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Genetic Variation in *Solanum tuberosum* Group Andigena Haploids

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Summary. A random sample of haploids, derived from 28 parental introductions from *Solanum tuberosum* Gp. Andigena, was used to estimate the quantitative genetic variation for six traits within this group. The six traits analyzed on a plot mean basis were: total tuber weight, fresh vine weight, total fresh weight (tuber + vine), dry vine weight, total dry matter (tuber + vine) and specific gravity. Progenies were obtained following the North Carolina mating Design I and were evaluated along with the female parental clones at two locations. Components of variance and narrow sense heritabilities were calculated by two methods: Design I and female parent-offspring regression. Heritability estimates calculated by the two procedures were in close agreement for most traits. The estimates for total tuber weight from the Design I procedure were twice that from parent offspring regression. The genetic coefficient of variation for these traits indicated a large amount of total genetic variance in this population. Genetic variability for total tuber weight was mostly additive, while both additive and dominant genetic variances were equally important for the remaining traits.

Key words: *Solanum* – Andigena – Potato – Haploids – Genetic variation

Introduction

Quantitative genetic variation in the cultivated tetraploid potato *Solanum tuberosum* Group Andigena has not been described. Its tetraploid nature has been associated with complex tetrasomic inheritance that makes the complete partitioning of the genetic components of variance difficult (Levings and Dudley 1963). Most genetic models have been developed to study quantitative inheritance at the diploid level, with most components of genetic variation being more easily partitioned. The availability of haploids derived from this tetraploid potato group provides the opportunity to obtain estimates of genetic variation at the diploid level. The measurement of the quantitative variation within a sample of haploids may provide knowledge of the type and amount of gene action present in the derived diploid population, which may be useful in extrapolation to the tetraploid population from which they originated. The present paper is part of an extensive study of the breeding potential of Gp. Andigena haploids and presents estimates of quantitative genetic variation in a sample of Andigena haploids.

Materials and Methods

The experimental material was developed by use of the mating design described as North Carolina Design I (Comstock and Robinson 1948, 1952). The female source was composed of a random sample of haploid clones derived by crossing the 4x Gp. Andigena parents as females with a 2x Gp. Phureja pollinator clone (PI 225682.22), commonly used in haploid extraction, using the method first described by Hougas and Peloquin (1957). These haploids originated from twenty-eight Gp. Andigena parental introductions representing five South American countries and Mexico. The haploid clones were crossed as females in sets to three male groups – Gp. Andigena haploids (2n = 2x = 24), Gp. Phureja (2n = 2x = 24), and Gp. Stenotomum (2n = 2x = 24) using a bulk pollen sample from each of the three Groups. The number of females per set was four, ten, and seven, respectively. The bulk pollen sample for each male group was created by combining the pollen from an equal number of flowers per clone taken from a random sample of clones from each Group.

The progenies and the parental female clones were evaluated in two different locations: University of Wisconsin Peninsular Branch Experiment Station at Sturgeon Bay and the University of Wisconsin Experiment Station at Hancock. A randomized complete block design with three replications was used to evaluate both progenies and female parents. Each progeny plot consisted of 40 individuals spaced 30 cm apart with 122 cm between rows at Sturgeon Bay and 91 cm at Hancock. The parental female clones consisted of five hills per plot. The seedlings and clones were transplanted to the field

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Table 1. Analysis of variance combined over locations and expected mean squares (EMS) used to estimate components of variance

Source of Variation	D. F.	M. S.	E. M. S.
Locations	$(l-1)$		
Rep/Locations	$l(r-1)$		
Males	$(m-1)$	M_1	$\sigma^2_W + K_1\sigma^2_{FL} + K_1/\sigma^2_F + K_2\sigma^2_{ML} + K_2/\sigma^2_M$
Females/Males	$\sum_i m_i(f_i-1)$	M_2	$\sigma^2_W + K_1\sigma^2_{FL} + K_1/\sigma^2_F$
Males × Loc	$(m-1)(l-1)$	M_3	$\sigma^2_W + K_1\sigma^2_{FL} + K_2\sigma^2_{ML}$
Females/Males × Loc	$\sum_i m_i(f_i-1)(l-1)$	M_4	$\sigma^2_W + K_1\sigma^2_{FL}$
Error	$l(r-1)[\sum_i m_i(f_i-1)]$	M_5	σ^2_W

l = locations; r = replications; m = males; f = females; K_1 = number of plots/maternal line; K_2 = number of plots/paternal line (harmonic mean is used because of unequal number of females within males)

on June 6 and 12, 1978 at Hancock and Sturgeon Bay, respectively. The tubers were harvested during the week of September 27 at Hancock and October 18 at Sturgeon Bay.

Measurements for six traits were recorded on a per plot basis. Total tuber weight and fresh vine weight were determined directly in the field at harvest. Percent dry matter of the vine was determined by sampling a branch of every plant per plot, weighing each sample fresh, then drying at 27 °C for three weeks and immediately determining the dry weight. The total dry matter of all vines per plot was determined by multiplying the percent vine dry matter times the total fresh vine weight. Specific gravity was determined following the standard weight-in-air/weight-in-water procedure sampling one tuber per plant per plot. Total fresh weight (tuber + vine) was determined by adding total tuber weight and fresh vine weight, and likewise, total dry matter (tuber + vine) was determined by adding vine dry matter to tuber dry matter. Tuber dry matter was derived directly from Maercker's table, based on specific gravity values (Behrend et al. 1880).

Two types of analyses of variances were conducted on a plot mean basis. One followed Design I procedures (Comstock and Robinson 1948, 1952), and a second type used parental information from the intra-male regression of offspring on the female parent (Becker 1967; Lush 1940). For both procedures, a computer program was developed to perform the analyses. The analysis of variance and the expected mean squares (EMS) for combined data are presented in Table 1, and the components of variance were calculated by equating the respective mean squares to their EMS and solving for the appropriate component. According to Design I, the variance component for males (σ^2_M), which is due to the half-sib relationship, equals the covariance of half-sibs. This estimate is equivalent to one-fourth of the additive genetic variance (σ^2_A). The variance component for females (σ^2_F) is estimated by one-fourth of σ^2_A and one-fourth of the dominant genetic variance (σ^2_D). According to the intra-male regression of offspring on female parent analysis, the covariance of progenies and their female parent will estimate one-half of σ^2_A, and twice the regression coefficient provides an estimate of heritability.

Results

Estimates of the variance components for the six traits and the unbiased estimates of narrow sense heritability, according to Design I, are presented in Table 2. The male × location interaction component (σ^2_{ML}), for most traits was large; therefore, a considerable amount of non-genetic variation was accounted for, which otherwise would have inflated the estimate of σ^2_M and consequently, σ^2_A and heritability. Although the error components of variance (σ^2_e) were also quite large for all

Table 2. Estimates of components of variance from Design I mating system and narrow sense heritabilities

Variances	Total tuber wt.	Fresh vine wt.	Total fresh wt. (tuber + vine)	Dry vine wt.	Total dry matter (tuber + vine)	Specific gravity
σ^2_M	0.0131	0.0991	0.0501	0.0024	0.0015	59×10^{-5}
σ^2_F	0.0034	0.2098	0.1800	0.0047	0.0043	20×10^{-4}
σ^2_{ML}	0.0034	0.0939	0.0649	0.0012	0.0010	95×10^{-5}
$\sigma^2_{F/ML}$	−0.0009	0.0824	0.1127	0.0006	0.0008	-26×10^{-5}
σ^2_e	0.0162	0.1824	0.1881	0.0072	0.0077	51×10^{-4}
h^2	0.741	0.318	0.303	0.352	0.359	0.270

$$h^2 = \frac{4\sigma^2_M}{4\sigma^2_M + \sigma^2_F + \frac{(4\sigma^2_{ML} + \sigma^2_{F/ML} + \sigma^2_e)}{l}}$$

Table 3. Heritability estimates using intra-male regression of offspring on female parent (combined over two locations)

Traits	Total tuber wt.	Fresh vine wt.	Total fresh wt. (tuber + vine)	Dry vine wt.	Total dry matter (tuber + vine)
h^2	0.338 ± 0.115	0.515 ± 0.106	0.523 ± 0.110	0.416 ± 0.098	0.374 ± 0.105

Table 4. Genetic variances, genetic coefficient of variation (G.C.V.) and means based on Design I

Genetic component	Total tuber wt.	Fresh vine wt.	Total fresh wt. (tuber + vine)	Dry vine wt.	Total dry matter (tuber + vine)	Specific gravity
σ^2_A	0.0524	0.3964	0.2004	0.0096	0.0060	24×10^{-4}
σ^2_D	0.0000	0.4428	0.5196	0.0094	0.0112	56×10^{-4}
G.C.V.	51.9	34.6	27.4	31.9	25.9	8.4
Mean	0.441	2.644	3.094	0.432	0.507	1.066

$$\text{Genetic C.V.} = \frac{\sqrt{\sigma^2_A + \sigma^2_D}}{\text{Mean}} \times 100$$

traits, heritability values for most traits were moderately high. The heritability value for total tuber weight was especially high considering the quantitative nature of inheritance for this trait.

Heritability estimates obtained from the intra-male regression of offspring on female parents are presented in Table 3 for all traits except specific gravity. The estimates for most traits, with the exception of tuber weight, were high and in reasonable agreement with Design I heritability estimates. The divergency in the estimates of heritability for total tuber weight between these two methods could have been due to sampling error.

Estimates of genetic variances, σ^2_A and σ^2_D, and genetic coefficients of variation (GCV) for all traits for Design I are presented in Table 4. The additive genetic variances for total tuber weight and dry vine weight in this study were larger than the respective estimates of dominant genetic variance. In fact, for total tuber weight, σ^2_D was negative and assumed to be the result of sampling error. Therefore, σ^2_D for this trait was assumed to be zero. The remaining traits indicated larger estimates of σ^2_D than σ^2_A.

The genetic coefficients of variation (GCV) for all traits ranged from 25.9 to 51.9, except specific gravity which had a rather low GCV (8.4%). A coefficient of 20 percent indicates a range in genetic value of approximately 50 to 150 percent of the mean for the character (Comstock et al. 1957). According to this criterion, the estimate of the total genetic variance was large for all traits except specific gravity. A similar conclusion can also be drawn from the heritability estimates.

Discussion

The estimates of variance components according to Design I and their genetic interpretation were based on the assumptions proposed elsewhere – regular diploid behavior at meiosis, no multiple allelism, arbitrary gene frequencies, no linkage, no epistasis (Cockerham 1956; Comstock and Robinson 1948, 1952). Deviation from the theoretical model in the present study may occur in that the distribution of genotypes, especially the equilibrium of linked groups, may not be at random in the haploid population because the process of extracting haploids may not be equivalent to a random sampling of gametes (haploids). The simple mechanism of $4x \times 2x$ crossing used to isolate haploids, though assumed to provide a random sample of living gametes, may not since it does require that an egg be capable of developing into a mature plant. It seems likely that not all eggs would have this potential, as reflected in part by the differences in frequency of haploid production of various 4x cultivars (Hougas et al. 1964; Frandsen 1967).

Design I also assumes the use of a single diploid male per female set, but since bulk pollen from a group of common taxonomic origin was used in this study instead of pollen from a single clone, the "no multiple allelism" assumption of Design I may have also been violated. The consequences of these discrepancies would be that the "female within males" component of phenotypic variance would be increased, biasing downward the σ^2_A and h^2 estimates derived from the intraclass correlation coefficient. The Design I heritabilities,

with the exception of tuber weight, were lower than those derived from the offspring on female parent regression analysis. The unusually high heritabilities for tuber weight may simply be a reflection of the simpler genetic mechanism underlying the tuberization response (Mendoza and Haynes 1977), which is confounded in this experiment because of the use of less adapted materials, than it is a direct measurement of the heritability of the quantitative trait, tuber yield.

The narrow sense heritability estimates for most traits, regardless of the two methods, clearly indicate the relative importance of the additive fraction of the total genetic variance in this particular population. These values will give estimates of the rate of progress to be expected if they were to undergo selection. Both methods give heritability estimates in reasonable agreement for most traits. The exception is total tuber weight, for which the estimated value according to Design I was twice as large as the estimate calculated from offspring-female parent regression. Occasionally, unexplainable discrepancies among different estimates of heritability originate as a result of sampling error. Robinson et al. (1949), working with F_2 corn populations from single hybrids, reported discrepancies of heritability estimates for several traits using both methods. They concluded that the estimates were in reasonable agreement and that sampling error could account for the discrepancies. The amount of the dominant genetic variance in this particular study for all traits except total tuber weight implies that it may be as important as the additive fraction; therefore, it should not be overlooked.

Although measurement of quantitative variation in a sample of haploids from *Solanum tuberosum* Gp. Andigena provides clues to the type and amount of genetic variation in the parental tetraploid population, its real value resides in the information it provides about the haploid population itself. The haploid population will constitute the initial experimental population on which breeding techniques will be applied. The present results are encouraging, particularly for increasing total tuber weight. The large proportion of the additive fraction of the total genetic variance provides an opportunity to obtain gains from selection as the population is subjected to various selection schemes. The present study, as part of an extensive exploration of the breeding potential of Gp. Andigena haploids, is intended to promote their use as one of the sources in a 2n-gamete breeding scheme (Chase 1963; Mendiburu et al. 1974). Intensive breeding and selection to achieve desired genetic combinations can be effectively done at this ploidy level prior to the use of a selected diploid genotype in uni- or bilateral sexual polyploidization. Crossability of these haploids within their own Group and with other diploid Groups has been demonstrated (Landeo and Hanneman 1979), and the occurrence of diplandroids and diplogynoids has been confirmed (unpublished).

The full potential and usefulness of the Gp. Andigena haploids will be attained as diploid breeding stocks are developed and used in the 2n-gamete approach to potato improvement.

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Literature

Becker, W.A. (1967): Manual of Procedures in Quantitative Genetics. The Program in Genetics. Pullman, Washington: Washington State University

Behrend, P.; Maercker, M.; Morgen, A. (1880): Über den Zusammenhang des spezifischen Gewichts mit dem Stärkemehl- und Trockensubstanzgehalt der Kartoffeln, sowie über die Methode der Stärkebestimmung in den Kartoffeln. Landwirtsch. Vers. Stn. **25,** 107–165

Chase, S.S. (1963): Analytic breeding in *Solanum tuberosum* L. – a scheme utilizing parthenotes and other diploid stocks. Can. J. Genet. Cytol. **5,** 359–363

Cockerham, C.C. (1956): Analysis of quantitative gene action. In: Genetics in Plant Breeding. Brookhaven Symp. Biol. **9,** 53–68

Comstock, R.E.; Kelleher, T.; Morrow, E.B. (1957): Genetic variation in an asexual species, the garden strawberry. Genetics **43,** 634–646

Comstock, R.E.; Robinson, H.F. (1948): The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics **4,** 254–266

Comstock, R.E.; Robinson, H.F. (1952): Estimation of average dominance of genes. In: Heterosis (ed. Gowen, J.W.), pp. 494–516. Ames, Iowa: Iowa State College Press

Frandsen, N.O. (1967): Haploidproduktion aus einem Kartoffelzuchtmaterial mit intensiver Wildarteinkreuzung. Züchter **37,** 120–134

Hougas, R.W.; Peloquin, S.J. (1957): A haploid plant of the potato variety Katahdin. Nature **180,** 1209–1210

Hougas, R.W.; Peloquin, S.J.; Gabert, A.C. (1964): The effect of the seedparent and pollination on haploid frequency in *Solanum tuberosum.* Crop Sci. **4,** 593–595

Landeo, J.A.; Hanneman, R.E. Jr. (1979): Crossability of *Solanum tuberosum* Gp. Andigena haploids. Am. Potato J. **56,** 427–434

Levings, C.S. III.; Dudley, J.W. (1963): Evaluation of certain mating designs for estimation of genetic variance in autotetraploid alfalfa. Crop Sci. **3,** 532–535

Lush, J.L. (1940): Intra-sire correlations or regressions of offspring on dams as a method of estimating heritabilities of characteristics. Proc. Am. Soc. Anim. Prod. **33,** 293–301

Mendiburu, A.O.; Peloquin, S.J.; Mok, D.W.S. (1974): Potato breeding with haploids and 2n gametes. In: Haploids in Higher Plants: Advances and Potential (ed. Kasha, K.J.), pp. 249–258. Guelph, Ontario: University of Guelph Press

Mendoza, H.A.; Haynes, F.L. (1977): Inheritance of tuber initiation in tuber-bearing *Solanum* as influenced by photoperiod. Amer. Potato J. **54,** 243–252

Robinson, H.F.; Comstock, R.E.; Harvey, P.H. (1949): Estimates of heritability and the degree of dominance in corn. Agron. J. **41,** 353–359

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