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Quantitative Genetic Analysis of Ten Characteristics in Sweet Corn (*Zea mays* L.)¹

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Abstract. Tassel date, silk date, plant height, ear height, shank length, husk extension, tip blanking, row number, ear length, and first ear weight were studied in a diallel involving 7 inbred sweet corn parents. Both general combining ability (GCA) and specific combining ability (SCA) were involved in the inheritance of all 10 characters. This was consistent for F₁ crosses in 2 years and for F₂ families. SCA variance (V_{SCA}) was larger than GCA variance (V_{GCA}) for ear length and first ear weight in the F₁ and ratios of V_{SCA}/V_{GCA} for these characters were slightly larger than 1.0. V_{GCA} was larger than V_{SCA} for all other characters in the F₁. Ratios of V_{SCA}/V_{GCA} ranged from .05 for row no. to .57 for plant height.

Variance ratios for most characters decreased in the F₂. The failure of some ratios to decrease in the F₂ was attributed to either differential interactions of GCA and SCA with environment or inadequate sampling of F₂ families. Genotype × year interactions influenced the expression of most characters. A greater portion of the genotype × year interaction was contained in estimates of SCA than in estimates of GCA. Heritability estimates from parent-progeny regression were generally larger than those from variance components, although these estimates were generally in close agreement.

The quantitative genetics of *Zea mays* has been extensively studied, but primarily in field corn types. Additional information, obtained for sweet corn, would be useful for the following characters of interest to sweet corn breeders: length of time from planting to anthesis (tassel date), length of time from planting to silk emergence (silk date), plant ht, ear ht, shank length, husk extension beyond the tip of the ear, tip blanking, no. of kernel rows, ear length, and first ear wt. Variation in each of these characters is continuous and assumed to be under quantitative genetic control.

Three characters, tip blanking, husk extension, and shank length, were of primary interest in this study. Tip blanking, the failure of kernels to develop at the tip of the ear, can be intensified by unfavorable environment or improper plant nutrition. However, tip blanking is genetically controlled and is expressed by inferior genotypes even when environmental and nutritional conditions are optimum. No reports on the inheritance of tip blanking have been found in the literature. Husk extension has been associated with resistance to the corn earworm [*Heliothis zea* (Boddie)] and dusky sap beetle (*Carpophilus lugubris* Murr.) in sweet corn and field corn (15), and with resistance to bird damage in field corn (19). Inheritance of husk extension has

been studied in limited populations of sweet and field corn (11, 15, 19). There have been no reported studies of the inheritance of length of the shank, the lateral branch that attaches the ear to the stalk.

The remaining characters have been studied extensively in field corn (1, 3, 5, 6, 11, 12, 14, 16, 17, 18, 20) but studies in sweet corn have been limited (2). They were included in this study to provide more information about inheritance in sweet corn germ plasm and to study their interrelationships with the characters of primary interest.

Our objectives were (1) to determine the relative importance of additive versus non-additive genetic variance for each of the 10 characters studied, (2) to compare the diallel analysis with covariance among relatives by comparing heritability estimates from variance components with those from parent-progeny regression, and (3) to determine the stability of types of genetic variance between years.

Materials and Methods

Diallel crosses among 7 sweet corn inbreds (Table 1) were made in 1973. F₂ seed was obtained by selfing the 21 F₁'s in 1974.

The parents and F₁'s were evaluated at Nampa, Idaho in 1974 using a randomized complete block design with 5 replications. They were reevaluated along with the 21 F₂'s in 1975 using the same design but 4 replications. Each plot in 1974 consisted of a row 457 cm long with plants spaced 23 cm within the row. Rows were 81 cm apart. Plot rows in 1975 were 610 cm long and each F₂ plot consisted of two rows. In 1974 it became apparent that the inbred parents could not compete equally with the more vigorous F₁ hybrids when randomized with them in the same block. Thus, the parents were replicated in separate blocks adjacent to the interrandomized F₁'s and F₂'s in 1975.

Character measurements were made on 10 equally competitive

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Table 1. Degree of inbreeding of sweet corn inbred lines included in the diallel.

Line	Inbred generation
320	S15
327	S10
362	S7
368	S8
372	S11
376	S7
T42-S	S7

plants in each parent and F₁ plot and on 20 plants in each F₂ plot. Characters measured were: tassel date (no. of days from planting until 50% of the plants in a plot were shedding pollen); silk date (no. of days from planting until 50% of the plants in the plot had silked); plant ht (distance in cm from the soil surface to the point of attachment of the lowest lateral tassel branch); ear ht (distance in cm from the soil surface to the butt of the uppermost ear); shank length (distance in cm from the butt of the ear to the point of attachment to the stalk); husk extension (distance in cm from the tip of the ear to the collar attaching the flag leaf of the longest husk sheath); tip blanking (distance in cm from the tip of the ear back to the last developed kernels); row no. (no. of kernel rows on each ear); ear length (distance in cm from the butt to the tip of the ear); first ear wt (bulk wt of 10 husked ears from each F₁ and parent plot, or 20 husked ears from each F₂ plot).

Plant and ear ht were measured 10 days past mid-silk. Re-measurement of several plots 25 days past mid-silk confirmed that extension growth had been completed at the time of the first measurement. The remaining characters were measured at 25 days past mid-silk when ears were just past the prime edible stage and dimensional ear characters had reached maximum.

Griffing's (7) method 4 – model I of the diallel analysis of variance was used to partition total genetic variation in the F₁'s and F₂'s into general combining ability (GCA) and specific combining ability (SCA). Plot means were used in the analyses of all characters except first ear wt, for which plot totals were used. The replication × crosses mean square was used as the error term to test significance of all other mean squares. Combining ability variance components (V) for single year data were extracted from mean squares based on expectations of mean squares given by Griffing (7).

The formula, $H = 2VGCA/2VGCA + VSCA + VE$, was used to obtain narrow sense heritability estimates from variance components of single year F₁ data. The formula, $H = 2VGCA/2VGCA + VSCA + 2VGCA \cdot y + VSCA \cdot y + VE$ was used for combined F₁ data. Variance components from F₂ data were used to obtain narrow sense heritability estimates by the

formula: $H = 2VGCA/2VGCA + 4VSCA + VE$. Regressions of F₂ on F₁ and F₁ on mid-parents were also used to estimate the heritability of each character.

The interactions of GCA and SCA with years were obtained by a combined analysis of 1974 and 1975 F₁ data. This analysis was patterned after those of Rojas and Sprague (13) and Matzinger, Sprague, and Cockerham (9). Because of the extreme differences between growing seasons and a later-than-normal planting date in 1975, years were considered as fixed. The expectations of mean squares used to derive components of variance and covariance are shown below.

Source	d.f.	Expectations of mean squares
Years (y)	1	
GCA	6	$VE + \bar{r}y(P-2)VGCA$
SCA	14	$VE + \bar{r}yVSCA$
Years × GCA	6	$VE + \hat{r}(P-2)VGCA \cdot y$
Years × SCA	14	$VE + \hat{r}VSCA \cdot y$
Reps (r) within years	7	
Error	140	VE

where \bar{r} = arithmetic mean of the number of replications
 \hat{r} = harmonic mean of the number of replications

Results

Combining ability. A diallel analysis of variance was calculated for each character on F₁ data for each year and on F₁ data from two years combined. Mean squares from the combined analyses only are shown in Table 2. Both GCA and SCA were significant at the 1% level for all characters indicating that both additive and non-additive genetic effects are involved. In addition, a related phase of this study (8) has indicated that reciprocal differences may also be involved in the inheritance of these characters.

Similar results were obtained from F₂ analyses (Table 3). GCA mean squares were significant at the 1% level for all characters. SCA mean squares were significant at the 1% level for all characters except tip blanking, which was significant at the 5% level.

Components of variance for GCA and SCA for each character from the 1974, 1975, and combined F₁ analyses, and the 1975 F₂ analysis are presented in Table 4, and ratios of VSCA/VGCA are shown in Table 5 to provide a measure of relative importance of GCA and SCA. GCA variance was larger than SCA variance (ratios <1) for all characters in the F₁ generation except ear length and first ear wt. The ratio was smallest for row no. and somewhat larger for characters such as plant ht, shank length, husk extension, and tip blanking. GCA in relation to SCA, in the F₁ generation, was larger for most characters in 1975 than in 1974. However, the reverse was true for ear length.

The ratio of VSCA/VGCA was expected to be smaller in the F₂ generation through loss of non-additive gene action with

Table 2. Mean squares from the combined analyses of variance² for 10 characters of 21 F₁ hybrids grown in 1974 and 1975.

Source	df	Tassel date	Silk date	Plant ht	Ear ht	Shank length	Husk extension	Tip blanking	Row no.	Ear length	First ear wt
Years	1	6118.12**	4912.03**	1576.45**	228.91**	373.18**	39.08**	.17	27.19**	.18	.003
Crosses	20	47.70**	69.33**	1059.47**	1280.38**	112.71**	33.89**	5.12**	45.04**	20.39**	.852**
GCA	6	137.85**	207.05**	2742.27**	3803.21**	323.71**	95.56**	13.97**	146.28**	44.02**	1.804**
SCA	14	9.06**	10.31**	338.27**	199.16**	22.28**	7.46**	1.34**	1.64**	10.27**	.444**
Years × Crosses	20	1.94*	4.47**	39.57	116.99**	6.89**	2.31**	.56**	1.77**	.56**	.030*
GCA × Years	6	1.70	9.57**	32.40	192.93**	5.66	5.58**	1.42**	3.23**	.86**	.006
SCA × Years	14	2.04*	2.28*	42.64	84.44**	7.41**	.91**	.19**	1.14**	.42**	.040**
Reps within years	7	2.57*	3.87**	90.55**	41.94	2.87	.29	.03	.61*	.24	.026
Error	140	1.04	1.12	31.51	22.37	2.64	.22	.08	.26	.14	.016

*, **Significant at 5% and 1% level of probability, respectively.

²Using Griffing's (7) method 4 – model 1.

Table 3. Mean squares from the diallel analyses of variance^z for 10 characters of 21 F₂ families grown in 1975.

Source	df	Tassel date	Silk date	Plant ht	Ear ht	Shank length	Husk extension	Tip blanking	Row no.	Ear length	First ear wt
Reps	3	.30	1.66	33.27	3.99	1.12	.66	.01	.88*	.12	.010
Crosses	20	21.99**	39.49**	507.48**	584.78**	42.87**	20.97**	2.23**	19.86**	7.49**	.288**
GCA	6	64.50**	123.19**	1390.04**	1645.14**	131.17**	60.28**	7.04**	64.21**	20.33**	.715**
SCA	14	3.77**	3.62**	129.24**	130.34**	5.02**	4.12**	.17*	.86**	1.99**	.105**
Error	60	.53	.88	23.71	19.37	1.03	.36	.08	.27	.19	.013

*, **Significant at 5% and 1% level of probability, respectively.

^zUsing Griffing's (7) method 4 – model I.

Table 4. Components of GCA and SCA variance (V) for 10 characters of sweet corn.

Character	1974 F ₁ analysis		1975 F ₁ analysis		Combined F ₁ analysis		1975 F ₂ analysis	
	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}	V _{GCA}	V _{SCA}
Tassel date	2.49	1.29	3.71	.79	3.04	.89	3.20	.81
Silk date	3.10	1.32	6.59	1.05	4.58	1.02	6.12	.68
Plant ht	52.90	48.63	69.17	23.11	60.24	34.08	68.32	26.38
Ear ht	90.83	35.35	87.08	18.84	84.02	19.64	81.29	27.74
Shank length	8.19	3.52	6.42	2.08	7.14	2.18	6.51	1.00
Husk extension	2.02	1.07	2.51	.72	2.12	.80	3.00	.94
Tip blanking	.27	.15	.42	.16	.31	.14	.35	.02
Row no.	2.87	.35	3.84	.16	3.24	.15	3.20	.15
Ear length	1.07	1.18	.94	1.17	.98	1.13	1.01	.45
First ear wt	.04	.05	.04	.05	.04	.05	.04	.02

Table 5. Ratio of SCA variance to GCA variance for 10 characters in sweet corn.

Character	1974 F ₁ analysis	1975 F ₁ analysis	Combined F ₁ analysis	1975 F ₂ analysis
	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}	V _{SCA} /V _{GCA}
Tassel date	.52	.21	.29	.25
Silk date	.43	.16	.22	.11
Plant ht	.92	.33	.57	.39
Ear ht	.39	.22	.23	.34
Shank length	.43	.32	.31	.15
Husk extension	.53	.29	.38	.31
Tip blanking	.55	.39	.45	.07
Row no.	.12	.04	.05	.04
Ear length	1.10	1.25	1.15	.45
First ear wt	1.31	1.23	1.20	.66

inbreeding. This was true for silk date, shank length, tip blanking, ear length, and first ear wt. This reduction was less evident for the other characters and for ear ht the ratio was substantially larger than in the corresponding F₁. This failure of the variance ratios for some characters to respond as expected in the F₂ analysis may be caused by a larger contribution of the genotype × environment interaction to SCA variance than to GCA variance as demonstrated in the combined F₁ analysis. Biased sampling of F₂ families (where plants with a preponderance of heterozygous loci for those characters were unintentionally selected for evaluation) could also be involved.

Interactions of GCA and SCA with years. GCA × years was significant at the 1% level for silk date, ear ht, husk extension, tip blanking, row no., and ear length (Table 2). SCA × years was significant at the 1% or 5% level for all characters except plant ht.

Mean squares for GCA × years were much smaller than mean squares for GCA main effects and even though most interactions were statistically significant, the interpretation of main effects is probably not substantially affected. Mean squares for SCA × years were, in some cases, relatively large in relation to those for SCA main effects. SCA effects must be interpreted with this

in mind.

The relationship between GCA and SCA over years was evaluated by comparing the ratio of V_{GCA·y}/V_{GCA} to the ratio of V_{SCA·y}/V_{SCA} (Table 6). For most characters, the ratio of V_{SCA·y}/V_{SCA} is substantially larger than the ratio of V_{GCA·y}/V_{GCA}, indicating that a substantial portion of the genotype × year interaction is contained in the estimate of SCA.

Heritability estimates. Narrow sense heritability estimates obtained from variance components and from parent-progeny regression were generally in agreement, although those from regression were usually larger (Table 7). Estimates within methods for an individual character were also in general agreement. However, for some characters such as tip blanking, regression estimates in 1974 were out of line with those in other years and generations. This may have resulted from unequal competition between parents and adjacent F₁'s in the common block in 1974. Several heritability estimates from regression were greater than 100% which indicates they were subject to sampling error.

These heritability estimates have not been evaluated by establishing a selection differential and comparing actual with predicted gain. The primary objective of calculating heritability in this study was to provide a means for comparing the results

Table 6. Variance components for GCA × years and SCA × years interactions and their ratios with GCA and SCA, respectively.

Character	V _{GCA•y}	V _{GCA•y}		V _{SCA•y}	
		V _{GCA}	V _{SCA•y}	V _{SCA}	V _{SCA•y}
Tassel date	.03	.010	.23	.253	
Silk date	.38	.083	.26	.256	
Plant ht	.04	.001	2.51	.074	
Ear ht	7.67	.091	13.97	.711	
Shank length	.14	.019	1.07	.492	
Husk extension	.24	.114	.15	.192	
Tip blanking	.06	.195	.02	.176	
Row no.	.13	.041	.20	1.293	
Ear length	.03	.033	.06	.057	
First ear wt	.002 ^z	—	.01	.112	

^zNegative variance component (−.0004) set to zero.

of the combining ability analysis with the method of covariance among relatives.

Heritabilities based on parent-progeny regression for the most part agree with the combining ability analysis. Relatively high heritability estimates by both methods indicate that genes acting in an additive manner are more important than non-additive gene interactions in the inheritance of most characters. However, larger heritabilities by regression for ear length and first ear wt in relation to heritabilities of other characters, may suggest that the importance of SCA for these characters was overestimated by the combining ability analyses.

GCA effects for individual lines were consistent from year to year and ranking of parents was the same whether GCA effects or parental means were used. SCA effects for individual crosses were not consistent from year to year. This was reflected in the relatively large interaction of SCA with years (Table 2).

Discussion

A fixed model was used in this study and the validity of extracting variance components may be questioned. These variance components are undoubtedly inflated by the variation due to reciprocal differences found in this material (8). This inflation would be slight because of the large differences in magnitude of variation due to reciprocals versus that due to GCA and SCA. It is recognized that some unknown biases are present in the estimates of these variance components, especially those obtained from F₂ data. However, the agreement between heritability estimates obtained from parent-progeny regressions and those obtained from variance components

indicate that these biases are not serious. It is possible that differential interactions of the non-vigorous parents, the vigorous F₁'s, and the variable F₂'s with the environment may render estimates obtained from parent-progeny regressions less reliable than those obtained from variance components.

Our estimates of genetic variance are in general agreement with results of others cited. Additive effects comprise a major portion of the genetic variation for tassel date, plant ht, ear ht, and row no., but non-additive effects are also important, indicating partial dominance. The relatively greater importance of non-additive effects for ear length found in this study was not reported by the majority of previous workers (5, 6, 11, 12, 20). Adjustment of SCA variance for the relatively large SCA × years interaction might bring this estimate into closer agreement with previous reports. This is not possible in this case because years must be considered fixed.

Variance estimates for first ear wt were comparable to those of Sprague and Tatum (16) for yield in previously selected field corn lines but were in opposition to those of Wright et al. (20) in a study of unselected material. The significant SCA × years interaction and nonsignificant GCA × years interaction may somewhat modify the indicated relationship between GCA and SCA variances. Ear diameter, not measured in this study, could also affect the expression of first ear wt.

Variance estimates for characters receiving little or no previous study (shank length, husk extension, and tip blanking) were in line with results for other characters. The ratios of additive to non-additive effects are roughly comparable to trends for plant and ear ht. Additive effects comprise most of the genetic variation but non-additive effects are important for all 3 characters.

Comparisons of F₁ analyses in individual years with F₁ analyses of combined data validates Gardner's (4) warning that gene action estimates based on experiments conducted in a single environment will be biased upward because of the genotype × environment interactions contained in estimates of genotypic effects. The conclusion that SCA estimates, for most characters, are inflated more by genotype × year interactions than are GCA estimates, is in agreement with the results of Rojas and Sprague (13) but in conflict with the results of Matzinger et al. (9). However, Matzinger et al. (9) were studying material previously unselected while the materials in both this study and that of Rojas and Sprague (13) were highly selected.

General support for the greater importance of additive effects found in this study is contained in a recent comprehensive review by Moll and Stuber (10). These authors reviewed the results of experiments to estimate genetic variance in a wide

Table 7. Heritability estimates (%) for 10 characters of sweet corn calculated by: 1) regression of progeny on parents, and 2) components of variance from the analyses of variance.

Character	Regression			Variance components			
	1974 F ₁	1975 F ₁	1975 F ₁	1974 F ₁	1975 F ₁	Combined	
	on mid-parent	on mid-parent	on F ₂			F ₁	1975 F ₂
Tassel date	77.1 ± 11.0 ^z	90.1 ± 8.7	87.6 ± 8.1	64.9	84.7	73.3	62.9
Silk date	62.8 ± 11.2	107.6 ± 9.1	88.1 ± 8.6	69.5	88.0	74.3	77.2
Plant ht	50.8 ± 21.2	71.1 ± 20.8	88.3 ± 10.7	56.4	72.5	63.9	51.4
Ear ht	113.6 ± 20.2	119.0 ± 21.2	88.7 ± 10.2	74.8	82.6	70.2	55.5
Shank length	142.4 ± 26.4	122.2 ± 29.9	86.2 ± 9.0	70.3	77.7	69.8	72.2
Husk extension	88.4 ± 18.6	86.2 ± 12.9	102.2 ± 9.4	75.8	84.4	71.8	59.3
Tip blanking	34.5 ± 11.6	76.6 ± 11.0	75.1 ± 9.5	68.0	79.2	62.7	80.7
Row no.	98.1 ± 7.4	112.9 ± 9.1	88.3 ± 5.5	90.3	94.9	88.1	88.2
Ear length	102.3 ± 18.3	72.3 ± 16.0	81.4 ± 9.4	61.6	59.4	58.3	50.3
First ear wt	87.1 ± 23.6	81.0 ± 16.6	75.9 ± 8.8	54.1	55.0	53.6	40.0

$$z_{sb} = \sqrt{\frac{sy^2 - (s_{xy})^2 / (n-2)s_x^2}{s_x^2}}$$

where sb is the standard error of the regression coefficient, s_y² is the sum of squares of the progeny, s_{xy} is the sum of cross products, and s_x² is the sum of squares of the parents.

range of crop species. Additive genetic variance has been found to be relatively more important than non-additive genetic variance for most characters in a range of crops including cross-pollinated species, self-pollinated species, and polyploid species.

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Cluster-thinning 'de Chaunac' French Hybrid Grapes Improves Vine Vigor and Fruit Quality in Ontario¹

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Abstract. Cluster-thinning of the French hybrid grape cultivar 'de Chaunac' (*Vitis* sp.) resulted in superior fruit quality and an increase in vigor of the vines in comparison to the unthinned vines in a similar pruning and management regime. The higher sugar levels associated with thinning are consistently desirable for wine making under Ontario conditions. The favorable test site used limited the expression of vine decline and winter injury usually associated with over-cropping of this cultivar in the Niagara Peninsula of Ontario.

Introduction of French direct-producer hybrid grapes to Ontario in the 1950's was part of a program to broaden the base of the wine industry in the province. Bradt (3,4) reported that among the most promising of these was 'de Chaunac' (Seibel

9549), a blue grape of complex genetic background, including *Vitis vinifera* L., *V. labrusca* L., *V. riparia* L. and others (1).

Differences in the response to management practices may be inferred from reports on *V. vinifera* L. and *V. labrusca* L. (8, 9, 10, 11) which might influence the choice of practices to apply to those direct-producer hybrids prone to winter injury (1). The cultivar 'de Chaunac' has a tendency to overbear, weakening the vine and risking winter injury and reduced productivity. Studies on the effect of pruning and cluster-thinning on 'de Chaunac' were begun at the Horticultural Research Institute of Ontario Grape Substation at Beamsville, Ontario. Both techniques have been widely used in grape production in North America (10, 11, 12, 13, 14) and the growth habit of this cultivar suggested a potential response to both.

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