

## Quantitative genetic analysis in *Phalaris tuberosa*

### III. Maternal effects on seedling growth and development

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#### SUMMARY

The genetic basis of variation in rate of seedling growth and development has been examined in the Australian commercial population of *Phalaris tuberosa*. A model of additive genetic maternal effects has been used, with seed weight of the female parent as an index of maternal ability. Rate of leaf appearance, rate of tillering and growth per tiller are all genetically variable in the population, with estimated heritabilities of 0.36, 0.23 and 0.34 respectively on an individual seedling basis. Total seedling growth has a lower heritability (0.17), due to a negative genetic correlation between tiller production and growth per tiller ( $-0.46$ ). These two components have also been shown to be subject to qualitatively different seed size maternal effects. Genetic differences in seed size in the female parent have been found to influence growth per tiller, while environmental differences in seed size affect primarily the rates of leaf appearance and tiller production.

#### 1. INTRODUCTION

A quantitative theory of genetically determined maternal effects in random-breeding populations has been developed by Dickerson (1947) and Kempthorne (1957) for non-epistatic genes. Kempthorne's theory allows for an arbitrary degree of dominance in respect of direct *and* maternal effects on a quantitative character but the expectations of observable covariances among relatives depend on a total of nine parameters if environmental maternal effects are included. The parameters cannot therefore be estimated from observations of sire-offspring, dam-offspring, full-sib and half-sib covariances alone, unless simplifications of the model can justifiably be introduced.

In earlier papers of this series, the genetic basis of differences in seedling growth rate in the Australian commercial population of *Phalaris tuberosa* has been studied (Latter, 1965*a, b*), using a model of *additive* genetic maternal effects. Mean seed size, measured as the weight of a sample of seed produced by an individual plant, has been shown to be highly correlated with maternal ability (Latter, 1965*b*; McWilliam & Latter, 1970). Since the additive genetic variance in seed weight is almost 80% of the total phenotypic variance among the parental individuals in the population, the model assumes dominance effects to be unimportant for seed

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weight and for the resultant genetically determined maternal effect on seedling growth rate (Latter, 1965*a*).

The present paper deals with seven physiological components of seedling growth and development in the same population, measuring rates of tillering, of leaf appearance and of growth per tiller. Three main questions are of interest:

- (1) Which variables are most subject to maternal influence?
- (2) Do the traits differ in the relative importance of genetic and environmental maternal effects due to seed size?
- (3) What is the nature of the maternal, genetic and environmental relationships among the seven components?

Recent studies with *Lolium multiflorum* and *L. perenne* have shown maternal effects to be significant for some components of seedling growth (Edwards & Emara, 1969; Edwards, 1970) but no attempt has been made to separate *environmental* from *genetic* maternal effects. The importance of the present analysis lies in the demonstration of a *qualitative* difference between the two in their effects on seedling growth and development.

## 2. RÉSUMÉ OF THEORY AND PROCEDURES

*Phalaris tuberosa* is a wind-pollinated perennial grass species showing a high level of self-incompatibility. Quantitative genetic analysis of a character of high heritability, namely seed weight, has shown no evidence of self-fertilization under open pollination (Latter, 1965*b*), and selfing has therefore been ignored in the genetic model used in the analysis. The model assumes the observed phenotypic value of the character subject to maternal influence (seedling growth rate or one of its components) to be the sum of (i) an additive genetic value, (ii) a dominance effect, (iii) an additive genetic maternal effect, (iv) an environmental maternal effect, and (v) an independent environmental deviation. The phenotypic value of the trait related to maternal ability (seed weight) is supposed to be the sum of (i) an additive genetic value and (ii) an independent environmental deviation.

It should be noted that the genetical model used in these analyses does not allow for the possibility of *paternal* effects on seed size. A small but highly significant effect of this sort has been reported by Bingham (1966) in wheat, involving parental varieties of markedly different grain size.

Seed weight has a heritability of  $0.79 \pm 0.06$  in the Australian commercial population, based on the covariance of maternal parent and offspring scored in separate years (Latter, 1965*b*). The *repeatability* of seed weight, estimated from samples of seed harvested from the same plants in different years, must therefore be due almost entirely to genetic factors rather than permanent environmental differences among individuals (Falconer, 1960). The covariance of maternal seed weight and offspring seedling growth normally includes both genetic and environmental maternal effects, since the measure of seed weight is taken from the seed sample used to produce offspring: a covariance of this sort is denoted by  $\text{cov}(D, O)$ . In a perennial species, however, the seed weight determination may be repeated using samples of seed collected from the female parent in later years, and the

covariance of dam seed weight and offspring seedling growth will then include only genetically determined maternal effects, plus any *permanent* environmental maternal influence: such a covariance is herein denoted by  $\text{cov}(D^*, O)$ . The expectations of all covariances used in this paper are given as equations 13–23 by Latter (1965*a*), and will be referred to directly by number.

Table 1. *Observed and derived variables involved in the analysis of maternal effects on seedling growth and development*

No.	Character	Scale of measurement	Mean	Standard deviation	c.v. (%)
$x_1$	Flowering date	Days after November 1	25.4	4.3	—
$x_2$	Seed weight	50 seed wt. (mg)	79.5	9.3	11.7
$x_3$	Seedling weight	Log <sub>10</sub> dry wt. (cg)	1.72	0.16	38.2‡
$x_4$	Time to 3rd leaf†	Leaves per day	0.193	0.017	8.7
$x_5$	Time to 6th leaf†	Leaves per day	0.190	0.015	7.9
$x_6$	Time to 1st tiller†	Tillers per day	0.040	0.005	12.1
$x_7$	Tiller number	Count at seedling harvest	7.34	1.89	25.8
$x_8$	Rate of leaf appearance	Leaves per day	0.188	0.020	10.4
$x_9$	Rate of tiller production	Tillers per day	0.152	0.040	26.2
$x_{10}$	Growth per tiller	Log <sub>10</sub> dry wt. (cg)	0.87	0.14	33.0‡

† Measured from the time of sowing pre-germinated seed.

‡ Coefficients of variation on the untransformed scale of measurement.

The data analysed in this paper are derived from experiments 2 and 4 of Latter (1965*b*). Experiment 2 involves 200 *maternal half-sib* families derived by open pollination (family size 21), whereas experiment 4 deals with 134 *full-sib* families produced by random pair-crossing, seed having been collected only from the designated *female* parent of a cross (family size 18). Seedling observations in each experiment were made on three separate replications sown through the late summer and autumn, providing three contrasting natural temperature regimes. The characters measured are listed in Table 1. Flowering date ( $x_1$ ) was scored as the day on which the third ear commenced to emerge from the leaf sheath. Seed weight ( $x_2$ ) refers to the weight in milligrams of 50 mature seeds shaken from heads of the plant concerned. Seedling weight ( $x_3$ ) was determined by harvesting the top growth of individual seedlings at approximately 2 months' of age: tiller number ( $x_7$ ) and growth per tiller ( $x_{10}$ ) refer to the date of seedling harvest. Rate of leaf appearance ( $x_8$ ) has been calculated from the number of days elapsing between the emergence of the 3rd and 6th leaves. Rate of tiller production ( $x_9$ ) refers to the period between emergence of the first tiller and final seedling harvest.

### 3. RESULTS AND DISCUSSION

The correlations among relatives estimated for the eight seedling variables are set out in Table 2, together with three derived statistics for each character. (i) The heritability ( $h^2$ ) of a trait subject to maternal influence includes only the *permanent*

Table 2. Correlations among relatives and derived statistics for the eight measures of seedling growth and development

Character	Correlations among relatives†			Derived statistics‡		
	$\tau(S, O)$	$\tau(D^*, O)$	$\tau(FS)$	$\tau(HS)$	$4[\tau(FS) - \tau(HS)]$	$\tau(HS) - \frac{1}{4}h^2$
$x_3$	0.093 ± 0.037	0.076 ± 0.037	0.109 ± 0.024	0.084 ± 0.015	0.169 ± 0.053	0.042 ± 0.020
$x_4$	0.125 ± 0.044	0.027 ± 0.045	0.164 ± 0.034	0.071 ± 0.013	0.152 ± 0.084	0.033 ± 0.021
$x_5$	0.214 ± 0.044	0.114 ± 0.045	0.168 ± 0.036	0.117 ± 0.017	0.328 ± 0.084	0.035 ± 0.023
$x_6$	0.125 ± 0.045	0.071 ± 0.045	0.179 ± 0.035	0.079 ± 0.014	0.196 ± 0.063	0.030 ± 0.021
$x_7$	0.161 ± 0.043	0.109 ± 0.043	0.166 ± 0.032	0.096 ± 0.015	0.270 ± 0.062	0.028 ± 0.022
$x_8$	0.231 ± 0.042	0.129 ± 0.043	0.147 ± 0.033	0.106 ± 0.016	0.360 ± 0.061	0.016 ± 0.022
$x_9$	0.143 ± 0.039	0.087 ± 0.039	0.115 ± 0.027	0.086 ± 0.014	0.230 ± 0.056	0.028 ± 0.020
$x_{10}$	0.147 ± 0.042	0.196 ± 0.041	0.166 ± 0.031	0.132 ± 0.018	0.343 ± 0.060	0.046 ± 0.023
Means	0.155	0.101	0.152	0.096	0.256	0.032

† Denoting respectively the correlations of sire and individual offspring, dam and individual offspring, of full sibs and half sibs.

‡ The three derived statistics are (i) the heritability [ $h^2 = \tau(S, O) + \tau(D^*, O)$ ]; (ii)  $4[\tau(FS) - \tau(HS)]$ , a measure of total genetic variance

excluding maternal effects; and (iii)  $[\tau(HS) - \frac{1}{4}h^2]$ , a statistic which is expected to be equal to zero in the absence of environmental and genetic maternal effects (Latter, 1965a).

contribution of parents to the performance of their offspring (Latter (1965*a*), equation 19), and is estimated as the sum of the sire-offspring and dam\*-offspring correlations (Latter (1965*a*), equations 17, 23). (ii) The statistic  $4[r(FS) - r(HS)]$  measures the total genetic variance excluding maternal effects, i.e. the additive genetic + dominance variances, as a fraction of the total phenotypic variance. (iii) The difference between  $r(HS)$  and  $\frac{1}{4}h^2$ , on the other hand, measures only the variance due to environmental maternal effects, plus a major fraction of that due to genetically determined maternal effects (Latter (1965*a*), equations 19, 21).

The data of Table 2, considered in isolation, illustrate the extreme difficulty of a detailed analysis of maternal effects. The eight variables have a mean heritability among individuals of 0.256, with coefficients of variation in the range 8–38% (Table 1). The estimates of total genetic variance as a fraction of the total phenotypic variance average 0.222, and there can be no doubt that extensive genetic variation exists in the Australian commercial population for all three major components of seedling growth, namely rate of leaf appearance ( $x_8$ ), rate of tillering ( $x_9$ ) and growth per tiller ( $x_{10}$ ). However, the statistic testing for maternal influence,  $r(HS) - \frac{1}{4}h^2$ , is statistically significant only for variables  $x_3$  and  $x_{10}$ , and the difference between  $r(S, O)$  and  $r(D^*, O)$  is not sufficiently accurate to provide a useful estimate of genetically determined maternal effects for any of the eight variables.

The resolution of the analysis can be greatly improved, however, by using seed size (the weight of 50 seeds produced by the maternal parent) as an index of maternal ability. The last column of Table 3 shows the correlations between seed weight of the maternal parent and individual offspring seedling performance to be statistically highly significant for all variables except rate of leaf appearance ( $x_8$ ). The corresponding correlation of sire and offspring,  $r(S_2, O_n)$ , which measures the strictly genetic relationship between seed weight and individual seedling growth, is, if anything, negative. There can therefore be no doubt about the reality of maternal influence via seed size on all measured seedling traits except rate of leaf appearance.

#### (i) Genetic and environmental maternal effects

The total correlation between the observed seed weight of the maternal parent and the true mean value of seedling trait  $x_n$  in the derived maternal half-sib group of offspring is given for each seedling character in the last column of Table 4. These correlations are calculated as  $r(D_2, O_n)/[r(HS)_n]^{\frac{1}{2}}$ . For seedling weight ( $x_3$ ) the correlation is 0.59 (i.e.  $0.127/\sqrt{0.084}$ ), indicating that seed size is a major factor in the determination of seedling growth. The correlations for component traits range from 0.12 for rate of leaf appearance ( $x_8$ ), which is not significant, to 0.57 for time to third leaf ( $x_4$ ).

Of particular interest are the correlations expressed separately in terms of genetic and environmental differences in seed size (Table 4). The correlation involving genetic differences in seed size is given by  $r(D_2^*, O_n)/[h_2^2 \cdot r(HS)_n]^{\frac{1}{2}}$ , where  $h_2^2 = 0.79 \pm 0.06$ . The corresponding correlation involving environmental differences in seed size is given by  $[r(D_2, O_n) - r(D_2^*, O_n)]/[(1 - h_2^2) \cdot r(HS)_n]^{\frac{1}{2}}$ . The genetic maternal effects due to seed size can be seen from Table 4 to be significant only for

Table 3. Correlations describing the relationship between mean seed weight ( $x_2$ ) and measures of individual seedling growth and development ( $x_n$ )

Character ( $x_n$ )	Phenotypic correlation, † $r_p(2, n)$	Maternal half-sib correlation, † $r(HS)_{2n}$	Parent-offspring correlations †		
			$r(S_2, O_n)$	$r(D_2^*, O_n)$	$r(D_2, O_n)$
$x_3$	0.123 ± 0.029	0.038 ± 0.020	0.001 ± 0.037	0.106 ± 0.037	0.172 ± 0.025
$x_4$	0.002 ± 0.029	0.019 ± 0.020	-0.035 ± 0.045	0.018 ± 0.045	0.151 ± 0.024
$x_5$	-0.048 ± 0.030	0.003 ± 0.022	-0.007 ± 0.046	-0.035 ± 0.046	0.109 ± 0.028
$x_6$	-0.020 ± 0.029	0.011 ± 0.021	-0.026 ± 0.045	-0.032 ± 0.045	0.117 ± 0.026
$x_7$	-0.025 ± 0.030	0.000 ± 0.021	-0.090 ± 0.043	-0.004 ± 0.044	0.102 ± 0.027
$x_8$	-0.083 ± 0.029	-0.018 ± 0.020	-0.011 ± 0.044	-0.064 ± 0.044	0.040 ± 0.029
$x_9$	-0.021 ± 0.029	-0.002 ± 0.021	-0.097 ± 0.039	0.012 ± 0.040	0.089 ± 0.026
$x_{10}$	0.174 ± 0.030	0.051 ± 0.021	0.075 ± 0.043	0.119 ± 0.042	0.112 ± 0.029
Means	0.013	0.013	-0.021	0.015	0.112

† Phenotypic correlations refer to measurements of seedling growth or development ( $x_n$ ), and of seed weight scored on the resulting mature plant ( $x_2$ ): maternal half-sib correlations are based on components of covariance for  $x_2$  and  $x_n$  among maternal half-sib groups.

† Denoting respectively (i) the correlation of sire seed weight and individual offspring seedling growth characters; (ii) the corresponding dam-offspring correlation in the absence of environmental maternal effects; and (iii) the dam-offspring correlation including both genetic and environmental maternal effects.

the two *growth* characters, seedling weight ( $x_3$ ) and growth per tiller ( $x_{10}$ ): completely independent verification of this phenomenon is provided by the half-sib and phenotypic correlations of Table 3. The *environmental* maternal effects due to seed size, on the other hand, are most readily detected for variables  $x_4 - x_7$ , i.e. time to emergence of third leaf, sixth leaf and first tiller, and final tiller number. The environmental correlations are not estimated with great accuracy, but it is nevertheless quite clear that a qualitative difference exists between the genetic and environmental maternal effects of seed size.

Table 4. *Maternal effects of seed weight on measures of seedling growth and development, subdivided into genetic and environmental components*

Character	Maternal correlation due to seed size†		
	Genetic	Environmental	Total
$x_3$	0.41*	0.50	0.59**
$x_4$	0.08	1.09*	0.57**
$x_5$	-0.12	0.92*	0.32**
$x_6$	-0.13	0.66*	0.42**
$x_7$	-0.01	0.75*	0.33**
$x_8$	-0.22	0.70	0.12
$x_9$	0.05	0.57	0.30**
$x_{10}$	0.37*	-0.04	0.31**

\*, \*\* Significantly different from zero at  $P < 0.05$ ,  $P < 0.01$  respectively.

† Correlations between the true mean value of character  $x_n$  in a maternal half-sib group, and the breeding value, environmental deviation and phenotypic values respectively, of seed weight in the maternal parent.

#### (ii) *Relationships among the seedling characters*

Table 5 sets out the estimated phenotypic correlations among the eight seedling characters (above diagonal), together with those due to maternal plus genetic factors (i.e. based on components of variance and covariance among maternal half-sib or full-sib groups). The estimates have been pooled from experiments 2 and 4, and are based on a total of 6150 individuals in 334 families.

The striking negative correlations are those involving growth per tiller ( $x_{10}$ ) and measures of rate of tiller production ( $x_6$ ,  $x_7$  and  $x_9$ ). The same phenomenon has been reported by Cooper & Edwards (1961) in *Lolium multiflorum* and *L. perenne*, the genetic correlation within varieties in their study averaging  $-0.44$ , compared with  $-0.46$  in the Australian commercial population of *Phalaris tuberosa*. Evans, Wardlaw & Williams (1964) have also noted an 'inverse relation between environmental conditions favouring leaf and stem growth on established tillers (long days and moderately high temperatures), and those favouring root growth and abundant tillering (short days and low temperatures)'.

The breakdown of seed size maternal effects in Table 4 shows these two facets of seedling growth also to be affected by seed size differences in qualitatively distinct ways. The genetic maternal effects may possibly depend on differences in the levels of endogenous gibberellins and auxins, while the environmental maternal

Table 5. Phenotypic correlations (above diagonal) and correlations due to genetic + maternal effects (below diagonal) for components of seedling growth and development

Characters	$x_3$	$x_4$	$x_5$	$x_6$	$x_7$	$x_8$	$x_9$	$x_{10}$
Seedling weight ( $x_3$ )	—	0.51**	0.47**	0.47**	0.49**	0.25**	0.41**	0.70**
Time to 3rd leaf ( $x_4$ )	0.50**	—	0.78**	0.61**	0.41**	0.31**	0.29**	0.23**
Time to 6th leaf ( $x_5$ )	0.32**	0.87**	—	0.59**	0.42**	0.83**	0.30**	0.17**
Time to 1st tiller ( $x_6$ )	0.35**	0.58**	0.51**	—	0.59**	0.34**	0.37**	0.04
Tiller number ( $x_7$ )	0.31**	0.51**	0.48**	0.91**	—	0.30**	0.96**	-0.25**
Leaf appearance ( $x_8$ )	0.13	0.61**	0.92**	0.37**	0.36**	—	0.20**	0.04
Tiller appearance ( $x_9$ )	0.29**	0.45**	0.43**	0.82**	0.99**	0.33**	—	-0.31**
Growth per tiller ( $x_{10}$ )	0.70**	0.09	-0.04	-0.36**	-0.46**	-0.14*	-0.47**	—

\*, \*\* Significantly different from zero at  $P < 0.05$ ,  $P < 0.01$  respectively. The standard error of a phenotypic correlation is approximately  $\pm 0.03$ , based on differences in the estimates obtained from ex-

periments 2 and 4. The corresponding standard error of a genetic + maternal correlation averaged  $\pm 0.07$ .

effects might be expected to involve primarily nutritional factors and differences in embryo size. The only evidence to support these conjectures is that gibberellic acid is known to inhibit tillering and root growth in a number of grasses, while promoting leaf and stem growth on established tillers (Evans, Wardlaw & Williams, 1964).

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