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COMPARATIVE EVALUATION OF CLONES AS TESTERS FOR YIELD, SPECIFIC GRAVITY AND TUBER APPEARANCE IN THE POTATO

by

Lind Lee Sanford

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In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

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Of Science and Technology
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INTRODUCTION

Cytological and genetic evidence indicates that Solanum tuberosum may be an old species. Since 1850, a great deal of effort has been directed toward selecting superior varieties. Beginning with the variety Garnet Chili, released in 1857 by Rev. Goodrich of Utica, New York, breeding procedure has been based largely upon single plant selection among sexually propagated progenies. Although selection of this type has been the major breeding method for the past 100 years, it has been observed that the potato is a crop difficult to improve through standard breeding methods. This difficulty is in part due to its tetraploid inheritance. Furthermore, it is highly probable that over a period of time some of the chromosomes have become differentiated to the extent that both allopolyploid and autopolyploid behavior exist. Pollen sterility barriers have been encountered, particularly in early generations of inbreeding. This has been accentuated by a tendency toward an inverse relationship between fertility and yield. Recently it has been noted that recombinations of inbred lines infrequently result in heterosis for yield. This is in sharp contrast to the relatively consistent appearance of hybrid vigor found within many vegetable crops. All of these factors combine to restrict efficiency of breeding and selection methods. It is only recently that new breeding methods have been proposed to increase the effectiveness of potato improvement. Many of these are adaptations of those used to improve corn inbreds or varieties. In testing any of these techniques, consideration should be given to the vegetative propagation of the potato, to its unit land requirement, and to its genetic complex.

This study was undertaken as part of a program to develop recurrent selection as a breeding method for potato improvement. Through evaluation of general and specific combining ability for total yield, specific gravity, and general tuber appearance, it was hoped that efficient testers for these characters could be found. Estimates of general and specific combining ability also were to be related eventually to the type of recurrent selection most efficient in improving each character.

REVIEW OF LITERATURE

Evaluation of Parental Material

Potatoes

The importance of superior parental material in a potato breeding program was stated by Krantz and Hutchins (28, p. 4) as follows:

> The problem of potato improvement is essentially one of developing individuals for breeding purposes. The usefulness of these individuals will not depend upon their own performance, but upon their breeding value as ascertained by a study of their progeny; and upon their ability when crossed, to produce other individuals of economic value. The physical limitations on the number of lines that can be grown makes it obligatory to practice some type of selection so desirable germ plasm can be sorted out and saved and the undesirable discarded.

In a study of 47 F_1 crosses, Krantz and Hutchins (28) found the regression of parental yields on F_1 yields to be 0.5564 ± 0.1079. It also appeared that selection within self-fertilized lines was a practical method of securing improved parental materials.

Gowen (11) indicated that tests of selfed progeny gave an evaluation of parental genotypes more accurate than those obtained through progenies from crosses of phenotypically superior heterozygous plants. Inbred selections with combining ability superior and inferior to that of their parents were tested. Significant differences in specific combining ability frequently were found between closely related inbreds. A greater dispersion of combining abilities occured among self-pollinated lines than among heterozygous lines.

Rieman *et al.* (39) proposed potato improvement through parental line breeding. The investigation of breeding methods for their efficiency in producing parental lines of high combining ability was felt to be desirable. In particular, the authors cited a need for finding the degree of homozygosity required in lines superior in disease resistance, tuber type, and total solids.

Corn

Hayes and Johnson (16), Jorgenson and Brewbaker (22), Nilsson-Leissner (37), and Kiesselbach (26) compared the productivity of pure line parents with their hybrid offspring and found a positive relationship. In contrast, Richey and Mayer (38), and Jenkins (19) reported data suggesting little or no relationship between the productivity of pure line parents and their hybrid offspring.

The use of the inbred-variety cross as a means of isolating higher yielding lines was first proposed by Davis (5). Jenkins and Brunson (20) suggested that crosses with a commercial variety could be used as a rapid method of preliminary tests of new inbred lines. On the basis of performance in such crosses, it was felt that 50 percent of the lines could be discarded without a serious loss of valuable material. Johnson and Hayes (21) compared the performance of 11 sweet corn lines crossed in all possible combinations with the performance of these lines in top-cross tests. Inbreds that showed low combining ability in top-cross tests were usually low in average single cross performance. Similar results were observed for high combining lines.

Federer and Sprague (9) analyzed a series of 11 top-cross tests containing two or more testers. The results suggested that, for a fixed number of plots, the greatest gain in combining ability would be expected by increasing the number of testers. An increase in the number of lines, and particularly in the number of replications, resulted in a progressive decline in breeding efficiency. It was suggested that the choice of a tester for a given set of lines should be determined by the future use of such lines. If maximum general combining ability were desired, the use of more than one tester would be recommended. Green (13) compared a high-yielding double cross with a low-yielding, open-pollinated line for use as testers of segregating F_2 progenies. The results generally revealed no differences between the two testers, although some interaction with F_2 segregates was observed. It was suggested that genes affecting specific combining ability were important in the gametic samples of the tester parents. The wide range of top-cross yields, using the double cross tester, appeared to be an indication of this sampling importance. The use of related and unrelated single crosses as tester parents in evaluating a group of selected F_2 plants was studied by Keller (25a). The difference between the testers was revealed by dissimilar ranking of F_2 plants. It was suggested that the different rankings were due to differences in specific combining ability between the testers and the F_2

plants. Results obtained by Grogan and Zuber (14) indicated that a tester closely related to the inbred lines under study should not be used when general combining ability information is desired. Matzinger (32) crossed eight inbred lines to three types of testers. These testers consisted of: (1) the eight inbred lines, (2) two double crosses, and (3) the four single crosses comprising each double cross. The three types of testers gave similar means and ranges for general combining ability in test-cross progenies. Each tester also gave a consistent ranking.

Lonnquist and Rumbough (31) found that lines selected for specific combining ability represented a random sample with respect to general combining ability. This was observed in a comparison of selected lines with unselected material from the same original source. These data seemed to support the accepted procedure of testing new lines for general combining ability before determining specific combining ability. Hull (18) proposed the use of a single homozygous line as a tester in selecting for specific combining ability. This method seemed to be relatively efficient in selecting lines for superior hybrid combinations.

Forage crops

The term "polycross" was first proposed by Tysdal *et al.*(45) to designate "the progeny from seed of a line that was subject to outcrossing with the other selected lines growing in the same nursery". The same procedure had been suggested earlier by Frandsen (10). Bolton (2) concluded that alfalfa clones of low and high combining ability performed with equal efficiency when used as testers. The results indicated that the use of testers could be helpful in determining combining ability in a large population of plants. Tysdal and Crandall (44) found that tested clones were ranked similarly by polycross progenies, top-cross progenies, and the average performance of single crosses having a common parent. The performance of parental clones was generally found to be indicative of the performance of their progenies, particularly for insect and disease resistance. Davis and Panton (6) compared single crosses, S_1 progenies, and two types of polycrosses for testing clones of high and low phenotypic performance. Variances for mature plant yield, components of yield, and seedling height were statistically significant when computed from means of S_1 and single cross progenies. No significance was found when polycross progeny means were analyzed. The clones characterized by high phenotypic performance generally produced superior yield in progenies.

Hanson et al. (15) used a polycross progeny test in orchard grass to relate the combining ability of 18 parental lines to that of 52 of their selfed progenies. The general combining ability of most of the inbred lines was not materially different from that of their parental clones. Results indicated, however, that lines with general combining ability higher and lower than that of original clones could be selected. Kalton et al. (24) found that clonal performance was of little value in predicting combining ability. Single cross, polycross, and top-cross progenies generally predicted combining ability in a similar manner.

Dhawan (7) found in timothy that the polycross progeny gave a reliable estimate of general combining ability for plant vigor and regrowth. Both polycross and S_1 progenies were found to be efficient in predicting general combining ability for leafiness and stem rust resistance.

Knowles (27), in studies of open-pollinated progenies from selected brome grass plants, found a relationship between the open-pollinated progenies and test-cross progenies with respect to forage production. It was concluded that a test of open-pollinated progenies of selected plants would be useful in obtaining superior combining ability for this character. Timothy et al. (43) showed that clones differed in general combining ability for forage yield, seed yield, and leaf spot reactions. Specific combining ability was significant for plant height, but general combining ability effects could not be shown. There was fair agreement of clone rankings between polycross progeny performance and the average single cross performance. Nielson and Kalton (36) studied the effect of one generation of inbreeding on combining ability and found it to be negligible.

Vegetable crops

Larson and Currence (29) found little relationship between variety yields and yields of their F_1 hybrids in tomatoes. In a later study, Currence et al. (4) found an agreement between variety yields and general combining ability for yield. It was suggested that varieties productive within an adapted area would probably produce superior yielding hybrids in this area. Moore and Currence (35) attempted to predict general combining ability by crossing each of 25 tomato varieties and two selections with two different F_1 hybrids. The resulting three-way crosses were then grown in a replicated trial along with the 27 parents. Eight strains, showing a range of combining ability, were selected and grown with all possible hybrid combinations, including reciprocals. The results indicated that the mean performance of a variety in a series of crosses provided the best measure of general combining ability. The three-way cross did not appear to be superior to varietal performance as an indication of combining ability. Horner and Lana (17), working with fruit size, early U.S. No. 1 yield, and yield of all grades, found that the best general combiners could be predicted from parental values with reasonable accuracy.

In progeny tests of asparagus plants, Currence (3) found that parents selected for higher phenotypic performance for seedling size and yield tended to produce superior progenies. The desirability of progeny tests was demonstrated by a 50 percent yield increase of two superior lines in comparison with the mean of all lines.

Statistical Investigations of General and Specific Combining Ability

Combining ability was divided into two types by Sprague and Tatum (42). General combining ability was defined as the average performance of a line in a number of hybrid combinations. Specific combining ability was meant to describe the extent to which a cross deviated from expectation on the basis of general combining ability.

General combining ability values are considered to be due predominantly to additive gene action, whereas specific effects are a result of such non-additive gene responses as dominance, epistasis, and other types of gene interaction.

Corn data presented by Sprague and Tatum (42) indicated that general combining ability was more important than specific combining ability in single crosses made up of untested material. However, in trials involving previously tested lines, specific combining ability appeared to be relatively important. The results of Federer and Sprague (9) agreed with those of Sprague and Tatum. Similar conclusions were reported by Kalton and Leffel (23) in a study of orchard grass clones. However, Matzinger et al. (34) analyzed diallel crosses of ten corn plants selected at random from the open-pollinated variety, Low Ear. The results showed little variance due to general combining ability. Considerable variance was found for specific combining ability. It was concluded that the estimate of general combining ability was of little use as a criterion for selection in this population. The use of specific combining ability was regarded as more valuable.

Models for obtaining estimates of variance components for general and specific combining ability and their interactions with years were presented by Rojas (40). Rojas and Sprague (41) tested these models by analyzing single crosses in corn, replicated by locations and years. Variance components for specific combining ability showed consistently greater interactions with environment than did those variance components for general combining ability. This indicated the presence of genotypic-environmental interaction in the estimate of specific combining ability variance. Interaction with environment appeared to decrease as the heterogeneity of the material increased. Matzinger (33) found additive variance to be negligible when estimated from a combined analysis of experiments run over locations and years. Additive variance interacted significantly with years, but not with locations. Dominance variance showed little interaction with either years or locations. Ballesteros (1) studied top-cross progenies of S_2 and S_3 lines of White Flint for two seasons in three locations. There was no significant interaction between top-crosses and locations and among top-crosses, locations, and seasons. It was concluded that a performance test to determine general combining ability, conducted at one location, would effectively eliminate lines for subsequent specific combining ability tests. In testing the same lines for specific combining ability with a selected single cross, however, a highly significant interaction between locations and hybrids was obtained. Thus, it was concluded that specific crosses must be tested at several locations and in several years to obtain sufficient information on their yielding potential.

Green (12) investigated the inheritance of combining ability in the F_2 generation of three single crosses in corn. These crosses represented combinations of high x high, high x low, and low x low combining inbreds. The frequency of high combining F_2 segregates in the progeny of the high x high cross was found to be higher than that in the other two crosses. This difference indicates that combining ability is an inherited characteristic. Lonnquist (30) demonstrated that combining ability, for a group of lines or families, remains relatively stable from S_1 through subsequent selfed generations.

MATERIALS AND METHODS

In 1956, six clones were selected for use as tester parents. These included: B962-32, ND457-1, B3131-8, TL1859, X96-56, and Katahdin. Each of the clones had demonstrated superiority in pollen fertility. Each clone also had shown superior combining ability for one or more of the characteristics, yield, specific gravity, and tuber type. This performance was observed in several varietal breeding programs. Pollen from each of the six tester parents was crossed with 45 phenotypically distinct clones. These clones included 34 lines from the breeding programs of Iowa, North Dakota, Nebraska, and the United States Department of Agriculture, as well as six released varieties and five species hybrids. The 45 lines were chosen at random from available material. The total number of possible crosses among testers and lines would be 270, but due to various failures, only 190 were successful. The crosses made are presented in Table 1. Samples of true seed of each cross were sent to Ithaca, New York. Progenies were further subdivided for trials at Ithaca and Riverhead, New York.

In 1957, seedling tubers of each of the crosses were planted for increase. One to three tubers were harvested from each seedling plant and bulked as family lines. The number of tubers harvested from each plant was determined by the number of such plants in the family line. Each tuber in a bulked line was cut once to obtain a sample of 66 seed pieces. If the number of tubers was insufficient to obtain

Table 1. Crosses obtained between six testers and 45 clonal lines of potatoes[a]

Line No.	Pedigree No.	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1	I957-1		(X)	X	X		X
2	I1015-2	X	(X)	(X)	X		(X)
3	I1077-16	X	X	X			X
4	I1077W28-5	X	X	X	X	X	X
5	I1114-2	X	X	(X)	X	X	X
6	Early Gem	X	(X)	X	X	(X)	(X)
7	B1396-N2	X	X	X	X	X	X
8	B2938-22		(X)		X		
9	B2903-17		(X)				
10	I1188-2	X		X		(X)	(X)
11	B922-3	X	(X)	X	X	(X)	(X)
12	B922-6	X	(X)	X	(X)	(X)	
13	B2834-3	(X)	(X)	X	(X)		(X)
14	B3014-10	X	X	(X)	X		
15	B3097-16		(X)	(X)	X		
16	B3131-N2	X	(X)	X	X		
17	B3428-31			X			(X)
18	B3428-41	X	(X)	(X)	X		(X)
19	B3556-12	X	(X)	X	X	(X)	(X)
20	PI194665		X	X	X	X	X
21	TL1859	(X)		X	(X)		
22	ND457-1	(X)	(X)	X			
23	OB2905-1	(X)	(X)		(X)		(X)
24	PI214372-1		X	X	X	X	X
25	PI214371-2	X	X			X	
26	PI214372-2	X	X	X		X	
27	P51. 1-53-15	X	(X)	X	(X)		
28	I1049-3	X	X			X	
29	I1092-2		(X)		X	X	X
30	I1165-14	X	X	(X)	X	X	X
31	I1216-1R	X	X	X	X	X	
32	B605-10	X	(X)	X		(X)	(X)
33	B2368-4	(X)		X	(X)	X	X
34	B3131-8	X	(X)	X	X	(X)	
35	B3556-1	X	(X)	X	X		
36	X927-3	(X)	(X)	X	(X)	X	
37	AC25953	X	X	X		X	
38	N154-47-2			X	X		
39	OB3596-1		(X)				
40	Earlaine	X	(X)		X	(X)	X
41	Katahdin		(X)	X		X	
42	Osage	(X)	(X)	(X)	(X)	X	(X)
43	Red Kote		(X)	(X)			(X)
44	I1077-14	X		X	X	X	X
45	B24-58		(X)	X	X	(X)	

[a] X - Tester and line with no common parent or grandparent
(X) - Tester and line with at least one common parent or grandparent

66 pieces with one cut, a second cut was made. This procedure was used in an attempt to obtain a representative sample for each family. Care was taken in cutting to assure that each seed piece weighed approximately two ounces.

In 1958, the 190 bulked test-cross lines and ten commercial check varieties were planted in a rectangular lattice design at Clear Lake, Iowa; Riverhead, New York; and Ithaca, New York. Six replications were used at each location. Each plot consisted of ten hills spaced one foot apart. The stand at all locations was excellent; therefore, no statistical adjustment was deemed necessary. Data taken from each plot at Clear Lake, Iowa, included total weight, specific gravity, and a general tuber appearance rating. Only total weight measurements were recorded at the two New York locations.

Specific gravity of tubers was obtained by the water displacement method. The tubers were first weighed in air. The same sample was then weighed in water, using a special counter-balanced scale. Specific gravity was calculated from the formula

$$\frac{\text{Weight in air}}{\text{Weight in air - Weight in water}} .$$

All tubers in a plot were used to determine specific gravity unless total weight exceeded 20 pounds. A maximum of 20 pounds was felt to be adequate for measuring this character.

The tuber appearance ratings were based upon an arbitrary numerical scale of one to eight. The figure eight represented the most desirable tuber appearance relative to existing varietal characteristics.

The least desirable tuber was designated by the number one. Four characteristics were used as a basis for the rating: (1) depth of eyes, (2) regularity of shape, (3) susceptibility to growth cracks, and (4) susceptibility to second growth. Such factors as susceptibility to scab, russet skin versus smooth skin, and skin color differences were disregarded. It should be emphasized, however, that these differences undoubtedly affect tuber appearance.

DESIGN AND ANALYSIS OF THE EXPERIMENT

The experimental design used for this experiment is an adaptation by Federer and Plaisted (8) of a triple rectangular lattice. The adaptation permits the comparison of $v = 2k$ treatments in $b = 2rk$ incomplete blocks of k treatments with $3q = r$ replicates. The structure is closely related to the structure of rectangular lattices in a way to be exemplified later. The basic plan, consisting of three replicates with different confounding, is repeated q times; therefore, the total of r equals 3q replicates. The experiment included 200 treatments. Ten treatments were assigned to each of 20 blocks in a replicate. A series of three arrangements was duplicated to give a total of six replicates.

The actual arrangement, apart from randomization, is given in Table 2. Treatments are designated by ijk, where i equals one or two, and both j and k range from one to k.

Treatments were randomly assigned field numbers from 1-200. These were then grouped into incomplete blocks according to the arrangements outlined in Table 2. The blocks were arranged at random in each replicate, and then each treatment was randomly assigned to the plots within incomplete blocks. The three arrangements were duplicated for replicates four, five, and six, but with different randomization. Thus, in the present design, q equals two. This experimental design completely confounds one degree of freedom (treatments 111 to 1kk versus treatments 211 to 2kk) with differences among incomplete blocks.

Table 2. Structure of the experiment

Block No.	Replicate Type I		
1	111	112	11k
2	121	122	12k
3	131	132	13k
.	.	.	.
.	.	.	.
k	1k1	1k2	1kk
k+1	211	212	21k
.	.	.	.
.	.	.	.
2k	2k1	2k2	2kk

Block No.	Replicate Type II		
1	111	121	1k1
2	112	122	1k2
3	113	123	1k3
.	.	.	.
.	.	.	.
k	11k	12k	1kk
k+1	211	221	2k1
.	.	.	.
.	.	.	.
2k	21k	22k.	2kk

Block No.	Replicate Type III			
1	111	122	133	1kk
2	112	123	134	1k1
3	113	124	135	1k2
.	.	.	.	.
.	.	.	.	.
k	11k	121	132	1kk-1
k+1	211	222	233	2kk
.	.	.	.	.
.	.	.	.	.
2k	21k	221	232	2kk-1

In order for the reader to be able to understand this design, the following description was abstracted from an unpublished paper of Federer and Plaisted (8):

The normal equations employed to compute totals for each effect are shown below. Y_{ijg} is the total yield of the i^{th} treatment of the j^{th} type replicate and the g^{th} block in that replicate. Sums over subscripts are represented by replacing the subscripts with dots; for example, $Y_{i..} = \sum_{jg} Y_{ijg}$.

1. $Y_{...}$ = Grand total = $urv + v\sum_{j=1}^{r} \rho_j + r\sum_{i=1}^{r} \tau_i + k\sum_{j=1}^{r}\sum_{g=1}^{2k} \beta_{jg}$;

2. $Y_{i..}$ = i^{th} treatment total = $r(u+\tau_i) + \sum \rho_j$ + sum of block effects for blocks in which i^{th} treatment occured;

3. $Y_{.j.}$ = j^{th} replicate total = $v(u+\rho_j) + \sum_i \tau_i + \sum_g \beta_{jg}$;

4. $Y_{.jg}$ = jg^{th} incomplete block total = $k(u+\rho_j+\beta_{jg})$ + sum of treatment effects for treatments occurring in block jg;

where u = grand mean,

τ_i = i^{th} treatment effect,

ρ_j = j^{th} replicate effect,

β_{jg} = jg^{th} incomplete block effect.

The above plus the following equations result in unique solutions for the μ, τ_i, ρ_j, and β_{jg} effects:

$$\sum_{i=1}^{2k^2} \tau_i = \sum_{j=1}^{r} \rho_j = \sum_{g} \beta_{jg} = 0 \qquad ;$$

$$\sum_{i=1}^{k^2} \tau_i = \sum_{g=1}^{k} \beta_{jg} = \frac{1}{r}\sum_{j=1}^{r}\sum_{g=1}^{k} \beta_{jg} \qquad ;$$

$$\sum_{i=k^2+1}^{2k^2} \tau_i = \sum_{g=k+1}^{2k} \beta_{jg} = \frac{1}{r} \sum_{j=1}^{r}\sum_{g=k-1}^{2k} \beta_{jg} \qquad .$$

The solutions for the β_{jg} are

$$\hat{\beta}_{jg} = \frac{1}{2qk^2} \left\{ 3kQ_{.jg} - \sum_{g=1}^{k} Q_{.jg} \right\} + \frac{1}{k(k+1)} \sum_{i=1}^{k^2} (\bar{y}_{i..} - \bar{y})$$

for g = 1, 2, ···, k, and

$$\hat{\beta}_{jg} = \frac{1}{2qk^2} \left\{ 3kQ_{.jg} - \sum_{g=k+1}^{2k} Q_{.jg} \right\} + \frac{1}{k(k+1)} \sum_{i=k^2+1}^{2k^2} (\bar{y}_{i..} - \bar{y})$$

for g = k 1, k 2, ···, 2k. If q equals one, the value for $Q_{.jg}$ equals the total for the gth block in the jth replicate minus the mean yield over all replicates of the treatments appearing in block g of the jth replicate. If q is greater than one, Q_{jg} is equal to the sum of the block totals, which contain the same treatments, minus q times the overall mean yield of the treatments occurring together in the blocks.

The adjusted variety means are $\hat{u} + \hat{\tau}_i = \bar{y} + \hat{\tau}_i$, and the $\hat{\tau}_i$ are obtained from the normal equations for the treatments. This formula expresses the variety mean adjusted for intrablock information only.

The analysis of variance for this design is presented in Table 3.

Table 3. Analysis of variance

Source of variation	d.f.	Sum of squares
Total	$2rk^2-1$	usual method
Replicates	$r-1$	$\sum_{j=1}^{r} Y^2_{.j.}/2k^2 - Y^2_{...}/2rk^2$
A = Treatments 1-100 versus 101-200	1	$\left[\sum_{i=1}^{k^2} Y_{i..} - \sum_{i=k^2+1}^{2k^2} Y_{i..}\right]^2 / 2rk^2$
A x replicates	$r-1$	usual method
Treatments within groups (ignoring blocks)	$2k^2-2$	$\sum_{i=1}^{200} Y^2_{i..}/r - Y^2_{...}/rv$
Incomplete blocks (eliminating treatments)	$6qk - 6q$	
Component (a)	$6(q-1)(k-1)$	see text
Component (b)	$6(k-1)$	see text
Intrablock error	$(2rk^2-1)$ $-(2r+2k^2+12k-15)$	subtraction

The component (b) sum of squares is computed as follows:

$$\sum_{j=1}^{3}\sum_{g=1}^{k} \beta_{jg}\, Q_{.jg}/q \quad \sum_{j=1}^{3}\sum_{j=k+1}^{2k} \beta_{jg}\, Q_{.jg}/q \quad .$$

The component (a) sum of squares is the interaction of block totals, $Y_{.jg}$ with the q replicates which have the same basic arrangement within sets of treatments 1 to k^2 and $k^2 + 1$ to $2k^2$.

Both the A x replicates and the component (a) mean squares have an expectation $\sigma_e^2 + k\,\sigma_\beta^2$; the expectation of the component (b) mean square is $\sigma_e^2 + 2/3\,k\,\sigma_\beta^2$ where σ_e^2 is the variance of plots within block errors and σ_β^2 is the variance of block errors on a per plot basis.

The preceding analysis, developed by Federer and Plaisted (8), was applied to the data for total yield for each of the three locations. It appeared subsequently that a slightly different method of analysis is desirable, because the mean square for A x replicates, in Table 3, is an estimate of $\sigma_e^2 + 10\,\sigma_\beta^2$ and thus provides information on the weights to be used in the combination of interblock and intrablock information. Specific gravity and tuber appearance data therefore, were computed by this modified analysis. The equations for estimation of the weights are as follows:

$\hat{\sigma}_e^2$ = intrablock error mean square,

$113\hat{\sigma}_e^2 + 950\hat{\sigma}_\beta^2$ = pooled sum of squares for A x replicates, and component (a) and component (b) of the sum of squares for blocks eliminating treatments in Table 3.

The intrablock weight, W, is estimated, in the customary manner, by $\frac{1}{\hat{\sigma}_e^2}$ and the interblock weight by $W' = \frac{1}{\hat{\sigma}_e^2 + 10\hat{\sigma}_\beta^2}$. The nature of the estimation procedure is that A, the comparison of treatments 1-100 versus 101-200 is estimated by the interblock comparisons; comparisons among treatments 1-100 and 101-200 are estimated by the usual procedure for the triple lattice. Thus, the comparison of treatments 1-100 versus treatments 101-200 is estimated by the observed mean difference, while comparisons within the first set of 100 and within the second set of 100 are estimated by the standard formulae; given, for example, by Kempthorne (25b, pp. 454-455). The letters w and w' are used to denote the estimates of W and W' respectively. Then, the variances of treatment differences are as follows:

1. difference of two treatments which occur together in a block,

$$V(\hat{t}_i - \hat{t}_j) = \frac{1}{10}\left[\frac{2}{2w+w'} + \frac{8}{3w}\right] \quad ;$$

2. difference of two treatments within a set which do not occur together in a block,

$$V(\hat{t}_i - \hat{t}_j) = \frac{1}{10}\left[\frac{3}{2w+w'} + \frac{7}{3w}\right] \quad ;$$

3. difference of treatments in different sets,

$$V(\hat{t}_i - \hat{t}_j) = \frac{1}{100}\left[\frac{27}{2w+w'} + \frac{72}{3w} + \frac{1}{3w'}\right] \quad .$$

It would be possible to take account, in analysis of line by tester crosses, of these differences in variances, but this would be rather complicated and tedious. Because the crosses were assigned at random to the two sets of 100 entries, it is appropriate to use half the average variance of all possible differences of pairs of treatments as the effective error mean square to be associated with each final treatment total. This effective error variance was found to be

$$\frac{36}{199}\left[\frac{27}{2w\ w'}+\frac{72}{3w}+\frac{1}{6w'}\right] ,$$

and this is designated by $\hat{\sigma}^2$.

To estimate the variances ascribed to general and specific combining ability, the adjusted treatment totals were arranged in a two-way layout as indicated below:

	Tester	1	2	3	4	5	6
Line 1							
2							
j		x_{1j}	x_{2j}	x_{3j}	x_{4j}	x_{5j}	x_{6j}
.							
.							
45							

In this layout, if the cross of line j and tester i was made, the entry is x_{ij}, the adjusted treatment total for that cross. A feature of the situation which presents difficulty is that the layout is incomplete, since some crosses could not be made. Just what this non-orthogonality does to the validity of the ensuing analysis is a moot point. It is assumed in the analysis that absence of a line-tester combination is due to the particular circumstance at the time and not to the genetic properties of the line and tester.

Table 4 gives a non-orthogonal analysis of variance which was used to estimate the components of variance for lines, testers, and interaction of lines and testers.

Table 4. Analysis of variance for estimating line, tester, and line x tester variance components

Source of variation	d.f.	Sum of squares[a]
Testers	T-1	$\sum_{j=1}^{6} \frac{X_{i.}^2}{6K_{i.}}$ - c.f.
Lines	L-1	$\sum_{1}^{45} \frac{X_{.j}^2}{6K_{.j}}$ - c.f.
Testers x Lines	$\sum$ (L-1) within testers - (L-1)	$\sum_i \sum_j \frac{K_{ij} X_{ij}^2}{6} - \sum_i \frac{X_{i.}^2}{6K_{i.}}$
		$- \sum_j \frac{X_{.j}^2}{6K_{.j}} +$ c.f.

[a]K_{ij} = O if the i^{th} tester was not crossed to the j^{th} line

K_{ij} = 1 if the i^{th} tester was crossed to the j^{th} line

$K_{i.} = \sum_j K_{ij}$

$K_{.j} = \sum_i K_{ij}$

The expectations of the sum of squares in Table 4 were developed by the use of the model,

$$Y_{ghij} = n_{ghij}\ m_{ij}\ (u + \rho_g + \alpha_i + \gamma_j + \alpha\gamma_{ij} + e_{ghij}),$$

where u = grand mean,

ρ_g = g^{th} replicate effect,

α_i = i^{th} tester effect,

γ_j = j^{th} line effect,

n_{ghij} = one if the ij^{th} treatment occurs in the h^{th} block of the g^{th} replication, otherwise it equals zero,

m_{ij} = one if the i^{th} tester was crossed to the j^{th} line,

and are expressed by the following formulae:

$$\text{Testers} = (a-1)\sigma^2 + r(a-1)\sigma^2_{\alpha\gamma} + r(a\frac{1}{m_{..}}\sum_j m_{.j}^2)\sigma^2_{\gamma} + r(a-\frac{1}{m_{..}}\sum_i m_{i.})^2\sigma^2_{\alpha}\ ;$$

$$\text{Lines} = (c-1)\sigma^2 + r(c-1)\sigma^2_{\alpha\gamma} + r(m_{..} - \frac{1}{m_{..}}\sum_j m_{.j}^2)\sigma^2_{\gamma} + r(c-\frac{1}{m_{..}}\sum_i m_{i.}^2)\sigma^2_{\alpha}\ ;$$

$$\text{Lines x Testers} = (m_{..}-a-c+1)\sigma^2 + r(m_{..}-a-c+1)\sigma^2_{\alpha\gamma}$$

$$+ r(-a\frac{1}{m_{..}}\sum_j m_{.j}^2)\sigma^2_{\gamma} + r(-c\frac{1}{m_{..}}\sum_i m_{i.}^2)\sigma^2_{\alpha}\ .$$

In these formulae, (a) equals the number of testers and (c) equals the number of lines.

The expected mean squares are obtained by dividing by the appropriate degrees of freedom for testers (a-1), lines (c-1), and lines x testers (c-1 within each tester minus c-1). The calculated expected mean squares are given in Table 5.

Table 5. Expected mean squares for testers, lines, and testers x lines

Source of variation	d.f.	Expected mean squares[a]
Testers	5	$\sigma^2 + 6\sigma^2_{lxt} + 188.91\sigma^2_t + 1.63\sigma^2_l$
Lines	44	$\sigma^2 + 6\sigma^2_{lxt} + 1.69\sigma^2_t + 25.28\sigma^2_l$
Testers x Lines	140	$\sigma^2 + 6\sigma^2_{lxt} \quad -0.53\sigma^2_t \quad -0.06\sigma^2_l$

[a]The quantity σ^2 is the effective error mean square previously described

It was also considered worthwhile to determine the effects of the six testers, assuming both testers and lines as fixed with no interaction. The following mathematical model was used:

$$Y_{ij} = u + t_i + l_j + e_{ij} \quad ,$$

where Y_{ij} = the response of the cross between the i^{th} tester and the j^{th} line,

u = grand mean,

t_i = effect of the i^{th} tester,

l_j = effect of the j^{th} line,

e_{ij} = the residual deviation, which is distributed with a constant variance and uncorrelated error.

The least square procedure of fitting $Y_{ij} = u + t_i + l_j$ was followed to construct the normal equations; these equations can be expressed in matrix form as follows:

$$\begin{bmatrix} t_i \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ l_{45} \end{bmatrix} = \begin{bmatrix} a_{11} & \cdots & a_{145} \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ a_{451} & & a_{4545} \end{bmatrix}^{-1} \begin{bmatrix} t_1 \\ t_2 \\ \cdot \\ \cdot \\ \cdot \\ l_{44} \\ l_{45} \end{bmatrix},$$

where t_i = the estimated effect of the i^{th} tester,

l_j = the estimated effect of the j^{th} line,

a_{11}-a_{4545} = the elements of the matrix of coefficients,

T_i = the total for the i^{th} tester,

L_j = the total for the j^{th} line.

Since the tester effects were of prime interest, a mathematical procedure of absorbing the lines was used to reduce the 45 x 45 matrix of coefficients to the following 6 x 6 matrix:

$$\begin{bmatrix} t_1 \\ t_2 \\ \cdot \\ \cdot \\ t_6 \end{bmatrix} = \begin{bmatrix} b_{11} & \cdots & b_{16} \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ \cdot & & \\ b_{61} & & b_{66} \end{bmatrix}^{-1} \begin{bmatrix} T_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ T_6 \end{bmatrix}.$$

The b_{ij}'s are the elements of the matrix of coefficients following the process of absorption. This matrix was then inverted after imposing the condition that the $\sum \hat{t}_i = 0$. The matrix equation was then solved to determine the effect of each tester.

In order to assess interactions of lines, testers, and lines x testers with locations (with an associated subscript p because the subscript l is already used for lines), a subset of the data consisting of eight lines crossed with all the six testers was evaluated by a complete orthogonal analysis of variance of the adjusted treatment means. The structure of the analysis of variance is given in Table 6. In this table, the σ^2 is again the effective error mean square referred to previously.

Table 6. Analysis of variance for an orthogonal set of 48 crosses

Source of variation	d. f.	Expected mean squares
Lines	7	$\sigma^2 + \sigma^2_{lxtxp} + 6\sigma^2_{lxp} + 3\sigma^2_{lxt} + 18\sigma^2_{l}$
Lines x Places	14	$\sigma^2 + \sigma^2_{lxtxp} + 6\sigma^2_{lxp}$
Testers	5	$\sigma^2 + \sigma^2_{lxtxp} + 8\sigma^2_{txp} + 3\sigma^2_{lxt} + 24\sigma^2_{t}$
Testers x Places	19	$\sigma^2 + \sigma^2_{lxtxp} + 8\sigma^2_{txp}$
Lines x Testers	35	$\sigma^2 + \sigma^2_{lxtxp} + 3\sigma^2_{lxt}$
Lines x Testers x Places	70	$\sigma^2 + \sigma^2_{lxtxp}$

EXPERIMENTAL RESULTS

Yield

The analyses of variance for Ithaca, Riverhead, and Clear Lake are shown in Tables 7, 8, and 9, respectively. Total variability appeared to be high at all locations. This was revealed by coefficients of variability of 24.2 percent at Ithaca, New York, 17.6 percent at Riverhead, New York, and 21.7 percent at Clear Lake, Iowa. Some of this variability appeared to be the result of sporadic virus infection of seedling plants in 1957. No attempt was made to index the crosses for any of the virus diseases.

Differences among crosses were found to be statistically significant at the one percent level at each of the three locations. The relatively low mean square for crosses 1-100 versus 101-200 seemed to verify the assumptions that the crosses had been randomly assigned to each triple lattice group and that the sample size was large enough in each group to be representative of this experimental population.

Yields for all tester x line crosses are shown in Tables 10, 11, and 12, for Ithaca, Riverhead, and Clear Lake, respectively. The mean yield of each tester represents performance in a wide variety of crosses and is therefore a relative measure of its general combining ability. As shown by the standard error of each mean, significant differences between averages of tester performance were not apparent at any location. This lack of significance suggests that general combining ability may be of relatively little prominence in the present study. Within each of the testers, however, the range of yield values representing individual crosses indicates the relative magnitude of specific combining ability. For example, the Ithaca location, TL1859 x line 2 yielded 146.2 pounds compared to a mean for this tester of 111.3 pounds.

Table 7. Analysis of variance for total yield at Ithaca, New York

Source of variation	d.f.	Mean square
Replication	5	
Crosses 1-100 versus 101-200	1	8.416
Error (a)	5	113.442
Crosses within groups (ignoring blocks)	198	60.466**
Blocks within groups (eliminating crosses)	108	90.952
Component (a)	54	97.062
Component (b)	54	84.841
Intrablock error	882	16.696

** Denotes significance at the one percent level

Table 8. Analysis of variance for total yield at Riverhead, New York

Source of variation	d. f.	Mean square
Replication	5	
Crosses 1-100 versus 101-200	1	3.330
Error (a)	5	152.200
Crosses within groups (ignoring blocks)	198	56.112**
Blocks within groups (eliminating crosses)	108	57.735
Component (a)	54	63.424
Component (b)	54	52.048
Intrablock error	882	9.359

** Denotes significance at the one percent level

Table 9. Analysis of variance for total yield at Clear Lake, Iowa

Source of variation	d. f.	Mean square
Replication	5	
Crosses 1-100 versus 101-200	1	2.891
Error (a)	5	22.205
Crosses within groups (ignoring blocks)	198	41.924**
Blocks within groups (eliminating crosses)	108	29.529
Component (a)	54	30.223
Component (b)	54	28.834
Intrablock error	882	10.105

** Denotes significance at the one percent level

Table 10. Adjusted total yields, in pounds, of line x tester crosses grown at Ithaca, New York[a]

Line	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1		114.6	133.8	103.2		135.0
2	95.4	146.4	111.0	87.6		122.4
3	88.8	104.4	111.6			84.6
4	102.6	88.2	91.2	105.5	153.0	75.0
5	105.0	40.8	120.0	97.2	69.6	43.8
6	116.4	132.0	89.4	120.6	81.0	82.2
7	82.2	123.0	108.0	124.8	70.8	106.2
8		72.0		116.4		
9		121.2				
10	99.6		122.4		94.2	132.0
11	117.6	104.4	87.6	111.6	155.4	118.2
12	142.2	119.4	98.4	85.8	75.0	
13	91.8	115.8	90.0	100.2		104.4
14	84.6	137.4	100.8	73.8		
15		131.4	112.8	103.2		
16	85.2	94.2	101.4	120.0		
17			79.8			121.8
18	71.4	118.2	65.4	79.8		72.0
19	95.4	117.6	88.2	77.4	76.8	112.8
20		79.8	96.0	118.8	119.4	109.8
21	88.2		140.4	103.2		
22	114.6	118.8	77.4			
23	84.6	117.0		58.2		86.4
24		111.0	78.6	69.0	117.0	84.6
25	80.4	49.8			83.4	
26	144.6	82.8	112.8		104.4	
27	109.8	139.2	106.2	85.8		
28	102.0	146.4			88.8	
29		118.8		111.6	93.0	100.8
30	111.6	76.8	48.0	107.4	128.4	99.6
31	91.2	108.6	76.8	79.8	58.8	
32	82.8	140.4	108.0		90.0	97.2
33	93.6		108.6	65.4	93.0	98.4
34	97.2	111.0	96.0	76.2	99.0	
35	123.0	142.8	118.8	109.8		
36	93.6	129.6	124.2	90.0	96.6	
37	114.6	123.6	93.6		74.4	
38			96.6	84.0		
39		109.2				
40	81.6	120.0		73.8	59.4	75.6
41		78.0	102.6		109.2	
42	99.0	79.0	79.2	98.4	139.2	119.4
43		149.4	70.2			90.6
44	98.4		60.6	125.4	118.2	123.0
45		129.0	97.8	108.0	125.4	
Mean	99.6	111.3	97.4	96.0	99.0	99.8
$s_{\bar{x}}$	3.0	4.2	3.3	3.3	3.4	4.5

a 180 square feet

Table 11. Adjusted total yields, in pounds, of line x tester crosses grown at Riverhead, New York[a]

Line	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1		119.4	132.0	102.6		57.0
2	112.8	146.4	117.0	74.4		91.2
3	115.8	109.2	97.2			95.4
4	90.0	120.6	106.2	113.4	111.6	121.2
5	94.8	107.4	102.0	100.2	100.8	89.4
6	118.2	118.2	123.6	130.2	107.4	93.6
7	87.6	125.4	102.6	112.8	124.8	106.2
8		70.8		113.4		
9		91.8				
10	96.6		121.2		124.2	122.4
11	87.6	124.8	98.4	100.4	110.4	70.8
12	73.2	116.4	102.6	102.0	73.8	
13	108.0	129.0	102.6	102.6		118.2
14	99.6	129.0	112.2	87.6		
15		97.2	102.0	114.6		
16	108.0	106.2	102.6	109.8		
17			106.8			88.8
18	85.2	113.4	96.6	70.2		41.4
19	104.4	123.0	109.2	105.0	99.6	79.2
20		153.0	130.2	100.2	73.8	106.2
21	112.2		123.0	121.8		
22	96.6	127.2	104.4			
23	111.6	132.6		123.0		107.4
24		115.8	104.4	89.4	115.8	105.6
25	84.6	126.0			118.2	
26	93.0	114.0	121.2		111.0	
27	97.8	112.8	95.4	63.6		
28	106.8	95.4			72.0	
29		145.8		92.4	107.4	110.4
30	97.2	92.4	61.2	96.6	85.8	102.6
31	86.4	133.8	124.2	76.8	79.2	
32	118.8	123.0	106.8		67.8	76.8
33	123.6		106.8	88.8	116.4	111.6
34	119.4	82.2	73.2	82.8	103.8	
35	111.0	102.6	48.0	94.8		
36	105.0	120.6	66.6	91.8	73.8	
37	102.0	85.8	127.8		124.8	
38			73.8	75.0		
39		109.2				
40	84.6	104.4		94.2	56.4	73.8
41		90.6	81.6		72.0	
42	72.0	101.4	103.8	129.0	121.2	97.2
43		136.2	80.4			98.4
44	129.0		97.8	126.0	93.6	115.8
45		124.2	85.2	123.6	128.4	
Mean	101.0	114.8	101.4	100.3	99.0	95.0
$s_{\bar{x}}$	2.5	2.9	3.2	3.1	4.2	4.1

[a] 180 square feet

Table 12. Adjusted total yields, in pounds, of line x tester crosses grown at Clear Lake, Iowa[a]

Line	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1		58.3	78.8	94.2		76.1
2	89.8	89.0	82.1	102.1		95.5
3	114.9	73.0	72.1			79.6
4	119.6	93.1	97.3	98.2	86.9	87.5
5	79.3	77.4	85.8	92.5	84.5	56.9
6	78.2	101.9	81.4	76.3	71.3	65.2
7	79.3	76.6	111.0	75.2	78.5	80.5
8		71.3		73.6		
9		67.8				
10	85.3		69.8		76.0	87.4
11	66.0	73.1	91.9	92.3	82.2	65.4
12	93.2	89.1	80.7	75.1	80.6	
13	93.8	92.5	78.1	101.0		92.0
14	79.0	101.5	104.5	93.5		
15		92.5	79.3	84.4		
16	84.5	88.2	96.3	116.4		
17			79.8			80.0
18	84.7	90.7	77.4	85.4		65.3
19	84.4	94.3	70.1	67.9	65.0	73.5
20		100.4	64.0	82.3	62.5	104.5
21	85.1		99.4	89.6		
22	79.4	97.0	92.5			
23	82.6	92.9		86.0		72.3
24		98.2	73.7	89.3	83.1	74.9
25	64.7	87.5			86.0	
26	94.8	64.8	67.1		103.4	
27	120.2	101.3	93.4	70.8		
28	71.4	81.1			92.5	
29		78.0		95.0	107.3	85.9
30	71.7	96.2	66.7	93.0	84.8	79.1
31	68.3	103.1	84.0	83.9	81.1	
32	95.6	91.5	94.7		78.5	68.9
33	107.8		106.4	113.6	121.5	122.5
34	104.4	90.5	88.0	91.1	73.6	
35	101.0	108.5	70.1	92.9		
36	99.2	118.0	98.9	73.4	89.0	
37	88.4	98.2	88.0		50.3	
38			109.7	121.6		
39		82.3				
40	105.6	96.1		96.8	111.8	97.5
41		114.4	100.2		101.3	
42	55.1	115.6	103.5	94.0	68.7	74.7
43		111.3	96.6			91.3
44	63.4		47.3	65.3	91.6	82.6
45		77.6	74.3	91.9	70.8	
Mean	87.2	90.6	85.3	89.3	83.9	81.6
$s_{\bar{x}}$	2.9	2.3	2.4	2.3	3.1	2.9

[a] 180 square feet

Estimates of the variance components used to measure general and specific combining ability at each location are presented in Tables 13, 14, and 15. The line x tester component was relatively large in comparison with those for lines and testers at each of the three locations. Therefore, it appears that specific combining ability was more important than general combining ability in determining yield at each of the locations. Since an incomplete set of crosses was used to estimate these components, the values were not measured by an F-test. However, the consistency of the results over three varied locations supports their biological significance.

The combined analysis for estimating general and specific combining ability is presented in Table 16. In this analysis, an orthogonal table of 48 of the 190 crosses was used to compute the variance components. The line x tester component was found to be approximately twice that of the tester or line, again indicating the importance of specific combining ability. The specific combining ability effects appeared to interact more with the environment than did general combining ability effects. This is shown by comparisons between the estimated components for line x tester x location and the components for tester x location and line x location. The line x tester x location mean square was shown to be statistically significant at the one percent level. This significance was revealed by using the effective error mean square, divided by six, as the denominator in the F-test.

Table 13. Analysis of variance for estimating general and specific combining ability for total yield at Ithaca, New York

Source of variation	d.f.	Mean square	Estimated variance component
Testers	5	188.296	σ_t^2 = 0.579
Lines	44	89.619	σ_l^2 = 0.412
Lines x Testers	140	77.888	σ_{lxt}^2 = 10.254

Table 14. Analysis of variance for estimating general and specific combining ability for total yield at Riverhead, New York

Source of variation	d.f.	Mean square	Estimated variance component
Testers	5	261.170	σ_t^2 = 1.099
Lines	44	76.643	σ_l^2 = 0.892
Lines x Testers	140	51.595	σ_{lxt}^2 = 7.145

Table 15. Analysis of variance for estimating general and specific combining ability for total yield at Clear Lake, Iowa

Source of variation	d.f.	Mean square	Estimated variance component
Testers	5	57.386	σ_t^2 = 0.143
Lines	44	63.625	σ_l^2 = 1.395
Lines x Testers	140	27.954	σ_{lxt}^2 = 3.001

Table 16. Analysis of variance of combined data for estimating general and specific combining ability for total yield[a]

Source of variation	d.f.	Mean square	Estimated variance component
Lines	7	18.353	σ_l^2 = 0.701
Lines x Places	14	9.337	σ_{lxp}^2 = 0.205
Testers	5	20.267	σ_t^2 = 0.701
Testers x Places	10	11.434	σ_{txp}^2 = 0.416
Lines x Testers	35	12.315	σ_{lxt}^2 = 1.402
Lines x Testers x Places	70	8.108	σ_{lxtxp}^2 = 6.099

[a]Orthogonal table of 48 line x tester crosses used for computations

In Table 17 the direct effect of testers is shown for each location and for combined locations. This direct effect primarily includes the yield contribution of the tester. Effects of individual lines had been mathematically absorbed. These data revealed that the greatest effect was due to tester TL1859. This effect was consistent at each location and in the combined analysis. B3131-8 gave the smallest effect over all locations. The tester effect calculated in this study apparently contains both specific and general effects. General combining ability differences among testers were shown to be insignificant and the importance of specific effects in this population was indicated from the estimated variance components. Therefore, it would seem that the large effect of TL1859 could be attributed primarily to specific combining ability, i.e., to non-additive gene action.

Table 17. Relative effects of testers in determining yield of crosses grown at Ithaca, New York, Riverhead, New York, Clear Lake, Iowa, and in combined locations[a]

Tester	Ithaca New York	Riverhead New York	Clear Lake Iowa	Combined locations
Katahdin	-20.8	-95.9	62.1	-18.2
TL1859	1093.3	1535.6	551.0	1059.9
B962-32	-518.9	-29.4	-222.3	-256.9
ND457-1	-510.5	-84.8	217.4	-125.9
X96-56	-34.4	-326.9	-169.6	-176.9
B3131-8	-8.7	-998.5	-438.6	-481.9

[a] Based upon total yield in pounds per 180 square feet

Specific Gravity

Table 18 presents the analysis of variance at the Clear Lake location. Total variability was low with a coefficient of variability of 6.5 percent. If virus infections caused some of the variation in the trials, it is apparent that such infections have little or no effect on specific gravity, assuming that the infected plant lives to maturity. The differences between crosses were found to be statistically significant at the one percent level. The random sample of these crosses in each lattice group was felt to be effective, since no significant difference was found between crosses 1-100 and 101-200.

Table 18. Analysis of variance for specific gravity at Clear Lake, Iowa

Source of variation	d.f.	Mean square
Replication	5	
Crosses 1-100 versus 101-200	1	71.050
Crosses within groups (ignoring blocks)	198	94.978**
Blocks within groups (eliminating crosses)	108	28.376
Component (a)	54	32.785
Component (b)	54	37.835
Intrablock error	882	18.179

**Denotes significance at the one percent level

Table 19. Adjusted mean specific gravity of line x tester crosses grown at Clear Lake, Iowa

Line	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1		1.064	1.066	1.068		1.065
2	1.058	1.059	1.067	1.060		1.066
3	1.067	1.066	1.066			1.070
4	1.065	1.067	1.070	1.065	1.068	1.066
5	1.065	1.065	1.072	1.071	1.068	1.071
6	1.057	1.063	1.066	1.060	1.060	1.063
7	1.059	1.061	1.066	1.062	1.061	1.068
8		1.058		1.066		
9		1.064				
10	1.064		1.073		1.066	1.070
11	1.060	1.057	1.061	1.065	1.061	1.064
12	1.064	1.061	1.068	1.065	1.061	
13	1.061	1.062	1.069	1.067		1.065
14	1.061	1.058	1.069	1.068		
15		1.061	1.065	1.067		
16	1.066	1.061	1.067	1.066		
17			1.071			1.071
18	1.063	1.059	1.068	1.064		1.064
19	1.065	1.065	1.072	1.067	1.071	1.074
20		1.065	1.066	1.072	1.073	1.067
21	1.063		1.070	1.063		
22	1.065	1.067	1.073			
23	1.056	1.061		1.066		1.064
24		1.067	1.070	1.070	1.066	1.070
25	1.066	1.067			1.072	
26	1.070	1.067	1.070		1.064	
27	1.061	1.062	1.066	1.067		
28	1.061	1.063			1.065	
29		1.069		1.067	1.069	1.073
30	1.065	1.068	1.066	1.071	1.064	1.070
31	1.059	1.062	1.068	1.070	1.066	
32	1.062	1.063	1.065		1.065	1.064
33	1.061		1.072	1.068	1.060	1.065
34	1.066	1.065	1.072	1.073	1.068	
35	1.066	1.065	1.071	1.069		
36	1.067	1.063	1.070	1.069	1.066	
37	1.064	1.067	1.074		1.068	
38			1.065	1.058		
39		1.063				
40	1.060	1.059		1.065	1.065	1.064
41		1.068	1.064		1.063	
42	1.064	1.062	1.066	1.066	1.063	1.068
43		1.064	1.067			1.064
44	1.067		1.076	1.071	1.070	1.070
45		1.065	1.071	1.068	1.071	
Mean	1.063	1.063	1.069	1.067	1.066	1.067
$s_{\bar{x}}$	0.006	0.005	0.005	0.006	0.007	0.007

The mean specific gravity reading for each cross is presented in Table 19. The mean for tester B962-32 was found to be significantly greater than those for Katahdin and TL1859 at the one percent level. This suggests that B962-32 may be a better general combiner for specific gravity than Katahdin or TL1859. No measurable differences were found between other tester means. Most of the values for individual crosses seemed to correspond closely to the respective tester mean indicating a relatively small specific effect.

The analysis of variance for estimating general and specific combining ability is presented in Table 20. The tester and line components were approximately twice that of line x tester. This analysis suggests that general combining ability, or additive effects, may be more important than specific combining ability, or non-additive effects, in determining specific gravity.

Table 20. Analysis of variance for estimating general and specific combining ability for specific gravity at Clear Lake, Iowa

Source of variation	d.f.	Mean square	Estimated variance component
Testers	5	995.014	$\sigma_t^2 = 5.033$
Lines	44	183.346	$\sigma_l^2 = 5.519$
Lines x Testers	140	32.326	$\sigma_{lxt}^2 = 2.858$

The relative tester effects calculated for specific gravity are as follows:

Katahdin	-1611.8
TL1859	-1404.1
B962-32	1740.2
ND457-1	721.8
X96-56	-380.7
B3131-8	934.6

Testers B962-32, ND457-1, and B3131-8 had rather strong effects. The magnitude of individual tester means and variance components suggest that additive gene effects contribute to the differences found in these effects.

Tuber Appearance

The analysis of variance is presented in Table 21. The coefficient of variability for this characteristic at Clear Lake was found to be 22 percent. A significant difference at the five percent level was discovered between crosses 1-100 and 101-200. Although the distribution of crosses within each tester was found to be nearly equal between the two groups, the sample size may have been too small to represent the entire population of crosses for tuber rating. The reason for this could be the subjective nature of the tuber appearance ratings. It is doubtful if this difference has any significance regarding other tuber rating results, however. The differences between crosses within groups was found to be significant at the one percent level.

Thus, most of the total variation can be accounted for by effect of crosses.

Table 21. Analysis of variance for tuber appearance at Clear Lake, Iowa

Source of variation	d. f.	Mean square
Replication	5	
Crosses 1-100 versus 101-200	1	11.600*
Error (a)	5	1.530
Crosses within groups (ignoring blocks)	198	2.711**
Blocks within groups (eliminating crosses)	108	0.854
Component (a)	54	0.869
Component (b)	54	0.839
Intrablock error	882	0.695

* Denotes significance at the five percent level
** Denotes significance at the one percent level

The cumulative tuber appearance indexes are presented for each cross in Table 22. The difference between the mean of tester ND457-1 and that of all other testers, except Katahdin, was found to be significant at the one percent level. The difference between ND457-1 and Katahdin was significant at the five percent level. All other differences between tester means were found to be non-significant. This indicates that ND457-1 has the best general combining ability of the six testers. When individual crosses of each

Table 22. Adjusted totals of tuber rating indexes of line x tester crosses grown at Clear Lake, Iowa

Line	Katahdin	TL1859	B962-32	ND457-1	X96-56	B3131-8
1		13.8	23.0	25.6		20.6
2	21.7	20.0	21.6	26.0		20.6
3	22.0	16.8	17.7			18.8
4	28.3	18.8	25.0	29.3	18.9	22.2
5	20.3	22.5	18.4	29.6	23.0	19.8
6	24.0	21.0	21.5	28.3	18.0	16.8
7	25.8	19.5	26.8	24.6	21.5	19.5
8		14.9		20.6		
9		20.1				
10	21.8		20.4		18.0	30.5
11	18.3	20.8	23.8	30.4	24.7	16.8
12	22.2	19.0	21.0	25.4	26.3	
13	25.2	19.0	24.2	34.3		25.0
14	23.2	21.3	28.8	27.0		
15		20.1	24.4	27.8		
16	30.6	20.8	20.0	23.2		
17			19.0			17.1
18	29.7	22.3	22.0	25.8		20.3
19	21.5	21.7	20.4	22.2	21.7	17.7
20		11.2	18.1	23.7	15.3	23.7
21	19.8		20.9	21.0		
22	25.8	23.6	29.7			
23	22.7	25.4		26.2		18.3
24		21.0	17.6	27.7	25.7	19.0
25	16.7	14.5			18.8	
26	25.0	16.0	22.1		23.8	
27	22.2	23.5	24.0	24.8		
28	25.2	24.9			19.0	
29		18.5		27.2	27.4	25.0
30	23.8	21.6	22.4	26.0	28.0	22.0
31	23.2	19.5	22.2	32.3	21.0	
32	24.9	23.0	20.3		21.2	24.0
33	25.6		22.8	24.0	19.0	25.1
34	26.0	18.7	21.5	27.2	18.9	
35	27.3	22.0	17.0	24.5		
36	21.4	19.8	23.5	20.6	18.8	
37	21.4	18.6	20.4		16.1	
38			20.8	25.9		
39		21.0				
40	26.3	22.7		28.3	21.1	21.7
41		28.6	26.8		25.7	
42	22.2	24.0	23.3	33.3	23.2	21.5
43		20.3	21.8			19.0
44	23.5		18.0	25.0	22.8	20.0
45		18.8	23.0	28.5	19.9	
Mean	23.7	20.2	22.0	26.4	21.4	21.0
$s_{\bar{x}}$	0.5	0.5	0.5	0.6	0.7	0.7

tester are compared with the tester mean, it is apparent that the specific effects are somewhat less than those found for yield data.

In Table 23 the variance components for estimating general and specific combining ability are presented. The estimates of these components seem to suggest that general and specific combining ability were of equal importance in determining tuber appearance in this population.

Table 23. Analysis of variance for estimating general and specific combining ability for tuber appearance at Clear Lake, Iowa.

Source of variation	d.f.	Mean square	Estimated variance component
Testers	5	261.170	$\sigma_t^2 = 0.138$
Lines	44	76.643	$\sigma_l^2 = 0.047$
Lines x Testers	140	51.595	$\sigma_{lxt}^2 = 0.126$

The relative tester effects calculated for tuber appearance are as follows:

Katahdin	114.4
TL1859	-231.8
B962-32	-47.2
ND457-1	408.5
X96-56	-107.7
B3131-8	-136.2

Testers ND457-1 and Katahdin had the largest relative effects. Both of these clones have been used extensively as parents in breeding programs and have been noted for the excellent tuber appearance transmitted to their progenies.

Relationship between Testers and Lines

Of the 190 crosses used in this study, 70 were between testers and lines having a common parent within the previous two generations. As shown in Table 1, tester TL1859 was related to 26 of the 39 lines with which it was crossed, and tester B3131-8 was related to 12 of a total of 24 lines.

A comparison of data pooled for related and unrelated crosses of each tester revealed no substantial difference for yield, specific gravity or tuber appearance. The results are shown in Tables 24, 25, and 26, respectively. These data suggest that the relationship between lines and testers apparently had little effect on yield, specific gravity, or tuber appearance.

Table 24. Pooled yield of crosses involving related and unrelated parents[a]

Tester	Related crosses	Unrelated crosses
Katahdin	95.1	96.2
TL1859	107.9	100.8
B962-32	90.8	95.8
ND457-1	92.2	96.2
X96-56	92.6	94.7
B3131-8	91.0	93.3

[a] Based upon total yield in pounds per 180 square feet

Table 25. Pooled mean specific gravity readings of crosses involving related and unrelated parents

Tester	Related crosses	Unrelated crosses
Katahdin	1.062	1.063
TL1859	1.063	1.064
B962-32	1.068	1.069
ND457-1	1.066	1.066
X96-56	1.065	1.066
B3131-8	1.066	1.068

Table 26. Pooled tuber appearance indexes of crosses involving related and unrelated parents

Tester	Related crosses	Unrelated crosses
Katahdin	23.2	23.8
TL1859	20.9	18.9
B962-32	22.8	21.8
ND457-1	26.2	26.5
X96-56	21.1	21.6
B3131-8	20.6	21.4

DISCUSSION

The line and tester clones used in this study originally were selected from F_1 crosses of heterozygous parents. Each clone had been tested for several years and retained because of one or more desirable attributes. Within this experimental population, there was no evidence of planned inbreeding. Therefore, it is assumed that the clones tested in the present study represent highly heterozygous parents. It is further assumed that this population is a representative sample of the genes found in clones used in the United States.

In efforts to determine the type of gene action present in a crop, it is of considerable importance to ascertain the population to which the results might apply. The information obtained concerning gene action in this study was felt to be relative to comparable populations of lines derived from American potato breeding programs. This reasoning assumes that the lines and testers comprise a diverse sample from a number of breeding programs.

Potato breeders have long recognized that it is extremely difficult to predict the results of a given cross. This has been especially true for yield and such characters influenced by environmental fluctuation. Most breeders have concluded that specific combining ability is more important than general combining ability in the potato for such quantitative characters. This conclusion is the result of observations made in practical breeding programs and not from specific studies to determine gene action. These potato breeders also consider the technique of recurrent selection to have potential as a method to increase the efficiency of potato improvement. Before such a method is used, however, the relative importance of additive and non-additive effects should be ascertained. This information has been obtained for a number of crops, such as corn, and has been helpful in developing new breeding techniques.

One of the purposes of this study was to obtain estimates of general and specific combining ability in F_1 crosses of potato clones. General combining ability is largely a result of additive effects, whereas specific combining ability is a combination of dominance, epistasis, and other genetic interactions.

The results of this study tend to verify the importance of specific combining ability for yield. In the analysis for line, tester, and line x tester components, the line and tester values are analagous to general combining ability, or the average effect of lines and testers. The line x tester variance component is similar to specific combining ability in that it is a measure of the variability of specific crosses of lines and testers.

These analyses show similar results for yield at each of the three locations. The line x tester component was consistently larger than the line and tester components. This difference was most noticeable at Ithaca, New York. Smaller differences were found in the data from Riverhead and Clear Lake. These data suggest that specific combining ability is of primary importance in determining yield as measured over widely differing environments. This evidence is in general agreement with that of Sprague and Tatum (42). In previously tested and selected corn lines, these authors reported that specific combining ability was more important than general combining ability. In the present study, it is felt that the importance of specific combining ability also can be related to the tetraploid inheritance of potatoes and to the heterozygous nature of the parental clones.

In the combined-location analysis for yield, the estimate of specific combining ability x location ($\sigma^2_{l \times t \times p}$) was approximately 12 times that of general combining ability x location($\sigma^2_{l \times p}$ and $\sigma^2_{t \times p}$). This result agrees with Rojas and Sprague (41) who reported that estimates of specific combining ability in corn tend to interact more with environment than do estimates of general combining ability.

From the comparison of tester means over lines, it appears that there is no difference in general combining ability for yield. Tester TL1859 gave the largest relative effect in determining yield at each location. This relative effect assumes that there is no interaction between lines and testers. Although a sizeable interaction was shown, it is felt that the relative effect values are indicative of the performance of testers. It would seem that the effect of tester TL1859 must be mostly specific in nature. A possible explanation for the predominance of specific combining ability is the close relationship between this tester and the lines with which it was crossed. Grogan and Zuber (14) and Keller (25a) found in corn that testers closely related to the inbred lines would not give an accurate estimate of the general combining ability of the lines because of the apparent increases in specific effects. In the present study, simple comparisons between related and unrelated crosses within each tester revealed no substantial differences, and would suggest that the existence of a relationship between testers and lines in potatoes has little effect on combining ability for yield. However, differences could exist in general and specific combining ability of related and unrelated material which might have been averaged out in such a comparison. The evidence in this study can be considered only as preliminary in an area where further study is needed.

The estimates for specific gravity of the σ^2_l, σ^2_t, and σ^2_{lxt} components reveal that general combining ability was more important than specific combining ability. The line and tester components were twice that of the line x tester component. This result coincides with observations of potato breeders after making crosses between clones of high specific gravity. In general, a large number of plants with high specific gravity can be found in progenies from crosses between parents of high specific gravity. The genes that affect specific gravity apparently are fewer in number than those affecting yielding ability. These data further indicate that gene effects are largely additive.

Comparisons among means of testers for specific gravity reveal a significant difference between the largest mean, B962-32, and two of the low means, Katahdin and TL1859. This indicates that B962-32 is superior as a general combiner. No other differences in the general combining ability of the testers could be detected.

It is of interest to note that the testers which are considered to have high specific gravity (B962-32, B3131-8, and ND457-1) had the highest relative effects for determining specific gravity. Those with relatively low specific gravity (Katahdin, TL1859, and X96-56) had the lowest effects. These data seem to indicate that the specific gravity phenotype of a parent gives a fair prediction of performance of its progeny in F_1 crosses.

The results of the analysis to determine general and specific combining ability for tuber appearance suggest a lack of predominance of either. A comparison of tester means over lines revealed that ND457-1 is a significantly better general combiner than the other five. The data for relative tester effects showed that the two testers, ND457-1 and Katahdin, which have been particularly noted for imparting desirable tuber appearance to their progeny, had the largest effects.

It is the present goal of many potato breeders to develop parental material of superior general combining ability for particular characteristics such as high yield, disease resistance, and high specific gravity. Efficient progress towards such a goal can be realized only if the character shows a predominance of additive genetic variance. The present study indicates that it may be difficult to obtain clones homozygous for general combining ability for yield. This conclusion is supported by the predominant non-additive effects found for yield in evaluating six testers. Selection for additive effects would appear to require a large number of testers in order that the specific effects of each tester could be averaged out. Information concerning the number of testers required for measurable genetic advance could not be adequately obtained in this experiment and is an area for further study. The data from this experiment indicate that specific effects in the potato react more to various environments than general effects. This observation suggests that progeny tests for yield should be conducted for more than one year and in more than one location.

Because of the relative importance of additive effects, it would seem possible to develop parental clones of good general combining ability for specific gravity. A substantial variance for additive gene action was found for this character. The number of testers needed would tend to be less than that required for evaluating yield. Since additive and non-additive genetic variances were found to be of equal importance for tuber appearance, it should be possible to develop good combiners for this character without recourse to large numbers of testers.

Data presented by Matzinger (33), Rojas and Sprague (41), and Federer and Sprague (9) have indicated that genetic responses are generally affected by the particular year and location in which the tests are grown. For this reason, these authors have suggested that tests be conducted in a number of locations and for more than one year. Data obtained in several environments increase the reliability of the results. Since this experiment includes data of but one year and is the first attempt to estimate gene action in a population of potato clones, the importance of additive and non-additive effects shown for the characters studied should be considered only as indications of possible genetic patterns. However, it is felt that the information obtained for yield is more reliable than that obtained for specific gravity or tuber appearance. This reliability is based upon the three locations from which yield data was obtained. These locations differed widely in soil type, light intensity, and other environmental forces. Further work, however, would undoubtedly be helpful in defining more precisely the effect of gene action in a potato breeding program.

SUMMARY

This study was designed to obtain estimates of general and specific combining ability variances from tests of 190 F_1 crosses and to evaluate six proposed tester clones for total yield, specific gravity, and tuber appearance.

Crosses were made between 45 diverse breeding lines and six clones selected as testers. The 190 crosses obtained were tested at Ithaca and Riverhead, New York, and at Clear Lake, Iowa, in a modified rectangular lattice design. Total yield data were taken at all locations. Specific gravity and tuber appearance measurements were recorded only at the Clear Lake location.

The calculation of line, tester, and line x tester variance components indicated that specific combining ability was relatively more important than general combining ability for yield. No substantial differences in the general combining ability of testers could be found in comparing their means. Significant interaction of specific combining ability with locations was observed in these data. Calculation of relative effects of each tester revealed that tester TL1859 was consistently high in all locations. It was concluded that its effect was largely non-additive. These yield data indicate that genetic improvement for this character would be difficult. A large number of testers would be required to select from the relatively small additive effects found.

General combining ability was found to be more important than

specific combining ability in determining specific gravity. Tester B962-32 was significantly superior in mean performance to the two poorest testers. Testers B962-32, ND457-1, and B3131-8 gave the largest relative effects. Each of these clones is of high specific gravity. The three low specific gravity testers gave relatively small effects. It was therefore concluded that the phenotypic response of a parent for specific gravity would give fair prediction of its progenies performance. The data suggested that good general combining clones could be obtained through recurrent selection for additive effects.

General and specific combining ability were found to be of equal importance in determining tuber appearance. Tester ND457-1 was found superior as a general combiner. This tester and Katahdin gave the largest relative effects. These results agree with previous observation of the excellence of both clones as parents. It was felt that additive variation for tuber appearance is of sufficient magnitude to realize substantial genetic progress through development of clones of high general combining ability.

Comparisons of crosses between related and unrelated lines and testers indicated that the relationship between testers and lines apparently has little or no effect on the resulting progeny. It was pointed out, however, that differences could have been averaged out by specific effects in such comparisons.

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