

A Method for Quantitative Genetic Analysis of Early Clonal Generation Seedlings of an Asexual Crop with Special Application to a Breeding Population of the Potato (*Solanum tuberosum* L.)

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Summary. Traditionally, the selection and breeding of asexual crops starts with a population of many thousands of seedlings derived from many crosses. Heavy screening of clones in the first field trial, sometimes up to 90% of the population, is a routine practice. The extent of such early selection pressure is questioned since plants in the early clonal generations are usually managed in an unconventional cultivation system as compared to that used in the later clonal generation trials or in the commercial practice. A method of quantitative genetic analysis is presented for analyzing data of quantitative traits which are collected from two different clonal generations. It is proposed to measure the regression type of heritability between two clonal generations in standard deviation unit and the expected response to selection in the first clonal generation with a physical unit used in the second clonal generation. Subsequently, the method was applied to a breeding population of potato. The results indicated that selection for quantitative traits in the first clonal generation was in most cases less efficient than direct selection in the second clonal generation.

Introduction

The breeding of an asexual crop differs from that of sexually reproduced crops in many aspects. For instance, once a seedling is established from true seed following hybridization, the integrity of its genotype is maintained through vegetative propagation. Hence, it is the whole, instead of part (i. e., additive, dominance and/or epistatic effect) of the genotypic value of a seedling which should be assessed in a breeding program.

The type of seed used in growing F_1 and initial clonal generations is frequently different from that used for later generation clones and commercial varieties. The quantity of sets is also limited in these early generations. This forces the breeder to handle his early generation clonal materials in a somewhat different manner than is the case with the later generations. Consequently, the early clonal generations are cultured in a micro-environment which differs also from that of the commercial crop. For example, in a potato breeding program the F_1 seedlings are usually raised in the greenhouse from true seeds. Field testing of progenies begins with the first clonal generation when plants are grown in single hills from small uncut tubers. The spacing between hills is usually much wider than that used for plants in the later generations in order to maintain the identity of individual genotypes. Only after the second clonal generation are there sufficient tubers for a field trial that simulates the standard cultural practice. In North America this implies spacing a clone derived from cut seed pieces in rows 91.4 cm (3') apart with 25.4–50.8 (10–20") between the hills.

The present study proposes a method for the genetic analysis of quantitative traits of an asexual crop. The genotypes in the breeding population are assumed to be tested in two separate clonal generations which are managed differently. Formulae for estimating heritability and genetic progress under different selection schemes are presented. The method is then applied to a breeding population of potato.

Heritability and Expected Response to Selection

A breeding population of an asexual crop always involves clones from many crosses. Let us start with a simple case, i. e., a population of n seedlings in one cross. Extension to a more complicated case with seedlings from many crosses will be considered later. Let x_s and y_s be the phenotypic values of a quantitative trait of the s th clone in a cross tested in two successive early clonal generation trials. We shall identify the two generations as the first (C_1) and second (C_2) clonal generations and abbreviate the two clonal generation trials as the C_1 and C_2 trials respectively. In practice, it may be set up such that clones in the C_1 trial are planted in an unconventional way because of management problems in the early generation, whereas the same clones in the C_2 trial are managed 'normally' as in commercial practice. Mathematical models corresponding to the two trials can be expressed as:

$$\left. \begin{aligned} x_s &= u_x + g_{xs} + e_{xs} \\ y_s &= u_y + g_{ys} + e_{ys} \\ s &= 1, 2, \dots, n \end{aligned} \right\} \quad (1.1)$$

where

u_x = population mean of clones in the C_1 trial,
 g_{xs} = genotypic effect of the s th clone in the C_1 trial,
 e_{xs} = non-heritable effect or error deviate of the s th clone in the C_1 trial,
 $u_y, g_{ys},$ and e_{ys} are the corresponding effects in the C_2 trial.

Assuming that the error deviates, e_{xs} and e_{ys} , in the two trials are independent of each other, heritability of a quantitative trait can be estimated by calculating a regression coefficient of data of the C_2 clones on those of the C_1 's. However, the differential management systems between the two trials may cause changes in scale from C_1 to C_2 and thus contribute to a special type of genotype-environment interaction. To cancel the scaling factor due to this type of interaction, Frey and Horner (1957) proposed a standard unit method for measuring heritability which is actually the correlation coefficient between the two trials. Let b_{yx} and b'_{yx} be the heritability values estimated by the conventional regression method and the standard unit method respectively. The expected response of clones in the C_2 trial due to selecting clones in the C_1 trial can be expressed as:

$$R_{yx} = ib_{yx}\sigma_x = ib'_{yx}\sigma_y$$

in which i is the intensity of selection and σ_x^2 and σ_y^2 are the phenotypic variances of clones in the C_1 and C_2 trials. Frey and Horner (1957) had also calculated the predicted gain to selection in standard unit which is the product of intensity of selection and standard unit heritability, i. e.,

$$R'_{yx} = ib'_{yx}. \quad (1.2)$$

Falconer and his co-worker (Falconer, 1952 and 1960; Falconer and Latyszewski, 1952) used a totally different concept to analyze the genotype-environment interaction problem. They proposed to treat a trait measured in two different environments as two different traits instead of one. The improvement of a trait in the C_2 trial as a result of selecting for the trait in the C_1 trial is then treated as a problem of measuring the correlated response. The expectation of the correlated response can be given as:

$$CR_{yx} = ih_x h_y r_g \sigma_y$$

where h_x^2 and h_y^2 are the heritabilities derived from the C_1 and C_2 trials and r_g is the genotypic correlation between the two trials. With the assumption that the error deviates are not correlated between the two trials, it can be shown that:

$$\left. \begin{aligned} b'_{yx} &= h_x h_y r_g \\ CR_{yx} &= R'_{yx} \sigma_y \end{aligned} \right\} \quad (1.3)$$

It is thus clear that the two approaches are different from each other only in the manner of expressing the expected response to selection: as gain in terms of standard deviation unit (1.2) by Frey and Horner

(1957) or as gain in a physical unit used in the C_2 trial (1.3) by Falconer (1960).

If R_y is the expected response to direct selection in the C_2 trial, the relative efficiency of selection in the C_1 trial to that of direct selection in the C_2 trial is determined:

$$CR_{yx}/R_y = i_{xy} b'_{yx} / i_y h_y.$$

This relation can be converted to a useful statistic for breeding work, i. e., the relative intensity of selection:

$$i_{yx}/i_y = h_y / b'_{yx}. \quad (1.4)$$

This, in turn, measures how the strength of the selection pressure which must be exerted on a first clonal generation population in order to reach a level of improvement which is identical to that achieved by direct selection in the second clonal generation population.

Extension to Different Selection Schemes

The above results can be extended to a breeding population of m crosses, each having n clones, i. e., a total of $N = mn$ clones. If x_{st} and y_{st} represent the phenotypic values of a quantitative trait of the t th clone in the s th cross tested in the C_1 and C_2 trials, respectively, the mathematical models in (1.1) can be modified as follows:

$$\left. \begin{aligned} x_{st} &= u_x + f_{xs} + w_{xst} + e_{xst} \\ y_{st} &= u_y + f_{ys} + w_{yst} + e_{yst} \\ s &= 1, 2, \dots, m; t = 1, 2, \dots, n. \end{aligned} \right\} \quad (2.1)$$

In this instance, f and w represent respectively, an average cross effect and a clone within cross deviate. It is assumed, as above, that the error deviates are independent of each other in the two trials. Three statistical analyses can be carried out on observed data of a quantitative trait. They are two analyses of variance for the C_1 and C_2 trials respectively and an analysis of covariance between the two trials. The expectations of four mean squares and two mean products derived from the three analyses are given in Table 1. In the table, the variance and covariance

Table 1. Variance component structure in the expectations of mean squares and mean products derived from analyses of variance and covariance

	Mean squares and products	Expectations
ANOVA of 1st clonal generation trial		
between crosses	M_1	$nV_{fx} + V_{wx} + V_{ex}$
clones w. crosses	M_2	$V_{wx} + V_{ex}$
ANOVA of 2nd clonal generation trial		
between crosses	M_3	$nV_{fy} + V_{wy} + V_{ey}$
clones w. crosses	M_4	$V_{wy} + V_{ey}$
ANOCOVA of 1st and 2nd clonal generation trials		
between crosses	M_5	$nW_f + W_w$
clones w. crosses	M_6	W_w

components in the expectations are represented by V and W respectively with a suitable subscript verifying the source of effect. For example, V_{fx} is the variance component due to the average cross effects in the C_1 trial and W_f the corresponding covariance component between the two trials.

There are three basic methods of selection when a breeding population is composed of genotypes from many crosses. If selection is based on the phenotypic values of individual genotypes only, we are using the method of *individual* (or mass) *selection*. Alternatively, selection may be practiced on the basis of the cross means without any concern for the variation of individual genotypes within crosses. This is known as *family selection*. Further, we may also use *within family selection* in which any genotype having better phenotypic performance than others in its own cross is selected. The mean merit of a cross is totally disregarded when within family selection is practiced. More detail interpretation of these selection methods can be found from Lerner (1958) and Falconer (1960).

Where h^2 , h_f^2 , and h_w^2 represent the standard unit heritabilities of individual values, cross means and within-cross deviations, they can be derived as follows:

$$\left. \begin{aligned} h^2 &= (W_f + W_w) / \{ (V_{fx} + V_{wx} + V_{cx}) \times \\ &\quad \times (V_{fy} + V_{wy} + V_{ey}) \}^{1/2} \\ h_f^2 &= (W_f + W_w/n) / \{ (V_{fx} + V_{wx}/n + V_{cx}/n) \times \\ &\quad \times (V_{fy} + V_{wy}/n + V_{ey}/n) \}^{1/2} \\ h_w^2 &= W_w / \{ (V_{wx} + V_{cx}) (V_{wy} + V_{ey}) \}^{1/2} \end{aligned} \right\} (2.2)$$

If CR , CR_f , and CR_w represent the expected responses in the C_2 trial due to individual, family and within family selection in the C_1 trial,

$$\left. \begin{aligned} CR &= ih^2\sigma_y, & \sigma_y^2 &= V_{fy} + V_{wy} + V_{ey} \\ CR_f &= ih_f^2\sigma_{fy}, & \sigma_{fy}^2 &= V_{fy} + V_{wy}/n + V_{ey}/n \\ CR_w &= ih_w^2\sigma_{wy}, & \sigma_{wy}^2 &= (n-1)(V_{wy} + V_{ey})/n \end{aligned} \right\} (2.3)$$

and i is the intensity of selection, σ_y^2 , σ_{fy}^2 , and σ_{wy}^2 are, respectively, the phenotypic variances for individual values, cross means and within-cross deviations in the C_2 trial. The various variances and covariances in the formulae can be estimated by using the mean squares (M_1 , M_2 , M_3 and M_4) and mean products (M_5 and M_6) in Table 1.

The relative intensity of selection due to individual, family and within-family selection can be evaluated when the genetic advances to direct selection in the C_2 trial can be estimated for these selection schemes. This can be done if we replicate at least partly the clones in the C_2 trial so that an estimate of the error variance is available to determine the heritability values in the C_2 trial.

Application to a Breeding Population of Potato

A set of data collected from a breeding population of potato is used to illustrate the analytic procedure.

The population contained 25 hybrid progenies derived from 20 parents. The parents included American and European varieties and parental lines, and Fredericton-derived lines. More information about the parental combinations of the 25 crosses and the performance of the parents can be found from the appendices at the end of the paper.

In 1969, 100 small uncut tubers derived from 1968 greenhouse-grown F_1 plants of each of the 25 crosses were planted in the field. A complete randomized block design with four replicates was used. Each replicate had 25 single-row plots and each plot contained 25 hills for 25 clones of a cross. The spacing between adjacent hills in a row was 76.2 cm, and that between adjacent plots was 91.4 cm. Five consecutive plants in a plot were sampled and recorded for various horticultural traits. This gave a total of 500 recorded clones with each cross having 20 clones.

Three to five medium-sized tubers from each of the 500 first clonal generation plants were reserved when tubers were dug in field. In 1970, tubers of each clone or parent were cut into 10 sets and planted in field in a single row plot of 2.54 m long. Four groups of tubers of each of 17 parents* were also included for comparisons. The field plots were completely randomized. The spacing between adjacent plants in a plot was 25.4 cm and that between plots was 91.4 cm. The 1969 and 1970 trials are referred to as the C_1 and C_2 trials respectively.

Seven horticultural traits were recorded for each of the 500 clones in the two trials. The physical units used to record each of the traits in the two trials are as follows:

Maturity of haulm: scored from 1 (early) to 5 (late) according to the degree of senescence of the haulm immediately prior to harvest.

Marketable yield: yield of marketable tubers (tubers ≥ 5.5 cm ($2\frac{1}{4}$ " in diameter) harvested (plot size: .67 m² for the C_1 trial and 2.24 m² for the C_2 trial).

Number of marketable tubers: number of marketable tubers harvested in a plot.

Average weight of marketable tuber: weight per tuber derived from the relation (marketable yield/no. marketable tubers).

Total yield: yield of all tubers harvested in a plot.

Total number of tubers: number of all tubers harvested in a plot.

Average tuber weight: weight per tuber derived from the relation (total yield/total no. of tubers).

Data from 499 clones in both trials were used for the analyses since there was one missing plot in the 1970 experiment. Four statistical analyses were carried out for each of the seven traits. These were: 1) analysis of variance for clones in the C_1 trial;

* Tubers of three parents were not available during the time of the 1970 experiment.

Table 2. *Analyses of variance and covariance for seven traits of clones in the first and second clonal generation trials* and analyses of variance for parental clones augmented with the second clonal generation clones*

	Degrees of freedom	Mean squares and mean products						
		Maturity	Mark. yield	No. mark. tubers	Av. wt. mark. tuber	Total yield	Total no. tubers	Av. tuber wt.
ANOVA, 1st clonal gen. trial, 1969								
Between crosses	24	9.72	1.19	12.92	0.01545	1.44	165.14	0.01715
Clones w. crosses	474	1.86	0.48	6.41	0.00426	0.53	31.01	0.00422
ANOVA, 2nd clonal gen. trial, 1970								
Between crosses	24	5.17	19.37	312.33	0.00587	20.72	4103.19	0.00572
Clones w. crosses	474	0.57	6.09	132.91	0.00212	6.16	882.38	0.00162
ANOCOVA, 1st & 2nd clonal gen. trials								
Between crosses	24	5.84	2.54	13.81	0.00555	2.53	384.79	0.00575
Clones w. crosses	474	0.43	0.82	6.76	0.00079	0.65	42.96	0.00090
ANOVA, parental clones, 1970								
Parents	16	1.23	7.76	131.41	0.00222	7.29	397.92	0.00176
Error	51	0.12	3.54	81.98	0.00097	2.92	192.22	0.00099

* Data of 499 seedlings were used for the analyses of both trials since one plot was missing in the second clonal generation trial.

2) analysis of variance for clones in the C_2 trial; 3) analysis of covariance for clones between the two trials; and 4) analysis of variance for the 17 parents in the 1970 experiment according to a completely randomized design with four replicates. The results of these analyses are shown in Table 2.

The mean squares and mean products derived from the first three analyses were used to estimate the standard unit heritabilities for individual values, cross means, and within cross deviations as described in the last section. The results are given in the 2nd, 3rd and 4th columns of Table 3. Another set of variance component estimates of heritabilities for clones in the C_2 trial was also calculated by using the variance components derived from the two mean squares in the second analysis and the error mean square from the fourth analysis. The results are given in the 5th, 6th and 7th columns of Table 3. In general, for both the standard unit and the variance com-

ponent estimates, the heritability values of the seven traits followed the order: cross means > individual values > within cross deviations. The variance component estimates were, in general, larger than the corresponding standard unit estimates with the exception of those based on individual values and within-cross deviations for marketable yield and average tuber weight which were closely related, regardless of the two methods of estimation.

Maturity and number of marketable tubers showed the highest and lowest heritability values respectively, irregardless of the methods of estimation. Total number of tubers, on the other hand, showed relatively low values for the three standard unit estimates but were the second highest for the three variance component estimates.

Estimates of the expected response to selection are presented (Table 4) for between clonal generation analyses (2nd, 3rd and 4th columns) and the second clonal generation analyses (5th, 6th and 7th columns). The intensities of selection (i) for individual, family and within family selection were, respectively, 1.75 (10% or 50 clones), 1.745 (8% or 2 crosses) and 1.64 (10% or 2 clones/cross). Most of the estimated gains from selection in the first clonal generation were less than those attributed to direct selection in the second clonal generation. The only exceptions were individual and within family selection for marketable yield in the first clonal generation which gave slightly better results than the corresponding direct selection in the second clonal generation. With respect to the three selection schemes, the gains followed the order: individual selection > within family selection > family selection with only one negligible exception. Family selection gave the lowest response even though a higher intensity of selection was used.

The results of relative intensity of selection for selection in the first clonal generation to direct

Table 3. *Heritability of seven traits estimated in standard unit by correlation analysis involving two clonal generation trials and estimated by variance components in the second clonal generation trial*

	Standard unit estimate*			Variance component estimate*		
	h^2	h_f^2	h_w^2	h^2	h_f^2	h_w^2
Maturity	0.52	0.82	0.42	0.85	0.98	0.79
Marketable Yield	0.48	0.53	0.48	0.48	0.82	0.42
No. mark. tubers	0.23	0.22	0.23	0.42	0.74	0.38
Av. wt. mark. tubers	0.31	0.58	0.26	0.58	0.83	0.54
Total yield	0.37	0.46	0.36	0.58	0.86	0.53
Total no. tubers	0.30	0.47	0.26	0.82	0.95	0.78
Av. tuber weight	0.38	0.58	0.35	0.46	0.83	0.39

* h^2 and h^2 ; h_f^2 and h_f^2 ; h_w^2 and h_w^2 represent heritabilities for individual values, cross means and within cross deviations, respectively.

Table 4. *Expected response to selection in the first clonal generation trial and to direct selection in the second clonal generation trial. The intensities of selection (i) for individual, family and within-family selection are taken to be 1.75 (10% or 50 clones), 1.745 (8% or 2 crosses) and 1.64 (10% or 2 clones of each cross) respectively*

	Select. in parent. trial			Select. in progeny trial		
	Ind.	Family	Within-family	Ind.	Family	Within-family
Maturity (1-5)	-.82	-.73	-.53	-1.33	-.87	-1.00
Mark. yield (kg/plot*)	2.19	.91	1.98	2.16	1.40	1.74
No. mark. tubers (#/plot)	4.80	1.50	4.49	8.80	5.09	7.43
Av. wt. mark. tuber (kg/tuber)	.0259	.0175	.0203	.0485	.0249	.0418
Total yield (kg/plot)	1.72	.82	1.51	2.65	1.53	2.20
Total no. tubers (#/plot)	17.12	11.70	12.98	46.13	23.85	39.10
Av. tuber wt. (kg/tuber)	.0288	0.0172	0.0234	0.0341	.0244	.0262

* 1 plot = 2.24 m²

selection in the second clonal generation are shown in Table 5. Again, except for individual and within-family selection for marketable yield, selection in the first clonal generation would require a higher intensity of selection to reach a similar order of genetic advance as direct selection in the second clonal generation. For example, using individual selection, the intensity of selection for total number of tubers in the first clonal generation should be 2.7 times stronger than that used in the second clonal generation in order to achieve an equivalent efficiency of selection. To translate this result into a technique for seedling screening, elimination of 50% ($i = .80$) of the clones in the second clonal generation would be required to achieve an order of genetic gain comparable to that achieved by eliminating 96% ($i = 2.16$) of the clones in the first clonal generation.

Table 5. *Relative intensity of selection for three selection schemes*

	Individual selection	Family selection	Within-family selection
Maturity	1.62	1.19	1.87
Mark. yield	.98	1.54	.88
No. mark. tubers	1.84	3.39	1.66
Av. wt. mark. tubers	1.87	1.43	2.06
Total yield	1.54	1.86	1.46
Total no. tubers	2.69	2.04	3.01
Av. tuber wt.	1.19	1.42	1.12

Discussion

The breeding of many asexual crops such as potato, sweet potato, sugarcane, usually begins with a population of many thousands of clones. Heavy screening of clones in the first trial, sometimes up to 90% of the population, is routinely practiced to reduce the number of genotypes so that the merit of the selected ones can be evaluated more accurately in later generations. The criteria for selection may be based solely on visual discrimination or alternatively on some easily scored traits. Few investigations have been carried in the past to reconcile the practice of discarding the bulk of the genotypes when the clones

are still being managed in an unconventional cultivation system. Most quantitative genetic analyses for asexual crops (e. g., Keller and Likens, 1955; Burton and Devane, 1953) measured heritability by intra-class correlation coefficient following analysis of variance of identical trials conducted over a sample of environments. In the present case, the different environmental conditions between the early clonal generations would cause the variances due to environmental and genotype-environmental interaction effects to be heterogeneous for clones grown in these generations. Hence, it is doubtful if the analysis of variance approach is a suitable method. The present study, which estimates genetic parameters following analysis of variance for data within a trial and analysis of covariance for data between two trials, may circumvent such a problem.

It is proposed that, based on the results of analyses of variance and covariance of the first and second clonal generation trials, the regression type of heritability of a quantitative trait is measured in standard units and the expected response to selection is expressed by the physical units compiled in the second clonal generation trial. This ensures that both parameters are comparable to those measured directly from the results of analysis of variance of the second clonal generation trial and thus offers a chance to compare the genetic advance between selection in the first clonal generation and that in the second clonal generation.

Another aspect of the present approach is that it considers only the total genotypic effect of a clone which is transmitted from one generation to another. No further partition of a genotypic effect is attempted in the method, since a superior genotype can be maintained by means of clonal propagation in the asexually reproduced crop. According to Hanson (1963), the method measures heritability in a broad sense. The reference unit of measurement is the physical unit of a trait used in the second clonal generation trial.

The results obtained from analysis of the potato data are helpful in establishing efficient breeding

methods. First of all, individual or mass selection offers the best selection method for those with the seven studied traits whether applied in the first or the second clonal generation. Both standard unit and variance component estimates of heritability have shown the highest values based on cross means of the seven traits. But the expected response to family selection was the lowest for any of the seven traits among the three selection schemes. This was apparently because of the rather small amount of genetic variability for cross means.

Considering the best selection method, i. e., individual selection, five out of the seven traits showed a much lesser gain from selecting seedlings in the first clonal generation than in the second clonal generation (Table 4). If a 50% screening rate is used for direct selection in the second generation, the rate required to obtain an equivalent efficiency for selection in the first clonal generation should be approximately 75,

50, 81, 80, 74, 96 and 58% for maturity, yield, number and average weight of marketable tubers; and yield, number and average weight of all tubers, respectively, based on results in Table 5. A heavy rate of screening reduces the chance of retaining the superior genotypes through the later stage of selection when more accurate identification procedures are employed.

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Appendix 1. Parental combinations of the 25 potato crosses

Cross No.	Parental combinations	Cross No.	Parental combinations	Cross No.	Parental combinations
4844	Grand Falls × F51013	4877	F60053 × F63054	4894	Majestic × F58050
4846	F47024 × Lenape	4880	F62008 × 96–56	4899	96–56 × Lenape
4857	F53048 × F47024	4881	F62008 × F51013	4901	Bake-King × F58050
4860	F53048 × F58050	4882	F62008 × F63054	4902	Bake-King × Lenape
4861	F53048 × Lenape	4883	F62042 × 96–56	4908	USSR # 32 × Penobscot
4870	F58010 × F51013	4884	F62042 × Lenape	4917	Majestic × Lenape
4871	F58010 × F61101	4890	Grand Falls × F61101	4918	Monona × Lenape
4872	F58010 × Monona	4891	Grand Falls × Lenape		
4876	F60053 × F51013	4892	Kennebec × Katahdin		

Appendix 2. Performances of 17 parents* and means of 499 clones for seven horticultural traits in the 1970 field trial

	Maturity (1–5)	Mark. yield (Kg/plot)	No. mark. tubers (No./plot)	Av. wt. mark. tuber (Kg/tuber)	Total yield (Kg/plot)	Total tuber no. (No./plot)	Average tuber wt. (Kg/tuber)
Kennebec	4.5	9.86	49.0	.201	12.87	93.7	.137
Katahdin	4.7	6.17	32.5	.189	9.06	74.5	.121
Grand Falls	4.7	9.40	39.0	.241	12.92	82.7	.156
Penobscot	4.6	5.69	32.0	.177	9.73	87.7	.110
Bake-King	4.6	7.43	34.3	.216	10.12	69.3	.146
Lenape	4.6	5.47	31.0	.176	8.07	69.7	.115
96–56	3.1	6.21	30.3	.204	9.37	75.3	.124
F47024	4.6	6.66	31.5	.211	8.98	66.5	.135
F51013	3.6	7.85	35.5	.221	9.97	64.3	.155
F53048	4.5	6.06	32.7	.185	9.16	67.7	.135
F58010	4.4	5.58	26.3	.212	8.85	76.5	.115
F58050	3.9	4.44	23.5	.188	8.44	75.5	.111
F60053	3.0	7.74	35.7	.216	9.30	53.5	.173
F61101	4.6	6.47	29.7	.217	9.68	74.5	.129
F62008	4.9	7.17	25.7	.278	9.53	60.5	.157
F62042	4.7	5.87	30.5	.192	8.72	69.5	.125
F63054	3.9	6.49	30.7	.211	8.59	62.0	.138
Mean of C ₂ clones	4.3	5.28	27.7	.190	8.82	86.5	.104

* The parents Majestic, USSR # 32, and Monona were not included in the 1970 trial.

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