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Computer Note

SASQuant: A SAS Software Program to Estimate Genetic Effects and Heritabilities of Quantitative Traits in Populations Consisting of 6 Related Generations

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Plant breeders are interested in the analysis of phenotypic data to measure genetic effects and heritability of quantitative traits and predict gain from selection. Measurement of phenotypic values of 6 related generations (parents, F_1, F_2, and backcrosses) allows for the simultaneous analysis of both Mendelian and quantitative traits. In 1997, Liu et al. released a SAS software based program (SASGENE) for the analysis of inheritance and linkage of qualitative traits. We have developed a new program (SASQuant) that estimates gene effects (Hayman's model), genetic variances, heritability, predicted gain from selection (Wright's and Warner's models), and number of effective factors (Wright's, Mather's, and Lande's models). SASQuant makes use of traditional genetic models and allows for their easy application to complex data sets. SASQuant is freely available and is intended for scientists studying quantitative traits in plant populations.

Analysis of phenotypic data for estimating genetic effects, heritability, and gain from selection for quantitative traits is an important statistical tool for plant breeders. Quantitative methods partition the total variance into genetic and environmental variances and the genetic variance into additive and dominance components and interallelic interaction effects, whenever the population structure and composition allows (Nyquist 1991; Holland et al. 2003). Variance of the F_2 provides an estimate of phenotypic variance, whereas the mean variance of the nonsegregating generations (P_1, P_2, and F_1) provides an estimate of environmental variance (Wright 1968). Additive variance is derived by subtracting the variances of the backcrosses (B_1, B_2) from twice the phenotypic (F_2) variance, as an extension of the single-locus model and assuming absence of linkage and of genotype by environment interaction (Warner 1952). The broad- and narrow-sense heritabilities and the predicted gain from selection can then be calculated from the available estimates of genetic, additive, and phenotypic variances. In addition, main and epistatic gene effects contributing to the phenotypic expression of a quantitative trait can be partitioned according to the model proposed by Hayman (1958) and reviewed by Gamble (1962).

In 1997, Liu et al. published SASGENE, a program using SAS software (SAS Institute, Cary, NC), for the analysis of inheritance and linkage of Mendelian genes. SASGENE required phenotypic ratings (discreet data) from families (or crosses) of 6 related generations (parents, F_1, F_2, and backcrosses) segregating for the traits of interest (Liu et al. 1997). However, SASGENE did not provide information on the genetics of quantitative traits segregating in those same families.

We have developed a new program, called SASQuant, for the genetic analysis of quantitative data. SASQuant uses the Output Delivery System (SAS Institute Inc. 2005) of SAS software (version 8 and higher). SASQuant is dimensioned for the analysis of an unlimited number of traits and unlimited number of individuals per generation and family. SASQuant, as required by the genetic models used, combines summary statistics (means and variances) in order to estimate genetic factors and their effects. The actual data set used to generate the estimates presented in the output of SASQuant is composed only by this summary statistics. Therefore, additional descriptive statistics, such as standard errors of the estimates or *F*-tests for significance of family mean differences, cannot be computed. This limitation is part of the genetics models adopted and cannot be overcome. Furthermore, SASQuant is intended solely as tool for breeders who are interested in deploying traditional genetic models such as those presented herein, not as an improvement over such models.

SASQuant is freely available and includes sample data set and instructions illustrating the use of the 2 macros and proper data-recording format. It also shows how to set up data properly for the analysis. The program files (dist.sas and estim.sas) and the sample data set (data.dat) can be obtained from the World Wide Web by visiting http://cucurbitbreeding.ncsu.edu/ and looking under the "Software" category.

Computational Methods

For each cross, SASQuant requires phenotypic data from multiple individuals of the 2 inbred parents (P_1, P_2), F_1

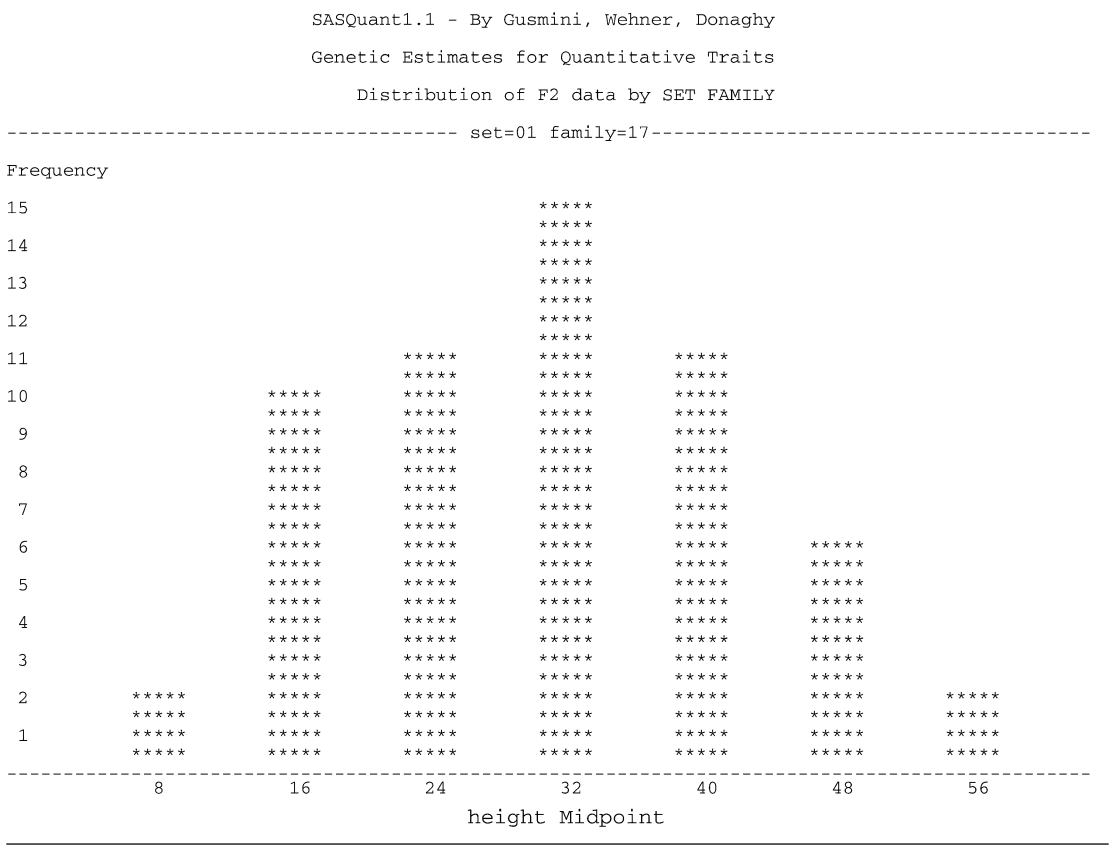

Figure 1. Distribution of F_2 data by Set Family. Output from DIST macro of SASQuant includes data distribution charts for the F_2 phenotypic values of each trait, which are useful, when visually inspected, to determine whether the data are normally distributed.

and F_2 hybrids, and the 2 backcrosses of the F_1 to the parents (B_1, B_2). SASQuant analyzes data from multiple phenotyping experiments (sets), in order to reduce the chances of complete loss of valuable and unique populations due to environmental adversities or disease epidemics at one location. In addition, sets could be considered as different environments, in order to reduce environmental effects on genotype. SASQuant analyzes an input data file that consists of plot number, set number, family number, and generation number, followed by the trait values. Families and sets can be assigned characters or numbers. The generation codes required by SASQuant are P_1 = '01', P_2 = '02', F_1 = '03', F_2 = '04', B_1 = '05', and B_2 = '06'.

Table 1. Homogeneity of variance test—Bartlett. Output from DIST macro of SASQuant includes chi squares and *P* values to test for homogeneity of variance of the F_2 phenotypic values of each trait, in order to verify the assumption of equal variance needed to pool data for a specific source. Bartlett's test is the default homogeneity of variance test for the SASQuant program, but other algorithms can be specified by the user

Dependent	Set	Family	Source	df	Chi square	Probability
Height			Set	1	34.4194	<0.0001
Height			Fam	8	53.8471	<0.0001
Height		17	Set	1	4.5620	0.0327
Height		18	Set	1	6.6999	0.0096
Height		19	Set	1	9.5673	0.0020
Height		20	Set	1	3.7412	0.0531
Height		21	Set	1	0.9134	0.3392
Height		22	Set	1	3.7600	0.0525
Height		23	Set	1	5.3446	0.0208
Height		24	Set	1	3.6507	0.0560
Height		25	Set	1	0.4492	0.5027
Height	01		Fam	8	36.2800	<0.0001
Height	02		Fam	8	25.4451	0.0013

SASQuant consists of 2 SAS macros. The first macro, DIST, plots the data from the F_2 generation so that the user can visually verify the normal distribution of the F_2 phenotypic data. In a second step, the DIST macro tests the homogeneity of variances of the F_2 data overall, by family over set and by set over family (Ostle and Malone 1988; Steel et al. 1997). From this analysis, the user can interpret the chi squares for the null hypothesis of homogeneous variances and decide how to pool the data for the analysis (overall, by set, by family, or not pooled). By default, the program performs Bartlett's test, but Levene's or any other test of homogeneity of variances available in SAS can be selected. The second macro, ESTIM, calculates means and variances by generation and pooling factor (overall, by set, by family, or not pooled), as indicated by the user. Generation means

Table 2. Number of observations and generation means by Set Family. Output from ESTIM macro of SASQuant lists the number of observations (*N*) and means (M) by generation (parents, F_1, F_2, and backcrosses, respectively) for each trait

Set	Family	*N*Pa	MPa	*N*Pb	MPb	NF_1	MF_1	NF_2	MF_2	*N*BCa	MBCa	*N*BCb	MBCb
01	17	7	16.7	6	54.8	10	33.5	57	30.2	22	24.7	26	43.8
01	18	10	17.2	10	40.8	16	28.8	87	26.7	29	21.8	30	30.2
01	19	8	10.0	7	47.0	13	32.5	92	32.8	22	22.0	29	40.6
01	20	9	10.1	3	23.0	14	27.7	30	27.1	24	18.0	28	36.3
01	21	8	10.9	10	38.8	8	27.9	74	26.0	24	16.7	16	35.1
01	22	3	10.3	3	49.3	10	42.3	48	31.4	15	20.3	17	35.5
01	23	5	5.6	5	44.4	12	20.4	81	20.6	22	11.8	29	30.3
01	24	7	5.1	5	48.0	9	15.8	53	20.5	14	11.9	30	30.1
01	25	6	7.0	5	50.0	10	26.2	45	25.0	17	14.1	29	29.0
02	17	9	12.0	4	39.0	13	23.2	91	26.0	19	20.5	26	29.1
02	18	7	15.9	6	28.7	17	22.8	99	20.2	25	17.8	30	25.8
02	19	8	11.8	4	38.8	17	23.5	106	22.4	29	17.3	27	31.6
02	20	8	8.8	3	32.7	15	18.8	41	20.2	27	16.6	21	24.2
02	21	8	9.4	6	11.8	20	15.5	105	17.7	30	11.1	25	16.0
02	22	9	7.7	5	18.4	12	15.6	102	20.0	26	14.9	24	22.1
02	23	6	3.3	2	30.0	14	11.1	56	15.0	22	8.7	25	25.6
02	24	10	3.3	7	18.7	16	15.8	37	13.5	30	9.3	30	18.3
02	25	10	2.6	5	43.4	18	19.8	64	18.0	30	8.6	24	29.6

and variances are then combined to estimate genetic variances, heritabilities (narrow and broad sense), number of effective factors, predicted gain from selection, and gene effects.

SASQuant estimates phenotypic (P), environmental (E), genotypic (G), and additive (A) effects from generation variances as follows (Warner 1952; Wright 1968):

$$\hat{\sigma}^2_{\mathrm{P}} = \hat{\sigma}^2_{\mathrm{F}_2} \quad \hat{\sigma}^2_{\mathrm{E}} = \frac{\hat{\sigma}^2_{\mathrm{P}_1} + \hat{\sigma}^2_{\mathrm{P}_2} + (2 \times \hat{\sigma}^2_{\mathrm{F}_1})}{4}$$

$$\hat{\sigma}^2_{\mathrm{G}} = \hat{\sigma}^2_{\mathrm{P}} - \hat{\sigma}^2_{\mathrm{E}} \quad \hat{\sigma}^2_{\mathrm{A}} = (2 \times \hat{\sigma}^2_{\mathrm{F}_2}) - (\hat{\sigma}^2_{\mathrm{B}_1} + \hat{\sigma}^2_{\mathrm{B}_2})$$

SASQuant estimates the number of effective factors using the following 5 methods (Wright 1968; Lande 1981; Mather and Jinks 1982):

Wright's method:

$$\frac{(\mu_{\mathrm{P}_1} - \mu_{\mathrm{P}_2})^2 \times \left\{1.5 - \left[2 \times \frac{\mu_{\mathrm{F}_1} - \mu_{\mathrm{P}_1}}{\mu_{\mathrm{P}_2} - \mu_{\mathrm{P}_1}} \times \left(1 - \frac{\mu_{\mathrm{F}1} - \mu_{\mathrm{P}_1}}{\mu_{\mathrm{P}_2} - \mu_{\mathrm{P}_1}}\right)\right]\right\}}{8 \times \left[\sigma^2_{\mathrm{F}_2} - \frac{\sigma^2_{\mathrm{P}_1} + \sigma^2_{\mathrm{P}_2} + (2 \times \sigma^2_{\mathrm{F}_1})}{4}\right]}$$

Mather's method: $\dfrac{\frac{(\mu_{\mathrm{P}_1} - \mu_{\mathrm{P}_2})^2}{2}}{(2 \times \sigma^2_{\mathrm{F}_2}) - (\sigma^2_{\mathrm{B}_1} + \sigma^2_{\mathrm{B}_2})}$

Lande's method I: $\dfrac{(\mu_{\mathrm{P}_1} - \mu_{\mathrm{P}_2})^2}{8 \times \left[\sigma^2_{\mathrm{F}_2} - \frac{\sigma^2_{\mathrm{P}_1} + \sigma^2_{\mathrm{P}_2} + (2 \times \sigma^2_{\mathrm{F}_1})}{4}\right]}$

Lande's method II: $\dfrac{(\mu_{\mathrm{P}_1} - \mu_{\mathrm{P}_2})^2}{8 \times [(2 \times \sigma^2_{\mathrm{F}_2}) - (\sigma^2_{\mathrm{B}_1} + \sigma^2_{\mathrm{B}_2})]}$

Table 3. Generation variances by Set Family. Output from ESTIM macro of SASQuant lists the variance (Var) by generation (parents, F_1, F_2, and backcrosses, respectively) for each trait

Set	Family	VarPa	VarPb	$VarF_1$	$VarF_2$	VarBCa	VarBCb
01	17	6.57	90.97	54.50	118.20	40.51	106.18
01	18	15.29	82.40	153.76	114.34	54.67	79.22
01	19	12.57	145.00	50.77	139.11	32.10	62.26
01	20	3.61	21.00	24.84	86.82	54.30	81.32
01	21	1.84	28.40	27.55	54.53	36.23	179.72
01	22	0.33	81.33	58.68	111.23	35.50	180.51
01	23	0.80	46.80	22.63	56.86	16.66	68.36
01	24	0.48	172.00	21.44	63.60	27.82	49.17
01	25	7.60	44.50	31.96	62.20	13.11	86.29
02	17	12.25	107.33	58.36	71.09	34.15	82.71
02	18	11.14	11.87	54.53	66.47	45.27	51.43
02	19	17.36	112.92	39.89	74.20	47.71	40.10
02	20	3.36	121.33	62.17	44.59	31.10	88.89
02	21	1.41	32.57	40.89	44.39	15.91	86.79
02	22	3.00	30.80	70.45	69.23	39.39	137.59
02	23	0.27	8.00	42.29	31.55	13.08	110.67
02	24	0.68	45.24	25.80	34.76	13.25	38.56
02	25	0.27	40.30	39.48	51.63	12.52	67.81

Table 4. Genetic variances and heritability by Set Family. Output from ESTIM macro of SASQuant lists genetic variances (phenotypic, environmental, genotypic, additive, and dominance, respectively) and broad- and narrow-sense heritability for each trait

Set	Family	VarP	VarE	VarG	VarA	VarD	HerB	HerN
01	17	118.20	51.63	66.57	89.71	−23.14	0.56	0.76
01	18	114.34	101.30	13.03	94.78	−81.75	0.11	0.83
01	19	139.11	64.78	74.33	183.87	−109.5	0.53	1.32
01	20	86.82	18.57	68.25	38.02	30.23	0.79	0.44
01	21	54.53	21.34	33.20	−106.9	140.08	0.61	−1.96
01	22	111.23	49.76	61.47	6.45	55.02	0.55	0.06
01	23	56.86	23.21	33.65	28.70	4.95	0.59	0.50
01	24	63.60	53.84	9.76	50.21	−40.45	0.15	0.79
01	25	62.20	29.00	33.20	25.01	8.19	0.53	0.40
02	17	71.09	59.08	12.01	25.31	−13.30	0.17	0.36
02	18	66.47	33.02	33.45	36.23	−2.78	0.50	0.55
02	19	74.20	52.51	21.68	60.58	−38.90	0.29	0.82
02	20	44.59	62.26	−17.67	−30.81	13.14	−0.40	−0.69
02	21	44.39	28.94	15.44	−13.93	29.38	0.35	−0.31
02	22	69.23	43.67	25.55	−38.53	64.08	0.37	−0.56
02	23	31.55	23.21	8.34	−60.67	69.00	0.26	−1.92
02	24	34.76	24.38	10.38	17.70	−7.32	0.30	0.51
02	25	51.63	29.88	21.75	22.94	−1.18	0.42	0.44

Lande's method III: $$\frac{(\mu_{P_1} - \mu_{P_2})^2}{[8 \times (\sigma^2_{B_1} + \sigma^2_{B_2} - \sigma^2_{F_1})] - \frac{(\sigma^2_{P_1} + \sigma^2_{P_2})}{2}}$$

SASQuant predicts gain from one cycle of selection as $h^2_n \times \sqrt{\sigma^2_P}$ multiplied by the selection differential in standard deviation units (k) for selection intensities of 5%, 10%, or 20% (Hallauer and Miranda 1988). The user can modify k to predict gain from one cycle of selection under a different magnitude of selection intensity.

SASQuant partitions additive, dominance, and epistatic effects based on the Hayman's mean separation analysis procedure (Hayman 1958; Gamble 1962), using the following formulae, and computes the standard errors for the estimates as square root of their variances:

$$m = \mu_{F_2} \quad a = \mu_{B_1} - \mu_{B_2}$$

$$d = -\frac{\mu_{P_1}}{2} - \frac{\mu_{P_2}}{2} + \mu_{F_1} - (4 \times \mu_{F_2}) + [2 \times (\mu_{B_1} + \mu_{B_2})]$$

$$aa = -(4 \times \mu_{F_1}) + [2 \times (\mu_{B_1} + \mu_{B_2})]$$

$$ad = -\frac{\mu_{P_1}}{2} + \frac{\mu_{P_2}}{2} + \mu_{B_1} - \mu_{B_2}$$

$$dd = \mu_{P_1} + \mu_{P_2} + (2 \times \mu_{F_1}) + (4 \times \mu_{F_2}) - [4 \times (\mu_{B_1} + \mu_{B_2})]$$

SASQuant tests the hypothesis that the estimates are significantly different from zero, performing a Fisher's t-test. The estimates a, d, aa, ad, and dd are obtained by combining the means of generations with different sample sizes (number of

Table 5. Effective factors and gain from selection by Set Family. Output from ESTIM macro of SASQuant lists the number of estimated effective factors (EF) (Wright's, Mather's, three Lande's, and average estimates) and the predicted gain from selection (GS) (selection intensity of 5%, 10%, and 20%, respectively) for each trait

Set	Family	EF1	EF2	EF3	EF4	EF5	EFm	GS05	GS10	GS20
01	17	2.7	8.1	2.7	2.0	4.2	4.0	17.0	14.5	11.6
01	18	5.3	2.9	5.3	0.7	−1.0	2.7	18.3	15.6	12.4
01	19	2.4	3.7	2.3	0.9	−4.9	0.9	32.1	27.4	21.8
01	20	0.8	2.2	0.3	0.5	0.2	0.8	8.4	7.2	5.7
01	21	3.0	−3.6	2.9	−0.9	0.6	0.4	−29.8	−25.5	−20.3
01	22	3.7	117.9	3.1	29.5	1.6	31.2	1.3	1.1	0.9
01	23	5.7	26.2	5.6	6.6	4.9	9.8	7.8	6.7	5.3
01	24	26.5	18.3	23.5	4.6	−7.5	13.1	13.0	11.1	8.8
01	25	7.0	37.0	7.0	9.2	5.6	13.1	6.5	5.6	4.4
02	17	7.7	14.4	7.6	3.6	−70.9	−7.5	6.2	5.3	4.2
02	18	0.6	2.3	0.6	0.6	0.7	0.9	9.2	7.8	6.2
02	19	4.2	6.0	4.2	1.5	−5.3	2.1	14.5	12.4	9.8
02	20	−4.1	−9.3	−4.0	−2.3	−15.8	−7.1	−9.5	−8.1	−6.5
02	21	0.4	−0.2	0.0	−0.1	0.0	0.0	−4.3	−3.7	−2.9
02	22	0.6	−1.5	0.6	−0.4	0.2	−0.1	−9.5	−8.1	−6.5
02	23	11.6	−5.9	10.7	−1.5	1.1	3.2	−22.3	−19.0	−15.1
02	24	3.4	6.7	2.9	1.7	9.7	4.9	6.2	5.3	4.2
02	25	9.7	36.3	9.6	9.1	10.1	14.9	6.6	5.6	4.5

Table 6. Hayman's main gene effects by Set Family. Output from ESTIM macro of SASQuant lists Hayman's estimates of main gene effects, their standard errors (SEs), and Student's *t* significance level (PROB) (mean, additive, and dominance effects, respectively) for each trait

Set	Family	*m*	SE*m*	*a*	SE*a*	P*a*	*d*	SE*d*	P*d*
01	17	30.21	1.44	−19.09	3.38	0.0000	13.79	17.28	0.4284
01	18	26.68	1.15	−8.44	3.00	0.0087	−2.85	15.74	0.8568
01	19	32.79	1.23	−18.55	2.67	0.0000	−2.11	15.14	0.8895
01	20	27.07	1.70	−18.24	3.21	0.0000	11.55	16.19	0.4815
01	21	25.99	0.86	−18.46	4.58	0.0007	2.67	15.53	0.8637
01	22	31.44	1.52	−15.20	4.80	0.0063	−1.81	20.88	0.9313
01	23	20.63	0.84	−18.54	2.41	0.0000	−2.94	11.27	0.7951
01	24	20.45	1.10	−18.21	2.69	0.0000	−8.76	14.37	0.5449
01	25	25.02	1.18	−14.88	2.60	0.0000	−16.15	13.75	0.2464
02	17	25.96	0.88	−8.60	3.12	0.0117	−6.99	15.08	0.6439
02	18	20.23	0.82	−8.01	2.65	0.0056	6.69	11.71	0.5694
02	19	22.37	0.84	−14.28	2.50	0.0000	6.47	13.27	0.6269
02	20	20.24	1.04	−7.65	3.13	0.0227	−1.22	15.97	0.9394
02	21	17.74	0.65	−4.91	2.59	0.0693	−11.73	10.59	0.2705
02	22	20.04	0.82	−7.24	3.63	0.0573	−3.59	14.50	0.8051
02	23	15.02	0.75	−16.88	2.88	0.0000	2.89	11.60	0.8042
02	24	13.46	0.97	−9.00	1.80	0.0000	6.11	10.14	0.5511
02	25	17.98	0.90	−21.03	2.33	0.0000	1.29	11.23	0.9089

individuals rated per generation). Thus, the computation of the degrees of freedom (df) to be used to fit the *t*-test is not obvious. The most conservative approach would be to calculate the df based on the minimum number of observations (n) common to all the generations that contribute to the estimates of each gene effect. For example, if a was estimated using 30 observations for one backcross generation and 35 for the other, then df should be equal to 29. However, n is typically largely unbalanced between nonsegregating (parents and F_1) and segregating generations (F_2 and backcrosses). Thus, the df of estimates built from generations of the 2 groups would use only few observations, and the *t*-test would have little power. According to a common practice among breeders (personal communications), SASQuant estimates the df as an average of the segregating generations used to estimate the gene effect, as follows:

$$\mathrm{df}_m = n_{\mathrm{F}_2} - 1$$

$$\mathrm{df}_a = \mathrm{df}_{aa} = \mathrm{df}_{ad} = \frac{n_{\mathrm{B}_1} + n_{\mathrm{B}_2}}{2} - 1$$

$$\mathrm{df}_d = \mathrm{df}_{dd} = \frac{n_{\mathrm{F}_2} + n_{\mathrm{B}_1} + n_{\mathrm{B}_2}}{3} - 1$$

The output of DIST includes the distribution plots of data from the F_2 families (Figure 1) and a table of tests of

Table 7. Hayman's epistatic gene effects by Set Family. Output from ESTIM macro of SASQuant lists Hayman's estimates of epistatic gene effects, their corresponding standard errors (SEs), and Student's *t* significance level (PROB) (additive × additive, additive × dominance, and dominance × dominance effects, respectively) for each trait

Set	Family	*aa*	SE*aa*	P*aa*	*ad*	SE*ad*	P*ad*	*dd*	SE*dd*	P*dd*
01	17	16.06	12.52	0.2081	−0.03	5.81	0.9962	−14.41	28.80	0.6200
01	18	−2.66	10.58	0.8026	3.36	5.05	0.5113	14.23	26.88	0.5990
01	19	−6.07	10.26	0.5571	−0.05	5.58	0.9927	2.89	25.37	0.9098
01	20	0.39	13.22	0.9768	−11.80	4.85	0.0224	−20.50	25.58	0.4300
01	21	−0.36	12.59	0.9772	−4.50	5.66	0.4370	2.20	27.63	0.9368
01	22	−14.28	15.68	0.3712	4.30	7.57	0.5786	47.07	35.66	0.1985
01	23	1.65	8.16	0.8410	0.86	4.14	0.8365	5.02	19.18	0.7948
01	24	2.04	9.76	0.8361	3.22	5.75	0.5817	−1.19	24.35	0.9615
01	25	−13.85	9.91	0.1726	6.62	4.66	0.1694	37.02	22.80	0.1151
02	17	−4.72	9.78	0.6317	4.90	6.30	0.4453	3.08	26.62	0.9083
02	18	6.12	8.59	0.4791	−1.60	3.99	0.6912	−3.01	20.15	0.8820
02	19	8.19	8.35	0.3310	−0.78	5.89	0.8957	−8.30	23.20	0.7221
02	20	0.69	10.43	0.9480	4.31	6.63	0.5221	−3.33	27.77	0.9054
02	21	−16.62	7.78	0.0374	−3.68	3.97	0.3622	14.49	18.58	0.4390
02	22	−6.14	10.55	0.5632	−1.87	5.15	0.7194	−10.65	25.70	0.6804
02	23	8.41	8.75	0.3434	−3.54	3.98	0.3826	−21.28	20.19	0.2995
02	24	1.36	7.47	0.8565	−1.29	3.20	0.6891	−3.05	16.41	0.8539
02	25	4.51	8.25	0.5874	−0.63	3.83	0.8716	4.59	18.87	0.8089

homogeneity of variances (Table 1). For example, the tests of homogeneity of variances in Table 1 indicate whether the data can be pooled as follows: 1) all data (tests 1 and 2), using sets and families as sources for the test, 2) data from all sets for a specific family (tests 3–11), and 3) data from all families for a specific set (tests 12 and 13). The output of ESTIM includes 6 tables (Tables 2–7) reporting the following: number of observations and means by generation (Table 2), variances by generation (Table 3), estimates of genetic variances and heritability (Table 4), number of effective factors and predicted gain from selection (Table 5), and Hayman's gene effects (Tables 6 and 7).

Formulas used by SASQuant may produce negative estimates, which should be considered equal to zero (Robinson et al. 1955). Both negative and positive estimates should be reported to permit unbiased estimates of genetic parameters in future meta-analysis or, as originally stated, "in order to contribute to the accumulation of knowledge, which may, in the future, be properly interpreted" (Dudley and Moll 1969). Furthermore, when a negative estimate results from derivation from another negative value (e.g., narrow-sense heritability and gain from selection, calculated from negative additive variance), it should be omitted.

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