A DIALLEL ANALYSIS OF CELLULAR MEMBRANE THERMOSTABILITY IN COMMON BEAN (PHASEOLUS VULGARIS L.)

by

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MANUSCRIPT

A Diallel Analysis of Cellular Membrane Thermostability in Common Bean (*Phaseolus vulgaris* L.)[1]

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Abstract. To estimate the genetic component of cellular membrane thermostability in *Phaseolus vulgaris*, parental and F_1 plants from a 6-parent half diallel cross were tested by electrical conductivity and the results were analyzed by Hayman's method. Membrane thermostability was found to be a quantitative trait, with environmental and dominance effects accounting for most of the phenotypic expression. Narrow sense heritability was low (5.4%).

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[1]Received for publication.....

[2]Graduate student and Professor.

It is well known that high temperature is one of the major factors limiting yield of common bean. In order to breed for heat tolerance, one needs information about the inheritance of the character and a suitable method of screening for it.

Screening methods and inheritance of heat tolerance in common beans have been studied by several researchers. Benepal and Rangappa (3) screened 5380 accessions for their ability to set pods in the field. Wien and Munger (31) also tested lines for heat tolerance in the field. Weaver et al. (29) suggested a possible screening procedure testing pollen growth *in vitro* or *in vivo*. Ng and Bouwkamp (21) rated more than 600 accessions according to their response to high temperature in the greenhouse. Bouwkamp and Summers (4) reported on the inheritance of combined temperature and drought stress resistance based on the number of pods set per plant.

In addition to morphological characters, methods of measuring cell viability have been tested in the hope of finding a rapid laboratory screening procedure. The electrical conductivity method is the most important of these. It tests for cell membrane thermostability as measured by leachate conductivity and has recently been

used as an index of viability after heat treatment. Various plant species and parts have been examined by the conductivity test. Laminar pieces of tomato and epidermal strips from onion bulb were tested by Onwueme (22), holly root cells by Ingram (12), and pear suspension cells by Wu (32). A diversity of turf grasses has been tested by with this method (28,30); and Chen et al. (6) have examined tomato, soybean, and potato.

Comparison of the electrical conductivity test with other methods and with field performance suggests that the electrical conductivity method is a moderately reliable and convenient screening procedure for measuring heat tolerance. Marsh et al. (18) measured heat tolerance in common bean by the conductivity test, a hot water dip, percent pod set, and pollen stainability. They concluded that the conductivity method best combined reliability with early testing convenience. Marsh et al. (17,19) reported for the conductivity method that the killing times for the 5 genotypes used were in agreement with previous ratings from yield data. They also studied heat tolerance inheritance by conductivity tests for the parents, F_1, backcross, and F_2 populations from 3 crosses of heat-

tolerant X heat-intolerant lines. Schaff (23) observed significant correlation of electrical conductivity with field performance under heat stress, developed a sigmoidal model to calculate killing temperature, and conducted a 6-parent weighted diallel analysis to determine the inheritance of heat tolerance. In soybean and sorghum, good correlation has been found between heat tolerance as measured by electrical conductivity and field performance measured by yield (20, 25).

The Hayman-Jinks diallel cross has been widely used for inheritance studies (5, 14), despite the fact that some reports have been openly critical of the diallel analysis as a method for studying the genetics of complex traits or as a tool in plant breeding (8). Johnson (14) pointed out two major advantages that the diallel cross provides: compared to other methods available, the diallel cross technique permits a more systematic approach to large scale studies of continuous variation and a better diciplined analysis of the resulting data; and the overall analysis provides reliable genetic information on dominance and recessiveness and on complementary non-allelic interaction.

The diallel analysis makes it possible to predict

the phenotypes of the completely dominant parents, which in turn suggests the possible limit of selection among genes showing dominance. Baker (2) emphasized the fact that similar information could be obtained from different methods of analyzing diallel crosses, such as those developed by Griffing (9) and Gardner and Eberhart (7). The assumptions required for the genetic interpretation in self-pollinating plants were evaluated by Sokol and Baker (24). Jones (15) modified the Hayman-Jinks method so that it can be conducted without reciprocal crosses (half-diallel analysis).

The objective of this experiment was to carry out a six parent half-diallel analysis to determine the inheritance of heat killing time in common bean.

Material and Methods

Three of the parents used in this study are cultivars previously reported to be heat tolerant (23, 31): PI 324607 (P_2), ND 364 (P_4), Wyoming 166 (P_5). The other three are heat intolerant (23): PI 271998 (P_1), Oregon 1604 (P_3), Valley (P_6). Valley, Wyoming 166, and ND 364 were obtained originally from M. LeBaron, University of Idaho, Kimberly; PI 271998 and PI 324607 from the USDA Plant Introduction Station, Pullman, WA; and Oregon 1604 from the Idaho Seed Bean Co., Twin Falls, ID. All cultivars have been maintained by single seed descent for at least four generations.

The half-diallel cross was made in winter 1984. The seeds of each parent were sown in 5.5 X 5.5 X 5.0 cm pots containing a potting mixture of vermiculite, peat, perlite, and soil; and the pots were put in a growth chamber set for 30 C and a 16-hr light period to ensure rapid and uniform germination. Ten days from seeding, the seedlings were transplanted into one-gallon pots containing the same soil mixture as in the seeding pots. The plants were maintained in a greenhouse set for 28/22 C day/night temperature and supplementally lighted to approximate a 12-hr photoperiod to ensure uniform timing of flower initiation. The crosses were made by hand

pollination as soon as the plants began flowering. Cultivars with dominant marker genes were used as male parents whenever possible.

In fall and winter of 1985, 4 runs of the conductivity test were carried out, each containing 1 plant for each of the 21 accessions (15 F_1 hybrids and 6 parents). In each run, 2 to 3 seeds of each genotype were sown, transplanted, and maintained in the greenhouse as previously described. One plant of each genotype was tested for membrane stability in a random sequence. The time schedule for each run is listed in Table 1.

The plants to be tested were acclimated at flowering stage for 24 hours in growth chambers set for a constant 37.5C and a 16-hr photoperiod at 900 μE sec^{-1} m^{-2}. Immediately after acclimation the young, fully expanded leaves were picked for testing by the procedure of Kinbacher (16) with the following modifications.

Leaf discs, one cm in diameter, were washed with deionized-distilled water, changed 3 times, and put into test tubes, 5 per tube, each containing 1 ml of water. The treatment tubes were kept in a water bath set at 47C for 30, 60, 90, 120, 150, and 180 minutes, for each of the accessions with 3 replications for each time.

Control discs were held at room temperature. After the tubes cooled, 20 ml of deionized-distilled water were added to each and they were incubated at 10 C for 24 hours. The first conductivity was determined at 25C after incubation. All of the tubes were put in boiling water for 15 minutes to kill the cells completely. After 24 hours at room temperature, the second conductivity reading was taken at 25C.

Relative leakage, or injury, was calculated using the equation:

$$\text{Relative leakage} = 1 - [(1-(C_1/C_2))/(1-(C_{1c}/C_{2c}))],$$

where C_1 = treatment first conductance, C_{1c} = control first conductance, C_2 = treatment second conductance, and C_{2c} = control second conductance.

The killing time (Time50) is defined as the time at which 50% cell were injured. Viability was estimated using the sigmoidal equation:

$$\text{Viability} = 1 / [1 + e^{-B(\text{Time}-\text{Time50})}] + \epsilon$$

where B is a rate parameter and ϵ is the deviation from the regression line (27).

The error term for the diallel analysis was the MS ERROR, the mean square interaction of cross X run, which can be obtained by fitting the sigmoidal model to

various sets of data (Table 2).

The diallel weighting and analysis procedure followed that of Schaff (23) with modifications and is given in the appendix. The same notation was used as by Hayman (10). The caculations were conducted using the SAS computer language.

Results and Discussion

The Hayman-Jinks diallel model assumes: parental homozygosity, diploid segregation, no differences between reciprocal crosses, no multiple alleles, no epistasis, and no linkage between the genes studied.

The first three assumptions were confirmed to be valid by observation of parental and hybrid phenotypes. The remaining three were tested with the methods of Hayman (10) and Jinks (13), namely, uniformity of $W_r - V_r$. The t-test for heterogeneity of $W_r - V_r$ is not significant (t=0.046, P=0.97), and Figure 1 shows that the regression slope of W_r on V_r is not significantly different from unity (for b=1, P = 0.30). Consequently, there is insufficient evidence to say that Hayman's model is inappropriate for this experiment.

The mean killing time (Time50) and its coefficient of the standard error (K) for each genotype are presented in Table 3. Due to the large standard errors of Time50 and the small mean square residuals of the sigmoidal model, K values are relatively large. The relative position of the parents for heat tolerance is similar to Schaff's results (23).

Since only six parents were intercrossed in the

present study (less than ten parents), the genetic components estimated are appropriate only for this particular set of parents, rather than for the entire population (10,11).

The main components of genetic variance are listed in Table 4, and the estimates of heritability parameters are given in Table 5. Since $(H_1/D)^{1/2}$, which estimates the degree of dominance, is larger than 1, overdominance exists, as also indicated by the negative intercept in Figure 1. Also, the correlation coefficent between the parental order of dominance (W_r+V_r) and the weighted parental values is very close to 0 ($r=0.00008$, $P=0.99$), indicating that there are equal numbers of positive and negative genes showing dominance. Marsh et al. (19) also found that the F_1 mean killing time exceeded the midparent for all 3 crosses studied and interpreted the fact as gene interaction. Since their data also fit the additive-dominant model with small epistatic effects, this "gene interaction" means dominance.

For our results, the ratio of dominant to recessive genes equals 1.40, indicating that there are more dominant than recessive genes for heat tolerance. There is at least one gene group showing some degree of dominance, as indicated by the estimate, $h^2/H_2 = 0.52$.

The proportion of genes with positive and negative effect in the parents, $H_2/4H_1$, is 0.23, possibly indicating slightly unequal distribution of positive or negative genes among parents.

Significant differences were found among runs (Table 6), which suggests that unknown environmental factors affected plants by causing different responses to the heat stress among runs even for the same cross. Tal and Shannon (26), also using the leaf disc conductivity test for membrane heat stability, found that all Lycopersicon and Solanum species tested had more injury in the winter than in the summer. The results of our experiment support this because, as shown in Table 1, overall means of each run decreased as the treatment date shifted. So weather conditions, such as light intensity and daylength, may account for some of the variation among runs, among crosses, and among plants of the same cross. In order to obtain a more accurate estimate of the inheritance, the present conductivity procedure needs to be refined to minimize environmental error. Additional replication of genotypes tested, both within and between runs, would give more accurate estimation of killing times.

The estimate of narrow sense heritability is low (5.4%), which contrasts with the high heritability (59%) observed by Schaff (23). Several factors should be taken into consideration when comparing these two results. Firstly, some of the bean lines he used differed from those of this study. Secondly, his experiment was an unbalanced split plot design using killing temperature, not killing time. Thirdly, his original data were not homogeneous for W_r-V_r until one parent, Oregon 1604, was removed.

By comparing the estimate of broad sense heritability (34.6%) and that of narrow sense heritability, it is clear that the dominant effects accounted for most of the genetic variation.

The narrow and broad sense heritabilities of heat tolerance calculated by Marsh et al. (19) for their different parental crosses ranged from 2.9% to 24% and 0.0% to 21.6%, respectively. Our narrow sense heritability (5.4%) is within their range, and its low value is due to the large environmental and dominant effects and the small additive effects. Also, the estimate of the heritability in this experiment was based on individual plant responses, where large errors of estimation were common.

We conclude that membrane thermostability in common bean is a quantitative trait and easily influenced by the environment. Dominant effects accounted for most of the genetic variation. Because of the low heritability of cellular membrane thermostability, should the conductivity method be employed in a breeding program, continuous evaluation and selection using large samples will be required in later generations. Even then, the time- and labor-consuming nature of this procedure makes it difficult to use. Unless the test can be improved in these respects, alternative testing procedures will have to be developed for an effective heat-tolerance breeding program.

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Table 1. Time schedule and overall mean Time50 for each run.

Run	Planting	Testing	Mean
1	09/25/85	11/06/85	120.4
2	10/16/85	11/26/85	112.2
3	11/08/85	12/18/85	111.0
4	12/09/85	01/16/86	85.3

Table 2. Error term calculation.

Source	Sum square residual	d.f.[z]
All plants	SSRes(ALL)	crtn-m
Run	SSRes(RUN)	r(ctn-m)
Cross	SSRes(CROSS)	c(rtn-m)
Each plant	SSRes(PLANT)	cr(tn-m)

[z] c = No. of genotypes, including parents; r = No. of runs; t = No. of time intervals tested/plant; n = No. of test tubes/time interval; and m = No. of parameters in the sigmoidal model.

$$SS(CROSSXRUN) = SS\ ERROR$$
$$= SSRes(CROSS)+SSRes(RUN)-SSRes(ALL)-SSRes(PLANT)$$

$$d.f._{ERROR} = d.f._{SSRes(CROSS)} + d.f._{SSRes(RUN)} - d.f._{SSRes(ALL)} - d.f._{SSRes(PLANT)}$$

$$MS\ ERROR = MS(CROSS\ X\ RUN) = SS\ ERROR\ /\ d.f._{ERROR}$$

Table 3. The killing time (Time50) and its coefficient of the standard deviation (K) for the parents and their F_1 hybrids.

	P1[z]	P2	P3	P4	P5	P6
P_1	76.8[y] 62.3[x]					
P_2	100.8 64.2	84.5 49.5				
P_3	111.3 55.4	114.1 93.9	108.3 49.5			
P_4	113.1 57.4	128.8 54.7	81.3 48.4	97.7 48.4		
P_5	101.1 54.9	140.9 61.1	124.0 54.7	107.1 52.7	123.3 55.6	
P_6	105.6 50.6	110.8 57.5	117.0 65.5	106.6 54.6	103.6 58.4	96.0 48.3

[z] P_1= PI 271998, P_2= PI 324607, P_3= Oregon 1604, P_4= ND 364, P_5= Wyoming 166, and P_6= Valley.

[y] Time50, mean value for 4 runs; $LSD_{0.05}$=28.65.

[x] K, mean value for 4 runs.

Table 4. Genetic variance components for killing time.

Genetic component[z]	Estimate and standard error[y]
D	74.9±125.5
H_1	468.7±318.5*
H_2	435.2±284.5*
F	61.9±306.5
h^2	226.0±191.5
E	227.6±47.4**

[z] D = additive effects of genes;

H_1 = dominance effects of genes;

H_2 = dominance indicated by asymmetry of positive and negative effects of genes;

F = covariance of dominance and additive effects;

h^2 = square of the dominance effects over all loci in heterozygous phase in all crosses; and

E = environmental error.

[y] *, ** significant at 20%, 1% level, respectively.

Table 5. Hayman's heritability parameters.

Inheritance parameters[z]	Estimate
$(H_1/D)^{1/2}$	2.50
$H_2/4H_1$	0.23
K_D/K_R	1.40
h^2/H_2	0.52
Narrow sense heritability	0.054
Broad sense heritability	0.346

[z] $(H_1/D)^{1/2}$ = average degree of dominance;

$H_2/4H_1$ = average frequency of positive vs negative alleles;

K_D/K_R = $((4DH_1)^{1/2}+F)/((4DH_1)^{1/2}-F)$ the ratio of dominant to recessive alleles;

h^2/H_2 = average number of genes showing dominanance;

Narrow sense heritability = $(1/4)D/[(1/4)(D-F+H_1)+E]$;

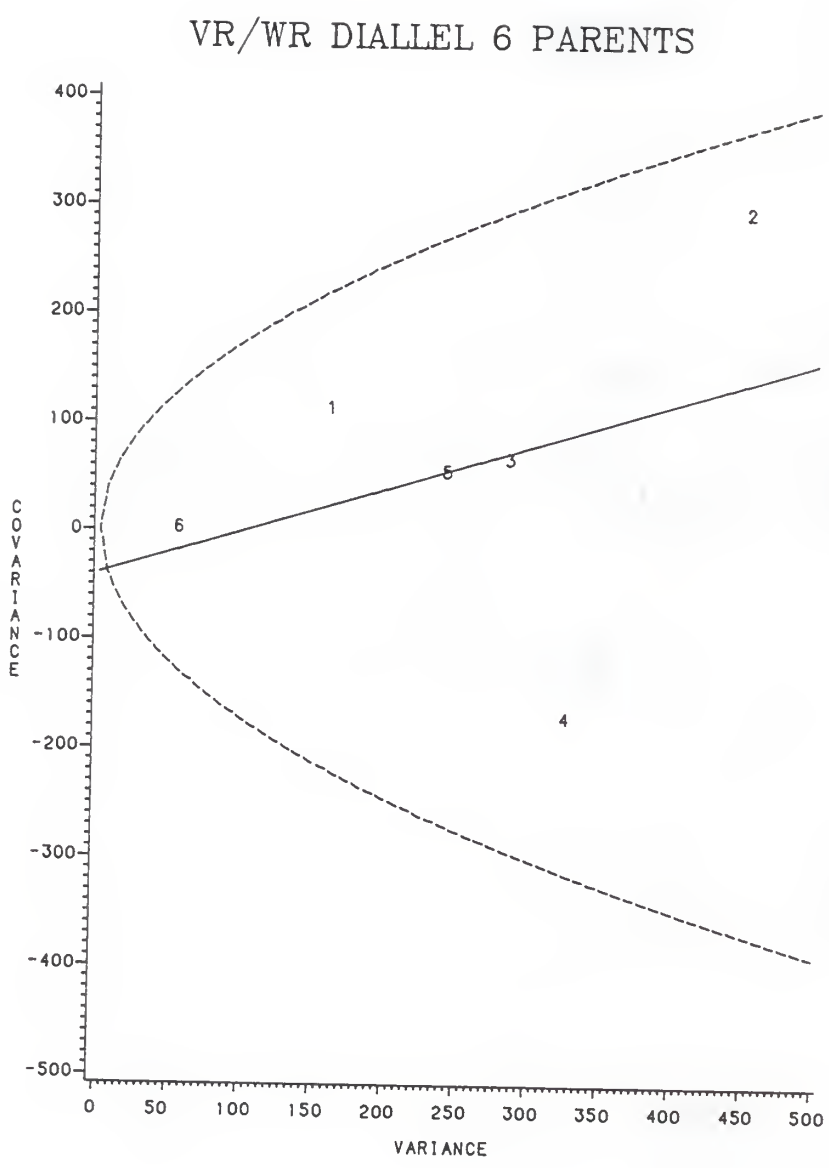
Broad sense heritability=$(1/4)(D-F+H_1)/[(1/4)(D-F+H_1)+E]$.

Table 6. ANOVA table of mean killing times for the half diallel cross.

Source	d.f.	Mean square
Cross	20	953.76**
Run	3	4848.77**
Error	60	410.29
Total	83	

** significant at 1% level.

Figure 1. Graph of variance vs. covariance (V_r, W_r) of 6 bean cultivars for heat tolerance.


VR/WR DIALLEL 6 PARENTS
400
300
200
100
0
-100
-200
-300
-400
-500
COVARIANCE
0
50
100
150
200
250
300
350
400
450
500
VARIANCE
1
2
3
4
5
6

APPENDIX A

```
*************************************************************
*************************************************************
*                                                           *
*                                                           *
*  FIT THE SIGMOIDAL MODEL TO ALL PLANT, TO RUN,            *
*          TO CROSS, AND TO EACH PLANT                      *
*                                                           *
*                                                           *
*************************************************************
*************************************************************
;
DATA ALL;
INPUT PLANT 1-2 TIME 5-7 A1 10-13 1 A2 15-18 1
A3 20-23 1 A4 25-28 1 A5 30-33 1 A6 35-38 1
RUN 40 P1 45 P2 50;
IF P1=3 OR P2=3 THEN DELETE;
IF P1=1 AND P2=1 OR P1=1 AND P2=1 THEN CROSS='1X1';
IF P1=1 AND P2=2 OR P1=2 AND P2=1 THEN CROSS='1X2';
IF P1=1 AND P2=3 OR P1=3 AND P2=1 THEN CROSS='1X3';
IF P1=1 AND P2=4 OR P1=4 AND P2=1 THEN CROSS='1X4';
IF P1=1 AND P2=5 OR P1=5 AND P2=1 THEN CROSS='1X5';
IF P1=1 AND P2=6 OR P1=6 AND P2=1 THEN CROSS='1X6';
IF P1=2 AND P2=3 OR P1=3 AND P2=2 THEN CROSS='2X3';
IF P1=2 AND P2=4 OR P1=4 AND P2=2 THEN CROSS='2X4';
IF P1=2 AND P2=5 OR P1=5 AND P2=2 THEN CROSS='2X5';
IF P1=2 AND P2=6 OR P1=6 AND P2=2 THEN CROSS='2X6';
IF P1=3 AND P2=3 OR P1=3 AND P2=3 THEN CROSS='3X3';
IF P1=2 AND P2=2 OR P1=2 AND P2=2 THEN CROSS='2X2';
IF P1=3 AND P2=4 OR P1=4 AND P2=3 THEN CROSS='3X4';
IF P1=3 AND P2=5 OR P1=5 AND P2=3 THEN CROSS='3X5';
IF P1=3 AND P2=6 OR P1=6 AND P2=3 THEN CROSS='3X6';
IF P1=4 AND P2=4 OR P1=4 AND P2=4 THEN CROSS='4X4';
IF P1=4 AND P2=5 OR P1=5 AND P2=4 THEN CROSS='4X5';
IF P1=4 AND P2=6 OR P1=6 AND P2=4 THEN CROSS='4X6';
IF P1=5 AND P2=5 OR P1=5 AND P2=5 THEN CROSS='5X5';
IF P1=5 AND P2=6 OR P1=6 AND P2=5 THEN CROSS='5X6';
IF P1=6 AND P2=6 OR P1=6 AND P2=6 THEN CROSS='6X6';
REP=1; R=1-(A1/A4); OUTPUT;
REP=2; R=1-(A2/A5); OUTPUT;
REP=3; R=1-(A3/A6); OUTPUT;
DROP A1-A6;
CARDS;
DATA ONE; SET ALL;
PROC SORT; BY  PLANT;
DATA TWO; SET ONE;
IF TIME > 0 THEN DELETE;
PROC MEANS NOPRINT; BY  PLANT; VAR R;
OUTPUT OUT=NEW MEAN=RC;
DATA THREE; SET NEW;
PROC SORT; BY  PLANT;
DATA CONO; MERGE ONE THREE; BY PLANT;
IF TIME = 0 THEN DELETE;
READ=1-(R/RC);
PROC NLIN;
PARMS B=.01 TO .3 BY .1 U=50 TO 180 BY 30;
L=EXP(-B*(TIME-U));
MODEL READ=1/(1+L);
DER.U=-L*B/(1+L)**2;
DER.B=(TIME-U)*L/(1+L)**2;
OUTPUT OUT=MOCALL R=READALL PARMS=BALL UALL ESS=SSRESALL;
```

```
PROC SORT DATA=COND; BY CROSS;
PROC NLIN ; BY CROSS;
PARMS B=.01 TO .3 BY .1 U=50 TO 180 BY 30;
L=EXP(-B*(TIME-U));
MODEL READ=1/(1+L);
DER.B=(TIME-U)*L/(1+L)**2;
OUTPUT OUT=NEWC P=PREADC PARMS=BC UC ESS=SSRESC;
PROC MEANS N NOPRINT; BY CROSS;VAR READ;
OUTPUT OUT=NEWC N=NC;
DATA NEWC;SET NEWC; BY CROSS; IF FIRST.CROSS;
DATA CROSS1; MERGE NEWC NEWO; BY CROSS;
DFC=NC-2;
DATA CROSS2;SET CROSS1;
PROC SORT;BY DESCENDING UC;
PROC MEANS SUM;VAR SSRESC DFC;
OUTPUT OUT=NEWC SUM=SSSRESC SDFC;
PROC SORT DATA=COND; BY RUN;
PROC NLIN;BY RUN;
PARMS B=.01 TO .3 BY .1 U=50 TO 180 BY 30;
L=EXP(-B*(TIME-U));
MODEL READ=1/(1+L);
DER.B=(TIME-U)*L/(1+L)**2;
DER.U=-L*B/(1+L)**2;
OUTPUT OUT=NEWR P=PREADR PARMS= BR UR ESS=SSRESR;
PROC MEANS N NOPRINT;BY RUN;VAR READ;
OUTPUT OUT=NEWS N=NR;
DATA NEWR;SET NEWR;BY RUN; IF FIRST.RUN;
DATA RUN1;MERGE NEWR NEWS;BY RUN;
DFR=NR-2;
DATA RUN2;SET RUN1;
PROC SORT;BY DESCENDING UR;
PROC MEANS SUM;VAR SSRESR DFR;
PROC PRINT;
PROC NLIN;BY PLANT;
PRAMS B=.01 TO .1 BY .02 U= 30 TO 150 BY 30;
L=EXP(-B*(TIME-U);
MODEL READ=1/(1+L);
DER.B=(TIME-U)*L/(1+L)**2;
DER.U=-L*B/(1+L)**2;
OUTPUT OUT=NEWA P=PREAD PARMS=BP UP ESS=SSRESP;
PROC PRINT;
```

APPENDIX-B

```
*                                                                                *
*****************************  WEIGHTED DIALLEL ANALYSIS  ****************************
*                                                                                *
*                                                                                *
**********************************  PARENTS OF CROSSES*****************************
*                                                                                *
*                PARENT 1 = PI 271998                                            *
*                       2 = PI 324607                                            *
*                       3 = OREGON 1604                                          *
*                       4 = ND 364                                               *
*                       5 = WYOMING 166                                          *
*                       6 = VALLEY                                               *
**********************************************************************************
;
DATA TEST;
INPUT RUN 5 TIME50 10-13 1 STDER 15-20 4 MSRES 25-28 5 P1 35 P2 40;
STEU=STDER/SQRT(MSRES);
STEU=STEU*STEU;
SIGCP=.066075;
CARDS;
PROC SORT; BY P1 P2;
PROC MEANS MEAN; BY P1 P2;VAR TIME50 STEU;
OUTPUT OUT=DATA MEAN=TIME50 K;
DATA DATA; SET DATA; K=SQRT(K);
PROC MEANS MEAN DATA=TEST NOPRINT;BY P1; VAR TIME50;
OUTPUT OUT=NUMB MEAN=TIME50;
PROC MEANS N DATA=NUMB NOPRINT; VAR TIME50;
OUTPUT OUT=NUMBER N=NP;
DATA NUMBER; SET NUMBER; KEEP NP;
DATA CO;INPUT L $ 22;CARDS;
CORR     STE_CORR     PR_COR=0
DATA A; INPUT A $ 22; CARDS;
VARIANCE COVAR W+V W-V Y YR STNCRD_Y PARAEQLA RANK_CRD
DATA B; INPUT B $ 22; CARDS;
D F H1 H2 SHGR E
DATA E; INPUT E $ 22; CARDS;
D_OF_DOM POS=NEG DOM=REC GENES
DATA G; INPUT G $ 22; CARDS;
VOLD VILI WCLOI VOLI MLI_MLO MLI_MLO2 D F H1 H2 HSQR ERROR
DATA X; INPUT X $ 22; CARDS;
INTERCPT SLOPE(B) B_ERROR
DATA GO; INPUT RUN $ 22;CARDS;
W-V_HOM   PR_W-V_HOM   B=0   PR_B=0   B=1  PR_B=1
DATA ERROR;SET TEST;
IF _N_ =1;
KEEP SIGCP;
PROC MATRIX;
FETCH P DATA=NUMBER;****DATA SET WITH NUMBER OF PARENTS ONLY;
FETCH Q DATA=DATA;  ****DATA SET WITH P1, P2, OBSERVATION AND WEIGHTING VALUES;
FETCH E DATA=ERROR; ****DATA SET WITH ERROR TERM ONLY;
U=J(P,P,0); ****OBSERVATION VALUES;
K=J(P,P,0);****K VALUES FOR WEIGHTING;
UR=J(P,I,0);
AR=J(P,1,0);
SR=J(P,1,0);
VR=J(P,1,0);****VARIANCE IN AN ARRAY;
WR=J(P,1,0);****COVARIANCE IN AN ARRAY;
*BUILD DIALLEL DATA ARRAY;
IK=NROW(Q);
*DETERMINE NUMBER OF MEANS IN DIALLEL;
```

```
DO I=1 TO IK;
P1=Q(I,1);          ****P1, PARENT 1;
P2=Q(I,2);          ****P2, PARENT 2;
U(P1,P2)=Q(I,3);     ****U, OBSERVARTION VALUES MATRIX;
U(P2,P1)=Q(I,3);     ****U, OBSERVARTION VALUES MATRIX;
K(P1,P2)=Q(I,4);    ****K, WEIGHT MATRIX;
K(P2,P1)=Q(I,4);    ****K, WEIGHT MATRIX;
END;
PRINT Q U K;
*DIALLEL ARRAY IS MATRIX U;
UII=VECDIAG(U);    **** PARENT OBSERVATION VALUES;
KOO=SSQ(K)#/(P#P);          **** AVERAGE VALUE OF WEIGHT;
E=E#KOO;                    **** ERROR CORRECTED FOR MEAN VALUES;
KII=VECDIAG(K);             **** PARENT WEIGHT VALUES;
UP=SUM(UII#/(KII#KII))#/SSQ(1#/KII);
PRINT UII KOO E KII UP;
DO I=1 TO P;
UR(I,1)=SUM(U(,I)#/(K(,I)#K(,1)))#/SUM((1#/(K(,I)#K(,I))));
AR(I,1)=SUM(U(,I)#/(K(,1)#K(,I)));
SR(I,1)=SUM(1#/(K(,I)#K(,I)));
VR(I,1)=(1#/(P-1))#(SSQ((U(,I)#/K(,I)))-(UR(I,1)#UR(I,1))#SUM((1#/(K(,I)#K(,I))
)))#KOO;
WR(I,1)=(1#/(P-1))#(SUM(((UII-UP)#/KII)#(U(,I)-UR(I,1))#/K(,I)))#KOO;
END;
PRINT UR AR SR VR WR;
VCLO=(1#/(P-1))#(SUM((UII#/KII)#(UII#/KII))-(UP#UP#SUM(1#/(KII#KII))))#KOO;
VILI=SUM(VR(,1))#/P;
WCLO1=SUM(WR(,1))#/P;
VCLI=(1#/(P-1))#(SSQ(AR)-(SUM(AR#SR)**2#/SSQ(SR)))#KOO#KOO#/(P#P);
MLI_MLO=((SUM(U#/(K#K))#/SUM(1#/(K#K)))-(SUM(UII#/(KII#KII))#/SUM(1#/(KII#KII)))
);
MLI_MLO2=MLI_MLO**2;
N=P;
PRINT VOLO VILI WCLO1 VOLI MLI_MLO2 MLI_MLO N P;
OOM=VCLO-E;
F=2*VOLO-4*WCLO1-((2*(N-2))*E)#/N;
H1=VCLO-4*WOLO1+4*VILI-(((3*N)-2)*E)#/N;
H2=4*VILI-4*VCLI-2*E;
HSQR=4*MLI_MLO2-(4*(N-1)*E)#/N**2;
OEG_OOM=SQRT(H1#/OOM);
POS_NEG=H2#/(4*H1);
OOM_REC=(SQRT(4*OOM*H1)+F)#/(SQRT(4*OOM*H1)-F);
GENES=HSQR#/H2;
COOM=(N**5+N**4)#/(N**5);
CF=((4*(N**5))+(20*(N**4))-(16*(N**3))+(16*(N**2)))#/(N**5);
CH1=(N**5+(41*(N**4))-(12*(N**3))+(4*(N**2)))#/(N**5);
CH2=(36*(N**4))#/(N**5);
CHSQR=((16*(N**4))+(16*(N**2))-(32*N)+16)#/(N**5);
CE=(N**4)#/(N**5);
W_V=WR-VR;
W_PLUS_V=WR+VR;
* STANDARD ERRORS OF ;
S2=((SSQ(W_V)-((SUM(W_V))**2)#/N)#/((N-1)#2));
SCOM=SQRT((COOM*S2));
SF=SQRT((CF*S2));
SH1=SQRT((CH1*S2));
SH2=SQRT((CH2*S2));
SHSQR=SQRT((CHSQR*S2));
SE=SQRT((CE*S2));
ERROR_OF= SOOM||SF||SH1||SH2||SHSQR||SE;
```

```
* T TEST STAST FOR O F H1 H2 HSQ ERROR;
OCMTT=COM#/SCCM;
IF OCMTT > 0 THEN OT=-1*OCMTT;
IF OCMTT < 0 THEN OT=OOMTT;
FTT=F#/SF;
IF FTT > C THEN FT=-1*FTT;
IF FTT < 0 THEN FT=FTT;
H1TT=H1#/SH1;
IF H1TT > 0 THEN H1T=-1*H1TT;
IF H1TT < C THEN H1T=H1TT;
H2TT=H2#/SH2;
IF H2TT > 0 THEN H2T=-1*H2TT;
IF H2TT < 0 THEN H2T=H2TT;
HSQRTT=HSQR#/SHSQR;
IF HSQRTT > C THEN HSQRT=-I*HSQRTT;
IF HSQRTT < 0 THEN HSQRT=HSQRTT;
ETT=E#/SE;
IF ETT > 0 THEN ET=-1*ETT;
IF ETT < 0 THEN ET=ETT;
POT=PROBT(OT,N-1);
PO=2*POT;
PFT=PROBT(FT,N-1);
PF=2*PFT;
PH1T=PROBT(H1T,N-I);
PH1=2*PH1T;
PH2T=PROBT(H2T,N-1);
PH2=2*PH2T;
PHSQRT=PROBT(HSQRT,N-1);
PHSQR=2*PHSQRT;
PET=PROBT(ET,N-1);
PE=2*PET;
PROB_T=PO||PF||PH1||PH2||PHSQR||PE;
NOTE DIALLEL CROSS DATA;
PARENT=UII*;
STDCCV=(SSQ(WR)-((SUM(WR)**2)#/N))#/(N-1);
STOPAR=SQRT(VCLC#KOO);
STOVAR=(SSQ(VR)-((SUM(VR)**2)#/N))#/(N-1);
PM=SUM(PARENT)#/N;
WM=SUM(WR)#/N;
VM=SUM(VR)#/N;
YR=UII*#/KII*;
STO_Y=(PARENT-LP)#/(STOPAR#KII*);
RO=RANK(W_PLUS_V);
PARABOLA=SQRT(VR#VOLO);
VR1=VR*;WRI=WR*;W_PLUSV=W_PLUS_V*;W_VI=W_V*;PARABCLI=PARABCLA*; RC1=RO*;
STATS=VR1//WR1//W_PLUSV//W_VI//PARENT//YR//STO_Y//PARABCL1//RO1;
FETCH C DATA=A TYPE=CHAR;
NOTE ARRAY STATISTICS; PRINT STATS ROWNAME=C;
PLOT=STATS*;
OUTPUT PLOT CUT=PLT1 (RENAME=(COL1=VARIANCE COL2=CCVAR COL3=W_PLUS_V
COL4=W_V COL5=Y COL6=YR
CCL7=STNORO_Y CCL8=PARABOLA COL9=RANK_ORO ROW=PLT));
CUTPUT STATS CUT=PLT;
MEANS=CEG_OOM||PCS_NEG||OCM_REC||GENES;
NOTE HAYMANS ANALYSIS QUANTIES;
QUANTITY=VOLO||VILI||WOLCI||VOLI||MLI_MLO||MLI_MLO2||OOM||F||H1||H2||HSQR||E;
CUTPUT QUANTITY CUT=VCLC (RENAME=(CCL1=VOLO COL2=VILI COL3=WOLOI COL4=VCLI
CCL5=MLI_MLO CCL6=MLI_MLC2 COL7=O COL8=F COL9=H1 COL10=H2 COL11=HSQR COL12=ERROR
));
FETCH Y DATA=G TYPE=CHAR;
```

```
PRINT QUANTITY COLNAME=Y;
FETCH X7 DATA=B TYPE=CHAR;
NOTE STANDARD ERRORS; PRINT ERROR_OF COLNAME=X7;
NOTE T PROB=C;PRINT PROB_T COLNAME=X7;
FETCH Z DATA=E TYPE=CHAR;
NOTE MEAN EFFECTS OVER ALL PARENTS; PRINT MEANS COLNAME=Z;
MWV=SUM(W_PLUSV)#/N;
C1=SUM((W_PLUSV-MWV)#(PARENT-UP)#/KII*);
C2=SSQ(W_PLUSV)-((SUM(W_PLUSV)**2)#/N);
C3=VOLO#KOO#(P-1);
CORR=C1#/SQRT(C2*C3);
STEC=SQRT((1-CORR**2)#/(N-2));
CORT=CORR#/STEC;
IF CORT > 0 THEN CT=-1*CORT;
IF CORT < 0 THEN CT=CORT;
PROBCA=PRCET(CT,N-2);
PROBC=2*PRCBCA;
CORR1=CORR||STEC||PROBC;
FETCH CO DATA=CO TYPE=CHAR;
NOTE CORRELATION OF Y AND W+V; PRINT CORR1 COLNAME=CO;
VV_VW=(STOVAR-STCCOV)**2;
VVXVW=(STOVAR*STCCOV);
PCOV=VR#WR;
CVRWR2=((SUM(PCOV)-((SUM(VR)*SUM(WR))#/N))#/(N-1))**2;
T2=((N-2)*VV_VW)#/((VVXVW-CVRWR2)*4);
B1=SUM(VR#WR)-((SUM(VR)*SUM(WR))#/N);
B2=SSQ(VR-VM);
B=B1#/B2;
SB=SQRT(((STCCOV*(N-1))-(B*B1))#/((N-2)*B2));
DIF_0=B#/SB;
DIF_1=(1-B)#/SB;
IF T2 > 0 THEN T2A=-1*T2;
IF T2 < 0 THEN T2A=T2;
IF DIF_0 > 0 THEN DIF0=-1*DIF_0;
IF DIF_1 > 0 THEN DIF1=-1*DIF_1;
IF DIF_0 < 0 THEN DIF0=DIF_0;
IF DIF_1 < 0 THEN DIF1=DIF_1;
PROBT2A=PRCBT(T2A,N-1);
PROBT2=2*PROBT2A;
PROBA0=PROBT(DIF0,N-2);
PROB0=2*PROBA0;
PROBA1=PROBT(DIF1,N-2);
PROB1=2*PROBA1;
INTERCEP=WM-B*VM;
NOTE GRAPH STATISTICS;
GRAPH=INTERCEP||B||SB;
FETCH X1 DATA=X TYPE=CHAR;
OUTPUT GRAPH OUT=LINE1 (RENAME=(COL1=INTERCPT COL2=SLOPE COL3=STERR_B));
PRINT GRAPH COLNAME=X1;
TTEST=T2||PRCET2||DIF_0||PROB0||DIF_1||PRCB1;
FETCH X2 DATA=GO TYPE=CHAR;
NOTE T TEST STATISTICS FOR; PRINT TTEST COLNAME=X2;
NOTE NARROW SENSE HERITABILITY ESTIMATES;
HRITBLTY=(0.25*OCM)#/((0.25*(OOM+H1-F))+E);
PRINT HRITBLTY;
PROC CORR DATA=PLT1;
VAR YR W_PLUS_V;
PROC REG DATA=PLT1;
MODEL COVAR=VARIANCE;
DATA PLT1;SET PLT1;
```

```
IF PLT='ROW1' THEN DO; C1=COVAR;PLANT='PI 271998   ';END;
IF PLT='ROW2' THEN DO; C2=COVAR;PLANT='PI 324607   ';END;
IF PLT='ROW3' THEN DO; C3=COVAR;PLANT='OREGON 1604';END;
IF PLT='ROW4' THEN DO; C4=COVAR;PLANT='ND 364      ';END;
IF PLT='ROW5' THEN DO; C5=COVAR;PLANT='WYOMING 166';END;
IF PLT='ROW6' THEN DO; C6=COVAR;PLANT='VALLEY      ';END;
DATA PARAB; SET VOLO;
X1=0.5+(0.5*SQRT(1-((4*(WOLOI-VILI))/VOLO)));
X2=0.5-(0.5*SQRT(1-((4*(WOLOI-VILI))/VOLO)));
VO1=VOLO*X1**2;
WO1=VOLO*X1;
VR1=VOLO*X2**2;
WR1=VOLO*X2;
INTER=WOLOI-VILI;
WPV=WOLOI+VILI;
PROC PRINT;
DATA PARAB1;SET PARAB;
X=VO1;Y1=WO1;VAR=0;COV=INTER;OUTPUT;
X=VR1;Y1=WR1;VAR=VR1;COV=WR1;OUTPUT;
X=VILI;Y1=WOLOI;VAR=.;COV=.; OUTPUT;
KEEP X Y1 VAR COV;
DATA RUN1; SET VOLO;
DO VARIANCE=0 TO 500 BY 5;
PAR82=-1*(SQRT(VARIANCE*VOLO));
OUTPUT;END;
KEEP PAR82 VARIANCE;
PROC SORT; BY DESCENDING VARIANCE;
DATA L2;SET LINE1;
DO VARIANCE=0.00 TO 500 BY 5;
L2=INTERCPT + (SLOPE*VARIANCE);
OUTPUT;END;
DATA RUN;SET VOLO;
DO VARIANCE=0.00 TO 500 BY 5;
PAR82=SQRT(VARIANCE*VOLO);
OUTPUT;END;
KEEP PAR82 VARIANCE;
PROC SORT; BY VARIANCE;
DATA RUN2;SET RUN1 RUN;
DATA PLOT;SET PLT1 RUN2;
LABEL C1=COVARIANCE;
PROC REG OUTEST=EST DATA=PLT1;
MODEL YR=W_PLUS_V;
PROC MEANS MEAN DATA=PLT1;VAR YR;
OUTPUT OUT=MEANY MEAN=YR;
DATA EST; SET EST;B=W_PLUS_V;
TEST=1;KEEP TEST B;
DATA PAR1;SET PARAB;
KEEP WPV;
DATA LINE;MERGE EST MEANY PAR1;
PROC SORT; BY TEST;
DATA WR;SET PLT1;TEST=1;
YR1=YR;
KEEP W_PLUS_V TEST YR1;
DATA WR1; SET PARAB;
W_PLUS_V=WO1+VO1;TEST=1;OUTPUT;
W_PLUS_V=WR1+VR1;TEST=1;OUTPUT;
KEEP TEST W_PLUS_V;
DATA WR2;SET WR WR1;
PROC SORT; BY TEST;
DATA GO;MERGE WR2 LINE ;BY TEST;
```

```
EST=YR+(B*(W_PLUS_V-WPV));
PROC PRINT;
PROC PRINT; VAR YRI EST YR B W_PLUS_V WPV;
DATA GPLOT; SET PLOT PARAB1 L2;
KEEP VARIANCE PARB2 X YI VAR COV C1 C2 C3 C4 C5 C6 PLANT L2;
PROC GPLOT;
TITLE1 VR/WR DIALLEL 6 PARENTS;
SYMBOL1 C=BLACK V=1 F=SIMPLEX;
SYMBOL2 C=BLACK V=2 F=SIMPLEX;
SYMBOL3 C=BLACK V=3 F=SIMPLEX;
SYMBOL4 C=BLACK V=4 F=SIMPLEX;
SYMBOL5 C=BLACK V=5 F=SIMPLEX;
SYMBOL6 C=BLACK V=6 F=SIMPLEX;
SYMBOL8 C=BLACK V=M H=2 F=SPECIAL L=1 I=JOIN;
SYMBOL9 C=BLACK L=1 I=JOIN;
SYMBOL10 C=BLACK L=1 I=SPLINE;
SYMBOL11 C=BLACK L=3 I=JOIN;
PLOT C1*VARIANCE=1 PARB2*VARIANCE=10 C6*VARIANCE=6
C2*VARIANCE=2 C3*VARIANCE=3 C4*VARIANCE=4 C5*VARIANCE=5 L2*VARIANCE=9/0 ;
```

DATA FOR DIALLEL ANALYSIS

1	1	845	63084	1830	2	2
1	2	1028	65752	1079	3	2
1	3	1213	37387	0652	3	3
2	1	1864	114026	0540	3	2
2	2	1235	58557	1450	4	4
2	3	1100	43536	0987	6	2
3	1	943	54162	1226	1	1
3	2	1349	51319	0995	5	2
3	3	1361	54394	0800	3	1
4	1	1204	59871	0861	6	4
4	2	847	60902	1091	2	1
4	3	1262	50405	0901	5	5
6	1	873	69718	1685	5	4
6	2	839	77033	1551	1	1
6	3	1057	62555	1266	4	4
7	1	1351	43001	0764	3	1
7	2	1145	50825	1021	5	3
7	3	1251	61250	1418	5	4
8	1	1282	57053	1091	3	3
8	2	1042	72143	1370	5	6
8	3	1202	60832	1195	2	1
9	1	1338	65940	0964	5	6
9	2	1159	30205	0269	6	4
9	3	1179	27855	0328	6	4
10	1	1016	65841	1636	6	6
10	2	1018	61908	1254	3	3
10	3	1300	48544	0648	5	3
11	1	1223	59766	1698	4	2
11	2	851	56808	1135	5	1
11	3	948	44423	0855	6	1
12	1	930	25178	0319	6	1
12	2	1547	52851	0675	5	5
12	3	918	36853	0612	4	3
13	1	1236	35018	0471	5	1
13	2	831	47529	0693	3	1
13	3	894	36708	0662	4	1
14	1	767	36962	0670	4	3
14	2	1015	60145	0822	6	2
14	3	1167	54144	1193	5	6
15	1	1807	107745	1374	5	2
15	2	958	40807	0494	2	2
15	3	1099	38644	0478	3	2
16	1	1521	45733	0421	4	1
16	2	994	69241	1340	4	1
16	3	1083	42863	0946	6	6
17	1	1367	85098	2150	5	3
17	2	884	27732	0347	4	3
17	3	950	35595	0598	2	2
18	1	1249	76041	1506	2	1
18	2	1227	52269	0873	6	3
18	3	1167	53654	0946	5	1
19	1	867	27896	0522	4	4
19	2	1590	89660	1457	4	2

19	3	1272	34306	0560	4	2
20	1	1364	49092	0515	6	2
20	2	1409	39389	0422	6	1
20	3	1341	60538	1066	6	3
21	1	958	63123	1391	5	5
21	2	1388	44630	0595	5	4
21	3	1212	31507	0448	5	2
1	4	791	67836	1286	5	1
2	4	817	32954	0680	3	3
3	4	598	55568	1082	5	6
4	4	1115	47725	0871	4	1
5	4	769	83919	3137	6	6
6	4	681	60516	1373	4	3
7	4	698	45314	1029	6	4
8	4	733	74729	0906	2	1
9	4	939	37583	0625	6	1
10	4	826	166782	5146	6	3
11	4	1163	71097	1980	5	5
12	4	772	28658	0365	5	4
13	4	954	44030	0805	6	2
14	4	628	28770	0384	2	2
15	4	1065	62766	1753	4	2
16	4	704	52774	1033	1	1
17	4	1147	66900	1852	5	3
18	4	750	39684	0644	4	4
19	4	909	51495	0919	3	1
20	4	573	65231	1051	3	2
21	4	1268	35342	0761	5	2

A DIALLEL ANALYSIS OF CELLULAR MEMBRANE THERMOSTABILITY IN COMMON BEAN (PHASEOLUS VULGARIS L.)

by

BIBO XU

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Abstract

To estimate the genetic component of cellular membrane thermostability in Phaseolus vulgaris, parental and F_1 plants from a 6-parent half diallel were tested by electric conductivity and the results were analyzed by Hayman's method. Membrane thermostability was found to be a quantitative trait, with environmental and dominant effects accounting for most of the phenotypic expression. Narrow sense heritability was relatively low (5.4%)