (1993) that more or less all 17 juvenile traits studied had equal predictive power. Some of the most laborious ones were not assessed in the present investigation. It is noteworthy that N productivity had only two strong, but non-significant, positive relationships. With the exception of the SLSI-trial, N concentration was in many cases negatively and strongly correlated with field traits. Thus all three significant and negative correlations for the two northern trials had N concentration as its juvenile component. This is expected since the more a plant or tree grows per N atom the lower the N concentration will be per gram dry matter.

In conclusion it was an unfortunate situation that the best series of field trials, designed to reveal any genetic differences in response to a broad span of site fertilities, had a tree material with an exceptionally low heritability. In spite of this, as well as the low genotype x site interaction, there were several strong J–M correlations with data from the two northern field trials when the juvenile data from the low-N treatment were included. Above ground biomass traits and N utilization seem to have the highest predictive power and might be focused on in future studies of J–M genetic correlations rather than N productivity which requires laborious experimentation.

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