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Quantitative Genetic Analysis in *Phalaris* and its Breeding Implications

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Summary. The genetic variation for a number of important agronomic characters within a widely based breeding population of *Phalaris tuberosa* has been analysed, and the interrelationships among the variables characterized.

Estimates of heritability for flowering date, seed retention and seed weight were higher than those for cool season growth measured in spaced plants or swards, but all characters showed appreciable additive genetic variation, which offers considerable scope for further selection. There was no evidence of any general loss of adaptation in the widely based population, though flowering date and seed weight tended to show increased environmental variability by comparison with the adapted Australian cultivar.

One of the most important changes in the genetic relationship between characters in the breeding population has been the elimination of undesirable ecotypic correlations which were present in the parental material prior to hybridization and recombination.

In the advanced breeding population significant intra-population correlations existed between the various estimates of growth made on single plants, but in general, estimates of growth made under these conditions were not significantly correlated with the performance of the same families in swards. Of particular interest, however, were the significant genetic correlations between seedling growth of full-sib families measured in controlled environments, and the growth of the same families as spaced plants and in swards.

The predicted response to either direct or indirect selection indicates considerable potential for improvement in a number of important characters including seedling growth, seed retention, and winter growth in swards. Of particular interest is the possibility of increasing sward production as a correlated response to intensive selection for seedling growth.

A selection procedure is described involving simultaneous selection in full-sib families grown as swards and spaced plants. This technique provides a useful compromise when progress is desired in a number of characters which are best assessed under one or the other regime.

I. Introduction

The initial step in any plant breeding programme is the choice of a suitable base population. With cross-pollinated species, the plant breeder is often faced with the choice of improving an established or accepted variety by intra-population selection, or by forming a more widely based breeding population by the incorporation of introduced material. The second alternative may often be necessary because of the limited variability present in a local population, but any increase in the genetic variability by this means must be balanced against the possible loss in adaptation to local conditions.

This problem has arisen in the breeding of *Phalaris tuberosa* L., a perennial grass which has been widely used as a component of sown pastures in southern Australia, and which is valued for its adaptability, persistence, and cool season production. The one commercial variety which has been in use in Australia for over 60 years is thought to have been derived from a single introduction of Mediterranean origin (Trumble 1935), and appears to have undergone no marked ecotypic differentiation at least during the early part of this period (Trumble and Cashmore 1934). Despite its virtues, the Australian cultivar has certain shortcomings, including slow seedling growth which makes its establishment more difficult, and a tendency to shed seed immediately after ripening which causes harvesting problems. In addition, the value of this grass could be enhanced by increasing productivity during the autumn and winter, which is often the period of greatest pasture shortage.

A breeding programme designed to remedy these deficiencies inevitably involves a choice between two alternative approaches. The first alternative of intra-population selection has been examined by Latter (1965 a, b), who assessed the potential for a change in the date of ear emergence and for increases in seed weight and seedling growth, through selective breeding within the locally adapted Australian cultivar. This analysis, and also selection for seed retention and vernalization requirement (McWilliam 1963, 1968) indicates that selection within the Australian cultivar could ultimately produce a population with a mean for each character outside the range shown by introduced ecotypes.

The second alternative involves the pooling of the variability found in a wide range of ecotypes of *P. tuberosa* by crossing these into the Australian population and selecting for desirable recombinants. The consequences of adopting this second approach are examined in the present paper, which represents a compromise between a practical breeding programme and an attempt to understand the nature of the genetic variability at various stages during selection.

The data have been derived from a study of two populations; one a base population representing the initial gene pool and the other a more advanced breeding population derived from it. The variability for a number of important agronomic characters in these synthetic populations has been compared with that available in the more restricted locally adapted Australian population. Also an attempt has been made to measure the nature and extent of genetic correlations between characters following the initial recombination, and to detect any conspicuous changes in these relationships during the course of selection.

II. Material and Methods

(a) Nature of the Breeding Material

(i) *Mediterranean Ecotypes.* Thirty introductions (ecotypes) of *P. tuberosa* were used to generate a broadly based breeding population. These were selected from a larger collection of over 100 introductions from the Mediterranean region (Neal-Smith 1955) which had undergone preliminary screening at Canberra. They were chosen to represent the range of morphological, physiological and geographic variation present in the species, and because they possessed desirable agronomic features. In particular, introductions from Morocco and Algeria were strongly represented because of their desirable seedling vigour and winter growth characteristics.

The nature of the variation present within representative samples of this collection has been studied for a range of growth and developmental characters including seed weight, germination, seed retention, flowering responses, seedling growth, and sward production (McWilliam 1961; 1963; 1968; Scurfield and Biddiscombe 1966; Cooper and McWilliam 1966). From these studies, and from the work of Latter (1965b), it is apparent that the range of variation for most characters is extensive, and that significant interpopulation correlations exist between a number of important agronomic characters when compared at the ecotypic level.

(ii) *Australian Cultivar.* The general agronomic features of this cultivar have been reviewed by Cameron (1963). The variation shown with respect to flowering time, seed weight, and seedling growth has been analysed, and the interrelationships among the variables characterized (Latter 1965b). Variation in the extent of seed retention and vernalization requirement has also been studied by McWilliam (1963; 1968). All characters show appreciable additive genetic variation, and by contrast with the close association found for characters at the ecotypic level in the Mediterranean collection, the correlations between characters within the commercial population were of a low order, and to a large extent the traits were genetically independent. The phenotypic and genetic correlations among a number of these variables and their heritabilities are shown in Table 1.

(b) Breeding Procedures

Before describing the populations analysed in this study, and the techniques used for the collection of the data, it is necessary to give a brief outline of the selection procedures used in the development of this material. A summary of the breeding programme is illustrated in Figure 1.

A top-crossing procedure followed by recombination was used to establish a genetically variable base population. The 30 selected ecotypes from the Mediterranean collection were used as pollen parents (sires) in crosses to genotypes of two testers; the Australian cultivar (V97) and a productive mid-season variety (CPI 15022) from Turkey. The tester genotypes were selected for high self-incompatibility to ensure maximum hybrid seed set without emasculation. Up to four genotypes of each Mediterranean ecotype were used in crosses to similar number of genotypes of each tester which, when combined, gave a total of 60 F_1 (tester × ecotype) families. Alternatively these may be classified as 30 sire groups in each of which the pollen parents were derived from the same ecotype.

All 60 F_1 families, together with the two testers, were grown as spaced plants and also as planted microswards, and their productivity was compared. In the first and second year after establishment about 25% of the families when compared under sward conditions significantly outyielded both testers, and for this reason two separate recombination blocks were established.

The first consisted of 100 genotypes selected in equal proportions from the ten most productive F_1 sire groups. The second was composed of lots of ten plants taken at random from each of the 30 F_1 sire groups. Flowering in these was synchronized to minimize assortative mating, and after randomizing, the plants within each group were allowed to interpollinate.

Equal weights of seed from each genotype were pooled on the basis of sire groups within each recombination block, and the seedlings from each group were raised in separate boxes. Approximately 100 well grown seedlings from each sire group were established as spaced plants in the field in two blocks, one representing F_2 progeny from

Table 1. *Heritabilities and genetic and phenotypic correlations for characters within the Australian cultivar (Latter 1965b; McWilliam 1963, 1968)*

Character	Mean $\bar{x}$	Variance σ_p^2	Heritability h^2	Genetic and Phenotypic Correlations		
				Characters	r_g	r_p
1. Date of Ear Emergence (Days after Nov. 1)	25.4	18.3	$0.53 \pm .02$	1 – 2	$-0.24 \pm .07$	$-0.10 \pm .03$
2. Seed Weight (50 seed wt.mg)	79.5	87.2	$0.79 \pm .06$	2 – 3	$0.16 \pm .02$**	$0.12 \pm .03$
3. Seedling Growth (log mg d.wt)	1.72	0.025	$0.17 \pm .05$	3 – 1	$0.05 \pm .10$	$-0.06 \pm .02$
4. Seed Retention* (% retained)	65.5	227.5	$0.92 \pm .11$	4 – 1	Negligible	—
5. Vernalization Requirement (Days below 10 °C)	16	88.4	$0.63 \pm .06$	—	—	—

* Based on a closely related Argentine population; retention measured on intact heads.

** Observed correlation between seed weight of the ovule parent and seedling growth of a member of the derived half-sib progeny group (Latter 1965b).

the restricted, and the other F_2 progeny from the unrestricted recombination block.

The plants were used for two purposes:

(1) Plants were selected at random from all of the 30 sire groups in the unrestricted block and were used to set up a base population for analysis (see Section c (1)).

(2) Outstanding plants selected from each of the sire groups in the unrestricted block, plus additional selections from each of the ten sire groups in the restricted block, were removed from the field prior to flowering and recombined in isolation to provide a heterogeneous population of F_3 individuals for further selection.

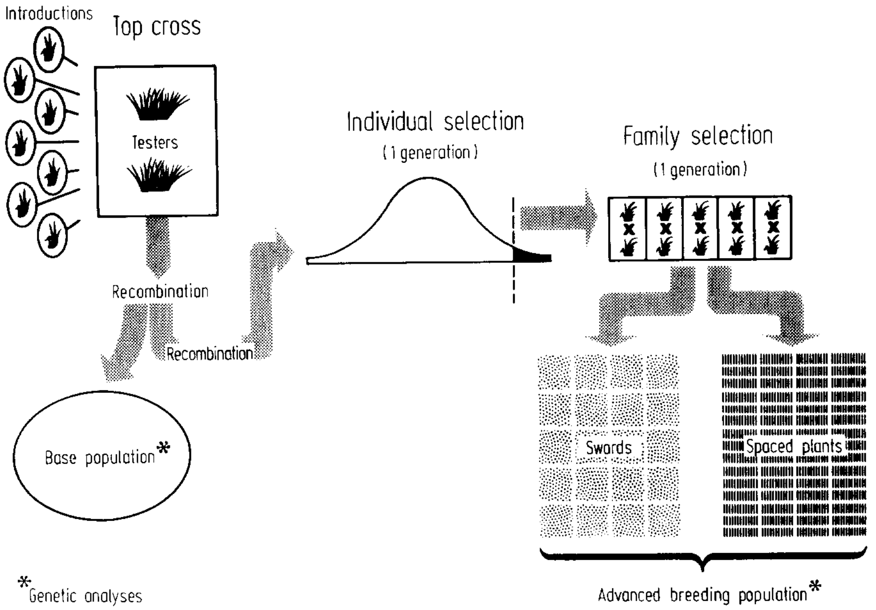

Fig. 1. Outline of the crossing and recombination procedure used to produce the base population, and a diagramatic representation of the selection procedure employed in the production of the advanced breeding population. These two populations were used for the genetic analysis as indicated

(i) *Individual Selection.* Approximately 75,000 F_3 seeds, made up of equal numbers from each of the recombined F_2 selections, were imbibed for 48 hr at 4 °C, then germinated for a further 48 hr at 25 °C. About 20 per cent of the seedlings in each half-sib family were retained, based on selection for germination vigour (rate and vigor of germination) which has been shown to be correlated with seedling vigour (McWilliam unpublished). These selected seedlings were grown outdoors in boxes for two months in the autumn when 10 per cent of the largest in each half-sib family (as judged by the size of the tops and tiller number) were transplanted to the field as spaced plants. The combined population of all F_3 seedling selections (approximately 2000 plants) was then passed through a further series of selection sieves by scoring for first year winter production, growth habit, date of ear emergence (only extremely early and late genotypes excluded) and seed retention as judged by the structure of the inflorescence (McWilliam 1963). Plants surviving the final screening were used in the second phase of family selection.

(ii) *Family Selection.* A family selection system with a two year generation interval was adopted because of the importance of winter and autumn growth as breeding objectives, and the need to assess these responses under sward conditions. Also for a character such as forage yield which can be expected to have a low heritability, of the order of 10 per cent, selection based on family means is likely to be a most accurate way of identifying superior genotypes (Latter 1964).

The parental genotypes for the crossing programme were selected at the end of the first cycle of individual selection. These selected plants were removed from the field just prior to anthesis and pair-crossed at random without emasculation. In each cross the reciprocal seed was bulked to provide a sufficient quantity for subsequent family testing in replicated swards. Of the 100 crosses made only 64 were used, the remainder being rejected because of insufficient self-incompatibility in either parent, or because of insufficient seed.

The progenies from these pair crosses were first grown in the Canberra phytotron in flats at two day/night temperature regimes (15/10 °C and 21/16 °C) in natural daylight extended with incandescent lamps to give a 16-hour photoperiod. Comparisons of seedling growth were based on the dry weight of seedlings measured at the 7th leaf stage.

Progenies from these crosses were also established in the field both as sown swards (6 sq. metres) and as rows of spaced plants (10 plants/row, spaced 1 × 1 metre) in separate experiments, each with four replicates. Selection was based largely on winter and autumn yield of swards as determined by harvests made in the second year. In addition, the spaced plants representing these same selected progenies were scored and measured for single plant characters, and the best individual genotypes from each selected family were removed for the next cycle of family selection.

(c) Populations Analysed

(i) *Base Population.* A base population was established by taking a random sample of five genotypes from each of the 30 F_2 sire groups described in Section (b), and after synchronizing flowering, plants were recombined under isolation. To ensure maximum randomisation of pollination, the position of all plants was changed several times during the flowering period. The mean weight of 50 seeds from each of the 150 genotypes was recorded, and the performance of the half-sib progenies was studied with respect to tiller number and seedling growth in boxes, and date of flowering (ear emergence) and seed weight, over a period of two years in the field. The field trials were located at Canberra and Wagga, N.S.W., and in these, and the seedling comparisons, four replicates of a basic 6-plant plot were used for each genotype in a randomised block design. The analyses of these data have given estimates of phenotypic variance, heritability and genetic correlations between the characters and estimates of correlations between offspring performance and seed weight of the ovule parent.

(ii) *Advanced Population.* The second analysis was carried out on a more advanced breeding population representing the first cycle of family selection. The origin of this material, and the design and details of the family structure, are set out in the previous section (Section (b)).

During the first year of establishment all spaced plants were scored for winter growth, and a record taken of the flowering date (emergence) and seed weight. In addition, two plants in each family were measured for seed retention using a mechanical shaking technique described by Bonin and Goplen (1963). Seedling growth of all families was measured in controlled environments as described previously. A measure was also made of the flowering date and seed weight of the parental genotypes grown under similar conditions.

In the following year 50 per cent of these plants in each full-sib family were harvested for autumn and winter yield. At the same time the identical families, grown as swards, were also measured for autumn and winter yield by harvesting a strip (3 sq. metres) from the centre of each plot. Analyses of these data have provided estimates of heritability and genetic correlations between the various characters at this stage in the selection programme. From measurements of the yields of seedlings and spaced plants in the first and second year of growth, and the sward yields taken in the second year, it has been possible to compare the relative efficiencies of a number of alternative breeding procedures.

III. Results

(*a*) *Analysis of Base Population*

A summary of the estimates derived for a number of parameters characterizing variation in the base population is given in Table 2. Comparable parameters in the Australian commercial population (Table 1) show the heritabilities to be of the same order in both populations, but the variability for each character in the Australian cultivar is appreciably less than in the base population. The estimate of heritability for flowering date in the base population (0.60 ± .02) has been calculated as the repeatability of the character measured on the same individual plants in consecutive years, since the half-sib correlation for this character (0.23 ± .04) is expected to be inflated by phenotypic assortative mating despite attempts to achieve random pollination among parents.

Table 2. *Estimates of population parameters in the base population*

Character	Mean $\bar{x}$	Variance σ_p^2	Heritability h^2
Tiller No.	10.1	8.5	0.22 ± .06
Seedling Growth (log mg d.wt)	2.16	0.053	0.17 ± .08
Flowering Date (Days after Nov. 1)	13.9	32.3	0.60* ± .02
Seed Wt. (50 seed wt.mg)	76.3	121.2	0.57 ± .10

* Estimated from the repeatability of flowering date in two consecutive years. Measured as date of ear emergence.

The estimate of heritability of seed weight in Table 2 is based on the dam-offspring correlation $r(\mathrm{D, O})$ given in Table 3. Offspring seed weight was measured in only one replication of the progeny trial, and no estimate of heritability based on the differences among progeny group means is therefore available. Heritabilities for both tiller number and seedling growth based on half-sib correlations, $r(\mathrm{HS})$, were comparatively low, possibly due to a high level of environmental variance among individuals under the conditions of this experiment.

The observed correlations between seed weight of ovule parent and four characters measured in the offspring are presented in Table 3, and the genetic and phenotypic correlations estimated from the offspring measurements themselves are given in Table 4. The maternal relationship between seed weight and seedling growth is not significant in this population, whereas a significant relationship was detectable in Australian cultivar (Table 1).

The only significant genetic correlation detected in the base population was that between tiller number and flowering date (0.34*) reflecting the greater tillering capacity of the late flowering genotypes in this population (Table 4). The genetic correlation between seedling growth and flowering date (0.35) approached significance, but the relationship is of opposite sign to that shown by the parental Mediterranean ecotypes (Table 10), and is unlikely therefore, to be more than a chance positive estimate. The corresponding correlation in the Australian cultivar is effectively zero (Table 1).

(*b*) *Analysis of Advanced Breeding Population*

Spaced Plant Performance: Estimates of the means, variances and heritabilities of the range of characters measured on spaced plants from full-sib family groups are given in Table 5.

Table 3. *Correlations in the base population between seed weight of the ovule parent and characters measured in offspring derived by open-pollination* $[r(D, \mathrm{O})]$

Character in Offspring	$r(\mathrm{D, O})$
Tiller No.	0.02 ± .03
Seedling Growth	0.04 ± .03
Flowering Date	−0.06 ± .04
Seed Weight	0.28 ± .05

Table 4. *Phenotypic and genetic correlations between characters in the base population. Above diagonal: genetic correlation* (r_g). *Below diagonal: phenotypic correlation* (r_p)

	Tiller No.	Seedling Growth	Flowering Date	Seed Wt.
Tiller No.	—	−0.04 (0.2)⁺	0.34* (2.1)	−0.43 (1.5)
Seedling Growth	0.55 ± .02	—	0.35 (2.0)	0.38 (1.0)
Flowering Date	−0.09 ± .02	−0.15 ± .05	—	−0.24 (1.4)
Seed Wt.⁺⁺	0.01 ± .02	0.13 ± .04	0.13 ± .04	—

* Significant at $P = 0.05$

⁺ The figure in brackets is the ratio of the between-family covariance component to its standard error. A ratio greater then 2.0 has been taken as significant at $P = 0.05$.

⁺⁺ Seed harvested from same plants in year following that in which other characters scored.

The magnitude of the variances and heritabilities for seedling growth at the two controlled temperatures were comparable, as expected from the high genetic correlation (0.97) based on the performance of members of the same families at each temperature. The estimates of heritability have been corrected for non-genetic maternal effects due to seed size differences among the ovule parents (Table 6). They may to some extent be positively biased by non-additive genetic effects, though they do not differ appreciably from the comparable estimates for the base population (Table 2) which is free of this source of bias.

Estimates of heritability of growth of spaced plants were generally low, though that of first year winter growth score was somewhat higher than for the second year cuts. All three measurements in fact show an appreciable genetic relationship with seedling growth at low temperatures (Table 7).

Table 5. *Estimates of population parameters for spaced plant characters in the advanced breeding population*

Character	Mean $\bar{x}$	Variance σ_p^2	Heritability h^2	Mean Australian Cultivar
*Seedling Growth 21/16 °C ^{1}(log mg d. wt.)	1.92	0.048	0.19±.07	1.82
*Seedling Growth 15/10 °C ^{2}(log mg d.wt.)	2.46	0.052	0.25±.08	—
Winter Growth Score 1st year (1 to 10)	6.25	3.39	0.29±.07	4.87
Autumn Growth 2nd year (g d.wt./plant)	189.9	6,515	0.21±.07	—
Winter Growth 2nd year (g d.wt./plant)	148.8	2,631	0.14±.06	—
Flowering Date^{+} (Days after Nov. 1)	12.6	41.7	0.56±.05	12.3
Seed Retention^{++} (% seed retained)	27.6	252.2	0.53±.13	21.4
Seed Weight (50 seed wt.mg)	84.8	161.6	0.54±.08	85.8

* Genetic correlation $r_{g_{12}} = 0.97 \pm .20$

$^{+}$ Measured as date of ear emergence.

$^{++}$ Based on % retained following mechanical shaking.

An estimate of the repeatability of flowering date measured on the same plants in consecutive years ($r = 0.56 \pm .07$) did not differ significantly from the estimate of heritability derived from the mid-parent-offspring regression, viz. 0.57 ± .07. The full-sib correlation r(FS) = 0.48 ± .09 is clearly inflated by a degree of phenotypic assortative mating in the population which has been estimated directly from observations on the parents to be $\varrho = 0.44 \pm .06$. Because of the existence of assortative mating and selection practised in the parental population, the precise interpretation of r(FS) is difficult. However, the mid-parent-offspring regression and the estimate of repeatability can be combined to give an unbiased estimate of the heritability of flowering date (0.56 ± .05).

Estimates of r(FS) and r(D,O) characterizing the variation for seed weight in the population did not differ significantly, and were used to derive the pooled estimate of heritability for seed weight given in Table 5 (0.54 ± .08). The estimates of heritability for flowering date and seed weight are comparable with those found for the same characters in the base population (Table 2) though the variances are somewhat greater in the advanced population. Such comparisons may indicate no more than year to year differences in variability (Latter 1965b), and it cannot necessarily be inferred from the present data that the two populations differ.

Dam-offspring and midparent-offspring correlations between seed weight and flowering time in the parents, and seedling growth and mature plant growth in the full-sib progeny, are presented in Table 6. The estimate for r(P, O), when seed weight and seedling growth were assessed on the same seed sample, includes environmental maternal effects which are absent when the progeny are derived from a seed sample produced in a different year from that used for the seed weight determination. The correlation between the seed weight of the ovule parent and the „true" mean performance for seedling growth of the derived full-sib group of offspring, can be estimated from these data to be greater than 0.76. This is somewhat higher than the comparable value in the Australian cultivar (Latter 1965b). Dam-offspring correlations between seed weight and second year growth of spaced plants were small and not significant, as was the parent-offspring correlation between flowering date and seedling growth.

Table 6. *Relationship between parental seed weight and flowering date and characters in the full-sib progenies measured as spaced plants. Data from advanced breeding population*

Character in Parent	Character in Offspring	Correlation Symbol	Estimate
Seed Wt.	Seedling Growth	r(D*, O)$^{+}$	0.16±.05
	Seedling Growth	r(P, O)$^{++}$	0.28±.05
	Autumn Growth (2nd year)	r(D, O)	0.08±.05
	Winter Growth (2nd year)	r(D, O)	0.11±.05
Flowering Date	Seedling Growth	r(P, O)$^{++}$	−0.05±.05

$^{+}$ r(D*, O) and r(D, O) refer to observed correlations between dam and offspring. r(D, O) included both genetic and environmental maternal effects; r(D*, O) includes only genetic maternal effects (Latter 1965a).

$^{++}$ r(P, O) denotes mid-parent offspring relationship.

Table 7. *Phenotypic and genetic correlations between spaced plant characters in the advanced breeding population. Above diagonal: genetic correlation* (r_g). *Below diagonal: phenotypic correlation* (r_p)

	Autumn Growth 2nd Year	Winter Growth 2nd Year	Winter Growth Score 1st Year	Flowering Date	Seed Retention	Seed Weight
Seedling Growth	0.68* (3.3)†	0.56* (2.5)	0.60* (3.5)	−0.23 (1.6)	−0.07 (0.4)	0.45* (2.7)
Autumn Growth 2nd Year	—	0.78* (2.6)	0.59* (2.5)	−0.50* (2.5)	−0.11 (0.7)	0.02 (0.1)
Winter Growth 2nd Year	0.37±.04	—	0.74* (3.0)	−0.13 (0.6)	−0.08 (0.3)	0.34 (1.5)
Winter Growth Score 1st Year	0.46±.04	0.28±.03	—	−0.34* (2.2)	−0.22 (1.3)	0.38* (2.3)
Flowering Date	−0.18±.04	−0.08±.04	−0.29±.03	—	0.16 (1.1)	−0.16 (1.2)
Seed Retention	—	—	—	—	—	−0.17 (1.1)
Seed Weight	0.11±.04	0.11±.03	0.19±.03	−0.12±.03	—	—

* Significant at $P = 0.05$. — † The figure in brackets is the ratio of the between-family covariance component to its standard error. A ratio greater than 2.0 has been taken as significant at $P = 0.05$.

Table 8. *Estimation of population parameters for autumn and winter growth in 2nd year swards in the advanced breeding population*

Character	Mean ($\bar{x}$)	Phenotypic Variance (σ_p^2)	Heritability of Single Plot Values (h^2)	Heritability of Family Means⁺	Standardized Genetic Covariance ($h_1 r_g h_2$)⁺⁺	Genetic Correlation (r_g)	Mean Australian Cultivar
Autumn Growth (d.wt.g/plot)	1073.8	54,094*	0.19±.08	0.48±.13	−0.046±.056	−0.25	1056
Winter Growth (d.wt.g/plot)	372.9	8,991*	0.18±.08	0.47±.13			314

* Within replication variance among plots. — ⁺ Based on 4 replications. — ⁺⁺ Brown, Daniels and Latter (1969).

Phenotypic and genotypic correlations between spaced plants' characters in the advanced breeding population are given in Table 7. Of particular interest are the significant genetic correlations between seedling growth of full-sib families as measured in controlled environments, and the growth of the same families both as first and second year spaced plants. First year winter growth score was also significantly correlated with autumn and winter growth of the same plants in the second year. These results indicate that either of these two methods of measuring seedling vigour (which are themselves correlated, $r_g = 0.60^*$) can be used in a preliminary screening for second year performance of spaced plants. The two first year growth characters, seedling growth and winter growth score, also are significantly correlated with seed weight measured on the same plants (0.45* and 0.38*) and the data of Table 6 have established the existence of a genetically controlled maternal component in certain of these relationships.

Seed retention was not shown to be significantly correlated genetically with any of the other characters measured on spaced plants. Flowering date shows significant genetic correlations with second year autumn growth and first year winter growth score. Earliness of flowering is in both cases associated genetically with more vigorous growth. The magnitude of the genetic correlations between flowering date and both seedling growth and winter growth is in each case low in marked contrast to the close relationship found between these characters in the Mediterranean ecotypes used in the initial crosses, although the sign of the correlations is the same in all cases.

Sward Performance: Under sward conditions only second year autumn and winter growth were measured, and estimates of population parameters for these characters are given in Table 8. Very similar estimates for heritability based on plot means were obtained for growth in both seasons, indicating that almost 20 per cent of the variation between plots within replications for sward yield in autumn and winter is genetic. The genetic correlation between autumn and winter yield (−0.25) is low and non-

Table 9. *Genetic correlations between spaced plant characters and sward performance in the advanced breeding population*

Spaced-plant Characters	Sward Performance (2nd Year)	
	Autumn Growth	Winter Growth
Seedling Growth	0.69*(2.7)**	0.55*(2.1)
Autumn Growth (2nd year)	0.78*(2.7)	0.05 (0.2)
Winter Growth (2nd year)	0.57 (2.0)	0.42 (1.4)
Winter Growth Score (1st year)	0.40 (1.7)	0.38 (1.6)
Flowering Date	0.19 (0.9)	0.07 (0.3)
Seed Retention	0.28 (1.2)	−0.72*(2.8)
Seed Weight	0.05 (0.3)	0.45*(2.0)

* Significant at $P = 0.05$.

** Ratio of between family component of covariance to its standard error. A ratio greater than 2.0 has been taken as significant at $P = .05$.

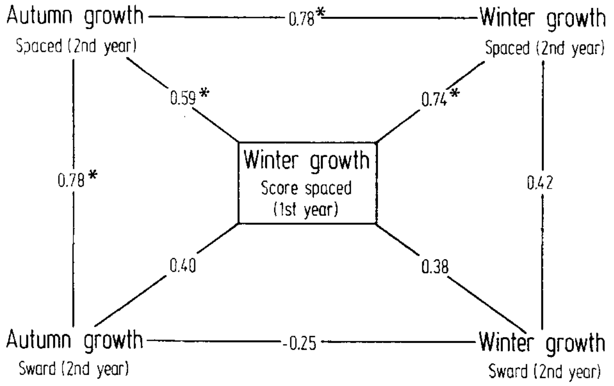

Fig. 2. Genetic correlations between autumn and winter growth assessed for the same full-sib families grown as spaced plants and swards

significant, at first sight suggesting that genetic responses in these two periods of the year are to a large extent independent.

Table 9 lists the genetic correlations between spaced plant characters and autumn and winter production in swards. There was a significant positive correlation between seedling growth and both autumn and winter growth under sward conditions. With the exception of autumn growth of spaced plants, which showed a significant positive correlation with autumn growth in swards, all other measures of the growth of spaced plants were not significantly correlated with production in swards, although the correlations were all positive. A significant negative correlation also existed between seed retention and winter growth in swards, although no corresponding relationship with seed retention exists in the case of autumn growth. This persistent negative correlation reflects the situation which exists in many of the winter active early flowering Mediterranean ecotypes (McWilliam 1963) used as parents in the original topcross. On the other hand, the breakdown of the close relationship between flowering date and growth in swards observed among the parental ecotypes appears to have been complete in this advanced breeding population, though a residual association has been detected for autumn growth in spaced plants (Table 7).

The genetic correlation between growth characters assessed for the same full-sib families grown both as spaced plants and as swards are summarized in Figure 2. It is clear from this figure that significant correlations exist between the various estimates of growth made in spaced plants, either in the first or second year. However, with the exception of autumn growth, estimates of growth in spaced plants are not significantly correlated with performance in swards, nor is the growth of swards in the autumn statistically correlated with growth in the winter. These results emphasize the difficulty of deriving economically meaningful measures of growth unless the material is grown under realistic sward conditions.

IV. Discussion

This study has provided an opportunity to compare the genetic relationships among variables at the inter-population level in a group of parental ecotypes, and to examine the magnitude of these same correlations at two stages following recombination with or without selection in a widely based breeding population. A summary of these data is presented in Table 10.

Table 10. *Comparisons of genetic correlations between characters in both parental and breeding populations*

Genetic Correlation (r_g)	Mediterranean⁺	Australian Cultivar⁺	Base Breeding Population	Advanced Breeding Population
Seed Wt. — Seedling Growth	0.76**	0.16	0.38	0.45*
Flowering Date — Seedling Growth	−0.79**	0.05	0.35	−0.23
Seed Wt. — Flowering Date	−0.62*	−0.24	−0.24	−0.16
Seed Wt. — Seedling Tiller No.	0.10	—	−0.43	—
Seedling Tiller No. — Seedling Growth	−0.35	—	−0.04	—
Seedling Tiller No. — Flowering Date	0.11	—	0.34*	—
Flowering Date — Winter Growth Swards	−0.82**	—	—	0.07
Flowering Date — Seed Retention	0.85*	Nil	—	0.16

*, ** Significant at $P = 0.05, 0.01$. — ⁺ Latter (1965b), McWilliam (1961, 1963).

The most obvious change in the genetic relationship between characters has been the marked reduction in the magnitude of a number of ecotypic correlations which were present in the parental material prior to hybridization and recombination. Correlations between flowering date and growth characters (seed weight, seedling growth, and winter growth in swards) and between flowering date and seed retention, which were significant and mostly negative in the Mediterranean ecotypes, are virtually non-existent at the intra-population level in the advanced breeding population. One significant correlation in the parental ecotypes, between seed weight and seedling growth, which is favourable to the breeding objectives, has persisted in the advanced breeding population, whereas other characters which showed no relationship early in the breeding programme have remained genetically independent.

These results clearly indicate the value of recombination and selection in disrupting strong ecotypic associations between characters which presumably evolved under the influence of natural selection. These associations, which are undoubtedly of value for survival in certain natural environments, are undesirable in terms of the breeding objectives. The rapidity and relative ease with which they have been dissociated indicates that they are controlled by virtually independent sets of genes.

Estimates of heritability for certain characters in the Australian cultivar, which was used as one of the parents in the top-cross, and for the same characters in the two breeding populations, are quite comparable in magnitude (Tables 1, 2, 5). This is surprising, in view of the considerable genetic variability which was introduced from the Mediterranean ecotypes. The effect of selection of parents in the advanced breeding population would have resulted in a slight underestimate of h^2 but this is not a factor in interpreting estimates of heritability in the base population. The measures of total phenotypic variance (σ_p^2) for flowering date and seed weight in Tables 1, 2 and 5 make it clear that the recombination of contrasting genotypes has had some disruptive effect on the adaptation of the breeding populations, resulting in increased environmental variability for those characters, as estimated by $(1 - h^2)\,\sigma_p^2$. Estimates of phenotypic variance are known to change significantly for both these characters from one year to the next, but the differences are small for a single population (Latter 1965b).

Predictions of selection response for a number of characters in the advanced population have been calculated as

$$\Delta G = \bar{i}\, h^2\, \sigma_p$$

using values of $\bar{i}$, the standardized selection differential, given by Finney (1958). These expectations of progress in a single generation have been used to calculate the superiority of the resultant population relative to (i) the advanced breeding population itself, and (ii) the Australian commercial population grown under identical conditions (Table 11). The results indicate that substantial progress can be made for the high selection intensities possible with single-plant characters. The considerable potential for improvement in seed retention is a reflection of the appreciable variation and moderately high heritability ($h^2 = 0.53$) exhibited by this character. For sward yields, where family selection is necessary, and the generation interval is two years, progress, although less spectacular, is still appreciable on a per generation basis.

The improvement expected in most characters is greater when expressed as a per cent of the mean of the Australian cultivar. This is particularly true of the three agronomic characters, seedling growth, winter growth in swards, and seed retention, and is a realistic measure of the substantial progress that has been achieved with these characters.

In most breeding programmes improvement is usually sought in a number of characters and the progress achieved will depend on the genetic relationship between the characters, and the particular selection technique employed. In the breeding pro-

Table 11. *Progress expected following one generation of selection for individual characters in advanced population*

Characters	Generation Interval (years)	Selection Intensity and ($\bar{i}$)	% Superiority* relative to mean of	
			Advanced population	Australian cultivar
Seedling Growth (21/16 °C)	1	20/20,000 ($\bar{i}$ = 3.37)	7.3	13.2
Flowering Time	1	20/5000 ($\bar{i}$ = 2.96)	10.7 days⁺	11.0 days⁺
Seed Retention⁺⁺	1	20/5000 ($\bar{i}$ = 2.96)	90.3	145.5
Seed Weight	2	20/5000 ($\bar{i}$ = 2.96)	24.0	22.2
Autumn Growth Swards	2	10/100 (4 reps) ($\bar{i}$ = 1.75)	10.5	12.3
Winter Growth Swards	2	10/100 (4 reps) ($\bar{i}$ = 1.75)	13.0	34.2

* Predicted mean $\hat{y} = \bar{y} + \bar{i}\, h^2 \sigma_p$: Percent superiority = 100 $(\hat{y} - \bar{y})/\bar{y}$.

⁺ Progress expressed as the predicted shift in flowering time measured as days after mean flowering time.

⁺⁺ Based on % of seed retained following mechanical shaking.

gramme described in this paper the major objectives were to increase cool season production (autumn and winter growth), seedling growth, and seed retention, while maintaining a flowering date comparable with the commercial population. With the exception of seed retention, which in the advanced population showed a negative correlation with winter growth, genetic correlations between the other spaced plant characters and sward yields were positive (Table 9), indicating that any selection for these characters under spaced plant conditions will have, in most cases, a beneficial effect on cool season growth in swards. The predicted responses in terms of autumn and winter sward growth in the advanced breeding population following selection for various growth characters measured on spaced plants in the same full-sib families are shown in Table 12. The response expected from direct selection for sward performance is also listed for comparison.

Individual or family selection based on yields from cuts of spaced plants in the second year (Methods B and C) were generally less efficient than direct selection for sward yield (A). However, individual selection for seedling growth (E) or winter growth score (D) in the first year, using a high selection intensity, can be theoretically more efficient than direct selection in terms of progress per annum. These predictions, however, can only be taken as a guide, as in each generation of selection both the heritability and the extent of the correlations between characters are likely to change. Nevertheless, these results do emphasize the possibility of achieving significant progress through intensive selection for a correlated response. This approach is especially applicable for a character such as seedling growth which is easily measured and can be subjected to a very high selection pressure.

Table 12. *Predicated response in autumn and winter yield of 2nd year swards following selection for different growth characters*

Methods for Selection.

A. Based on (the yield of) swards in the 2nd year (10/100) averaged over 4 reps

B. Based on yield of spaced plants cut in 2nd year (20/5000)

C. Based on yield of spaced plants cut in 2nd year (10 fams/100: 5 reps)

D. Based on 1st year winter yield scores of spaced plants (20/5000)

E. Based on 1st year growth of seedlings (20/20,000)

Method	Character Selected	Sward character for which response assessed	Response (%)	
			Per gen.	Per annum
A	Winter yield	Winter yield	13.0	6.5*
	Autumn yield	Autumn yield	10.5	5.2*
B	Winter cut	Winter yield	7.2	3.6
	Autumn cut	Autumn yield	13.0	6.5*
C	Winter cut	Winter yield	5.9	3.0
	Autumn cut	Autumn yield	9.0	4.5*
D	Winter score	Winter yield	10.8	10.8
	Winter score	Autumn yield	7.8	7.8
E	Seedling growth	Winter yield	11.4	11.4*
	Seedling growth	Autumn yield	11.3	11.3*

* Based on genetic correlations significantly different from zero (cf. Table 9).

The data of Tables 8 and 9 indicate that the partial genetic correlation between autumn and winter sward production, at a constant level of seedling growth rate, is close to —1.0; the non-significant genetic relationship between the two sward characters overall is therefore likely to involve components showing both positive and negative associations. Indirect selection based on seedling growth can be expected to influence those components which are positively correlated, but additional direct selection would be necessary to establish the desired balance between the two sward characters.

In the phalaris breeding programme, illustrated in Figure 1, both individual selection based on spaced plants, and family selection based on swards were used in separate phases of the programme to combine the virtues of both techniques. This may well be the most efficient compromise when progress is desired in characters which are best assessed under one or the other regime. In addition, using pair-crosses it is possible to select the most productive full-sib families in swards in the second year, and then from these same families represented as replicated spaced plant rows, select individual plants on the bases of single plant characters.

The data presented in this study indicate that appreciable additive genetic variation exists for a number of characters in the advanced breeding population which offers considerable scope for further selection. The loss of adaptation which is often predicted following the incorporation of additional genetic variability has not been observed, apart from an apparent increase in environmental variability for some characters. Of particular significance has been the demonstration that a number of undesirable ecotypic correlations which were present in the parental breeding material have been eliminated after a relatively short period of recombination and selective breeding. The results clearly support the suggestion (Latter 1965b) that a study of genetic relationships in an adapted interbreeding population can indicate the likely magnitude of residual correlations following recombination in a widely based breeding population.

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Zusammenfassung

An einer Zuchtpopulation von *Phalaris tuberosa*, die aus Kreuzungen von 30 Ökotypen mediterraner Herkunft mit einer australischen und einer türkischen Sorte stammte, wurden die genetische Variation einer Anzahl agronomisch wichtiger Merkmale untersucht und die Beziehung zwischen den Variablen charakterisiert.

Die an Einzelpflanzen wie im geschlossenen Bestand ermittelten Schätzungen der Heritabilität für den Blühtermin, die Verringerung des Samenausfalls und das Samengewicht waren höher als für das Wachstum während der kühlen Jahreszeit; alle Merkmale wiesen aber eine beachtliche additive genetische Variation auf, die Aussichten für eine weitere Selektion eröffnet. Ein allgemeiner Adaptationsverlust war in der umfangreichen Population nicht festzustellen, wenn auch die Merkmale Blütezeit und Samengewicht im Vergleich mit der adaptierten australischen Sorte zu einer erhöhten umweltbedingten Variabilität neigten.

Eine der bedeutendsten Veränderungen in den genetischen Beziehungen zwischen Merkmalen der Zuchtpopulation war die Elimination unerwünschter, für die genannten Ökotypen zutreffender Korrelationen, wie sie im Eltermaterial vor der Hybridisierung und Rekombination vorhanden waren. Es gab in der vorgeschrittenen Zuchtpopulation signifikante Intrapopulations-Korrelationen zwischen den verschiedenen an Einzelpflanzen ermittelten Wachstums-Schätzungen, im allgemeinen waren die unter diesen Bedingungen gemachten Schätzungen aber nicht signifikant mit der Leistung der gleichen Familien im geschlossenen Bestand korreliert. Von besonderem Interesse waren jedoch die signifikanten genetischen Korrelationen zwischen dem Keimlingswachstum von Vollgeschwisterfamilien, die unter kontrollierten Umweltbedingungen gemessen wurden, und dem Wachstum der gleichen Familien als Einzelpflanzen und im geschlossenen Bestand.

Die vorausgesagte Reaktion auf direkte oder indirekte Selektion läßt beträchtliche Möglichkeiten zur Verbesserung einer Anzahl wichtiger Merkmale einschl. des Keimlingswachstums, der Verringerung des Samenausfalls und des winterlichen Wachstums im geschlossenen Bestand erwarten.

Die Möglichkeit der Steigerung des Bestandsertrages als Folge einer intensiven Selektion auf Keimlingswachstum ist von besonderer Bedeutung.

Es wird ein Selektionsverfahren beschrieben, das eine gleichzeitige Selektion in Vollgeschwisterfamilien ermöglicht, die sowohl im Bestand wie als Einzelpflanzen angezogen wurden. Diese Technik bietet einen nützlichen Kompromiß, wenn eine Verbesserung einiger Merkmale erzielt werden soll, die sich entweder beim Anbau in der einen oder in der anderen Form am besten abschätzen lassen.

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