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Genetic variation in nutrient response functions

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Summary. Genetic differences in the non-linear growth response function of *Pinus sylvestris* seedlings to five nutrient levels are analyzed to estimate the causes of variation. Analyses of genotypic differences as quadratic response functions, as stability coefficients, and as separable functions indicate that the estimation of genetic effects can vary widely depending on the analytical model assumed. The existence of different reaction norms is demonstrated.

Key words: Nutrient response – Genetic variance – Genotype × environment interaction – *Pinus sylvestris* – Seedling growth

Introduction

At low levels of soil nutrients, pine seedlings respond strongly and positively to nutrition supplements. At levels above optimum, growth can be reduced if seedlings are over-fertilized to the point of salt toxicity (Kramer and Kozlowski 1979). This general form of response varies among genotypes (Squillace 1970; Goddard et al. 1976; Jahromi et al. 1976; Jonsson et al. 1992; Mason and Pelham 1976; Bevege 1981; Li et al. 1991). For example, open pollinated *Pinus taeda* families differ in their height growth response to urea fertilization (Roberds et al. 1976). In some families height growth is not strongly affected by urea applications, while in other families there is a strong monotonic response or a growth depression around an optimum. Thus, various patterns of family response exist, heritable differences occur, and the variance among families differs among nutrient levels.

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To analyze gene effects and variances, the nutrient response function of each genotype and the differences among genotypes are usually linearized and estimated using standard forms of analysis of variance. Any failure to fit additivity is included in an interaction effect. Polynomial models may be fitted to the data, or stability parameters may be estimated (McKeand et al. 1990) to discriminate among response levels. However, since the responses of any genotype to nutrients are rarely linear, and may be inherently non-linearizable, attempts to force linearity can be misleading (Knight 1970; Namkoong 1978, 1980) and may produce results useful only for descriptive purposes (Lin et al. 1986). Thus, Baker (1988) concludes that "regression analysis has *not* helped develop a better understanding of the nature of genotype-environmental interaction, nor of how to cope with interactions in breeding programs."

It would, therefore, be desirable to characterize how gene effects change the response to nutrient additions. When nutrient responses are nonlinear, genotypes usually cannot be characterized as having a simple constant difference at all nutrient levels. Neither do they usually differ by a constant multiplier of the nutrient level. In fact, there is no obvious way to characterize the differences in response functions among genotypes. To analyze genotypic difference in response functions, consider the simplest case where responses are actually linear. In that case it is possible that over j nutrient levels (x_j), the response function $f(x_j)$ is the same for all i genotypes except that responses differ either by a simple constant, a_i, or as a multiple, b_i, of the basic response. Then, the genotypic growth responses, y_{ij}, can be characterized by

$$y_{ij}=a_i+b_i f(x_j) \quad (1)$$

This expression simplifies to an additive or multiplicative growth model of nutrient levels if $f(x_j)=x_j$ (see e.g.,

Freeman and Perkins 1971). It is also equivalent to the models of Finlay and Wilkinson (1963), in which $f(x_j)$ is defined as the mean response of genotypes at test sites with unmeasured x_j. Deviations from the fitted model are attributed to an instability of response (Shukla 1972). Thus, stability models assume an inherent genetically additive effect on whatever average response function may actually exist. If $f(x_j)$ is a polynomial function of x, then the first two parameters still reflect this linear fit. For any $f(x_j)$, a genetically multiplicative effect could be modelled by simply replacing the plus with a multiplication operation.

There are, of course, many other forms of gene effect that may influence differences in nutrient response functions not describable by a linear operation. Genotypes could differ in maximal or asymptotic levels of growth reflecting some limits in abilities to obtain or use nutrients, and they could differ in the rate at which nutrient increments allow trees to reach their maximal response. For such effects, the growth function $f(x_j)$ may be logarithmic while genotypes differ multiplicatively (a_i) and exponentially (b_i). For example:

$$y_{ci} = a_i\,[f(x_j)]^{bi} \tag{2}$$

Obviously there are many other forms of joint genotypic and nutrient effects. If there are functional relationships among g_i genotypes, then the genetic effects may also be described as $\gamma\,(g_i)$ functions, and the analytical problem is to describe $f(x_j)$, $\gamma\,(g_i)$ and the operation of their joint effects on growth as

$$y_{ij} = \gamma\,(g_i) \times f(x_j) \tag{3}$$

While genotypic and nutrient effects are not as simply separated as in linear models, they may be separable and estimable (Gregorius and Namkoong 1986, 1987). If we write $f(x_j)$ as ε (e), and y_{ij} as Ω, our bivariate notation can be seen to be the same as Gregorius and Namkoong's. As they suggest, the measure of genotypic and environmental effects depends on the form of these joint effects on growth. Therefore, what we estimate as genotypic effects and variances depends on the model of joint genotypic and nutrient effects. By discerning the joint operation, we may be able to understand the joint actions of genotypes and environments and be able to better cope with them in breeding programs.

Analyses

For this paper, we analyzed the stem dry weight and height growth responses to five nutrient levels in phytotron-grown seedlings of *Pinus sylvestris*. These data were derived from a nearly completely balanced, eight-replicate phytotron experiment. Ten female parents were crossed with four common males to produce a total of 35 families (Fig. 1). The parents, their mating design, and the nutrient (N) treatments in this phytotron experiment over three growth periods are described by Jonsson et al. (1992). The nutrient solution used as a standard in the phytotron was diluted to concentrations of 5, 15, 25, 35, and 45 mg. N per liter. Jonsson et al. (1992) report that there is a strong relationship between the nitrogen level applied and the amount of nitrogen available to the roots. Milligrams of nitrogen was our independent variable and mean growth of seedlings in each family, in all replications, was the dependent variable. We estimated the mean female family effect over the three or four crosses in which it was the maternal parent. Male effects are not estimated in these analyses but see Jonsson et al. (1992) for the analysis of the complete model. Hereafter, we refer to family effects by their female parent designation as modified from Jonsson et al. (1992). When analyzed for each nutrient level separately, significantly different genotypic effects for total stem dry weight and for total height exist at least at the higher nutrient levels (Table 1).

Table 1. Female mean stem dry weight and height response to nutrients

Female	Mean stem dry weight (g)					Mean height (mm)				
	Concentrations of N (mg/l)					Concentrations of N (mg/l)				
	5	15	25	35	45	5	15	25	35	45
2	0.548	2.421	3.267	5.004	2.867	100.8	241.9	288.5	344.5	306.0
3	0.438	1.952	2.229	2.992	3.717	112.5	234.7	278.6	305.4	341.1
4	0.528	2.116	2.316	2.744	3.597	130.2	245.1	280.6	302.5	379.7
5	0.625	2.854	2.717	3.592	2.333	132.0	275.8	293.0	320.3	306.0
6	0.859	3.674	4.609	5.381	5.197	131.2	296.6	335.1	363.0	388.1
7	0.566	2.422	3.758	3.884	3.578	131.2	253.8	319.2	331.2	347.5
8	0.533	2.568	3.242	4.138	4.133	129.9	272.0	306.0	331.0	343.9
9	1.009	3.500	4.690	5.112	4.562	172.2	297.7	366.7	379.3	384.2
10	0.579	3.488	4.467	5.312	4.833	136.6	308.8	356.0	376.0	385.5
11	0.619	2.874	3.709	4.556	3.562	137.1	277.4	340.1	375.2	356.1
Genetic variance	0.026	0.0183	0.0418	0.0506*	0.0216**	285.18**	457.21**	660.07**	569.71**	516.00*

* Significantly greater than zero at the 0.05 level of probability
** Significantly greater than zero at the 0.01 level of probability

Since female families differed significantly in their growth responses, we considered analyses of models of the form of Equations (1) and (3). For linear joint effects, we fitted a quadratic model and contrasted those results with a stability analysis. For nonlinear joint effects, we used a transformation developed by Gregorius and Namkoong (1986) and arbitrarily chose a reference genotype (g_0), and scaled the growth of the other genotypes to that of the reference. The growth of g_0 was used as if it were the independent variable, and every other genotype's growth was estimated as the dependent variable. The growth of g_0 was thus transformed to a straight 45° line with an intercept at the origin, and all other genotypic responses were scaled relative to g_0. If genotypes differ linearly for whatever $f(x_j)$ may be represented by g_0, their resulting responses in this transformation would appear as parallel 45° lines. If the differences were linear in the sense of (1), but were multiplicative, so that the b_i differed, then the transformations would appear as straight lines with different slopes. If genotypic effects were not thus linearizable, their graphs would be nonlinear, and could be better understood to affect nutrient response by some other mathematical function.

Fig. 1. The mating design for the 35 families. Identification numbers are revised from Jonsson et al. (1992)

Female	Male			
	3	5	8	10
2	x	x	x	
3		x	x	x
4	x	x	x	x
5	x		x	x
6	x	x	x	x
7	x	x	x	x
8	x	x		x
9	x	x	x	x
10	x	x	x	
11	x	x	x	x

Results and discussion

Fitting a quadratic model to the female families,

$$Y_{ij} = a_i + b_i x_j + c_i x_{ij}^2, \quad (4)$$

resulted in all mean female responses being apparently well approximated with R^2 ranging from 0.870 to 0.998 (Table 2). The variances among females for the a_i, b_i, and c_i parameters indicate that no significant differences exist for stem dry weight. Significant differences for height growth exist only for the a and b parameters. Though not significantly different for dry weight, females 4 and 3 have the highest a_i, while females 10 and 9 have the highest b_i. For height, females 9 and 4 have the highest a_i, while 10 and 11 have the highest b_i. No outstandingly good female can be identified (Fig. 2).

A linearizable model of genotypic and nutrient effects can also be considered, though $f(x_j)$ appears to be strongly nonlinear. That is, equation (1) can be considered to model how genetic variations affect $f(x_j)$. Since the Finlay-Wilkinson analysis parameterized genotypic differences as linear responses to the average response at each treatment level, we fit the female data for the stability parameters and for Shukla's deviations from linearity (Fig. 3). These estimates (Table 3) indicate that females 6, 10, and 11 are more responsive in height, while 4 and 5 are less responsive. In stem dry weight, females 3, 4, and 5 are less responsive than average. While the linearized fit for both traits has high R^2, the pooled error of estimate for the parameters is high. Duncan's Multiple Range Test fails to demonstrate that any of these differences for either trait are statistically significant. While significant growth differences exist at some nutrient levels (Table 1), the apparent differences in female response functions cannot be significantly distinguished.

Table 2. Female parameters for quadratic function

Female	Stem dry weight				Height			
	Parameters fit				Parameters fit			
	a	b	c	R^2	a	b	c	R^2
2	−0.1216	3.311	−5.1429	0.8702	0.03785	1.652	−2.328	0.9833
3	0.0035	1.150	−0.7800	0.9645	0.06527	1.202	−1.350	0.9758
4	0.0192	1.120	−0.8871	0.9292	0.08812	1.096	−1.250	0.9651
5	−0.0425	2.545	−4.2600	0.8743	0.07450	1.485	−2.186	0.9466
6	−0.0522	3.238	−4.4007	0.9872	0.06915	1.622	−2.085	0.9581
7	−0.0710	2.725	−3.9529	0.9960	0.06279	1.531	−2.014	0.9969
8	−0.0441	2.255	−2.7557	0.9858	0.07379	1.441	−1.907	0.9642
9	−0.0484	3.318	−4.8929	0.9983	0.10298	1.573	−2.136	0.9911
10	−0.0945	3.501	−4.9357	0.9885	0.06338	1.832	−2.836	0.9664
11	−0.0800	3.073	−4.6329	0.9807	0.05796	1.772	−2.471	0.9964
Genetic variance	0	0.008	0		0.002580**	0.2013*	0	

* Significantly greater than zero at the 0.05 level of probability
** Significantly greater than zero at the 0.01 level of probability

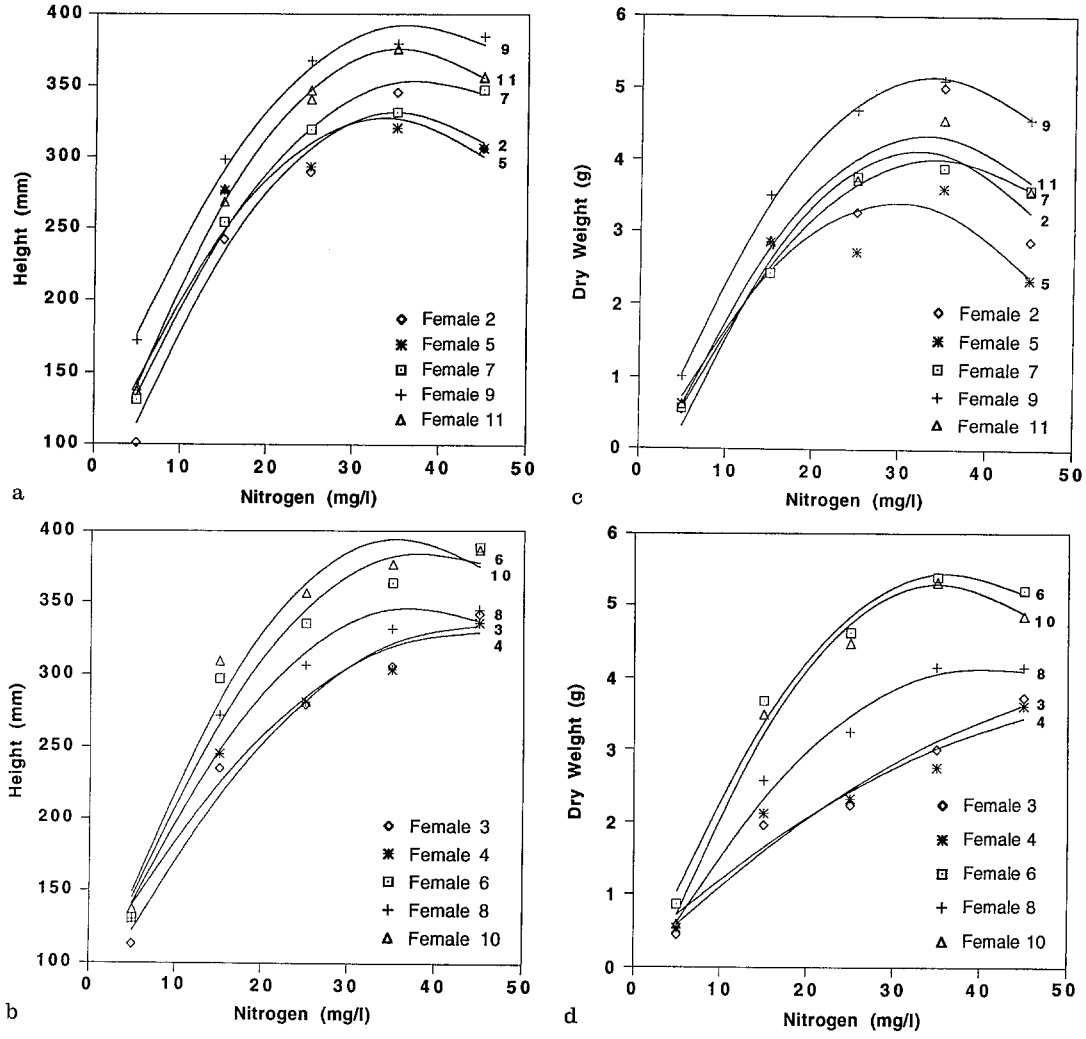

Fig. 2a–d. Quadratic function fit for female family response to five nutrient levels. **a** Height of female families 2, 5, 7, 9, 11; **b** Height of female families 3, 4, 6, 8, 10; **c** Stem dry weight of female families 2, 5, 7, 9, 11; **d** Stem dry weight of female families 3, 4, 6, 8, 10

In terms of the departure from linearity estimated by Shukla's test, females 2, 4, and 5 are identifiable as contributing most of the nonlinearity in both traits. Females 7, 8, and 9 are least irregular, while 3, 6, 10, and 11 are moderately irregular.

Considering the Finlay-Wilkinson and the Shukla analyses for both traits, females 4 and 5 have lower than average growth responses to nutrient increments accompanied by irregular departures from the average response function. Only female 9 combines a high mean with a relatively low sensitivity and low irregularity. Females 6 and 10 have relatively high means but also seem to be more sensitive to nutrient level and are somewhat irregular in that response. Females 2, 4, and 5, on the other hand, have relatively low mean growth and high variability. They could be conjectured to be in a different class of response functions than the other females, since their responses do not conform to a linear fit. The remaining females (3, 7, 8, and 11) could be thought to belong to an average growth class with moderate responsiveness. However, the failure of the multiple range test to reveal statistically significant differences in any of the parameters for the ten females implies that our test is too insensitive to clearly detect any such genotypic effects as may exist.

In contrast, using the Gregorius-Namkoong transformation, separation of the female responses could not be achieved in less than two sets. However, two sets of five females each could be formed for which, with the exception of females 2 and 4, the response curves do not appear to intersect. These two sets (A and B) are females 3, 4, 6, 8, 10 and 2, 5, 7, 9, 11, respectively (Fig. 4). Hence, two classes of response are hypothesized to exist. In both sets and for both traits, there is less variance among genotypic means at low and high levels of response to nutrition (Table 1), suggesting that the linear model of

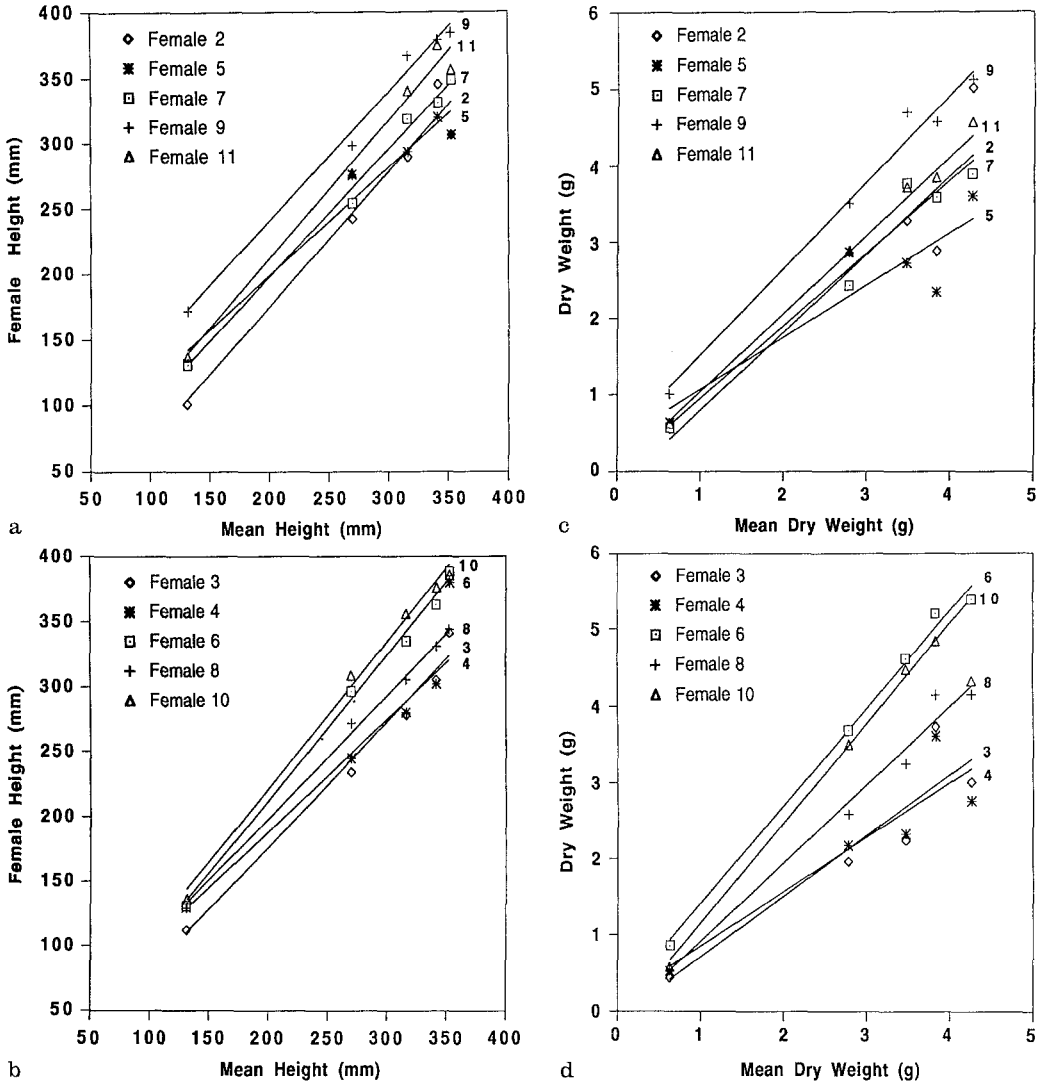

Fig. 3a–d. Linear fit of female families to mean response at five nutrient levels. **a** Height of female families 2, 5, 7, 9, 11; **b** Height of female families 3, 4, 6, 8, 10; **c** Stem dry weight of female families 2, 5, 7, 9, 11; **d** Stem dry weight of female families 3, 4, 6, 8, 10

genotypic effects may not be a good approximation. For both sets, the exponential function suggested by Gregorius and Namkoong (1986) fits the data better in the sense that a two-parameter model has higher R^2 values for all females (Table 4). The model we fit is:

$$Y_{ij}=a_i\{1-[(a_i-x_j)/a_i]^{b_i}\} \quad (5)$$

This is an exponential model for genotypic effects. If $b_i>1$, then a_i is the maximum height or weight that genotype i can attain and still have greater height or weight than the base genotype. If $b_i<1$, then a_i is the maximum height or weight that genotype i can attain and still have smaller height or weight than the base genotype. In the model, the a_i expresses the range of sizes on the domain of nutrients over which superiority or inferiority is maintained, and the b_i is the rate at which the difference between genotype i and the base genotype is reduced. It is assumed that no growth occurs if nutrients are absent. We tested all females for service as the base genotype and found that female 3 in Set A and female 11 in Set B provide the highest R^2 for fitting all other females. We estimate a_i and b_i by Marquardt's procedure using the NLIN estimation procedure from SAS. The values for these fits are listed in Table 4.

Set A

In Set A, the responses of all females are well approximated by the exponential model of genotypic effects. Females 3 and 4 are very similar in all respects, since b_4 is very close to 1.0. Responses of females 6 and 10 are larger since a_6 and a_{10} are large, but in both traits they

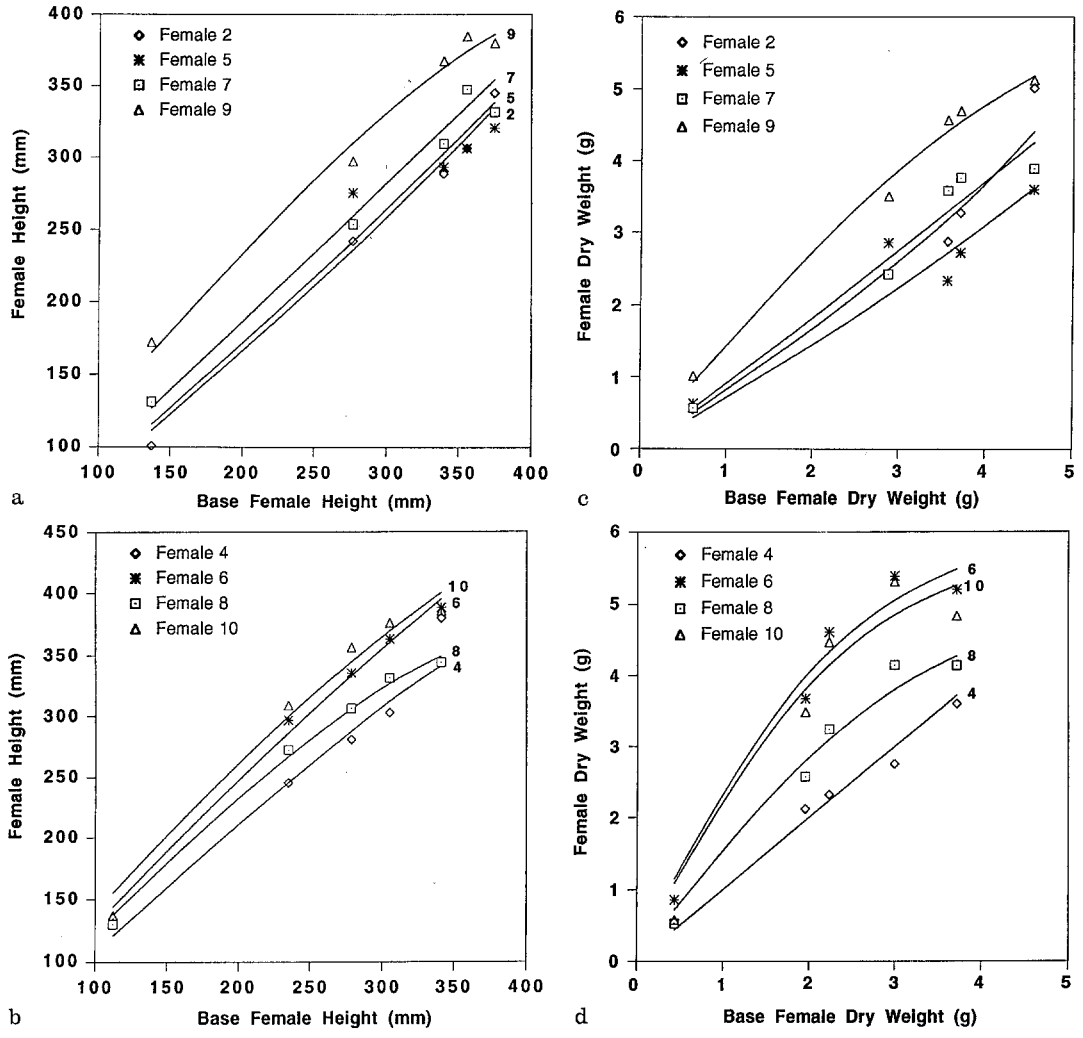

Fig. 4a–d. Nonlinear fit of female families to response of base families. **a** Height of female families 2, 5, 7, 9 relative to base family 11; **b** Height of female families 4, 6, 8, 10 relative to base family 3; **c** Stem dry weight of female families 2, 5, 7, 9 relative to base family 11; **d** Stem dry weight of female families 4, 6, 8, 10 relative to base family 3

also are more responsive to nutrients than 3 since both b_6 and b_{10} are large.

Based on pooled estimates of error variances, Duncan's Multiple Range Tests were run to estimate significant differences among families in a_i and b_i. For dry weight, the a_i coefficient for female 6 is significantly larger than that for female 4. It is also larger than that for the other females but not significantly so. By an approximate t-test, female 10 also has a significantly higher a_i coefficient than female 4, but is not significantly different from females 6 and 8. Thus, females 6 and 10 form a distinct set with a high a_i. The other females, including the intermediate female 8, are not statistically distinguishable from each other.

Unlike the a_i coefficients, the b_i coefficients are not significantly different for dry weight. While the pattern of females 6 and 10 having larger coefficients than the others, with female 8 being intermediate, holds for the b_i coefficients as well, the differences are not large enough to detect, given the standard error of the estimates. This contrast between the relative magnitude of the standardized differences between the a_i and b_i coefficients implies that genotypic differences most strongly affect the range of nutrients over which differences can be attained, and less strongly affect the rate at which those differences change.

In set A, the same basic segregation of response types exists for height growth as for dry weight. Females 3 and 4 have similarly low responses to nutrients while females 6 and 10 have strong responses and female 8 is intermediate. Duncan's Multiple Range Test did not indicate any significant differences among the b_i coefficients. Among the a_i coefficients, females 6 and 10 are significantly higher than female 8, and 8 is significantly higher than

Table 3. Stability and variance parameters

Female	Height			Stem dry weight		
	Stability b_i	S.E. (b_i)	σ_i^2 (Shukla)	Stability b_i	S.E. (b_i)	σ_i^2 (Shukla)
2	1.02	0.107	2,636	1.02	0.246	0.035*
3	0.96	0.077	1,398	0.79	0.186	0.029
4	0.86	0.072	2,609	0.71	0.178	0.035*
5	0.82	0.093	4,570**	0.68	0.198	0.043*
6	1.11	0.052	1,431	1.27	0.053	0.015
7	0.97	0.042	302	0.95	0.095	0.004
8	0.94	0.034	331	1.02	0.081	0.002
9	0.98	0.047	375	1.13	0.080	0.005
10	1.12	0.049	1,569	1.30	0.035	0.018
11	1.05	0.068	1,127	1.02	0.091	0.003
Pooled SE		0.071			0.145	

* Significantly greater than zero at the 0.05 level of probability
** Significantly greater than zero at the 0.01 level of probability

Table 4. Female parameters for exponential effects model

Female	Stem dry weight			Height		
	a_i	b_i	R^2_{exp}	a_i	b_i	R^2_{exp}
Set A						
4	0.3903	0.9818	0.9986	341.0	1.089	0.9994
6	0.5802	2.8236	0.9989	527.7	1.329	0.9992
8	0.4503	1.6975	0.9986	354.8	1.286	0.9998
10	0.5552	2.6665	0.9970	473.6	1.465	0.9983
Pooled SE	0.0439	0.8209		22.28	0.2276	
Set B						
2	0.4705	0.7959	0.9922	486.1	0.7874	0.9993
5	0.7000	0.6900	0.9767	524.0	0.8283	0.9947
7	0.8000	0.8990	0.9908	747.4	0.9206	0.9994
9	0.5596	1.5350	0.9982	394.7	1.2718	0.9993
Pooled SE	0.1989	0.6215		60.88	0.2769	

females 3 and 4. Otherwise, the difference in the a_i coefficients between 3 and 4 is not significant, nor is the difference between 6 and 10. Thus, the relatively large differences in the a_i coefficients again support an argument for genotypic effects to be most strongly expressed in the different ranges of response and less clearly in the rate of response.

All females conform to the same functional forms of response, but females 6 and 10 are distinct from females 3 and 4, while female 8 lies between, at least in the range of responses over which growth differences are maintained. The response function of the base female 3 to the range of nutrient levels is as close to linear as any of the females. Hence, $f(x_j)$ can be approximated by a linear function of nutrients. The way that genotypes differ from the base genotype for females 4, 6, 8, and 10, however, is better described as exponential for both dry weight and height, with strongest discrimination expressed by the range over which the females differ.

Set B

In set B, the exponential functions fit very well, and the R^2 values are always better than for the linear stability analysis. Female 9 is relatively highly responsive while females 2 and 5 are low and females 7 and 11 are intermediate. As in set A, the parameter differences among females relative to the standard errors of estimate are relatively larger for the a_i than for the b_i coefficients. However, the differences in a_i are statistically significant only in height growth. In contrast to set A, the female with the highest b_i (9) has a significantly lower a_i coefficient than the female with the highest a_i (7). Since female 7 has a b_i coefficient less than 1 for both traits, and the highest ranking a_i coefficient, it is both lower in growth than base female 11 and is lower over a broader range of nutrients than others. Hence, female 7 can be identified as a poor choice for growth. In contrast, female 9 may have a better growth than female 11, but it is not significantly more responsive than others, and is superior over a relatively small range of nutrients. Thus, female 9 is not predicted to be an unequivocally good choice for growth for a wide range of nutrient conditions.

The responses of all females in this set are well described by a single response function. Female 7 is the only distinctive female in the range of nutrients over which it grows relatively poorly. The response of base female 11 to the experimental range of nutrients is non-monotonic and is better described as quadratic rather than linear. The $f(x_j)$ can be approximated by a quadratic function of nutrient level, but the genotypic effects of females 2, 5, 7, and 9 are better described as exponential for both height and dry weight. However, strongest discrimination is expressed in the range at which female 7 grows relatively poorly.

Conclusions

For both sets A and B, genotypic differences are most sharply discriminated by the range over which growth superiority or inferiority is predicted. In both sets, female differences relative to the standard error of estimate of the coefficient are more strongly expressed in height than in dry weight. While the females tended to maintain the same parameter rankings for the two traits, the distinctive females (6, 10) in set A had both larger a_i and b_i coefficients with $b_i > 1$; in set B, the distinctive female (7) had a moderate b_i less than 1, but the largest a_i coefficient. Thus in set A, the relatively superior mean sizes of females 6 and 10 are likely to be maintained over a wide

range of nutrient concentrations and they respond relatively strongly to nutrient increments. However, in set B, the relatively poor growth of female 7 is predicted to persist. In both sets, height growth is more responsive to nutrient variations than is dry weight, and all female response functions are well fit as exponential departures from their base female responses.

In contrast to the stability analyses, our nonlinear analysis shows that female 9 is not a generally superior performer over a wide range of nutrient concentrations. While both analyses identify females 6 and 10 to be superior in dry weight and height, our analysis can also predict that their superiority will be maintained over a wide range of nutrient concentrations. The stability analysis can only predict a high responsiveness and higher-than-average deviations from the linear fit. No females are identified in our analyses as failing to fit within the range of the two-parameter response functions we used. All females would appear to display predictable effects and genetic variation could be described in terms of one or two parameters.

While we can claim that our model is better than those that force linear genotypic effects, we cannot claim that our model is uniquely descriptive. Some models with more than two parameters could fit the data better than ours does. If we had chosen different base genotypes, other nonlinear functions or even other exponentials might provide better fits. Wider genotypic sampling and experimental breeding is needed to support any claims of improved approximations to true genotypic differences. Nevertheless, nonlinear parameterizations such as ours can give different insights and possibly more useful functions for breeding than can linear functions. The methods used allow breeders to examine a wider range of functional operations that can describe genotypic and environmental effects and a wider range of environmental norms of reaction without resort to a non-analyzable interaction component.

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