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## Genetic Parameters Estimated for an Advanced-cycle Strawberry Breeding Population at Two Locations

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**Abstract.** Strawberry (*Fragaria* × *ananassa*) seedlings were evaluated for yield, fruit weight, and commercial appearance in two field trials established in 1985 and 1986. Genetic analyses for unbalanced diallels were performed to quantify genetic, environmental, and interaction variance for each trial separately, and for crosses common to two locations in a single year. When data from crosses common to two test locations were analyzed simultaneously, narrow-sense heritabilities ( $h^2$ ) averaged 0.35 ( $\pm 0.11$ ), 0.21 ( $\pm 0.07$ ), and 0.08 ( $\pm 0.06$ ) for yield, fruit weight, and appearance score. Broad-sense heritabilities ( $H^2$ ) were 0.35 ( $\pm 0.11$ ), 0.27 ( $\pm 0.12$ ), and 0.21 ( $\pm 0.11$ ) for the same traits, respectively. These estimates do not differ significantly from heritabilities estimated from the ancestral breeding population 20 years ago. Estimates of  $H^2$  for single-location analyses were biased upwards by dominance × location interactions for all traits. Additive × location interactions were detected for appearance score and contributed a small bias to single-location estimates of  $h^2$ . Use of biased estimates in predicting genetic gain could lead to errors in choice of appropriate selection strategy.

Improved cultivars and cultural practices have contributed to the substantial improvements in production traits of strawberries in California over the past four decades (1). The objective of the Univ. of California breeding program is to develop new cultivars with improved performance, and adaptation to the superior environments created by improved cultural practices. Over time, successful selection is expected to alter the amount and distribution of genetic variation within the breeding population. Periodic assessments and information regarding directional change

in genetic parameters are important, because the effectiveness of different breeding, testing, and selection strategies depends on the availability and distribution of genetic variation.

Hansche et al. (7) estimated narrow-sense heritabilities for strawberry fruit yield, fruit weight, and a commercial appearance score as 0.48, 0.20, and -0.02, respectively, using data from a large sample of offspring-parent pairs collected in California between 1960 and 1966. They also compared estimates of genotypic and additive genetic variance, concluding that dominance effects were unimportant for yield, detectable for fruit weight, and large for appearance score. Conversely, Comstock et al. (3) and Spangelo et al. (11) have detected different patterns of inheritance for yield and fruit weight in cultivated strawberries, concluding that these traits are conditioned largely

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by genes with dominance effects. Several explanations for this discrepancy have been offered, including differences in genetic materials, cultural practices, and environments.

The studies cited above each used information from plantings established in a single year and location. Hansche et al. (7) used data from offspring-parent pairs collected in a single location but over several years, sampling more than a single environment both climatically and culturally; however, they could not estimate genotype  $\times$  environment (G $\times$ E) interactions variance. The objective of our study was to obtain information about genetic and environmental parameters that describe an advance breeding population, particularly with respect to the consequences of using different or multiple test environments. Heritabilities were also estimated to compare this population with its ancestral population.

### Materials and Methods

*Plant materials and cultural methods.* The advance breeding population studied was derived from the ancestral population described by Hansche et al. (7). The exact number of mass selection cycles separating the ancestral and present populations is difficult to quantify because generations are not discrete, and important parents have been included in more than one cycle.

Seedlings were planted at two locations in Sept. 1985 and 1986: Wolfskill Experimental Orchard (WEO) near Davis, Calif. and the Watsonville Strawberry Research Facility (WAT) located on the central coast of California. The environment at WEO differs from that of WAT, having colder winters (Jan. means of 7.5 vs. 10.0C) and warmer summers (June means 23.9 vs. 17.2C).

Seedlings from 63 and 66 biparental crosses among 18 parents were planted at WEO and WAT, respectively, in Sept. 1985. Fifteen of the crosses tested at WAT were reciprocals, so 51 unique full-sib families were used in further analyses. Twenty-eight of the full-sib families from 15 parents were common to both locations in the 1985 trial. Seedlings from 39 crosses among 15 parents were planted at WEO and WAT in 1986, with all crosses common to both locations. Five full-sib families among four of the parents were common to all four trials.

The parents of all crosses were a random sample of named cultivars and advanced selections from current California breeding populations. Inbreeding coefficients predicted from pedigrees (5) averaged 0.17 and 0.15 for the crosses tested in 1985 and 1986, respectively. None of the crosses were performed with parents that shared more than one grandparent (i.e., recent half-sibs), and the crosses approximate random mating among the parental genotypes, with avoidance of close inbreeding. Cumulative inbreeding coefficients estimated from complex pedigrees are poor predictors of genomic homozygosity when selection is performed each generation, and are included here as a reference to the relatedness among the parents used for estimation of genetic parameters.

Twenty seedlings chosen randomly from each cross were planted at WEO and 10 from each at WAT in 1985; 12 seedlings from each cross were planted at each location in 1986. The test designs differed between years; the 1985 trial was established using completely random plots of 10 plants, whereas seedlings for the 1986 trials were divided into two replicates, each with six seedlings, and planted in a randomized complete block design.

*Measurements and analyses.* Fruit from individual plants was harvested weekly during the spring following planting (1986

and 1987) for the first 12 weeks of production. Data were collected for fruit yield (g/plant), fruit number, and an appearance score. Fruit weight (g/fruit) was determined by dividing the total yield by the fruit number; appearance score results from subjective evaluation based on fruit size, shape, color, seed position, and various defects. This appearance rating was recorded on a scale of 1 to 5, where 5 = the highest quality rating (7).

The crosses established in each trial form a partially filled half-diallel design (6). Parents were represented by an average of 4.7 full-sib families each, and the minimum number of families per parent was three. Analyses of variance (ANOVA) and estimation of variance components for general combining ability (GCA) and specific combining ability (SCA) were performed for all trials using the least-squares procedure DIALL (9). Preliminary analyses indicated that reciprocal effects were not significant, and reciprocal data were pooled for further analyses.

Statistical tests were conducted for single-location analyses using the expected mean squares given in Table 1. Families common to both locations in a single year were analyzed for GCA, SCA, and GCA  $\times$  location interaction (G $\times$ L) effects using DIALL. To complete each two-location analysis, the SCA  $\times$  location interaction (S $\times$ L) sum of squares was determined by subtraction of the G $\times$ L sum of squares from family  $\times$  location interaction sum of squares obtained from a supplemental analysis using the SAS procedure GLM (8). Error degrees of freedom and sum of squares for the DIALL results were adjusted, and the form and expected mean squares for the two-location analysis is given in Table 2. These supplemental steps were necessary because the DIALL procedure pools S $\times$ L sums of squares into a combined error term. Estimates of variance components due to factors in the two-location analyses were obtained as linear functions of the expected mean squares in Table 2.

Translation of model variance components to causal components follows Hallauer and Miranda (6):

$$\sigma_A^2 = 4 (\sigma_{GC\Lambda}^2)$$

$$\sigma_D^2 = 4 (\sigma_{SC\Lambda}^2)$$

$$\sigma_{\Lambda \times L}^2 = 4 (\sigma_{G \times L}^2)$$

$$\sigma_{D \times L}^2 = 4 (\sigma_{S \times L}^2)$$

$$h^2 = [4(\sigma_{GC\Lambda}^2)]/[2(\sigma_{GC\Lambda}^2) + \sigma_{SC\Lambda}^2 + 2(\sigma_{G \times L}^2) + \sigma_{S \times L}^2 + \sigma_W^2]$$

$$H^2 = [4(\sigma_{GC\Lambda}^2 + \sigma_{SC\Lambda}^2)]/[2(\sigma_{GC\Lambda}^2 + \sigma_{SC\Lambda}^2) + 2(\sigma_{G \times L}^2) + \sigma_{S \times L}^2 + \sigma_W^2]$$

In the above equations,  $\sigma_A^2$ ,  $\sigma_D^2$ ,  $\sigma_{\Lambda \times L}^2$ , and  $\sigma_{D \times L}^2$  are estimates of variance components due to additive and dominance genetic effects, and additive and dominance by location interaction effects;  $\sigma_W^2$  is a residual error term that includes within-family genetic, interaction and experimental sources of variance;  $h^2$  and  $H^2$  are estimates of narrow-sense and broad-sense heritabilities. The assumptions necessary for translation of model variances into causal components and heritabilities have been discussed for strawberries by Comstock et al. (3) and by Shaw et al. (10) for the California breeding populations. The primary caution for this analysis relates to epistatic genetic variance for metric traits that has been detected in commercial strawberries (3,11). Epistatic components are not estimable with our experimental methods, but could bias heritability estimates either upwards or downwards, depending on which epistatic effects are

Table 1. Expected mean squares (EMS) for the analysis of variance of yield, fruit weight, and appearance score, with results from the two test locations considered separately.

Source <sup>z</sup>	df				EMS
	Wolfskill		Watsonville		
	1985	1986	1985	1986	
Replications	---	1	---	1	$\sigma_w^2 + k_1\sigma_R^2$
GCA	17	14	17	14	$\sigma_w^2 + k_2\sigma_{SCA}^2 + k_3\sigma_{CSA}^2$
SCA	48	24	33	24	$\sigma_w^2 + k_2\sigma_{SCA}^2$
Residual	1134	433	581	438	$\sigma_w^2$
<i>Coefficients<sup>y</sup></i>					
k <sub>1</sub>	---	237.0	---	240.0	
k <sub>2</sub>	18.5	11.7	12.4	12.0	
k <sub>3</sub>	123.0	57.7	67.8	57.9	

<sup>z</sup>GCA and SCA = general and specific combining ability, respectively.

<sup>y</sup>Coefficients for model components of variance.

important. Because most epistatic variance occurs within families (2) and because our estimates of genetic variance components use among-family comparisons, serious bias is not expected.

### Results

Yield and fruit weight were substantially greater for WAT than for WEO for both 1985 and 1986 trials, and means for these traits were larger for the 1985 than for the 1986 trials (Table 3). Average appearance scores were consistent across the four trials, ranging from 2.3 to 2.6. Between-year differences in trait means at a single location could result either from environmental effects or from genetic sampling, because different crosses were tested in each year. Trait means for the five families common to all trials were very similar to the trial means given in Table 3, (611, 1310, 530, and 799 g/plant; 10.8, 16.7, 9.2 and 11.8 g/fruit for the WEO 1985, WAT 1985, WEO 1986,

and WAT 1986 trials, respectively), suggesting that much of the difference was due to the effects of environment.

Statistically significant ( $P < 0.05$ ) GCA and SCA effects were detected for yield and fruit weight in all single-location analyses (Table 4) with the single exception of SCA for fruit weight in the WEO 1986 trial. GCA effects were significant for appearance scores in all single-location analyses, SCA effects for appearance were significant for only the 1985 trials.

A somewhat different pattern was detected for analyses that combine data from families common to both locations in a single year. GCA effects for yield and fruit weight remain significant, but SCA effects for these traits were nonsignificant in both years (Table 5). Genetic  $\times$  location ( $G \times L$  and/or  $S \times L$ ) effects for yield and fruit weight were significant. Therefore, some of the variance attributed to genetic effects in single-location analyses is recognized as interaction variance by two-location analyses.

Results for two-location analyses of appearance scores were less consistent than for yield and fruit weight. Significant SCA effects were detected for the 1985 trials and GCA effects were significant for the 1986 trials (Table 5).  $G \times L$  interaction effects were significant for appearance score in both years, whereas  $S \times L$  effects were significant only for the 1986 trials. Also, location effects were highly significant for yield and fruit weight, but were nonsignificant for appearance in both years.

Narrow-sense heritabilities estimated for yield at both locations in 1985 and 1986 ranged from 0.26 ( $\pm 0.12$ ) to 0.38 ( $\pm 0.18$ ) for single-location analyses and were consistent with those estimated for corresponding two-location analyses—0.34 ( $\pm 0.19$ ) and 0.36 ( $\pm 0.11$ ) for the 1985 and 1986 trials, respectively (Table 6). Conversely, broad-sense heritabilities for yield were large for single-location analyses, ranging from 0.61 ( $\pm 0.23$ ) to 0.87 ( $\pm 0.29$ ), but were much smaller [0.34 ( $\pm 0.19$ ) and 0.36 ( $\pm 0.11$ )] for two-location analyses. Single-location estimates of  $H^2$  were biased upwards by  $G \times L$  interaction variance, which can be estimated and eliminated from heritability estimates only for multiple-location analysis (4). Single-location estimates of  $h^2$  for yield did not differ from two-location esti-

Table 2. Expected mean squares (EMS) for the analysis of variance of yield, fruit weight, and appearance score, with results from the two test locations considered simultaneously.

Source <sup>z</sup>	df		EMS
	1985	1986	
Location (L)	1	1	$\sigma_w^2 + k_1\sigma_{S \times L}^2 + k_2\sigma_{G \times L}^2 + k_3\sigma_{R(L)}^2 + k_4\sigma_L^2$
Replications/L	---	2	$\sigma_w^2 + k_5\sigma_{R(L)}^2$
GCA (G)	12	14	$\sigma_w^2 + k_1\sigma_{S \times L}^2 + k_2\sigma_{G \times L}^2 + k_3\sigma_{SCA}^2 + k_4\sigma_{GCA}^2$
SCA (S)	14	25	$\sigma_w^2 + k_1\sigma_{S \times L}^2 + k_3\sigma_{SCA}^2$
$G \times L$	12	14	$\sigma_w^2 + k_1\sigma_{S \times L}^2 + k_2\sigma_{G \times L}^2$
$S \times L$	14	25	$\sigma_w^2 + k_1\sigma_{S \times L}^2$
Residual	586	859	$\sigma_w^2$
<i>Coefficients<sup>y</sup></i>			
k <sub>1</sub>	11.7	12.0	
k <sub>2</sub>	42.6	57.2	
k <sub>3</sub>	23.9	23.4	
k <sub>4</sub>	90.6	115.4	
k <sub>5</sub>	---	238.4	
k <sub>6</sub>	328.0	476.0	

<sup>z</sup>GCA and SCA = general and specific combining ability, respectively.

<sup>y</sup>Coefficients for model components of variance.

Table 3. Means and SDs for yield, fruit weight, and appearance score at Wolfskill (WEO) and Watsonville (WAT).

Trait	Location	1985 Trial		1986 Trial	
		Mean	SD	Mean	SD
Yield (g/plant)	WEO	536	236	499	223
	WAT	1191	486	788	365
	Both	804	403	644	335
Fruit weight (g/fruit)	WEO	10.7	2.4	9.8	2.1
	WAT	17.2	4.1	12.7	3.3
	Both	13.8	4.5	11.2	3.1
Appearance score	WEO	2.57	0.34	2.42	0.42
	WAT	2.55	0.39	2.28	0.47
	Both	2.59	0.37	2.37	0.49

mates only for multiple-location analysis (4). Single-location estimates of  $h^2$  for yield did not differ from two-location estimates because  $G \times L$  variance resulted primarily from the interaction of dominance genetic and location effects ( $\sigma_{S \times L}^2$ , Table 5).

Heritabilities estimated for fruit weight followed a pattern similar to that detected for yield, with  $h^2$  ranging from 0.13 ( $\pm 0.07$ ) to 0.34 ( $\pm 0.12$ ) and  $H^2$  from 0.14 ( $\pm 0.08$ ) to 0.53 ( $\pm 0.19$ ) for all test-location combinations (Table 6). Estimates of  $h^2$  averaged 0.25 for single-location and 0.21 for two-location analyses, whereas  $H^2$  averaged 0.42 and 0.27 for corresponding comparisons (see Table 6). Both  $A \times L$  and  $D \times L$  effects contribute to bias in single-location heritability estimates for fruit weight with the latter causing substantially larger bias.

The genetic interpretations of two-location heritabilities for yield and fruit weight differ:  $H^2$  estimated for fruit weight was larger than  $h^2$  and SCA effects were significant in both years

(Table 5), whereas no differences were detected for yield. Significant SCA effects indicate the presence of dominance variation independent of  $D \times L$  interactions.

Estimates of  $h^2$  for appearance score range from 0.10 ( $\pm 0.06$ ) to 0.42 ( $\pm 0.18$ ) for single-location analyses and were small [0.0 ( $\pm 0.09$ ) and 0.16 ( $\pm 0.08$ )] for 1985 and 1986 two-location analyses, respectively. Dominance effects were detected for the 1985 trials, but not for the 1986 trials. All two-location heritability estimates for appearance were smaller than corresponding single-location estimates and the biased results from both additive and  $D \times L$  interactions.

## Discussion

Heritability estimates obtained from two-location analyses averaged over both years were similar to those estimated for the ancestral population by Hansche et al. (7). Estimated  $h^2$  for yield was 0.35 ( $\pm 0.11$ ) for our study, slightly smaller than the 0.48 estimated for the ancestral population, but this difference was not significant. Our estimates of  $h^2$  for fruit weight and appearance score ( $0.21 \pm 0.07$  and  $0.08 \pm 0.06$ ) were not substantially different from those estimated 20 years ago (0.20 and  $-0.02$ ). The genetic variation available for further improvement of the traits studied appears similar to that for the ancestral population, despite changes in cultural practices and a history of intensive selection with little infusion of new germplasm.

The absence of detectable dominance effects for yield and detection of small dominance effects for fruit weight is consistent with results obtained for the ancestral population (7), but differs from the results of similar studies of genetic variation in breeding populations of commercial strawberries in other locations (3, 11). Two-location analyses demonstrate that environments can have a large effect on estimates of genetic parameters when  $G \times E$  interaction effects are important, and may offer a partial explanation for the above discrepancy. Our results, interpreted for any single location and year, would not differ substantially from those of the other studies cited.

Interactions resulting from differences in scale across locations affect heritability, and thus the potential for predicting

Table 4. Analysis of variance for yield, fruit weight, and appearance score, with the results for each location considered separately.

Trait	Source <sup>a</sup>	Wolfskill				Watsonville			
		1985		1986		1985		1986	
		MS	F	MS	F	MS	F	MS	F
Yield	Replications	---		780,462	20.3**	---		152,969	1.56
	GCA	672,505	3.3**	321,530	4.8**	1,604,923	3.77**	937,933	3.2**
	SCA	205,830	4.5**	67,137	1.7*	438,780	2.2**	296,279	3.0**
	Residual	45,947		38,480		202,194		98,186	
Fruit weight	Replications	---		33.7	8.2**	---		0.7	<1
	GCA	69.0	3.8**	11.7	2.8*	85.8	2.9*	59.5	3.7**
	SCA	18.3	1.9**	4.2	1.0	30.1	2.1**	16.1	1.8**
	Residual	9.7		4.1		14.1		8.8	
Appearance score	Replications	---		0.91	4.8*	---		0.01	<1
	GCA	0.60	2.14*	1.57	6.3**	0.95	4.52**	0.92	3.8**
	SCA	0.28	3.11**	0.25	1.3	0.21	1.75**	0.24	1.26
	Residual	0.09		0.19	0.12			0.19	

<sup>a</sup>GCA and SCA = general and specific combining ability, respectively.

\*\*\*Statistical significance at  $P = 0.05$  and  $0.01$ , respectively.

Table 5. Analysis of variance for yield, fruit weight, and appearance score, with results for the two test locations considered simultaneously.

Source <sup>z</sup>	Yield				Fruit Wt				Appearance			
	1985		1986		1985		1986		1985		1986	
	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Location(L) <sup>y</sup>	46364969	147.1**	19806949	30.6*	6393.1	340.1**	1995.3	54.3*	0.57	1.54	7.68	6.2
Replication/L	---	---	466716	6.8**	---	---	17.2	2.69	---	---	0.49	2.56
GCA(G) <sup>x</sup>	1266043	2.52*	1071203	3.49**	84.8	2.65**	50.1	1.92*	0.51	<1	1.67	2.12*
SCA(S)	302164	1.03	176754	<1	19.1	1.22	11.3	1.22	0.33	2.53*	0.18	<1
G × L	315237	1.07	181140	1.01	18.8	1.21	19.6	2.11*	0.37	2.85*	0.77	2.26*
S × L	293022	2.58**	178507	2.60*	15.6	1.79**	9.3	1.45	0.13	1.08	0.34	1.79*
Residual	113446		68592		8.7		6.4		0.12		0.19	

<sup>z</sup>GCA and SCA = general and specific combining ability, respectively.

<sup>y</sup>Tested with a synthetic F ratio for the 1986 trial with 1 and 2 df.

<sup>x</sup>Tested with a synthetic F ratio: 17 and 26 df for the 1986 trial, 19 and 36 df for the 1986 trial.

\*\*\*Statistical significance at  $P = 0.05$  and  $0.01$ , respectively.

Table 6. Estimated narrow-sense ( $h^2$ ) and broad-sense ( $H^2$ ) heritabilities for yield, fruit weight, and appearance score with results from Wolfskill (WEO) and Watsonville (WAT) considered separately and simultaneously.

Trait	Location	1985 <sup>z</sup>		1986 <sup>z</sup>	
		$h^2$	$H^2$	$h^2$	$H^2$
Yield	WEO	0.26 (0.12)	0.85 (0.20)	0.38 (0.18)	0.61 (0.23)
	WAT	0.30 (0.16)	0.62 (0.19)	0.35 (0.19)	0.87 (0.29)
	Both	0.34 (0.19)	0.34 (0.20)	0.36 (0.11)	0.36 (0.11)
Fruit weight	WEO	0.34 (0.12)	0.48 (0.14)	0.13 (0.07)	0.14 (0.08)
	WAT	0.22 (0.11)	0.53 (0.19)	0.30 (0.15)	0.54 (0.31)
	Both	0.28 (0.14)	0.34 (0.20)	0.14 (0.03)	0.19 (0.11)
Appearance score	WEO	0.10 (0.06)	0.55 (0.14)	0.42 (0.18)	0.51 (0.21)
	WAT	0.30 (0.13)	0.49 (0.17)	0.23 (0.11)	0.31 (0.21)
	Both	0.00 (0.09)	0.26 (0.15)	0.16 (0.08)	0.16 (0.08)

<sup>z</sup>Value in parentheses are SES of heritability estimates (6).

selection response, but do not change the relative ranking of unselected genotypes. Interactions that result in rank shifts are of more serious consequence for selection decisions, because individuals selected in one environment may not be superior in others. Some scale-induced interactions are expected for yield and fruit weight in our study, due to the large and significant between-location differences observed for these traits. Average appearance scores were consistent across locations, suggesting that interactions result in changes in rank, although it is possible to alter scales without affecting trait means. A preliminary indication of interaction type was obtained by analysis of log-transformed data for individual traits; such a transformation is expected to eliminate the multiplicative effects of scale difference (5). ANOVA results and heritabilities for transformed yield and appearance data (not shown) were essentially unchanged from those presented in Tables 5 and 6 demonstrating that interactions for these traits result in rank shifts. Conversely,  $G \times L$  interactions were nonsignificant for transformed fruit weight data, indicating that such interactions were largely the consequence

of scale effects, and selections can be expected to perform with similar ranking in different locations. Each seedling has a unique genotype, and can be tested in only a single environment. However, information from relatives grown in diverse environments can be used to reduce the consequences of shifts in performance rank. Simple procedures, such as making selections from families that are stable across environments, might be useful, but more specific strategies can be developed using indirect selection approaches (5).

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