EFFECTS OF NITROGEN STRESS ON ADAPTIVE GENETIC VARIATION IN *ACER PLATANOIDES* L. AND *BETULA PENDULA* ROTH.

Sanna Black-Samuelsson[1] **& Gösta Eriksson**

Department of Forest Genetics, Swedish University of Agricultural Sciences (SLU), P.O. Box 7027, S– 750 07 Uppsala, Sweden.

[1)] Corresponding author: Sanna Black-Samuelsson. Tel: +46(0)18- 67 12 43. Fax: +46(0)18- 67 27 18, E-mail: Sanna.Black@sgen.slu.se

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ABSTRACT

Seedlings from one Swedish and one Norwegian population of *Acer platanoides* L. (Norway maple) and *Betula pendula* Roth. (silver birch) were cultivated for one growing season in both a controlled free access (non-stressful) and a low nutrient (stressful) condition. We analysed whether the nutrient treatments had an effect on genetic variation in growth and phenology traits, and investigated the population and family rank changes between environments. The nutrient effect was strong indicating high phenotypic plasticity in both species. Populations of Norway maple differed little whereas the family variation was high between and within treatments. Treatment rank changes were also higher at the family than at the population level. In silver birch, populations differed for half of the traits between and within both treatments. Except the high variation among non-stressed Norwegian families, family differentiation was generally low and the treatment interaction at the population and family levels were moderate. The relation between the species life-history traits and the partitioning of genetic variation within and between populations were unclear. According to our knowledege, this is the first study of reaction norm variation in fitness-related traits in temperate deciduous tree species.

Key words: Norway maple, silver birch, low nutrient, reaction norm variation, fitness-related traits

INTRODUCTION

Additive genetic variation in fitness-related traits is a prerequisite for response to selection and for adaptation to environmental changes. It has been hypothesized that stressful environments might affect the amount of additive genetic variance of a trait and its narrow-sense heritability (HOFFMANN & PARSONS 1991, HOFFMANN & MERILÄ 1999). Most hypotheses suggest that genetic variation increases in stressful conditions: For instance, in common favourable environments, the heritable variation in fitness-related traits might decrease due to stabilizing selection, whereas in a novel stressful environment, selection is initially less effective on unfavourable alleles which results in higher additive genetic variance (HOLLOWAY *et al.* 1990). However, other hypotheses suggest that genetic variation decreases in unfavourable conditions (cf. BLUM 1988).

At the individual level, organsisms' responses to environmental heterogeneity can be assessed as phenotypic plasticity, i.e. the degree of modification of a phenotype to environmental changes. Phenotypic plasticity represents a rapid means of adjustment and is of adaptive significance when it results in increased relative fitness across environments (SULTAN 1987). In addition, genetic variation for phenotypic plasticity (the interaction between genotype and environment) is of evolutionary importance as it reflects the ability of genotypes to differ in adaptation across environments. The reaction norm may be described in terms of genetic variation, phenotypic plasticity and genotype × environment (g × e) interaction. Particularly in species with long generation times and which might experience large environmental heterogeneity during their lifetime, reaction norm parameters in relation to environmental stress are interesting to study. In temperate forest trees, such investigations have almost exclusively been conducted on conifers (see references in SONESSON 2000). Moreover, studies of the additive genetic variation in insect-pollinated temperate tree species are rare as a consequence of their minor importance in commercial forestry.

The relationship between a species' life-history traits and the partitioning of genetic variation within and between populations has been reviewed previously (e.g. LOVELESS & HAMRICK 1984, HAMRICK & GODT 1996). Among other life-history traits, a species' breeding system, pollination mechanism and mode of

seed dispersal have a major influence on the genetic structure: generally, a predominantly outcrossed wind-pollinated species with wind-dispersed seeds is expected to have high genetic variation within and among populations. For a selfing insect-pollinated species with gravity- or animal-dispersed seeds, a likely pattern might show less variation within populations whereas geographical distance would promote among population variation.

Acer platanoides L. (Norway maple) and *Betula pendula* Roth. (silver birch) (both species are hereafter referred to by their english names) are two temperate deciduous tree species that are monoecious and outcrossing (DE JONG 1976, HAGMAN 1971). The species exhibit several differences in life-history traits: Norway maple is mainly insect-pollinated but may also be partly wind-pollinated as is the case in sugar maple (GABRIEL & GARRETT 1984), whereas silver birch is exclusively wind-pollinated (HAGMAN 1971). Norway maple has fairly specific habitat requirements compared with the more general habitat demands of silver birch. The distribution of Norway maple is fragmented and populations are often small. This is a result of afforestation with conifers and unfavourable forest management practices due to the species low economic value. Unlike Norway maple, silver birch has a continuous distribution and large populations. In Sweden, the species ranks third among tree species in total volume and is the only deciduous tree species that is the subject of any active forest tree breeding.

The objectives of the present study was to study the effect of high and low nutrient availability on amounts of genetic variation in growth and phenology traits in seedlings of Norway maple and silver birch. We studied the effects of nitrogen availability since it has been suggested that this is one of the most important factors besides temperature and photoperiod for long-term growth (TAMM 1991). Furthermore, we investigated the population and family rank changes between environments (g × e interaction), and examined the relationship between the species' life-history traits and the partitioning of genetic variation within and between populations.

MATERIAL AND METHODS

Plant material and cultivation

Birch and maple seeds were collected during September 1998 from one Swedish population: a browsed meadow adjacent to cultivated land, located on the Baltic island of Öland (latitude 56°43´N, longitude 16°40´E), and from one Norwegian population situated in Lillehammer (latitude 61°10´N, longitude 10°25´E) within the south-boreal zone. Both populations of both species were represented by ten families with 20 open-pollinated seedlings per family and treatment. In a growth chamber study, with its limited space, a compromise between numbers of populations and number of families per population must be reached. Our reason for including only two populations of each species was that population differences for both species have previously been observed for the latitudinal range involved (JOHNSSON 1977, HÅBJØRG 1978).

Norway maple: seeds were imbibed in water for 24 h to release dormancy and then stratified in pots containing a mixture of perlite, vermiculite, sand and gravel in a phytotron (3 °C, 24 h darkness). After approximately 15 weeks, seeds started to germinate and seedlings were planted in mineral wool ("Grodan") and cultivated at 20 °C, photoperiod 21 h day / 3 h night for three weeks. Then the initial length of each plant (Height1) was measured before transferring to the two nutrient treatments. The 800 plants were grown in randomized single-tree plots divided into 35 blocks with 24 plants per block.

Silver birch: seeds were kept at +4 °C until being sown in a mixture of perlite, vermiculite, sand and gravel, and placed in controlled cultivation conditions in a phytotron (photoperiod 16 h day, 20 °C / 8 h night, 12 °C). After one week, the first seedlings developed: At a size of approximately six cm, 40 open-pollinated progenies of each family were planted in individual pots containing mineral wool ("Grodan"). After approximately four weeks, the initial length of each plant (Height1) was measured before transfer to the two nutrient treatments. The 812 plants were randomized single-tree-plots divided into 63 blocks with 14 plants per block.

Environmental conditions

The cultivation conditions in the growth chambers were controlled in order to reduce the environmental variance and to be able to specifically study the effect of nutrient availability on reaction norm parameters. The chosen nutrient treatments had previously indicated large variation in growth and phenology characters in birch and maple seedlings (data not shown). The non-stressful treatment consisted of free access to nutrients, i.e. all plants were watered frequently with a 50 % nutrient solution, 2L-6513, as described by INGESTAD (1967). In the low-N (stress) treatment, plants were first given water, followed by nutrient solution 2L-6513 pippetted in quantities calculated for a growth rate of three percent. This method allows high accuracy so that the amounts of nutrients added correspond to the amounts

Table 1. Photoperiod and day and night temperatures used in the nutrient study of Norway maple and silver birch.

	Week no.	Night length (h)	Night temp. (°C)	Day length (h)	Day temp. (°C)
Norway maple	1–6	8	15	16	20
	7–8	10	15	14	20
	9–10	12	15	12	20
	11–12	14	10	10	15
	13–14	16	5	8	10
	15–17	16	2	8	5
Silver birch	1–6	8	15	16	20
	7–8	10	10	14	15
	9–10	12	5	12	10
	11–12	14	5	10	10
	13–14	16	5	8	10
	15–17	16	2	8	5

of nutrients taken up, and increases exponentially with time and in relation to the exponential increase in plant biomass (INGESTAD & LUND 1979). All other cultivation conditions were identical between the treatments: the light from 250 W daylight Osram HQi-E lamps provided an irradiance of 300 mmol $m^{-2}s^{-1}$ in the 400–650 nm spectrum, and the relative air humidity was 75 %. The photoperiod and temperatures (see Table 1) were intended to be similar to natural conditions in the spring to autumn period.

Trait registration

Norway maple: Individual plant height was measured on three occasions in the low-N and on four occasions in the high-N treatments. Budset was registered on a three-point scale (0 = no visible bud, 1 = beginning of bud development, 2 = clear bud). At the time of the first registration (Bud1 = day 28), no visible buds were scored among non-stressed plants, however at the time of the second registration (Bud2 = day 77), all bud-stages of plants in both treatments were recorded. For percentage of individual leaf coloring, a five-point scale was used (0 = 0–20 % colored leaves, 1 = 20–40 % colored leaves, 2 = 41–60 % colored leaves, 3 = 61–80 % colored leaves, and 4 = 81–100 % colored leaves). At the first registration (Color1 = day 77), all non-stressed plants had completely green leaves, whereas at the two following registrations (Color2 = day 88, Color3 = day 98), all leaf color stages were present in both treatments. At harvest, number of nodes (>10 cm length) was registered.

Silver birch: Height was measured on five occasions in the low-N and on nine occasions in the high-N treatments. Budset was recorded using the same scale as for maple. By the time of the first registration (Bud1 = day 35), all low-N plants had already set clear buds whereas no visible buds were found among non-stressed plants. Thus, during the following three occasions (Bud2 = day 56, Bud3 = day 70, Bud4 = day 78), only the non-stressed plants were recorded. For leaf coloring, the same scale as for maple was used. Leaf coloring was recorded at harvest for low-N plants only, as all non-stressed plants had completely green leaves. In addition, number of branches (>15 cm length) was registered at harvest.

Norway maple and silver birch: At harvest, after separating each plant into roots and above ground material (stem and leaves), dry weight was recorded after 40 h at 70 °C. In the statistical analyses, different increment measures and shoot / root dry weight ratio were also included (Table 2).

Statistical analyses

Character mean values were calculated for each treatment. The amount of phenotypic plasticity, i.e. the slope of the reaction norm, was quantified as the coefficient of variation: (the difference between the highest and the lowest treatment mean value / the overall mean) × 100. Reaction norm variation was illustrated using the Delta Graph Program 3.5.

Prior to analysis of variance, examination of the residuals revealed that some traits needed to be log-transformed in order to be normally distributed (Table 2). Nested factorial analysis of variance was then conducted for each trait using type III sum of squares (PROC GLM, SAS 1989). Preliminary analyses revealed significant effects of covariate (Height1 = initial plant length when transferred to each treatment) and block, so these effects were included in the final analyses. Appropriate denominators for each F-test were synthesized with the Satterthwaite approximation using the TEST option in the RANDOM statement of

Table 2. Abbreviations and description of growth and phenology traits measured in Norway maple and silver birch. Traits are measured in both treatments unless otherwise indicated. The day number refers to the number of days after plants were transferred to the nutrient treatments. M = Norway maple, B = silver birch, low = low nitrogen treatment, high = high nitrogen treatment.

Trait	Species	Description, unit, transformation type
Height 1 (covariate)	M, B	Plant height when transferred to nutrient treatments, day 0 (mm)
Height 2	B	Plant height day 14 (mm)
Height 5	B	Plant height day 35 (mm, log-transf.)
Maxheight	M	Plant heights day 28 (low), day 42 (high) (mm)
Maxheight	B	Plant heights day 42 (low), day 78 (high) (mm, log-transf.)
Increment 21	M	Height 2 - Height 1 (mm)
Increment 42	M	Height 4 - Height 2 (high) (mm)
Increment 41	B	Height 4 - Height 1 (mm)
Increment 94	B	Height 9 - Height 4 (mm)
Maxincrement	B	Height 6 - Height 1 (low), Height 9 - Height 1 (high) (mm, log-transf.)
Shoot	M, B	Dry weight of stem and leaves (g, B: log-transf.)
Root	M, B	Dry weight of root (g)
Dwsr	M, B	Shoot/Root dry weight ratio (B: log-transf.)
Node	M	Node number >10 cm length at harvest
Branch	B	Branch number > 15 cm length at harvest (high) (arscin-transf.)
Bud 1	M	Bud set stage day 28 (low)
Bud 2	M	Bud set stage day 77
Bud 2	B	Bud set stage day 56 (high)
Bud 3	B	Bud set stage day 70 (high)
Bud 4	B	Bud set stage day 78 (high)
Color 1	M	Leaf color stage day 77 (low)
Color 2	M	Leaf color stage day 88
Color 3	M	Leaf color stage day 98
Color 1	B	Leaf color stage (low)

PROC GLM (SAS 1989). Phenotypic plasticity was estimated as the treatment effect, and genetic variation for phenotypic plasticity was estimated as the genotype × environment (g × e) term in the ANOVAs. In order to estimate genetic variation within and between treatments and populations, the following statistical ANOVA models were used for all traits except for budset:

$$y_{hijkl} = \mu + cx_{hijkl} + t_i + b_{j(i)} + p_k + f_{l(k)} + (tp)_{ik} + tf_{il(k)} + e_{hijkl} \quad \text{(Model 1)}$$

$$y_{hjkl} = \mu + cx_{hjkl} + b_j + p_k + f_{l(k)} + e_{hjkl} \quad \text{(Model 2)}$$

$$y_{hjl} = \mu + cx_{hjl} + b_j + f_l + e_{hjl} \quad \text{(Model 3)}$$

where y_{hijkl}, y_{hjkl} and y_{hjl} are values of single observations, μ = grand mean, c = coefficient, x_{hijkl} = covariate (initial plant height), t_i = fixed effect of nutrient treatment i, b_j = random effect of block j, $b_{j(i)}$ = random effect of block j within treatment i, p_k = fixed effect of population k, f_l = random effect of family l, $f_{l(k)}$ = random effect of family l within population k, $(tp)_{ik}$ = fixed interaction effect of treatment i and population k, $tf_{il(k)}$ = random interaction effect of treatment i and family l within population k, e_{hijkl} = residual error.

The variance components for each of the random factors were calculated as the ratio of the variance component to the sum of all components. Estimates of the variance components were obtained using the REML option in PROC VARCOMP (SAS 1989) and the standard errors of the relative components were found using the Delta technique (BULMER 1980).

Budset analysis

Prior to statistical analysis, budset was classified into cumulative bud-stages based on the bud developmental scale (0, 1, 2) used during assessments. For silver birch in the low-N condition, ten different patterns of bud development were identified for the Bud 2, Bud 3 and Bud 4 records: The most developed bud-stage pattern had clear buds on all three registration occasions, corresponding to "222". The second most developed bud-stage pattern corresponded to "122", i.e. a plant beginning to develop buds at Bud 2 and with visible

Table 3. Treatment means (X) and coefficients of variation (CV) for growth and phenology traits cultivated under low-N and high-N conditions in two populations of Norway maple and silver birch. CV is quantified as (the difference between the highest and the lowest treatment mean value divided by the mean value for both treatments) × 100.

Trait	low-N X	high-N X	CV
Norway maple			
Height 1 (covariate) (mm)	67.9	65.1	4
Maxheight (mm)	119.6	183.8	42
Increment 21 (mm)	44.8	62.0	32
Increment 42 (mm)	-	56.0	-
Shoot (g)	3.0	4.4	37
Root (g)	1.3	1.4	10
Dwsr	2.5	3.3	26
Node	3.7	5.2	33
Bud 1	1.9	0	200
Bud 2	2.0	1.5	25
Color 1	0.7	0	200
Color 2	1.8	1.1	49
Color 3	3.1	2.2	33
Silver birch			
Height 1 (covariate) (mm)	71.6	55.9	25
Height 2 (mm)	147.6	168.8	13
Height 5 (mm)	181.8	405.8	76
Maxheight (mm)	190.6	629.4	108
Increment 41 (mm)	-	272.7	-
Increment 94 (mm)	-	301.7	-
Maxincrement (mm)	118.9	575.5	133
Shoot (g)	2.7	8.8	107
Root (g)	3.4	3.9	14
Dwsr	0.8	2.3	92
Branch	0	4.2	200[1]
Bud 2	2.0	1.0	64
Bud 3	2.0	1.4	36
Bud 4	2.0	1.6	20
Color 1	2.1	0	200[1]

[1] Note the mean value in one of the treatments was zero

buds at Bud 3 and Bud 4. In an analogous way, the following bud patterns were denoted "022", "112", "012", "002", "111", "011", "001" and "000". The sorting of bud-stage pattern is not clear-cut but approximately reflects the budset development from the third to the first registration time. In Norway maple, the budset assessments over treatments at the two registration times (Bud 1, Bud 2) resulted in six cumulative bud-stage patterns "22", "12", "02", "11", "01" and "00". For low-N (Bud 1), the three bud-stages were "2", "1" and "0". Using Generalized Linear Models (Mccullagh & Nelder 1989) extended with random effects, the log-odds ratio was written:

$$\ln (q_{jkl}/(1- q_{jkl})) = \mu + cx_{jkl} + b_j + p_k + f_{l(k)}$$

(birch and maple, low nitrogen)

$$\ln (q_{ijkl}/(1- q_{ijkl})) = \mu + cx_{ijkl} + t_i + b_{j(i)} + p_k + f_{l(k)} + (tp)_{ik} + tf_{il(k)}$$

(maple, both treatments)

where q is the conditional probability of obtaining a certain bud-stage pattern or a faster development.

For both populations, least square means were calculated and re-transformed to the probability scale. Under the log-odds ratio, a 95 % confidence interval was found for the difference of the least square means. To determine whether the difference between the populations was significant or not, the interval was centered as the average of the least square means. The end-points of the interval were re-transformed to the probability scale. The numerical calculations were done with the help of the Glimmix macro (SAS 1989).

Table 4.

Trait df	Tr (1)	Block (Tr) (maple 33 birch 61)	Cov (1)	Pop (1)	Tr*Pop (1)	Fam(Pop) (18)	Tr*Fam (Pop) (18)	Block(Tr) varcomp	Fam(Pop) varcomp	Tr*Fam(Pop) varcomp	Error varcomp
Norway maple											
Maxheight	92.1***	5.12***	410.***	7.41*	1.16	2.18	2.75***	3.9 (1.8)	13.3 (5.4)	4.6 (2.8)	78.3 (5.1)
Increment 21	24.6***	4.34***	95.1***	14.9**	2.14	4.34***	3.76**	6.7 (2.5)	11.8 (4.3)	0.9 (1.7)	80.6 (4.6)
Shoot	168.***	3.31***	299.***	3.25	1.39	1.46	3.86***	2.8 (1.5)	11.7 (5.8)	8.3 (4.0)	77.2 (5.1)
Root	12.6**	3.82***	210.***	0.54	0.48	2.54*	2.31**	5.5 (2.1)	13.2 (5.4)	4.9 (2.9)	76.4 (5.1)
Dwsr	95.4***	2.63***	1.44	0.44	0.47	1.98	2.79***	5.8 (2.2)	5.5 (4.1)	7.5 (3.8)	81.2 (4.1)
Node	130.***	2.80***	57.7***	0.15	7.64*	2.99*	1.46	4.6 (2.0)	6.2 (3.1)	1.7 (2.1)	87.5 (3.5)
Color 2	55.6***	2.04***	164.***	0.83	1.00	4.63***	1.73*	1.6 (1.3)	21.5 (6.6)	2.0 (2.0)	74.9 (6.4)
Color 3	70.9***	2.31***	178.***	0.11	0	2.15	2.22**	4.7 (2.0)	13.8 (5.1)	2.6 (2.3)	78.8 (5.0)
Silver birch											
Height 2	146.***	3.35***	1599.****	12.0**	17.7***	1.37	1.89*	26.9 (4.5)	9.7 (3.7)	0.8 (1.3)	62.6 (4.7)
Height 5	1354.***	1.41*	293.***	0.64	2.91	1.00	1.55	10.0 (3.4)	5.8 (3.2)	2.7 (2.3)	81.6 (4.2)
Maxheight	1630.***	1.37*	159.***	0.88	7.29*	1.02	2.46***	8.5 (2.7)	3.9 (3.5)	6.5 (3.5)	81.1 (3.9)
Maxincrement	1728.***	1.37*	12.9***	0.95	0.11	0.93	2.58***	3.7 (2.1)	0.7 (3.0)	7.7 (4.0)	87.9 (3.5)
Shoot	856.***	1.25	337.***	3.90	12.9**	0.87	1.96**	5.6 (2.3)	4.0 (2.8)	2.8 (2.4)	87.6 (3.4)
Root	53.3***	2.03***	367.***	17.1***	6.92*	0.98	1.96**	7.2 (2.5)	0.4 (2.6)	2.1 (2.2)	86.7 (3.4)
Dwsr	1020.***	1.36*	10.18**	7.36*	0.01	1.52	1.27	3.5 (2.2)	1.3 (1.9)	1.8 (2.6)	93.3 (2.9)

RESULTS

Norway maple

Trait mean values over all populations for each treatment revealed that the growth traits showed a positive response to increased nutrients whereas the development of buds and autumn leaf color was faster among low-N than among high-N plants (Table 3). This was also shown by the increment curves within treatments (Figure 1) and in the reaction norm diagrams (Figure 2). Coefficients of variation (CVs) over all populations for traits measured in both treatments ranged from four (Height 1) to 200 (Bud 1, Color 1) (Table 3) and all traits had strongly significant treatment effects and were therefore highly plastic (Table 4). For the complete data set (ANOVA model 1, Table 4), populations differed for maximum height and first increment, and family variation was found for first increment, root biomass, node numbers and Color 2. The g × e interaction was significant only for node number at the population level, whereas all traits but node number were

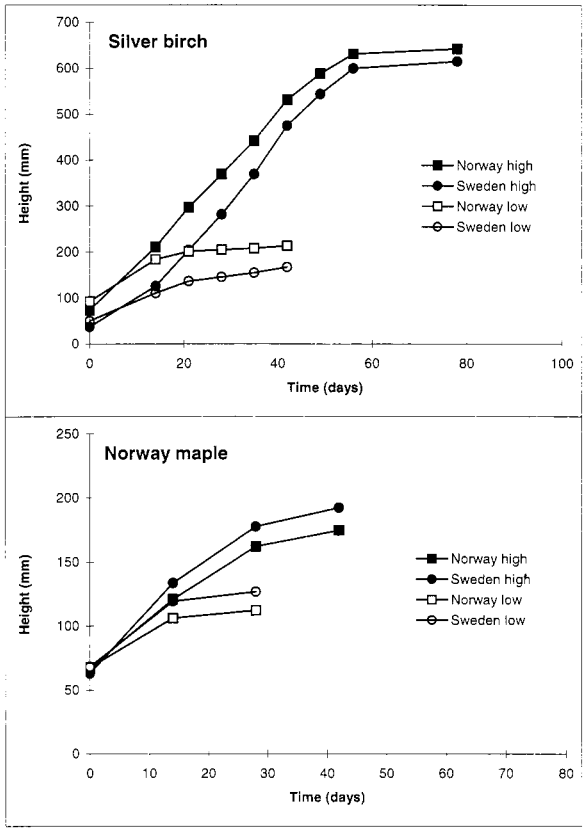

Figure 1. Increment curves based on population mean values for height recorded on several occasions for silver birch and Norway maple cultivated in carefully conrolled high (filled symbols) and low (open symbols) nutrient conditions. The Norwegian population is denoted with squares and the Swedish population is denoted with circles.

significant at the family level. Family variance components for all traits but node number and biomass ratio were high (>10 %) compared with lower (<5 %) variance components for most traits at the family × treatment level. Within treatments (ANOVA model 2, Table 5), populations differed for three of seven traits (low-N) and two of nine traits (high-N), respectively whereas families within populations were significantly different and had high variance components for a majority of the traits. In the ANOVAs including separate populations and treatments (ANOVA model 3, Tables 6, 7), all traits except node number (low-N, Sweden) and first increment (high-N, Sweden) showed significant family variation. Variance components among the Norwegian families were remarkably high for a number of the traits (10.5–29.6 % for low-N plants and 3.9–28.6 % for high-N plants). Variances were somewhat lower among the Swedish families (2.4–20.3 % and 8.1–19.3 % for low-N and high-N plants, respectively). The block and covariate effects reached statistical significance for a majority of the traits for all models (Tables 4–7). The budset analysis in the low nutrient treatment detected family variation within Sweden for the bud-stage "01", whereas assessments including both treatments revealed no significant effects of genotype or g × e interaction (data not shown).

Silver birch

As illustrated in the increment curves within treatments (Figure 1) and the reaction norm diagrams (Figure 3), all growth traits had higher mean values in the free access than in the low-N treatment while the phenology traits showed the opposite tendency (Table 3). CV-values over all populations ranged from 13 (Height 2) to 200 (Branch, Color 1) (Table 3), and all traits showed strongly significant treatment effects in the ANOVA (Table 4). In the joint analysis (ANOVA model 1, Table 4), genetic variation was observed for approximately half of the traits for populations and in the population interaction with treatment. Family differentiation was absent although family rank changes were significant for all but two traits (Height5 and biomass allocation). Variance components were relatively low at the family (0.4–9.7 %) and family × treatment levels (0.8–7.7 %). Within treatments (ANOVA model 2, Table 5), populations differed for five of eight traits in the low-N treatment and for four of ten traits in the high-N treatment. Family variation was observed only for root biomass in the low-N treatment as compared with all traits but shoot biomass in the high-N treatment. Family variances exceeded 10 % only

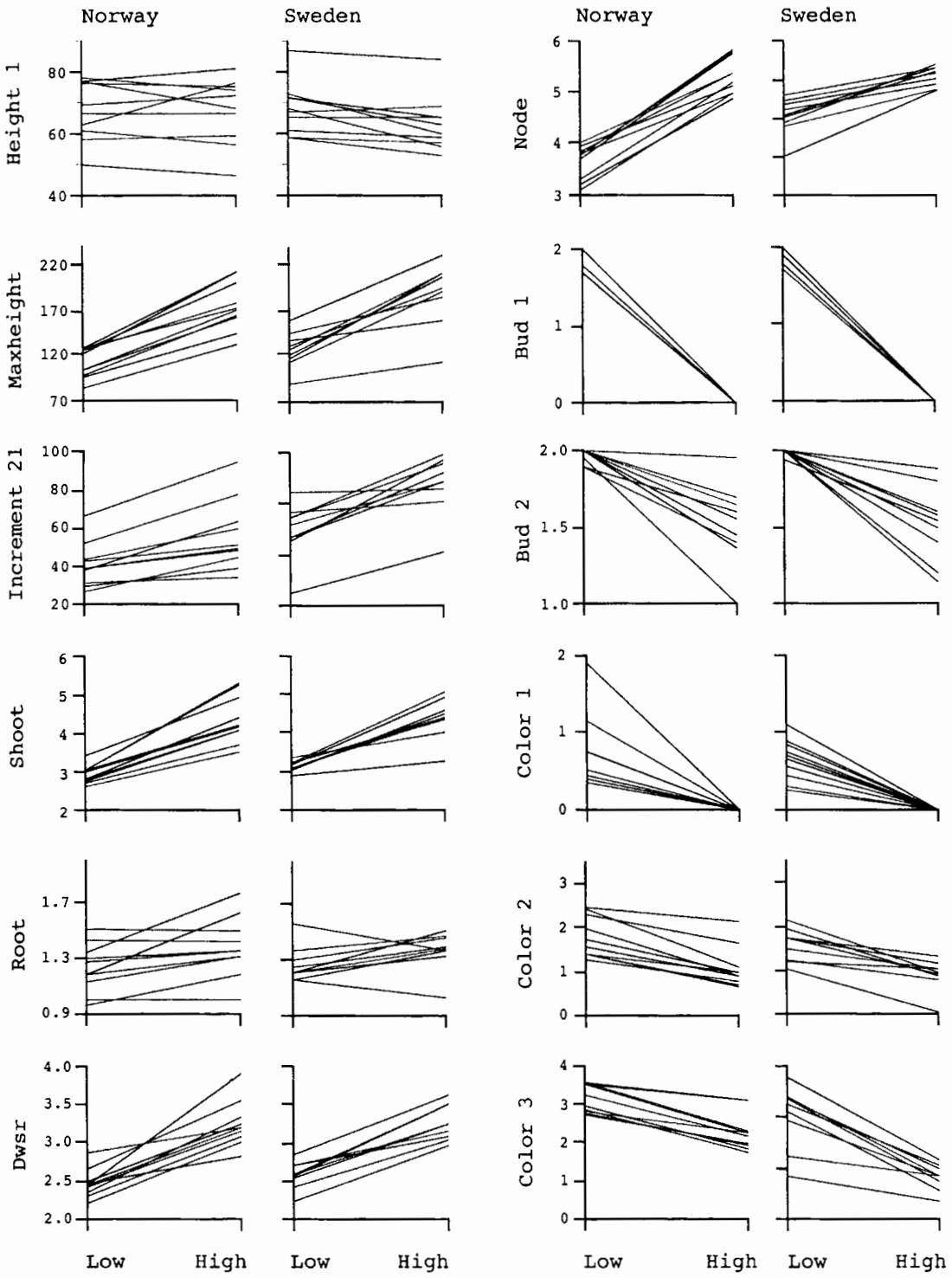

Figure 2. Reaction norm diagrams of growth and phenology traits of ten families from a Norwegian and a Swedish population of Norway maple grown under low and high nutrient treatments. The y-axis represents the values of the phenotypic character. For further explanations, see Table 2.

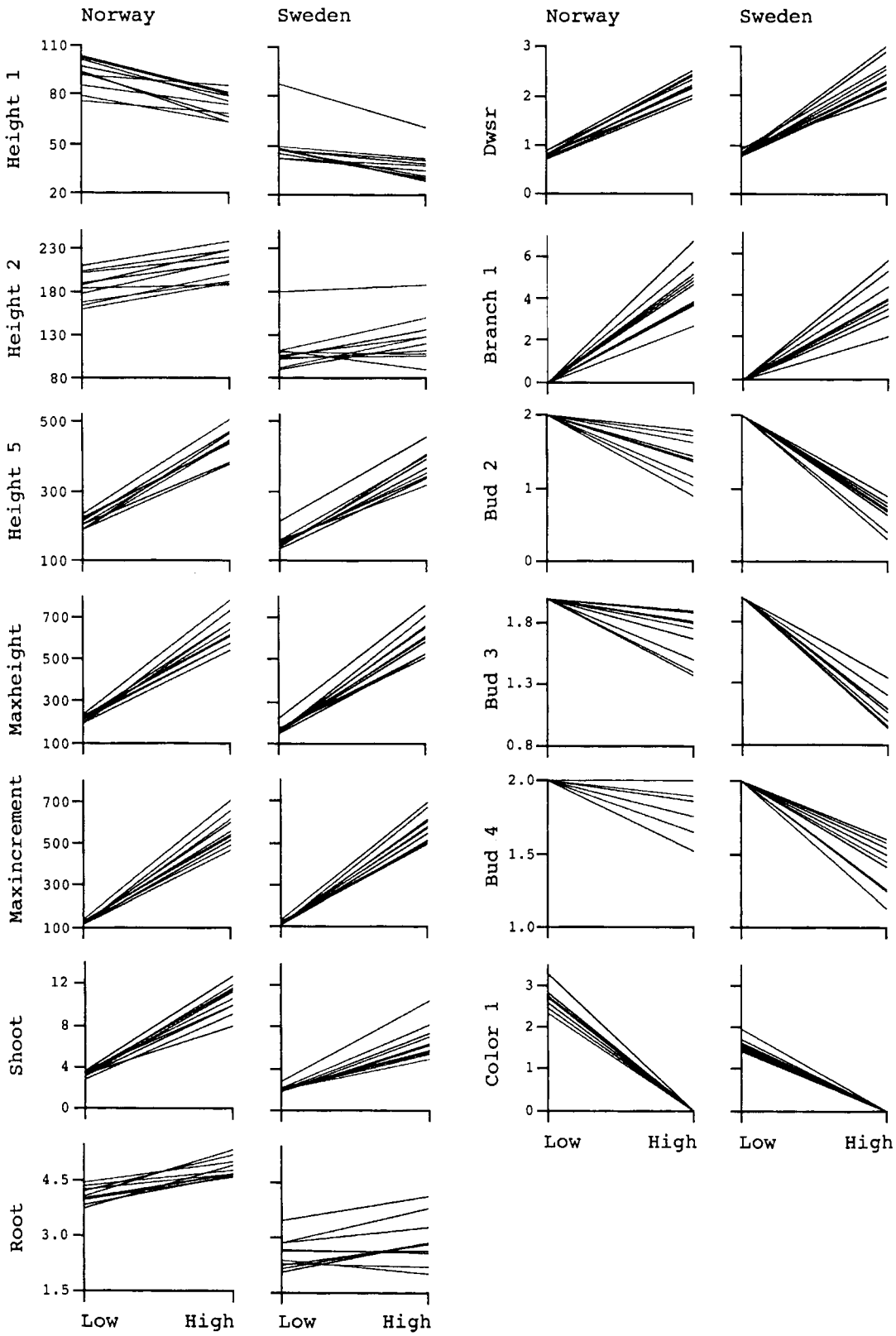

Figure 3. Reaction norm diagrams of growth and phenology traits of ten families from a Norwegian and a Swedish population of silver birch grown under low and high nutrient treatments. The y-axis represents the values of the phenotypic character. For further explanations, see Table 2.

Table 5. F-ratios and percentage of variance components (standard error in brackets) for growth and phenology traits in two populations of Norway maple and silver birch cultivated under low-N and high-N treatments. Analysis of variance according to model 2. df = degrees of freedom, Cov = covariate, Pop = population, Fam = family, varcomp = variance component.

Trait (df)	Block (maple 16 birch 33)	Cov (1)	Pop (1)	Fam (Pop) (18)	Block varcomp	Fam (Pop) varcomp	Error varcomp
Maple Low N							
Maxheight	3.86***	430.***	10.6**	3.59***	2.0 (2.0)	20.3 (6.6)	77.7 (6.7)
Increment 21	3.31***	45.3***	10.5**	3.24***	5.7 (3.3)	13.2 (5.2)	81.0 (5.8)
Shoot	2.40**	264.***	33.6***	2.68***	2.3 (2.1)	17.2 (6.1)	80.5 (6.2)
Root	5.12***	107.***	1.38	3.82***	9.3 (4.0)	17.0 (6.0)	73.7 (6.3)
Dwsr	4.36***	15.6***	1.73	3.43***	10.8 (4..5)	11.4 (4.5)	77.7 (5.7)
Node	1.96*	31.0***	2.95	2.00**	3.8 (2.7)	5.7 (3.4)	90.5 (4.2)
Color 1	1.30	59.4***	0.25	5.33***	0	23.3 (7.1)	16.7 (7.1)
Maple High N							
Maxheight	6.12***	178.***	5.38*	4.53***	4.6 (2.8)	17.1 (6.0)	78.3 (6.2)
Increment 21	5.22***	53.2***	14.9**	2.62***	7.3 (3.6)	12.6 (5.0)	80.2 (5.7)
Increment 42	3.42***	16.9***	0.85	3.74***	6.3 (3.4)	10.4 (4.5)	83.3 (5.3)
Shoot	4.26***	167.***	0.49	4.77***	2.8 (2.1)	20.6 (6.6)	76.5 (6.7)
Root	3.10***	107.***	0.09	4.17***	2.9 (2.2)	18.6 (6.4)	78.5 (6.5)
Dwsr	1.98*	1.76	0.06	4.44***	3.2 (2.3)	13.9 (5.3)	82.8 (5.6)
Node	3.35***	30.9***	1.59	3.32***	5.1 (3.0)	8.7 (4.1)	86.2 (4.9)
Color 2	69.2***	2.10**	0.17	4.71***	2.3 (2.0)	21.5 (6.9)	76.2 (6.9)
Color 3	2.70***	70.4***	0.04	3.93***	6.1 (3.2)	17.8 (6.2)	76.0 (6.4)
Birch Low N							
Height 2	1.00	908.***	9.67**	1.50	13.2 (4.5)	14.4 (5.3)	72.4 (6.0)
Height 5	1.33	295.***	0.83	0.74	10.8 (4.2)	8.2 (3.9)	81.0 (5.3)
Maxheight	1.07	295.***	0.005	0.92	10.4 (4.0)	9.1 (4.1)	80.5 (5.3)
Maxincrement	1.11	7.64**	0.11	1.22	0.7 (2.2)	2.2 (2.3)	97.1 (3.3)
Shoot	1.64*	357.***	7.08*	1.00	14.1 (4.8)	4.6 (2.8)	81.3 (5.3)
Root	2.17***	225.***	19.6***	1.82*	20.5 (5.8)	5.3 (3.0)	74.2 (6.1)
Dwsr	0.87	10.1**	10.2**	1.13	0	0	1
Color 1	3.32***	91.3***	38.7***	1.57	13.3 (4.6)	5.2 (3.1)	81.5 (5.2)
Birch High N							
Height 2	2.40***	827.***	5.51*	2.73***	33.3 (6.6)	8.4 (3.7)	58.3 (6.3)
Height 5	1.49*	71.6***	0.21	1.98*	14.4 (4.6)	8.4 (4.2)	77.3 (6.0)
Maxheight	1.37	24.2***	0.91	2.85***	7.2 (3.5)	11.3 (4.8)	81.5 (5.4)
Increment 41	2.14***	43.5***	1.06	2.01**	23.9 (5.9)	6.5 (3.3)	69.6 (6.0)
Increment 94	1.49*	0.002	5.40*	4.04***	4.3 (2.8)	14.7 (5.5)	81.0 (5.8)
Maxincrement	1.34	6.32*	0.88	2.90***	4.7 (3.0)	10.6 (4.6)	84.7 (5.2)
Shoot	1.35	159.***	1.40	1.54	2.8 (2.7)	7.4 (3.9)	89.8 (4.7)
Root	2.52***	195.***	5.04*	1.67*	0	6.6 (3.6)	93.4 (3.6)
Dwsr	1.22	4.48*	3.52	1.65*	4.3 (3.1)	3.8 (2.8)	91.9 (4.1)
Branch	3.41***	176.***	12.9**	2.58***	5.5 (3.1)	7.1 (3.7)	87.4 (4.6)

for Height 2 in the low-N treatment and for maximum height, increment 94 and maximum increment under the high-N treatment. Treating population and treatments separately (ANOVA model 3, Tables 6, 7), remarkably more variation was revealed in the Norwegian population in the high-N treatment (all traits but root biomass) than in the low-N treatment (maximum increment and Color 1), and variance components were also on

Table 6. F-ratios and percentage of variance components (standard error in brackets) for growth and phenology traits in a Norweigan and a Swedish population of Norway maple and silver birch cultivated under a *low-N* treatment. Analysis of variance according to model 3. df = degrees of freedom, Cov = covariate, Pop = population, Fam = family, varcomp = variance component.

Trait df	Block (maple 16 birch 28)	Covariate (1)	Family (9)	Block varcomp	Fam (Pop) varcomp	Error varcomp
Maple Norway						
Maxheight	2.05*	236.***	3.23**	4.6 (4.2)	20.3 (9.3)	75.1 (9.8)
Increment 21	2.13**	18.1***	2.97**	3.6 (4.2)	11.2 (6.7)	85.2 (7.6)
Shoot	1.45*	163.***	4.52***	0	28.6 (11.4)	71.4 (11.4)
Root	2.68***	46.1***	4.51***	4.7 (3.7)	23.6 (9.9)	71.7 (9.8)
Dwsr	2.53**	5.07*	3.50***	9.0 (4.8)	13.0 (7.3)	78.0 (7.9)
Node	1.94*	26.1***	2.56**	3.8 (3.9)	10.5 (6.4)	85.7 (7.2)
Color 1	0.74	27.0***	6.77***	0	28.6 (11.1)	71.4 (11.1)
Color 2	1.27	47.7***	5.78***	0.3 (2.3)	29.6 (11.2)	70.1 (11.5)
Color 3	1.03	63.4***	0.02*	1.5 (3.5)	16.4 (8.8)	82.1 (9.3)
Maple Sweden						
Maxheight	2.35**	190.***	3.69***	4.6 (4.2)	20.3 (9.3)	75.1 (9.8)
Increment 21	2.09**	27.3***	3.19**	6.4 (5.0)	14.5 (7.7)	79.2 (8.7)
Shoot	1.58	107.***	2.16*	4.1 (4.2)	9.7 (6.2)	86.2 (7.6)
Root	2.55**	52.3***	3.32***	10.8 (5.8)	12.5 (7.1)	76.7 (8.3)
Dwsr	2.06*	8.90**	3.17**	8.8 (5.3)	9.7 (6.2)	81.6 (7.5)
Node	0.98	8.74**	1.50	1.9 (3.5)	2.4 (3.4)	95.8 (5.1)
Color 1	1.56	28.2***	2.86**	1.7 (3.6)	13.6 (7.4)	84.6 (8.1)
Color 2	1.74*	40.5***	3.21**	2.5 (3.5)	19.9 (9.3)	77.6 (9.6)
Color 3	0.88	52.9***	2.11*	0	9.8 (6.3)	90.2 (6.3)
Birch Norway						
Height 2	1.08	436.***	2.36	19.5 (6.9)	10.5 (6.2)	70.0 (7.8)
Height 5	1.36	258.***	1.66	14.6 (6.3)	7.6 (5.2)	77.8 (7.4)
Maxheight	1.32	255.***	1.69	13.2 (6.1)	8.3 (5.5)	78.5 (7.5)
Maxincrement	1.52	6.02*	2.02*	5.6 (5.0)	6.6 (5.1)	87.8 (6.9)
Shoot	1.74*	134.***	1.08	16.7 (7.1)	2.6 (3.0)	80.7 (7.7)
Root	1.36	70.3***	0.99	22.6 (7.5)	0.1 (2.0)	77.3 (7.7)
Dwsr	1.17	8.62**	1.50	0.3 (4.2)	2.0 (3.3)	97.8 (5.8)
Color 1	3.25***	44.2***	2.34*	20.7 (7.3)	6.4 (4.7)	72.9 (7.9)
Birch Sweden						
Height 2	0.82	457.***	0.47	8.6 (5.1)	17.3 (8.5)	74.1 (9.1)
Height 5	0.93	116.***	0.41	9.2 (5.8)	8.4 (5.8)	82.4 (8.0)
Maxheight	0.73	94.3***	0.58	8.0 (5.5)	9.6 (6.0)	82.4 (8.0)
Maxincrement	0.68	2.30	0.78	0	0	1
Shoot	1.16	223.***	1.63	11.8 (6.2)	7.7 (5.3)	80.5 (8.0)
Root	1.15	144.***	2.28*	15.4 (6.7)	10.8 (6.4)	73.9 (8.5)
Dwsr	0.69	1.76	0.54	0	0	1
Color 1	1.47	44.0***	0.42	7.7 (5.5)	3.0 (3.8)	89.3 (7.0)

average higher under high-N (1.6–16.8 %) than under low-N (0.1–11.9 %) conditions. In the Swedish population, root biomass within the low-N treatment and increment 94 and root biomass in the free access treatment reached statistical significance and variances were generally of the same magnitude within the low-N (0–17.3 %) and free access (2.6–12.6 %) treatments. As for the block and covariate effects, significant variation was found for a number of the traits in all ANOVA models (Tables 4–7). The budset analysis revealed that populations differed for all bud-stages

Table 7. F-ratios and percentage of variance components (standard error in brackets) for growth and phenology traits in a Norweigan and a Swedish population of Norway maple and silver birch cultivated under a *high-N* treatment. Analysis of variance according to model 3. df = degrees of freedom, Cov = covariate, Pop = population, Fam = family, varcomp = variance component.

Trait / df	Block (maple 16 birch 33)	Covariate (1)	Family (9)	Block varcomp	Fam (Pop) varcomp	Error varcomp
Maple Norway						
Maxheight	3.48***	123.***	4.01***	3.5 (3.7)	16.1 (8.2)	80.4 (8.5)
Increment 21	3.96***	38.3***	4.25***	9.1 (5.2)	16.9 (8.3)	73.9 (8.6)
Increment 42	1.24	6.15*	1.99*	0.5 (3.3)	3.9 (4.0)	95.7 (5.3)
Shoot	1.69	90.4***	5.74***	1.7 (2.7)	26.6 (10.6)	71.7 (10.7)
Root	1.61	58.0***	7.11***	4.0 (3.5)	28.6 (11.0)	67.3 (10.8)
Dwsr	1.53	0.39	5.54***	3.2 (3.6)	17.3 (8.5)	79.5 (9.0)
Node	2.16**	20.3***	2.61**	6.2 (4.7)	5.4 (4.5)	88.3 (6.3)
Color 2	1.17	32.9***	6.04***	1.1 (2.8)	27.0 (10.8)	71.9 (10.9)
Color 3	1.27	42.5***	3.85***	4.6 (4.0)	16.5 (8.3)	78.9 (8.5)
Maple Sweden						
Maxheight	4.09***	73.8***	4.78***	5.3 (4.2)	17.1 (8.4)	77.6 (8.9)
Increment 21	2.61**	20.6***	1.60	5.3 (4.4)	9.0 (5.9)	85.7 (7.1)
Increment 42	3.57***	13.8***	5.28***	11.5 (5.9)	14.1 (7.5)	74.4 (8.4)
Shoot	4.14***	75.4***	3.94***	7.7 (4.8)	14.3 (7.5)	78.0 (8.2)
Root	3.15***	45.6***	2.40*	6.7 (4.8)	8.1 (5.5)	85.2 (7.0)
Dwsr	1.23	2.27	3.04**	1.8 (3.3)	9.5 (6.2)	88.7 (6.9)
Node	3.07***	11.4***	4.08***	10.0 (5.5)	11.1 (6.6)	78.9 (7.9)
Color 2	1.92*	36.6***	3.11**	1.9 (3.3)	14.8 (8.1)	83.3 (8.8)
Color 3	24.8***	2.39**	3.95***	8.1 (5.1)	19.3 (9.2)	72.6 (9.6)
Birch Norway						
Height 2	2.30***	413.***	3.64***	49.3 (7.9)	4.0 (3.0)	46.7 (7.5)
Height 5	1.28	14.3***	3.76***	23.5 (7.2)	11.7 (6.5)	64.9 (8.0)
Maxheight	1.50	0.42	4.74***	10.8 (5.8)	15.0 (7.8)	74.2 (8.7)
Increment 41	2.03**	2.94	3.60***	27.2 (7.5)	9.8 (5.8)	63.0 (7.9)
Growt 94	1.54*	19.0***	5.78***	0.4 (4.1)	16.8 (8.4)	82.8 (9.5)
Maxincrement	1.50	7.42**	4.85***	2.8 (4.5)	15.5 (8.1)	81.7 (9.0)
Shoot	0.91	44.7***	2.12*	13.4 (6.2)	8.3 (5.6)	78.3 (7.4)
Root	1.44	66.6***	0.46	1.4 (4.5)	1.6 (3.2)	97.0 (5.3)
Dwsr	1.43	0.76	2.69**	10.7 (6.1)	8.0 (5.5)	81.2 (7.6)
Branch	2.24***	79.0***	3.99***	9.5 (5.6)	11.4 (6.7)	79.1 (7.8)
Birch Sweden						
Height 2	1.88**	454.***	1.65	20.6 (6.8)	12.6 (6.9)	66.8 (8.2)
Height 5	1.53*	76.7***	1.07	12.0 (6.4)	6.3 (5.1)	81.7 (7.6)
Maxheight	1.84**	58.5***	1.88	7.1 (6.0)	9.2 (6.2)	83.7 (7.9)
Increment 41	1.77*	85.4***	0.87	21.5 (7.4)	5.2 (4.2)	73.3 (8.0)
Growt 94	2.33***	37.3***	2.62**	10.8 (6.4)	11.4 (6.9)	77.9 (8.2)
Maxincrement	1.90**	2.61***	1.67	5.5 (6.1)	7.8 (5.6)	86.8 (7.8)
Shoot	1.85**	156.***	1.14	0	6.4 (5.2)	93.6 (5.2)
Root	2.44***	158.***	2.87**	0	10.8 (6.6)	89.2 (6.6)
Dwsr	1.16	6.51*	1.33	3.6 (5.6)	2.6 (3.5)	93.8 (6.5)
Branch	2.21***	101.***	1.74	1.8 (4.6)	4.1 (4.1)	94.1 (6.1)

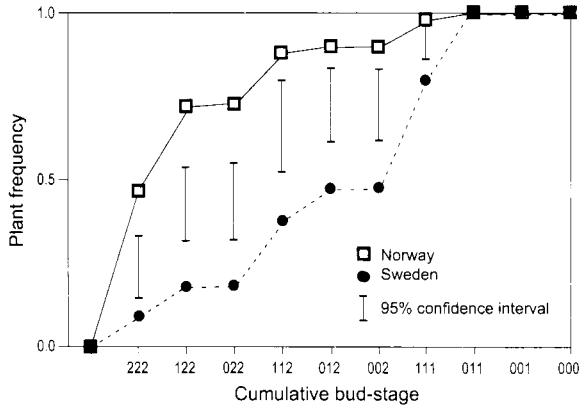

Figure 4. Cumulative bud-stages sorted after budset development during three registration occasions (Bud 2, Bud 3 and Bud 4) in silver birch cultivated under low nutrient conditions. The most developed bud-stage pattern ("222") had clear buds at all three registration times, the second most developed bud-stage pattern ("122") represents a plant beginning to develop buds at Bud 2 and with a visible bud at Bud 3 and Bud 4. The values on the y axis denote the estimated frequencies of plants which have reached at least that particular bud-stage pattern, e.g. at least 90% and 47% of the Norwegian and Swedish families, respectively have reached bud-stage pattern "012". Population differences were significant for all bud-stages except 001, as illustrated using 95% confidence intervals for the difference of the least square means. The intervals are obtained by re-transformation from the log-odds scale.

except for "001", and it was evident that budset was completed more rapidly in the Norwegian than in the Swedish population (Figure 4). Family variation was observed for the bud-stages "001" (Norway, Sweden) and "222" (Norway) (data not shown).

DISCUSSION

The effect of nutrient treatment on genetic variation

It should be noted that we have used the initial plant height at the start of the nutrient treatments as a covariate in all ANOVAs since it was significant for most traits. This was done to avoid bias caused by maternal effects. It should also be stressed that the comparisons between amounts of genetic variation within the low-N and high-N treatments were complicated by the difficulty of finding suitable occasions for joint recording of phenology traits: in silver birch, budset of all low-N plants took place within a short time-span and at an early stage. Even though high-N plants eventually completed their growth and budset, no autumn color had appeared at harvest time. Leaves of low-N plants however, were bright yellow and about to defoliate. Consequently there was a total lack of genetic variation for budset in low-N plants and for leaf color in high-N plants. For Norway maple it was also evident that budset and leaf coloring started earlier for the low-N plants than for the high-N plants. Accordingly, the assessments for Bud 1 and Color 1 were carried out only within the low-N treatment.

For both Norway maple and silver birch, the proportion of traits showing a significant population effect were lower in the high-N than in the low-N treatment. In contrast, the family genetic variation in birch in creased substantially in the high-N treatment with on average only slightly higher variance components, and the variation was attributed to the Norwegian population (Table 7). The nutrient stressed Norwegian birch seedlings were less variable in biomass allocation and had more uniform increment rates than non-stressed Norwegian families. In maple, the family variation was high within both treatments.

Our study revealed no consistent effect of nutrient stress on amounts of quantitative genetic variation with the exception of the Norwegian non-stressed silver birch families being more variable than the nutrient stressed ones for most traits. This finding would support the prediction by BLUM (1988) that heritable variation decreases under stressful conditions as a consequence of increased environmental and phenotypic variance leading to reduced heritabilities. In our experiment, the treatments were controlled to obtain equivalent and uniform conditions within each nutrient treatment which probably reduces the impact of environmental variance. Most data on size-related traits in natural populations of birds and some studies of size-related traits in *Drosophila*, indicate that heritabilities and treatment mean values decrease under environmental stress, although numerous *Drosophila* studies indicate the opposite (see references in HOFFMANN & MERILÄ 1999). In agricultural plant studies, heritabilities are reported both to decrease (BLUM 1988) and increase (CECCARELLI 1994) in relation to unfavourable growth conditions. Thus, as supported by our study, the effect of environmental stress on additive genetic variance is not clear-cut and seems to depend on the organism, type of stress environment and the traits studied.

Among population and family variation

Significant population effects were observed for fewer than half of the traits in both species (Table 4). The low number of populations makes it hard to detect population differences although the geographic distance between the Norwegian and Swedish populations was expected to result in genetic differences between these populations.

Earlier budset and leaf coloring was observed for Norwegian birch plants which also were larger and grew faster compared to Swedish plants (Figure 1). The Norwegian populations of both species are located further north than the Swedish populations. According to numerous studies of forest trees, night length is the main factor involved in growth termination and photoperiodic change and is most pronounced at high latitudes (ERIKSSON & EKBERG 2001). Consequently northern populations are generally exposed to a harsher climate and respond to shorter nights with growth cessation to prevent early autumn frost damage. The shorter growing season results in an earlier budset than is found in southern populations. The observed earlier budset of the Norwegian birch population agrees with this expectation, although the better growth of this population was unexpected (Figure 1). This growth-differentiation was non-significant and far reaching speculations are premature. In another study of genetic variation in silver birch, clinal variation in critical photoperiod was observed for growth cessation in latitudinal and altitudinal provenances (HÅBJØRG 1978). Genetic variation between families has been demonstrated in growth rhythm (e.g. ERIKSSON & JONSSON 1986, WANG & TIGERSTEDT 1993), as well as clinal responses in bud burst and dormancy release in silver birch populations of different latitudinal origin (MYKING & HEIDE 1995, MYKING 1997).

In Norway maple, population phenological differences were non-significant, but Swedish plants were taller and more fast-growing than Norwegian plants (Table 4). The literature on genetic variation in Norway maple is scarce, only few studies exist on growth and phenology traits assessed in field trials. WESTERGAARD & ERIKSEN (1997) reported that, for growth cessation, northern populations responded more rapidly to shorter nights than conspecific southern ones. Differences in growth performance have also been demonstrated between provenances (KERR & NILES 1988) and families (WESTERGAARD 1997). Using isozyme markers, RUSANEN *et al.* (2000) reported that the population differentiation in 29 Finnish populations of Norway maple were relatively high but with no geographical structuring. In fact, more genetic variation was observed among populations within geographic regions than among regions (RUSANEN *et al.* 2000).

As seen from Tables 6 and 7, the family variance components were higher in Norway maple than in silver birch. This was true for both populations and both treatments. It is noteworthy that the family variance components within the Norwegian maple population exceeded the permitted 25 % for some of the traits. This population grows close to the margin of the species distribution area and it may be speculated that pollination within this population mainly occurs among trees in small groups. This leads to genetic drift and occurrence of full-sibs in the offspring, thereby exaggerating the true family additive variance. A similar speculation was made by BALIUCKAS *et al.* (1999) in their nursery study of growth and phenology in Swedish populations of Norway maple. The family variance components in their study were lower than in the present case which agrees well with the generally larger variance components obtained under controlled than under field conditions (e.g. SONESSON 2000).

In conclusion, the estimated family variances for growth and phenology traits suggest that the maple and birch populations studied here possess the ability to respond to selection and have a high potential to cope with future heterogeneity in soil nutrient levels.

Phenotypic plasticity and genotype × environment interaction

This study clearly showed that there were strong treatment effects for all traits in both species (Table 4). Plant growth, overall size, node number (maple) and branch number (birch) were positively affected by high nutrient availability. The low-N individuals showed typical nitrogen deficiency symptoms, with pale plants and with the oldest leaves sometimes yellow. Mean values for the partitioning of biomass allocation revealed that the root system was well developed in comparison with the shoots. In non-stressed plants, roots seemed poorly developed compared with the abundant shoot biomass.

Phenotypic plasticity was also estimated as the coefficient of variation, CV. CV-values ranged from 4 to 200 in Norway maple and from 13 to 200 in silver birch. The particularly high CVs of 200 for some of the phenology traits (both species) and for branch number (birch) is explained by the mean value in one of the treatments being zero and the CVs may in these cases be exaggerated. The large variation in CV-values suggests that the assessed traits have different functions and are expressed by different genes. High phenotypic plasticity can be considered adaptive as it indicates the potential of individual plants to endure environmental variation. As regards g × e interaction, population rank changes were small in Norway maple but intermediate in silver birch. For several traits in both species, we observed significant family × treatment interaction indicating differences in family adaptedness to different nutrient availabilities for several traits. G × e interaction indicates differences among genotypes in ability to survive under environmental change and allows individuals to exploit new environments. Therefore, this interaction is regarded as important for adaptation,

particularly in long-lived trees.

To our knowledge, this is the first study to examine phenotypic plasticity, genetic variation and g × e interaction in general, and low nutrients in particular, in Norway maple and silver birch. Reaction norm parameters under controlled nutrient environments have until now only been assessed in conifers: JONSSON *et al.* (1997) reported weak family × nutrient interaction but significant family variation in seedlings of *Pinus sylvestris* for nitrogen productivity (see INGESTAD 1979 for a definition). In a growth chamber study of *Picea abies* (JONSSON *et al.* 2000), no family × nutrient interaction was observed for growth but such interaction was observed for nitrogen concentration and for the efficiency with which the plants made use of the uptaken nutrients (nitrogen utilization).

Relationship between life-history traits and genetic variation

According to the assumptions of LOVELESS & HAMRICK (1984), one would expect the insect-pollinated Norway maple, with its small and scattered populations and gravity-dispersed seeds, to show more divergence among than within populations. As for the wind-pollinated silver birch with its continuous distribution, large population sizes and wind-dispersed seeds, genetic variation would be expected to be high both within and between populations. Moreover, birch exhibits important outcrossing mechanisms such as self-incompatibility and dichogamy which promote within-population genetic variation. Based on these assumptions, a higher among family variance was expected for silver birch than for Norway maple. Scrutiny of the family variance components in Tables 6 and 7 clearly shows that there is no support for this assumption. Even if there are some differences in the traits analysed in the two species, it is evident that family variance components are generally higher in Norway maple than in silver birch. One explanation might be that, although the seeds of Norway maple are relatively heavy, the samaras use microgeographical winds to promote gene flow as has been reported for *Acer saccharum* (GREENE & JOHNSON 1992). In addition, we speculated above that some of our Norway maple seedlings were full-sibs rather than half-sibs. Even if all Norway maple seedlings are assumed to be full-sibs and all silver birch seedlings are assumed to be half-sibs, the heritabilities would be of the same magnitude but certainly not higher in silver birch than in Norway maple. Based on our data, it is probably premature to reject the hypothesis of a larger genetic within-population variation of a species with the life-history traits of silver birch than in a species with the life-history traits of Norway maple. Studies of quantitative genetic variation should be complemented with detailed studies of the mating pattern (i.e. the zygotes formed in a population) in populations of the two types of species in order to shed light on the validity of this hypothesis.

Concluding remarks

This study of first-year seedlings of Norway maple and silver birch demonstrated high phenotypic plasticity in growth and phenology traits in response to nutrient stress. The nutrient treatments had no consistent effect on amounts of additive genetic variation except for a higher family differentiation within the Norweigan birch population in the high-N than in the low-N treatment. Judging from the significant family and/or population differentiation, as well as from the family rank changes, both species seem to possess the ability to respond to selection and to cope with changes in soil nutrient levels. The impact of the species' life-history traits on their genetic structure was ambiguous. Joint studies of isozyme diversity and additional quantitative genetic data from a field trail in the same populations of Norway maple and silver birch as were included in this study are underway and will further reveal the partitioning of genetic variation assessed in isozyme markers and in fitness-related traits.

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