Diallel Analysis and Least Square Estimators of Genetic Parameters

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Individual effects of genes controlling quantitative traits can not ordinarily be distinguished from one another. Consequently, it is not possible to determine the mode of inheritance for single genes. By studying their combined effectsin segregating generations, however, one can gain some insight into their behavior and can make statistical inferences about their average gene action.

The investigation reported herein was to extend genetic variance components and variance and covariance analyses, special attention was given to the genetic statistics from which least square estimators of genetic parameters are obtained.

Theory

The genotypes II, ii and I$_i$ at the i^{th} locus have phenotypes $c+d_i$, $c-d_i$ and $c+h_i$ respectively where c is constant, $d_i>0$ and h_i may take either sign. Let us represent the genotype by variable θ_i which takes the value $1, -1$ and 0 respectively, so that the phenotype is the polynomial $c+d_i\theta_i+h_i(1-\theta_i^2)$. When the genotype controlling character is the set, $\theta=(\theta_1, \theta_2, \ldots, \theta_k)$, and when genes at non-homologus loci act independently, the phenotype is

$$\sum_{i=1}^{k}\{d_i\theta_i+h_i(1-\theta_i^2)\}$$

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Some general results of this representation are:

1. Since $\theta_i^3=\theta_i$, $\sum_i\{d_i\theta_i+h_i(1-\theta_i^2)\}$ is the most general polynomial involving $\theta_1, \theta_2, \dots, \theta_k$ independently, and excludes products like $\theta_i\theta_j$.
2. The individual with genotype θ produces gametes containing I and i in the freguencies $\frac{1}{2}(1+\theta_i)$ and $\frac{1}{2}(1-\theta_i)$.
3. The cross $\theta'\times\theta''$ produces progeny II, ii and Ii in the frequencies $\frac{1}{4}(1+\theta_i')(1+\theta_i'')$, $\frac{1}{4}(1-\theta_i')(1-\theta_i'')$ and $\frac{1}{2}(1-\theta_i'\theta_i'')$.
4. In the progeny of the cross $\theta'\times\theta''$ the expectation of θ_i and $1-\theta_i^2$ are $\frac{1}{2}(\theta_i'+\theta_i'')$ and $\frac{1}{2}(1-\theta_i'\theta_i'')$. The expected mean phenotype of these progeny is thus

$$\frac{1}{2}\sum_i\{d_i(\theta_i'+\theta_i'')+h_i(1-\theta_i'\theta'')\}.$$

The genotypes of the offspring in the $n\times n$ diallel cross are determined by the parental genotypes which are also the genotypes corresponding to the leading diagonal of the diallel table. The parents are assumed to be homozygous with u_i and $v_i(u_i+v_i=1)$ as the frequencies of parents with positive and negative homozygotes at the i^{th} locus. Thus $\theta_i=1$ in nu_i parents and $\theta_i=-1$ in nv_i parents. The mean of θ_i is $u_i-v_i=w_i$. Also $\theta_i^2=1$ and var $\theta_i=1-w_i^2=4u_iv_i$. Since the genes are assumed distributed independently in the parents $\mathrm{cov}(\theta_i, \theta_j)=0$ $(i=j)$.

Let the genotypes of the n parents be $\theta_r=(\theta_{r1}, \theta_{r2}, \dots, \theta_{rk})$ $(r=1, \dots, n)$ so that their phenotypes are $y_r=\sum_i d_i\theta_{ri}$ with mean $m_{.0}=\sum_i d_iw_i$. The progeny of $\theta_r\times\theta_s$ (or $\theta_s\times\theta_r$) all have the phenotype $y_{rs}=\frac{1}{2}\sum_i\{d_i(\theta_{ri}+\theta_{si})+h_i(1-\theta_{ri}\theta_{si})\}=\frac{1}{2}\sum_i\{(d_i-h_i\theta_{si})\theta_{ri}+d_i\theta_{si}+h_i\}$. The mean of all the progeny of θ_r is $\underline{\bar{y}_r}=\frac{1}{2}\sum_i\{(d_i-h_iw_i)\theta_{ri}+d_iw_i+h_i\}$ and the mean of the whole n^2

progeny is $m_{L1}=\sum_i\left\{d_iw_i+\frac{1}{2}h_i(1-w_i^2)\right\}$. The difference between the mean of the parents and the mean of their n^2 progeny is $m_{L1}-m_{L0}=\frac{1}{2}\sum_i h_i(1-w_i^2)$.

Consider the set of parents, the r^{th} array and the set of array means of the diallel table. The variance of the parents,

$$V_{0L0}=\underset{r}{\text{var}}\sum_i d_i\theta_{ri}=\sum_i d_i^2\text{var}\theta_{ri}=\sum_i d_i^2(1-w_i^2).$$

The covariance between the parents and their offspring in the r^{th} array,

$$W_{01L01}=\underset{s}{\text{cov}}\left[\sum_i d_i\theta_{si},\ \frac{1}{2}\sum_i\{(d_i-h_i\theta_{ri})\theta_{si}+d_i\theta_{ri}+h_i\}\right]$$

$$=\frac{1}{2}\sum_i d_i(d_i-h_i\theta_{ri})\ \underset{s}{\text{var}}\theta_{si}$$

$$=\frac{1}{2}\sum_i d_i(d_i-h_i\theta_{ri})(1-w_i^2)$$

The variance of the r^{th} array,

$$V_{1L1}=1/4\underset{s}{\text{var}}\sum\{(d_i-h_i\theta_{ri})\theta_{si}+d_i\theta_{ri}+h_i\}$$

$$=1/4\sum(d_i-h_i\theta_{ri})^2(1-w_i^2).$$

The covariance between the array means and the r^{th} array,

$$W_{01L1}=1/4\sum(d_i-h_i\theta_{ri})(d_i-h_iw_i)(1-w_i^2).$$

The means of the last three statistics are

$$W_{0L01}=1/2\sum d_i(d_i-h_iw_i)(1-w_i^2)$$

which is also the covariance between the parents and the means of their offspring,

$$V_{1L1}=1/4\sum(d_i^2-2d_ih_iw_i+h_i^2)(1-w_i^2),$$

and $V_{0L0}=1/4\sum(d_i-h_iw_i)^2(1-w_i^2)$

which is also the variance of the means of the arrays.

The statistics in the above may be written in a form similar to that used by Mather and Jinks [5] as

$$V_{0L0}=D$$

$$W_r=1/2D-1/4F_r$$

$$W_{0L01}=1/2D-1/4F$$

$$V_r=1/4D-1/4F_r+1/4H_1$$

$$V_{1L1}=1/4D-1/4F+1/4H_1$$

$$V_{0L1}=1/4D-1/4F+1/4H_1-1/4H_2$$

and $$m_{L1}-m_{L0}=1/2h \qquad (1)$$

where $$D=\sum d_i^2(1-w_i^2)$$

$$F_r=2\sum d_ih_i\theta_{ri}(1-w_i^2)$$

$$F=2\sum d_ih_iw_i(1-w_i^2)$$

$$H_1=\sum h_1^2(1-w_i^2)$$

$$H_2=\sum h_i^2(1-w_i^2)^2$$

and $$h=\sum h_i(1-w_i^2)$$

Quantitatively we may consider any degree of dominance (measured by $|h_i|/d_i$ at the i^{th} locus), the dominant homozygote deviating from the mid-homozygote in the same direction as the heterozygote so that $h_i\theta_i=|h_i|$. Similarly $h_i\theta_i=-|h_i|$ for the recessive homozygote. ($|h_i|$ means the positive value of h_i.)

In the diallel cross an overall measure of dominance is provided by $(H_1/D)^{1/2}$, the square root of the ratio of weighted means of h_i^2 and d_i^2. If we define the completely dominant parent to be the parent carrying the dominant homozygotes of all the genes and the completely recessive parent that carrying all the recessive homozygotes then, for the complete dominant,

$$V_D=1/4\sum(d_i-h_i)^2(1-w_i^2)$$

and for the complete recessive

$$V_R=1/4\sum(d_i+h_i)^2(1-w_i^2).$$

Now, unless the degree of dominance, $|h_i|/d_i$, of every gene is the same, (V_D, W_D) and (V_R, W_R) lie just inside the parabola. However, assuming that the points where the straight line cuts the parabola correspond to the completely dominant and recessive parents, it is found that

$$(V_D, W_D)=V_{0L0}X_1^2, V_{0L0}X_1)$$

and $(V_R, W_R) = (V_{0L0}X_2^2, V_{0L0}X_2)$
where x_1 and x_2 are the roots of $V_{0L0}X^2 - V_{0L0}X + W_{0L01} - V_{1L1} = 0$.

Suppose that the parent θ_r contains k_rD dominant genes and k_rR recessive genes. Then, with certain restrictions about equality of gene effects, $k_rD/k_rR = (V_R - V_r)/(V_r - V_D)$ = the ratio of the lengths of the two segments into which the point (V_r, W_r) divides the chord joining (V_R, W_R) to (V_D, W_D). The ratio of the total numbers of dominant to recessive genes in all the parents is

$$\frac{k_D}{k_R} = \frac{V_R - V_{1L1}}{V_{1L1} - V_D} = \frac{(4DH_1)^{1/2} + F}{(4DH_1)^{1/2} - F}$$

An estimate of the summed value of h_i is $2(m_{L1} - m_{L0}) = h = h_i(1 - w_i^2)$. In general, this underestimates mean dominance because positive and negative values of h_i cancel out, but its sign does show whether positive or negative dominants are in the majority, or which exhibit the greatest degree of domince.

Let k_+ and k_- be the number of groups of genes distributed independently in the parents for which the dominance is respectively positive and negative. Then $h^2/H^2 = (k_+ - k_-)^2/(k_+ + k_-)$ again with certain restrictions about equality of gene effects.

The sign of h gives the mean direction of dominance. A measure of association between the signs of dominant genes is the correlation between parental size and parental order of dominance. The parental measurement, y_r, is closely correlated with the number of positive homozyotes in the parent while $(W_r + V_r)$ bears the same relation to the number of recessive homozygotes.

Components of Variation

Interaction among environmental fluctuations and the genotypes in a diallel cross is revealed by heterogeneity of the variances within parental and F_1 families. Such heterogeneity may be handled in at least three cases.

(1) when the sole source of heterogeneity is a difference between parental and F_1 variances the environmental variances of y_r and y_{rs} $(r=s)$ may be denoted by E and $1/2E'$ respectively. E is estimated from differences between duplicate plots, E' is estimated from same source or from reciprocal differences, and the factor of 1/2 compensates for the replacement of each pair of measurements of reciprocals by their common mean. With the environmental expections included the equation of 1 become

$$
\begin{aligned}
&V_{0L0}=D+E\\
&W_r=1/2D-1/4F_r+E/n\\
&W_{0L01}=1/2D-1/4F+E/n\\
&V_r=1/4D-1/4F_r+1/4H_1+(E+1/2(n-1)E')/n\\
&V_{1L1}=1/4D-1/4F+1/4H_1+(E+1/2(n-1)E')/n\\
&V_{0L_1}=1/4D-1/4F+1/4H_1-1/4H_2+(E+1/2(n-2)E')/n^2\\
&(m_{L1}-m_{L0}{}^2=1/4h^2+(n-1)((n-1)E+E')/n^3.
\end{aligned}
\qquad (2)
$$

(2) when each F_1 variance can be expressed as the sum of two components corresponding to its parents those of the above equations which are independent of r hold with $E=E'=$overall mean family variance.

(3) when a trend exists between all the L_1 family means and variances the genotype-environment interaction may be removed by rescaling.

In obtaining the least squares solution of the above equations we omit W_{0L01} and V_{1L2} and weight with a factor $n^{1/2}$ the equations for V_{0L1} and $(m_{L1}-m_{L0})^2$ and the estimates of E since these three statistics depend on all the measurements of the diallel table. The solution is

$$
\begin{aligned}
&\hat{D}=V_{0L0}-E\\
&\hat{F}=2V_{0L0}-4W_{0L01}-2(n-2)E/n\\
&\hat{H}_1=V_{0L0}-4W_{0L01}+4V_{1L1}-(3n-2)E/n\\
&\hat{H}_2=4V_{1L1}-4V_{0L1}-2E\\
&\hat{h}^2=4(m_{L1}-m_{L0})^2-4(n-1)E/n^2\\
&\hat{F}_r=2(V_{0L0}-W_{0L01}+V_{1L1}-W_r-V_r)-2(n-2)E/n
\end{aligned}
\qquad (3)
$$

where we have used W_{0L01} and V_{1L1} for the means of W_r and V_r. The estimates of D, F, H_1, H_2 and h^2 are the same as in the exact solution. Only the estimate of F_r is new, and it shows that (W_r+V_r), and not just V_r or W_r, provides the better measure of dominance order.

The expected values of the statistics, derived from the estimates of the components, are identical with the observed values for V_{0L0}, V_{0L1}, $(m_{L1}-m_{L0})^2$ and E, but

$$\hat{W}_r=1/2(W_{0L01}-V_{1L1}+W_r+V_r)$$

and $$V_r=1/4(-W_{\overline{0L}01}+V_{1L1}+W_r+V_r)=1/2\{\sum(W_r-V_r)^2-n(W_{0L01}-V_{1L1})^2\}$$

so that the residual sum of squares with $n-1$ degrees of freedom. The mean square, $s^2=1/2$ var $(\mathrm{W}_r-\mathrm{V}_r)$. The covariance matrix of $\hat{D}, \hat{F}_r, \hat{H}_1, \hat{H}_2, \hat{h}_2$ and $\hat{E}$ is the inverse of the matrix of the coefficients of these components in the least square equations and, as the important components are D, F, H_1, H_2, h^2 and E, the covariance matrix may be contracted to refer only to these quantities.

Tests for Validity of the Assumptions in the Diallel

A consequence of those assumptions is that W_r-V_r is constant, i.e. independent of r. We therefore expect that failures of the assumptions may upset this constancy, and this is borne out in the investigations below. Heterogeneity of W_r-V_r is thus a good indication of such failures. Homogeneity of W_r-V_r, while always implied by the validity of the assumptions, may also be attained in certain cases of balanced failure. Two tests for heterogeneity of W_r-V_r are available.

(1) When the experimenter is replicated the variance of W_r-V_r may be analyzed for line and replication differences. A significant line effect indicates failure of the assumptions.

(2) A test which is useful when the experiment is not replicated depends on the (V_r, W_r) graph. This is not a line slope if W_r-V_r varies. To provide a test which gives equal weight to both W_r and V_r the axes of

the graph are rotated through 45 degree so that the coordinates of points become proportional to W_r+V_r and W_r-V_r. The t-testing of the significance of regression in the new axes is given by

$$t^2=\frac{n-2}{4}\cdot\frac{(\mathrm{Var}V_r-\mathrm{Var}W_r)^2}{\mathrm{Var}V_r-\mathrm{Var}W_r-\mathrm{Cov}^2(V_r, W_r)} \text{ with } n-2 \text{ degrees of freedom.}$$

Significance indicates failure of the assumptions. The weakness of this test is that it only detects variation in W_r-V_r which is correlated with the dominance order of the parents. Variations which merely increases the scatter of points about the regression line without altering its slope can only be decected by the first test.

Results and Discussion

1. Validlty of assumptions

Assumptions of diallel analysis include (1) parental homozygosity, (2) normal diploid segregation, (3) no difference between reciprocal crosses, (4) no multiple alleles, (5) no linkage, and (6) no non-allelic genic interactions [1, 5]. The assumptions of (4), (5), and (6) were tested by the analysis of variance of the quantity (W_r-V_r) where W_r is the covariance of the members of the r^{th} array with their nonrecurrent parents, V_r is the variance of the members of the r^{th} array, and the r^{th} array includes the r^{th} parent as well as all the crosses in which it is involved. If the assumptions are valid, (W_r-V_r) is expected to be constant over arrays [3, 4].

Mean squares obtained from (W_r-V_r) values for each of ten agronomic traits are presented in Table 1. Mean squares for (W_r-V_r) attributable to arrays were not significant at 5 percent probability level for all the traits except for plant height in April, ear height in June and ear height in combined dates. This indicates that a partial failure of assumptions (4), (5), and (6) occurred only for plant height in April, ear height in June and ear height incombined dates. The non-significant mean squares for $(W_r - V_r)$ among other arrays indicated that assumptions (4), (5), and (6) were valid for those traits.

Table 1.

Analyses of Variance of $(W_r - V_r)$ Values for Plant Height(X_1), Ear Height (X_2), Ear Length(X_3), Shank Length(X_4), Ear Diameter(X_5), Cob Diameter (X_6), Kernel Depth(X_7), Weight with Husk(X_8), Weight Husked(X_9), and Mid-silking Days(X_{10}) for April, June, and Combined Dates

		M.S. (April)			M.S(Combined)		
Source	D.F.	X_1	X_2	X_3	X_1	X_2	X_3
Replication	1	56958.8*	14288.7	0.68	107677.5*	25034.5	0.48
Arrays($W_r - V_r$)	7	46734.0*	41895.7	0.74	22440.7	23063.8*	0.16
Error	7	9027.5	11663.3	0.85	6846.1	5081.2	0.26

		Mean Squares(June)									
Source	D.F.	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
Replication	1	58572.5	43408.9**	0.25	1.29	0.007	0.011	0.002	0.016	0.001	5.598
Arrays($W_r - V_r$)	7	12256.7	22163.1*	0.35	2.71	0.018**	0.008	0.003	0.007	0.002	3.947
Error	7	13933.1	3393.9	0.09	2.50	0.004	0.009	0.001	0.005	0.001	1.708

*, **Significant at P=.05, 01 respectively

2. Least square estimators

D is the additive genetic variance parameter which may also include a portion of the additive additive epistatic variance as well as the additive genetic variance itself. H_1 and H_2 are dominance genetic variance parameters which may include the dominance genetic variance, dominance x dominance epistatic variance, and additive x dominance variance as well as the portion of the additive x additive variance not included in D. F is an indicator of the relative frequency of dominant and recessive alleles in the parents and may take sign, whereas the other parameters are expected to be positive. Least square estimators of genetic variance components are presented in Table 2.

Table 2.

Mean Estimator of Genetic Variance Componets and Environmental Variances together with Their Standard Errors for Plant Height(X_1), Ear Height(X_2), Ear Length(X_3), Shank Length(X_4), Ear Diameter(X_5), Cob Diameter(X_6), Kernel Depth(X_7), Weight with Husk(X_8), Weight Husked(X_9), and Mid-silking Days(X_{10}) for April, June and Combined Dates

	April			Combined		
	X_1	X_2	X_3	X_1	X_2	X_3
D	355.8±70.7	689.1±66.8	1.70±0.44	446.7±63.0	700.5±50.2	1.44±0.19
F	225.1±167.0	384.0±157.8	1.57±1.03	214.0±149.0	263.5±118.7	1.34±0.47
H_1	1057.8±162.5	851.2±153.6	2.21±1.00	706.1±144.9	683.2±115.5	2.07±0.45
H_2	886.4±141.4	669.5±133.6	1.40±0.87	585.1±126.1	554.6±100.5	0.87±0.39
h_2	252.2±94.8	127.2±89.6	0.07±0.58	271.5±84.5	130.1±67.4	0.22±0.26
E	63.2±23.5	41.1±22.2	0.94±0.15	58.3±21.0	41.3±16.7	0.49±0.06

	June Planting				
	X_1	X_2	X_3	X_4	X_5
D	614.9±52.0	762.9±52.1	1.50±0.20	1.78±0.75	0.08±0.01
F	237.5±122.9	189.2±123.1	1.90±0.46	−1.16±1.77	0.03±0.02
H_1	622.1±119.6	582.4±119.8	4.17±0.45	1.24±1.72	0.09±0.01
H_2	513.0±104.1	515.3±104.2	2.08±0.39	1.31±1.50	0.06±0.01
h_2	248.0±69.8	81.9±69.9	0.22±0.26	1.44±1.00	0.03±0.01
E	73.0±17.3	38.2±17.3	0.32±0.07	3.25±0.25	0.01±0.00

	June Planting				
	X_6	X_7	X_8	X_9	X_{10}
D	0.035±0.0006	0.003±0.001	0.378±0.035	0.157±0.016	12.08±0.86
F	0.021±0.013	0.001±0.002	0.344±0.083	0.174±0.038	9.71±2.02
H_1	0.024±0.013	0.007±0.002	0.417±0.081	0.227±0.037	11.42±1.97
H_2	0.012±0.011	0.006±0.002	0.200±0.070	0.116±0.032	8.48±1.71
h_2	−0.001±0.007	0.002±0.001	0.033±0.047	0.024±0.022	14.60±1.15
E	0.014±0.002	0.002±0.000	0.027±0.012	0.014±0.005	1.16±0.29

All estimates of additive effects (D) and environmental variations (E) were significantly different from zero for April, June, and combined dates.

Estimates of the component of variation due to dominance effects (H_1 and H_2) were significantly different from zero except for shank length and cob diameter in June and ear length in April. This lack of significance was due to the lack of consistency of the estimates from replication to replication and to the large *t* value associated with the degrees of freedom. Since only one estimate of each parameter is possible for each replication, the number of estimates that can be made becomes a matter of practical concern. Because the number of replications that can be included is limited, degree of freedom are therefore small, and *t* values used for significance level on means are large, which in turn caused large calculated *t* values.

The parameter F was positive and significant for plant height, ear length, weight with husk, weight without husk, mid silking days in June and ear height in April whereas ear height, shank length, ear diameter, cob diameter, and kernel depth in June and plant height, and ear length in April were not significantly different from zero. Results indicated that the parents carried an excess of dominant genes for plant height, ear length, weight with husk, weight without husk, and mid-silking days in June and ear height in April.

Estimates of overall dominance effects of heterozygous loci (h^2) were significantly different from zero for the traits plant height, ear diameter, and mid-silking days in June, and plant height in April and plant height over combined dates.

Genetic ratios and heritability estimators are presented in Table 3. $(H_1/D)^{\frac{1}{2}}$ are weighted overall measures of the degree of dominance. Values between zero and one indicate partial dominance, a value of one indicate complete dominance, values above one indicate overdominance. It should be noticed that these are overall estimates of the degree of dominance, and that each individual cross does not necessarily display the same degree of dominance for the same trait.

The average frequency of negative and positive alleles in the parents were estimated by $(\bar{p}, \bar{q}=H_2/4H_1)$[4]. Estimates of the average frequency of negative vs. positive alleles at loci exhibiting dominance, showed that the positive and negative alleles were not distributed equally among the parents for each traits (Table 3). This provides information about those genes with some degree of dominance. When negative and positive alleles are distibuted equally among the parents, the quantity equals $\frac{1}{4}$.

Table 3.

Ratio of Components and Heritability for Plant Height(X_1), Ear Height(X_2), Ear Length(X_3), Shank Length(X_4), Ear Diameter(X_5), Cob Diameter(X_6), Kernel Depth(X_7), Weight with Husk(X_8), Weight Husked(X_9), and Mid-silking Days(X_{10}) for April, June and Combined Dates

	April			June		
Ratios	X_1	X_2	X_3	X_1	X_2	X_3
$(H_1/D)^{1/2}$	1.72	1.11	1.14	1.25	0.98	1.19
$\overline{p}\,\overline{q}=H_2/4H_1$	0.21	0.19	0.15	0.20	0.20	0.10
$K_D/K_R=(4DH_1)^{1/2}+F/(4DH_1)^{1/2}-F$	1.44	1.66	2.35	1.47	1.47	2.26
$K=h^2/H_2$	0.28	0.19	0.04	0.46	0.23	0.26
Heritability	0.25	0.52	0.28	0.38	0.54	0.35

	June Planting									
Ratios	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
$(H_1/D)^{1/2}$	1.00	0.87	1.67	0.83	1.06	0.83	1.50	1.05	1.20	0.97
$\overline{p}\,\overline{q}=H_2/4H_1$	0.20	0.22	0.12	0.26	0.15	0.12	0.19	0.12	0.12	0.18
$K_D/K_R=(4DH_1)^{1/2}+F/(4DH_1)^{1/2}-F$	1.47	1.33	2.22	0.44	1.44	2.09	1.24	2.53	2.70	2.40
$K=h^2/H_2$	0.48	0.15	0.10	1.09	0.48	−0.04	0.26	0.16	0.20	1.72
Heritability	0.48	0.58	0.30	0.10	0.49	0.38	0.17	0.68	0.59	0.66

The ratio of dominant to recessive genes, k_D/k_R, showed an excess of dominant alleles in the parents for all traits in both April, June and combined date except for shank length of June planting which showed excess of recessive alleles.

An estimate of the number of effective factors, K, that control the traits and exhibit dominance to some degree, showed that at least one effective factor controlled each trait except for shank length and mid-silking days of june planting. However, K is underestimated when the gene effects are not equal.

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