

Quantitative genetic analysis in *Phalaris tuberosa*

II. ASSORTATIVE MATING AND MATERNAL EFFECTS IN THE INHERITANCE OF DATE OF EAR EMERGENCE, SEED WEIGHT AND SEEDLING GROWTH RATE

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1. INTRODUCTION

Phalaris tuberosa is a perennial grass which has been widely used as a component of sown pastures in southern Australia, due to its productivity during autumn and winter, high drought tolerance, and persistence under grazing. The Australian strain is thought to be derived from a single introduction of material of Mediterranean origin (Trumble, 1935) and has been grown commercially for over 50 years. Trumble & Cashmore (1934) found no evidence of ecotypic differentiation among samples from various parts of Australia, despite the fact that the species had at that time been established in relatively small but widespread areas for a period of about 30 years.

Agronomically the commercial strain suffers from two deficiencies, viz. a tendency to lose seed by shattering, and a susceptibility to competition from weeds and other grasses in the year of establishment, due to its slow rate of seedling development. In the more favourable areas of its distribution, the value of the commercial strain would also be greatly enhanced by an increase in the length of the growing season, and by increased growth during the autumn and winter periods.

It is of considerable interest to assess the potential improvement due to selective breeding within such a locally adapted cross-fertilized population. Variation in the degree of seed retention shown by individual plants of a closely related Argentine strain has been found by McWilliam (1963) to be almost entirely genetic, and virtually independent of date of ear emergence: a single cycle of selection within the strain brought about a 29% increase in the average level of seed retention following ripening. The present paper is concerned with the nature and extent of the variation in the Australian population for date of ear emergence, seed weight and seedling growth rate. The necessary statistical theory has been set out in the first paper of this series (Latter, 1965).

2. EXPERIMENTAL PROCEDURES

The data to be discussed in this paper have been derived from four separate experiments. In *Experiment 1*, conducted in 1961, the mean performance of a range of Mediterranean ecotypes has been determined in respect of seed weight, seedling growth rate, tiller number and winter growth rate. The experiment

involved a total of seventeen replications, spread over three sowing dates, of a randomized blocks design with six plants per plot. The extent of the variation shown by these characters throughout the species, and the magnitudes of the ecotypic correlations among them, provide the background necessary for an appraisal of the scope for selective breeding within the commercial strain. The remaining three experiments have provided the data for an analysis of the variation shown by the Australian population.

The material for *Experiment 2* originated from seed collected from each of 200 single plants of the Australian Commercial strain following open-pollination in 1959. The mean weight of fifty seeds from each ovule parent was recorded, and the performance of the open-pollinated progeny groups was studied in 1960 in respect of various measures of seedling growth rate in flats, and of date of ear emergence and seed weight in the field at the end of the first growing season. These comparisons were made using three replications separated in time, in each of which a total of 1400 plants, seven from each progeny group, were sown in a *completely randomized* layout. The analysis of these data has furnished estimates of the maternal half-sib correlations displayed by each character, and of the correlations between offspring performance and the mean seed weight of the ovule parent.

Experiment 3 represents a one-generation selection experiment undertaken to determine the parent-offspring correlation and repeatability from season to season of date of ear emergence, and to provide additional information on the genetic relationship between seed weight and date of ear emergence. From one replication of *Experiment 2*, an equal quantity of seed produced in 1960 under open-pollination was taken from each of the eighty earliest and eighty latest flowering plants. A similar sample made up of equal contributions from each of 400 randomly chosen plants was taken as a control population. Note that the use of open-pollinated seed from *Experiment 2*, in the measurement of the regression of offspring on parent for date of ear emergence, is justified in view of the completely randomized design adopted in that experiment.

The offspring of selected parents and controls were scored in 1961 for date of ear emergence, and again in 1962 for date of ear emergence and seed weight. In this study fifteen replications of a randomized blocks design were involved, with plots each of six plants: in each replication two plots were planted to control material, and four to each of the early and late selected populations.

The material for *Experiment 4* was also derived from one of the replicates of *Experiment 2*. In the early spring of 1961, a number of randomly chosen plants were removed from the field and their flowering times synchronized by appropriate environmental treatment in the glasshouse and shadehouse. A total of 134 random pair-crosses were then made by bringing together under bags single heads of previously designated ovule and pollen parents. No attempt was made to emasculate the ovule parent, because of the high level of self-incompatibility prevailing in the species. Seed was collected only from the ovule parent of each cross. The mean weight per fifty seeds was recorded for each female parent, and the full-sib offspring were scored in 1962 for the same measures of seedling growth rate as were

observed in Experiment 2. The comparisons were made in three randomized blocks, using plots of six plants each. Since the performance of the parents of each family had been fully documented in Experiment 2, it was possible to estimate from these data all the required sire-offspring and dam-offspring correlations, in addition to the various correlations among full-sibs.

3. THE EXTENT OF VARIATION WITHIN THE SPECIES

A wide range of introductions of *P. tuberosa* from the Mediterranean region is available for incorporation in programmes aimed at the breeding of improved

Table 1. *Mean performance of a sample of ecotypes of P. tuberosa*

C.P.I. number	Origin	Date of ear emergence (days after 1 November)	Seed weight* (mg./50 seeds)	Seedling growth (log dry wt. in cg.)	Seedling tiller number	Winter growth (log dry wt. in cg.)
19,351	Greece	44.2	80	1.76	11.3	1.51
14,279	Greece	40.2	80	1.71	11.0	1.46
15,022	Turkey	34.2	96	1.78	11.0	1.58
19,344	Portugal	33.0	74	1.73	10.2	1.54
14,693	Morocco	24.1	72	1.79	9.2	1.59
19,299	Algeria	23.3	94	1.98	11.5	1.69
14,498	Algeria	20.1	93	1.79	13.8	1.64
19,331	Morocco	19.9	97	2.07	7.9	1.79
19,305	Morocco	8.8	105	2.11	10.6	1.95
Commercial	Australia	28.4	80	1.83	11.2	1.62
L.S.D. (0.05)		3.6	—	0.091	1.2	0.097

* Single weighings of bulked samples of seed.

locally adapted varieties (Neal-Smith, 1955). A sample of those of potential value as breeding material under southern Australian conditions, has been characterized under a regime similar to that adopted in the more detailed study of the commercial strain. This survey has been designated Experiment 1 in the previous section.

At 10-day intervals during March 1961, three sowings of each of ten ecotypes were made in flats in the glasshouse using pre-germinated seed. A six-plant row of each ecotype was included in each flat, with a spacing of 2 in. both between rows and between plants within rows. The depth of soil in the flats averaged 3½ in. At approximately 10 weeks of age, the seedlings were clipped individually and the dry weight of top growth measured: counts of the numbers of tillers per plant were also taken a week later. The flats were then transferred to the shade-house, and were fertilized when necessary to prevent yellowing of the foliage. The regrowth of each plant was subsequently harvested at the end of the 3-month winter period.

The comparisons are summarized in Table 1. The data for date of ear emergence, kindly furnished by Mr C. Neal-Smith, represents means of an average of fifty

plants of each ecotype scored in two consecutive years (1955, 1956). An analysis of the data showed the ecotypes \times years interaction to be of little importance biologically, though it was statistically highly significant: the interaction component of variance was 2.0 days² compared with a pooled within-ecotype variance of 29.6 days².

There are two main points to be emphasized here. The first is the wide range covered by the ecotype means in respect of each of the five characters: the dates of ear emergence span a period of well over one month; the largest seeded introduction has seeds almost 50% heavier than those of the smallest seeded ecotype; and the fastest growing introduction produces seedlings under these particular conditions which are 2.5 times the weight of the slowest growing ecotype. Note also that the Australian Commercial population is intermediate in performance for all characters studied.

The second point is brought out more clearly in Table 2, i.e. the existence of

Table 2. *Correlations between means of introduced populations*

	Seed weight	Seedling growth	Tiller number	Winter growth
Ear emergence	-0.62*	-0.79**	0.11	-0.90***
Seed weight		0.76**	0.10	0.77**
Seedling growth			-0.35	0.94***
Tiller number				-0.22

*, **, *** Significant at $P = 0.05, 0.01, 0.001$.

high positive correlations among three of the characters, viz. seed weight, seedling growth and winter growth; and a high negative correlation between each of these related characters and date of ear emergence (Fig. 1). Note also that the rate of tiller production in the seedling stage is very largely independent of the other four characters, though there is a tendency for the fastest growing seedlings to produce a smaller number of tillers.

4. VARIATION WITHIN THE AUSTRALIAN STRAIN

P. tuberosa regularly forms fourteen bivalents at diakinesis (McWilliam, 1962) and is presumably of allopolyploid origin, so that we may safely assume its inheritance to be disomic. The species is predominantly out-breeding, and under conditions of enforced self-pollination the seed set averages only four to five seeds per plant, compared with a mean of 120 seeds per plant under controlled hybridization. Occasional genotypes set appreciable quantities of seed under selfing, however, and little is known of the behaviour of these self-compatible individuals under open-pollination. The possibility of bias due to selfing will therefore have to be considered in the interpretation of observed covariances among relatives.

(i) *Variation in date of ear emergence*

Flowering time has been scored as the date on which the third ear commenced to emerge from the leaf sheath in plants grown in the field at a spacing of 16 in.

The distribution of this criterion in the Australian population is close to normal, and the variable analysed has been the number of days after 1 November. Since the phenotypic variance of the population differs considerably from year to year, care has been taken to work in terms of the prevailing phenotypic standard deviation wherever necessary. Standard errors have been calculated by means of large sample formulae which take account of the covariances among the estimates involved (Mode & Robinson, 1959).

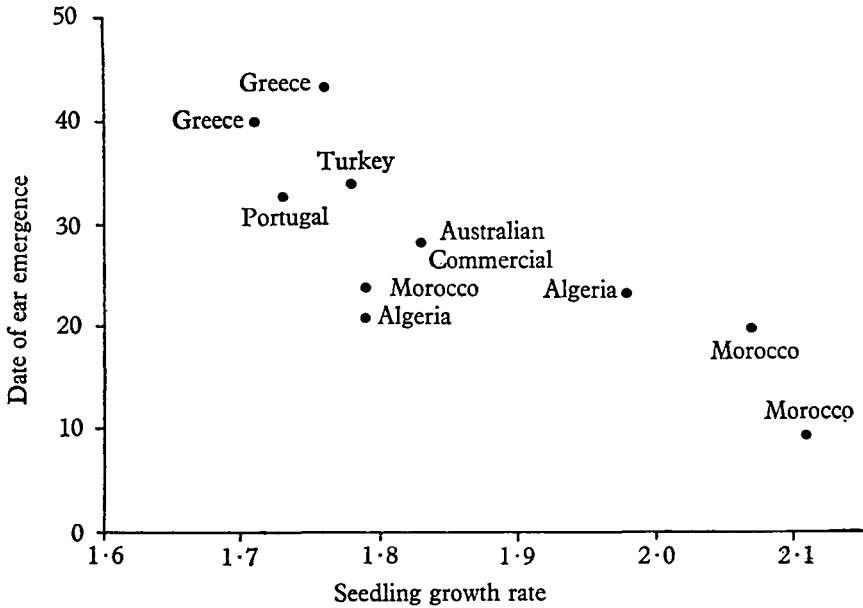


Fig. 1. The relationship between date of ear emergence and seedling growth rate among ecotypes of *P. tuberosa*.

In Table 3 is presented the analysis of variation shown by the open-pollinated progeny groups in Experiment 2. Since a number of plants were lost in the seedling stage, the data have been analysed by the method of unweighted means (Snedecor, 1956). The correlation between half-sibs for this variable can be estimated to be

$$r(HS) = 7.133/24.947 = 0.286 \pm 0.024$$

Leaving aside the possibility of bias due to selfing, this correlation will have the expectation given as equation (10) in the first paper of this series (Latter, 1965).

Table 3. Analysis of variation in date of ear emergence shown by open-pollinated progeny groups (1960)

Source	d.f.	Mean squares	Components
Blocks	2	32.348	0.011
Progeny groups	199	157.523	7.133
Interaction	398	18.438	0.113
Residual	3300	17.701	17.701
Total	3899	24.920	24.958

The results of two-way selection for date of ear emergence (Experiment 3) are summarized in Table 4. The selection differential between early and late selection was 3.63 ± 0.04 phenotypic standard deviations (σ_p), the standard error of estimation deriving solely from that of $\hat{\sigma}_p$. The overall response to selection was $1.62 \pm 0.08 \sigma_p$ measured in 1961, and $1.79 \pm 0.09 \sigma_p$ in 1962, giving a mean response of $1.71 \pm 0.06 \sigma_p$. The dam offspring correlation, $r(DO)$, can then be estimated to be

$$r(DO) = 1.71/3.63 = 0.470 \pm 0.028$$

This will have the expectation given as equation (6) in the earlier paper. The standard error of this estimate has two components: one which reflects the accuracy with which the population means and phenotypic standard deviations have been measured; and a second which is due to the finite sample of parents contributing to each selected group (Prout, 1962).

Table 4. *Average dates of ear emergence in selected and control material, scored as days after 1 November*

Selections	Parents	Offspring	
		1961	1962
Late	39.63	27.19 \pm 0.23	26.24 \pm 0.17
Control	29.78	23.02 \pm 0.33	23.50 \pm 0.25
Early	21.54	20.07 \pm 0.23	20.32 \pm 0.17
Phenotypic standard deviation	4.98 \pm 0.06	4.38 \pm 0.10	3.30 \pm 0.08

From the data of this experiment, an estimate has also been derived of the *repeatability* of the character measured on the same individuals in consecutive years. The value obtained from a pooled within-population analysis of the two selected lines and the control population is $r = 0.529 \pm 0.024$. The difference of 0.059 ± 0.039 between this estimate of repeatability and that of the parent-offspring correlation is statistically non-significant. According to the theory of assortative mating developed by Fisher (1918), this comparison is a joint test for the significance of dominance effects and for the departure of the degree of assortative mating from unity. It is in addition a test for correlated environmental effects from year to year.

The expectations of the three available estimates characterizing variation in date of ear emergence, assuming all the genetic variance to be additive, are set out in Table 5. The degree of phenotypic assortative mating in the population can be estimated to be

$$\hat{\rho} = 2(0.470/0.529) - 1 = 0.78 \pm 0.14$$

This estimate and that of $\hat{h}_1^2 = 0.529 \pm 0.024$ have a covariance of estimation equal to -2.326×10^{-3} . Substitution in the expectation for $r(HS)$ leads to the following estimate of the within-season heritability:

$$\hat{h}_{w1}^2 = 4(0.286) - 0.78(2.78)(0.529)^2 = 0.54 \pm 0.13$$

There is therefore no conspicuous evidence of variance due to genotype \times season interaction, though the test is not one of great accuracy.

Table 5. *Estimates of parameters characterizing variation in date of ear emergence*

Parameter	Symbol	Estimate	Expectation	Covariance of estimation
Repeatability	r	0.529 ± 0.024	h_1^2	} -0.100×10^{-3} 0.156×10^{-3}
Dam-offspring correlation	$r(DO)$	0.470 ± 0.028	$\frac{1}{2}h_1^2(1 + \rho)$	
Half-sib correlation	$r(HS)$	0.286 ± 0.024	$\frac{1}{4}[h_{w1}^2 + \rho h_1^2(2 + \rho)]$	

(ii) *Variation in seed weight and its relation to date of ear emergence*

Seed weight has been scored throughout as the weight in mg. of fifty mature seeds shaken from heads of the plant concerned. This variable has been found to be normally distributed in the population under study, with a phenotypic standard deviation σ_p which differs significantly from year to year, though this is less marked than in the case of date of ear emergence. Observed values of σ_p were 9.94 ± 0.50 , 9.39 ± 0.21 , and 8.64 ± 0.26 respectively in 1959, 1960 and 1962.

Estimates of the correlation between dam and open-pollinated offspring, and of the correlation among half-sibs, have been derived from observations of seed weight in one of the three replicates of Experiment 2 (Table 6). These estimates have expectations given by equations (9) and (11) in Part I of this series of papers.

Table 6. *Estimates of parameters characterizing variation in seed weight*

Parameter	Symbol	Estimate	Expectation	Covariance of estimation
Dam-offspring correlation	$r(DO)$	0.396 ± 0.032	$\frac{1}{2}[h_2^2 + \rho(h_1 r_g h_2) r_p]$	} 0.696×10^{-3}
Half-sib correlation	$r(HS)$	0.231 ± 0.029	$\frac{1}{4}[h_{w2}^2 + \rho(h_1 r_g h_2)^2(2 + \rho)]$	

The phenotypic correlation, r_p , between seed weight and date of ear emergence in Experiment 2 was -0.038 ± 0.032 , and the pooled intra-population estimate from Experiment 3 was -0.156 ± 0.043 . These estimates differ significantly, and it is possible that the environmental correlation between the two variables varies with seasonal conditions. We may take an unweighted mean estimate of $r_p = -0.097 \pm 0.027$. Information on the genetic relationship between the two characters is available from three sources (Table 7): (i) the correlation between seed weight of the ovule parent and flowering date of the offspring, $r(D_2O_1)$, from Experiment 2; (ii) the half-sib correlation, $r(HS_{12})$, estimated from the open-pollinated progeny groups of Experiment 2; and (iii) the correlation between the flowering date of the ovule parent and the seed weight of the offspring, $r(D_1O_2)$, estimated from the correlated response in seed weight measured in Experiment 3.

All three estimates indicate the existence of a negative genetic association between seed weight and flowering date, apparently of a low order of magnitude. A preliminary assessment of the data is sufficient to establish that the bias involved

in estimating the heritability of seed weight from the dam-offspring correlation (Table 6) is of the order of 2%, compared with a standard error of estimation of 8%. We may therefore take the heritability of seed weight to be simply

$$h_2^2 = 0.792 \pm 0.064$$

In the context of the present study, the most useful estimate characterizing the genetic relationship between seed weight and date of ear emergence is

$$r(D_2 O_1) + \frac{1}{2}r(D_1 O_2) = -0.154 \pm 0.044$$

Taken as an estimate of $h_1 r_g h_2$, this statistic has a bias due to assortative mating which is trivial by comparison with its standard error, and corresponds to a value of

$$\hat{r}_g = -0.24 \pm 0.07$$

Let us return now to the data of Table 6. Note that the value of $2r(HS) - r(DO)$ is 0.066 ± 0.040 , i.e. positive but statistically non-significant. The effects of assortative mating for date of ear emergence in this study are such as to make this com-

Table 7. *Estimates of parameters characterizing covariation between date of ear emergence and seed weight*

Parameter	Symbol	Estimate	Expectation
Phenotypic correlation	r_p	-0.097 ± 0.027	r_p
Dam-offspring correlations	$r(D_2 O_1)$	-0.116 ± 0.037	$\frac{1}{2}[(h_1 r_g h_2) + \rho h_1^2 r_p]$
	$r(D_1 O_2)$	-0.076 ± 0.045	$\frac{1}{2}(h_1 r_g h_2) (1 + \rho)$
Half-sib correlation	$r(HS_{12})$	-0.047 ± 0.025	$\frac{1}{4}(h_1 r_g h_2) [1 + \rho h_1^2 (2 + \rho)]$

parison positive, and there are three additional sources of bias which may produce the same effect. These are

- (i) genotype \times season interaction for seed weight;
- (ii) partial self-fertilization under open-pollination; and
- (iii) restricted male parentage under open-pollination.

The existence of genotype \times season interaction for seed weight leads to a value of h_{w2}^2 , the within-season heritability, which is greater than h_2^2 . Partial self-fertilization has been shown by Latter (1965) to inflate the estimate of heritability based on $r(HS)$ to a greater extent than that derived from $r(DO)$. The restriction of male parentage under open-pollination does not affect the dam-offspring correlation, but inflates the component of variance among progeny groups. In view of the non-significant value of the above comparison, we may therefore judge each of these three sources of bias to be unimportant within the limits of accuracy of the experiment.

(iii) *Variation in seedling growth and its relation to seed weight*

In this paper, the analysis of variation in seedling growth rate will be based solely on measurements of the dry weight of top growth, leaving the other measures

of growth rate to be treated in the next paper in this series. The seedlings were grown in flats in the glasshouse under conditions similar to those described in Section 3, the top growth being harvested at approximately 2 months of age.

A logarithmic transformation of the dry weights gave an approximately normal distribution in each replication of Experiment 2 and 4, but the phenotypic variance on the transformed scale differed markedly from one replication to the next, without any obvious relationship to the mean (Table 8). Accordingly the observations were analysed by the method of unweighted means in three different ways. The first analysis ignored the heterogeneity of variance; the second involved standardization of the observations by dividing by the prevailing phenotypic standard deviation; and the third made use of the 'genetic correlation' approach to the characterization of genotype × environment interaction (Falconer, 1952; Robertson, 1959).

Table 8. *Heterogeneity of variance in seedling weight measured as log dry weight in centigrams*

Experiment	Replication	Mean	Standard deviation
2	1	1.68	0.169 ± 0.003
2	2	1.78	0.170 ± 0.003
2	3	1.69	0.133 ± 0.003
4	1	1.77	0.134 ± 0.003
4	2	1.80	0.186 ± 0.005
4	3	1.57	0.169 ± 0.004

It was of some interest to find that the three methods of analysis led to quite similar results. In Experiment 2, the crude analysis gave an estimated intra-progeny group correlation of 0.082, compared with 0.084 from the standardized analysis: in Experiment 4 the corresponding correlations for full-sib groups were 0.104 and 0.109. The relative importance of genetic variance and that due to genotype × environment interaction, measured as the ratio of the between-groups and interaction components, was estimated to be 0.67 from the crude analysis of Experiment 2, 0.69 from the standardized analysis, and 0.74 by the genetic correlation approach. In the analyses of Experiment 4, the respective measures of the importance of interaction were 0.48, 0.50 and 0.50.

In the analysis of variation in seedling growth, the effects of phenotypic assortative mating for date of ear emergence can safely be ignored. A standardized analysis of covariance of the observations in Experiment 2 gave an estimate of the phenotypic correlation between the two variables of -0.059 ± 0.016 , and a correlation coefficient of 0.05 ± 0.10 based on components of variance and covariance among progeny groups. The phenotypic correlation coefficient is significant statistically, but it is of such a low order of magnitude that we may consider the two variables to be independent.

In Table 9 are given estimates of the available correlations among relatives for seedling growth, derived from standardized analyses of Experiments 2 and 4.

The accuracy of the estimates is not sufficient to permit a detailed breakdown of the variation into all its components, nor is it possible to detect maternal effects in the usual way by a comparison of sire-offspring and dam-offspring correlations. However, evidence of maternal influence is provided by the value of

$$4r(HS) - [r(S, O) + r(D^*, O)] = 0.167 \pm 0.076$$

which has zero expectation under a conventional model in the absence of epistasis. An unbiased estimate of the heritability of the character (Latter, 1965) is given by

$$h_3^2 = r(S, O) + r(D^*, O) = 0.169 \pm 0.053$$

It is clear from observations of the relationship between seed weight and seedling growth (Table 10) that seed weight is a factor of considerable importance in the

Table 9. *Estimates of parameters characterizing variation in seedling weight*

Parameter	Symbol	Estimate	Expectation
Sire-offspring correlation	$r(S, O)$	0.093 ± 0.037	(17)
Dam*-offspring correlation	$r(D^*, O)$	0.076 ± 0.037	(23)
Full-sib correlation	$r(FS)$	0.109 ± 0.019	(20)
Half-sib correlation	$r(HS)$	0.084 ± 0.014	(21)

Numbers in parentheses refer to equations given by Latter (1965).

* Offspring derived from seed harvested in a different year from that in which the dams' seedling growth was measured.

determination of maternal influence. The observed correlation between the seed weight of a pollen parent and the seedling growth of its offspring, $r(S_2, O_3)$, is effectively zero, and we must therefore consider any 'genetic' relationship between the two characters to be the result of genetically determined maternal effects. Making use of the expectations given as equation (13), (15) and (22) by Latter (1965), two independent estimates may be obtained of $r(a_2, am'_3)$, i.e. the correlation between the additive genetic value of the dam for seed weight and the additive genetic maternal effect on seedling growth common to a maternal half-sib group of offspring. Predictions of the *permanent* correlated response in seedling growth to be expected as a result of artificial selection for seed weight, can be made directly from this statistic. The combined estimate from the two sources is

$$r(a_2, am'_3) = \frac{\text{COV}(a_2, am'_3)}{\sigma_{p2} \sigma_{p3}} = 0.091 \pm 0.027$$

The importance of seed weight in the determination of seedling growth can most readily be appreciated in terms of the correlation between the seed weight of the ovule parent, and the 'true' mean performance for seedling growth of the derived maternal half-sib group. This may be estimated as

$$r = (0.084)^{-1} r(D_2, O_3) = 0.57 \pm 0.06$$

It is this statistic which will be found most useful in the comparison of the susceptibility to maternal influence of different measures of seedling growth rate.

Table 10. *The relationship between seed weight and seedling weight*

Parameter	Symbol	Estimate	Covariance of estimation	Expectation
Phenotypic correlation	r_p	0.123 ± 0.029		(16)
Sire-offspring correlation	$r(S_2, O_3)$	0.001 ± 0.037		(13)
Dam-offspring correlations	$\left\{ \begin{array}{l} r(D_2^*, O_3) \\ r(D_2, O_3) \end{array} \right\}$	0.106 ± 0.036	0.239 × 10 ⁻³	(22)
		0.164 ± 0.020		(14)
Half-sib correlation	$r(HS_{23})$	0.038 ± 0.020	0.364 × 10 ⁻³	(15)

Numbers in parentheses refer to equations given by Latter (1965).

The variation in seedling growth may then be partitioned as in Table 11. The relative importance of genotype × environment interaction has legitimately been estimated from the progeny groups × blocks interaction in Experiment 2, because of the completely randomized layout within blocks in that experiment. The ‘genetic correlation’ between blocks in Experiment 4 is considerably lower than that in Experiment 2, due to an inflation of the interaction mean square by plot errors.

Table 11. *Components of variation in seedling weight*

Source of variation	Component (%)
Among open-pollinated progeny groups	
(i) Due to seed weight of ovule parent	2.7
(ii) Genotype × environment interaction	3.7
(iii) Remainder	5.7
Within open-pollinated progeny groups	
(i) Among seedling flats	10.7
(ii) Residual	77.2
Total	100.0

5. DISCUSSION

In the first paper in this series, a theoretical discussion has been given of possible complications arising in quantitative genetic analysis with an open-pollinated species, due to assortative mating, maternal effects or partial self-fertilization. No attempt has been made to examine the joint effects of these phenomena, since no character involved in the present studies is seriously influenced by more than one of the possible sources of complexity. A comparison of the dam-offspring and half-sib-correlations for seed weight has indicated that partial self-fertilization under open-pollination is an unimportant source of bias in *P. tuberosa*. Date of ear emergence is subject to phenotypic assortative mating in the population, but it has been considered unlikely that the character is subject to maternal influence in view of the virtual independence of flowering time and seedling growth rate. Seedling weight has been found to be subject to maternal influence, but the effects of assortative mating for flowering time on seedling characters may safely be ignored.

As a result of the preceding analyses, the genetic variability present in the locally adapted population can be compared with that available from introduced material. The ecotypes studied in Experiment 1 collectively represent potential breeding material which covers a wide range in each of the three variables, but which would require genetic adjustment for use in the more favoured areas of south-eastern Australia.

Variation in seed weight within the Australian strain is very extensive and highly heritable, with a coefficient of variation of 11.7% and a heritability of 0.79. The additive genetic standard deviation in the population (σ_a) is of the order of 8.3 units, so that the range spanned by the sample of ecotypes represents only four additive genetic standard deviations. The response to individual selection in the Australian strain may be calculated as

$$\Delta G = \bar{i}h\sigma_a$$

where a selection intensity of 5% leads to a value of \bar{i} equal to 2.06. Under this regime the change in the population mean would be expected to be 1.83 σ_a per generation, so that two generations of selection should be sufficient to increase mean seed weight beyond that of the heaviest seeded ecotype included in the sample.

Variation in date of ear emergence within the Australian strain is also appreciable and moderately heritable, with a phenotypic standard deviation (averaged over three seasons) of 4.2 days, and a heritability of 0.53. However, it has been shown that under open-pollination the character is subject to phenotypic assortative mating of degree $\rho = 0.78$. Under random mating in a population under artificial selection, the additive genetic variance in the population would be expected to be reduced by a factor of the order of $1 - h^2\rho$, leading to a phenotypic standard deviation of 3.7 days and a heritability of 0.40. The range in mean flowering time of the sample of ecotypes studied in Experiment 1 is 35 days, representing approximately fifteen additive genetic standard deviations. One can therefore estimate that between five and seven generations of selection would be required to move the mean of the Australian strain beyond the limits of this range.

Seedling growth in the Australian Commercial population, measured as log dry weight of the shoots of seedlings surviving to 2 months of age, shows a phenotypic standard deviation of approximately 0.16 units (Table 8), and a heritability of 0.17 which includes variation due to genetically determined maternal effects. In a selection programme devoted specifically to a character of this heritability one would normally advocate the method of family selection (Latter, 1964), but the efficiency of this procedure would be considerably reduced in the presence of important environmentally determined maternal effects. We will therefore consider the response to be expected from a regime of individual selection. The range in mean seedling growth spanned by the sample of ecotypes in Experiment 1 is 0.40 units, and one would predict that something like five generations of selection would be necessary to increase the mean of the Australian population to the level of the most vigorous ecotype.

All three characters must therefore be judged to show appreciable additive genetic variation in the Australian Commercial population, in the sense that roughly seven generations of artificial selection would be sufficient to push the population mean for each character beyond the range shown by promising introductions. Similar conclusions with respect to variability within established strains or varieties of cross-fertilized species have been drawn by Cooper (1959) with respect to date of ear emergence in *Lolium*, by Gardner (1963) in his review of studies of yield in open-pollinated varieties of maize, and by Kehr & Gardner (1960) from a study of forage yield in lucerne.

The genetic relationships among the three variables in the Australian strain differ considerably from those shown by the means of the ecotypes studied in

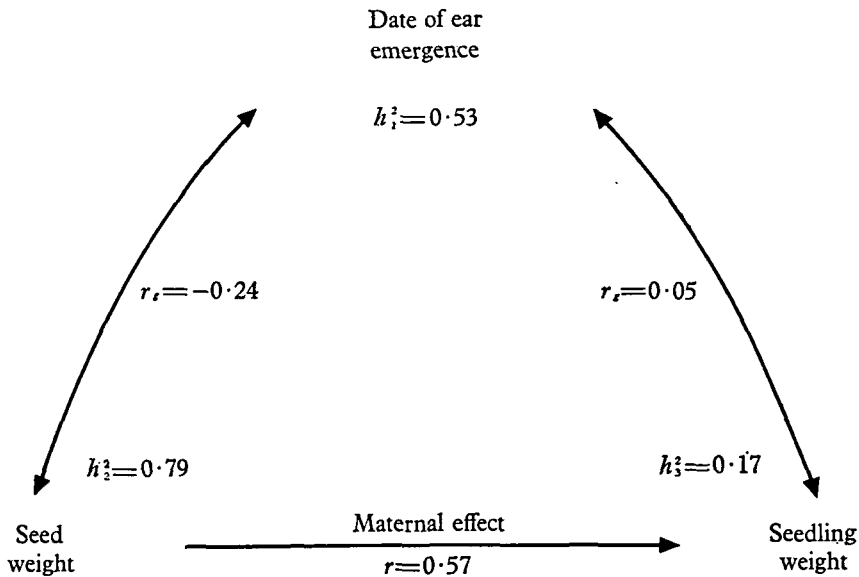


Fig. 2. Heritabilities and genetic correlations summarizing relationships among variables in the Australian Commercial strain.

Experiment 1 (Table 2). In particular, it was of interest to find that seedling growth rate and date of ear emergence are almost completely independent at the intra-population level (Fig. 2), in contrast to the close negative relationship displayed at the interpopulation level (Fig. 1). The genetic correlation between seed weight and date of ear emergence in the Australian strain is also of a comparatively low order, though it is of the same sign as that prevailing between ecotypes.

Variation in seed weight among parents in the Australian population is positively correlated with variation among their open-pollinated progeny groups in seedling growth (Fig. 2), though the association is less pronounced than that involving differences among ecotypes in the two characters. The emphasis to be placed on increased seed weight as a breeding objective depends primarily on its relationship to seedling growth rate, and the relevant prediction from an applied viewpoint is therefore the magnitude of the correlated response. The genetic component of the

relationship between the two characters in the Australian strain has been shown to be due solely to the maternal effect involved, so that under a regime of individual selection for increased seed weight, the response in seedling growth is a function only of $r(a_2, am'_3)$, i.e. the correlation between the additive genetic value of the ovule parent for seed weight, and the additive genetic maternal effect on seedling growth shared by a maternal half-sib group of offspring. The prediction formula is

$$\Delta X_3 = \bar{i}r(a_2, am'_3) \sigma_{p_3}$$

The correlated response in seedling growth per generation is therefore λ times that expected from direct selection, where

$$\lambda = r(a_2, am'_3)/h_3^2 = 0.54$$

It must also be considered that selection for seed weight will involve a generation interval of 2 years, unless environmental conditions can be provided which will induce a second flowering in selected genotypes. The relative efficiency of indirect selection *per annum* may then be reduced to 0.27.

In conclusion it should be emphasized that a detailed genetic analysis of a locally adapted commercial population may be of practical interest in two ways. The initial step in any plant breeding programme is the choice of a suitable base population, and the alternatives in the case of a cross-fertilized species will often include

- (i) the improvement of an established strain or variety by intra-population selection, or
- (ii) the formation of a more widely based breeding population by the incorporation of introduced material.

The breeder must balance up the sacrifice involved in the latter alternative in terms of adaptation to the local or agricultural environment, against the enhanced scope for selection due to the introduction of additional genetic variability.

The useful genetic variation present in the locally adapted population of *P. tuberosa* has been found to be quite appreciable for the three characters studied. Additional experiments are at present being conducted by members of this Division to assess the magnitude of the genetic variability in a synthetic population created by the crossing of introduced strains into the Australian population. The combined information from these two series of studies will greatly facilitate decisions as to the emphasis to be given to each of the two alternative breeding procedures.

The second application of this type of analysis has to do with the observed interrelationships among the variables. A study of the genetic correlations prevailing in an inter-breeding population, which may be assumed to be in linkage equilibrium, will indicate the likely magnitude of the residual correlations following recombination in a more widely based breeding population. The results of the present analysis suggest in particular that the ecotypic correlation between seedling growth rate and date of ear emergence should rapidly disappear under random

mating in a synthetic population, since variation in the two characters appears to be controlled by almost completely independent sets of genes.

SUMMARY

The variation shown by the Australian Commercial population of *P. tuberosa* in respect of date of ear emergence, seed weight and seedling weight has been analysed, and the interrelationships among the variables characterized. All three characters show appreciable additive genetic variation, in the sense that approximately seven generations of artificial selection would be sufficient to push the population mean for each trait beyond the range shown by introduced ecotypes.

Apart from the positive association between seed weight and seedling weight due to maternal influence, the three variables are to a large extent genetically independent in this locally adapted interbreeding population. It is therefore probable that the negative ecotypic correlations between seedling growth rate and date of ear emergence, and between seed weight and date of ear emergence, would rapidly be dispelled under random mating in a synthetic population.

Under open-pollination, date of ear emergence has been shown to be subject to phenotypic assortative mating of degree $\rho = 0.78$, approximately 53% of the variation being additive genetic. Variation in seed weight within the strain is extensive, with a heritability of 0.79. Neither character shows evidence of important genotype \times years interaction.

Variation in seedling weight involves an appreciable genotype \times environment interaction component, and has a heritability of only 0.17 which includes variation due to genetically determined maternal effects. The correlation between the seed weight of an ovule parent and the 'true' mean seedling weight of the derived maternal half-sib group is of the order of 0.57. It has been estimated that the correlated response per generation in seedling weight, due to selection for seed weight, is 0.54 times that expected from direct selection.

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