Diallel analysis of yield components of snap beans exposed to two temperature stress environments

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Summary

Ten snap beans ('Barrier', 'Brio', 'Carson', 'Cornell 502', 'CT 70', 'HB 1880', 'Hystyle', 'Labrador', 'Opus' and 'Venture') were selected for differential temperature tolerance and used as parents in a complete diallel mating design. The 45 F_1 hybrid lines (with reciprocals) and parents were screened at 32 °C day/28 °C night, and in a separate experiment, 16 °C day/10 °C night, during reproductive development in replicated controlled environments. Variation for yield under temperature treatments was observed among parents and hybrids, with certain hybrids exceeding parental performance. Significant ($P \leq 0.0001$) general combining ability (GCA), and significant ($P \leq 0.05$) specific combining ability (SCA) were observed for yield components including pod number, seed number, and seeds per pod. There was evidence that pod number and seeds per pod under temperature stress are under separate genetic control. Reciprocal effects and heterosis were not significant. GCA could not be predicted from parental performance. The breeding line 'Cornell 502' had the highest GCA under high temperature, and the cultivar 'Brio' had the highest GCA under low temperature. The cross 'Brio' × 'Venture' was high yielding in both temperature treatments. Heat tolerance and chilling tolerance were associated in certain parents and hybrids. However, performance under high and low temperature treatments was not generally correlated in the parents and hybrids, indicating that these traits should be selected separately.

Introduction

Common bean (*Phaseolus vulgaris* L.) is a warm season annual crop that grows best at moderate temperatures (Hall, 2001). The ideal growing temperature is considered to be 23 °C (Dickson & Boettger, 1984a), or between 15 and 27 °C (Bliss, 1980), with optimal temperatures for pod set between 15 and 25 °C (Inoue & Suzuki, 1959). A temperature of 10 °C is close to the lower limit for growth in common bean (Austin & Maclean, 1972). Research in common bean on the effects of sub-optimal temperatures has focused on germination, emergence, and seedling growth (Dickson, 1971; Otubo et al., 1996). Very little information is available on the effects of low temperatures during reproductive development. There is evidence that chilling tolerance at juvenile stages of development (germination, emergence, and seedling growth) is under independent genetic control from chilling tolerance during reproductive development (Dickson & Petzoldt, 1987; Kemp, 1973; Melo et al., 1997). Dickson & Boettger (1984a) reported night temperatures of 8 and 12 °C significantly lowered pollen germination *in vivo* compared to 18 °C. Low night temperatures also reduced seeds per pod, with a combination of low day and night causing the lowest seed set. This reduction was attributed to ovule dysfunction, as pollen appeared normal. Farlow (1981) observed similar results of reduced fertility of the female gamete at 13.9 °C, with undeveloped ovules (i.e. missing seeds) distributed throughout

pods, and no seed set. Kemp (1973) observed damage or destruction of flower primordial at constant 7 °C. In a separate study, Dickson & Boettger (1984b), established that controlled environment temperature conditions of 16 °C day/8 °C night identified snap beans that were early maturing under low temperatures, and that were also tolerant to low temperature field conditions.

Snap bean is crop for which product quality is important and optimal timing for a single destructive harvest represents a moving target (Myers & Baggett, 1999). High temperature stress (>30 °C day and/or >20 °C night) during reproductive development reduces both yield and quality in snap bean (Singh, 2001) and is a major production constraint in temperate growing areas. Brief periods of high temperatures cause split sets in snap bean fields due to abscission of reproductive organs, which can be the primary determinant of pod number under heat stress (Ofir et al., 1993). Reciprocal pollinations between heat-stressed plants to plants grown at optimal temperatures indicated that pollen is more affected by heat stress than female reproductive structures (Gross & Kigel, 1994; Monterroso & Wien, 1990). High temperatures negatively affect other aspects of reproductive development, such as anther dehiscence, pollen germination, and pollen tube growth. Failure of anther dehiscence occurred with heat treatment during sporogenesis (13–8 days before anthesis [DBA]) in heat tolerant and heat sensitive cultivars (Gross & Kigel, 1994), or only in heat sensitive lines (Porch & Jahn, 2001). Gross & Kigel (1994) observed that the number of pollen tubes penetrating the stigma was reduced with high temperatures applied 7-0 DBA, but that there were still more pollen tubes penetrating the stigma than there were ovules to fertilize. Also, under heat stress conditions, the most likely ovules to develop were those positioned nearest to the blossom end of the pod, this can be attributed to high temperature constraints on pollen tube growth, sensitivity of the gynoecium to high temperatures at anthesis, or both. This result suggested some combination of impaired pollen development, reduction of pollen tube length, failure of fertilization, and embryo abortion is occurring with heat stress in common bean. Also, high temperatures around anthesis disrupt fertilization and ovule development (Gross & Kigel, 1994; Porch & Jahn, 2001), causing deformed pods in pods in snap bean due to reduced seed set.

Coincidence of tolerances to high and low temperature stress has been reported in snap beans (Dickson, 1993; Dickson & Boettger, 1984a), oat [*Avena sativa* L.] (Coffman, 1957; Mashiringi & Harahwa, 1985), and maize [*Zea mays* L.] (Yacoob & Filion, 1986). Porch (2001) found that snap bean lines developed for cold tolerance had significant positive general combining ability (GCA) under high temperatures for traits related to heat tolerance. A cowpea line selected for low temperature conditions in Minnesota was also very tolerant to high temperature; however, the correlation may have been related to earliness (Hall, 2004). It is possible that heat tolerant snap bean cultivars and lines may also possess cold tolerance. Correlation of these traits in snap bean material could enhance selection strategies, and provide evidence for yield stability in the materials studied. Evidence for correlation might also provide clues to stress tolerance mechanisms and enhance molecular studies. For example, recent studies have uncovered cross-talk between signaling pathways for plant perception of salt, drought, and cold stresses (Chinnusamy et al., 2004).

Tolerance to high and low temperature stresses is not always associated in bean. Nakano et al. (1997) developed a heat tolerant, black-seeded, indeterminate snap bean breeding line ('Haibushi') from South Asian germplasm, and found it performed poorly under low temperature (monthly mean air temperature of 17 °C) compared to standard cultivars. Tolerance to chilling germination and heat tolerance were not correlated in cowpea (El-kholy et al., 1997).

Using a diallel mating design, this study focuses on identifying snap bean cultivars and lines for developing heat tolerant snap bean cultivars, and also examines possible associations between tolerance to high and low temperatures at reproductive development. A previous diallel analyses by Shonnard & Gepts (1994) showed that additive genetic effects are important contributors to yield under heat stress in dry bean, indicating that improvement of reproductive heat tolerance could be possible through combinations of heat tolerant lines. The snap bean parents used in this study were all large sieve size (4–5), determinate type I growth habit, self-pollinated lines. This approach reduced genetic and phenotypic variability in the parents and hybrids associated with growth habit, maturity, and pod and seed size and number.

The objectives of this study were to (a) estimate GCA, SCA, and reciprocal effects for yield components of selected snap bean parents and progeny under high and low temperature stress, and (b) investigate potential association between high and low temperature stress tolerances during reproductive development in snap bean.

Materials and methods

Ten snap bean breeding lines and cultivars comprised of one chilling tolerant inbred breeding line ('CT 70', Cornell breeding line), two heat sensitive cultivars ('Hystyle', Harris Moran; 'Labrador', Seminis) and seven heat tolerant inbred lines and cultivars ('Barrier', Alpha Seeds; 'Brio', Seminis; 'Carson' [wax bean], Syngenta; 'Cornell 502', Cornell breeding line; 'HB1880', Syngenta; 'Opus', Seminis; 'Venture', Syngenta). The snap bean parents used were all large sieve size (4–5), determinate type I growth habit, self-pollinated lines. Parents were crossed in all possible combinations using the hooking method without emasculation (Bliss, 1980). A complete set of 90 F_1's (45 hybrids with 45 reciprocals) was created for each temperature treatment. A sample of 100 progeny assayed with RAPD markers (Williams et al., 1990) unique to each parent (University of British Columbia primers, Vancouver, B.C., Canada) indicated that the percentage of selfs was close to zero (data not shown).

The cold test was planted April 12, 2003 and the heat test was planted June 5, 2003. For each temperature treatment, the 90 F_1's and 10 parents were planted and randomized in four replications divided between two identical 90 m^2 greenhouses. To account for reciprocal/maternal effects among F_1's, reciprocal crosses in one direction were planted in two of the replications, and crosses in the other direction were planted in the other two replications. Seeds of F_1 hybrids and parents were sown in 14.6 cm $\times$ 14.6 cm square pots filled with 'Cornell mix' (Boodley & Sheldrake, 1972). Greenhouses were set for a 14 hr photoperiod with supplemental lighting provided by 1000 W metal halide bulbs (SunSystem III from Sunlight Supply, Inc., Vancouver, WA) at a rate of 300 μM m^{-2} s^{-1} of photosynthetically active radiation at bench level. Greenhouse temperatures were set at 24 °C day/21 °C night for germination and development of seedlings.

Temperature treatments were imposed two weeks after seedling emergence, corresponding to microsporogenesis, and continued through plant senescence. Low temperature treatment was 16 °C day/10 °C night, high temperature treatment was 32 °C day/28 °C night. Plants were irrigated as needed and fertilized equally. A guard row surrounded each experiment to maintain uniform light and temperature distribution, microclimate humidity, and air movement. After complete plant senescence all pods were harvested from individual plants. Pod and seed counts, and seed weight (to 1 $\times$ 10^{-2} g) were recorded separately for each plant in the experiment.

Yield component data were analyzed using the general linear model (GLM) analysis, where type III sums of squares comparisons were used to obtain F-values for experimental variables, and comparisons of means of yield components were obtained using Duncan's multiple range test ($P \leq 0.05$) (SAS, 1997). GLM analysis indicated reciprocal effects were not significant, so reciprocal values were used for missing crosses in the diallel analysis (only one hybrid in one direction, 'Venture' $\times$ 'Labrador' [female $\times$ male], did not germinate in any case). Means for treatment replications were used to calculate GCA, SCA, reciprocal, and maternal effects with the program DIALLEL-SAS (Zhang & Kang, 1997), based on Griffing's model I, method I diallel analysis (fixed effects) (Griffing, 1956). Correlations among yield component means and GCA values within separate temperature treatments were calculated using Pearson product-moment correlations (SAS, 1997). Correlations among yield components and GCA values across temperature treatments were calculated using Spearman's rank-correlation coefficient (SAS, 1997).

Results and discussion

Significant variation for yield components (YC) was observed among parents and F_1's at high and low temperatures (Tables 1 and 2). High temperature treatment of the F_1's and parents resulted in significantly lower ($P \leq 0.01$) means for all YC as compared to the low temperature treatment (data not shown). Analysis of variance indicated significant ($P \leq 0.0001$) greenhouse and replication effects in the heat treatment, and significant ($P \leq 0.0001$) replication effects in the chilling treatment (data not shown). Yield component means under high and low temperature treatment, respectively, were 10.04 and 10.76 for pod number, 27.23 and 33.38 for seed number, 4.46 and 10.23 g for seed weight, 0.162 and 0.317 g for mean seed weight, and 2.56 and 3.10 for seeds per pod. Pod number, seed number, and seeds per pod were the best indicators of yield in this study. Reciprocal effects were not significant for any full-sib family (i.e. cross) (data not shown), or YC except seed number in high temperature at $P \leq 0.05$ (Table 3).

Variation in GCA was highly significant ($P \leq 0.0001$) for pod number, seed number, and seeds per pod in both temperature treatments (Table 3).

Table 1. Mean pod number, mean seed number, and mean seeds per pod for the 10 parents and 45 hybrids of a diallel analysis when grown in a high temperature (32 °C day/28 °C night) controlled environment

Rank	Hybrid or parent	Pods (no.)		Seeds (no.)		Seeds (no./pod)		Mean rank
		Value	YC rank	Value	YC rank	Value	YC rank	
1	Car × CT 70	12.5 a–c	2	45.3 a	1	3.65 a	2	1.7
2	C 502 × HB	11.89 a–e	5	42.56 a–c	3	3.55 ab	3	3.7
3	Brio × C 502	13.6 a	1	43.9 ab	2	3.21 a–g	10	4.3
4	CT 70 × HB	11.89 a–e	6	42.56 a–c	4	3.55 ab	4	4.7
5	Brio × Ven	11.7 a–e	8	40.7 a–e	5	3.39 a–d	7	6.7
6	C 502 × Ven	11.45 a–e	13	38.35 a–f	6	3.45 a–c	5	8.0
7	CT 70 × Ven	11.45 a–e	14	38.35 a–f	7	3.45 a–c	6	9.0
8	Brio × HB	12.2 a–d	3	36.95 b–g	8	2.99 b–k	16	9.0
9	Brio × CT 70	11.6 a–e	9	35.55 c–i	12	3.08 a–j	15	12.0
10	Bar × C 502	11.75 a–e	7	34.7 d–j	14	2.85 c–l	22	14.3
11	C 502 × Lab	10.9 a–g	24	35.9 c–h	9	3.18 a–h	12	15.0
12	CT 70 × Lab	10.9 a–g	25	35.9 c–h	10	3.18 a–h	13	16.0
13	Bar × Ven	11.45 a–e	12	34.15 d–k	15	2.92 b–l	21	16.0
14	HB × Ven	9.74 d–i	37	35.63 c–i	11	3.70 a	1	16.3
15	Car × Ven	10.53 b–h	28	34.74 d–j	13	3.31 a–e	8	16.3
16	C 502 × Opus	11.2 a–g	19	33.9 d–l	16	2.99 b–k	17	17.3
17	CT 70 × Opus	11.2 a–g	20	33.9 d–l	17	2.99 b–k	18	18.3
18	Car × Lab	11.95 a–d	4	31.1 f–o	24	2.57 h–p	30	19.3
19	C 502 × CT 70	11.3 a–f	16	33.65 e–m	18	2.79 d–m	26	20.0
20	Car × HB	10.2 b–h	32	32.05 f–n	21	3.23 a–f	9	20.7
21	Lab × Ven	11.5 a–e	11	30.1 g–p	25	2.66 g–p	28	21.3
22	Brio × Car	11.2 a–f	18	31.5 f–n	23	2.8 d–n	25	22.0
23	Car × Hys	10.1 b–h	33	32.3 f–m	20	3.16 a–i	14	22.3
24	Car × C5	10.5 c–h	29	33.2 e–m	19	2.99 b–k	19	22.3
25	Car × Opus	10 b–i	35	31.75 f–n	22	3.21 a–g	11	22.7
26	Opus × Ven	11.3 a–f	17	27.7 i–r	28	2.42 l–s	33	26.0
27	Hys × Ven	10.05 b–h	34	29 g–q	26	2.95 b–l	20	26.7
28	Bar × Brio	10.25 b–h	30	28.6 h–r	27	2.74 e–o	27	28.0
29	Brio × Hys	10.9 a–g	22	27.2 j–s	30	2.47 k–q	32	28.0
30	Bar × Car	10.65 b–h	27	27.55 h–r	29	2.59 g–q	29	28.3
31	Bar × Lab	11.35 a–f	15	26.05 l–t	33	2.31 l–u	37	28.3
32	Hys × Opus	11.6 a–e	10	24.07 n–u	36	2.07 p–v	43	29.7
33	C 502 × Hys	9.32 e–j	39	26.9 j-s	31	2.83 c–m	23	31.0
34	Lab × Opus	10.89 a–g	26	25.94 l–t	34	2.41 k–s	35	31.7
35	CT 70 × Hys	9.32 e–j	40	26.9 j–s	32	2.83 c–m	24	32.0
36	Bar × Hys	10.25 b–h	31	25.69 m–t	35	2.42 l–s	34	33.3
37	Brio × Lab	10.9 a–g	23	23.35 o–v	37	2.15 o–v	41	33.7
38	HB × Opus	11.2 a–g	21	22.13 p–v	38	2.01 q–w	45	34.7
39	Carson	9.55 d–i	38	21.05 q–v	40	2.19 n–v	39	39.0
40	Bar × CT 70	7.43 i–l	48	21.43 q–v	39	2.53 i–q	31	39.33
41	Bar × HB	8.55 g–k	45	20.9 r–w	41	2.37 l–r	36	40.7
42	HB 1880	8.65 f–j	44	20 s–w	43	2.21 m–v	38	41.7
43	Brio × Opus	8.65 f–k	43	20.2 s–w	42	2.07 p–v	44	43.0

Table 1. (*Continued*)

Rank	Hybrid or parent	Pods (no.)		Seeds (no.)		Seeds (no./pod)		Mean rank
		Value	YC rank	Value	YC rank	Value	YC rank	
44	HB × Lab	9.8 d–i	36	18.8 t–x	44	1.76 t–x	49	43.0
45	Brio	8.05 h–l	47	16.65 u–x	45	2.15 q–o	42	44.7
46	Bar × Opus	6.95 j–m	49	16.6 u–y	46	2.18 n–v	40	45.0
47	Hys × Lab	8.2 h–k	46	16.55 u–y	47	1.98 q–w	46	46.3
48	HB × Hys	9.27 e–j	42	16 v–y	48	1.74 u–x	50	46.7
49	Cornell 502	9.3 e–j	41	15.6 v–y	49	1.59 v–x	51	47.0
50	Opus	6.42 k–m	50	13.16 w–z	50	1.87 r–x	47	49.0
51	CT 70	6.05 lm	51	11.95 x–z	51	1.82 s–x	48	50.0
52	Barrier	5.37 m	54	10.05 yz	52	1.46 w–y	52	52.7
53	Venture	5.95 lm	52	9.3 yz	53	1.33 xy	53	52.7
54	Hystyle	5.42 m	53	6.16 z–aa	54	1.02 yz	54	53.7
55	Labrador	2.95 n	55	2.2 aa	55	0.54 z	55	55.0
	S.D.	±3.39		±11.78		±0.78		

Hybrids and parents are arranged according to mean rank. Overall rank in the first column of hybrid or parent is based on mean rank. Mean rank is the mean of the three YC ranks. YC rank: yield component rank (rank of hybrid or parent for pod number, seed number, or seeds per pod); Car: 'Carson'; C 502: 'Cornell 502'; HB: 'HB 1880'; Ven: 'Venture'; Lab: 'Labrador'; Hys: 'Hystyle'. Within each yield component the means followed by different letters are significantly different ($P \leq 0.01$) according to Duncan's multiple range test.

The observation of significant GCA in each treatment indicated additive genetic variance contributed to heat tolerance in the parental population. However, additive genetic variance may be overestimated in a diallel analysis of non-randomly selected parents. The predominance of GCA contribution to genotypic variance for seed number is typical in common bean (Dickson, 1967; Kornegay et al., 1992; Nienhuis & Singh, 1988; Porch, 2001; Singh et al., 1992), and significant positive GCA for seed number in common bean has been observed previously in populations from diverse gene pools and races (Abreau et al., 1999; Nienhuis & Singh, 1988; Singh et al., 1992). Large additive effects also have been reported for pod number (Dickson, 1967; Nienhuis & Singh, 1988; Porch, 2001) and seeds per pod (Dickson, 1967; Mumba & Galwey, 1999; Nienhuis & Singh, 1988; Porch, 2001).

Significant ($P \leq 0.05$) SCA variance was observed in both temperature treatments (Table 3), indicating non-additive genetic contribution to yield as well. The statistical significance of the components of genetic variance indicated that genetic variation for pod number, seed number, and seeds per pod under both temperature treatments was present in the diallel mating design, and that experimental conditions allowed for the detection of genetic differences among the parents and progeny. SCA variance is unlikely to be overestimated

in this study as analysis of variance indicated heterosis was insignificant within families. Observation of non-additive gene action under temperature stress due to significant SCA contribution to variance provides further evidence that evaluation beyond the F1 generation may be necessary. This result differs from previous studies in which heterosis for yield and yield components was found to be significant in dry bean (Foolad & Bassiri, 1983; Nienhuis & Singh, 1986; Shonnard & Gepts, 1994). The lack of heterosis in this study may be attributed to uniformity of parents used in this experiment, as high F_1 heterosis in bean is associated with increasing phenotypic and genotypic divergence between parents (Evans, 1970; Nienhuis & Singh, 1986). Observation of insignificant heterosis suggests SCA can be utilized in selecting the best parental combinations for developing heat tolerant snap beans.

A number of interactions occurred between genotype and temperature. Parental performance suggested different alleles, genes, and combinations of genes may be available for breeding improved cultivars. For example, 'Cornell 502', was heat tolerant and chilling sensitive; thus, the gene or genes influencing yield under high temperature in 'Cornell 502' did not contribute to cold tolerance. Conversely, the cultivar 'Labrador' was chilling tolerant and heat sensitive. Parental performance under high and low temperatures was associated

Table 2. Mean pod number, mean seed number, and mean seeds per pod for the 10 parents and 45 hybrids of a diallel analysis when grown in a low temperature (16 °C day/10 °C night) controlled environment

Rank	Hybrid or parent	Pods (no.)		Seeds (no.)		Seeds (no./pod)		Mean rank
		Value	YC rank	Value	YC rank	Value	YC rank	
1	Brio	13.7 ab	2	50 a	1	3.67 a–h	11	4.7
2	Brio × CT 70	12.84 a–f	7	43.79 a–d	4	3.7 a–h	10	7.0
3	Brio × HB	12.88 a–e	6	46.53 ab	2	3.63 a–i	15	7.7
4	Brio × Lab	12.75 a–g	8	44.35 a–c	3	3.44 b–l	21	10.7
5	Brio × Ven	10.76 c–n	27	41.53 b–f	6	3.92 ab	2	11.7
6	Brio × C 502	12.35 b–h	11	43.2 a–e	5	3.52 b–k	20	12.0
7	Bar × Lab	13.11 a–d	4	41.39 b–f	7	3.23 e–q	26	12.3
8	Bar × Ven	12.2 b–i	14	41.25 b–f	8	3.38 b–m	22	14.7
9	Lab × Ven	10 g–n	38	41 b–f	9	4.1 a	1	16.0
10	Brio × Car	11.8 b–j	16	39.45 b–g	10	3.35 b–n	23	16.3
11	Car × Lab	10.21 e–n	32	38.68 b–h	14	3.82 a–d	5	17.0
12	HB × Ven	10.43 d–n	30	38.71 b–h	13	3.79 a–f	8	17.0
13	HB × Lab	10.82 c–n	24	38.77 b–h	12	3.61 a–j	16	17.3
14	Car × Opus	12.3 b–i	13	38.95 b–h	11	3.18 g–q	34	19.3
15	Car × HB	10.78 c–n	26	38.56 b–i	15	3.57 a–j	18	19.7
16	Brio × Opus	11.94 b–j	15	37.61 e–i	17	3.23 e–q	27	19.7
17	Opus × Ven	11.3 b–n	21	37.55 c–i	18	3.33 c–o	24	21.0
18	Bar × CT 70	12.33 d–h	12	38.5 b–i	16	3.16 h–q	35	21.0
19	C 502 × Opus	11.5 b–m	18	36.67 c–j	20	3.21 h–q	29	22.3
20	Bar × Car	13.05 a–d	5	37.47 d–i	19	2.85 m–t	43	22.3
21	C 502 × Lab	9.5 i–o	43	35.58 d–l	24	3.85 a–c	3	23.3
22	CT 70 × Opus	11.5 b–m	19	36.67 c–j	21	3.21 h–q	30	23.3
23	Brio × Hys	11.25 b–n	22	36.2 c–k	22	3.22 g–q	28	24.0
24	CT 70 × Lab	9.5 i–o	44	35.58 d–l	25	3.85 a–c	4	24.3
25	Car × CT 70	9.6 h–n	41	35.55 d–l	26	3.74 a–g	9	25.3
26	HB × Opus	13.31 a–c	3	35.31 d–l	27	2.68 q–u	46	25.3
27	Car × Ven	10.05 f–n	37	35.8 c–l	23	3.6 a–j	17	25.7
28	C 502 × HB	9.61 h–o	39	34.83 e–m	30	3.64 a–i	13	27.3
29	Bar × Brio	12.5 b–g	9	35 f–m	28	2.66 q–u	47	28.0
30	CT 70 × HB	9.61 h–o	40	34.83 e–m	31	3.64 a–i	14	28.3
31	Labrador	9.35 j–o	45	34.95 e–m	29	3.65 a–i	12	28.7
32	C 502 × Ven	8.89 l–o	49	33.16 f–n	33	3.81 a–e	6	29.3
33	Bar × Opus	15.15 a	1	31.55 g–n	37	2.08 vw	52	30.0
34	CT 70 × Ven	8.89 l–o	50	33.16 f–n	34	3.81 a–e	7	30.3
35	Lab × Opus	10.75 c–n	28	34.5 e–n	32	3.2 h–q	31	30.3
36	Bar × HB	12.47 b–g	10	31.47 h–n	39	2.54 r–v	48	32.3
37	C 502 × Hys	10.17 e–n	33	31.67 h–n	35	3.2 f–q	32	33.3
38	CT 70 × Hys	10.17 e–n	34	31.67 h–n	36	3.2 f–q	33	34.3
39	Hys × Lab	10.46 d–n	29	31.54 b–h	38	3.02 j–t	37	34.7
40	Car × C5	10.8 c–n	25	30.75 g–o	40	2.86 l–t	42	35.7
41	Hys × Opus	11.56 b–l	17	29.75 i–p	42	2.53 s–v	49	36.0
42	Hys × Ven	8.62 on	52	30.69 g–o	41	3.55 a–k	19	37.3
43	Bar × C 502	10.35 d–n	31	28.25 j–q	43	2.76 o–u	44	39.3
44	Bar × Hys	11.21 b–n	23	28 j–q	44	2.27 u–w	51	39.3

Table 2. (*Continued*)

| Rank | Hybrid or parent | Pods (no.) | | Seeds (no.) | | Seeds (no./pod) | | Mean rank |
		Value	YC rank	Value	YC rank	Value	YC rank	
45	CT 70	8.7 m–o	51	27.75 k–q	46	3.26 d–p	25	40.7
46	Barrier	11.35 b–n	20	22.7 o–r	51	1.95 wx	53	41.3
47	HB × Hys	9.57 h–n	42	27.79 k–q	45	2.9 l–t	41	42.7
48	HB 1880	10.16 f–n	35	27.05 l–q	49	2.73 q–u	45	43.0
49	Car × Hys	8.94 k–o	48	27.47 k–q	48	3.08 i–r	36	44.0
50	C 502 × CT 70	9.3 j–o	46	27.6 k–q	47	2.93 l–t	40	44.3
51	Carson	8.95 k–o	47	26.4 m–r	50	2.97 k–q	39	45.3
52	Opus	10.1 e–n	36	19.6 r	54	1.94 wx	54	48.0
53	Venture	7.05 o	54	20.35 rq	53	2.98 k–t	38	48.3
54	Hystyle	8.6 on	53	21.7 p–r	52	2.47 t–w	50	51.7
55	Cornell 502	2.25 p	55	4.5 s	55	1.56 x	55	55.0
	S.E.	±3.75		±14.71		±0.78		

Hybrids and parents are arranged according to mean rank. Overall rank in the first column of hybrid or parent is based on mean rank. Mean rank is the mean of the three YC ranks. YC rank: yield component rank (rank of hybrid or parent for pod number, seed number, or seeds per pod); Car: 'Carson'; C 502: 'Cornell 502'; HB: 'HB 1880'; Ven: 'Venture'; Lab: 'Labrador'; Hys: 'Hystyle'. Within each yield component the means followed by different letters are significantly different ($P \leq 0.01$) according to Duncan's multiple range test.

Table 3. Mean squares for pod number, seed number, and seeds per pod for the 10 parents and 45 hybrids of a diallel analysis when grown in a high temperature (32 °C day/28 °C night) or a low temperature (16 °C day/10 °C night) a controlled environment

| Source | df | Pods (no.) | | Seeds (no.) | | Seeds (no./pod) | |
		High temp.	Low temp.	High temp.	Low temp.	High temp.	Low temp.
Cross	89	17.22***	14.85***	297.5***	233.0***	1.85***	1.12***
GCA	9	19.66***	42.88***	602.6***	654.6***	2.98***	4.82***
SCA	35	16.77***	8.16*	245.4*	129.8*	1.62*	0.39*
Rec	45	4.12	3.98	99.9*	51.89	0.24	0.14
Error	108	4.27	3.70	83.99	39.90	0.22	0.15

*Indicates significance at $P \leq 0.05$.
***Indicates significance at $P \leq 0.0001$.

in other diallel parents. 'Brio', 'Carson', and 'HB 1880' were chilling tolerant and heat tolerant, and genes for these traits may be associated, linked, or pleiotropic in these parents. The unique responses of 'Labrador' and 'Cornell 502', for which tolerance or sensitivity to high and low temperatures were negatively associated, suggests these parents may possess different genes or alleles than parents with greater yield stability. Tolerance to high temperature also varied with yield components, such as for 'Barrier' and 'Venture', which both showed relatively high pod set, but relatively low seed set, in the heat treatment. This result suggests pod number and seed number under temperature stress may be under

separate genetic control, an observation supported by the lack of correlation between mean pod number and mean seed number (Table 4).

The diverse responses of parental performance to temperature stress were also observed for breeding value (i.e. GCA), with significant positive and

Table 4. Pearson product-moment correlations between general combining ability (GCA) and yield component means for the 10 diallel parents when grown in a high temperature (32 °C day/28 °C night) or a low temperature (16 °C day/10 °C night) controlled environment

	GCA seeds (no.)	GCA seeds (no./pod)	Mean pods (no.)	Mean seeds (no.)	Mean seeds (no./pod)
High temperature					
GCA pods (no.)	0.62	0.85*	0.61	0.52	0.32
GCA seeds (no.)		0.68*	0.95***	0.29	0.86*
GCA seeds (no./pod)			0.65*	0.49	0.47
Mean pods (no.)				0.42	0.93*
Mean seeds (no.)					0.38
Low temperature					
GCA pods (no.)	0.81*	0.55*	0.59	−0.19	0.14
GCA seeds (no.)		0.71*	0.86*	0.18	0.55
GCA seeds (no./pod)			0.90***	0.70*	0.835*
Mean pods (no.)				0.547	0.85*
Mean seeds (no.)					0.87*

*Indicates significance at $P \leq 0.05$.
***Indicates significance at $P \leq 0.0001$.

Table 5. General combining ability (GCA) of the 10 diallel parents for pod number, seed number, and seeds per pod when grown in a high temperature (32 °C day/28 °C night) or a low temperature (16 °C day/10 °C night) controlled environment

Parent	Pods (no.)		Seeds (no.)		Seeds (no./pod)	
	High temp.	Low temp.	High temp.	Low temp.	High temp.	Low temp.
Barrier	−1.03*	1.42***	−3.90*	−0.91	−2.09*	−0.48***
Brio	0.57	1.38***	2.38*	7.37***	0.07	0.28***
Carson	0.38	−0.31	3.51*	0.35	0.33***	0.14*
Cornell 502	1.27*	−1.15*	5.90***	−5.50***	0.15*	−0.32***
CT 70	0.01	−0.50	4.00*	0.67	0.33***	0.28***
HB 1880	−0.05	0.22	−2.01	0.75	0.04	0.04
Hystyle	−0.76*	−0.97*	−3.24*	−5.60***	−0.29*	−0.30***
Labrador	−0.26	0.04	−4.37*	3.57*	−0.35***	0.32***
Opus	−0.31	0.96*	−2.07*	−1.25	−0.27*	−0.35***
Venture	0.18	−1.09*	−0.20	0.5336	0.20*	0.39***
Standard error	±0.35	±0.27	±0.97	±0.81	±0.06	±0.04

*Indicates significance at $P \leq 0.05$.
***Indicates significance at $P \leq 0.0001$.

significant negative GCA values present in both temperature treatments (Table 5). For example, 'Cornell 502', a breeding line selected for heat tolerance, showed significant positive GCA for all of the YC under high temperature, but had a significant negative GCA for all the YC under low temperature. Parental combining ability also varied with yield components, with 'Venture' possessing significant positive GCA for seeds per pod, and significant negative GCA for pod number, under low temperature. Under low temperature, 'Barrier' had significant positive GCA for pod number, significant negative GCA for seeds per pod, and under high temperature, significant negative GCA for pod number. The variation in GCA for pod number and seeds per pod in 'Barrier' and 'Venture' provides additional evidence that these traits are under separate genetic control. The parents with the best combining ability under high temperature were 'Brio', 'Carson, 'Cornell 502', and 'CT 70', and 'Brio' under low temperature.

General combining ability could not be predicted from parental performance under temperature stress. For example, 'HB 1880' showed yield stability under both high and low temperature, but GCA was insignificant in all cases for this parent (Table 5). 'Barrier' showed high pod set under heat stress, but had significant negative GCA for this trait, and low pod set under chilling stress, with significant positive GCA for that trait. Additionally, within yield components, GCA and YC means (with the exception of seeds per pod in the low temperature treatment) were not correlated (Table 4). Parents with high yield potential under temperature stress were equally likely to have significant negative GCA as significant positive GCA for the three YC. The association of negative GCA with lines of high yield potential is a phenomenon that hinders yield improvement in common bean (Nienhuis & Singh, 1988; Porch, 2001). These observations confirm the value of diallel analysis in choosing parents for improvement of heat tolerance in common bean. Choosing effective heat tolerant or chilling tolerant parents may require knowledge of combining ability and evaluation of segregating populations developed from the F_1's.

The hybrids 'Brio' × 'Cornell 502', 'Brio' × 'CT 70', 'Brio' × 'HB 1880', and 'Brio' × 'Venture' (reciprocals combined) were among the 10 highest yielding F_1's in both temperature treatments (Tables 1 and 2). The best overall hybrid in the high temperature treatment was 'Carson' × 'CT 70', which had the most seeds and seeds per pod (Table 1). 'Brio' × 'Cornell 502' had the highest pod number under high temperature treatment. These two hybrids, in addition to 'Cornell 502' × 'HB 1880', had significantly ($P \leq 0.05$) higher YC means under high temperature than the highest yielding parent, 'Carson'. In the low temperature treatment no hybrids yielded significantly more than 'Brio', and six of the 10 highest yielding hybrids in the low temperature treatment had this cultivar as a parent (Table 2).

Crosses with significant positive SCA are listed in Table 6. 'Barrier' × 'Venture' and 'Brio' × 'Cornell 502' were the only hybrids that possessed significant positive SCA for a yield component (seed number) under both temperature treatments. In general, significant positive SCA in the high temperature treatment resulted from tolerant × tolerant crosses, indicating that transgressive segregation may be observed in segregating populations generated from these crosses. Two heat tolerant × heat sensitive crosses are listed in Table 6 as having significant positive SCA under high temperature ('CT 70' × 'Labrador' and 'Carson' × 'Hystyle), though these crosses did not rank highly among all crosses for performance. These two crosses yielded better than would be expected from the GCA values of 'Labrador' and 'Hystyle', suggesting heat sensitive lines may be improved by crossing to heat tolerant lines.

There was no general trend towards association of high and low temperature stress tolerances in this analysis, both in terms of parental or hybrid performance, or GCA and SCA values. Significant GCA and SCA interaction with temperature treatment indicated that

Table 6. F_1 hybrids from a diallel mating design with significant ($P \leq 0.05$) specific combining ability (SCA) for pod number, seed number, or seeds per pod when grown in a high temperature (32 °C day/28 °C night) or a low temperature (16 °C day/10 °C night) controlled environment

	High temperature (32 °C/28 °C)		Low temperature (16 °C/10 °C)	
Pods (no.)	n/a	n/a	'Barrier' × 'Opus'	1.85[a]
Seeds (no.)	'Barrier' × 'Venture'	9.70	'Barrier' × 'Venture'	7.21
	'Carson' × 'CT 70'	8.58	'Brio' × 'Cornell 502'	6.91
	'Cornell 502' × 'Hystyle'	8.29	'CT 70' × 'Labrador'	0.54
	'CT 70' × 'Labrador'	7.48	'Carson' × 'Opus'	0.50
	'Carson' × 'Hystyle'	7.32	'Brio' × 'Venture'	0.49
	'Brio' × 'Venture'	2.52	'Carson' × 'Hystyle'	0.48
			'Cornell 502' × 'Hystyle'	0.48
Seeds (no./pod)	'HB 1880' × 'Venture'	0.80	'Brio' × 'Cornell 502'	0.39
	'Cornell 502' × 'HB 1880'	0.60	'Barrier' × 'Cornell 502'	0.39
			'Barrier' × 'Venture'	0.30

[a]SCA value.

Table 7. Mean squares for interaction between general combining ability (GCA) or specific combining ability (SCA) with temperature treatment for pod number, seed number, and seeds per pod for the 10 parents and 45 hybrids of a diallel analysis when grown in high temperature (32 °C day/28 °C night) or a low temperature (16 °C day/10 °C night) treatment in a controlled environment

Source	df	Pods (no.)	Seeds (no.)	Seeds (no./pod)
GCA × treatment	9	41.28***	647.97***	2.13***
SCA × treatment	35	7.12*	70.95	0.44***

*Indicates significance at $P \leq 0.05$.
***Indicates significance at $P \leq 0.0001$.

combining ability under high and low temperature stress was not correlated (with the exception of seed number and SCA) (Table 7). For this reason, heat and chilling tolerance should be selected independently. Moreover, Spearman's rank-correlation coefficients between parental performance *per se* and GCA across temperature treatments showed no significant correlation (data not shown). However, breeding value was correlated in three cases. Under both high and low temperature treatments 'Brio' showed significant positive GCA for seed number, and 'Carson' and 'CT 70' show significant positive GCA for seeds per pod. Additionally, as mentioned previously, parental performance under heat and chilling stress was associated in lines such as 'Brio' and 'HB 1880'.

Conclusions

General and specific combining ability (GCA and SCA) were significant in both temperature treatments, indicating genetic variation for pod number, seed number, and seeds per pod under both temperature treatments was present in the diallel mating design, and that experimental conditions allowed for the detection of genetic differences among the parents and progeny. Pod number, seed number, and seeds per pod were the best indicators of yield in this study. Pod number and seed number under temperature stress may be under separate genetic control. Reciprocal effects and heterosis were not significant. Observation of insignificant heterosis suggests SCA can be utilized in selecting the best parental combinations for developing heat tolerant snap beans.

A number of interactions occurred between genotype and temperature. Parental performance under high and low temperatures was associated in some diallel parents; however, the responses of 'Labrador' and 'Cornell 502', for which tolerance or sensitivity to high and low temperatures were negatively associated, suggests different alleles, genes, and combinations of genes may be available for breeding improved cultivars. Diverse responses to temperature stress were also observed for breeding value, confirming the value of diallel analysis in choosing parents for improvement of stress tolerance in common bean. Additionally, GCA could not be predicted from parental performance. Choosing effective heat tolerant or chilling tolerant parents may require knowledge of combining ability and evaluation of segregating populations developed from the F_1's. Breeding value, parental performance, or both, under heat and chilling stress were associated in certain parents.

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