Genetics of Heat Tolerance during Reproductive Development in Common Bean

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ABSTRACT

Common bean (*Phaseolus vulgaris* L.) is grown in regions where high temperatures during reproductive development reduce yields. The purpose of this study was to identify sensitive growth stages during reproductive development and to investigate the genetics of heat tolerance during these stages. Exposure to high temperatures during two reproductive growth stages, namely flower bud formation and pod filling, resulted in particularly severe damage. This damage was evaluated by scoring two corresponding traits—flower bud abortion and reduced pod fill. For each trait, two tolerant and two susceptible large-seeded dry bean genotypes were chosen and crossed in all combinations, including reciprocals. The parents and control cultivars were evaluated under heat stress conditions at two locations in the Central Valley of California; this allowed us to determine that genotype × environment interactions were present for both traits. Genetic studies included parents, F_1 and F_2 progenies, and control cultivars at one of the above locations. Both traits displayed continuous variation, indicating quantitative inheritance. Generation means analyses demonstrated that additive genetic effects were significant for both heat tolerance traits, but were more important for tolerance to bud abortion. Significant dominance effects for tolerance to bud abortion were attributed to either linkage or pleiotropy of the single dominant gene conferring indeterminate growth habit. Both generation means and diallel analyses demonstrated the presence of cytoplasmic effects including interactions of cytoplasmic with nuclear genes. The significant additive effects observed indicate that gain from selection for improved heat tolerance should be possible for both traits.

HEAT STRESS, especially during reproductive development, causes severe yield reductions in common bean. This crop evolved under cool conditions in the highlands of Central and South America where temperatures during the growing season average 12 to 24°C (Debouck and Tohme, 1988). Despite this, common bean is grown commercially in climates that pose a marked temperature stress, such as the Central Valley of California where maximum daytime temperatures during the growing season reach 45°C. Temperatures of this magnitude inhibit processes in common bean that affect overall productivity such as photosynthesis (Chaisompongpan et al., 1990) and nitrogen fixation (Hernandez et al., 1987) and can cause damage by disrupting plasma membrane integrity (Chen et al., 1982). More importantly, exposure to less extreme temperatures during critical reproductive stages can directly affect seed yield.

Most reproductive stages in common bean are sensitive to high temperatures, including flower bud formation, flowering, pollen formation and function, fertilization, and pod and seed set (Konsens et al., 1991; Monterroso and Wien, 1990; Smith and Pryor, 1962; Weaver et al., 1985). Heat-induced abscission of flower buds before anthesis could be due to decreased carbohydrate levels or translocation constraints (Konsens et al., 1991). However, heat damage occurring after anthesis, such as flower abscission and low pod and seed set, is likely to include lack of pollination or fertilization as an important factor (Bouwkamp and Summers, 1982; Konsens et al., 1991). The extreme sensitivity of common bean pollen to heat, as documented by stainability (Halterlein, 1980; Weaver et al., 1985) and germination tests (Dickson and Boettger, 1984; Weaver and Timm, 1988), could account for a lack of fertilization under heat stress. It appears that pollen is more sensitive to high temperatures than are female reproductive structures (Dickson and Boettger, 1984; Monterroso and Wien, 1990). In particular, high night temperatures are very detrimental to pod and seed set in legumes, including common bean (Konsens et al., 1991), lima bean (*Phaseolus lunatus* L.; Fisher and Weaver, 1974), and cowpea [*Vigna unguiculata* (L.) Walp.; Hall, 1990]. In both common bean (Konsens et al., 1991) and lima bean (Fisher and Weaver, 1974), high temperatures and not water stress were responsible for the damage, since increased irrigation or relative humidity did not prevent the low pod set.

Despite the well documented sensitivity of common bean to high temperatures, literature on the genetics of heat tolerance during reproductive development is limited. Quantitative inheritance with large environmental effects was reported for heat tolerance at pod and seed set in snap bean (*P. vulgaris*) by Dickson and Petzoldt (1989). Bouwkamp and Summers (1982), however, concluded that heat and drought tolerance at pod set was due to a single dominant gene in one snap bean accession and to two genes with epistatic action in another.

Heat tolerance during reproductive development in cowpea has been more thoroughly characterized (Hall, 1990; Hall, 1992). Tolerance to inhibition of flower bud development under high temperatures and long day conditions was due to one recessive gene (Hall, 1992, data not presented). Tolerance during pollen formation, which affects pod set, was controlled by a single dominant gene, but was greatly influenced by environmental factors (Marfo and Hall, 1992).

The goal of this study was to investigate the genetic control of heat tolerance in common bean at two reproductive growth stages particularly sensitive to high temperatures. Improved tolerance during reproductive development could lead to improved yield under heat stress conditions.

MATERIALS AND METHODS

Screening Trial

A total of 187 common bean lines, including cultivars, plant introductions, and advanced breeding lines, were evaluated

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Abbreviations: ANOVA, analysis of variance; GCA, general combining ability; LSD, least significant difference; MS, mean square; SCA, specific combining ability; SS, sums of squares; WSFS, West Side Field Station, Five Points, CA.

for heat tolerance under field conditions during 1987 in the Central Valley of California. Seeds were obtained from various breeding programs in the USA and from the Centro International de Agricultura Tropical, Cali, Colombia. Some lines were reported to be heat tolerant in their respective environments (personal communication by contributors). A complete list is available from the corresponding author. Two locations, the West Side Field Station (WSFS) and Davis, were chosen because of their high temperatures, which often occur during reproductive development of common bean. The July and August average daily maximum/minimum temperatures over a 10-yr period (1981-1990) were 35/17°C and 34/13°C at WSFS and Davis, respectively. Night temperatures, which appear to be critical for pod and seed set in legumes, were especially high at WSFS. Production practices, including furrow irrigation every 10 to 14 d, were the same as those used in the U.C. Davis bean breeding program. Lines with sufficient seeds were planted in a randomized complete block design with two replications at each location; a number of lines were planted at WSFS only.

All lines were scored weekly for stress symptoms affecting reproductive development. Traits included abortion of flower buds, flowers, pollen, pods and seeds, and the yield components, pods/plant, seeds/pod and seed weight. Early flower bud formation and pod filling (proportion of fully developed seeds/pod) were the most sensitive stages, especially among the large-seeded, determinate types similar to the kidney bean (*P. vulgaris*) cultivars grown in California. Growth chamber experiments, at 35/25°C and 25/15°C day/night temperatures, confirmed that high temperatures resulted in symptoms at bud formation and pod filling similar to but more severe than those observed in the field (Shonnard, 1991).

Based on this preliminary screening of heat tolerance, two traits were chosen for further evaluation, flower bud abortion and percent pod fill. For each trait, two tolerant and two susceptible lines were selected as parents for an inheritance study (Table 1). An additional tolerant line, PA8, the only small-seeded line used as a parent, was later discontinued because of problems with F_1 seedling lethality, which was due to the presence of *Dl* genes (Gepts and Bliss, 1985; Shii et al., 1980), in crosses with the other, large-seeded lines. All of the parents used in the inheritance study had large seed size similar to kidney beans and, with the exception of PA2, had a determinate growth habit (Singh, 1982).

Inheritance Study

Field Evaluation

For each of the two traits evaluated, a complete diallel crossing program including reciprocals was established involving the two tolerant and two susceptible parents (Table 1). The F_1 and F_2 seeds of all 12 combinations and of the four parents were produced for each diallel during the fall, winter, and spring of 1987-1988 in the greenhouse at Davis.

One trial was planted at WSFS in the summer of 1988. It included the tolerant and susceptible parents and their F_1 and F_2 progenies for both traits, as well as cultivars representing the major market classes in California (Table 1). A second trial, consisting of parents and control cultivars only, was planted at Davis to evaluate the effect of environment on bud abortion and percent pod fill. Materials were planted in a randomized complete block design with two replications. Each plot consisted of a single row of 40 plants (15 plants for F_1s). Spacing was 15 cm within rows and 152 cm between rows (F_1 plots had identical within row spacing, but were shorter).

All plots were scored on a single plant basis for tolerance to bud abortion or percent pod fill; cultivars were scored for both traits. Bud abortion was scored on a visual scale from 2 = no damage to 9 = complete abortion of all buds (Shonnard, 1991). Scoring was initiated approximately 1 wk prior to first flower (between stages R5 and R6; Gepts, 1987). We noticed a positive association between indeterminate growth habit and tolerance to bud abortion, and therefore, took data on growth

Table 1. Parents, tolerant (T) and susceptible (S) to heat stress at bud formation and pod filling, and cultivars representative of California market classes, evaluated for heat tolerance at Davis and West Side Field Station in 1988.

Parents–bud abortion†				
Parent	Tolerance	Line	Growth habit‡	Seed type
PA1	T	G122	I A	Cream, elongated, red streaks
PA2	T	G5273	III B	Tan, elongated
PA3	S	CDRK×(C17×7756)	I A	Dark red kidney
PA4	S	BAT1558	I A	Light cream, pinto shape
Parents–Pod fill†				
Parent	Tolerance	Line§	Growth habit‡	Seed type
PA1	T	G122	I A	Cream, elongated, red streaks
PA5	T	BAN26	I A	Tan, elongated
PA6	S	GLP1127A	I A	Cream, elongated, black speckled (Mwezi Moja type)
PA7	S	Sac×(2602×C17)	I A	Light red kidney
PA8	T	Negro Argel	II B	Small black, discontinued as parent due to F_1 seedling lethality
Cultivars–Bud abortion and pod fill†				
Cultivar		Line	Growth habit‡	Seed type
CV1		Sal	III B	Small white
CV2		Turtle Soup 39	II B	Small black
CV3		Sutter Pink	III A	Pink
CV4		Linden	I A	Light red kidney
CV5		Red Kidney	I A	Light red kidney
CV6		California Dark Red Kidney	I A	Dark red kidney

† The parents G122, G5273, BAT1558, and Negro Argel were CIAT lines; GLP1127A from Kenya was supplied by J.G. Waines, UC Riverside; CDRK×(C17×7756), BAN26, Sac×(2602×C17) and the cultivars were supplied by D. Helms, UC Davis.
‡ I: determinate; II: indeterminate upright; III: indeterminate prostrate; A: without runners; B: with runners.
§ Carriers of *Dl-1* gene (PA8) and *Dl-2* gene (PA1, PA5, PA6, PA7).

habit for the F_2 families segregating for this trait at WSFS. Pod fill was calculated as the percentage of ovules/pod that developed into mature seeds, based on six pods/plant at harvest. Seed yield was obtained on single plant data at WSFS, and on plot means at Davis.

Statistical Analysis

Statistical Analysis System (SAS, 1985), a Fortran computer program DIALL (Schaffer and Usanis, 1969), and Microsoft Excell version 4.0 (Microsoft Corp., Redmond, WA) were used for analyses. Analyses of variance (ANOVAs) were conducted on plot means for bud abortion, percent pod fill, and yield. Error deviates of plot means for all of the data were tested for normality. Mean square error (MS_e) terms for each location were tested for homogeneity before ANOVAs were pooled over locations. Replications and locations were considered random effects, while groups (cultivars, parents, F_1s, and F_2s) and entries within groups were considered fixed effects. To test for effects of the environment, a first ANOVA was conducted on the cultivars and parents which were grown at both locations. A second ANOVA permitted comparisons among all four groups, cultivars, parents, F_1s, and F_2s, evaluated at WSFS. For main effects, Fisher's protected LSDs(0.05) were calculated. For the Group main effect, which had different numbers of entries per group, LSDs(0.05) were calculated for pairwise comparisons with equal variance (pooled MS_e) but unequal replication (Steel and Torrie, 1980; p. 191). Crosses with the small-seeded line PA8 were not included in any of the remaining analyses due to problems with seedling lethality.

A generation means analysis according to Mather and Jinks (1977) was conducted for either bud abortion or percent pod fill for each cross. Their model describes the phenotype in terms of the midparent value m, additive effects [d], dominance effects [h], and three types of digenic interactions: additive × additive [i], additive × dominance [j], and dominance × dominance [l]. Without backcross generations, as in this study, additive × dominance interactions [j] cannot be estimated, and in the presence of epistasis, these interactions are confounded with additive effects [d] (Hayman, 1958).

Reciprocal differences were significant ($P < 0.01$) for F_1 and/or F_2 families of several crosses, as determined by t tests with single plant values. Data from reciprocals were separated for these crosses, resulting in six generations: tolerant parent, susceptible parent, F_1, reciprocal F_1, F_2, and reciprocal F_2. Because reciprocal differences were not constant between the F_1 and F_2 generations, we used a model which accounts for interactions between nuclear and cytoplasmic genomes (Model B of Mosjidis et al.; 1989). This model, assuming no paternal cytoplasmic inheritance, includes two additional terms: maternal cytoplasmic effects on the homozygote [cd] and maternal cytoplasmic effects on the heterozygote [ch] (notation altered to correspond with above model of Mather and Jinks, 1977). Only terms for maternal cytoplasmic effects were included in the model, because evidence from cytoplasmic male sterility in common bean indicates that cytoplasm is maternally inherited (Khairallah et al., 1992; H. Bannerot, 1993, personal communication). With six generations, a model with up to five parameters (midparent value plus up to four effects) can be tested. First the adequacy of an additive-dominance model with cytoplasmic effects, including m, [d], [h], and [cd] and/or [ch] was tested (Mather and Jinks, 1977; Mosjidis et al., 1989), by weighted least squares regression (Foolad and Jones, 1991). If the model did not fit (significant chi-square), this indicated the presence of epistasis. Further models including interaction effects were then tested. Effects that were considered to be unimportant (nonsignificant t test and low sums of squares) were subsequently dropped from the model. However, to be biologically meaningful, models were required to include main effects if the corresponding interaction terms were present. In the presence of epistasis, approximate epistasis-free expectations of the genetic parameters [d] and [h] were derived from the m, [d], [h] model on the assumption of no epistasis, according to Hayman (1958).

For crosses without reciprocal differences, reciprocals were pooled, resulting in four generations only: tolerant parent, susceptible parent, F_1, and F_2. With four generations, only m (the midparent value) plus two effects could be included in the model. First, the adequacy of a simple, additive-dominance model, including m, [d], and [h] was tested (Mather and Jinks, 1977). If the model did not fit, a second model including m, [d], and [i] was tested. No other three parameter model was deemed to be biologically meaningful.

Coefficients of the genetic effects for the generation means model are presented for crosses with reciprocal differences (Table 2). Only coefficients involving cytoplasmic effects differ between reciprocals; therefore, for crosses with reciprocals pooled, coefficients for the nuclear effects can be read from the same table.

Midparent heterosis was calculated as the difference between the mean of the reciprocal F_1s and the mean of the parents for each cross. Significance was determined with a t test using the MS_e from the ANOVA (Delaney and Lower, 1987).

In progeny of crosses of the indeterminate tolerant parent (PA2) with any of the determinate parents (PA1, PA3, or PA4), observations indicated an association between indeterminate growth habit and tolerance to bud abortion. Tests of independence (Strickberger, 1968) determined if segregation data for determinacy from reciprocals could be pooled. Fit to the expected 3 indeterminate: 1 determinate segregation ratio (Norton, 1915) was evaluated with a goodness-of-fit test (Strickberger, 1968). Finally, t tests compared the mean bud abortion score of the indeterminate vs. determinate F_2 progenies for each cross, to determine if factor(s) for heat tolerance at flower bud formation were linked to the gene controlling indeterminate growth habit.

Diallel analyses were conducted separately on the F_1 and F_2 generations according to Griffing's (1956) Method 3 (crosses and reciprocals) Model I (fixed parents) with plot means. The sums of squares (SS) of reciprocal effects were partitioned further into either reciprocal general SS and reciprocal specific SS according to Cockerham and Weir (1977) or into the corresponding maternal SS and reciprocal SS of Schaffer and Usanis (1960). Both methods of partitioning yielded identical results; therefore, only results from the Cockerham and Weir analyses will be presented. The MS_e values from the ANOVA at WSFS were used as error terms for F tests. General and specific

Table 2. Coefficients of genetic effects in the model used for the generation means analysis.

	Genetic effects†						
Generation	m	[d]	[h]	[i]	[l]	[cd]	[ch]
P_1 (larger mean)	1	1	0	1	0	1	0
P_2 (smaller mean)	1	−1	0	1	0	−1	0
F_1 ($P_1 \times P_2$)	1	0	1	0	1	0	1
F_{1R} ($P_2 \times P_1$)	1	0	1	0	1	0	−1
F_2 ($P_1 \times P_2$) selfed	1	0	1/2	0	1/4	1/2	1/2
F_{2R} ($P_2 \times P_1$) selfed	1	0	1/2	0	1/4	−1/2	−1/2

† m = mean; [d] = additive effects; [h] = dominance effects; [i] = additive × additive interactions; [l] = dominance × dominance interactions; [cd] = maternal cytoplasmic effects on the homozygotes; [ch] = maternal cytoplasmic effects on the heterozygotes. Without additional generations (i.e. backcrosses) the [j] = additive × dominance interaction cannot be estimated, and is confounded with [d].

combining ability effects, instead of variance components, were estimated (Griffing, 1956) since the parents represented a fixed sample (Cockerham, 1963; Hallauer and Miranda, 1981).

RESULTS AND DISCUSSION

Analyses of Variance

Inbred Lines Grown at Two Locations

For the control cultivars (CV) and parents (PA) grown at both locations in 1988, the effect of location was not significant for any trait, while the Location × Group (L × G) interaction was significant for percent pod fill, and the Location × Entry /Groups (L × E/G) interaction was significant for all traits (Table 3). This indicates that while severity of overall stress levels was similar at both locations, performance of individual genotypes was affected by local differences in timing or type of stress. Due to the significant L × E/G interaction, means of entries were presented at each location separately (Table 4).

For bud abortion, the cultivars as a group were more tolerant than the parents, largely due to the extreme susceptibility of PA3 and PA4. Depending on the location, the tolerant large-seeded parent with determinate growth habit (PA1) was similar to, or more tolerant than, the large-seeded kidney cultivars (CV4, CV5, CV6), while the other tolerant large-seeded parent with indeterminate growth habit (PA2) was approximately as tolerant as the indeterminate small-seeded cultivars (CV1, CV2) with almost no bud abortion (Table 4).

For percent pod fill, no difference was found between the parental and cultivar groups; however, significant differences were found among the parents (Table 3). At each location, the two susceptible parents (PA6, PA7) had the lowest percent pod fill, while the two large-seeded, tolerant parents (PA1, PA5) had pod fill values similar to, or somewhat lower than, most of the cultivars (Table 4). At WSFS, performance of PA5 was intermediate with only 56% pod fill. The two small, black-seeded lines (PA8, CV2) consistently had very high pod fill levels.

As a group, the cultivars had significantly higher yields than those parents evaluated for bud abortion. However, for both traits, the large-seeded parents had yields similar to the kidney cultivars (CV4, CV5, CV6), and were appropriate for a study seeking to improve heat tolerance of this commercial bean class.

Genetic Study at WSFS

A second ANOVA compared all four groups grown at WSFS: control cultivars, parents, and the F_1 and F_2 progenies (Table 5). The four Groups (G) and individual Entries/Groups (E/G) differed significantly for bud abortion and percent pod fill.

The cultivars were the most tolerant group to bud abortion as determined by LSD tests. The F_1 generation was more tolerant than both the parents and the F_2 progenies, suggesting that there may be heterosis for tolerance at flower bud formation in these materials. The performance of both F_1 and F_2 groups was predictable; progenies from crosses of tolerant by tolerant parents were tolerant, of susceptible by susceptible parents were susceptible, and of tolerant by susceptible parents were intermediate (Table 6).

For percent pod fill, LSD tests indicated that the cultivars as a whole were more tolerant than the other three groups which did not differ from each other. Differences in percent pod fill were not significant among the F_1, but were highly significant among the F_2 progenies

Table 3. Mean squares from analyses of variance for bud abortion and yield or for percent pod fill and yield of cultivars and parents grown at Davis and West Side Field Station.

		Materials scored for bud abortion			Materials scored for pod fill	
Source of variation†	df	Bud abortion	Yield	df	Pod fill	Yield
		visual score	g/plant		% fill	g/plant
Locations (L)	1	0.49	4943	1	531	4258
Reps/L (R/L)	2	0.10	447**	2	55*	402**
Groups (G)	1	19.80***	3684***	1	1148	4056
L × G	1	0.07	265	1	154**	58
R/L × G	2	0.31	143	2	43	285*
Entries/G (E/G)	8	10.64***	927	9	337**	1107*
Among cultivars‡	5	4.36**	1138*	5	154	1138*
Among parents‡	3	21.11**	576	4	566**	1068*
L × E/G	8	0.33*	281**	9	61**	241**
Error (R/L × E/G)	16	0.12	78	18	14	64
Total	39			43		
CV, %		8	20		6	18

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

† The appropriate error terms for *F* tests were as follows: Error (R/L × E/G) was the error term for L × E/G, R/L × G, and R/L; L × E/G was the error term for Among entries and E/G; R/L × G was the error term for L × G; L × G was the error term for G; and R/L was the error term for L. Nonsignificant effects were assumed to be zero, and were dropped from the Expected MS of further *F* tests.

‡ To test for differences among entries within each group (cultivars or parents), MS for Among entries were obtained from ANOVAs for each group separately and divided by the appropriate error MS (L × E/G) from this combined ANOVA.

Table 4. Mean bud abortion and percent pod fill values of cultivars and parents grown at both Davis and West Side Field Station (WSFS). Calculations based on plot means.

	Bud abortion†			Pod fill†	
	Davis	WSFS		Davis	WSFS
	visual score			% fill	
Cultivars			Cultivars		
CV1	2.2‡	2.6	CV1	68§	64
CV2	2.4	2.0	CV2	80	83
CV3	4.0	4.0	CV3	83	71
CV4	4.7	4.3	CV4	77	74
CV5	5.0	4.4	CV5	70	73
CV6	4.2	3.3	CV6	69	63
Parents			Parents		
PA1	4.5	3.3	PA1	67	66
PA2	2.1	2.7	PA5	68	56
PA3	6.3	6.4	PA6	58	50
PA4	7.6	7.4	PA7	64	36
			PA8¶	83	78

† For bud abortion, 2 = no damage to 9 = complete abortion of all buds; percent pod fill is the percentage of ovules/pod that developed into mature seeds.

‡ LSD(0.05) for comparison of individual entry × location means for bud abortion is 0.8.

§ LSD(0.05) for comparison of individual entry × location means for pod fill is 9.

¶ PA8 was not used in genetic analyses due to seedling lethality in crosses with other parents.

Table 5. Mean squares from analyses of variance for bud abortion and yield or for percent pod fill and yield of cultivars, parents, F_1 and F_2 families grown at West Side Field Station.

		Materials scored for bud abortion			Materials scored for pod fill	
Source of Variation†	df	Bud abortion	Yield	df	Pod fill	Yield
		visual score	g/plant		% fill	g/plant
Reps (R)	1	0.22	269	1	171	79
Groups (G)	3	5.95**	1975***	3	502**	1803
R × G	3	0.09	342	3	29	370**
Entries/G (E/G)	30	5.72**	346**	35	167**	298***
Among cultivars‡	5	1.91**	1123**§	5	103*	1123**
Among parents‡	3	10.38**	119§	4	486**	296**
Among F_1‡	11	6.66**	316§	11	57	136
Among F_2‡	11	5.24**	133*§	15	184**	143
Error (R × E/G)	30	0.10	147	35	32	75
Total	67			77		
CV, %		7			9	

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

† The appropriate error terms for *F* tests were as follows: Error (R × E/G) was the error term for Among entries, E/G, R × G, and R; and R × G was the error term for G. Nonsignificant effects were assumed to be zero, and were dropped from the Expected MS of further *F* tests.

‡ To test for differences among entries within each group (cultivars, parents, F_1s, or F_2s), MS for Among entries were obtained from ANOVAs for each group separately and divided by the appropriate error MS, Error (R × E/G), from this combined ANOVA.

§ For yield of materials scored for bud abortion, the MS_e of the four ANOVAs for each group separately were not homogeneous. *F* tests among entries within each group, for this trait only, were therefore calculated by using the MS_e terms from the four separate ANOVAs (separate MS_e terms not shown).

Table 6. Mean bud abortion and percent pod fill values of F_1 and F_2 families, with reciprocals (F_1R and F_2R) separate, grown at West Side Field Station. Calculations based on plot means.

	Bud abortion†					Pod fill†			
	F_1	F_1R	F_2	F_2R		F_1	F_1R	F_2	F_2R
	visual score					% fill			
Cross					Cross				
PA1 × PA2	2.1‡	2.3	3.0	3.0	PA1 × PA5	65§	67	55	72
PA1 × PA3	4.9	4.9	4.3	5.9	PA1 × PA6	66	58	63	62
PA1 × PA4	6.0	6.0	6.8	5.4	PA1 × PA7	64	57	60	60
PA2 × PA3	3.0	3.0	4.0	3.6	PA5 × PA6	65	62	72	64
PA2 × PA4	3.0	3.0	3.7	3.7	PA5 × PA7	56	70	46	57
PA3 × PA4	6.9	7.1	7.3	7.1	PA6 × PA7	56	53	54	57
					PA1 × PA8¶				59
					PA5 × PA8¶				40
					PA6 × PA8¶				61
					PA7 × PA8¶				76

† For bud abortion, 2 = no damage to 9 = complete abortion of all buds; percent pod fill is the percentage of ovules/pod that developed into mature seeds.

‡ LSD(0.05) for comparison of individual cross by family means for bud abortion is 0.6.

§ LSD(0.05) for comparison of individual cross by family means for pod fill is 11.

¶ Crosses with PA8 were not used in genetic analyses due to seedling lethality with other crosses. Even though no plants from F_1 families with PA8 survived in the field, F_2 seeds were obtained in the greenhouse, since seedling lethality is temperature sensitive.

(Table 5); in addition, tolerance of the F_2 progenies was not predictable based on tolerance of the parents (Table 6), suggesting the presence of epistasis.

Generation Means Analyses

Tolerance to Bud Abortion

The six models from the stepwise regression (one model for each cross) explained from 90 to almost 100% of the variation in bud abortion present among the generation means (Table 7). The significant departure from the model (significant Chi-square) for cross PA2 × PA1 could be due to the presence of digenic or higher order interactions, interactions among linked genes, or environmental effects (Mather and Jinks, 1977). Additive effects [d] were present and significant in the models for all four crosses between the two tolerant (PA1, PA2) and two susceptible (PA3, PA4) parents, indicating that selection for tolerance to bud abortion should be effective in these crosses. Two crosses (PA1 × PA3 and PA1 × PA4) had significant differences among reciprocal F_2 families. Maternal cytoplasmic effects on the homozygotes [cd], which would be expected to become apparent in the more inbred F_2, were highly significant for both of these crosses. Dominance effects [h] were present and significant only for crosses involving the indeterminate line PA2. Highly significant values for midparent heterosis also suggested the presence of dominance effects in the three crosses involving PA2 (Shonnard, 1991).

PA2 was the only indeterminate parent used in this study, and the strong association, observed between indeterminate growth habit (a dominant trait) and tolerance to bud abortion in the F_2, was investigated. Segregation for the three sets of crosses involving PA2 fit the expected ratio of 3 indeterminate: 1 determinate F_2 plant (Shonnard, 1991). For each cross, the indeterminate F_2s (with mean bud abortion scores of 2.4 for PA2 × PA1 plus reciprocal, 2.8 for PA2 × PA3, 3.0 for PA3 × PA2, and 3.0 for PA2 × PA4 plus reciprocal) were significantly ($P < 0.001$) more tolerant to bud abortion than the

Table 7. Genetic effects included in the generation means analysis model for bud abortion and their estimates (± SE), the proportion of the variation accounted for by the model (R^2), and the Chi-square statistic to test the fit of the proposed model, for each cross evaluated (including reciprocals).

	Model			Fit of model		
Cross†	Genetic effects (± SE)			R^2 (%)	χ^2	df
PA2 × PA1	[d] = 0.3 ± 0.2	[h] = −0.8 ± 0.3		90	10.0**	1
PA1 × PA3‡	[d] = 1.5 ± 0.3*		[cd] = 1.6 ± 0.2**	99	1.3	3
PA1 × PA4‡	[d] = 1.9 ± 0.4**	[i] = −0.7 ± 0.0**	[cd] = −1.5 ± 0.1**	99.95	0.3	2
PA2 × PA3	[d] = 2.0 ± 0.0**	[h] = −1.6 ± 0.1*		99.97	0.5	1
PA2 × PA4	[d] = 2.5 ± 0.0**	[h] = −2.1 ± 0.0**		99.99	0.4	1
PA3 × PA4	[d] = 0.4 ± 0.2	[i] = −0.2 ± 0.2		94	3.7	1

*, ** Significant at the 0.05 and 0.01 probability levels, respectively (*t* test for effects; χ^2 for model). Significant χ^2 indicates that the model does not fully explain the data.

† More tolerant parent × more susceptible parent.

‡ Crosses for which reciprocal F_2 families differed significantly for bud abortion.

Table 8. Genetic effects included in the generation means analysis model for percent pod fill and their estimates (± SE), the proportion of the variation accounted for by the model (R^2), and the Chi-square statistic to test the fit of the proposed model, for each cross evaluated (including reciprocals).

Cross†	Model: Genetic effects (± SE)			Fit of model		
				R^2 (%)	χ^2	df
PA1 × PA5‡	[d] = 4 ± 5	[h] = 6 ± 8	[cd] = −17 ± 1**	99	0.2	2
PA1 × PA6§	[d] = 7 ± 2*	[h] = 3 ± 4	[ch] = 4 ± 2	93	2.7	2
PA1 × PA7	[d] = 13 ± 4	[i] = −10 ± 0**		99.99	0.01	1
PA5 × PA6‡	[d] = 4 ± 5	[i] = −13 ± 3*	[cd] = 8 ± 4	93	3.6	2
PA5 × PA7‡§	[d] = 10 ± 7	[h] = 16 ± 9	[ch] = −8 ± 1*	98	1.2	2
PA6 × PA7	[d] = 6 ± 5	[i] = −13 ± 0*		99.85	0.05	1

*, ** Significant at the 0.05 and 0.01 probability levels, respectively (*t* test for effects; χ^2 for model). Lack of significant χ^2 indicates that the model fully explains the data.
† More tolerant parent × more susceptible parent.
‡ Crosses for which reciprocal F_2 families differed significantly for percent pod fill.
§ Crosses for which reciprocal F_1 families differed significantly for percent pod fill.

corresponding determinate plants (with corresponding scores of 4.5, 6.3, 6.0, and 5.9). Thus, segregation for a single gene, controlling the easily scorable trait of growth habit, had a major influence on the quantitative trait of bud abortion. This gene controlling growth habit is either linked to factor(s) affecting heat tolerance during flower bud formation or has a pleiotropic effect.

Tolerance to Reduced Pod Fill

Midparent heterosis for percent pod fill was significant for four of the six crosses evaluated (all except PA1 × PA5 and PA1 × PA6; Shonnard, 1991). The presence of heterosis in common bean has been previously reported for yield, yield components, and architectural traits (e.g. Foolad and Bassiri, 1983; Nienhuis and Singh, 1986; and Wassimi et al., 1986).

All of the models for percent pod fill (Table 8) adequately described the data (nonsignificant Chi-squares) and explained from 93 to almost 100% of the variation among the generation means. Additive effects were significant in the model for only one cross (PA1 × PA6), indicating that effective selection for this trait may be more difficult. Additive × additive interactions [i] appeared to significantly decrease percent pod fill for three of the crosses. When these interactions make up a large portion of the genetic variance, Matzinger (1963) cautioned against severe selection in early generations in order to allow fixation of desirable epistatic combinations. Both crosses with significant differences between reciprocal F_1 families (PA1 × PA6 and PA5 × PA7) had models which included maternal cytoplasmic effects on the heterozygotes [ch]; these effects would be expected to be present to the greatest degree in the F_1. Among the three crosses with significant differences between reciprocal F_2 families, two (PA1 × PA5 and PA5 × PA6) had models which included maternal cytoplasmic effects on the homozygotes [cd]; these effects would be greater with the increased homozygosity present in the F_2 families.

The generation means analyses allowed us to separately evaluate the type of genetic effects present in each cross. This permitted the identification of the large dominance effects present for bud abortion in crosses with the indeterminate PA2. However, first order statistics can result in cancellation of positive and negative values of effects in the model, unless all positive alleles (those increasing the tolerance) are associated in one parent, and all negative alleles in the other. Thus, the analysis is theoretically best suited to crosses between very tolerant and very susceptible parents.

Diallel Analyses

The general combining ability (GCA) mean squares (MS) for bud abortion were highly significant and of substantially greater magnitude than any of the other MS for both the F_1 and F_2 generations (Table 9). PA2 with large negative GCA effects contributed tolerance to bud abortion to its F_1 and F_2 progenies, while use of PA3 and PA4 resulted in susceptible offspring (Table 10). The specific combining ability (SCA) MS for bud abor-

Table 9. Mean squares from diallel analyses conducted on two sets of parents for the F_1 and F_2 generations.

	Materials scored for bud abortion						Materials scored for pod fill					
	Bud abortion			Yield			Pod fill			Yield		
Source	df	F_1	F_2	df	F_1	F_2	df	F_1	F_2	df	F_1	F_2
Among F_1/F_2	11	6.63**	5.24**	11	316	133*	11	57	107**†	11	136	84†
GCA	3	23.63**	16.81**	3	701	385**	3	95*	161**	3	180	156
SCA	2	0.96**	1.05**	2	354	36	2	7	105	2	236	35
Reciprocal general	3	0.02	0.40*	3	39	30	3	26	65	3	80	7
Reciprocal specific	3	0.01	1.30**	3	183	49	3	83	96*	3	81	120
Error	30	0.10	0.10	11‡	280‡	45‡	35	32	32	35	75	75

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
† The df and MS for Among F_2 of materials evaluated for pod fill are smaller than the corresponding Among F_2 values in Table 5, since four F_2 families with PA8 were not included in the diallel analysis.
‡ For yield of materials scored for bud abortion, the MS_e of the four ANOVAs for each group separately were not homogenous. Therefore, MS_e terms from the separate ANOVAs for F_1 and F_2 generations were used (as in Table 5).

Table 10. General combining ability (GCA) effects (± SE) of two sets of parents from diallel analyses of F_1 and F_2 generations.

	Materials scored for bud abortion					Materials scored for pod fill			
	Bud abortion†		Yield			Pod fill†		Yield	
Parent	F_1	F_2	F_1	F_2	Parent	F_1	F_2	F_1	F_2
	visual score		g/plant			% fill		g/plant	
PA1	0.03	−0.14	−6.11	3.13	PA1	1.98	2.87	1.76	−1.21
PA2	−2.42	−1.98	13.96	8.27	PA5	3.80	1.28	−4.60	−4.89
PA3	0.92	0.84	−3.63	−6.44	PA6	−2.36	2.50	−0.22	0.37
PA4	1.47	1.28	−4.22	−4.96	PA7	−3.43	−6.65	6.58	5.73
SE	±0.10	±0.10	±5.12	±2.06	SE	±1.74	±1.74	±2.65	±2.65

† Negative GCA effects indicate improved tolerance at bud abortion, while positive GCA effects indicate improved tolerance at pod fill.

tion were also highly significant for both F_1 and F_2 families (Table 9). The SCA effects indicated that F_1 and F_2 families from crosses of PA1 × PA3 and of PA2 × PA4 were especially tolerant. The reciprocal general and reciprocal specific MS for bud abortion were significant only in the F_2 generation. This was surprising, since theoretically, the additive component of the genetic variance should remain constant and the dominance component of the genetic variance should decrease by one half due to the increased inbreeding in the F_2. One would, therefore, expect the magnitude of the reciprocal general MS to remain unchanged and the reciprocal specific MS to be reduced in the F_2 generation as compared to the F_1 (Cockerham, 1963; Nienhuis and Singh, 1986; Shonnard, 1991).

The GCA MS for percent pod fill were significant for both the F_1 and the F_2 diallels (Table 9). The GCA effects for pod fill differed in magnitude between the F_1 and F_2 generations for each parent; the GCA effects for both diallels were positive for the two tolerant parents (PA1 and PA5), negative for the very susceptible PA7, but changed sign for susceptible PA6 (Table 10). The SCA and reciprocal general MS for pod fill were not significant in either diallel. The reciprocal specific MS in the F_2 diallel was slightly larger than in the F_1 diallel and was significant (Table 9).

For materials scored for bud abortion, only GCA mean squares were significant for yield and only in the F_2 diallel. For materials scored for pod fill, no mean squares were significant for yield in either diallel.

CONCLUSIONS

We were able to identify two developmental stages, flower bud formation and pod filling, at which severe stress symptoms were observed following exposure to high temperatures. Genetic variability was present among large-seeded materials at both of these stages. Significant genotype × environment (G × E) interactions were observed for heat tolerance of parents and cultivars evaluated at both Davis and WSFS. The presence of G × E interactions in the ANOVA for materials evaluated at WSFS only may have resulted in inflated estimates of phenotypic variance (Dudley and Moll, 1969).

Use of generation means analyses permitted us to evaluate genetic effects in individual crosses. The presence of significant additive effects for heat tolerance during flower bud formation in four of the crosses and during pod filling in one cross suggest an opportunity for gain from selection at these developmental stages. Significant negative additive × additive interactions for percent pod fill caution against severe selection in early generations. Significant cytoplasmic interactions for several of the crosses at both bud formation and pod filling indicate the importance of choosing the direction of the cross carefully. Significant midparent heterosis estimates may have been due to repulsion-phase linkages of dominant genes, or simply due to allele associations in the inbred parents (Wassimi et al., 1986).

The diallel analyses involving the F_2 generation not only confirmed the importance of GCA effects observed in the F_1 generation for both traits, but also indicated the presence of reciprocal general and reciprocal specific effects not seen in the F_1 diallels. While the study of specific developmental stages did not identify simple genetic control of heat tolerance, with the exception of the association between tolerance to bud abortion and indeterminate growth habit, it did point to the possibility of gain from selection for both traits in these materials.

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