

Genetic Basis of Heterosis for Yield in the Autotetraploid Potato

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Summary. A model of overdominant gene action to explain heterosis for yield in the autotetraploid potato has been presented. Loci with multiple alleles and a maximum heterotic value for quadrigenic genotypic structures have been postulated. Various experimental results have been analyzed on the basis of such a model in contrast with a dominance situation. The analysis suggests a close positive correlation between heterozygosity and yield. The implication of the proposed overdominant model to potato breeding would be that substantial genetic advance in yield should be made upon increasing the genetic diversity of the parental clones. However, the alien sources of germplasm should undergo some previous selection for adaptation. A proper balance between heterozygosity and adaptation, mainly to photo-period, should maximize the heterosis for yield.

Introduction

The cultivated autotetraploid potato, *Solanum tuberosum* L. subsp. *tuberosum* and *andigena*, is considered an outbreeder species which suffers from inbreeding depression and also expresses heterosis upon crossing of suitable parents.

Hybrid vigor was recognized prior to Mendel's work and theories to explain its nature have been presented. The two main hypotheses, i.e., dominance of favourable alleles and overdominance, although conflicting, are not mutually exclusive. Extensive reviews have been published on the subject but basically only diploid organisms have been considered. The genetic basis of heterosis in autotetraploids has received much less attention.

The present paper is an attempt to analyze the nature of heterosis for yield in the autotetraploid potato on the basis of current theoretical knowledge and certain published experimental data.

Review of Literature

Rowe (1967a) compared the performance of 15 high yielding diploid potato hybrid (*Tuberosum* dihaploid \times Phureja) clones and their vegetatively doubled counterparts. The tuber production of the diploid hybrids was significantly superior to that of the autotetraploids. Later, Rowe (1967b) compared the performance and variability of 11 diploid and autotetraploid potato families. The hybrids originated from matings between the diploid clones cited above and equivalent crosses between their vegetatively doubled counterparts. The autotetraploid families were superior in yield not only to their mid-parent value but usually to their higher yielding parent. The performance of the diploid families was inferior to that of their parents. Mendiburu and Pelo-

quin (1974), carrying out crosses $2x - 2x$ (*Tuberosum* dihaploid \times Phureja), obtained sexual polyploidization. The $4x$ clones resulting from the union of non-reduced gametes outyielded by 50% their diploid "full-sibs" formed by the union of normally reduced gametes. Also, in matings of $4x - 2x$ [tetraploid commercial potato \times (*Tuberosum* dihaploid \times Phureja hybrids)] tetraploid progenies were obtained. These were produced by the functioning of non-reduced gametes from the diploid parent. These tetraploid hybrid families outyielded the leading cultivars presently grown.

Krantz (1946) reported studies on selfing potatoes for 6 generations. The performance of the S_1 was 83% of the F_1 and the S_6 yielded only 19% of the F_1 . It has been shown (Mendoza and Haynes, 1973a) that 92.7% of the variance of the percent reduction in yield was due to its linear regression on the inbreeding coefficient of the successive generations of inbreeding. De Jong and Rowe (1971), studying the effect of inbreeding in diploid potatoes, found a linear relationship between the decrease in tuber production and the expected coefficient of inbreeding of the successive generations of selfing.

Only a few studies for measuring the quantitative variability for yield have been conducted in the autotetraploid potato. Sandford (1960) found that specific combining ability was twice as large as general combining ability. Plaisted *et al.* (1962) made crosses between 45 female lines and six testers. The estimated specific combining ability was nearly four times larger than the general combining ability. Rowe (1969), working with diploid potatoes and using a nested mating design, obtained an estimate of additive genetic variance not different from 0, while the component for dominance variance was 0.56. However, when the estimates were obtained by using a factorial mating design, both additive and dominance components were of the same magnitude.

Discussion

To discuss the published results we shall schematically present Rowe's (1967a) work, assigning to the genotypes arbitrary values which will be explained later (assumptions 5 and 6).

Parents	Tuberosum dihaploid ($2n$)	\times	Phureja ($2n$)	
	$a_1a_2b_3b_4c_1c_2d_1d_2$		$a_3a_4b_2b_3c_2c_4d_1d_4$	
	18		16	
	↓			
F_1 generation genotypes selected for high yielding ability	$a_1a_3b_2b_4c_1c_2d_1d_2$		22	
	$a_1a_4b_2b_3c_1c_4d_1d_4$		22	
	$a_2a_4b_1b_3c_3c_4d_1d_2$		18	
	↓			
		Vegetative chromosome doubling (Colchicine treatment)		
	$a_1a_1a_3a_3b_2b_2b_4b_4c_1c_1c_2c_2d_1d_1d_2d_2$		22 (16)*	
	$a_1a_1a_4a_4b_2b_2b_3b_3c_1c_1c_4c_4d_1d_1d_4d_4$		22 (16)	
	$a_2a_2a_4a_4b_1b_1b_3b_3c_3c_3c_4c_4d_1d_1d_2d_2$		18 (16)	

The results obtained by Rowe (1967a) are indicated in Table 1.

Table 1. Average per hill performance of 15 diploid clones and their vegetatively doubled counterparts. After Rowe (1967a)

Ploidy	Year	Harvest	Total tuber production	
			No.	Weight (Pounds)
2x	1964		22.8	2.30
	1965	1	28.2	2.75
	1965	2	27.6	4.23
Average			26.2	3.09
4x	1964		12.8	2.02
	1965	1	14.9	1.78
	1965	2	14.3	2.59
Average			14.0	2.13

The superiority of the diploids over the tetraploids was highly significant in all trials.

Certain assumptions are necessary before these results are analyzed.

1. The Tuberosum dihaploid and Phureja parents were considerably heterozygous. This assumption agrees with our own observations and many published experimental results.

2. In the F_1 hybrids of the matings Tuberosum dihaploid \times Phureja, more than two allelic forms would have been present at most of the loci.

3. Due to the genetic divergence existing between Tuberosum and Phureja, it is reasonable to postulate that a high number of loci in the F_1 were heterozygous.

* The figures outside and within the parentheses are arbitrary genotypic values for the dominance and over dominance gene action models, respectively.

4. The high yielding clones selected from the F_1 generation are to be considered as heterotic peaks.

5. Under a dominance model we assume that $a_1 > a_2 > a_3 > a_4$, $b_1 > b_2 > b_3 > b_4$, and so on for the other loci. The arbitrary genotypic values for locus "a" will be: $a_{1-} = 6$, $a_{2-} = 4$, $a_{3-} = 2$, and $a_{4-} = 0$. Similar values are assumed for the other loci, so that the genotypic value of the individual will be obtained by the summing of all loci.

6. Under an overdominance model we assume the superiority of the quadrigenic genotypes. For locus "a", $a_1a_2a_3a_4 > a_1a_1a_2a_3 > a_1a_1a_2a_2 > a_1a_1a_1a_2 > a_1a_1a_1a_1$. Note that for the trigenic, duplex, triplex, and quadruplex genotypes there are several possible combinations. The genotypic values will be 6, 5, 4, 3, and 0 respectively. These values represent the total number of heterogeneous pairs of alleles or the total number of first order interactions within a locus. The same genotypic values will be assigned to the other loci so that the genotypic value of the individual will consist of the sum of all loci.

7. We shall assume chromosome segregation ($\alpha = 0$).

What is the explanation for the highly significant superiority in yield consistently shown by the diploid over the tetraploid genotypes? There are important facts which should be pointed out:

All the arrangement of the genetic material in the high yielding diploids remained unchanged in the genotypically equivalent autotetraploids obtained by colchicine chromosome doubling. This implies that the frequency of favourable alleles as well as the correlations between loci (linkage) were not disturbed by the vegetative doubling of the chromosome complement.

The carry-over effect of colchicine can be disregarded because of the generations of vegetative propagation which followed the chromosome doubling.

We can discard a possible lack of balance between nucleus and cytoplasm, or a superiority in the original material in the sense that diploidy was favored because of sexual polyploidization (Mendiburu and Peloquin 1971) where unreduced gametes of diploid parents produced superior tetraploids.

Apparently then, the expected performance of both levels of ploidy should have been about the same.

Mendoza and Haynes (1973a) showed that the chromosome doubling automatically generates a certain amount of inbreeding in the doubled genotype. A heterozygous diploid such as $a_i a_j$ will have an inbreeding coefficient equal to 0 since $F = p(a_i \equiv a_j) = 0$, where $p(a_i \equiv a_j)$ is the probability of identity by descent. The autotetraploid obtained by doubling $a_i a_j$ will have a genotype such as $a_i a_i a_j a_j$ where a_i is identical to a_i by duplication rather than by descent.

The same is true for a_j . Hence, the inbreeding coefficient of the autotetraploid is:

$$F = 1/6 [p(a_i \equiv a_i) + 4p(a_i \equiv a_j) + p(a_j \equiv a_j)] = 1/3$$

Since $p(a_i \equiv a_i) = p(a_j \equiv a_j) = 1$ and $p(a_i \equiv a_j) = 0$.

On the basis of these theoretical considerations, the expected performance of the autotetraploids was to be low and inferior to the high yielding diploids.

It is important to analyze how inbreeding produced a reduction in performance. Consider the following facts:

It was not the uncovering of deleterious or sub vital alleles since they were already covered in the high yielding diploids. So the genetic load was unchanged.

It was not due to the reduction of the general level of heterozygosity, i.e., all the heterozygous loci in the diploids were duplex in the autotetraploids.

Under a complete dominance type of gene action these results would be hard to understand.

It is hazardous to make extrapolations from the diploid to the tetraploid level but in this specific case where the same genes were involved at single doses at one level of ploidy and at double doses at the other level, perhaps it should be possible to make some inferences.

Using the general expressions provided by Kempthorne (1957) to represent genotypic values of diploid and tetraploid genotypes, the genotypic value of the diploid Tuberosum $2x$ -Phureja hybrids may be written as:

$$g_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij}$$

Where μ is the population mean, α_i and α_j are the average effects of the alleles a_i and a_j ; and δ_{ij} denotes the dominance deviation.

The genotypic value of the autotetraploids obtained by chromosome doubling of the above cited diploids may be written as:

$$g_{ijkl} = \mu + 2\alpha_i + 2\alpha_j + \beta_{ii} + \beta_{jj} + 4\beta_{ij} + 2\gamma_{iij} + 2\gamma_{iji} + \delta_{iij}$$

Where μ is the population mean; α_i and α_j are the average effects of the alleles a_i and a_j ; the β 's denote the first order interactions, the γ 's represent the second order interactions, and δ_{iij} denotes the third order interaction.

Intuitively one could expect the tetraploid genotype to perform at least as high as the diploid genotype, unless interactions such as β_{ii} , β_{jj} and δ_{iij} would have a very negative value.

The extension of the one locus situation to multiple loci would not have any influence since any linkage or linkage disequilibrium present in the diploids would remain in the autotetraploids. Under the

dominance of favorable alleles, the explanation of reduction in performance due to inbreeding depression should be rejected. Therefore, a diploid such as $a_1a_3b_2b_4c_1c_2d_1d_2$ to which an arbitrary genotypic value equal to 22 was given in the scheme earlier, after chromosome doubling should produce an autotetraploid such as $a_1a_1a_3a_3b_2b_2b_4b_4c_1c_1c_2c_2d_1d_1d_2d_2$ with a genotypic value equal to 22.

Table 2. Average performance of diploid and autotetraploid hybrids and their parents. After Rowe (1967b)

Character	Ploidy Level							
	2x				4x			
	P_1	F_1	P_2	F_1-MP	P_1	F_1	P_2	F_1-MP
Tuber No.	17.1	16.6	26.8	-5.4	7.2	15.0	11.6	+5.6
Tuber weight (pounds)	2.2	2.0	2.7	-0.4	0.9	2.3	1.3	+1.2

If we invoke a genetic model giving superiority to the heterozygous condition with a heterotic peak represented by the quadrigenic genotypes, the inferiority of the autotetraploids would be explainable. In fact, the inbreeding generated by doubling had the effect of reducing the relative level of heterozygosity, not the general level since all heterozygous loci remained as such, but were duplex. Therefore, an individual such as $a_1a_3b_2b_4c_1c_2d_1d_2$ with an assigned value of 22 should yield after doubling an individual such as $a_1a_1a_3a_3b_2b_2b_4b_4c_1c_1c_2c_2d_1d_1d_2d_2$ which would have a genotypic value of 16.

The results presented in Table 1 agree with these expectations.

The results obtained by Rowe (1967b) on performance of diploid and autotetraploid hybrid families from matings between high yielding diploid clones and equivalent crosses between their vegetatively doubled counterparts are presented in Table 2.

Ploidy level was not statistically significant for tuber weight.

These results were analyzed on an inbreeding basis (Mendoza and Haynes, 1973a) and it was shown that the experimental data were in agreement with the predicted performance. On the average, the diploid hybrid families should not have performed as well as the parents since they were at or near heterotic peaks. Moreover, related matings were made which generated inbreeding. On the other hand, the cross of partially inbred autotetraploid parents ($F = 1/3$) should have produced superior hybrid families. However, the heterosis for yield exhibited by the hybrids should not have been, on the average, at its maximum expression because there was still some inbreeding involved ($F = 1/9$).

The crosses made by Rowe (1967b) may be constructed on a one locus basis. These are presented in Tables 3 and 4.

Table 3. *Expected genotypic values of various diploid × diploid crosses on a one locus dominance model*

Crosses	F ₁ Population Mean	P ₁	P ₂	MP
a ₁ a ₃ × a ₁ a ₄	5.0	6	6	6
a ₁ a ₃ × a ₂ a ₄	4.5	6	4	5
a ₁ a ₄ × a ₂ a ₄	4.0	6	4	5

The expected mean population values agree with the experimental results regardless of the crosses involved. The F₁ is inferior to the MP value.

Table 4. *Expected genotypic values of various tetraploid × tetraploid crosses on a one locus basis under dominance D and overdominance OD models*

Crosses	F ₁ Pop. Mean		P ₁		P ₂		MP	
	D	OD	D	OD	D	OD	D	OD
a ₁ a ₁ a ₃ a ₃ × a ₁ a ₁ a ₄ a ₄	5.9	4.4	6	4	6	4	6	4
a ₁ a ₁ a ₃ a ₃ × a ₂ a ₂ a ₄ a ₄	5.6	5.3	6	4	4	4	5	4
a ₁ a ₁ a ₄ a ₄ × a ₂ a ₂ a ₄ a ₄	5.5	4.4	6	4	4	4	5	4

From this table it is shown that the overdominance model explains the pattern of experimental results while the dominance model fails to account for the data. To elaborate, in a cross such as a_ia_j × a_ka_i, where a_i is a dominant favorable allele, one half of the offspring will carry a_i. In an equivalent cross between the colchicine doubled genotypes, a_ia_ia_ja_j × a_ka_ka_ia_i, 5/6 of the offspring will carry a_i. The expected average performance of the tetraploid F₁'s is superior to that of the diploid F₁'s. The expectation was not realized.

To explain these results on a multiple loci basis is more complicated since correlations between loci have to be taken into consideration. Assume that two diploids such as a₁b₁c₂d₂/a₃b₃c₄d₄ with a value of 20 and a₂b₂c₁d₁/a₄b₃c₂d₄ also with a value of 20 are crossed. Note that all the most favorable alleles at each locus are linked in coupling phase. Let's further assume a complete linkage (λ = 1). The expected F₁ mean population value is 18 and inferior to the parental performance.

The equivalent mating at the autotetraploid level is a₁a₁b₁b₁c₂c₂d₂d₂/a₃a₃b₃b₃c₄c₄d₄d₄ with a value of 20 under the dominance hypothesis and 16 under overdominance. The genotype of the second mate is a₂a₂b₂b₂c₁c₁d₁d₁/a₄a₄b₃b₃c₂c₂d₄d₄ with the same values as the first parent. The F₁ mean population value should be 22.4 under dominance and 18.6 under overdominance. Under both genetic models the expectation of a F₁ superior to parental performance was realized. However, under the dominance model, the F₁ population mean of the autotetraploids should be superior to the diploid parents and to the diploid F₁ as approximately 70% of the autotetraploid hybrid genotypes carried the 4 dominant genes a₁b₁c₁d₁. The expectation, assuming a superiority of heterozygous genotypes, agrees completely with the

reported results. Several combinations, regardless of the number of loci involved, have been worked out either under linkage or independence. In most of the cases the dominance of favorable alleles has failed to explain the experimental data while in most of the cases the assumption of heterozygote superiority has agreed with the observed results.

The report of certain measurements of quantitative variability for yield give support to the above discussion. The few studies made on the subject have had the same trend. The estimates of specific combining ability were always larger, in varying degree, than those of general combining ability. Levings and Dudley (1963), using Kempthorne's (1957) model for partitioning of genetic variance, provided expressions for the general and specific combining ability variances in function of the components of genetic variance assuming autotetraploid inheritance.

$$\sigma_g^2 = \frac{1}{4} \sigma_A^2 + \frac{1}{36} \sigma_D^2 + \frac{1}{16} \sigma_{AA}^2 + \frac{1}{144} \sigma_{AD}^2 + \frac{1}{1296} \sigma_{DD}^2 + \dots,$$

$$\sigma_s^2 = \frac{1}{6} \sigma_D^2 + \frac{1}{12} \sigma_T^2 + \frac{1}{36} \sigma_F^2 + \frac{1}{8} \sigma_{AA}^2 + \frac{7}{72} \sigma_{AD}^2 + \frac{31}{648} \sigma_{DD}^2 + \dots,$$

where σ_A^2 is the additive variance; σ_D^2 , the variance due to digenic effects; σ_T^2 , the variance due to trigenic effects; σ_F^2 , the variance due to quadrigenic effects. The remaining terms of the equations are variances due to epistasis or inter-locus interactions. It is worthy of note that in autotetraploids the dominance variance, arising from the within locus interactions, includes variances due to digenic, trigenic and quadrigenic effects.

We could assume that, on the average, the effects of epistasis would not be significant after the average linear decrease of yield on the expected coefficient of inbreeding of the successive generations of selfing (Mendoza and Haynes, 1973 a). Under this assumption the general combining ability variance would be composed of:

$$\sigma_g^2 = \frac{1}{4} \sigma_A^2 + \frac{1}{36} \sigma_D^2.$$

On the other hand, the specific combining ability variance would be formed by:

$$\sigma_s^2 = \frac{1}{6} \sigma_D^2 + \frac{1}{12} \sigma_T^2 + \frac{1}{36} \sigma_F^2.$$

Even after this simplification it is not possible to obtain a "clean" estimate of Comstock and Robinson's (1948) average degree of dominance. However, after the sizable estimates reported by Plaisted *et al.* (1962) and Sandford (1960) where the ratio of specific combining ability to general combining ability was 4 to 1 and 2 to 1 respectively, one can infer that the average degree of dominance was large in those auto-

tetraploid potato populations. Moll *et al.* (1964) working with corn have demonstrated that reduction in estimates of dominance variance and average degree of dominance were noted following random mating, indicating that linkage effects cause an upward bias in estimates from F_2 populations. It is very likely that the estimates obtained from potato populations would have suffered from this linkage bias since they were obtained from F_1 populations which were most likely not at equilibrium. However, the estimates of specific combining ability seem to be too large to be explained only by the upward bias caused by coupling phase linkages. This, in addition to the results discussed earlier in this paper, would indicate that in the autotetraploid potato, overdominant gene action is important.

Let us examine results obtained in potato breeding. In every instance in which the subspecies *Tuberosum* has been crossed with foreign sources of germplasm which had undergone some selection for adaptation to long days, the increase in yield has been spectacular. It would be impossible to deny that the level of heterozygosity of the hybrids has been tremendously increased. Now, the questions suggested by those results are: Is the increase of yield directly related to the enhancement of heterozygosity? Is the increase of yield due to a major input of favorable dominant genes? It is evident that one possibility does not exclude the other. However, since the process of adaptation, i.e., selection of genotypes able to form tubers under long days, has not yet produced high yielding clones competitive with the commercial varieties, it is likely that their major contribution to the striking heterosis has been primarily an increase in the heterozygosity of the present U.S. varieties. Mendoza and Haynes (1973b) have shown the close genetic relationship which characterizes the majority of the North American potato cultivars. This is due to a very close breeding system which began with a base of a small number of introductions and which has not received any major contribution of new germplasm. It seems that the outcome of this breeding system has been a reduction in the relative level of heterozygosity which has limited the genetic ad-

vance for yield. The experience of the past 20 years in which no variety with an outstanding increase in yield has been released in spite of the operation of large breeding programs, dramatically demonstrates this point.

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