77

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Selection Criteria in Germplasm Improvement for Heat Tolerance in Phaseolus Beans

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Selection criteria in germplasm improvement for heat tolerance in

Phaseolus beans.

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*THIS FINAL REPORT IS DEDICATED TO THE MEMORY
OF OUR FRIEND AND COLLEAGUE PROF. YESHOHUA RUDICH, A DRIVING
FORCE DURING THE INITIAL STAGES OF THE PROJECT.*

Table of Contents

	Page
Introduction	1
Part A: the work done in the U.S.	3
I. Acclimation potential of <u>Phaseolus vulgaris</u> genotypes to high temperature:	5
Abstract	
Introduction	
Materials and methods	
Results	
Discussion	
II. Photosynthetic responses to heat stress in <u>Phaseolus vulgaris</u> genotypes differing in heat acclimation potential:	33
Abstract	
Introduction	
Materials and methods	
Results	
Discussion	
III. Breeding and Inheritance Phase	55
Part B: the work carried out in Israel	93
I. Abstract	94
II. Introduction	95
III. Experiments under controlled conditions:	96
a) Phytotron	
Materials and methods	
Screening for heat tolerance at 32°/27°C	
Time distribution of flowering and pod production	
HT effects at different stages of reproductive development	
- exposure to 32°/27°C at sporogenesis stage	
- exposure to 32°/27°C at anthesis and early pod development	
b) Greenhouse experiments	

	Page
IV. Field experiments:	135
Materials and methods	
Climatic conditions	
a) Snap-bean varieties	
b) Dry-bean varieties	
V. Temperature effects on photosynthesis and dark-respiration	182
VI. Discussion and conclusion	186
Cooperation and Achievements	195

Introduction

The work to be reported in this final report was begun during the late season of 1985. It covers the work that was done at the University of Minnesota, St. Paul (Part A) and the work that was carried out at the Hebrew University of Jerusalem (Part B).

Part A dealt with 3 areas of studies:

- I. Acclimation potential of Phaseolus vulgaris genotypes to high temperature.
- II. Photosynthetic responses to heat stress in Phaseolus vulgaris genotypes differing in heat acclimation potential.
- III. Breeding and inheritance phase

Paul H. Li was the leader for Projects I and II. David W. Davis was the leader for Project III.

Part B covers the following studies:

- I. Experiments under controlled conditions.
- II. Field experiments.
- III. Temperature effects on photosynthesis and dark-respiration.

Both Jaime Kigel and Micha Ofir were the leaders for these projects.

Following objectives were proposed in project US-851-84: I. To provide Phaseolus bean germplasm identified as to heat adaptability; II. To refine and search methods for screening germplasm for heat tolerance; III. To provide information on tolerance as an inherited character; IV. To determine the effectiveness of selection factor for improved heat tolerance; and V. To make a comparative study of high temperature effects on the vegetative and reproductive processes that determine yield in heat tolerant and sensitive beans.

The work which was reported in Part A-I attempted to answer objectives I, II and V; Part A-II to objective V; Part A-III to objectives II, III and IV. The work which was reported in Part B-I, II and III attempted to also answer objectives II and V.

Part A

Work done in the U.S.

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I. Acclimation potential of Phaseolus vulgaris genotypes to high temperature:

Can it be used as a selection criterion for improving crop performance in high temperature environments?

Abstract

The common bean (Phaseolus vulgaris L.) is a heat-sensitive plant species in which excessive abscission of reproductive organs occurs during hot weather. This results in split sets and yield reductions, and, in extreme heat stress, plants produce few or no pods. We evaluated 74 bean genotypes in terms of leaf heat tolerance (HT) and leaf heat acclimation potential (HAP), as expressed by heat killing time (HKT), the time in minutes needed to result in 50% ion leakage from leaf tissue heat stressed at 50°C. Leaf HT is defined as the leaf HKT of plants without prior conditioning at 37°C day/night temperature and leaf HAP as the change in leaf HT following exposure of the plant at 37°C day/night for 24-h. Among 74 bean genotypes examined, leaf HT ranged from 5 to 30 min HKT, whereas leaf HAP ranged from 35 to 130 min HKT. Positive significant correlations were observed between leaf HAP and post-stress performance in plant dry weight, pod set, pod weight and yield among bean genotypes. Correlations, however, were not significant between leaf HT and post-stress performance.

A relationship between heat resistance, consisting of the combination of HT and HAP, and heat injury is proposed. Interpretation of the differential amounts of heat injury among genotypes having different HAP, is discussed. We view leaf HT and leaf HAP as two distinguishable phenomena. We suggest that in breeding programs HAP may be the more important of the two, and should be evaluated as a selection criterion for improving crop performance in high temperature environments.

Introduction

High temperature is one of the major environmental factors that limit crop performance, especially when temperature extremes coincide with the critical stages of plant development (McWilliam, 1980). For example, when the common bean (Phaseolus vulgaris L.), a heat-sensitive plant species, is grown during the summer in the temperate zone, excessive abscission of reproductive organs occurs during hot weather (Smith and Pryor, 1962). The degree and duration of high temperatures contribute to the intensity of heat stress. When heat stress occurs, it is important that plants possess a certain degree of tolerance to minimize the heat injury. Plant species have the capability to increase heat tolerance when ambient temperatures increase to certain levels (Alexandrov, 1964), and differ in their thermal tolerance response to high temperature (Berry and Bjorkman, 1980). Heat acclimation enables plants to reduce heat injury. Acclimation potential of populations within the same species has been reviewed by Berry and Bjorkman (1980). The activation of heat acclimation may occur only within a narrow range of ambient temperatures. Above the range, increasing tolerance is less efficient, and below it, there is no increase in tolerance. In the common bean, for example, the range is somewhere between 30° and 37°C (Chen et al., 1982). We hypothesize that an initially rapid activation of heat acclimation plays a more important role to counteract an imposed heat stress in reducing the extent of heat injury than the maximum level of heat acclimation that eventually is developed.

Based on fruit set or yield under high temperature conditions, several genotypes of tomato (Lycopersicon esculentum Mill.), soybean (Glycine max Merr.), potato (Solanum tuberosum L.) and common bean (Phaseolus vulgaris L.) have been defined as heat tolerant, due to improved performance, as compared to less heat tolerant genotypes (Al-Ahmadi and Stevens, 1979; Stevens and Rudich, 1978; Martineau et al., 1979; Mendoza and Estrada, 1979; Halterlein et al., 1980). Leaf heat tolerances of these genotypes were examined and compared (Chen et al., 1982), using the conductivity test. Surprisingly, no differences in heat tolerance of the leaf tissues were found between the so-called tolerant and sensitive

genotypes of a species when plants had been grown in a non-heat-acclimating regime. However, significant differences in heat tolerance became apparent only after plants had been heat acclimated. The efficiently performing (heat tolerant) genotypes, regardless of whether the final products are fruits, seeds or tubers, were those which possessed high potential for heat acclimation (Chen et al., 1982).

Various response criteria, such as yield (Mendoza and Estrada, 1979), pollen stainability (Weaver et al., 1985), pollen tube growth (Halterlein et al., 1980), and/or fruit set (Al-Ahmadi and Stevens, 1979; Dickson and Petzoldt, 1989) have been used by researchers to define heat tolerance of crop genotypes. The response to heat stress in terms of these criteria has always been useful and effective. We propose the term "Heat Acclimation Potential" (HAP) to describe the change in heat tolerance following exposure of plants for a certain length of time to temperatures in an acclimation range and propose HAP to be an additional parameter to define heat tolerance of crop genotypes. Our view is that HAP is a phenomenon distinguishable from heat tolerance (HT) and that the latter refers to the status of tolerance of the plant prior to conditioning at an acclimation temperature. We hypothesize that HAP may be more important than HT and should be investigated as a selection criterion to improve crop performance in high temperature environments. We have chosen the common bean (Phaseolus vulgaris L.) as a testing model in conducting experiments designed to test the hypothesis. Preliminary results appear to support our reasoning.

Materials and Methods

Plant materials and culture.

Seeds of the collected bean (Phaseolus vulgaris L.) germplasm (Table 2) were germinated for all experiments in moist vermiculite-filled flats in a growth chamber. Seven to ten-day-old seedlings were transplanted to 15-cm diameter pots containing a mixture of soil, sand and vermiculite (1:1:1 by volume) with 1 seedling in each container, and placed in a greenhouse at 25°C/20°C day/night temperature. Pots were irrigated as needed to keep the mixture moist, and fertilized at each irrigation at a rate of 200 mgL⁻¹ of a soluble commercial starter fertilizer (20:8.7:16.6, NPK). Plants were grown under these conditions until further use.

Heat acclimation procedure.

In preliminary experiments, one-month-old plants (pre-floral growth stage) were transferred to a growth chamber for heat acclimation at constant 37°C day/night temperature and a 12-h photoperiod with 450 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ for 24-h. Later, this heat acclimation method was modified by using excised leaves instead of pot-grown plants. A sharp blade was used to excise the youngest fully expanded trifoliolate leaf from each one-month-old plant. Cut petiole ends were inserted immediately into tubes filled with water. Leaves were placed in the growth chamber as described above, with a humidifier to maintain high relative humidity, for 24-h.

Heat tolerance determinations.

Heat tolerance in leaf tissues of both heat acclimated and non-acclimated plants of the 74 bean genotypes (Table 2) was estimated by the conductivity test (Onwueme, 1979) after heat treatment, and expressed by heat killing time (Chen et al, 1982).

Heat treatment.

Leaflets selected for heat treatment, were excised, rinsed in distilled water, and placed in 25 x 150 mm test tubes. The bottoms of the test tubes were lined with moist tissue paper to ensure high humidity during treatment. Tubes were stopped with rubber stoppers and a thermocouple was inserted through a hole in the center of the stopper to monitor the tissue temperature of the leaf. The tubes were maintained in a water bath at 50°C constant temperature for determining tissue heat killing time.

Viability determination.

Ion leakage measurement (conductivity test) from the tissues after heat treatment was used to determine viability. Leaf disc of 2-cm diameter was cut from heat-treated leaves and immersed in 10 ml of double distilled deionized water in a plastic vial, vacuum-infiltrated and shaken for 1-h in a shaker. The conductance (R_1) of the liquid in each vial was measured with a conductivity bridge. Samples were then frozen in a freezer (-70°C) to kill the tissue, and, after warming to room temperature and shaken for 1-h, the conductance (R_2) was measured again. The ratio of R_1/R_2 was used as a measure of relative heat injury. Tests were repeated at least twice, and, for each test, three duplicate readings were made. Data were subjected to the analysis of variance, and means were compared by Least Significant Difference at the 5% level (LSD 0.05). The time (minutes) required to cause 50% ion leakage at 50°C was defined as the heat killing time (HKT), and by definition the tissue at this point no longer is viable.

Evaluation of plant growth and development responses to heat stress.

Twenty genotypes, randomly chosen from the tested collection (Table 2) were established in the greenhouse as described above. At about 30-35 days, i.e., immediately prior to the pre-floral growth stage, they were divided into two 12-plant groups of each genotype. One, a control group, was kept in the greenhouse. The other group was heat treated in a growth chamber with 37°C/35°C day/night temperature and a 12-h photoperiod with 450 $\mu\text{mol photo m}^{-2} \text{s}^{-1}$ for one week. They were then returned to the greenhouse.

Total plant dry weight was measured 2 weeks later, and, in 13 of the 20 genotypes, pod numbers were also counted. These 13 were chosen so as to have high, intermediate and low HAP.

Evaluation of reproductive response to heat stress.

Six genotypes, representing high, intermediate and low HAP (Table 2), were selected to study post-stress reproductive response. They were GNUI 59, PI 271998, 85CT-4976-2, Iguacu, BBL-47 and Pinto UI 111. Plants were grown in the greenhouse until one to three flowers had opened, i.e., the beginning of the anthesis. Individual flower buds were then classified as follows: 1) Flowering (F) - flower open or opening; 2) Large bud (LB) - petal length at least 3 times greater than sepal length, and anthers may or may not have released pollen; 3) Medium bud (MB) - petal length equal to or greater than sepal length, and bud about 2-3 days from anthesis; 4) Small bud (SB) - petal length equal to or less than sepal length, and bud about 5-7 days from anthesis. Fifteen to 20 flowers and/or buds were tagged for each of the four stages. Ten plants were used for each of the four stages of flower bud development. Plants were divided into 3 groups. One group was subjected to heat stress in a growth chamber at 37°C/35°C day/night temperature for 2 days, and a second for 4 days to provide a longer duration of heat stress. The third was kept in a chamber at 25°C/20°C day/night temperature with 12-h photoperiod as the control. The photoperiod in the chambers was 12-h with 450 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. After heat treatment, the three groups of plants were returned to the greenhouse, as described above. One week later, all tagged flowers and/or buds were examined and pod set recorded. After about 10-15 days in the greenhouse, when more than 80% of the pods on control plants were ready for fresh market harvest, all pods with seeds were harvested, and pod set, pod weight and seed number were recorded. The remaining pods were harvested 7-9 days later. At this time, all pods, whether mature or not, were harvested. Pod set, pod weight and seed number, if any, were again recorded.

Results

Modification of heat acclimation procedure.

The optimum acclimation temperature and duration of acclimation and appropriate plant age for heat acclimation were previously determined for the common bean and reported elsewhere (Chen et al., 1982). When the present study was initiated, pot-grown plants were used for heat acclimation. However, for efficient utilization of the limited controlled environment space for heat acclimation, a modified method was developed by using excised leaves instead of pot-grown plants. A t-test ($t = 0.66$, not significant) indicates that results are similar between excised leaves and pot-grown plants acclimated at 37°C day/night temperature for 24-h (Table 1).

Heat acclimation potential of bean germplasm.

Degree of heat injury in leaf tissues of 74 acclimated and non-acclimated bean genotypes estimated by measuring electrolyte leakage and expressed as heat killing time (HKT) is summarized in Table 2. Leaf HT of the 74 genotypes ranged from 5 to 30 min HKT, and leaf HAP ranged from 35 to 130 min HKT. Leaf HT and leaf HAP are not correlated ($r = 0.30$). For example, both GO 3698 and 85CT-4984-1 have a similar level of HT, 15 min HKT (Table 2), but the former has a much higher HAP, 130 min HKT, than the later, 60 min HKT. On the other hand, PI 324607, 5 min HKT, is less heat tolerant than G 6-6, 30 min. HKT, but both genotypes have shown similar HAP, 90 to 92 min HKT.

Post-stress plant growth and development.

There was a significant correlation ($r = 0.73$) between HAP, expressed by HKT, and relative plant dry weight at harvest when plants of 20 genotypes were stressed at 37°C/35°C day/night temperature for 1 week at one month of age (Fig. 1). However, heat stress in this temperature regime, for either 2 or 4 days was not sufficient to cause a significant depression in haulm dry weight (Data not shown). There was also a significant correlation

Table 1. Comparison of heat acclimation potentials (HAP) between pot-grown plants and excised leaves after acclimation for 24-h at 37°C day/night temperature. HAP was expressed by heat killing time (HKT) in minutes needed to result in 50% electrolyte leakage at 50°C.

Genotypes	HKT	
	Pot-grown plants	Excised leaves
Pinto UI III	45	50
Geneva 4416	45	50
BBL 47	62	70
GN Valley	67	59
Hebei NO. 1	80	75
PI 265695	75	78
PI 324607	82	77
PI 271998	80	93
Geneva 4416*	10	10

t = 0.66, not significant

*Plants were grown in a 25°C/20°C day/night temperature regime without exposure to 37°C.

Table 2. Heat acclimation potential (HAP) of the bean germplasm collected. Leaf heat tolerance and leaf HAP are expressed by heat killing time (HKT). Leaf heat tolerance refers to tolerance of leaf tissue which are tested from plants prior to conditioning at 37°C. Leaf HAP refers to the change in leaf heat tolerance of plants after 24-h at 37°C day/night temperature. HKT refers to the min needed to result in 50% electrolyte leakage at 50°C.

Germplasm	HAP	Leaf heat tolerance	Sources*
GO 3689	130	15	1
GO 3696	130	15	1
GO 3702	125	10	1
GO 4495	120	10	1
P 730	120	10	1
GO 0893	115	15	1
BAT 336	110	15	1
GNUI 59	110	20	2
PI 281711	107	25	Spain
Bronco	101	10	Asgrow
G 4727 Ancash 66	100	15	1
Aurora	100	5	2
PI 165616 (Dubbels Witte)	99	20	Netherlands
GN Tara	99	10	2
Labrador	97	20	Asgrew
Super Gloss Tory	97	10	Netherlands
Strike	95	10	Asgrew
V 8025	95	20	1
PI 271998 (Garrofon)	94	10	Spain
VR-Romano	93	15	3

Continued

Germplasm	HAP	Leaf heat tolerance	Source*
P. Checa	92	10	2
G 6-6	92	30	4
5W-372-B	91	25	8
Monument	90	10	2
BTS 3	90	10	2
GN Harris	90	10	2
85CT-4976-2	90	25	3
85CT-4983-2	90	10	3
85CT-4986-3	90	10	3
PI 324607 (La Victorie 270)	90	5	Hungary
NY 590	90	5	5
Top Crop	88	20	
Early Galatin	85	25	Gallatin
85CT-4992-3	85	10	3
G 2525	85	10	1
PI 285695 (Itota Saxa)	83	5	Poland
Tenderette	82	15	Musser
Hebei No. 1	80	20	6
BBL 94	80	5	4
Midnight	80	10	2
85CT-4991-2	80	10	3
Astro	79	10	4
Flo	78	10	4

Continued

Germplasm	HAP	Leaf heat tolerance	Source*
5W-372-A	77	15	8
C 20	76	10	4
PI 324616 (Metis Morocchino 215)	76	20	Hungary
PI 313241 (Veracruzano)	76	10	Mexico
85CT-4978-2	75	20	3
Iguacu	75	15	4
Upland	74	10	4
NY 5-161	72	5	5
85CT-4993-2	70	10	3
85CT-4999-1	70	10	3
G 3645 Jamapa	70	5	1
Domino	70	15	2
WIS(MDR) 147	70	10	7
A 463	67	5	1
Super Gloss Waterfall	66	10	Netherlands
G 14016 ICA (Tondan)	65	10	1
85CT-4971-2	65	15	3
85CT-4975-2	65	10	3
Musser	61	5	Musser
G 5701 Rojo 70	60	10	1
BBL 47	60	10	Asgrew
85CT-4984-1	60	15	3

Continued

Germplasm	HAP	Leaf heat tolerance	Source*
GN Valley	60	5	2
BBL 92	55	10	5
BBL 240	55	10	4
GN 1140	50	10	2
Pinto UI 111	50	10	2
OSU 1604	50	10	5
Geneva 4416	50	10	2
Sentry	45	5	Asgrew
Legacy	35	5	Netherlands

*Seed sources for bean germplasm: 1 = CIAT, Cali, Colombia; 2 = Dept. of Hort., University of Nebraska, Lincoln, NE; 3 = Irrig. Agr. Res. & Develop. CTR, Prosser, WA; 4 = Dept. of Hort., Univ. of Wisconsin, Madison, WI; 5 = Dept. of Hort. Sci., NY State Agr. Expt. Station, Geneva, NY; 6 = Inst. of Veg., Hebei Acad. of Agr. Sciences, Shijiazhuang, Hebei, China; 7 = Dept. of Plant Path., Univ. of Wisconsin, Madison, WI; 8 = USDA, Mayaguez, PR.

Figure 1. Relationship between post-stress relative plant dry weight and heat killing time among 20 bean genotypes of known heat acclimation potential ($r = 0.73$, significant at 5% level), where slope of the regression line $y = 33.25 + 0.59x$.

($r = 0.78$) between HAP and relative number of pods at harvest after a 1 week heat stress at one month of age (Fig. 2). In general, beans which have high HAPs show high post-stress assimilation, as expressed by the increase in plant dry weight and pod. Correlations between leaf HT and plant dry weight ($r = 0.32$), and between leaf HT and relative number of pods ($r = 0.45$) were not significant. High correlation coefficient for post-stress pod set performance in relation to the status of leaf HAPs suggests that the response rate of leaves to the high temperature as the means of increasing thermal tolerance might be an effective selection criterion for improving crop performance in a high temperature environment without directly testing reproductive response to stress.

Post-stress reproductive response.

Pod set.

The 6 bean genotypes used for the post-stress reproductive response test were similar in pod-set ability (about 70% of the tagged open flowers) in the control regime (25°C/20°C day/night temperature). However, after heat stress, i.e. a 2 or 4 day exposure to 37°/35°C day/night temperature, the 6 genotypes differed in pod set (Fig. 3). The high HAP PI 271998 had an even higher percentage pod set after stress than the control, but pods were empty. Pod set of 85CT-4976-2 (high HAP genotype) was decreased by 12 and 54% after 2- and 4-day stress periods, respectively, and pod set of GNUI 59, another high HAP bean, was reduced by 40 and 75% after 2- and 4-day stress, respectively. Intermediate to low HAP genotypes have more flower abscission when exposed to the same intensity of heat stress than high HAP ones. After a 4-day heat stress, pod-set was only 7% in Pinto UI 111, a low HAP genotype.

Flower buds at different stages of development differ in response to heat stress. It appears that open flowers are more tolerant than flower buds, in terms of percent pod set (Fig. 4). Genotypes with intermediate and low HAP show no pod set at the late bud (LB) and medium bud (MB) stages after heat stress, whereas high HAP genotypes still show some pod set. At the small bud (SB) stage, there is a higher percent pod set after heat stress

Figure 2. Relationship between post-stress pod setting capability and heat killing time for high, intermediate and low heat-acclimation-potential bean genotypes ($r = 0.78$, significant at 5% level), where slope of the line $y = 25.17 + 0.65x$.

Figure 3. Pod setting capability in the six bean genotypes after different intensities of heat stress. Pod set was expressed as the percentage of total open flowers tagged prior to heat treatment.

Figure 4. Effect of heat stress at different stages of flowering on pod setting capability in the six bean genotypes, where F = open flower; LB = large buds; MB = medium buds; SB = small buds. Pod set was expressed as the percentage of total tagged flowers and/or flower buds prior to heat treatment.

than at the LB and MB stages. PI 271998, an exception, showed high pod set rates from all stages of flower bud development. Although flowers and young pods on PI 271998 did not abscise after heat stress, all of the pods were seedless and did not develop to normal size. PI 271998 appears to have a strong tendency for parthenocarpy, and stress, such as 37°C/35°C day/night temperature for 2 or 4 days, may promote it. Johnson and Hall (1954) found that high temperature was associated with parthenocarpy in tomatoes.

Pod weight.

Heat stress affects pod weight (Fig. 5). Compared to the control, decrease in pod weight was much less in high HAP than in low HAP genotypes. For example, after a 2-day stress at 37°C/35°C day/night temperature, the average weight of pods per plant was 65, 57 and 40% of the control in high HAP PI 271998, 85CT-4976-2 and GNUI 59, but was 35, 23 and 22% in intermediate HAP Iguacu and in low HAP BBL-47 and Pinto UI 111, respectively.

Seed.

Seed number also reflected degree of sensitivity to heat stress. In all 6 genotypes tested, most of the seeds aborted after a 2-day heat stress. Only a few pods developed seeds (Table 3). Although there was some tendency for greater seed set in the high HAP genotypes GNUI 59 and 85CT-4976-2 than in low HAP BBL-47 and Pinto UI 111, more work would be needed before drawing a conclusion. Nevertheless, the data agree with those of Smith and Pryor (1962), who reported that there was high flower mortality and few seeds per pod when plants were in bloom on high temperature days.

Table 3. Number of seeds per plant for 6 common bean genotypes* heat stressed for 0 (control), 2 or 4 days at 37°C/35°C day/night temperature at the onset of anthesis.

Duration	Genotypes					
of treatment	PI 271998	85CT 4976-2	GNUI 59	Iguacu	BBL 47	Pinto UI 111
0 days	110	95	76	90	162	42
2 days	0	27	40	17	23	0
4 days	0	14	10	6	6	0

*For HAP status, see Table 2.

Figure 5. Total pod weight (per plant) as % of the control after heat treatment in six bean genotypes.

Discussion

Heat injury of plants has been thought to interrelate the 3 variables of temperature level, duration of exposure, and genotypic sensitivity. We hypothesize in the simplest case that there are 2 types of genotypes with regard to genotypic sensitivity (degree of tolerance), i.e., those that can acclimate rapidly to high temperatures and those that adjust slowly. As suggested by Levitt (1980), thermal tolerance of different genotypes should be compared only when plants are at the acclimated stage. Because post-stress plant growth and development determine crop performance, it can be hypothesized that plants with less heat injury will have better growth and development during post-stress, and those possessing high HAP will have less heat injury. Heat acclimation in beans can be considered to be a rapid process (Chen et al., 1982). It may offer an advantage in minimizing heat injury upon exposure to high ambient temperatures. Although there is a lack of scientific documentation, some researchers have suggested that genotypes with extremely high heat tolerance per se very often are poor yielders or have undesirable crop quality. We do not believe that these types of examples existed in our bean germplasm collection (Table 2).

A relationship between the heat resistance and the heat injury of genotypes of a plant species, such as Phaseolus vulgaris L., is proposed (Figure 6). Thus, whenever the level of heat resistance (the combination of initial heat tolerance and increased heat tolerance from acclimation) of a genotype is lower than the level of critical resistance (as shown in Figure 6) at a specific moment during heat stress, plant injury will begin. During exposure, the levels of heat resistance of genotypes are changing, as shown in genotypes 1, 2, and 3 in Figure 6. We hypothesize that the change in resistance is likely controlled by 2 parameters, the initial level of HT and HAP, and suggest that in beans the HAP, not the initial level of HT, mostly determines the heat resistance. Thus genotype with high HAP, such as genotype 1, which at the outset is less heat tolerant than genotype 2, may end up with a high level of heat resistance. Assume that 1, 2 and 3, as illustrated in Figure 6, are genotypes 'GO 3689', 'G 6-6' and 'BBL-47', respectively. They differ in heat tolerance, i.e.,

Figure 6. A proposed relationship between heat resistance (heat tolerance plus heat acclimation potential) and heat injury among three hypothetical genotypes (as shown 1, 2 and 3) of a species such as *Phaseolus vulgaris* L. exposed to heat stress. It is suggested that the genotype heat acclimation potential is the major determinant of: (1) the changes in heat resistance (curved lines) during heat exposure, and (2) the amounts of heat-injury (shaded areas) at the end of a stress (days). Injury will begin whenever the level of heat resistance of a genotype is lower than the level of critical resistance during a stress. HKT = heat killing time in minutes.

2>1>3 (Table 2), but their differences in HT may be insignificant for improving bean performance in high temperature environments because correlations between HT and both post-stress plant dry weight and number of pods are insignificant. However, as seen in Table 2, their HAPs vary greatly, i.e., 'GO 3689' (HKT:130), 'G 6-6' (HKT:92), and 'BBL-47' (HKT:60). Hence, when plants are exposed to heat stress, they all begin to increase in heat tolerance through the acclimation process, as shown in Figure 6. Because of genotypic differences in HAP, the levels of heat resistance increase differentially. At the end of a stress, the amount of heat injury (shaded areas) differs among genotypes with 3 (BBL-47) receiving more injury than 2 (G 6-6) and 2 more than 1 (GO 3689).

When heat stress is removed, the increased HT during heat exposure will rapidly dissipate and the plant more or less will be restored to the initial level of HT. The time course for loss of the high-temperature-induced HT in common bean leaves is about 12-h in a non-temperature stress regime (Chen et al., 1982). Consequently, GO 3689 (Genotype 1) would have better post-stress growth and development than G 6-6 (genotype 2), and G 6-6 than BBL-47 (Genotype 3) because of less heat injury. Genotypes GO 3689, G 6-6, and BBL-47 are known to be good performers when grown in a non-stress environment. With higher HAP in GO 3689 than G 6-6, and G 6-6 than in BBL-47, the possibility for improving crop performance in high temperature environments by selecting GO 3689 would be greater than G 6-6, and G 6-6 than BBL-47.

We have attempted to provide evidence supporting our hypothesis. Two parameters have been utilized as a gross measure of post-stress crop performance, i.e., the relative percent plant dry weight (stressed plants/controlled plants) and the relative percent number of pods (number of pods of stressed plants vs controls). The former is a final result of total assimilation. Injury due to heat stress affects photosynthesis (Berry and Bjorkman, 1980), and thus leads to depression of plant dry weight. Relative plant dry weight should be a reliable indicator of the relationship between HAP and post-stress plant performance. Number of pods per plant is a contributing factor in yield. Again, it may serve as an additional indicator, pointing out the relationship between HAP and plant performance. As

shown in figures 1 and 2, significant correlations are observed between HAP and post-stress plant dry weight, and relative number of pods.

In a separate study of the photosynthetic response of beans differing in HAP to heat stress (42°C or 45°C for 5 min.) (Chaisompongpan et al., 1990), suggests that genotypes may have different mechanisms to cope with heat stress, i.e. a) differential capability to acclimate faster at high temperatures, and b) differential capability to recover from heat injury when stress is removed. It appears that high HAP beans may possess mechanism a) or both a) and b). On the other hand, low HAP genotypes have low capability in both mechanisms. Genotypes with high HAP that showed less heat injury (or faster recovery from heat injury) than low HAP genotypes, as measured by photosynthetic response to heat stress (Chaisompongpan, et al., 1990), help interpret the significant correlation that was observed between HAP status and post-stress plant dry weight in beans (Fig. 1).

A 37°C/35°C, day/night, temperature stress for either 2 or 4 days exposure did not produce as much measurable depression in post-stress plant dry weight as compared to a 7-day exposure in the 6 genotypes tested (Data not shown). However, this same intensity of heat stress did result in significant abscission of flowers and flower buds, and responses differed among genotypes (Fig. 3). Evidence suggests that reproductive organs are more sensitive to heat stress than the vegetative organs in beans. Open flowers are shown to be less sensitive to heat stress than flower buds, as measured by percent abscission. Dickson and Petzoldt (1989) reported that bean plants are most sensitive to heat at or near bloom, and the most critical growth stage was 2 to 3 days before anthesis. During the stages of LB and MB, pollen grains and ovules are developing. They may be at a critical stage and more sensitive to temperature extremes than at the SB stage and open flowers, thus resulting in abscission either before or during anthesis as suggested by Warrag and Hall (1983). Different rates of flower abortion at different developmental stages in Phaseolus vulgaris L. have been reported by Pechan and Webster (1986).

We propose the term "Heat Acclimation Potential" to describe the potential for reaching a higher level of tolerance when the plant is subjected to an acclimating

temperature. Our view is that leaf HT and leaf HAP are two distinguishable phenomena. The increased HT will be dissipated when the impetus for heat acclimation is removed and the plant regains its initial level of heat tolerance. Based on post-stress plant growth and pod number, abscission of flowers/flower buds after heat stress, and yield, we suggest that HAP may be more important than HT and might serve as a selection criterion in a breeding program for improving bean performance in high temperature environments. A similar strategy has been reported for screening wheat heat tolerance (Saadalla et al., 1988). The key consideration in the effective use of HAP would be subjection of the breeding materials or progenies (in the case of the common bean) to a suitable heat acclimation regime (37°C day/night for 24-h) prior to heat tolerance evaluation (50°C for a number of min to result in a 50% electrolyte leakage).

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- II. Photosynthetic responses to heat stress in Phaseolus vulgaris genotypes differing in heat acclimation potential.

ABSTRACT

Photosynthesis is one of the most heat sensitive processes in plants. The common bean (Phaseolus vulgaris L.) is notoriously sensitive to heat. The objectives of this study were to determine the photosynthetic activities of six common bean genotypes under heat stress and whether these activities correspond with genotypes ranking in purported heat acclimation potential (HAP). The HAP is defined as the change in leaf heat tolerance, based on plasmalemma thermostability measured by electrolyte leakage, at the pre-floral growth stage of plants after acclimation at 37°C day/night for 24 hr. Photosynthetic response to short-term heat stress (5 min at 42°C or 45°C) was expressed by O₂ evolution and chlorophyll fluorescence. Without heat acclimation, heat stress at 42°C decreased O₂ evolution in the six genotypes from 50% to more than 95% as compared to the controls and heat stress at 45°C almost totally inhibited O₂ evolution in all genotypes. Heat stress had less effect on peak fluorescence level than on O₂ evolution. Heat acclimation slightly reduced O₂ evolution compared to nonacclimated controls. In heat-acclimated plants, heat stress at 42°C had no effect on O₂ evolution, whereas stress at 45°C significantly reduced O₂ evolution. Changes in levels of peak fluorescence under heat stress in heat-acclimated plants showed patterns similar to changes in O₂ evolution. Photosynthetic responses to heat stress did not totally correspond with the ranking of HAPs of the six genotypes obtained by conductivity test. Full recovery of O₂ evolution from heat injury at 42°C for 5 min occurred within 4 hr in GNUI 59, whereas O₂ evolution rates were still lower than the controls after 6 hr in the other genotypes. The recovery of chlorophyll fluorescence was more slowly than that of O₂ evolution.

INTRODUCTION

Heat stress affects many physiological processes such as photosynthesis, respiration, translocation, and membrane permeability (5,18). Among these processes, photosynthesis is the most heat sensitive (5,15). Oxygen evolution and chlorophyll fluorescence are greatly altered by high temperatures and are widely used as indicators of heat injury to the photosynthetic apparatus (2,3,4,5,9,15,17,19,22). The impact of high temperature on photosynthesis depends on plant genotype and growth conditions. Plants exposed to or grown at moderately high temperature have greater thermal stability of the photosynthetic apparatus than plants grown at lower temperature (5). The ability of plants to acclimate at moderately high temperatures, thereby reducing heat injury (1) and the ability to recover from heat injury are important factors in determining plant performance in high temperature environments.

The conductivity test, based on thermostability of the plasmalemma, has been used to estimate heat tolerance in beans and other crops (6,14). Germplasm of common bean has been screened using the conductivity test for heat acclimation potential (HAP) (13). The HAP is defined as the change in leaf heat tolerance after plants have been acclimated at 37°C day/night for 24 hr. The plasmalemma impairment due to heat stress occurs at higher temperatures than that which damages the photosynthetic apparatus (5). The objectives of this experiment were to determine photosynthetic responses to heat stress in six common bean genotypes with high or low HAP and to determine whether photosynthetic responses to heat stress correspond to their HAP rankings.

MATERIALS AND METHODS

Plant Materials

Six genotypes of common bean having different levels of HAP as determined by the conductivity test (6,13) were used. Three genotypes have high HAP, including 'GNUI 59', PI 271998, and 85CT-4976-2, and three have low HAP, including 'BBL 47', 'GN 1140', and 'PINTO UI 111' (Table 1). Plants were grown in a growth chamber in a sand:soil mixture (1:1, v/v) under a 12-hr light/12-hr dark cycle with a photosynthetic photon flux density (PPFD) of $450 \mu\text{mol m}^{-2} \text{s}^{-1}$. The temperature was 25°C/20°C day/night, and the vapor pressure deficit (VPD) was 0.95 kPa. Plants were watered daily to the drip point with a half-strength modified Hoagland's solution.

Chlorophyll Fluorescence and Oxygen Evolution Measurement

Chlorophyll fluorescence and oxygen evolution were measured in a Hansatech leaf disc chamber (7,8,20). Temperature during the measurements was controlled at 25°C by flowing water through a water jacket. A 10-cm² leaf disc was cut from the middle leaflet of the youngest fully-expanded trifoliate leaf of a 25-day-old plant. Before the measurement, leaf discs were kept in the dark in a petri-dish with moist filter paper for 30 min at room temperature. A red light source (680 nm) with PPFD of $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ was provided for fluorescence measurement. The measurement was carried out for 5 min. The fast fluorescence induction was recorded by MTU 130 microcomputer (Microtechnology Unlimited, N.C.) for 10 sec ($500 \text{ points sec}^{-1}$) with software developed from the same laboratory. Fluorescence was also recorded on a chart recorder for 5 min.

Oxygen evolution was measured for 10 min at light and CO₂ saturation. Carbon dioxide was supplied from 0.5M NaHCO₃. Light was provided by 100-W projector lamp with PPFD of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. After measurement of oxygen evolution, chlorophyll content in the leaf disc was determined according to the method of Knudson et al. (11).

Ion Leakage Measurement

Ion leakage was measured by the conductivity (6). After the leaf disc was removed for photosynthesis determination, two 1-cm-diameter discs were cut from the remaining part of the leaf. Leaf discs were put in vials with 10 mL distilled water, vacuum infiltrated for 15 min, and shaken at room temperature for 1 hr. Electrical conductance (R_1) of the solution was measured with a Wescan conductivity meter. The samples were frozen overnight at -70°C, warmed to room temperature, shaken for 1 hr, and electrical conductance (R_2) of the solution was measured. The ratio (R_1/R_2) was used as a measure of relative heat injury.

Determination of Plant Response to Heat Stress

With and Without Heat Acclimation

Two levels of heat stress were imposed for 5 min: 42°C or 45°C. The middle leaflet of the youngest fully-expanded trifoliolate leaves of 25-d-old plants were harvested and immediately placed into test tubes along with moist filter paper. The leaves were heat treated in a water bath at 42°C or 45°C for 5 min in the dark. After heat treatment, chlorophyll fluorescence, oxygen evolution, and ion leakage were measured as described above.

Another group of plants was acclimated in a growth chamber at 37°C for 24 hr under 12-hr light/12-hr dark cycle with PPFD of 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a VPD of 0.94 kPa. The VPD was kept constant by providing higher relative humidity in the acclimation chamber using a humidifier. The leaflets were harvested and also stressed at 42°C or 45°C for 5 min. Chlorophyll fluorescence, oxygen evolution, and ion leakage were then measured as described above. The response of photosynthesis to the acclimation temperature was also measured immediately after acclimation. Controls were plants grown at 25°C/20°C day/night.

Recovery of Photosynthetic Activity after Heat Stress

Recovery of photosynthetic activities from injury following 42°C for 5 min stress was examined in the six genotypes. After heat stress, the leaves were left in the test tubes in the dark at room temperature for 0, 2, 4, and 6 hr. Chlorophyll fluorescence and oxygen evolution were then measured as described above.

Experimental Design and Statistical Analysis

In heat stress response study, two similar experiments sharing 3*6 factorial design with four replicates were conducted. One plant was used in each replicate and one sample was taken from each plant. There were three treatments (acclimation, heat stress with acclimation, and heat stress without acclimation) and six genotypes. Responses were O_2 evolution and fluorescence each of which was expressed as a percentage of an internal control. Controls were the leaves harvested from plants grown at 25°C/20°C day/night. Plants were exposed to heat stress temperatures for 5 minutes. The heat stress temperatures were 42°C in one experiment and 45°C in the other. Analysis of variance and Fisher's

protected least significant difference ($LSD_{0.05}$) were used for data analysis in each experiment.

Similar design was utilized in the ion leakage experiment having three treatments (control, heat stress without acclimation, and heat stress with acclimation) and six genotypes. The heat stress temperature was 42°C for 5 minutes. Responses were described under 'Ion Leakage Measurement'. Controls, acclimation, and data analysis were the same as those described earlier.

In the recovery experiment, four treatments (0 hr recovery, 2 hr recovery, 4 hr recovery, and 6 hr recovery) and six genotypes were also organized in a factorial design. The heat stress temperature was 42°C for 5 minutes. Controls and statistical procedures used for data analysis were the same as above.

Data analyses were performed using Statistix software (Statistix is a registered trademark of NH Analytical Software).

Several preliminary experiments were conducted. The results presented herein are from one main experiment.

RESULTS

Response of Plasmalemma to Heat Stress in Heat-acclimated and Nonacclimated Plants

Heat stress at 42°C for 5 min did not cause lethal ion leakage in either heat-acclimated or nonacclimated plants (Table 1), since 50% (0.50) ion leakage is considered a critical level resulting in irreversible plasma membrane damage in bean (13).

Response of Photosynthesis to Heat Stress in Heat-acclimated and Nonacclimated Plants

Rates of O_2 evolution after heat stress in heat-acclimated and nonacclimated plants are presented in Fig.1. Since the rates of O_2 evolution of the controls differed among the six genotypes, percentage of control is used to express the effects of heat stress on photosynthesis. Stress at 42°C for 5 min decreased O_2 evolution from 50 to more than 95% among the genotypes tested (Fig.1A). Without heat acclimation, decrease in O_2 evolution after heat stress at 42°C was least in genotypes purportedly heat tolerant (GNUI 59) (Table 1), and heat sensitive (PINTO UI 111). The decrease in O_2 evolution was greatest in PI 271998 and 'BBL 47'. Heat stress at 45°C for 5 min almost totally inhibited the photosynthetic activity in all six genotypes (Fig.1A).

Acclimation treatment at 37°C reduced O_2 evolution by 20 to 30% in all genotypes, except 'GNUI 59' and PI 271998, which are high-HAP genotypes (Fig.1B). After acclimation, the 42°C stress did not significantly reduce O_2 evolution compared to those from acclimation treatment alone (Fig.1B and 1C,), whereas exposure to the 45°C stress significantly decreased O_2 evolution (Fig.1C,). Heat injury at 45°C after acclimation was least in PI

Table 1 The effects of high temperatures on ion leakage in six genotypes of *P. vulgaris* L. previously classified based on heat acclimation potential.

Genotypes	Leaf Heat	Leaf HAP ‡	Ion Leakage (R_1/R_2) §		
	Tolerance †		Control	42°C, 5 min	37°C, 24 hr+ 42°C, 5 min
	min	min	ratio		
GNUI 59	20	110 High	0.13	0.14	0.11
PI 271998	10	94 High	0.21	0.25	0.17
85CT-4976-2	25	90 High	0.13	0.13	0.10
BBL 47	10	60 Low	0.23	0.24	0.19
GN 1140	9	50 Low	0.15	0.14	0.10
PINTO UI 111	7	50 Low	0.13	0.14	0.12
LSD (0.05) ¶	-	-	0.03		

† Leaf heat tolerance, the tolerance of leaves from plants grown in a non-stress environment and expressed by time in minutes needed to result in 50% electrolyte leakage at 50°C (heat killing time or HKT).

‡ Leaf heat acclimation potential, the change in leaf heat tolerance following the exposure of plants for 24 hr to 37°C, day/night, and expressed by HKT.

§ R_1 , the first conductivity reading taken after the leaf was heat treated.

R_2 , the second conductivity reading taken after the leaf tissue was frozen overnight and thawed, thus releasing the total ions in the tissue.

¶ LSD (0.05) between means of all treatment and genotype combinations.

Fig.1 Oxygen evolution (as percentage of control) in six genotypes of *P. vulgaris* L. when nonacclimated leaves were heat stressed at 42°C or 45°C for 5 min (A), acclimated at 37°C for 24 hr (B), and heat stressed at 42°C or 45°C for 5 min after acclimation at 37°C for 24 hr (C). Controls were the leaves harvested from plants grown at 25°C/20°C, day/night, without heat treatment. Vertical bars indicate standard errors of means. Data from heat acclimated groups of heat stress experiments were pooled.

271998, a high-HAP genotype, which strongly indicates that PI 271998 has very high potential to acclimate to high temperatures.

Peak fluorescence (Fp) was determined by subtracting terminal fluorescence (Ft) from maximum fluorescence (21). Because of the difference in chlorophyll content in each sample, Fp values were also corrected by expressing Fp emitted per mg chlorophyll. The Fp for all genotypes did not decrease as much as O₂ evolution after exposure to 42°C for 5 min (Fig.2A). Decrease in Fp was least in 'PINTO UI 111' and greatest in 'BBL 47' and 'GN 1140'. These three genotypes belong to the heat sensitive group with 7 to 10 min HKT (Table 1). Acclimation treatment reduced Fp from 10 to 30% of controls (Fig.2B). The 42°C stress did not affect Fp of heat-acclimated plants (Fig.2C,). Although the 45°C stress affected the level of Fp less than O₂ evolution, it significantly decreased the level of Fp compared to acclimated nonstressed plants (Fig.2C,). Consistent with O₂ evolution, the decrease of Fp was also least in PI 271998 (a high-HAP genotype) after acclimation. Changes in levels of peak fluorescence and rates of O₂ evolution were highly correlated ($r=0.96$).

When treatment effects were held constant , GNUI 59 and PINTO UI 111 performed the best under 42°C stress, whereas 85CT-4976-2 performed poorly even though it has been ranked as heat tolerant genotype. Interestingly enough, PI 271998 significantly outperformed any other genotypes under 45°C stress.

Recovery of Photosynthetic Activity after Heat Stress

Oxygen evolution almost fully recovered from heat injury at 42°C for 5 min within several hours at room temperature in all genotypes (Fig.3). After 2 hr, O₂ evolution in 'GNUI 59' (a heat-tolerant genotype) reached the control level,

Fig.2 Peak fluorescence in six genotypes of *P. vulgaris* L. when nonacclimated leaves were heat stressed at 42°C or 45°C for 5 min (A), acclimated at 37°C for 24 hr (B), and heat stressed at 42°C or 45°C for 5 min after acclimation at 37°C for 24 hr (C). Vertical bars indicate standard errors of means. Data from heat acclimated groups of heat stress experiments were pooled.

Fig.3 Recovery of O_2 evolution in six genotypes of *P. vulgaris* L. at room temperature after exposure of leaves to heat stress at 42°C for 5 min. LSD (0.05) is the least significant difference between all treatment and genotype combinations.

whereas others were still significantly lower than the controls. Six hours after stress, O_2 evolution had returned to approximately 80% of the controls in all genotypes except 'GNUI 59', which was about 100% of the control.

The level of Fp decreased to 80% of the control after 42°C for 5 min stress in 'GNUI 59', whereas the levels of Fp in other genotypes were between 40 and 60% of the controls (Fig.4). The Fp decreased to 50% after 2 hr at room temperature in 'GNUI 59' and returned to 80% of the control level after 4 hr and stayed at the same level after 6 hr. In the other genotypes, the levels of Fp remained below 70% of the control level during the 6-hr recovery period. There was no correlation between the recovery of O_2 evolution and that of Fp ($r=0.43$).

Fig.4 Recovery of Peak fluorescence in six genotypes of *P. vulgaris* L. at room temperature after exposure of leaves to heat stress at 42°C for 5 min. LSD (0.05) is the least significant difference between all treatment and genotype combinations.

DISCUSSION

Photosynthetic sensitivity to heat stress differed among the six genotypes. 'GNUI 59' and 'PINTO UI 111' had the highest ability to withstand heat stress, whereas PI 271998 and 'BBL 47' had the lowest ability. Despite the sensitivity of PI 271998 to heat stress, it had high potential to acclimate to moderately high temperature. 'GNUI 59' had high ability both to withstand heat stress and to acclimate to high temperature. 'BBL 47' was one of the most heat sensitive genotypes among the six. 85CT-4976-2, a heat-tolerant (25 min HKT) and high-HAP (Table 1), was one of the most heat sensitive genotypes with the lowest level of photosynthetic activity. Even though it was not as heat sensitive as 'BBL 47', it had much lower photosynthetic activity than 'BBL 47' under heat stress after acclimation.

At the intensity of heat stress used (42°C, 5 min and 45°C, 5 min), photosynthetic responses among the six genotypes did not totally correspond with their rank of HAP as estimated by conductivity (Table 1). However, after acclimation, 'GNUI 59' and PI 271998 (high-HAP genotypes) had less heat injury at 42°C for 5 min, and 'BBL 47', 'GN 1140', and 'PINTO UI 111' (low-HAP genotypes) were injured more, based on photosynthetic responses.

Results from this study confirm that the photosynthetic apparatus is more heat sensitive than plasma membrane integrity. Heat stress at 42°C was not sufficient to cause damage to the plasma membrane in the six genotypes (Table 1). The critical level of ion leakage that is considered to be irreversible membrane damage in bean is 50% (13). However, the same intensity of heat stress significantly inactivated O₂ evolution (Fig.1A). Bjorkman and co-workers (5) found that much higher temperatures were required to induce ion leakage than to

reduce photosynthesis. This suggests that the reduction in photosynthesis occurs before plasmalemma impairment.

If photochemical reactions are inhibited by the heat stress, the rate of reoxidation of quencher Q_A , the first electron acceptor of PSII, will be reduced and cause an increase in the level of terminal fluorescence (F_t) (12). The reduced level of F_p , coupled with no change in the level of F_t (data not shown), indicates that heat damage occurred on the oxidizing side of PSII and not in the photochemical reactions. Initial fluorescence (F_o) cannot be used as an indicator of heat damage on PSII in this study since there was no change (data not shown). This contradicts reports in the literature (12,16,19), but may have resulted from the fact that the large proportion of F_o measured in this experiment was the reflection of light derived from the exciting light source. This interpretation is supported by similar levels of F_o observed from the measurements made with a piece of filter paper.

It has been known that exposure of a plant to high temperatures may result in acclimation of photosynthetic apparatus and improvement of photosynthetic rates (5). Acclimation at 37°C for 24 hr resulted in subsequently less heat injury to O_2 evolution under both levels of heat stress used in this study (Fig.1). Acclimation reduced heat injury to the F_p under 42°C stress in all genotypes but reduced heat injury of the F_p under 45°C stress only in PI 271998 (Fig.2).

Recovery from heat injury was also studied as another mean for plants to cope with heat stress. O_2 evolution recovered from heat inactivation faster in 'GNUI 59' than in other genotypes studied (Fig.3). This might be due to the fact that the decrease in O_2 evolution in 'GNUI 59' was much less than in other genotypes. After 6 hours, O_2 evolution returned to the control level in 'GNUI 59', but remained lower than the control levels in others.

The Fp decreased under heat stress condition and continued to decrease after a 2-hr recovery at room temperature in 'GNUI 59' but remained at the same levels in the other genotypes. Kislyuk (10) found, that when photosynthesis was not totally inhibited by heat stress, recovery of the photosynthetic apparatus is faster after cessation of heat stress when exposed to photosynthetically active radiation. In this study, the leaves were left in the dark for recovery.

The results from heat stress response experiment with and without acclimation showed high correlation between O_2 evolution and Fp ($r=0.96$). This suggests that the effects of heat stress on one parameter can be indicative to the other and that either one of the parameters can be used as a screening tool for heat tolerance and HAP. In contrast, the results from recovery experiment showed no correlation between O_2 evolution and Fp ($r=0.43$). O_2 evolution recovered from heat injury with time, whereas Fp showed different pattern of recovery. We, therefore, suggest that O_2 evolution is a better screening tool for recovery ability.

The results from this study indicate that 'GNUI 59' possesses three mechanisms to cope with heat stress : 1) inherent tolerance to heat stress ; 2) acclimation to moderately high temperature with improved tolerance to higher intensity of heat stress ; and 3) rapid recovery from heat injury. PI 271998 showed high sensitivity to initial heat stress, but has high potential to acclimate to moderately high temperature. The results also indicate that the photosynthetic apparatus is much more sensitive to heat than the plasmalemma. Photosynthetic response to heat stress did not totally correspond with the ranking of HAP based on ion leakage, suggesting that photosynthetic response to heat stress is independent of plasmalemma damage.

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III. Breeding and Inheritance Phase.

Abstract

Based on information from generation means analysis and on the results from recurrent selection, the improvement of bean heat tolerance is considered to have good potential in bean breeding programs.

BREEDING AND INHERITANCE PHASE

Introduction

The primary objectives of this phase, as reviewed at the outset of this report, were to determine the inheritance of heat tolerance and to determine if selection progress for greater tolerance might be possible.

However, the availability of an inexpensive, reliable method permitting the rapid screening of large numbers of progeny is critical to the success of breeding studies. Accordingly, further evaluation of other screening methods, and of potential screening methods, was undertaken. This search led to the adoption of both conductivity and leaf ethylene evolution in screening of progenies but did delay overall progress in the breeding phase.

Literature Review

Methods for Screening Breeding Material. Heat stress in plants has long been induced either by high air temperatures or by submersion of potted plants or plant parts in a hot water bath. In the evaluation of stress impact, i.e. degree of tolerance, numerous criteria have been used, such as visual damage to foliage, reproductive failure, loss of cell membrane integrity and tissue ethylene evolution. All, albeit on a very limited scale, have been used with common bean, Phaseolus vulgaris L., a species well known for heat sensitivity, as manifested by pod and blossom drop.

Farlow et al (1979) examined in vitro pollen viability following hot water immersion of plants and plant parts. Others have used warm greenhouse or field environments (Bouwkamp and Summers, 1982; Dickson and Petzoldt, 1989). Several studies have shown that high temperatures reduce pollen viability of P. vulgaris (Dickson and Boettger, 1984; Farlow et al., 1979; and Halterlein et al., 1980). Marsh and Davis (1985) showed that Phaseolus species differed in cell membrane integrity, as estimated by conductivity (Alexandrov, 1964; and Chen et al., 1982), when temperatures of 27, 32 and 37°C were applied at 3 growth stages. Conductivity has been used in germplasm screening (Li et al., In Press) but, because it is very time consuming, more rapid methods may be needed. The use

of conductivity in the estimation of bean heat acclimation potential (HAP) has been reviewed in earlier sections of this report, and the conceptual basis of HAP was discussed. Hence, hereinafter we will refer primarily to "HAP" rather than to "tolerance."

Ethylene Production by Heat Stressed Tissue. Even though light conditions markedly affect the yield of common bean, it is known that plant development is strongly influenced also by night temperature (Viglierchio and Went, 1957) and that heat stress is more effective in causing flower and pod abscission when applied at night than during the day (Konsens, 1983). This complicated relationship between the dependence of common bean yield on photosynthesis and the special sensitivity to heat stress during the night may be at least partly explained by taking into account the participation of ethylene in the response to high temperature.

The production of 1-aminocyclopropane-1-carboxylic acid (ACC), which is a precursor of ethylene, and of ethylene by the common bean, increases under high-temperature stress (Field, 1985; Yang and Hoffman, 1984). Processes known to be triggered or controlled by ethylene, such as abscission of flowers and pods, are likely to be affected by high-temperature stress (Konsens, 1983; Mack and Singh, 1969; Smith and Pryor, 1982; Viglierchio and Went, 1957). It thus seems reasonable to suggest that measurement of ethylene evolution rates (EER) under heat stress may provide a useful indication of the tolerance of bean to heat stress.

Under a high-CO₂ environment, the rate of ethylene conversion from ACC may be increased (Grodzinski et al, 1982; Horton, 1985; Kao and Yang, 1982). It follows that high light intensity, photosynthetic efficiency and respiration rate may be important factors in the control of ethylene evolution (Gepstein and Thimann, 1980; Grodzinski et al, 1982; Preger and Gepstein, 1984). An increased rate of ethylene evolution may in turn decrease the efficiency of photosynthesis (Taylor and Gunderson, 1986). Thus, a high-temperature effect on ethylene production during the day may result in a decrease in photosynthetic efficiency and hence in accumulation of dry matter and carbohydrates. Because of the CO₂ effect on EER, the effect of high temperature stress on EER is likely to be stronger during the night when the increased respiration rate is not compensated for by photosynthesis. The differences among plants in their EER under the influence of high CO₂ level may be related also to the presence of light, since in some cases CO₂ caused increase in EER only in the light (Yang and Hoffman, 1984) while in others the CO₂ effect was found also in the dark (Kao

and Yang, 1982; Preger and Gepstein, 1984).

Light intensity may affect the EER in two kinetically different ways. The first effect is the change in EER in response to the photosynthetic-dependent CO_2 level (Yang and Hoffman, 1984); it is rapid, reversible, and time-limited by the amount of ACC available (Bassi and Spencer, 1982; Gepstein and Thimann, 1980). The second effect of light intensity is based on the stimulation of ACC and ethylene production caused by increased levels of carbohydrates (Meir et al, 1984; Philosoph-Hadas et al, 1984) accumulated during growth.

Inheritance of heat tolerance. There are few reports on the genetic nature of heat tolerance in beans. Resistance of beans to temperature-drought stress (estimated by pod production) has been reported to be due to a single dominant gene in one cultivar, and to 2 genes with epistatic action in a second cultivar (Bouwkamp and Summers, 1982). Marsh et al (1985) measured HT tolerance by electrolyte conductivity and concluded that additive and dominance gene action accounted for the major genetic differences in two HT-tolerant x HT-sensitive crosses. It was concluded that epistasis had to be taken into account to explain the genetic differences in a third cross (Marsh et al, 1985). Dickson and Petzoldt (1989) estimated broad sense heritabilities (H_b) for yield of seeds and pods under HT conditions. H_b ranged from 19 to 79% and their results indicated quantitative inheritance. Good agreement was found between growth chamber and field results.

Our inheritance investigations utilized both conductivity and ethylene evolution rate (EER) under HT stress as indicators of degree of HT tolerance. Earlier research showed a strong negative association between HT-stress EER and plant growth (Tingey, 1980). Pepper (*Capsicum frutescens* L.) cultivars previously known to be HT stress tolerant based on flower bud abscission also were found by Wien (1988) to have less bud abscission following the application of ethephon. Wien et al (1989) concluded that increased ethylene level was the primary cause of pepper flower bud abscission under low light intensities. They suggested that the role of ethylene in their experiments may be similar to that observed in the dropping of young cotton bolls subjected to low light or high night temperatures (Guinn, 1976). Ethylene may play a similar role in the dropping of flower buds, flowers and small pods in beans as a response to HT conditions.

Materials and Methods

Further Evaluation of Screening Methods

Major effort was given to the integration and interpretation of germplasm screening data so that a firm genetic resource base could be identified for the breeding phase. Emphasis was placed on electrolyte conductivity (cell membrane integrity) and on ethylene evolution rate from heat stressed leaf tissue. Screening proceeded more slowly than expected because of variability in results from the conductivity method. The methods require great operator care and skill, and do not permit rapid screening of large numbers of plants, a necessity for inheritance and selection studies. Furthermore, it was desirable to have some confirmation of conductivity results by test results from field and biotron tests in Israel before other than preliminary commitment could be made to hybridization and progeny testing.

New methods were examined that might be useful in screening germplasm and for the study of progeny in the selection and inheritance research. Near the beginning of the project, we were fortunate to have Dr. I. Wallerstein of the Volcani Center at the University of Minnesota as a Visiting Scientist. The following describes the cooperative approach with Dr. Wallerstein by which leaf ethylene evolution rate (EER) was researched as a possible screening tool which we then used under the BARD project for the evaluation of progenies in the breeding phase.

Comparison of PI 271998 (tolerant) and BBL-47 (sensitive) Germplasm by Leaf Ethylene Evolution Rate (EER). Two common bean genotypes of Type I growth habit and maturity, and previously identified as "heat-tolerant" (PI 271998) and "heat-sensitive" (BBL-47) (Marsh et al. 1985), were grown in a greenhouse in Minnesota at 25/18C day/night temperatures and natural photoperiod. Previous work, presented in an earlier section of this report, described PI 271998 and BBL 47 as having high and low heat acclimation potential (HAP), respectively.

Plants were grown in 20 cm pots containing a mixture of sand, soil, peat and vermiculite (1:1:1:1 by volume) and fertilized at each irrigation with 200 mg.l⁻¹ of a commercial fertilizer (20 N : 8.7 P : 16.6 K). Sixty days after planting, when the plants were reaching the end of the pod-filling phase, the dry weight of the plant (cut at the soil level) and the numbers of pods, pods with seeds and seeds, were determined for each plant. Harvested plants were dried for 72-h at 72C in a forced-air

oven.

For heat-stress treatments, applied at different growth stages, plants were transferred to growth chambers and subjected to 24-h daily cycles with a 12-h photoperiod under a light intensity of $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ photosynthetically active radiation (PAR) supplied by mercury lamps. Included in each daily cycle was a 12-h period (light or dark) of heat stress at 30C and a complementary 12-h period at 20C. For experiments conducted under low light intensity ($150 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR), fluorescent lamps were used. The higher light intensity was used for all experiments except where otherwise noted. Depending on the experiment, 2, 3, 10 or 30 daily cycles of heat stress were applied. Following completion of the last cycle, plants were returned to the greenhouse.

At different growth stages and at different times during the daily cycle, EER was measured from 1 g (fresh weight) samples of primary leaf tissue in 32-ml flasks sealed with rubber serum caps. A one ml sample of gas was withdrawn from each flask after incubation for 2 h at room temperature (25C) in the dark. Samples were injected into a Hewlett Packard 5880A gas chromatograph equipped with a flame ionization detector. A Poro Pak Q column with a gas flow of N_2 (30 ml.min^{-1}), H_2 ($28 - 30 \text{ ml.min}^{-1}$) and air ($400 - 450 \text{ ml.min}^{-1}$) was used at an oven temperature of 70C, detector temperature of 150C and a junction temperature of 100C. The peak areas obtained for ethylene were compared with those of known ethylene standards. The rate of ethylene accumulation in the incubation flask was constant during 2 h of incubation and there was no detectable wound effect on EER. The primary leaves sampled for ethylene measurement remained green until the plants were at least 60 days old.

Variables consisted of planting dates, plant age at application of heat stress, number of daily cycles of heat stress, and light intensity during daily heat-stress cycles.

The effect of planting date of greenhouse-grown plants (i.e., under controlled temperatures and changing natural photoperiods) on all yields components was determined from seven dates in autumn, winter and spring. In order to study the combined effect of heat-stress and light intensity (during growth and under stress) on all yield components we used a combination of planting date, plant age, number of daily heat-stress cycles, and light intensity at the time of stress, as follows: May 7, 36 days, two cycles and $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR; and August 22, 30 days, 30 cycles and $150 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR.

The effect of seasonal changes in natural daylight during growth on EER under heat stress was studied by subjecting 23-day-old plants planted on January 15, February 21, and April 23 to two daily cycles of daytime ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or nighttime heat stress at 30C. In studies of the direct effects of natural and growth-chamber light intensity on EER with or without heat stress, we used non-stressed 37-day-old plants planted on May 15 and examined in the greenhouse on cloudy or sunny days (100 or $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR, respectively); and 28-day-old plants started in February 15 and exposed to daytime or nighttime heat stress at 30C and daytime light intensities of 150 or $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR in the growth chamber.

The effect of plant developmental stage on response to heat stress in terms of all the yield parameters was studied in plants at the flowering (36-day-old) or vegetative (20 - or 17-day-old) stage, after being subjected to 2, 3 or 10 daily cycles of daytime ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or nighttime heat stress, (30C). These plants were grown from seed planted on May 7 or 15.

The EER of nonstressed plants at different growth stages (23-, 27-, 35-, 42- and 60-days-old) was determined in plants from seed planted on April 23 and grown under greenhouse conditions. The effect of developmental stage on response to heat stress in terms of EER was examined in vegetative (28-day-old) or flowering (36-day-old) plants, all of which had been started from seed planted on April 23 and subjected to two daily cycles of heat stress at 30C and a daytime light intensity of $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR.

As a control for the heat stress treatments we used greenhouse growth conditions, since no differences were found in yield, plant dry weight or EER between plants treated for 10 days at 20C under a daytime light intensity of $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR in a growth chamber and plants grown continuously under greenhouse conditions.

Evaluation of Field Grown Germplasm for EER. Additional germplasm was screened for EER via the procedure described above. Ten *P. vulgaris* genotypes ('BBL 47', 'UI 111', PI 271998, 'Strike', 'Labrador', 'Red Kidney', 'GNUI 59', 'Hebei No. 1', G 4727 (Ancash 66), USDA 85-CT-4986-3)) and a *P. acutifolius* (tepariy bean) entry were field-grown 80 km from the laboratory on an irrigated Hubbard series soil (Sandy, mixed udorthentic haploborolls) under standard cultural practice. BBL 47 and UI 111 (a 'Pinto' type) had been identified in earlier work as HT sensitive via conductivity, while all others had been identified as HT tolerant (unpublished data). Plants were

spaced 0.1 m apart in 1.5 m long unreplicated, single-row plots with 0.75 m between rows. Plants were evaluated the morning following a 33/27C day/night which had been preceded by several diurnal cycles of cooler temperatures (30/25C day/night). Leaf samples were collected for EER determination and prepared for incubation prior to transit to the laboratory. The transit time constituted their 2-hr incubation. Ten samples, each from a single plant, were evaluated from each plot.

Comparison of Conductivity, Hot Water Immersion and Pollen Viability as Screening

Methods. Seventeen genotypes of *P. vulgaris* were used. These were: PI 271998 (high HAP), 5BP-7 and 80BP-2 (heat tolerant breeding lines, USDA/ARS/Prosser, WA), BBL 47 (a low HAP cultivar from Asgrow Seed Company, Kalamazoo, MI), 80BP-6 (a heat sensitive breeding line, USDA/ARS/Prosser, WA), and BAT 11, G2206, G1951, G1401, G3689, 81C-4883-B, ICA Palmer, G4461, A 162, A 70, BAT 258 and BAT 332 (all possibly having some tolerance, and obtained from the International Center for Tropical Agriculture (CIAT), Cali, Colombia). The response of PI 271998 and BBL-47 has been documented (Li et al., 1990; Marsh and Davis, 1985; and Sauter et al., 1987).

All experiments were conducted on uniform plants grown in plastic pots in a 1: sand: 1 peat: 1 vermiculite (by volume) steam-pasteurized medium fertilized weekly with 200 ml of tap water with 400 N:174 P:332 K mg/liter of water (supplied by Peters soluble 20N:8.7P:16.6K fertilizer). Pots were overseeded and thinned to maximize uniformity.

To evaluate hot water immersion, plants were thinned to 2 per each of ten 20 cm diameter pots of each of the 17 genotypes and maintained in the greenhouse at 30/20C, day/night. At the initiation of anthesis, plants, except for the roots, were immersed in a water bath at 35 or 40C for 4 min. These temperatures and the 4 min time were chosen because preliminary work showed that they produced greatest separation among genotypes; both higher and lower temperatures at 2, 4 and 6 min were either ineffective or killed the plants (Marsh and Davis, 1985). Flower buds from one to about 5 days from anthesis were tagged immediately after heat treatment, and 3 weeks later the numbers of pods and seeds per pod from these buds were counted; the number of pods with seed was used to determine the percent pod set. The experiment was repeated.

Conductivity was evaluated on replicated single plants of the 17 genotypes established in 15

cm diameter pots and grown in a growth chamber under 15 hr photoperiod, a light intensity of $450 \mu\text{mol.s}^{-1}\text{m}^{-2}$, and 20/15C day/night temperature. The 17 genotypes were each represented as single plants in each of 7 growth chamber runs (replications). At 32 days after planting, the plants were acclimated at 37C for 24 hours in the chamber. Following acclimation, 10 fully expanded leaflets were excised from each plant for evaluation of cell membrane integrity (as heat-killing time) via electrical conductivity (Alexandrov, 1964; Chen et al., 1982). Estimation of heat tolerance following acclimation at 37C for 24 h, prior to stress application, is more correctly an estimate of HAP rather than of tolerance per se (Levitt, 1972).

Pollen viability and pod set of 5 genotypes were evaluated as criteria of heat tolerance, in 2 randomized complete block design experiments conducted with 5 single-plant and 4 double-plant (per pot) replications, respectively. Plants were grown in 20 cm diameter pots in the greenhouse at 30 to 40/30 to 20C, day/night temperature. At the third day of flowering, and the following 4 days, flower buds of uniform size and development (and one-day from anthesis) were randomly selected from each plant for estimation of pollen viability. Following pollen staining with acetocarmine, 500 grains from each sample were counted under 10X magnification. Stained grains regular in shape were considered viable. To determine pod set, flower buds and open flowers and pods were tagged, and percent pod set was determined by calculating the percentage of pods produced from total flower buds on each plant.

Inheritance Studies (See Objective III)

Generation Means Experiment: After 2 generations of single plant selection for EER reaction to HT stress, PI 271998 (high HAP) and BBL 47 (low HAP) were crossed and F_2 and reciprocal BC_1 populations were produced in the greenhouse. A generation means analysis of progenies was conducted from growth chamber HT tests according to the following protocols. Scarified seeds of the parent and progeny populations (Table 1) were germinated in compartmentalized (4.5 cm diam. cones) flats filled with commercial starter mix. Uniform seedlings were transplanted into 0.15m diameter/1.5 l pots of a 2 soil : 1 peat : 1 sand (by volume) pasteurized medium when the primary leaves had unfolded but not yet expanded, and grown in a greenhouse at 23/18C day/night. A

randomized complete block design was used, with 9 benches as blocks. Each block contained 4 plants of each parent, 2 and 6 of each reciprocal F_1 and F_2 , respectively, and 12 of each of the 2 backcrosses. Blocks were separated by a 2-day planting sequence because of limitations in growth chamber space. Thus each block constituted a separate experiment in the chamber.

At full bloom (2 viable pods set on the first raceme to reach anthesis, with several flowers opening on other racemes), approximately 36 days after planting, plants were transferred to the growth chamber for HT treatment at 35/30C day/night, and a 12-hr photoperiod ($600 \mu\text{mol}\cdot\text{sec}^{-1}\cdot\text{m}^{-2}$ PAR from High Intensity Discharge lamps). At 48 hr, leaf EER determinations were made according to protocols described earlier in this report. After 96 hrs of HT, the plants were returned to the greenhouse. Pods and seeds were harvested at dry maturity and were placed in a forced-air drying room for 7 days at 37C before weighing.

High HAP by High HAP Crosses for Leaf EER Evaluation. PI 271998 was crossed also with 3 other cultivars (Hebei No. 1, BTS 3 and Upland) identified as having high HAP relative to BBL 47, as determined by their electrolyte leakage response to HT stress in our laboratory. These 3 were screened more recently in our testing program than PI 271998 and BBL 47 and were concluded to be superior in HAP to PI 271998.

From the F_1 of the cross between PI 271998 and Hebei No. 1 an F_2 was generated in the greenhouse. The 4 parents, the 4 F_1 's and the single F_2 population were evaluated for EER following HT Stress in the growth chamber by the same procedure as used for the parents and progenies for the generation means analysis.

Progenies Generated for Evaluation by Electrolyte Conductivity Plus EER. The following crosses and/or their reciprocals were made and from each of these crosses F_2 and F_3 families were generated.

High HAP x High HAP

GNUI 59 x Strike

" x Labrador

" x Aurora

" x Pinto UI-3

Aurora x Strike

High HAP x Low HAP

GNUI 59 x BBL-47

Aurora x BBL-47

"	x Labrador	
"	x Pinto UI-3	
Labrador	x Strike	Labrador x BBL-47
"	x Pinto UI-3	
Strike	x Pinto UI-3	Strike x BBL-47

Selection Studies (see Objective IV)

Investigation of the effectiveness of selection for improved HAP proceeded along two avenues. The first consisted of repeated bidirectional selection for leaf EER within the relatively high HAP cv PI 271998 ('Garrofon') and within the relatively low HAP cv BBL-47, and was directed at the issue of whether or not genetic material previously unselected for HAP would possess residual variability for HAP. In this study 30 to 40 plants of each cultivar were evaluated for EER according to the protocols described above for the EER inheritance study.

The second investigation of effectiveness of selection for improved HAP was designed to compare the efficiency of 3 methods of selection applied successively on a population of plants in a single seed descent program derived from the cross between relatively high HAP cv GO 4495 and relatively low HAP cv BBL 47. GO 4495 was chosen as a high HAP parent among several other high HAP potential parents because it contrasted with BBL 47 for several pod and seed quality traits, thus permitting the study of trait associations during recurrent selection for HAP among the progeny of cross.

Beginning in the F_2 , 184 plants were categorized as to their HAP by each of 3 methods--electrolyte conductivity, EER, and pollen viability. All plants were advanced to the F_3 , retested, and advanced to the F_4 by single seed descent without elimination, and so on through the F_6 , at which time field and greenhouse tests will be conducted, after a seed increase, to determine pod and seed set under high temperature conditions. In addition, at each generation the data used to classify each plant for HAP by each of the three methods can be evaluated as to its predictive ability for HAP level in the subsequent generation.

Results and Discussion

Because of the slowness with which the collected germplasm was screened, and because it was desirable to begin the breeding and inheritance studies as early as possible in the life of the grant, parental choice had to be made before all of the germplasm had been screened. Hence, parents chosen were relatively tolerant or sensitive and were not the extremes in the collected germplasm pool. The following were identified as the screened germplasm having the greatest potential for the breeding phase.

Germplasm Identified for Breeding Studies. Based on the conductivity work and on tests in Israel by early 1987 the following were identified to be of greatest interest for future breeding studies:

<u>Most Tolerant</u>		
<u>Conductivity (US)</u>	<u>Phytotron (Israel)</u>	<u>Field (Israel)</u>
GO-3689	Musser 175	Strike
GO-3696	Bronco	
GO-3702	BAT-1289	
GO-4495		
GO-0893		
P 730		
BAT 366		
PI 281711		
PI 165616		
Super Gloss Tory		
GNUI 59		
G 4727 (ANCASH 66)		
Aurora		
Labrador		
Strike		

PI 271998

BTS #3

85CT-4976-2

Iguaco

Most Sensitive		
<u>Conductivity (US)</u>	<u>Phytotron (Israel)</u>	<u>Field (Israel)</u>
BBL-47	Strike	Early Galatin
85CT-4984-1	Dor	Waterfall
	Lake Superior	Legacy
	Sentry	

Evaluation of Field Grown Germplasm for EER. A four-fold range in mean EER (0.62 to $2.52 \mu\text{g}^{-1}\text{h}^{-1}$) was found among the field-grown entries, and for most of the entries the standard deviation was less than one-half of the mean (Table 1). The 2 previously identified HT-sensitive entries, BBL 47 and UI 111, showed the greatest EER among the 11 entries. The 9 HT-tolerant entries, as determined by conductivity, had considerably lower EER, further suggesting that a relationship may exist between EER and heat tolerance. Results for 9 of the 11 entries were compared to data obtained by Li et al. (1990) via electrical conductivity (Table 1). Both methods identified the HT-sensitive material and were correlated, having a Pearson correlation coefficient of -0.70 ($P \geq 0.05$). A weaker relationship was observed for comparisons within the HT-tolerant entries. These results suggest that substantial variation exists for EER.

Yield Response of a Relatively High (PI 271998) and a Relatively Low (BBL-47) HAP Genotype to Heat Stress. The combined effects of heat stress at flowering and light conditions during growth and at the time of stress on all the yield components are shown in Tables 2 and 3. For the high HAP genotype PI 271998, two daily cycles of heat stress applied under high light intensity to plants planted in May (Table 2) had the same effect on yield reduction as 30 cycles applied under low light intensity to plants started in August (Table 3). In both cases only daytime heat stress was effective, causing a reduction of ca. 40% in each of the yield parameters. The response of the low

HAP genotype BBL-47 to heat stress was less strongly affected by the light conditions. Even though applied under low light intensities, 30 cycles of heat stress were more effective in reducing yield components than two cycles under high light intensity. Moreover, in the latter case only nighttime heat stress was effective, causing a mean reduction of 36.6% in all parameters; in the plants subjected to 30 heat-stress cycles, the mean yield reduction was 56.2% when the heat stress was applied at night and 41.8% when applied during the day.

The difference between the two genotypes in their response to heat-stress treatments was dependent also on the stage of plant development at the time of exposure to stress. During the vegetative stage PI 271998 showed no significant yield reduction in response to three daily cycles of stress (Table 4); however, extension of the stress period to 10 daily cycles led to a reduction in all yield parameters (Table 5). The application of three daily cycles of heat stress to BBL-47 resulted in a reduction only in the number of seeds, while after 10 cycles a reduction was noted in all yield parameters. In both genotypes the effect of 10 heat-stress cycles was independent of the time of day at which they were applied. When plants of both genotypes reached the flowering stage, they became more sensitive to heat stress (Table 2,4). However, the stress effects at flowering differed according to genotype and depending on whether the heat treatment was applied during the day or the night (Table 2). PI 271998 was more sensitive to daytime and BBL-47 to nighttime heat-stress. The effects of high day temperature on PI 271998 and of high night temperature on BBL-47 were very similar in terms of the resulting numbers of pods, seeded pods, and seeds per plant.

EER of PI 271998 and BBL-47 in Response to Heat Stress. The EER from primary leaves of 23-day-old plants changed with planting date (Fig.1). As the days lengthened (from January to May), the EER from unstressed plants of both genotypes also increased. On each date the EER at the end of the light period was lower than at the end of the dark period; this finding was especially pronounced in PI 271998. The response of the two genotypes to heat stress also increased with the elongating photoperiod, but they differed in their response to daytime or nighttime heat stress. When planted in April, PI 271998 responded to either daytime or nighttime heat stress with an increased EER at the end of the light period; its response to nighttime stress was evident 12 h after stress termination, but the response to daytime stress was greater than to nighttime stress. BBL-47, on the other hand, responded to nighttime heat stress with an increased EER at the end of the dark period,

and to daytime heat stress with an increased EER at the end of light. Plants of both genotypes planted in January scarcely responded to heat stress. The response of February planted plants was intermediate between those of January- and April-planted plants: PI 271998 was sensitive only to daytime heat stress, while BBL-47 was sensitive only to nighttime heat stress.

Different light intensities during the daily cycle significantly altered the pattern and rate of ethylene evolution. On a sunny day ($600 \mu\text{mol.m}^{-2}\text{s}^{-1}$ PAR) in the greenhouse (25/18C day/night), 37-day-old flowering plants typically released ethylene at low rates during the daytime and at significantly higher rates during the night (Fig. 2). The patterns of change in the EER between day and night and the EER values were similar in the two genotypes. One day earlier the same plants in the same greenhouse, but under a cloudy sky ($100 \mu\text{mol.m}^{-2}\text{s}^{-1}$ PAR), released ethylene in quite a different pattern: there was no daytime reduction in EER, which was nearly the same during day and night. The EER under $600 \mu\text{mol.m}^{-2}\text{s}^{-1}$ PAR was very similar to that found in the greenhouse in other experiments; therefore, $600 \mu\text{mol.m}^{-2}\text{s}^{-1}$ PAR was chosen as the high light intensity value for the following experiments.

The effects of light intensity during the light period of the daily heat-stress cycles were examined in 28-day-old plants planted in February (Fig. 3). As noted, February started plants responded primarily to the kind of heat stress (i.e., daytime or nighttime) to which the genotype is most sensitive. During the two daily heat-stress cycles the EER of both genotypes was highly dependent on light intensity, which had a direct effect during the daytime and an indirect effect during the night. Under high light intensity ($600 \mu\text{mol.m}^{-2}\text{s}^{-1}$ PAR) it was possible to observe the typical response of PI 271998 to daytime heat stress and of BBL-47 to nighttime heat stress, while under low light intensity the EER in both genotypes was very low and their typical responses to light and to heat stress disappeared.

For most of their lives the leaves of both genotypes evolved ethylene in a typical day-night cycle, and the EER changed very little from the age of 23 days until pod filling (42 days), when it started to decrease (Fig. 4). In the greenhouse the daily pattern of EER was essentially the same for both genotypes and at the two growth stages examined, viz., just before flowering (28 days old) (Fig. 5) and at flowering (36 days old) (Fig. 6), but the effect of heat stress on EER changed with growth stage, genotype and time in the daily cycle. Before flowering, both genotypes responded to daytime

and to nighttime heat stress with an increased EER (Fig. 5). PI 271998 responded to daytime and to nighttime stress in the same way, with an increased EER at the end of the light period; in the case of nighttime stress the main effect appeared 12 h after the end of night. The effect of heat stress on PI 271998 during the day was greater than at night. The response of BBL-47 to heat stress depended on the time of stress; nighttime stress increased the EER during the dark period while day stress increased it at the end of the light period.

The special sensitivity of PI 271998 to daytime heat stress and BBL-47 to nighttime heat stress was greater during the flowering (Fig. 6) than during the vegetative stage (Fig 5). During flowering, PI 271998 responded mainly to daytime heat stress and BBL-47 to nighttime heat stress.

Comparison of Conductivity, Hot Water Immersion and Pollen Viability as Germplasm Screening Methods. Based on percent pod set and numbers of seed produced, hot water submersion at 40C was more effective in separating genotypes than was either conductivity or submersion at 35C (Table 6). Correlation coefficients ('r' values) were not high, i.e. hot water submersion at 35C vs 40C, 0.54; at 35C vs conductivity, 0.03; and at 40C vs conductivity, 0.43). The conductivity method was tedious and only a few plants could be screened each day. More refinement as to time and temperature of exposure in the hot water submersion test is needed.

At the high ambient greenhouse temperatures, differences ($P \leq 0.05$) were found for pod set but not for pollen viability, (Table 7), although at the 10% level PI 271998 had a higher percent of stained pollen than 5BP-7, BBL 47 and 80BP-6. Other workers have found variability in pollen viability of *P. vulgaris* at 35/20, 35 and 41C (Halterlein et al., 1980 and Weaver et al., 1984). The small differences in pollen stainability in our study may have been due to greater fluctuation of greenhouse temperature compared to the greater temperature precision obtained in the growth chamber studies by these workers. Pollen viability and conductivity were closely associated ($r = 0.92$).

Percent pod set provided a more distinct separation of the 5 genotypes. However, high temperature tends to result in parthenocarpy. Hence, in germplasm screening one should choose a temperature level permitting seed formation in tolerant genotypes. Temperatures up to 35C seem to have the greatest effect on pod set through post-fertilization barriers (Halterlein et al., 1980 and Ormrod et al., 1967), while higher temperatures affect pod set by first inhibiting pre-fertilization factors, such as pollen viability and pollen production (Halterlein et al., 1980).

Generations Means Experiment. Differences ($P < 0.01$) were detected among progeny means for EER in the generation means analysis (Table 8). Variation was high but could be removed as a block effect in the analysis of variance. EER for the F_1 of the cross between PI 271998 and BBL 47 was 15% below the midparent and similar to the EER of PI 271998 (Table 8). The F_2 was closer to the midparent, although variability was high. The 2 BC means differed from one another ($P \leq 0.01$). Backcrossing to PI 271998, the HT tolerant parent, was more effective for recovery of low EER than was backcrossing to BBL 47 for recovery of high EER.

Gene effects (Hayman and Mather, 1955) indicate additive, dominance, and epistatic effects to be important in the inheritance of EER in this cross (Table 9). Variance components were in agreement with the genic effects (Table 9). The genic effects and a unimodal segregation pattern in the segregating generations suggest that more than one gene is important in this system, but variation was too great to permit precise interpretation of inheritance. The high environmental effect was shown by the greater magnitude of environmental variance, as opposed to the genetic variance. The estimated broad sense heritability (H_b) of 0.46 for EER in the presence of the additive effects suggests that selection progress for lower EER can be made.

Dry weight of pods and seeds of BBL 47 was about 10% below that of PI 271998 (Table 8). The mean of the F_2 was identical to that of the tolerant parent and backcross means approached the mean of the respective recurrent parent.

The degree of association between EER and seed weight, pod number and seed number (all on an individual plant basis) across the segregating generations was virtually non-existent ($r = 0.03$ to 0.15). However, data on these yield-related traits were obtained at the end of the plant life cycle, and thus there was opportunity for recovery from HT stress. No attempt was made to evaluate pod and seed set shortly after HT treatment, as a way of estimating a temporary HT effect. The "split-set" phenomenon frequently seen as an immediate response to HT stress in the field may represent only a temporary loss of biological yield, but the economic impact in once-over harvesting of snap beans can be severe.

Evaluation of High HAP by High HAP Crosses for Leaf EER. Except for the cross between PI 271998 and Upland, the 2 parents in each combination differed ($P \leq 0.05$) in EER, with the F_1 's tending to fall below the midparent in one cross and below the lower parent in another (Table 8).

The mean (1.99) of the single F_2 population fell closer to the less tolerant of the 2 parents. Results from these crosses demonstrate the degree of variability which can be found in the ethylene work. While they could be interpreted as supportive of the generation means analysis, they should instead serve to urge a cautious approach in interpretation. The EER for PI 271998 (2.83) was considerably larger than in the generation means experiment (1.13), due probably to growing season differences. The plant material for the generation means analysis was planted in October while for the analysis of tolerant by tolerant crosses the plants were started in June. Fall and winter grown bean plants typically have had a lower EER in our laboratory.

These results suggest that lower EER should be transferable from a donor parent by backcrossing. Evidence in the literature for association between higher EER and flower and flower bud abscission in response to heat stress is increasing. The screening of plants at an early vegetative stage for EER as a response to heat stress could be useful in the breeding program.

Evaluation of Additional Progenies by Electrolyte Conductivity Plus EER. As shown in Table 10, selected parents and F_1 and F_3 progenies were evaluated in 2 different tests with only a partial overlapping between the two. Hence the data are too limited to permit a covariance analysis between EER and conductivity.

In all 4 parentages some F_3 means fell below the lower parent for EER and some fell above the higher parent, indicating good opportunity for selecting among F_3 s.

Responses to Selection. The recurrent selection study for low vs high EER, low vs high HAP via electrolyte conductivity, and low vs high pollen viability from the cross between high HAP GO 4495 and low HAP BBL 47 has not been completed and will continue for another year on funds from other sources. Currently at the F_3 level, this study will be continued to the F_6 , with resulting tolerant and sensitive lines evaluated in the field and greenhouse for pod and seed yield.

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Table 1. A comparison of leaf ethylene evolution rate for field grown bean cultivars and breeding lines, and their heat acclimation potential as determined by heat killing time from electrolyte leakage via a conductivity test applied to leaflet tissue from greenhouse-grown plants.

Entry	Ethylene evolution rate ^x ($\mu\text{l} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)	Heat killing time (min.) ^y
BBL 47	$2.52 \pm 1.61 \text{ a}^z$	60
UI 111	$2.45 \pm 1.19 \text{ a}$	50
Strike	$1.71 \pm 0.48 \text{ ab}$	95
Labrador	$1.59 \pm 0.46 \text{ ab}$	97
Red Cloud	$1.48 \pm 0.40 \text{ ab}$	--
GNUI 59	$1.39 \pm 0.65 \text{ ab}$	110
PI 271998	$1.37 \pm 0.38 \text{ ab}$	94
<u>P. acutifolius</u>	$1.09 \pm 0.54 \text{ b}$	--
Hebei No. 1	$1.08 \pm 0.45 \text{ b}$	80
G 4727 (Ancash 66)	$0.96 \pm 0.47 \text{ b}$	100
85-CT-4986-3	$0.62 \pm 0.29 \text{ b}$	90
LSD (5%)	1.00	

^zMean $\pm$ standard deviation; mean separation 5% level, based on Duncan's New Multiple Range Test.

^yAdapted from Li, P.H., D.W. Davis and Z.Y. Shen. Heat Killing Time is the time in minutes to 50% electrolyte leakage as determined by electrical conductivity. Correlation ('r') for ethylene vs. heat killing time = -0.70 ($\alpha = 0.95$).

^xEach value is the mean of 10 observations (plants).

Table 2. Yield per plant of two common bean genotypes, PI 271998 and BBL-47, following exposure to two daily cycles of heat stress (30C) applied to 36-day-old plants (planted on May 7) during the 12 h light ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the 12 h dark period.

Location	Temperature		No. of			Total
			_____	_____	_____	plant
	day	night	_____	_____	_____	dry
	(°C)		no./plant	no./plant	no./plant	weight
						g/plant
<u>PI 271998</u>						
Growth chamber	20	30	23.4ab	18.0ab	79.0ab	64.9ab
Growth chamber	30	20	8.6b	14.4b	62.4b	51.2b
Greenhouse	25	18	27.0a	22.4a	96.2a	73.6a
<u>BBL-47</u>						
Growth chamber	20	30	20.2b	14.5b	62.8b	38.9b
Growth chamber	30	20	25.6ab	20.4ab	77.8ab	49.6ab
Greenhouse	25	18	34.1a	22.9a	94.6a	58.8a

All data are means of five plants. Mean separation for each genotype and within columns by Duncan's New Multiple Range Test, 5% level.

Table 3: Yield per plant of two common bean genotypes, PI 271998 and BBL-47, following exposure to 30 daily cycles of heat stress (30C) applied to 30-day-old plants (planted on August 22) during the 12 h light ($150 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the 12 h dark period.

Location	Temperature		No. of			Total
	day	night	_____	_____	_____	plant dry weight
			_____	_____	_____	
	(°C)		_____	_____	_____	_____
<u>PI 271998</u>						
Growth chamber	20	30	18.3a	12.0a	37.5a	27.8a
Growth chamber	30	20	12.7b	7.0b	22.2b	17.7b
Greenhouse	25	18	19.3a	12.8a	38.2a	28.5a
<u>BBL-47</u>						
Growth chamber	20	30	6.6c	5.4b	18.6b	16.6b
Growth chamber	30	20	12.5b	7.7b	26.7b	14.0b
Greenhouse	25	18	19.7a	13.2a	42.3a	29.2a

All data are means of five plants. Mean separation for each genotype and within columns by Duncan's New Multiple Range Test, 5% level.

Table 4. Yield per plant of two common bean genotypes, PI 271998 and BBL-47, following exposure to three daily cycles of heat stress (30°C) applied to 20-day-old plants (planted on May 15) during the 12 h light ($150 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the 12 h dark period.

Location	Temperature		No. of			Total
			_____	_____	_____	_____
	_____	_____	_____	_____	_____	_____
	day	night	_____	_____	_____	_____
	(°C)		no./plant	no./plant	no./plant	g/plant
<u>PI 271998</u>						
Growth chamber	20	30	28.0a	20.4a	89.4a	59.4a
Growth chamber	30	20	30.4b	21.2b	94.0b	61.9b
Greenhouse	25	18	32.2a	20.0a	88.6a	62.5a
<u>BBL-47</u>						
Growth chamber	20	30	32.2a	21.4a	49.8b	39.9a
Growth chamber	30	20	35.8a	22.2a	56.2b	45.0a
Greenhouse	25	18	38.4a	27.4a	96.4a	49.1a

All data are means of five plants. Mean separation for each genotype and within columns by Duncan's New Multiple Range Test, 5% level.

Table 5. Yield per plant of two common bean genotypes, PI 271998 and BBL-47, following exposure to 10 daily cycles of heat stress (30C) applied to 17-day-old plants (planted on May 15) during the 12 h light (600 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the 12 h dark period.

Location	Temperature		No. of			Total
	day	night	_____	_____	_____	plant dry weight
			_____	_____	_____	
	(°C)		_____	_____	_____	_____
<u>PI 271998</u>						
Growth chamber	20	30	20.6b	13.0b	45.4b	35.2b
Growth chamber	30	20	18.2b	12.2b	47.8b	38.2ab
Greenhouse	25	18	29.4a	19.0a	75.6a	53.1a
<u>BBL-47</u>						
Growth chamber	20	30	21.4b	13.6a	45.4b	25.7b
Growth chamber	30	20	21.4b	12.2b	42.8b	23.4b
Greenhouse	25	18	36.6a	26.4a	82.8a	54.9a

All data are means of five plants. Mean separation for each genotype and within columns by Duncan's New Multiple Range Test, 5% level.

Table 6. Mean leaf heat killing times of 17 genotypes of *Phaseolus vulgaris* at 50C (conductivity test), and percent pod set following a 2 minute hot water immersion at 35 and 40C.

Genotype	Heat killing time (min.)	Pod set (%) ²	
		35°C	40°C
PI 271998	109 ^{ay}	75 ^{bcd}	75 ^{abc}
5BP-7	99 ^{ab}	69 ^{cd}	67 ^{bcd}
80BP-2	96 ^{abc}	89 ^{ab}	73 ^{abcd}
BBL 47	83 ^{abcd}	67 ^{cd}	66 ^{bcd}
80BP-6	80 ^{bcde}	48 ^e	48 ^{efg}
Bat 11	70 ^{cde}	74 ^{bcd}	69 ^{bcd}
G 2206	69 ^{cde}	96 ^a	79 ^{ab}
G 1951	66 ^{de}	81 ^{bc}	87 ^a
G 1401	66 ^{de}	80 ^{bc}	72 ^{abcd}
G 3689	64 ^{de}	81 ^{bc}	84 ^a
81C-4883-B	60 ^{de}	70 ^{cd}	61 ^{cde}
ICA Palmar	59 ^{de}	67 ^{cd}	15 ^h
G 4461	57 ^{de}	63 ^d	44 ^g
A 162	56 ^{de}	72 ^{cd}	34 ^a
A 70	54 ^{de}	79 ^{bcd}	46 ^{fg}
BAT 258	53 ^e	76 ^{bcd}	48 ^{efg}
BAT 332	53 ^e	69 ^{cd}	59 ^{def}

²% Pod set = $\frac{\text{No. of seeded pods from tagged buds} \times 100}{\text{Total number of tagged buds}}$

Total number of tagged buds

^yMean separation within columns by Duncan's New Multiple Range Test, 5% level.

Table 7. Percent pollen viability and pod set for 5 genotypes of common bean grown at high air temperatures in the greenhouse.

Genotypes	Pollen Viability (%)	Pod set (%) ^z
PI 271998	70 ^{ay}	73 ^c
80BP-2	54 ^a	50 ^{bc}
5BP-7	46 ^a	40 ^b
BBL 47	42 ^a	11 ^a
80BP-6	42 ^a	58 ^{bc}

$$^z\% \text{ Pod set} = \frac{\text{Total no. pods produced per plant} \times 100}{\text{Total no. floral structures produced per plant}}$$

^yMean separation within columns by Duncan's New Multiple Range Test, 5% level.

Table 8. Leaf ethylene evolution rate and pod and seed weight for the parents, BC₁P₁, F₁, F₂ and BC₁P₂, and the midparent of the heat tolerant by heat sensitive cross PI 271998 x BBL 47, and leaf ethylene evolution rate for progenies of three tolerant by tolerant crosses also involving PI 271998.

Generation	Number of plants	Ethylene evolution rate ($\mu\text{l}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	Percent of control ^y	Dry weight of pods & seeds (g)	Percent of control
P1(PI 271998)	36	$1.13 \pm 0.93 \text{ b}^z$	96	22.1 ± 5.4	88
BC ₁ P ₁	108	$1.14 \pm 0.77 \text{ b}$	102	23.1 ± 5.4	85
F ₁	36	$1.24 \pm 1.08 \text{ b}$	79	22.2 ± 5.0	97
Midparent ^x		1.46			
F ₂	108	$1.50 \pm 1.57 \text{ ab}$	109	20.6 ± 5.8	88
BC ₁ P ₂	108	$1.50 \pm 1.05 \text{ ab}$	117	19.7 ± 5.1	78
P2 (BBL 47)	36	$1.78 \pm 1.39 \text{ a}$	148	17.8 ± 5.0	78
LSD (5%)		0.39			

Table 8. (continued)

Generation	Number of plants	Ethylene evolution rate ($\mu\text{l}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)	Percent of control ^y	Dry weight of pods & seeds (g)	*Percent of control
P1 (PI 271998)		2.83 ± 1.27			
P3 (Hebei No. 1)		0.68 ± 0.13			
F ₁		1.50 ± 1.00			
Midparent		1.75			
F ₂		1.99 ± 1.88			
P4 (BTS 3)		0.74 ± 0.25			
F ₁		0.58 ± 0.36			
Midparent		1.79			
P5 (Upland)		2.18 ± 1.72			
F ₁		2.62 ± 1.17			
Midparent		2.50			

^zMean $\pm$ standard deviation; mean separation at 5% level based on Duncan's New Multiple Range Test. Separate analyses of variance were conducted for each parentage.

^yControls in the generation means analysis consisted of 8 to 14 non-HT-stressed plants for each generation.

^xMidparent = (P1 + P2)/2.

Table 9. Estimates of genic effects, variance components and broad-sense heritability for the generation means analysis of the cross PI 271998 x BBL 47.

Genic effects ^z		Variance components ^z		H_b^2
m	>1.50	σ_E^2	1.32	0.46
d	-0.36	σ_G^2	1.13	
h	-0.94	σ_A^2	3.20	
i	-0.72	σ_D^2	-2.07	
j	-0.04			
l	0.83			

^z All estimates smaller than their standard error.

Table 10. Heat acclimation potential of selected parents, their F_1 hybrids and random F_3 families.

Genotype	Test 1		Test 2	
	Heat killing time (HKT)		Mean	
	Non-acclimated	Acclimated	HKT Acclimated	EER ($\mu\text{l.g}^{-1}.\text{h}^{-1}$)
PI 271998 (control)			73	0.81
Labrador (P_1)	19	75	61	0.98
Strike (P_2)	5	51	62	1.00
F_1	10	79		
F_3 #3			58	1.39
F_3 #4			57	1.81
F_3 #8			64	1.59
F_3 #11			68	0.80
PI 271998 (P_1)				1.40
BTS 3 (P_2)			100	1.46
F_1				
F_3 #1				0.98
F_3 #3				2.29
F_3 #6				1.34

Table 10. continued

Genotype	Test 1		Test 2	
	Heat killing time (HKT)		Mean	
			HKT	EER
	Non-acclimated	Acclimated	Acclimated	($\mu\text{l.g}^{-1}.\text{h}^{-1}$)
PI 271998 (control)			65	1.50
GNUI 59 (P_1)	17	84	61	1.76
Aurora (P_2)	14	48	<40	2.54
F_1	30	76		
F_3 #1			<40	1.38
F_3 #3			<40	1.85
F_3 #4			43	1.89
F_3 #7			74	3.41
PI 271998 (control)			71	
Labrador (P_1)	14	75	81	
Aurora (P_2)	14	48	82	
F^1	8	80		
F_3 #1			58	
F_3 #2			67	
F^3 #3			60	
F_3 #4			81	

- Fig. 1 Effects of planting date in the greenhouse (25/18C day/night temperatures) and two daily cycles of daytime or nighttime heat stress (30C) on ethylene evolution rate from 23-day-old plants of PI 271998 (A) and BBL-47 (B). Bars indicate standard errors.
- Fig. 2 Ethylene evolution rates measured at 6-hour intervals in 37-day-old plants of PI 271998 (A) and BBL-47 (B) on cloudy ($100 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or sunny ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) days in the greenhouse (25/18C day/night temperatures). Planting was on May 15. Bars indicate standard errors.
- Fig. 3 Ethylene evolution rates in 28-day-old plants of PI 271998 (A) and BBL-47 (B) exposed to two daily cycles of heat stress (30C) during the day or the night and to daytime light intensities of 150 or $600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR in the growth chamber. Planting was on February 15. Bars indicate standard errors.
- Fig. 4 Ethylene evolution rates in plants of PI 271998 (A) and BBL-47 (B) measured in the greenhouse (25/18C) day/night temperatures) at two times during the daily cycle and as a function of plant development. Planting was on April 23. Bars indicate standard errors.
- Fig. 5 Ethylene evolution rates measured at 6-hour intervals in 28-day-old vegetative plants of PI 271998 (A) and BBL-47 (B) exposed to two daily cycles of heat stress (30C) during the day ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the night. Planting was on April 23. Bars indicate standard errors.
- Fig. 6 Ethylene evolution rates measured at 6-hour intervals in 36-day-old flowering plants of PI 271998 (A) and BBL-47 (B) exposed to two daily cycles of heat stress (30C) during the day ($600 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR) or the night. Planting was on April 23. Bars indicate standard errors.

Fig 1

Fig. 2

Fig. 3

91

Fig. 4

Fig 5

Fig. 6

Part B

Final Report of the work carried out in Israel.

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ABSTRACT

Yields of snap-bean and dry-bean were reduced under summer conditions in field trials in Israel. Ample irrigation diminished and even cancelled this reduction. Experiments under controlled conditions (phytotron) indicate that HT at sporogenesis resulted in unviable pollen and failure of anther dehiscence. HT at anthesis reduced pod and seed set due to negative effects on pollen germination, pollen tube growth and fertilization. Female development was unaffected by HT. Bean genotypes largely differed in their yield responses to HT under controlled conditions, and to summer effects in the field. However, summer performance of genotypes was not correlated with HT effects in the phytotron, nor with their HAP. It is suggested that, in the coastal plain of Israel, HT is not the main limiting factor if water stress is prevented.

INTRODUCTION

The common bean is grown in temperate and subtropical regions, both as a pulse crop and as a vegetable. In these regions large fluctuations in yield are of common occurrence and frequently they are associated with hot weather spells. While the negative effects of relatively mild water stress on bean yield are well known, information as to the effects of high temperatures (HT) is scarce. Theoretically, HT may limit pod and seed set in the field even under ample irrigation. Furthermore, while it is possible to alleviate water stress in the field by irrigation, the possibilities of reducing the impact of HT are much more limited. Thus, although we are aware of possible water-heat interactive effects on bean yield, the approach in our project was to study first the effects of HT under conditions where water was not a major limiting factor. Our main goals were: (1) to determine the relative importance of HT for bean yield; and (2) to identify genotypes with higher tolerance and/or adaptability to heat for further investigations on the effects of drought in hot environments.

Experiments were carried out under controlled conditions (phytotron and greenhouse) or in the field. In the phytotron, plants were grown under moderate temperatures (22/17°C or 27/22°C, day/night temperature) and transferred at various stages of reproductive development to a higher temperature (32/27°C) for different lengths of time. Pollen and ovule development, pollen germination and ovule fertilization, seed and pod set were studied under low and high temperatures, as potential determinants of yield under HT.

In the field experiments, an attempt was made to analyze the effects of HT by comparing "spring" and "summer" yields (sown in April and June, respectively) produced by different genotypes of beans (snap bean and dry bean). In these experiments, the effects of moderate

(spring) and high (summer) temperatures on yield were studied under ample irrigation to minimize the influence of water stress.

Commercial varieties and seed accessions of snap and dry beans from numerous sources were studied in field and/or phytotron experiments (Tables 1 and 2).

For several varieties or accessions, heat acclimation potential (HAP) was estimated by a conductivity test carried out at St. Paul, Minnesota. HAP values of tested varieties are indicated in the tables.

EXPERIMENTS UNDER CONTROLLED CONDITIONS: PHYTOTRON

In previous work (Kigel & Ofir) we found that exposure of bean plants to relatively high temperature (32/27°C) at anthesis strongly reduced pod production due to increased abscission of flower buds, flowers, and young pods. At the same time, 32/27°C increased flower production. Thus the lower pod set was not due to high temperature constraints on flower production.

In the present project we studied further the effects of 32/27°C on the reproductive development of bean plants. The main goals of these experiments were;

- 1) to examine whether the response to 32/27°C can be used as a method for screening bean germplasm for higher tolerance to heat in relation to pod production;
- 2) to identify the reproductive processes affected by 32/27°C that result in the reduction of pod set

Table 1 : Snap-Bean Varieties. Bush-type varieties with terminal raceme. Score : 0=no effect, 4=most severe effect.

<u>Code</u>	<u>Variety</u>	<u>Source</u>	<u>Seed & Color¹</u>	<u>--SCORE-----</u>		<u>Heat⁴ Acclim. Potential</u>
				<u>Rust²</u>	<u>Wilting³</u>	
BBL-15	Bush Blue Lake-15	Asgrow	W	-	4.0	-
BBL-47	Bush Blue Lake-47	Asgrow	W	2.6	2.3	60
BBL-92	Bush Blue Lake-92	Asgrow	W	3.5	-	55
BRD	Bronco	Asgrow	W	2.9	2.3	100
CONT	Contender	Keystone	W	-	-	-
EAG	Eagle	Asgrow	W	-	3.5	-
EG	Early Galatine	Galatin	W	2.4	2.5	85
LAB	Labrador	Asgrow	W	2.0	1.6	97
LS	Lake Superior	Sunseeds	W	-	2.5	-
LEG	Legacy	Royal Sluis	W	3.1	1.9	35
MUS	Musser-175	Musser	W	2.5	0.9	60
PR	Purple Rouge	Bakker	B	3.5	-	-
PQ	Purple Queen	Bakker	B	2.4	-	-
ROG	Rogers-73183	Rogers	W	1.6	-	-
SEN	Sentry	Asgrow	W	-	4.0	45
SHAN	Shanon	Sunseeds	W	-	2.3	-
STR	Strike	Asgrow	W	2.1	1.6	95
TEND	Tenderette	Rogers	W	1.7	1.4	82
TORY	Supergloss Tory	Bakker	B	1.9	2.0	100
WAT	S. Waterfall	Bakker	W	2.2	2.0	70
WAX	Supergloss Wax	Bakker	W	-	0.0	-
PI	PI-271998(Garrofon)Spain		W	2.1	0.5	94
2102	2102		W	-	3.1	-

1 - W=white ; B=black.

2 - Rust Incidence - summer 1986.

3 - Wilting and leaf scorching of young leaves after severe dry hot weather (chamsin) on 27/5/1987, approx. 1 week after onset of flowering.

4 - Heat Acclimation Potential - the change in leaf heat tolerance after 24 hr exposure to 37°C, expressed in time (min) needed for 50% electrolyte leakage at 50°C (HKT), as measured by conductivity test.

Table 2 : Dry bean accessions

<u>Accession</u>	<u>Growth</u> <u>Habit</u> ¹	<u>Seed</u> <u>Colour</u>	<u>Source</u> ²	<u>Wilting</u> <u>Score</u> ³	<u>Heat</u> <u>Acclimation</u> <u>Potential</u> ⁴
BAT-336	B	cream	1	2.1	110
BAT-447	B	cream	1	-	-
BAT-1289	B	red	1	2.1	-
V-8025	C	black	1	1.8	95
G-2525	C	cream	1	-	85
G-3645 (Jamapa)	B	black	1	1.0	70
G-4495	C	black	1	2.8	120
P-729	C	black	1	-	-
P-730	C	black	1	-	120
G-0893	C	red	1	1.0	115
G-1050	C	brown	1	2.3	-
G-3696	B	black	1	3.2	130
G-3670	C	black	1	3.0	-
G-3689	C	black	1	2.4	>130
G-3702	C	black	1	3.0	125
ALUBIO	B	white	8	-	-
DOR-41	B	black	8	-	-
GNUI-59	C	white	2	-	110
GUANACO	C	black	4	-	-
HEBEI 1	C	white	7	-	80
IGUACU	B	black	5	-	75
PINTO UI-111	C	spotted	3	-	50
SANILAC	B	white	4	-	100
WA-2289	C	white	8	2.0	-
WAF-9	B	white	8	1.8	-
XFB-74	B	white	8	4.0	-
23-52	C	white	4	-	-
NY-5-161	B	brown	5	-	72
85-CT-4976-2	C	white	4	-	90
C-20	B	white	5	-	76

1 - B=bush type ; C=climbing type

2 - Sources;

1. CIAT, Cali, Colombia
2. Dept. of Hort., Univ. of Nebraska, Lincoln
3. Irrig. Agr. Res. & Dev. Center, Prosser, Washington
4. Dept. of Hort., Univ. of Wisconsin, Madison
5. Dept. of Hort. Sci., NY State Agr. Expt. Station, Geneva
6. Inst. Veg., Hebei Acad. Agr. Sc., Shijiazun, Hebei, China
7. Dept. Plant Pathology, Univ. of Wisconsin, Madison
8. INTA, Salta, Argentina

3,4 - As in Table 1.

Materials and Methods

Experiments under controlled conditions were carried out in the phytotron at the Faculty of Agriculture, Rehovot (Ofir & Koller, 1974, Aust. J. Plant Physiol. 1:259-270). Plants were grown in 16 hr photoperiods (04:00 - 20:00), obtained by extending the natural day length from 04:00 until dawn and from dusk until 20:00 with artificial light from 75 watt incandescent lamps providing 0.5 W/m^2 at plant level. Solar radiation reaching the plants in the phytotron was 70-80% of outdoor levels.

Thermoperiods combining different day temperatures (DT - 8 hr: 08:00-16:00) and night temperatures (NT - 16 hr: 16:00-08:00) were controlled within $\pm 1^\circ\text{C}$ of indicated values. A saturation deficit of ca. 0.8 KPa was maintained under the different DT to ensure approximately the same evaporative demand in all temperature treatments.

Plants were grown singly in 1.5 L or 1 L drained pots containing a mixture of tuff gravel (0.5-1.0 cm) and vermiculite (grade 4) (1:1 v/v). Plants were irrigated every day with a half strength Hoagland solution (including a chelated source of iron), in the morning, and with tap water (to prevent salt accumulation) in the afternoon.

Seeds were sown at $27/22^\circ\text{C}$. Seedlings selected for uniformity were transferred 10 days later to $22/17^\circ\text{C}$. Phytotron experiments were arranged in a completely randomized block design with 10-15 plants for treatment. ANOVA was carried out for statistical analysis of data. Multiple Range Tests (Duncan's test) were run at significance a level of $P=0.05$.

Screening for Heat Tolerance at $32/27^\circ\text{C}$

Plants grown at $22/17^\circ\text{C}$ were subjected to 5 days at $32/27^\circ\text{C}$, starting 2-3 days before anthesis of first flowers. Thus, pollination, pollen tube growth, fertilization and initial embryo development in the first 10-15 flowers occurred during the exposure to

32/27°C. In determinate snap bean varieties these flowers provide about 90% of mature pods in the phytotron under 22/17°C. After the HT, the plants were transferred back to 22/17°C, where they continued to develop until harvest time. Yield parameters were recorded 4-5 weeks after the HT (about 2 months from sowing) and compared to the controls. Two experiments were carried out under the light conditions of the summer (higher natural light intensities for more hours daily), (Exp I, sown 1/6/87; Exp II, sown 16/8/87) in which 14 varieties of snap bean were examined. A third experiment (Exp III, sown 8/3/88) was carried out at the lower light intensities of early spring. In this experiment an additional three varieties were examined, together with 4 varieties previously studied that were tested again for constancy of response (BBL-47, LEG, TEND, WAT). Detailed results and statistical analysis are presented in Tables 3, 4 and 5. A graphic comparative summary for each yield parameter appears in Figures 1, 2 and 3.

In the three experiments yield components pods/plant, seeds/pod and pod length were strongly reduced by 32/27°C in most varieties, while pod curvature was increased. Varieties greatly differed in their responses to 32/27°C. Pod set was practically unaffected in MUSSER-175 (2%) and LAKE SUPERIOR (12%), while it was greatly reduced in STRIKE (91%), SENTRY (84%), WAX and 2102 (80%). On the other hand, the effects of 32/27°C on seed/pod were much smaller in LEGACY, STRIKE, and BBL-47 (13-30%) than in WAX, PI-271998 and TORY (65-73%).

Yield parameters pods/plant and seeds/pod were differentially influenced by 32/27°C. While in STRIKE, BBL-47, 2102, SENTRY, BRONCO, WAT and EAGLE the decrease in pods/plant was larger than in seeds/pod, the opposite was true for MUSSER-175 and LAKE SUPERIOR. On the other hand, similar reductions were observed for both parameters in LAB, TORY, EG, WAX, TEND and PI-271998 (differences < 10%).

Table 3: Effects of exposure of *P. vulgaris* plants to high temperature at flowering stage on yield parameters.

Phytotron experiments. Sowing date: 1.6.87.

Variety	Control 22/17				5 days at 32/27			
	Mean $\pm$ S.E.	M	R	T % of mean	Mean $\pm$ S.E.	M	R	T % of mean % change
Number of mature pods per plant.								
SENTRY	22.6 $\pm$ 1.1	A	a	152	3.6 $\pm$ 0.8	C	b	59 -84
BRONCO	17.1 $\pm$ 1.2	B	a	115	4.5 $\pm$ 0.6	C	b	74 -74
STRIKE	15.9 $\pm$ 0.7	BC	a	107	1.5 $\pm$ 0.4	D	b	25 -91
E.G.	15.1 $\pm$ 1.1	BC	a	101	7.5 $\pm$ 1.0	B	b	123 -50
MUSSER	13.2 $\pm$ 0.7	CD	a	89	12.9 $\pm$ 0.8	A	a	211 -2
LABRADOR	11.5 $\pm$ 0.8	DE	a	77	4.9 $\pm$ 0.4	C	b	80 -57
L.S.	9.0 $\pm$ 1.0	E	a	60	7.9 $\pm$ 0.6	B	a	130 -12
Mean	14.9				6.1			

Number of seeds per plant.

SENTRY	100.9 $\pm$ 5.3	A	a	149	8.2 $\pm$ 1.9	C	b	48 -92
BRONCO	71.4 $\pm$ 5.4	B	a	105	10.6 $\pm$ 1.6	C	b	62 -85
STRIKE	68.8 $\pm$ 4.4	B	a	102	6.6 $\pm$ 1.9	C	b	39 -90
E.G.	67.2 $\pm$ 4.9	B	a	99	22.2 $\pm$ 3.7	B	b	131 -67
MUSSER	69.3 $\pm$ 4.4	B	a	102	43.3 $\pm$ 2.0	A	b	255 -38
LABRADOR	56.6 $\pm$ 3.4	B	a	84	9.1 $\pm$ 0.9	C	b	54 -84
L.S.	39.6 $\pm$ 5.7	C	a	58	19.1 $\pm$ 1.9	B	b	112 -52
Mean	67.7				17.0			

Degree of curvature of mature pods.

Pod curvature range: 1 - straight, to 4 - very curved.

SENTRY	1.4 $\pm$ 0.0	D	b	74	2.2 $\pm$ 0.3	B	a	85 57
BRONCO	1.6 $\pm$ 0.1	CD	b	84	2.5 $\pm$ 0.1	B	a	96 56
STRIKE	1.6 $\pm$ 0.1	CD	b	84	2.5 $\pm$ 0.2	B	a	96 56
E.G.	2.1 $\pm$ 0.1	B	b	110	2.7 $\pm$ 0.1	B	a	104 29
MUSSER	2.0 $\pm$ 0.1	B	b	105	2.5 $\pm$ 0.1	B	a	96 25
LABRADOR	1.7 $\pm$ 0.1	C	b	89	2.7 $\pm$ 0.1	B	a	104 59
L.S.	3.0 $\pm$ 0.1	A	a	158	3.4 $\pm$ 0.3	A	a	131 13
Mean	1.9				2.6			

Length of mature pods (cm.)

SENTRY	10.6 $\pm$ 0.1	C	a	95	6.9 $\pm$ 0.8	D	b	81 -35
BRONCO	11.3 $\pm$ 0.1	AB	a	101	8.8 $\pm$ 0.3	AB	b	104 -21
STRIKE	11.1 $\pm$ 0.1	BC	a	99	9.6 $\pm$ 0.1	A	b	113 -14
E.G.	11.0 $\pm$ 0.1	BC	a	98	9.0 $\pm$ 0.2	AB	b	106 -18
MUSSER	11.2 $\pm$ 0.1	AB	a	100	9.6 $\pm$ 0.2	A	b	113 -14
LABRADOR	11.7 $\pm$ 0.2	A	a	104	7.5 $\pm$ 0.3	CD	b	88 -36
L.S.	11.4 $\pm$ 0.4	AB	a	102	8.2 $\pm$ 0.3	BC	b	96 -28
Mean	11.2				8.5			

Number of seeds per mature pod.

SENTRY	4.48 $\pm$ 0.17	B	a	98	1.97 $\pm$ 0.29	C	b	77 -56
BRONCO	4.22 $\pm$ 0.14	B	a	93	2.37 $\pm$ 0.25	BC	b	93 -44
STRIKE	4.28 $\pm$ 0.14	B	a	94	3.08 $\pm$ 0.55	AB	b	120 -28
E.G.	4.46 $\pm$ 0.11	B	a	98	2.69 $\pm$ 0.20	ABC	b	105 -40
MUSSER	5.21 $\pm$ 0.10	A	a	114	3.44 $\pm$ 0.14	A	b	134 -34
LABRADOR	4.99 $\pm$ 0.16	A	a	110	1.93 $\pm$ 0.18	C	b	75 -61
L.S.	4.18 $\pm$ 0.30	B	a	92	2.42 $\pm$ 0.20	BC	b	94 -42
Mean	4.55				2.56			

M R T Duncan's Multiple Range Test at $p = 0.05$.

Upper case letters - differences among varieties.

Lower case letters - differences among treatments in varieties.

Table 4: Effects of exposure of *P. vulgaris* plants to high temperature at flowering stage on yield parameters.

Phytotron experiments. Sowing date: 16.8.87.

Treatment: Control 22/17					5 days at 32/27						
Variety	Mean $\pm$ S.E.	M	R	T	% of mean	Mean $\pm$ S.E.	M	R	T	% of mean	% change
Number of mature pods per plant.											
WAT	15.9 $\pm$ 1.1	A	a	123		4.3 $\pm$ 0.4	AB	b	105		-73
WAX	14.3 $\pm$ 1.0	AB	a	111		2.9 $\pm$ 0.7	B	b	71		-80
BBL47	13.6 $\pm$ 1.2	ABC	a	105		2.8 $\pm$ 0.4	B	b	68		-79
TEND	12.8 $\pm$ 1.0	BCD	a	99		5.8 $\pm$ 0.9	A	b	141		-55
LEG	11.8 $\pm$ 0.7	BCD	a	91		3.0 $\pm$ 0.5	B	b	73		-75
TORY	11.4 $\pm$ 0.7	CD	a	88		5.7 $\pm$ 1.0	A	b	139		-50
PI	10.3 $\pm$ 0.5	D	a	80		4.0 $\pm$ 1.0	AB	b	98		-61
Mean	12.9					4.1					

Number of seeds per plant.

WAT	73.6 $\pm$ 6.3	A	a	124		12.0 $\pm$ 1.5	AB	b	108		-84
WAX	71.9 $\pm$ 4.6	A	a	121		5.6 $\pm$ 1.2	B	b	50		-92
BBL47	55.5 $\pm$ 5.9	B	a	94		10.3 $\pm$ 2.0	AB	b	93		-81
TEND	55.4 $\pm$ 5.3	B	a	93		16.2 $\pm$ 2.7	A	b	146		-71
LEG	49.5 $\pm$ 4.0	B	a	83		11.5 $\pm$ 3.0	AB	b	104		-77
TORY	59.4 $\pm$ 3.7	AB	a	100		13.3 $\pm$ 2.5	A	b	120		-78
PI	50.1 $\pm$ 3.2	B	a	84		8.9 $\pm$ 2.5	AB	b	80		-82
Mean	59.3					11.1					

Degree of curvature of mature pods.

Pod curvatures range: 1 - straight, to 4 - very curved.

WAT	2.3 $\pm$ 0.1	A	a	115		2.4 $\pm$ 0.2	AB	a	100		4
WAX	2.0 $\pm$ 0.1	BC	b	100		2.7 $\pm$ 0.1	A	a	112		35
BBL47	1.9 $\pm$ 0.1	CD	a	95		1.6 $\pm$ 0.2	C	a	67		-16
TEND	1.7 $\pm$ 0.1	D	b	85		2.1 $\pm$ 0.1	B	a	87		24
LEG	1.9 $\pm$ 0.1	CD	b	95		2.5 $\pm$ 0.2	AB	a	104		32
TORY	2.2 $\pm$ 0.1	AB	b	110		2.7 $\pm$ 0.1	A	a	112		23
PI	1.8 $\pm$ 0.1	CD	b	90		2.5 $\pm$ 0.1	AB	a	104		39
Mean	2.0					2.4					

Length of mature pods (cm).

WAT	13.3 $\pm$ 0.2	AB	a	96		12.3 $\pm$ 0.2	A	b	118		-8
WAX	10.6 $\pm$ 0.2	D	a	77		7.9 $\pm$ 0.3	D	b	76		-25
BBL47	13.0 $\pm$ 0.2	AB	a	94		12.1 $\pm$ 0.4	A	a	116		-7
TEND	11.9 $\pm$ 0.2	C	a	86		10.3 $\pm$ 0.3	BC	b	99		-13
LEG	13.8 $\pm$ 0.2	A	a	100		10.9 $\pm$ 0.5	B	b	105		-21
TORY	13.0 $\pm$ 0.8	AB	a	94		10.2 $\pm$ 0.1	BC	b	98		-22
PI	12.3 $\pm$ 0.2	BC	a	89		9.4 $\pm$ 0.2	C	b	90		-24
Mean	12.6					10.4					

Number of seeds per mature pod.

WAT	4.61 $\pm$ 0.17	BC	a	100		2.72 $\pm$ 0.15	AB	b	115		-41
WAX	5.05 $\pm$ 0.12	AB	a	110		1.38 $\pm$ 0.11	D	b	58		-73
BBL47	3.99 $\pm$ 0.26	D	a	87		3.47 $\pm$ 0.29	A	a	146		-13
TEND	4.30 $\pm$ 0.19	CD	a	93		2.47 $\pm$ 0.23	BC	b	104		-43
LEG	4.20 $\pm$ 0.20	CD	a	91		3.06 $\pm$ 0.51	AB	a	129		-27
TORY	5.24 $\pm$ 0.16	A	a	114		1.87 $\pm$ 0.16	CD	b	79		-64
PI	4.86 $\pm$ 0.15	AB	a	105		1.65 $\pm$ 0.15	CD	b	70		-66
Mean	4.61					2.37					

M R T Duncan's Multiple Range Test at $p = 0.05$.

Upper case letters - differences among varieties.

Lower case letters - differences among treatments in varieties.

Table 5: Effects of exposure of *P. vulgaris* plants to high temperature at flowering stage on yield parameters.

Phytotron experiments. Sowing date: 18.3.88.

Treatment: Control 22/17					5 days at 32/27						
Variety	Mean $\pm$ S.E.	M	R	T	% of mean	Mean $\pm$ S.E.	M	R	T	% of mean	% change
Number of mature pods per plant											
BBL47	10.2 $\pm$ 0.6	A	a	121		1.6 $\pm$ 0.3	B	b	53		-84
BLUE	9.4 $\pm$ 0.7	AB	a	111		1.9 $\pm$ 0.4	B	b	63		-80
EAGLE	8.6 $\pm$ 0.6	AB	a	102		2.0 $\pm$ 0.4	B	b	66		-77
LEGACY	8.6 $\pm$ 0.5	AB	a	102		5.1 $\pm$ 0.7	A	b	169		-41
2102	8.4 $\pm$ 0.5	AB	a	99		1.7 $\pm$ 0.4	B	b	56		-80
TEND	7.8 $\pm$ 0.6	BC	a	92		4.6 $\pm$ 0.6	A	b	153		-41
WAT	6.1 $\pm$ 0.6	C	a	72		4.2 $\pm$ 0.5	A	b	139		-31
Mean:	8.4					3.0					

Number of seeds per plant.

BBL47	41.7 $\pm$ 3.2	A	a	112		5.2 $\pm$ 1.2	C	b	50		-88
BLUE	37.8 $\pm$ 3.4	A	a	102		8.6 $\pm$ 0.6	BC	b	82		-77
EAGLE	37.2 $\pm$ 2.8	A	a	100		5.7 $\pm$ 1.6	C	b	54		-85
LEGACY	43.6 $\pm$ 2.3	A	a	117		17.5 $\pm$ 2.4	A	b	167		-60
2102	38.8 $\pm$ 2.6	A	a	104		5.8 $\pm$ 1.2	C	b	55		-85
TEND	35.0 $\pm$ 3.4	AB	a	94		13.5 $\pm$ 1.9	AB	b	129		-61
WAT	26.4 $\pm$ 3.3	B	a	71		17.0 $\pm$ 2.5	A	b	162		-36
Mean	37.2					10.5					

Degree of curvature of mature pods.

Pod curvature range: 1 - straight, to 4 - very curved.

BBL47	2.2 $\pm$ 0.1	B	b	96		3.1 $\pm$ 0.2	A	a	104		40
BLUE	2.5 $\pm$ 0.2	AB	a	108		2.6 $\pm$ 0.2	B	a	87		4
EAGLE	2.2 $\pm$ 0.2	B	b	93		2.8 $\pm$ 0.2	AB	a	93		28
LEGACY	2.4 $\pm$ 0.1	AB	b	102		3.2 $\pm$ 0.1	A	a	106		34
2102	2.2 $\pm$ 0.1	B	b	93		3.1 $\pm$ 0.1	A	a	105		44
TEND	2.1 $\pm$ 0.1	B	b	92		2.9 $\pm$ 0.1	AB	a	97		36
WAT	2.7 $\pm$ 0.1	A	b	116		3.2 $\pm$ 0.1	A	a	107		19
Mean:	2.3					3.0					

Length of mature pods (cm).

BBL47	13.1 $\pm$ 0.2	BC	a	99		11.4 $\pm$ 0.7	ABC	b	98		-13
BLUE	13.3 $\pm$ 0.4	B	a	101		12.6 $\pm$ 0.5	A	a	109		-5
EAGLE	13.6 $\pm$ 0.2	B	a	103		10.8 $\pm$ 0.5	BC	b	93		-21
LEGACY	14.9 $\pm$ 0.2	A	a	113		12.8 $\pm$ 0.3	A	b	110		-14
2102	12.2 $\pm$ 0.2	D	a	92		10.5 $\pm$ 0.5	C	b	91		-14
TEND	12.3 $\pm$ 0.4	CD	a	93		10.9 $\pm$ 0.7	BC	a	94		-11
WAT	13.1 $\pm$ 0.4	BC	a	99		12.2 $\pm$ 0.4	AB	a	105		-7
Mean:	13.2					11.6					

Number of seeds per mature pod.

BBL47	4.06 $\pm$ 0.14	BC	a	92		2.58 $\pm$ 0.50	BC	b	86		-36
BLUE	3.94 $\pm$ 0.21	C	a	89		3.42 $\pm$ 0.41	AB	a	114		-13
EAGLE	4.34 $\pm$ 0.10	BC	a	98		2.27 $\pm$ 0.31	C	b	76		-48
LEGACY	5.11 $\pm$ 0.19	A	a	116		3.46 $\pm$ 0.16	AB	b	116		-32
2102	4.65 $\pm$ 0.14	AB	a	105		2.49 $\pm$ 0.34	BC	b	83		-46
TEND	4.43 $\pm$ 0.19	BC	a	100		2.91 $\pm$ 0.18	ABC	b	97		-34
WAT	4.35 $\pm$ 0.40	BC	a	99		3.80 $\pm$ 0.28	A	a	127		-13
Mean:	4.41					2.99					

M R T Duncan's Multiple Range Test at $p = 0.05$.

Upper case letters - differences among varieties.

Lower case letters - differences among treatments in varieties.

Seeds per pod.

Relative effect of H.T.

Fig. 2 :

Top : Effects of exposure to 5 day 32/27°C at anthesis on seed number for pod in bush-bean varieties. Results are from three different experiments. Sowing dates are indicated.

Bottom : Relative decrease (%) in seeds/pod after exposure to 5 days of 32/27°C at anthesis. Results from above experiment.

Mature pods
% of mean at 22/17

Relative effect of H.T.

Fig. 1 :

Top : Yields (pods/plant) of bush-bean varieties at 22/17°C in three different experiments. Sowing dates and mean yield for each experiment are indicated.

Bottom : Relative decrease (%) in pod/plant after exposure to 5 days of 32/27°C at anthesis, as compared to 22/17°C. Results are from above experiments.

Seeds per plant.

Relative effect of H.T.

Fig. 3 :

Top : Effects of exposure to 5 days of 32/27°C at anthesis on seed production per plant in bush-bean varieties. Results are from three different experiments - sowing dates are indicated.

Bottom : Relative reduction (%) in seeds/plant resulting from exposure to 5 days at 32/27°C at anthesis. Results from above experiments.

The effects of 32/27°C on the distribution of pods according to the number of seeds they contain was examined in Exp. I (Fig 4). Under 22/17°C, distribution of pods was quite similar in the 7 varieties tested. The mean number of seeds/pod ranged between 4.2 ± 0.3 and 5.2 ± 0.1 . Distribution was skewed towards pods with higher seed content. Exposure to 32/27°C resulted in a significant ($P=0.001$) reduction in the number of seeds/pod (from 4.6 ± 0.1 to 2.6 ± 0.1 , range 1.9-3.4). This decrease resulted from a great increase in the frequency of pods with 1 to 3 seeds. These seeds usually developed from the ovules most proximal to the stigma (results not shown; but see Fig. 8). Interactions between high temperature and ovule position in the pods were examined in other experiments (see Fig. 8). Production of one seed/pod was enough to prevent its abscission in all varieties studied. Therefore, no correlation was found between mean number seeds/pod after 32/27°C at anthesis and the relative reduction in pods/plant (Tables 3, 4, 5). For example, in Exp. I, seeds/pod in LAKE SUPERIOR and BRONCO was 2.4, but they differed extremely in the number of pods/plant : 7.8 vs. 4.5, representing a 12% and 74% reduction compared to 22/17°C. On the other hand, the larger the total number of seeds produced per plant after exposure to 32/27°C, the smaller was the reduction in the number of pods produced per plant ($r=0.803$, $P=0.001$; Fig. 5). This inverse correlation suggests that the low pod production under HT is due to its negative effects on processes determining seed set.

EFFECT OF HIGH TEMPERATURE (32/27 °C) AT ANTHESIS ON SEED SET/POD

Fig. 4 : Effect of 5 days of 32/27°C at anthesis on pod distribution according to seed/pod in bush-bean varieties.

Fig. 5 - Relationship between relative reduction (%) of pods/plant by 5 days 32/27°C at anthesis and total number of seeds/plant at 32/27°C. ($Y = -88.7 - 2.2X$; $r = 0.803$; $P = 0.001$)

Pod set under 22/17°C in Exp. III was significantly lower ($P=0.001$) than in the other 2 experiments (Tables 3, 4 and 5: Mean Yields 8.4 vs. 12.9 and 14.9 for Exp. III, II and I respectively). This reduction probably resulted from lower natural light intensity and duration that prevailed during Exp. III, and was not a chance consequence of the varieties being tested. The reduction in pod yield occurred in 3 of the 4 varieties grown in both experiments (Table 6).

Table 6 : Relative reduction in yield parameters by 5 days of 32/27°C at anthesis in two different experiments (data from Tables 2 and 3)

Exp*	% reduction					
	pods/plant		seeds/pod		seeds/plant	
	II	III	II	III	II	III
WAT	73	31	41	13	84	36
BBL-47	79	84	13	36	81	88
TEND	55	41	43	34	71	61
LEG	75	41	27	32	77	60

* Sowing dates : Exp. II : 16.8.87 ; Exp. III : 18.3.88

The reduction in pod/plant by HT in Exp. III was not necessarily associated with a comparable decrease of seeds/pod (see different behaviour of TEND and LEG compared to WAT). Possibly, the lower light intensity prevailing in Exp. III enhanced the abscission of flowers and/or young pods, without affecting seed set.

Generally, a higher yield (pods or seeds per plant) under the optimal temperature regime was associated with a larger relative reduction of yield after exposure to HT at anthesis (Figs. 1 and 3). This relation is shown by plotting the yield (pods/plant and seeds/plant) at 22/17°C against the relative decrease in yield due to HT (Fig. 6).

Fig. 6 - Relationship between relative reduction (%) of pods/plant (top) and seeds/plant (bottom) by 5 days 32/27°C at anthesis and pod or seed yield at 22/17°C.

	<u>pods/plant</u>	<u>seeds/plant</u>
Summer Exp. (□)	$r = 0.645$	$r = 0.664$
(1.6.87 and 1.8.87)	$P = 0.05$	$P = 0.05$
Early Spring Exp. (Δ)	$r = 0.786$	$r = 0.682$
(18.3.88)	$P = 0.05$	NS

The results clearly indicate a tendency of high yielding varieties to be more adversely affected by exposure to 32/27°C. Thus, while relative reduction in yield is a measure of variety tolerance to HT, it does not necessarily represent potential productivity under heat stress. Theoretically, a similar yield can be attained under HT by low and high yielding varieties showing contrasting relative yield reductions under heat stress.

Time distribution of flowering and pod production

In the phytotron experiments it was observed that varieties differed in the degree of anthesis synchronization. For example, SENTRY had a very concentrated flowering, while in PI-271998 flowering was more spread out over time. The timing of exposure of the developing flower to 32/27°C may be critical for HT effects on pod and seed set. Therefore, differences in flower synchronization may be the underlying cause for intervarietal differences in yield as measured in the phytotron experiments. In varieties in which flowering is more concentrated, a larger number of flowers will be exposed to the applied HT than in varieties with a less concentrated flowering. Less concentrated flowering may reduce the impact of heat stress on yield and represent a beneficial strategy in the field. The fact that flower buds at different developmental stages are subjected to the HT treatment may confound interpretation of its effects on specific reproductive processes determining pod and seed set. Therefore, in the following experiments only the first 10-15 flowers that opened 2-3 days after transfer to 32/27°C were left on the plants. Likewise, a similar number of flowers were left on the control (22/17°C) plants. Flowers reaching anthesis after the plants were transferred back to 27/17°C were removed. These experiments were carried out during the summer of 1988, with snap-bean (LAB, LEG, SENTRY, WAT) and dry-bean (WAF, G-3696, G-3689, G-3702, NY-5-161 and 85-CT-4976) genotypes (Tables 7A and 7B).

Table 7-A : Effects of 5 days of 32/27°C at anthesis on yield parameters of snap-bean varieties.

Only flowers reaching anthesis during heat treatment were left. Later opening flowers were removed.

		Pods/	reduction	Seeds/	reduction	Seeds/	reduction	
<u>Varieties</u>		<u>Plant</u>	(%)	<u>Pod</u>	(%)	<u>Plant</u>	(%)	<u>HAP</u>
LAB	22-17°C	9.8 ±0.8		3.9 ±0.4		38.2		
			-69		-41		-77	97
	32/27°	3.0 ±0.3		2.3 ±0.6		8.9		
LEG	22/17°C	7.6 ±0.5		3.5 ±0.5		26.6		
			-73		-29		-74	35
	32/27°C	2.8 ±0.4		2.5 ±0.3		7.0		
SEN	22/17°C	10.3 ±0.8		4.9 ±0.3		50.5		
			-45		-41		-67	45
	32/27°C	5.7 ±1.1		2.9 ±0.3		16.5		
WAT	22/17°C	8.0 ±0.9		3.3 ±0.3		26.4		
			-34		-33		-46	70
	32/27°C	5.3 ±1.1		2.2 ±0.4		11.7		
<hr/>								
<u>MEAN</u>	22/17°C	8.9		3.9		35.4		
			-53		-36		-66	
	32/27°C	4.2		2.5		12.0		

Table 7-B : Effects of 5 days of 32/27°C at anthesis on yield parameters of dry-bean varieties. Only flowers reaching anthesis during heat treatment were left. Later opening flowers were removed.

<u>Varieties</u>		reduction <u>Pods/Plant (%)</u>	reduction <u>Seeds/Pod (%)</u>	reduction <u>Seeds/Plant (%)</u>	<u>HAP</u>
WAF-9					
22/17 °C	6.9 ±0.2		3.7 ±0.3	25.5	
		-61	-22	-69	—
32/27 °C	2.7 ±0.4		2.9 ±0.1	7.8	
G-3696					
22/17 °C	14.2 ±0.9		5.2 ±0.1	73.8	
		-77	-42	-87	130
32/27 °C	3.2 ±0.5		3.0 ±0.2	9.6	
G-3689					
22/17 °C	15.4 ±1.0		4.9 ±0.1	75.5	
		-45	-35	-64	>130
32/27 °C	8.4 ±1.1		3.2 ±0.2	26.9	
G-3702					
22/17 °C	6.9 ±0.6		5.6 ±0.1	38.6	
		-77	-46	-88	125
32/27 °C	1.6 ±0.4		3.0 ±0.6	4.8	
NY-5-161					
22/17 °C	8.8 ±1.0		3.8 ±0.4	33.4	
		-46	-60	-86	72
32/27 °C	3.2 ±0.6		1.5 ±0.6	4.8	
85-CT-4976					
22/17 °C	4.7 ±0.4		3.8 ±0.4	17.9	
		-51	-55	-78	90
32/27 °C	2.3 ±0.5		1.7 ±0.3	3.9	
<hr/>					
<u>MEAN</u> 22/17 °C	9.5		4.5	44.1	
		-62	-43	-73	
32/27 °C	3.6		2.6	12.1	

Pods/plant and seeds/pod were reduced after an exposure to 32/27°C (at anthesis) by 53% and 36% for snap-bean, and by 62% and 43% in dry-bean varieties, respectively (mean values). Thus, a similar range of reduction in the different yield parameters was found for snap-bean and dry-bean varieties. Some seed-bearing pods developed even after the HT. The extent of the reduction was similar to that observed in previous experiments in which later opening flowers were not removed. Thus, although yield parameters were lower after HT treatment, reproductive processes involved - e.g. pollination, pollen-tube growth, fertilization and early embryo development, exhibited a moderate tolerance to 32/27°C at anthesis.

Varieties differed quantitatively in their responses to 32/27°C, as shown in previous experiments in which later opening flowers were not removed. Since the method of removing later opening flowers that were not exposed at anthesis to 32/27°C resulted in a much better defined system, it was adopted in the following experiments under controlled conditions.

HT Effects at different stages of reproductive development

Effects of HT on abscission as well as on the reproductive processes determining pod and seed set were studied in more detail in BBL-47 and PI-271-998 (PI in the following text). These varieties differed in their heat acclimation potential (HAP: 50 vs. 94 min heat killing time, HKT) and, in preliminary experiments, they also differed in pod set at 32/27°C. Additional varieties were examined with less detail to corroborate specific observation.

In order to identify the reproductive processes affected by HT and leading to lower yields, plants were grown at 22/17°C and exposed to 32/27°C at different developmental stages:

- a) at micro and macrosporogenesis in first flowers (approx. 20-23 days after sowing): to study effects on pollen and ovule development,
- b) at the time of anthesis of first flowers (approx. 30-32 days after sowing): to study effects on pollination, pollen tube growth and fertilization,
- c) at early pod development (1-3 day old pods): to study effects on early embryo and seed growth.

Exposure to 32/27°C at sporogenesis stage

In this series of experiments plants were transferred to 32/27°C when the first flower buds reached a length of about 2 mm (20-23 days after sowing). At this stage anthers and ovules had completed their morphological differentiation, but pollen and megaspore mother cells had not reached meiosis (microscopic observations). After exposure to 32/27°C for 5 days, plants were returned to 22/17°C where flowers reached anthesis and continued their development into pods. Only the first 10-12 flowers were left on the plants. Flowers that opened later were removed, since they may set normal pods. These are capable of inducing the abscission of pods developing from earlier flowers exposed to 32/27°C at sporogenesis. Thus, in this experiment we examined direct effects of HT on sporogenesis and the resulting pod and seed set, avoiding indirect effects on pod development due to interactions with later normally developing pods.

Most flowers of both varieties that were exposed to 5 days of 32/27°C at the sporogenesis stage reached anthesis. However, in all flowers the anthers failed to dehisce, pollen viability (determined by

Alexander Stain) was very low, and most pollen grains were deformed and/or empty. Mature pods (with at least one normal seed) did not develop in any of the varieties exposed to HT at microsporogenesis (Tables 8 and 9). Nevertheless, in most flowers the ovary developed into a narrow pod (4-5 mm), with a slow growth rate, reaching a length of 50-60 mm before stopping growth. At their maximal length, the ovules were 1.00 to 1.25 mm long, but did not develop into seeds. These pods were considered as parthenocarpic. Surprisingly, they did not abscise up to 2-3 weeks after anthesis, even though they lacked developing seeds. In plants developing at 22/17°C, pods abscise 3 to 6 days after anthesis, and are shorter than 30-40 mm at abscission time. Nevertheless, parthenocarpic pods were induced to abscise earlier if normal pods were allowed to develop from flowers reaching anthesis later. These flowers were exposed to HT at pre-sporogenous stages. In experiments in which 14 day old plants were transferred to 32/27°C for 5 days, yield was not reduced (results not shown). Thus these early stages are not affected by HT.

Since micro and megasporogenesis occur more or less simultaneously during exposure to 32/27°C, lack of pod and seed set can be attributed to a failure in one or both processes. Microscopic observations clearly showed that pollen from flowers exposed to 32/27°C at sporogenesis was unviable. The possibility of differential effects of HT on pollen and ovule development was examined in PI. Viability of their ovules after exposure to 32/27°C at sporogenesis was studied by hand pollination, with viable pollen from plants growing continuously under 22/17°C (Table 8).

Pollination of flowers exposed at sporogenesis to 32/27°C with viable pollen resulted in pod and seed set similar to that observed in plants under 22/17°C. Thus, ovule development at sporogenesis is unaffected by HT and lack of seed set is due solely to failure in pollen development at HT.

Table 8 : Effect of pollination of PI-271998 flowers exposed at sporogenesis to 5 days of 32/27°C with viable pollen from flowers continuously grown under 22/17°C. 65-70 flowers, 8-10 plants.

	pod set (%)	pod length (mm)	seeds/pod
<u>Not-emasculated</u>			
22/17°C	82	94	3.6
32/27°C	97 ¹	53	0.0
<u>Emasculated (and hand-pollinated)</u>			
22/17°C	72	81	3.3
32/27°C	82	118	3.5

1 - parthenocarpic

The possibility that parthenocarpic pods resulted from lack of pollination was studied further by anther emasculation under 22/17°C. Emasculation was carried out by 2 techniques:

- a) removal of anthers after slitting the keel
- b) by cutting the distal end of the twisted keel, removing anthers and stigma at the same time.

Non-emasculated flowers were removed to avoid development of normal pods. Emasculation by both techniques resulted in parthenocarpic pods in PI - as well as in BBL-47 in all treated flowers (Table 8). These parthenocarpic pods had a slower growth, elongated to 60-70mm (Fig. 7) and showed delayed abscission, similar to pods developing after HT. Onset of abscission of parthenocarpic pods occurred earlier in BBL-47

than in PI (ca 12 vs. 24 days, respectively). If non-emasculated flowers were left together with emasculated ones on the same plant, abscission of parthenocarpic pods started 5 to 6 days after anthesis in both varieties. This time lag is similar to that observed under 22/17°C for "normal" pods that are inhibited by pods more advanced in their development.

These results suggest that the abscission of late developing young pods on plants not exposed to HT is due to inhibitory effects originating from more advanced pods possessing normal developing seeds.

Parthenocarpic pods do not induce abscission of later developing parthenocarpic pods. In one particular experiment, PI produced and retained 31.8 ± 4 parthenocarpic pods/plant in plants transferred to continuous 32/27°C 20 days after sowing (Table 9). Furthermore, lack of abscission of parthenocarpic pods after exposure to 32/27°C was not due to a direct specific inhibition of abscission layer differentiation by the HT. This may be deduced, since abscission in similar pods developing from emasculated flowers, where seed set is inhibited, is also prevented under 22/17°C by lack of seed development.

HT effects at sporogenesis were studied in detail in another 5 varieties (BRONCO, DOR, LAKE SUPERIOR, SENTRY and STRIKE) which were transferred at the age of 20 days to 32/27°C where they continued to develop until harvest. Similar effects of 32/27°C were observed for anther dehiscence, pollen viability and parthenocarpic pod development in all varieties (Table 9). In another less detailed experiment with SUPERGLOSS TORY, SUPERGLOSS WATERFALL, LEGACY and LABRADOR, 32/27°C at sporogenesis also resulted in anther dehiscence failure and in non-viable pollen (results not shown). Thus, the high sensitivity of microsporogenesis to HT is of common occurrence in bean plants. Between the 11 varieties of bush-bean examined, none of them exhibited tolerance to this HT effect.

Fig. 7 - Elongation of pods at 22/17°C in PI-271998 and BBL-47 as affected by lack of pollination (anther emasculation). Pods developed from emasculated flowers were parthenocarpic. Normal pods from pollinated flowers (O). Parthenocarpic pods from flowers emasculated by removing anthers (Δ) or cutting twisted keel with anthers and stigma (●). Parthenocarpic pods that develop on plants bearing normal pods from pollinated flowers (□). ↓ indicates onset of abscission.

Table 9 : Effects of 32/27°C at time of microsporogenesis on pollen viability, anther dehiscence, and parthenocarpic pods. Plants grown at 22/17°C and transferred to 32/27°C 20 days after sowing. At 22/17°C all anthers were open and pollen was found on the stigma. Pollen viability determined by Alexander stain.

<u>Variety</u>	<u>Open Anthers</u>	<u>Pollen on Stigma</u>	<u>Pollen Viability</u>		<u>Parthenocarpic Pods at 32/27°C</u>
			<u>22/17°C</u> (%)	<u>32/27°C</u> (%)	
BRONCO	+	+(few) ¹	75	50	19.2
DOR	-	-	80	10	²
LAKE SUPERIOR	-	-	75	<5	11.4
SENTRY	-	-	65	<5	12.3
STRIKE	-	-	75	10	21.2
PI-271998	-	-	85	<10	31.8

1 - Viable pollen grains germinated inside anthers, no pollen tube penetration into stigma.

2 - In this variety, flowers and young pods abscised under LD conditions at 22/17°C and 32/27°C.

Exposure to 32/27°C at anthesis and early pod development

In this series of experiments plants were grown under 22/17°C and transferred for 5 days to 32/27°C 2-3 days before anthesis of first flowers, or when their pods were 1 day old (1 day after anthesis).

In the first case, only the first 10 to 12 flowers to open in 32/27°C were left on the plant and continued their development into pods at 22/17°C. Later opening flowers were removed. In the second case, 10-12 pods one day old were left on the plants when transferred to 32/27°C. Flowers reaching anthesis after the transfer were removed.

Since BBL-47 showed a stronger response to 32/27°C, another 2 treatments were carried out with this variety;

- a) exposure of plants with 10-12 flowers just before anthesis to 1 day of 32/27°C,
- b) exposure of plants with 10-12 three day old pods to 5 days at 32/27°C.

In contrast to the negative effect of 32/27°C at sporogenesis (age 20-23 days), exposure of plants with first flowers just before anthesis (age 30-32 days) to 5 days of 32/27°C did not affect anther dehiscence, or pollen viability (Alexander stain, Table 10).

However, the pollination picture in flowers exposed to 32/27°C at anthesis was different to that observed in flowers from 22/17°C. Closer examination revealed that heat stressed flowers had their anthers tightly pressed around the stigma, and a large proportion of the pollen germinated inside the anthers. When anthers were removed from the stigma, a larger portion of the germinated pollen mass remained attached to the anthers, while the stigma was left with few pollen grains, and sometimes practically naked. Thus, in the HT treated flowers most pollen grain germination did not occur on the stigma surface. In flowers from 22/17°C, the anthers were loosely

attached to the stigma, and when removed most of the pollen grains remained on the stigma.

The effects of temperature on anther dehiscence, pollen deposition and germination were examined in greater detail in-vitro in detached flowers obtained from PI, BBL-47, SENTRY and STRIKE. Flower buds were removed the night before anthesis from plants growing under 22/17°C and 32/27°C, and placed in Petri dishes on wet filter paper. Stressed and non-stressed flowers were kept overnight at 25°C or 35°C and examined the next morning, after 12-15 hours of incubation. During this period flowers reached anthesis. In practically all flowers from 32/27°C, most of the pollen germinated inside the anthers, and very few on the stigma, as in the attached flowers. In BBL-47 and PI-27199 8 pollination in detached flowers from 22/17°C was quite similar to that observed in attached flowers (Tables 10 and 11). However, in the four varieties examined, pollen germination under 35°C was much lower than under 25°C (Table 11).

Table 10: Anther dehiscence, pollen viability and pollen-tube growth as affected by exposure to 32/27°C at anthesis in BBL-47 and PI-271998. N=10

	(%) anther <u>dehiscence</u>	(%) pollen <u>viability*</u>	pollen tubes <u>in style**</u>	% ovaries in which pollen tubes reached <u>distal ovule</u>
BBL-47				
22/17°C	100	>90	42 ±5	90
32/27°C:1 day	100	80-90	18 ±2	-
32/27°C:5 day	100	80-90	13 ±2	40
PI-271998				
22/17°C	100	>90	28 ±4	100
32/27°C:5 day	100	80-90	25 ±3	100

* Alexander stain

** Pollen tubes penetrating stigma

Table 11: Temperature effects on pollen germination in detached flowers from plants grown at 22/17°C. Flowers were collected at 20:00 hr. and germination counted 12 to 15 hr later.

<u>Temp.</u>	<u>pollen germination (%)</u>			
	<u>STRIKE</u>	<u>SENTRY</u>	<u>BBL-47</u>	<u>PI-271998</u>
25°C	83 ±10	87 ±3	45 ±3	23 ±4
35°C	10 ±2	21 ±4	3 ±2	1 ±1

Data in Table 10 show that in attached flowers of BBL-47, exposure to even one day of 32/27°C strongly reduced the number of pollen tubes penetrating the style. In PI, the number of pollen tubes in the style at 22/17°C was significantly smaller than in BBL-47 ($P=0.001$) and not affected by temperature. Furthermore, while in BBL-47 the proportion of ovaries in which the pollen tubes reached the most distal ovule (farthest from the stigma) was reduced by half at 32/27°C. In PI, this parameter was unaffected. In other words, "potential maximal fertilization" was reduced by HT in BBL but not in PI.

The stronger inhibitory effect of 32/27°C on the pollination and potential fertilization of BBL-47 was reflected also in the larger proportion of abscised and aborted pods (pods where all seeds are aborted) found in this variety compared to PI (Table 12). In contrast, in PI 32/27°C did not affect the proportion of flowers producing mature normal pods. Furthermore, in BBL-47 exposure to 32/27°C at anthesis significantly reduced the number of seeds/pods (by 43%, $P=0.001$), while in PI the reduction was smaller (24%) and not significant. In BBL-47 even one day at 32/27°C at anthesis was effective in reducing the proportion of pods reaching maturity (by 21%), and of the number of seeds/pod (by 39%).

The reduction of seeds/pod in BBL-47 was due both to a higher proportion of unfertilized ovules ($< 1\text{mm}$ at harvest time), and to a greater proportion of aborted seeds (Table 13). In PI ovule fertilization and seed set were unaffected by HT.

Table 12 : Effect of 32/27°C at anthesis or early pod development on flower or pod abscission, pod abortion, seeds/pod, and seed weight in PI-271998 and BBL-47. At 22/17°C 32/27°C transfer, 10-12 flowers or 1d or 3d old pods were left on each plant. 10-14 plants.

	% abscission		% aborted		% normal ⁵		seed weight	
	flowers		pods ²		pods		seeds/pod	
	or pods						(mg)	
<u>BBL-47</u>								
22/17°C	7	B a ¹	15	AB a	78	A a	4.4	A a
32/27°C								
1d at anthesis ³	12	B	26	A	62	AB	2.7	B
5d at flowering ⁴	31	A b	26	A a	43	B b	2.5	B a
5d at 1d pods	7	B a	3	B a	90	A a	3.9	A a
5d at 3d pods	4	B	1	B	94	A	4.1	A
<u>PI-271998</u>								
22/17°C	18	A a	11	A a	71	A a	3.8	A b
32/27°C								
5d at flowering	16	A a	9	A b	75	A a	2.9	A a
5d at 1d pods	17	A a	11	A a	65	A b	3.5	A a

1 - Duncan's Multiple Range test at P=0.05. Treatments that share common letters are not statistically different. Uppercase letters: differences between treatments within temperature treatment. Lowercase letters: differences between varieties at same treatment.

2 - pods with all seeds aborted.

3 - onset of exposure at 32/27°C the night before anthesis.

4 - onset of exposure 2-3 days before anthesis.

5 - pods with at least one normal seed.

Table 13 : Effects of 32/27°C on ovule fertilization, ovule abortion and seed set in PI-271998 and BBL-47. 10-14 plants.

	% unfertilized			% aborted ¹			% normal		
	<u>ovules/plant</u>			<u>seeds/plant</u>			<u>seeds/plant</u>		
<u>BBL-47</u>									
22/17°C	6	C	a ²	24	A	a	70	A	a
32/27°C									
1d at anthesis ³	20	B		43	A		37	B	
5d at flowering ⁴	36	A	a	31	A	a	33	B	b
5d at 1d pods	8	C	a	21	B	a	71	A	a
5d at 3d pods	7	C		20	B		73	A	
<u>PI-271998</u>									
22/17°C	8	C	a	34	A	a	58	A	a
32/27°C									
5d at flowering	18	AB	b	35	A	a	47	A	b
5d at 1d pods	11	BC	a	35	A	a	55	A	b

1 - fertilized ovules that did not reach maturity

2, 3, 4 - as in table b

Position of the ovule in the ovary affects its chances of becoming a seed. The further the ovule is from the stigma, the smaller are its chances to be fertilized and to develop into a seed (Fig. 8). At 22/17°C the proportion of fertilized ovules (<1mm) was quite similar in PI and BBL-47. Both varieties showed a small decline with position in this parameter. However, ovules of BBL-47 have a slightly greater chance (10-25%) to develop into a mature seed at each position. Under 32/27°C the chances of fertilization and seed set in BBL-47 were smaller compared to 22/17°C. The farther the ovule was from the

stigma, the smaller were its chances to become fertilized or to set a seed. In contrast, the reduction in fertilization and seed set in PI by HT were smaller and more or less similar at each position along the pod.

Exposure of young pods (1 or 3 days old) to 5 days of 32/27°C did not affect pod development, or seeds/pod in both varieties (Table 12). The effects of 32/27°C on seed size were more pronounced in PI than in BBL-47 (Table 12). While in PI seed weight was significantly reduced by exposure to HT at anthesis (14%, $P=0.01$) and at the young pod stage (29%, $P=0.01$), the reduction in BBL-47 was smaller (<12%) and not significant.

In PI the effect of HT on seeds/pod was small, while seed size was significantly affected (Table 12). In BBL-47, on the other hand, significant reductions in seeds/pod were not accompanied by a decline in seed size. Thus, a simple mechanism of compensation cannot explain these differences. In PI, the larger seeds that characterize this variety may bring a stronger intrapod competition in stressed plants resulting in a reduction of seed size at maturity. On the other hand, pod size (length) was reduced to the same extent (ca. 15%) by 32/27°C in both varieties.

These results clearly indicate that in BBL-47 the decrease in pod and seed set after exposure to 32/27°C at anthesis is due to negative effects of HT on pollen germination, pollen tube growth and/or fertilization. These effects may lead to a larger abscission and/or abortion of young pods in BBL-47, compared to PI, after an exposure to HT at anthesis. The fact that exposure of very young pods to 32/27°C did not reduce pod and seed set shows that early embryo and endosperm development tolerates exposures to 32/27°C.

Fig. B - Effects of ovule position in pod and exposure to 32/27°C at anthesis on ovule fertilization (ovules>1mm) and seed set in PI-271998 (□, ■) and BBL-47 (○, ●). Control plants were grown continuously under 22/17°C (□, ○) or exposed to 5 days of 32/27 at anthesis (■, ●).

Spring

Fig. 9 :

Changes in maximal (●) and minimal (+) daily temperature, relative humidity (% RH) and daily pan evaporation (bars) during the springs of 1986-88. Data is for the main reproductive period (pre-flowering to pod filling stages) of snap-bean and dry-bean accessions. Determinate accessions flowered earlier than indeterminate ones. Shaded bars indicate period of onset of flowering in most accessions of each growth type.

Summer

Fig. 10 :

Changes in maximal (•) and minimal (+) daily temperature, relative humidity (% RH) and daily pan evaporation (bars) during the summers of 1986-88. Data is for the main reproductive period (pre-flowering to pod filling stages) of snap-bean and dry-bean accessions. Determinate accessions flowered earlier than indeterminate ones. Shaded bars indicate period of onset of flowering in most accessions of each growth type.

GREENHOUSE EXPERIMENT

The objective of this experiment was to test the feasibility of screening for HT tolerance on a large scale under semi-controlled greenhouse conditions. Since high night temperature at anthesis resulted in lower yields in the phytotron, the same HT treatment was used in the greenhouse experiments.

Materials and methods

13 snap-bean varieties were tested. Plants were sown on 7/5/1986 and harvested on 1-8/7/1986. Plants were grown singly in 5 L pots, containing a mixture of peat, foam and osmocot (3 gr/L), and were drip irrigated every day to avoid effects of water stress. Plants were arranged in a randomized block design with 4 blocks, 20 plants in each block.

Temperatures after the onset of flowering were;

<u>Treatments</u>	<u>Temperature (°C)</u>	
	<u>Min (night)</u>	<u>Max day)</u>
Control	19-21	32-35
HT at anthesis	27-28	33-35

Results

Control plants attained a similar biomass and yield as plants grown in the field during the same period of the year (date not shown).

Furthermore, a good correlation ($b=1.103$; $r=0.712$; $P=0.02$) was found between the relative reduction (%) in yield (gr/plant) in the greenhouse and the yield (gr/m²) in the field. On the other hand no correlation was found between the reduction in yield in the greenhouse and the phytotron (see Table 23), although in both cases plants were

subjected to more or less the same HT treatment during the night. One possible explanation for this discrepancy is the large difference in pod production per plant between the phytotron and the greenhouse. While in the phytotron 14.9 and 12.9 pods/plant were produced in Exp. I and Exp. II under the light conditions of the summer (Fig. 1), in the greenhouse plants produced an average of ca 35 pods/plant. The larger pots used in the greenhouse (5 L) enabled a much better root development than in the phytotron (1 or 1.5 L pots), and plants produced more or less the same number of pods as in the field (results not shown). The better correlation between field and greenhouse yields is probably related to non-constrained root development. Larger roots not only improve water and mineral uptake under stress, but may also affect plant development, and pod and seed set. It is worthwhile to note that the summer reduction in yield was also smaller than that recorded in the phytotron (see next section).

Varieties differed in the relative effect of the HT treatment on pod/plant and FW/pod. In most varieties FW/pod was reduced by HT (except in WATERFALL), while in 7 out of 13 varieties pod/plant was unaffected (Table 14). The highest reduction in yield was observed in WATERFALL (-65%), that is also one of the varieties with the lowest stability in the field (Table 23).

On the other hand, TENDERETTE and LAKE SUPERIOR were the less affected by the HT. These varieties were also among those showing the smallest summer decrease in yield in the field trials (Fig. 14).

Thus, screening bean germplasm for HT tolerance is possible under greenhouse conditions, provided that root development is not constrained and plants reach similar biomass and yield levels as in the field.

Table 14 : Effects of high night temperature (27-28°C) at anthesis on snap-bean yield under greenhouse conditions. HT was applied during 5 nights at onset of anthesis. (%) indicates relative reduction under HT.

<u>Variety</u>	<u>Treatmnt</u>	<u>FW/plant (%)</u>		<u># pods/plant (%)</u>		<u>FW/pod (%)</u>	
BUSH BLUE LAKE	C	239	a	38.3	a	6.3	a
	HT	172	b -28	32.1	b -16	5.4	b -13
LAKE SUPERIOR	C	232	a	37.1	a	6.3	a
	HT	201	b -13	37.4	a -1	5.5	b -13
MUSSEY-175	C	216	a	40.7	a	5.3	a
	HT	154	b -29	34.4	b -15	4.6	b -15
BBL-47	C	205	a	33.5	a	6.2	a
	HT	147	b -28	29.4	a -12	4.8	b -22
EARLY GALLATINE	C	203	a	38.7	a	5.3	a
	HT	127	b -47	28.5	b -26	4.5	b -14
SUPERGLOSS WATERFALL	C	196	a	35.1	a	5.6	a
	HT	68	b -65	14.6	b -58	4.5	b -19
PURPLE ROUGE	C	192	a	35.0	a	5.0	a
	HT	148	b -23	29.5	b -16	5.4	a +7
LEGACY	C	181	a	33.7	a	5.6	a
	HT	130	b -28	34.4	a +2	3.8	b -14
SHANNON	C	178	a	40.3	a	4.5	a
	HT	149	b -18	41.8	a +4	3.8	b -33
TENDERETTE	C	167	a	38.4	a	4.4	a
	HT	147	a -12	40.0	a +4	3.6	b -18
SUPERGLOSS TORY	C	153	a	32.2	a	4.4	a
	HT	125	b -18	31.8	a -1	4.0	b -16
PI-271998	C	135	a	27.7	a	4.8	a
	HT	113	b -16	31.7	a +14	3.6	b -27
CONTENDER	C	118	a	24.1	a	5.0	a
	HT	77	b -35	17.6	b -27	4.0	b -19
AVERAGE	C	185	a	34.9	a	5.3	a
	HT	131	b -29	30.1	b -14	4.4	b -19

FIELD EXPERIMENTS

In order to study differences in the response of bean genotypes to HT, 26 accessions of snap-bean and 27 accessions of dry-bean were grown in the spring and the summer during 3 years (1986-88), and seasonal yields were compared. Our purpose was to use the climatic conditions of the hot Israeli summer to screen bean genotypes under ample irrigation for higher yield tolerance to HT. Furthermore, seasonal effects on total yield and yield components were analyzed to determine developmental factors which limit yield under summer conditions.

Materials and methods

The experiments were carried out in the experimental farm of the Faculty of Agriculture in Rehovot. The soil in the farm is a light, sandy loam (0-30 cm): Sand 95%, silt 1%, clay 4%, organic matter 0.1%, pH 7.7. "Field capacity" moisture content is 8-10% (dry weight basis). Moisture content at -2 bars water potential, is 2%.

Pre-sowing treatments

Mineral fertilization (applied ca 1 month before sowing): Ammonium sulphate 500 kg/ha, super phosphate (granulated) 500 kg/ha, potassium chloride 250 kg/ha. One month before sowing the soil was fumigated with methyl bromide to eradicate weeds and soil pests.

	<u>Sowing dates</u>		
	<u>1986</u>	<u>1987</u>	<u>1988</u>
Spring	7/4	6/4	28/3
Summer	24/6	12/6	10/6

The experiments were done in a randomized block design. Each accession was replicated 4 times. The plots were 4.5 by 1 m (in 1987, plots were 3 by 1 m for some accessions), two rows per plot, 30 cm apart. Granulated 10% Diazinone at a rate of 20 kg/ha and Terachlor (in water suspension) at 5 kg/ha were applied after sowing to prevent insect damage and fungal diseases, respectively, at seedling stage.

During plant development fungicides and insecticides were applied when necessary to control diseases (e.g. rust, or fungal diseases of the roots and lower stem), mites, aphids etc.

Plant stand was thinned to 12 ± 3 plants/m² at 3 weeks after sowing. During the first 3 weeks the plants were sprinkler irrigated. Later, drip irrigation was used alone, or in combination with sprinkling on very hot and dry days. Drippers were 25 cm apart on the irrigation line. A dripper line was located between 2 adjacent plant rows, lines were 1 m apart. Irrigation timing and amount was assessed according to plant development and climate. Affluent watering was practiced, especially towards flowering and onwards, to eliminate the effects of water stress. The light texture of the soil enabled sufficient drainage, but demanded frequent watering.

Liquid fertilizer was applied via the drip-irrigation system, starting 5-7 days before the onset of flowering.

<u>L/ha</u>	<u>Spring</u>	<u>Summer</u>
	<u>Days from Sowing</u>	
100	35	28
120	38	31
120	44	35
80	49	42
80	53	49

The liquid fertilizer was "Shefer 737" (from Fertilizers & Chemicals Ltd, Haifa), containing:

Total N	7.3% (4.3% as NO_3 and 3% as NH_4)
P_2O_5	3.2%
K_2O	6.5%
Fe (chelated)	300 ppm
Mn	126 ppm
Zn	36 ppm
Cu	9 ppm
Mo	6 ppm

The irrigation water contains plenty of Ca and Mg.

Field trials were arranged in a randomized block design with 3-4 replicates. The plants in the beginning and the end 25 cm of each plot were discarded, so that sampling was done from 4 m² per plot. Analysis of data variance was carried out according to experiment design. Multiple range tests were run at a significance level of $P=0.05$ (Duncan's test).

Climatic conditions

In Israel the climatic differences between the spring and summer seasons are extreme. Data in Figs. 9 & 10 show maximal and minimal daily temperatures, minimal RH(%) and daily evaporation during the period from flower bud production to pod set in the springs and summers of 1986, 1987 and 1988. Summer temperatures during reproduction were usually higher than spring temperatures, except during hot dry weather spells (chamsins) that occurred in the springs of 1987 and 1988. Day-night differential in temperature was greater during the spring, mainly due to the fact that the spring nights were relatively cooler than summer nights. Furthermore, evaporation in the summer was usually much higher than in the spring (7 vs. 5 mm/day).

Another major difference between the spring and summer growing seasons was related to the uniformity and stability of the climatic conditions. While summer conditions were quite stable during the reproductive period, spring conditions were extremely variable. During the spring of 1987 and 1988 chamsins occurred at the time of flowering and pod set, but not in the spring of 1986. Thus, although spring is considered to be the optimal season for bean yields in Israel, the impact of unpredictable hot weather spells must be taken into account.

Data on climatic conditions during the main flowering period of snap- and dry-bean accessions are presented in Table 15. This stage of development is particularly sensitive to HT and water stress. Data clearly shows that in 1987 and 1988 maximum temperature and daily pan evaporation during the flowering period in the spring were similar to those recorded during flowering in the summer. Furthermore, minimum RH(%) during spring flowering in 1987 and 1988 was even lower than in the summer. On the other hand, plants at the flowering stage were exposed to more hours of relatively high temperature ($>25^{\circ}\text{C}$) at night during the summer than during the spring.

In 1987 three chamsins coincided with the reproductive stages (6-7/5, 16-17/5 and 22/5), during which maximal temperatures of 39°C and minimal RH of 12% were recorded (Fig. A). On these dates sprinkler irrigation was unavailable, and wilting of young leaves was observed in several varieties, despite continuous trickle irrigation. In the spring of 1988 two extremely hot and dry chamsins occurred during the reproductive stages. However, in 1988 sprinkler irrigation was added during these extremely hot days, and plant wilting was prevented. Thus, varying amounts of irrigation were supplied during the same season in different years, according to the climatic conditions, in order to minimize the effects of water stress (Table 16).

Table 15 : Climatic conditions during main flowering period of snap- and dry-bean accessions grown in the spring and summer field experiments.

	Onset	Temp. °C		Min.	Evap.	Number of		
	Flow.					Hours at Night		
	Period	Max.	Min.	RH (%)	mm/24hr	With Temp. (°C)		
						>23°	>25°	>27°
<u>BUSH-BEAN</u>								
<u>Spring</u>								
1986	16-26/5	25.3	12.2	48.4	6.2	0	0	0
1987	13-23/5	28.5	13.1	32.5	6.1	8	3	0
1988	7-17/5	32.4	12.9	33.4	7.6	38	24	18
<u>Summer</u>								
1986	18-28/7	31.2	19.9	53.5	7.1	50	31	14
1987	8-18/7	30.4	18.0	53.0	7.2	43	29	8
1988	6-16/7	32.7	21.1	47.8	7.8	77	38	22
<hr/>								
<u>DRY-BEAN</u>								
<u>Spring</u>								
1987	20-30/5	28.9	14.6	42.6	6.3	14	9	0
1988	12-27/5	34.2	17.0	25.6	8.4	32	31	22
<u>Summer</u>								
1987	18-28/7	32.9	20.6	49.2	7.2	82	37	27
1988	17-27/7	31.7	22.4	57.0	7.2	99	49	32

Values are means for a 10 day period comprising the main flowering wave of all varieties in each season (see Figs. 9 & 10).

Table 16 : Amounts of water (sprinkler and drip irrigation) applied during the spring and summer trials.

	<u>irrigation (in mm)</u>		
	<u>1986</u>	<u>1987</u>	<u>1988</u>
Spring	395	556	830
Summer	711	820	1175

Snap bean varieties

In the first year of the project (1986) 17 commercial varieties were tested in the field. Of those, 5 varieties were found to be very susceptible to bean rust during the summer, and were excluded from the following field trials (Rogers-79183, BLUE LECT, CIMBOLA, PURPLE ROUGE, and PURPLE QUEEN). Instead of them, another 6 varieties were included in the 1987 and 1988 trials. In 1988 a further 3 varieties that were studied for heat adaptability in St. Paul were included in the field trials (85-CI-4976, BBL-15, BBL-92). Thus, 12 varieties were tested during 3 years (1986-88), 18 varieties during 2 years (1987-88), and 21 varieties in 1988. Detailed data for spring and summer yields of each variety in the different years are presented in Tables 1 to 5 in the Appendix. Summarized data for summer and spring averages is shown in Tables 18 to 22. Average spring and summer yields are graphically compared in Figs. 11 to 17.

Average yields for all the varieties in each of the three years were smaller in the summer than in the spring (26% reduction in overall mean; Table 17). Lower summer yields were mostly due to a decrease in the fresh weight of individual pods (by ca 21%), while the number of pods produced per unit area was only slightly reduced (by 9%).

Table 17 : Seasonal effects (spring vs. summer) on yield and yield components of 18 snap-bean varieties.

	<u>1986^a</u>	<u>1987^b</u>	<u>1988^b</u>	<u>Average</u>
<u>Yield (gr FW/m²)</u>				
spring	1891 ±49	1333 ±45	1738 ±44	1653
summer	937 ±42	1096 ±34	1632 ±46	1219
	***	***	NS	(-26%)
<u># Pods/m²</u>				
spring	362 ±9	250 ±8	306 ±8	306
summer	228 ±11	272 ±8	335 ±9	278
	***	NS	*	(-9%)
<u>gr FW/Pod</u>				
spring	5.58 ±0.08	5.37 ±0.10	5.51 ±0.11	5.49
summer	4.08 ±0.10	4.09 ±0.10	4.85 ±0.11	4.34
	***	***	***	(-21%)

a - Values for 12 varieties

b - Values for 18 varieties, including varieties grown in 1986. Differences in averages calculated for 12 or 18 varieties were smaller than 2.5%.

In addition to the seasonal reduction in yield, large differences were found between years in seasonal yields. The highest average spring yield was obtained in 1986, when no hot weather spells occurred during the reproductive stages, and temperatures were generally lower than in 1987 and 1988 (Fig. 9, Table 17). On the other hand, the lowest spring mean yield was in 1987, when sprinkler irrigation was not available during chamsins, which caused wilting in several

varieties at the time of flowering. Thus, yield reductions in the spring of 1987 were probably due to a short period of water stress at the reproductive stage.

Summer yields in 1986 and 1987 were significantly lower than spring yields. The reduction in yield is particularly high (51 and 43%) when compared to the mean yield in the spring of 1986, during which temperatures were lower and plants did not suffer from hot weather spells.

After the first two years of field experiments we suspected that the lower summer yields were caused not only by the high temperature, but also by insufficient water supply. To further reduce any possible effect of water stress on yield, irrigation was increased in the spring and summer of 1988 (Table 6). Trickle irrigation was more frequent, larger amounts of water were provided, and sprinkler irrigation was added during chamsins. The ample irrigation in 1988 resulted in large increases (ca 60%) in summer yields, compared to previous years (Table 11). Furthermore, the 1988 summer yield was of the same order as the spring yields of all three years (19% and 9% lower, or 20% higher than the 1986, 1988 and 1987 spring yields, respectively).

The exceptionally hot and dry weather spells during the spring in 1988 presented a unique opportunity to evaluate the relative importance of high temperature and adequate irrigation on bean yield. During this growing season, 2 chamsins occurred during the 10 days that followed the onset of flowering (Fig. 9). Temperature readings during this period were as high as 43.7°C, and RH of 4% and evaporation of 10.8 mm/day were recorded. However, the added sprinkler irrigation combined with larger amounts of trickle irrigation prevented reduction of yield. Thus, yields in the spring of 1988 were high, even in comparison to the highest average spring yield attained in 1986.

It can therefore be concluded that in certain snap bean varieties summer yields can be improved and even reach yields typical to the

spring by optimal irrigation. Thus, at least in the coastal plain of Israel, high summer temperatures per-se may not be the main yield limiting factor, if water constraints in the field are prevented.

Inter-varietal differences

Varieties can be evaluated for their yield response under summer conditions in two ways:

- a) by comparing their absolute yields in the summer trials,
- b) by comparing the relative reduction in yield for each variety, e.g. spring vs. summer yield.

However, the fact that the highest spring and lowest summer yields were attained in 1986 (Table 17) renders it difficult to assess an inter-varietal comparison in which some of the varieties were tested only during 1987 and 1988. Pooling together all varieties in one statistical analysis will result in spurious larger spring vs. summer differences in yield for those varieties grown during 1986. Thus, to avoid a biased comparison between varieties, two separate statistical analysis are presented: one for the 12 varieties grown in 1986-88, and another for the 18 varieties grown in 1987-88 (Tables 18-22; Figs. 11-17).

Table 18: Effects of season on yield of snap bean under field conditions.

VARIETY	YIELD (gm/m ²)	M.R.T [^]	% OF MEAN	YIELD (gm/m ²)	M.R.T [^]	% OF MEAN	EFFECT (%)	SIGNIF [^]
SPRING				SUMMER				
				1986 - 1988				
BBL47	1687 ± 62	AB	102	1401 ± 180	A	115	-16.9	n.s.
BLUE	1787 ± 106	AB	108	1377 ± 135	A	113	-22.9	*
BRON	1819 ± 118	AB	110	1378 ± 133	A	114	-24.3	*
E.G	1720 ± 106	AB	104	1190 ± 151	AB	98	-30.8	**
LAB	1484 ± 117	BC	90	1143 ± 124	AB	94	-23.0	*
LEG	1711 ± 152	AB	104	1120 ± 99	AB	92	-34.5	**
MUS	1775 ± 108	AB	108	1287 ± 110	A	106	-27.5	**
PI	1226 ± 74	C	74	853 ± 30	B	70	-30.4	***
STR	1568 ± 110	BC	95	1439 ± 92	A	119	-8.2	n.s.
TEND	1500 ± 97	BC	91	1197 ± 143	AB	99	-20.2	*
TORY	1460 ± 153	BC	88	1039 ± 102	AB	86	-28.8	*
WAT	2038 ± 93	A	124	1138 ± 104	AB	94	-44.2	***
MEAN:	1648			1213				
				1987 - 1988				
2102	1352 ± 197	CD	89	1324 ± 114	ABCD	99	-2.0	n.s.
BBL47	1616 ± 82	BC	106	1545 ± 193	AB	115	-4.4	n.s.
BLUE	1721 ± 143	BC	113	1529 ± 163	AB	114	-11.2	n.s.
BRON	1575 ± 84	BC	103	1555 ± 134	AB	116	-1.3	n.s.
E.G	1506 ± 55	C	99	1253 ± 156	ABCD	94	-16.8	n.s.
EAGLE	1446 ± 76	CD	95	1658 ± 184	A	124	14.7	n.s.
L.S	1524 ± 115	BC	100	1637 ± 142	A	122	7.4	n.s.
LAB	1302 ± 112	CD	85	1205 ± 167	ABCD	90	-7.5	n.s.
LEG	1558 ± 189	BC	102	1150 ± 123	BCD	86	-26.2	n.s.
MUS	1676 ± 132	BC	110	1338 ± 148	ABC	100	-20.1	n.s.
PI	1049 ± 52	D	69	863 ± 57	D	64	-17.8	*
SENT	2170 ± 178	A	142	1490 ± 182	AB	111	-31.3	*
SHAN	1431 ± 62	CD	99	1210 ± 71	ABCD	90	-15.4	*
STR	1484 ± 153	CD	97	1537 ± 116	AB	115	3.6	n.s.
TEND	1345 ± 97	CD	88	1477 ± 110	AB	110	9.8	n.s.
TORY	1430 ± 237	CD	94	1100 ± 135	BCD	82	-23.1	n.s.
WAT	1954 ± 125	AB	128	1331 ± 95	ABCD	99	-31.9	**
WAX	1316 ± 138	CD	86	899 ± 80	CD	66	-31.7	*
MEAN:	1525			1339				

[^] Duncan's Multiple Range Test at $p = 0.05$.

[^] Significance of season effect: n.s - not significant; * - $0.05 \leq p < 0.01$;
** - $0.01 \leq p < 0.001$; *** - $p \leq 0.001$

Table 19: Effects of season on pod production / m² under field conditions.

VARIETY	No. OF PODS	M.R.T ^a	% OF MEAN	NO. OF PODS	M.R.T ^a	% OF MEAN	EFFECT (%)	SIGNIF ^b
<u>SPRING</u>				<u>SUMMER</u>				
<u>1986 - 1988</u>								
BBL47	292 ± 17	BCD	97	267 ± 25	C	97	-8.5	n.s.
BLUE	272 ± 12	CDE	90	274 ± 20	C	100	0.7	n.s.
BRON	387 ± 20	A	128	344 ± 23	AB	125	-11.1	n.s.
E.G	298 ± 16	BCD	99	257 ± 22	C	93	-13.6	n.s.
LAB	285 ± 22	CD	95	297 ± 21	BC	108	4.2	n.s.
LEG	308 ± 19	BCD	102	262 ± 19	C	95	-14.8	n.s.
MUS	323 ± 22	BC	107	277 ± 19	C	101	-14.4	n.s.
PI	221 ± 19	E	73	189 ± 6	D	69	-14.7	n.s.
STR	353 ± 19	AB	117	386 ± 18	A	140	9.3	n.s.
TEND	292 ± 22	BCD	97	269 ± 22	C	98	-7.9	n.s.
TORY	258 ± 22	DE	86	238 ± 21	CD	86	-7.8	n.s.
WAT	323 ± 17	BC	107	238 ± 15	CD	86	-26.3	**
MEAN:	301			275				
<u>1987 - 1988</u>								
2102	251 ± 33	DEF	90	272 ± 20	E	90	8.4	n.s.
BBL47	258 ± 8	DEF	92	292 ± 23	DE	96	13.2	n.s.
BLUE	260 ± 93	DEF	93	307 ± 19	DE	101	18.1	n.s.
BRON	349 ± 15	B	125	375 ± 23	ABC	124	7.4	n.s.
E.G	268 ± 13	CDEF	96	271 ± 19	E	89	1.1	n.s.
EAGLE	262 ± 14	DEF	94	352 ± 24	BCD	116	34.4	**
L.S	224 ± 14	FG	80	271 ± 20	E	89	21.0	n.s.
LAB	254 ± 25	DEF	91	307 ± 28	DE	101	20.9	n.s.
LEG	280 ± 22	CDEF	100	271 ± 23	E	89	-3.2	n.s.
MUS	288 ± 18	BCDEF	103	282 ± 23	E	93	-1.7	n.s.
PI	180 ± 6	G	64	189 ± 9	F	62	5.0	n.s.
SENT	438 ± 32	A	156	434 ± 29	A	143	-0.9	n.s.
SHAN	303 ± 10	BCDE	108	311 ± 10	CDE	103	2.6	n.s.
STR	330 ± 25	BC	118	407 ± 22	AB	134	23.3	*
TEND	245 ± 15	EF	87	313 ± 13	CDE	103	27.8	**
TORY	237 ± 29	EF	85	246 ± 29	EF	81	3.8	n.s.
WAT	294 ± 18	BCDE	105	266 ± 13	E	88	-9.5	n.s.
WAX	314 ± 24	BCD	112	297 ± 19	DE	98	-5.4	n.s.
MEAN:	280			303				

^a Duncan's Multiple Range Test at p = 0.05.^b Significance of season effect: n.s - not significant; * - 0.05 ≤ p < 0.01;

** - 0.01 ≤ p < 0.001;

Table 20: Effects of season on fresh weight of pods in snap bean varieties under field conditions.

VARIETY	WEIGHT OF POD (gm)	M.R.T [^]	% OF MEAN	WEIGHT OF POD (gm)	M.R.T [^]	% OF MEAN	EFFECT (%)	SIGNIF [^]
<u>SPRING</u>				<u>SUMMER</u>				
<u>1986 - 1988</u>								
BBL47	6.01 ± 0.13	BC	108	5.10 ± 0.26	A	116	-15.0	**
BLUE	6.48 ± 0.21	A	116	5.02 ± 0.22	AB	114	-22.5	***
BRON	4.79 ± 0.15	E	86	3.98 ± 0.15	DEF	90	-16.9	**
E.G	5.78 ± 0.13	CD	104	4.58 ± 0.26	ABCD	104	-20.8	***
LAB	5.44 ± 0.14	D	98	3.68 ± 0.17	F	83	-32.4	***
LEG	5.37 ± 0.19	D	97	4.30 ± 0.20	CDEF	97	-19.9	***
MUS	5.68 ± 0.08	CD	102	4.68 ± 0.18	ABC	106	-17.6	***
PI	5.35 ± 0.11	D	96	4.33 ± 0.11	CDE	98	-19.1	***
STR	4.50 ± 0.13	E	98	3.73 ± 0.09	EF	85	-17.1	***
TEND	5.36 ± 0.13	D	96	4.39 ± 0.34	BCD	100	-18.1	**
TORY	5.56 ± 0.22	CD	100	4.35 ± 0.10	CDE	99	-21.8	***
WAT	6.39 ± 0.10	AB	115	4.74 ± 0.15	ABC	107	-25.8	***
MEAN:	5.56			4.41				
<u>1987 - 1988</u>								
2102	5.31 ± 0.23	DE	98	4.86 ± 0.16	BCD	109	-8.5	n.s.
BBL47	6.13 ± 0.14	BC	113	5.21 ± 0.30	B	117	-15.0	*
BLUE	6.50 ± 0.32	AB	119	5.07 ± 0.34	BC	114	-22.0	**
BRON	4.48 ± 0.09	GH	82	4.19 ± 0.15	DEF	94	-6.4	n.s.
E.G	5.67 ± 0.14	CD	104	4.57 ± 0.29	BCDE	102	-19.5	**
EAGLE	5.41 ± 0.13	DE	99	4.67 ± 0.29	BCDE	105	-13.7	*
L.S	6.75 ± 0.22	A	125	6.09 ± 0.15	A	136	-9.8	*
LAB	5.20 ± 0.14	DEF	96	3.72 ± 0.23	FG	83	-28.4	***
LEG	5.35 ± 0.24	DE	98	4.31 ± 0.25	CDEF	97	-19.4	**
MUS	5.69 ± 0.11	CD	104	4.84 ± 0.22	BCD	108	-14.9	**
PI	5.53 ± 0.11	DE	102	4.25 ± 0.18	DEF	95	-23.2	***
SFNT	4.94 ± 0.11	EFG	91	3.40 ± 0.21	GH	76	-31.2	***
SHAN	4.72 ± 0.14	FG	87	3.95 ± 0.19	EFG	88	-16.3	**
STR	4.42 ± 0.18	GH	81	3.87 ± 0.12	FG	87	-13.9	*
TEND	5.39 ± 0.19	DE	99	4.87 ± 0.41	BCD	109	-9.7	n.s.
TORY	5.73 ± 0.33	CD	105	4.48 ± 0.09	BCDEF	100	-21.8	**
WAT	6.59 ± 0.06	AB	121	5.03 ± 0.12	BC	113	-23.8	***
WAX	4.10 ± 0.12	H	75	3.02 ± 0.13	H	68	-26.4	***
MEAN:	5.44			4.46				

[^] Duncan's Multiple Range Test at $p = 0.05$.

[^] Significance of season effect: n.s - not significant; * - $0.05 \leq p < 0.01$;
** - $0.01 \leq p < 0.001$; *** - $p \leq 0.001$;

Table 21: Effects of season on seed set / pod in snap bean under field conditions during 1987 - 1988.

VARIETY	S P R I N G				S U M M E R				SIGNIF ^b
	SEEDS /POD	M.R.T ^a	% OF MEAN		SEEDS /POD	M.R.T ^a	% OF MEAN	EFFECT (%)	
2102	3.70 ± 0.24	F	81		4.15 ± 0.25	BC	88	12.2	n.s.
BBL47	4.50 ± 0.19	CE	98		4.70 ± 0.27	AC	100	4.4	n.s.
BLUE	4.51 ± 0.16	CE	98		4.56 ± 0.37	AC	97	1.1	n.s.
BRON	5.37 ± 0.26	AB	117		4.90 ± 0.47	AC	104	-8.8	n.s.
E.G	4.14 ± 0.17	DF	90		4.60 ± 0.3A	AC	98	11.1	n.s.
EAGLE	4.48 ± 0.24	CE	98		4.46 ± 0.48	AC	95	-0.4	n.s.
L.S	4.60 ± 0.26	CE	100		5.27 ± 0.24	A	112	14.6	n.s.
LAB	4.88 ± 0.24	AD	106		4.02 ± 0.40	C	85	-17.7	*
LEG	4.83 ± 0.15	AD	105		4.89 ± 0.23	AC	104	1.2	n.s.
MUS	4.66 ± 0.32	BE	102		5.13 ± 0.12	BC	109	10.1	n.s.
PI	3.92 ± 0.29	EF	85		4.06 ± 0.27	AC	86	3.6	n.s.
SENT	5.44 ± 0.09	A	119		4.67 ± 0.33	AC	99	14.2	*
SHAN	4.56 ± 0.25	CE	99		4.91 ± 0.26	AC	104	7.7	n.s.
STR	4.78 ± 0.32	AD	104		4.75 ± 0.26	AC	101	-0.7	n.s.
TEND	4.27 ± 0.23	DF	93		4.89 ± 0.39	AC	104	14.5	n.s.
TORY	4.32 ± 0.24	CF	94		4.96 ± 0.15	AC	105	14.8	*
WAT	4.69 ± 0.16	AE	102		5.25 ± 0.27	A	112	11.9	n.s.
WAX	5.00 ± 0.20	AC	109		4.63 ± 0.24	AC	98	-7.4	n.s.
MEAN:	4.59				4.71				

^a Duncan's Multiple Range Test at $p = 0.05$.

^b Significance of season effect: n.s - not significant; * - $0.05 \geq p > 0.01$; ** - $0.01 \geq p > 0.001$; *** - $p \leq 0.001$

Table 22: Effects of season on pod curvature of snap bean under field conditions. Pod curvature range: 1 - straight to 4 - very curved.

VARIETY	YIELD (g/m ²)	M.R.T [^]	% OF MEAN	YIELD (g/m ²)	M.R.T [^]	% OF MEAN	EFFECT (%)	SIGNIF [^]
<u>SPRING</u>				<u>SUMMER</u>				
<u>1986 - 1988</u>								
BBL47	2.53 ± 0.04	AB	106	2.53 ± 0.06	AC	103	0.2	
BLUE	2.39 ± 0.06	BC	100	2.77 ± 0.06	B	113	15.9	***
BRON	2.32 ± 0.11	BC	98	2.37 ± 0.09	BD	96	2.0	
E.G	2.18 ± 0.08	C	92	2.33 ± 0.06	CD	95	6.9	
LAB	1.93 ± 0.07	D	81	2.27 ± 0.07	CD	92	18.1	**
LEG	2.67 ± 0.05	A	112	2.62 ± 0.08	AB	107	-1.7	
MUS	2.36 ± 0.03	BC	99	2.54 ± 0.08	AC	103	7.5	
PI	2.22 ± 0.08	C	93	2.15 ± 0.15	D	87	-3.4	
STR	1.87 ± 0.06	D	79	2.30 ± 0.09	CD	94	23.4	***
TEND	2.87 ± 0.07	C	121	2.36 ± 0.06	BD	96	3.1	
TORY	2.67 ± 0.09	A	112	2.46 ± 0.06	BC	100	-7.8	
WAT	2.60 ± 0.06	A	109	2.80 ± 0.13	A	114	7.8	
MEAN:	2.38			2.46				
<u>1987 - 1988</u>								
2102	2.71 ± 0.05	AB	115	2.62 ± 0.07	AD	110	-3.3	n.s.
BBL47	2.47 ± 0.04	BD	105	2.51 ± 0.06	BG	105	1.6	n.s.
BLUE	2.38 ± 0.08	DF	101	2.67 ± 0.04	AB	112	12.2	**
BRON	2.33 ± 0.17	DF	99	2.28 ± 0.11	GI	95	2.1	n.s.
E.G	2.28 ± 0.07	DF	97	2.31 ± 0.06	FI	97	1.3	n.s.
EAGLE	2.37 ± 0.07	DF	100	2.55 ± 0.05	BE	107	7.6	n.s.
L.S	2.77 ± 0.05	A	117	2.82 ± 0.09	A	118	1.8	n.s.
LAB	1.78 ± 0.06	H	75	2.22 ± 0.08	HJ	93	24.7	***
LEG	2.65 ± 0.06	AC	112	2.52 ± 0.06	BG	105	-4.9	n.s.
MUS	2.40 ± 0.04	CE	102	2.38 ± 0.06	DI	100	-0.8	n.s.
PI	2.16 ± 0.08	EG	92	1.88 ± 0.21	K	79	-13.0	*
SENT	1.75 ± 0.05	H	74	2.23 ± 0.05	HJ	93	27.4	***
SHAN	2.50 ± 0.06	BD	106	2.57 ± 0.08	BE	108	2.8	n.s.
STR	1.94 ± 0.07	GH	82	2.15 ± 0.09	J	90	10.8	n.s.
TEND	2.30 ± 0.09	DF	98	2.33 ± 0.08	EI	98	1.3	n.s.
TORY	2.84 ± 0.06	A	120	2.35 ± 0.04	EI	98	-18.3	***
WAT	2.67 ± 0.06	AB	113	2.52 ± 0.07	BG	106	5.6	n.s.
WAX	2.26 ± 0.11	DF	96	2.16 ± 0.04	IJ	90	4.4	n.s.
MEAN:	2.36			2.39				

[^] Duncan's Multiple Range Test at p = 0.05.

[^] Significance of season effect: n.s - not significant; * - 0.05 ≤ p < 0.01;
** - 0.01 ≤ p < 0.001; *** - p ≤ 0.001

Yields for 1986 - 1988 Fresh weight gm / m square

No. of pods / m square

Mean fresh weight of pod

Figure 11 :

Inter-variatal differences in yield (FW/m²), pod production (pods/m²) and pod size (FW/pod) in spring and summer field trials during 1986-88.

Yields for 1987 - 1988 Fresh weight gm / m square

No. of pods / m square

Mean fresh weight of pod

Figure 12 :

Inter-variatal differences in yield (FW/m²), pod production (pods/m²) and pod size (FW/pod) in spring and summer field trials during 1987-88.

% effect of summer (1986-88)
Fresh weight: gm / m square

No. of pods / m square

Mean pod fresh weight

Figure 13 :

Intervarietal differences in relative effects (%) of summer conditions on yield (FW/m²), pod production (pods/m²) and pod size (FW/pod) compared to the spring in 1986-88 field trials.

% effect of summer (1987-88)
Fresh weight gm / m square

No. of pods / m square

Mean pod fresh weight

Figure 14 :

Intervarietal differences in relative effects (%) of summer conditions on yield (FW/m²), pod production (pods/m²) and pod size (FW/pod) compared to the spring in 1987-88 field trials.

Mean number of seeds per pod 1987 -1988

% effect of summer

Figure 15 :

Intervarietal differences in seed set/pod in spring and summer field trials during 1987-88, and in relative effect of summer conditions.

Pod curvature 1986 - 1988

% effect of summer

Figure 16 :

Intervarietal differences in pod-curvature in spring and summer field trials during 1986-88, and in relative effect (%) of summer conditions.

Pod curvature 1987 - 1988

% effect of summer

Figure 17 :

Intervarietal differences in pod-curvature in spring and summer field trials during 1987-88, and in relative effect (%) of summer conditions.

A highly significant variety effect ($P=0.001$) on yield (FW/m^2) was observed within the spring and summer seasons, respectively. WAT and SENTRY had the highest yields in the spring, while STRIKE, EAGLE and LS were the better performing varieties in the summer. The lowest yielding varieties in the spring were PI, LAB and WAX, while in the summer they were PI, WAX and TORY. The poor performance of PI was due to the smaller number of pods produced by each plant compared to other varieties (see Figs. 11 & 12, Table 19). In the case of WAX, the lower yields were caused by the smaller size of the pods (Fig. 12, Table 20), and also by the small plant size characteristic to this variety. WAX was the earliest variety producing pods ready for harvest.

However, closer examination of mean yields in spring and summer reveals that, within each season, most varieties fell within the $\pm 10\%$ range of the overall seasonal yield (Table 18, Figs. 11 & 12).

On the other hand, in many varieties yields were reduced by summer conditions (Figs. 13 & 14). This reduction was significant ($P=0.05$) in 9 out of 12 varieties grown in 1986-88, and in 5 out of 18 varieties grown in 1987-88. Furthermore, varieties greatly differed in their response to the summer. For example, in WAT, SENTRY, LEGACY, WAX and TORY yields were reduced by 25-30%, while in STRIKE, TEND, LS, 2102, BBL-47 and BRONCO the reduction was much smaller ($<10\%$; NS), or yields were not reduced at all.

An analysis of the relationship between the level of the yield in the spring and its relative decrease in the summer shows that the highest spring yielding varieties (WAT, SENTRY) were those showing the greatest reduction in the summer.

However, the correlation between spring yield and the summer decrease in yield was not significant ($r=0.088$) for the varieties tested during 3 years (1986-88). The correlation was higher and significant ($r=0.663$, $P=0.01$) if only the varieties grown in 1987-88 are included in the regression analysis. But, if the high spring

yielding varieties WAT and SENTRY are excluded from the analysis, the regression is again not significant.

The low, or the lack of correlation found between spring yield and summer decrease may result from the fact that, in most of the varieties examined, the spring yield falls within a narrow range around the varieties' average (ca. 1450 gr $\pm 10\%$). One possible explanation for this narrow range (of spring yields) is that most of the snap-bean varieties used in our field trials have been bred under more or less similar climatic conditions in the USA, from a common genetic pool. On the other hand, the low correlation between spring yield and the relative decrease in yield in the summer may indicate that even within the narrow spectra of available varieties, large intervarietal differences in tolerance to summer conditions can be found and used in further breeding programs.

Pod production and pod weight

Effects of variety and growth conditions on yield are the result of their combined action on yield components, e.g. number of pods per m² (pods/m²) and fresh weight per pod (FW/pod). Pod weight is, in turn, affected by the number of ovules that succeeded in setting seeds.

Pod production was unaffected or even significantly ($P=0.05$) increased in some varieties (EAGLE 34%; TEND 28%; STRIKE 23%) in the summer (Table 18, Figs. 13 & 14). In the 1986-88 analysis, WAT was the only variety in which pod production was significantly reduced. This was due to the great differences in production between the spring and summer in 1986. SENTRY, STRIKE and BRONCO were the varieties producing the largest number of pods/m² in both the spring and summer trials. PI, LS and TORY were the varieties with the lowest pod production (Table 19, Figs. 11 & 12).

Average pod fresh weight was significantly ($P=0.05$) reduced by the summer conditions in all varieties examined (Figs. 13 & 14, Table 20).

Reduction in pod weight occurred even when pod production was increased in the summer.

These results clearly show that in each variety the lower yields in the summer were mainly due to a reduction in pod weight.

Pod production and pod weight were differently affected by the summer conditions. For example, in the 1987-88 trials pod production was somewhat increased in several varieties, while pod weight was concomitantly reduced (Figs. 13 & 14). Thus, in some varieties the opposite effects of summer conditions on pod production and pod weight compensated and reduced the overall effect on total yield.

The relative effect of summer on the number of seeds produced per pod was small, inconsistent and not statistically significant for most varieties (except in: LAB -18%; SENTRY -16%; and TORY +15%, $P=0.05$, Fig. 15, Table 21). Thus, the reduction in pod weight in the summer cannot be attributed in most varieties to a lower seed set per pod.

Pod curvature is one of the parameters determining pod quality. Pod curvature increases the larger the number of ovules that fail to develop into seeds. In most varieties pod curvature was unaffected by the summer conditions (Figs. 16 & 17, Table 22). However, in BLUE, LAB, STRIKE and SENTRY pod curvature was increased by ca 15-25%, while in TORY it was reduced by 18%. It is worthwhile to note that seed number was reduced in LAB and SENTRY and increased in TORY by the summer conditions (Figs. 15 & 17).

Compared with the HT effects in the phytotron, the lack of effect of the summer conditions on pod number, seed set per pod and on pod curvature, are a further indication that the HT during the summer is only one of the factors limiting production during the summer in the coastal plain of Israel.

Yield stability

One of the main goals of our research was to screen for bean varieties with high yields in the summer and/or smaller reduction in yield during the summer (compared to the spring).

However, the great fluctuations in yields observed in the same season between years indicated that screening for yield stability may be a better strategy than just screening for higher yields in the summer. This is particularly true in Israel since hot dry weather may occur during the spring, the season considered as optimal by bean growers.

The statistical analysis used to compare the yield performance and yield stability of the different varieties was the one developed by Finley and Wilkinson (Aust. J. Agric. Res. 1963, 14: 742-754). For each variety a linear regression of individual variety yield on the mean yield of all varieties for each trial (each block, season and each year) was computed. The mean yield of all varieties in each trial provides a quantitative measure of the environmental complex under which the plants grew. In this way the average yield of a relatively large number of bean varieties is used to "describe" the environment during each trial.

The Finley and Wilkinson analysis of stability is based on two main parameters:

- a) variety average yield over all environments
- b) regression coefficients (b)

Variety average yield provides a comparative measure of performance of the individual varieties.

Regression coefficients (b) of the order of one ($b=1$) indicate average stability. $b>1.0$ will characterize varieties with increasing sensitivity to environmental change (low stability), while $b<1.0$

indicates greater resistance to environmental change (high stability).

As an example, in Fig. 18 we present data for 4 contrasting varieties. TORY has a medium stability ($b=1.013$) but a significantly ($P=0.05$) higher yield (1608 gr/m^2). On the other hand, WATERFALL has one of the highest average yields (1588 gr/m^2), but has a low stability ($b=1.366$). Thus, WATERFALL is a high yielding variety under optimal conditions, but suffers more than others under sub-optimal conditions. Conversely, STRIKE has a high stability ($b=0.699$) and more or less maintains an average yield over all the environmental conditions tested.

Tested snap-bean varieties greatly differed in their stability (range b : $0.596-1.602$) and overall (spring and summer) average yield (range yield: $1094-1807 \text{ g/m}^2$) (Table 23, Fig. 19). According to these two criteria the varieties can be ordered in several groups (within each group varieties are ordered by yield) (Table 24).

Varieties with higher yields tend to be less stable, as indicated by the relatively small but significant regression between b and average variety yield: $b=0.00077*(\text{variety yield}) - 0.106$ ($r=0.581$; $P=0.02$). Thus, no varieties with: high yield - high stability or low yield - low stability characteristics were found in the tested sample of snap-bean (18 varieties).

Figure 18: Yield stability analysis for contrasting varieties of snap bean. Individual variety yields are plotted against average yield for all varieties. Data are for different seasons (spring and summer) and years (1986-88).

Table 23 : Yield stability (b) and average yield of snap-bean varieties grown in the spring and summer seasons.

Variety	yield		field	% reduction in yield				HAP
	stability		average	green-				
	b	r ¹	yield (gr/m ²)	field ²	phytotron ³	house ⁴		
*SHANNON	0.596	0.803	1321	-15	—	-18	—	
*EAGLE	0.604	0.441	1559	15	-77	—	—	
PI-271998	0.611	0.930	1040	-30	-61	-16	98	
STRIKE	0.669	0.728	1504	-8	-91	—	95	
*LS	0.904	0.733	1581	+7	-12	-13	—	
TENDERETTE	0.906	0.765	1349	-20	-48	-12	82	
LABRADOR	0.931	0.777	1329	-23	-57	—	98	
WAX	0.947	0.780	1094	-32	-80	—	—	
MUSSER-175	0.960	0.804	1531	-28	-2	-29	60	
BRONCO	1.003	0.770	1608	-24	-74	—	100	
TORY	1.013	0.789	1249	-29	-50	-18	100	
BBL-47	1.055	0.867	1556	-20	-81	-28	60	
*2102	1.057	0.697	1352	-2	-80	—	—	
EG	1.170	0.834	1493	-31	-50	-47	85	
LEGACY	1.282	0.856	1.442	-35	-58	-65	35	
WATERFALL	1.366	0.897	1588	-44	-31	-65	70	
*SENTRY	1.602	0.800	1807	-31	-84	—	—	

* Varieties tested 2 years only (1987-88)

1) Regression coefficient. All r's P<0.01-0.001, except EAGLE.

2) Reduction in summer compared to spring.

3) Reduction after 5 days of 32/27°C at anthesis vs. continuous 22/17°C.

4) Reduction after 5 days exposure to 25-28°C at night during anthesis.

Table 24 : Yield performance and yield stability of snap-bean varieties grown in the field (1986-88). Numbers in () indicate yield reduction in the summer compared to the spring trials. * indicates varieties tested in 1987-88 only. In each group varieties are ordered by decreasing yield.

<u>Yield (all varieties mean = 1440 gr/m²)</u>			
Yield	<u>High</u>	<u>Medium</u>	<u>Low</u>
Stability	(>1584 gr/m ²)	(1296-1584 gr/m ²)	(<1296 gr/m ²)
High (b<0.8)	—	STRIKE (-8)	PI-271998 (-30) *SHANNON (-15)
Medium (0.8<b<1.2)	BRONCO (-24)	*LAKE SUPERIOR (+7) BBL-47 (BLUE)(-20) MUSSEY (-28) EARLY-GELATINE (-31) TENDERETTE (-20) *2102 (-2) LABRADOR (-23)	TORY (-29) WAX (-32)
Low (b>1.2)	*SENTRY (-31) WATERFALL (-44)	LEGACY (-35)	—

Figure 19: Relationship between yield stability (b) and average yield for different varieties of snap bean - all varieties average: 1440 g/m².

STRIKE was the best variety in the sense that it has a relatively high yield stability and medium yield. On the other extreme, SENTRY and WATERFALL were the highest yielding varieties with the lowest stability. These varieties reached the highest yields in the spring, but were those with the highest yield reduction in the summer. LAKE SUPERIOR showed relatively high average yield, a quite good stability (0.904) and no summer decrease in yield. However, this variety was tested in 1987-88 only, and warrants further examination.

In most varieties a fairly good agreement was found between yield stability and the relative reduction in yield in the summer (Fig. 20). The main exception was PI-271998, a variety showing high stability ($b=0.611$) but a large summer decrease in yield (-30%).

The fact that in most varieties both classification procedures gave similar results indicate their feasibility for screening programs for summer tolerance.

Figure 20: Relationship between yield stability (b) and relative reduction (%) in yield (gr FW/m²) in the summer for different snap-bean varieties ($r=0.663$; $P=0.001$).

Dry-bean accessions

In 1987-88 16 dry-bean accessions were tested in the field in spring and summer trials. Two collections of Tepary bean (Phaseolus acutifolius) were included in the 1987-88 trials: TEP 1 (brown seeds) and TEP 3 (spotted seeds), from Sonora Desert, Mexico. In 1988 an additional 11 accessions, received from St. Paul, were included in the spring and summer trials. Results and statistical analysis for the 1987-88 and 1988 trials are presented separately.

Yield (seed weight/m²) was significantly ($P=0.05$) reduced (range 21-31%) in the summer in 8 of the 16 accessions tested during 1987-88 (Table 25, Fig. 21). However, accessions G-3702, G-4495 and PI-271998 exhibited a greater tolerance to the summer conditions and their yields were practically unaffected ($< \pm 10\%$). A remarkable result was that yields of G-893, TEP 1 and TEP 3 were greatly increased (45-66%) in the summer. The higher summer yields of Tepary bean in the summer are probably related to its origin from deserts with summer rains. On the other hand, although G-893 showed the highest relative yield increase in the summer, its yield potential was the lowest of all the tested accessions. Thus, the most promising dry-bean accessions for seed production were G-3702 and G-3670. With ample irrigation they had the highest yield in both the spring and summer trials, and the summer reduction in yield was only 5% for G-3702 (Table 25). The highest average spring yield was recorded for G-3696, but its yield was strongly reduced (31%) in the summer. TEP 1 showed an average yield in the spring and an outstanding production in the summer.

Table 25: Effect of season on seed yield (g/m²) of dry-bean under field conditions. Accessions tested in 1987-88.

Accessions	SPRING			SUMMER			Effect (%)	Signif.
	yield (g/m ²)	% of MRT	Mean	yield (g/m ²)	% of MRT	Mean		
BAT-336	330 ±40	AC	112	244 ±36	C	102	-26.1	*
BAT-1289	267 ±20	BC	91	203 ±10	CD	85	-23.9	*
G-0893	79 ±6	E	27	131 ±18	E	55	65.6	*
G-1050	319 ±23	AC	109	224 ±13	C	94	-29.8	**
G-3645	304 ±17	AC	103	266 ±26	BC	111	-12.7	
G-3670	357 ±54	AB	121	291 ±26	BC	122	-18.6	
G-3689	295 ±22	AC	100	250 ±38	BC	105	-15.3	
G-3696	373 ±26	A	127	256 ±20	BC	107	-31.3	**
G-3702	354 ±44	AB	121	337 ±49	AB	141	-4.9	
G-4495	247 ±23	CD	84	263 ±42	BC	110	6.4	
V-8025	300 ±25	AC	102	208 ±22	CD	87	-30.7	*
5-161-E	276 ±14	BC	94	217 ±8	CD	91	-21.5	**
ALUBIO	326 ±23	AC	111	227 ±38	C	95	-30.4	*
PI-271998	238 ±12	CD	81	212 ±9	CD	88	-10.4	
WA-2289	320 ±31	AC	109	230 ±29	C	96	-28.3	*
WAF-9	326 ±27	AC	111	263 ±21	BC	110	-19.2	
MEAN	294			239				
TEP 1	281 ±20	BC	96	409 ±24	A	171	45.6	***
TEP 3	178 ±13	D	61	296 ±28	BC	124	65.9	**

MRT - Duncan's Multiple Range Test at P=0.05.

Significance - significance of season effect: * - 0.05 ≥ P > 0.01,

** - 0.01 ≥ P > 0.001, *** - P ≤ 0.001

Seed yield / m square 1987 -1988

% effect of summer

Figure 21: Seed yield (g/m^2) in different accession of dry bean in spring and summer trials during 1987 - 1988.

Of the additional accessions tested only during 1988, G-2525 and GUANACO were the most promising ones. Their spring yields were among the highest ones (even when compared to accessions tested in 1987-88), and their yields were unaffected or even slightly increased by the conditions in the summer (Table 30, Fig. 25).

In dry-bean, seed yield is the compound result of effects on pod production (pods/m²), seed set per pod (seeds/pod) and seed weight. Data for the different yield parameters in spring and summer of 1987-88 are presented in Tables 26 to 28, and Figs. 22 to 24. A comparative summary of the relative effects of the summer conditions on the different yield components is presented in Table 29, where accessions are ordered by their yield potential in the spring.

The data clearly shows that yield components were differently affected by the summer conditions, and not, necessarily, in the same direction. In BAT-336, G-3645 and G-3696 reduction in seed yield in the summer was mostly due to a decline in pods/m². In WAF-9, PI-271998, and G-1050, on the other hand, the lower summer yield was caused mainly by a reduction in seed size, while in WA-2289 it was due to a lower seed set/pod. Summer effects on the other yield components of these accessions were not significant. In other accessions (e.g. ALUBIO, V-8025, G-3670 and BAT-1289) at least two yield components contributed to the summer decrease in yield. 5-161-E is a special case in which a significant compensatory effect was observed between yield components, e.g. - the increase in pods/m² in the summer (24%), partially compensated for the decrease in seeds/pod (-17%) and seed size (-24%). This compensation resulted in a relatively smaller reduction of the yield in the summer (-22%). No other cases of significant compensatory changes were observed in the 16 dry-bean accessions tested in 1987-88. In G-3702 and G-4495, accessions in which summer yields were similar to those in the spring, the three yield components were unaffected. The increase in yield observed in the summer in G-893 and TEP 3 was mainly due to a larger production of pods. The increase in TEP 1 was compounded by an equal increase in all three yield components.

Table 26: Effect of season on pod production (pods/m²) of dry-bean under field conditions. Accessions tested in 1987-88.

Accessions	SPRING			SUMMER			Effect (%)	Signif.
	pods/m ²	% of MRT	Mean	pods/m ²	% of MRT	Mean		
BAT-336	327 ±17	CF	115	265 ±22	CF	101	-18.8	*
BAT-1289	275 ±18	GI	97	247 ±9	DF	94	-10.1	
G-0893	144 ±G	K	51	214 ±24	FG	81	48.2	*
G-1050	244 ±29	HJ	86	219 ±19	EG	83	-10.2	
G-3645	360 ±13	CF	126	289 ±15	CE	110	-19.9	*
G-3670	378 ±22	BD	133	332 ±17	C	126	-12.2	
G-3689	367 ±22	BE	129	332 ±20	C	126	-9.5	
G-3696	424 ±20	B	149	296 ±17	CD	112	-30.2	***
G-3720	322 ±23	DG	113	279 ±27	CF	106	-13.4	
G-4495	236 ±17	IJ	83	266 ±26	EF	101	12.3	
V-8025	302 ±18	FH	106	259 ±12	DG	98	-14.2	*
5-161-E	231 ±10	IJ	81	287 ±21	CE	109	24.2	*
ALUBIO	200 ±7	JK	70	214 ±18	FG	81	7.1	
PI-271998	188 ±4	JK	66	194 ±7	G	74	3.4	
WA-2289	316 ±23	EG	111	270 ±22	CF	102	-14.3	
WAF-9	244 ±13	HJ	86	255 ±11	DG	97	4.6	
MEAN	285			264				
TEP 1	549 ±37	A		660 ±66	A	250	20.3	
TEP 3	386 ±13	BC		474 ±38	B	180	22.8	

MRT - Duncan's Multiple Range Test at P=0.05.

Significance - significance of season effect: * - 0.05≥P>0.01,

** - 0.01≥P>0.001, *** - P≤0.001

Table 27: Effect of season on seed set/pod in dry-bean under field conditions. Accessions tested in 1987-88.

Acces.	SPRING				SUMMER				Effect (%)	Signif.
	Seeds/pod	% of		MRT Mean	Seeds/pod	% of		MRT Mean		
BAT-336	4.95 ±0.41	AB	125		4.39 ±0.47	AC	118		-11.3	
BAT-1289	4.36 ±0.29	AD	110		4.01 ±0.22	BD	108		-8.0	
G-0893	2.46 ±0.17	G	62		2.68 ±0.19	FG	72		8.9	
G-1050	2.95 ±0.15	GF	74		2.71 ±0.10	FG	73		8.4	
G-3645	4.93 ±0.15	AB	124		4.90 ±0.27	AB	132		-0.6	
G-3670	4.17 ±0.56	AD	105		4.19 ±0.26	AD	113		0.5	
G-3689	4.06 ±0.32	BE	102		3.81 ±0.37	CD	103		-6.2	
G-3696	4.92 ±0.28	AB	124		4.81 ±0.34	AC	130		-2.2	
G-3720	4.40 ±0.33	AD	111		4.74 ±0.42	AC	128		7.7	
G-4495	4.70 ±0.33	AC	118		4.56 ±0.45	AC	123		-3.0	
V-8025	5.07 ±0.24	A	127		4.09 ±0.44	AD	110		-19.3	*
5-161-E	3.47 ±0.16	DF	87		2.89 ±0.12	EF	78		-16.7	**
ALUBIO	3.00 ±0.17	GF	75		2.10 ±0.27	G	57		-30.0	**
PI-271998	3.35 ±0.13	EG	84		3.36 ±0.11	EF	91		0.3	
WA-2289	3.98 ±0.20	BE	100		3.31 ±0.27	EF	89		-16.8	*
WAF-9	2.94 ±0.24	GF	74		2.75 ±0.12	FG	74		-6.5	
MEAN	3.98				3.71					
TEP 1	3.85 ±0.29	CF	97		4.82 ±0.22	AC	130		25.2	*
TEP 3	4.43 ±0.20	AD	111		5.08 ±0.35	A	137		14.7	

MRT - Duncan's Multiple Range Test at P=0.05.

Significance - significance of season effect: * - 0.05 ≥ P > 0.01,

** - 0.01 ≥ P > 0.001, *** - P ≤ 0.001

Table 28: Effect of season and seed weight (g/1000 seeds) in dry bean under field conditions. Seed weight corrected to 14% water content. Accessions tested in 1987-88.

Acces.	SPRING		SUMMER		Effect		Signif.
	seed wgt	% of	seed wgt	% of			
	(g/1000)	MRT Mean	(g/1000)	MRT Mean	(%)		
BAT-336	200 ±3	FG 71	207 ±8	GH 80	3.5		
BAT-1289	227 ±9	EF 80	206 ±4	GH 79	-9.3	*	
G-0893	223 ±6	EF 79	230 ±13	FE 88	3.1		
G-1050	455 ±18	B 160	385 ±6	B 148	-15.4	*	
G-3645	172 ±7	G 61	185 ±5	HI 71	7.6		
G-3670	226 ±10	EF 80	198 ±7	GI 76	-12.4	*	
G-3689	202 ±8	FG 71	199 ±3	GI 77	-1.5		
G-3696	180 ±3	G 64	181 ±4	I 70	0.6		
G-3702	248 ±9	E 87	249 ±5	DE 96	0.4		
G-4495	223 ±3	EF 79	215 ±10	FG 83	-3.6		
V-8025	195 ±3	FG 69	198 ±7	GI 76	2.1		
5-161-E	348 ±11	D 123	266 ±4	D 102	-23.6	***	
ALUBIO	544 ±10	A 192	488 ±9	A 188	-10.3	***	
PI-271998	378 ±12	C 133	326 ±11	C 125	-13.8	**	
WA-2289	255 ±8	E 90	255 ±10	D 98	0.0		
WAF-9	462 ±9	B 163	373 ±8	B 143	-19.3	**	
MEAN	284		260				
TEP 1	119 ±7	H 42	142 ±5	J 56	21.8	**	
TEP 3	118 ±1	H 42	123 ±4	K 47	4.2		

MRT - Duncan's Multiple Range Test at P=0.05.

Significance - significance of season effect: * - 0.05 ≥ P > 0.01,

** - 0.01 ≥ P > 0.001, *** - P ≤ 0.001

Table 29: Relationship between average spring yield, yield stability (b), heat acclimation potential (HAP) and the relative reduction in different components of yield by the summer conditions.

	Spring seed yield (g/m ²)	Relative (%) Effect of Summer vs. Spring					b	HAP
		yield	Pods	seed	weight			
		(g/m ²)	/m ²	/pod	/seed			
G-3696	373	-31*	-30*	-2	1	1.14	130	
G-3670	357	-19	-12	-1	-12*	1.97	-	
G-3702	354	-5	-13	8	0	2.33	125	
BAT-336	330	-26*	-19*	-11	4	2.02	110	
ALUBIO	326	-30*	7	-30**	-10***	1.54	-	
WAF-9	326	-19	5	-7	-19**	1.08	-	
WA-2289	320	-28*	-14	-17**	0	1.41	-	
G-1050	319	-30*	-10	-8	-15*	0.77	-	
G-3645	304	-13	-20*	-1	8	0.95	70	
V-8025	300	-31*	-14*	-19*	2	1.10	95	
G-3689	295	-15	-10	-6	-2	1.30	>130	
5-161-E	276	-22*	24*	-17**	-24***	0.65	72	
BAT-1289	267	-24*	-10	-8	-9*	0.51	-	
G-4495	247	6	12	-3	-4	1.00	120	
PI-271998	238	-10	3	0	-14**	0.30	94	
G-0893	79	66*	48*	9	3	-	115	
TEP 1	281	46*	20*	25*	22*	-	-	
TEP 3	178	66*	23*	15	4	-	-	

Significance of season effect: * - $0.05 \geq P > 0.01$; ** - $0.01 \geq P > 0.001$;
*** - $P \leq 0.001$.

Number of pods / m square 1987 - 1988

% effect of summer

Figure 22: Pod production (pods/m²) in different accessions of dry bean in spring and summer trials during 1987 -1988

Mean number of seeds / pod 1987 - 1988

% effect of summer

Figure 23: Seed set/pod in different accessions of dry bean in spring and summer trial during 1987 - 1988

Seed weight (gm/1000 seeds) 1987 - 1988

% effect of summer

Figure 24: seed size (g/1000 seed) in different accessions of dry bean in spring and summer trial during 1987 - 1988

Similar trends were observed in the additional 11 accessions tested in 1988 (Tables 30 and 31, Fig. 25). Yield was significantly ($P=0.05$) reduced in the summer in 5 accessions. In 23-52 and PINTO the reduction was caused by a lower pods/m² and seed size, while in SANILAC the main causes were lower seed set/pod and seed weight. In HEBEI the reduction in yield was due to a smaller seed weight, while in IGUACU all three yield parameters were reduced in the summer.

P-730 behaved like G-893, TEP 1 and TEP 3. In the spring it had the lowest yield. However, in the summer yield was greatly increased (225%, Table 30), mainly due to a larger pod production and a somewhat greater seed size.

In the 1987-88 trials a clear cut relationship was found between seed size and the summer effects (Fig. 26). Accessions with larger seeds showed a larger decrease in seed size in the summer ($b = -0.079\%/gr$; $r=0.808$; $P=0.001$). Thus, if no compensatory effects are present, genotypes with larger seeds are more prone to larger decreases in yield under summer conditions.

Stability Analysis

Dry-bean accessions tested in the 1987-88 trials greatly differed in their average yields, and yield stability (b) (Fig. 27, Table 25). Accessions with larger yields tend to be less stable. A positive significant correlation exists between yield stability and the average yield ($b=0.0014$; $r=0.803$; $P=0.01$). If both yield level and yield stability are rated as positive features for selection, varieties such as G-3696, WAF-9 and G-3645 may be considered as promising ones.

Table 30: Effect of season on seed yield (g/msq, top) and on pod production (pods/msq, bottom) by dry - bean accessions tested in 1988. Highest and lowest yielding accessions tested in 1987-8 are included for comparison (above and below dashed lines respectively).

ACCESSION	S P R I N G			S U M M E R			EFFECT (%)	SIGNIF.
	YIELD (g/msq)	M.R.T	% OF MEAN	YIELD (g/msq)	M.R.T	% OF MEAN		
G-3670	508	A	158	334	B-E	115	-34	*
G-3702	452	AB	140	449	A	154	-1	
G-2525	438	A-C	136	452	A	155	3	
P-730	122	IJ	38	274	D-H	94	225	**
23-52	422	A-C	131	239	F-I	82	-43	**
C-20	372	B-F	115	298	C-G	102	-20	
DOR	310	D-H	96	314	C-F	108	1	
GNUL-59	271	F-H	34	238	F-I	82	-12	
GUANACO	336	C-G	104	385	A-C	132	15	
HEBEI	295	E-H	91	213	G-I	73	-28	*
IGUACU	343	C-G	106	259	E-I	88	-24	
PINTO	362	B-G	112	263	D-H	91	-27	
SANILAC	272	F-H	85	197	HI	68	-28	*
G-4495	258	GH	80	355	B-D	122	38	*
PI-271998	259	GH	80	207	G-I	71	-20	*
MEAN	330			285				

ACCESSION	S P R I N G			S U M M E R			EFFECT (%)	SIGNIF.
	PODS /MSQ	M.R.T	% OF MEAN	PODS /MSQ	M.R.T	% OF MEAN		
G-3670	432	B	142	342	C-G	110	-21	*
G-3702	364	B-F	120	329	C-H	106	-10	
G-2525	415	BC	136	402	CD	129	-3	
P-730	148	K	49	251	G-K	80	70	*
23-52	329	D-G	108	217	JK	70	-34	*
C-20	430	B	141	370	CF	119	-14	
DOR	266	G-J	87	303	D-J	97	14	
GNUL-59	229	H-J	75	222	I-K	71	-3	
GUANACO	329	D-J	108	374	C-E	120	14	
HEBEI	242	H-J	81	225	J-K	78	-7	
IGUACU	346	C-G	114	267	G-K	86	-23	*
PINTO	242	H-J	79	196	K	63	-19	
SANILAC	351	B-F	115	407	C	131	16	
G-4495	210	I-K	69	322	C-I	103	53	**
PI-271998	186	JK	61	186	K	60	0	
MEAN	298			290				

M.R.T - Duncan's Multiple Range Test at $p=0.05$.

Significance of season effect: * - $0.05 \geq p > 0.01$; ** - $0.01 \geq p > 0.001$;

*** - $p \leq 0.001$

Table 31: Effect of season on seed set/pod (top) and seed size (g/1000 seeds, bottom) in dry bean accessions tested in 1988. Highest and lowest yielding accessions tested in 1987-8 are included for comparison (above and below dashed lines respectively).

ACCESSION	S P R I N G SEED/ POD	M.R.T	% OF MEAN	S U M M E R SEED/ POD	M.R.T	% OF MEAN	EFFECT (%)	SIGNIF.
G-3670	5.8	AB	131	5.5	A-D	122	-5	
G-3702	5.2	A-F	117	5.8	AB	130	12	
G-2525	5.4	A-E	123	6.0	A	133	10	
P-730	3.9	H-M	89	4.7	D-F	104	14	
23-52	5.1	B-G	116	5.7	AB	127	9	
C-20	4.4	F-H	101	4.2	F-H	95	-5	
DOR	5.6	A-C	128	5.5	A-D	123	-3	
GNUL-59	3.3	LM	75	3.6	H-J	80	9	
GUANACO	4.6	E-I	104	5.1	B-E	113	11	
HEBEI	4.3	F-K	97	4.1	F-H	91	-5	
IGUACU	4.4	D-H	106	5.1	B-E	113	16	*
PINTO	3.5	K-M	80	3.7	G-J	82	5	
SANILAC	4.0	H-L	91	3.1	I-K	69	-21	*
G-4495	5.4	A-E	123	5.7	AB	128	6	
PI-271998	3.6	J-M	82	3.2	I-K	72	-11	
MEAN	4.4			4.5				

ACCESSION	S P R I N G G/ 1000	M.R.T	% OF MEAN	S U M M E R G/ 1000	M.R.T	% OF MEAN	EFFECT (%)	SIGNIF.
G-3670	203	J-L	78	180	G	78	-11	*
G-3702	240	H	93	237	F	102	-1	
G-2525	194	J-L	77	196	G	84	-2	
P-730	209	J-L	81	234	F	101	12	*
23-52	245	H	95	202	G	87	-17	*
C-20	194	KL	75	188	G	81	-3	
DOR	207	J-L	81	188	G	81	-9	*
GNUL-59	358	E	138	308	D	132	-14	*
GUANACO	223	H-J	86	205	G	88	-8	*
HEBEI	283	G	109	231	F	99	-18	*
IGUACU	226	H-J	87	189	G	81	-16	*
PINTO	433	B	167	368	B	158	-15	*
SANILAC	198	KL	75	158	H	68	-20	*
G-4495	227	H-J	88	190	G	82	-16	*
PI-271998	389	D	150	342	G	147	-12	*
MEAN	265			240				

M.R.T - Duncan's Multiple Range Test at $p=0.05$.

Significance of season effect: * - $0.05 \geq p > 0.01$; ** - $0.01 \geq p > 0.001$; *** - $p \leq 0.001$

Seed yield / m square 1988

% effect of summer

Figure 25: seed yield (g/m²) of dry bean in spring and summer trials of accessions tested in 1988.

Figure 26: Relationship between seed size of different dry bean accessions and relative effect of summer conditions on seed size.

Figure 27: Relationship between yield stability (b) and average yield in dry bean accessions.

Temperature effects on photosynthesis and dark respiration

Inhibitory effects of HT on net-photosynthesis and/or increased dark-respiration are among the possible causes resulting in the yield reduction observed under HT (spring vs. summer in the field; 22/17°C vs. 32/27°C in the phytotron). To examine this hypothesis we measured the rate of net-photosynthesis (CO_2 uptake) and of dark-respiration (CO_2 release)¹ in plants of several snap-bean varieties growing at 22/17°C continuously, or that were exposed when 20 days old to 7 days of 32/27°C before measurement. At this age plants were at the sporogenesis stage of the first flowers. This stage is particularly sensitive to the 32/27°C treatment that causes a drastic reduction in pod and seed set (Tables 8 and 9).

Net-photosynthesis rate was unaffected, or even slightly increased, by transferring plants from 22/17°C to 32/27°C in the 5 varieties examined (Table 32). Thus, the yield reduction after exposure to 32/27°C is not due to lower rates of net-photosynthesis. In previous work (Kigel and Ofir) we have shown that biomass accumulation in Tenderette is also unaffected by increasing temperature from 27/17°C to 32/27°C.

Rates of CO_2 -uptake measured in the phytotron were of the same order as those measured in the field during the same period of the year (July 1986; Table 32). Large intervarietal differences in net-photosynthesis were observed in the field, and these differences were maintained in the phytotron (Table 32). However, no correlation was found between net-photosynthesis and average yield, yield stability or heat acclimation potential (HAP) (compare Tables 23 and 32).

1) CO_2 -uptake or release were measured in the phytotron and in the field with a Li-Cor portable system.

Table 32 : Rate of net photosynthesis of snap-bean varieties grown in the field or in the phytotron (27/17°C vs. 32/27°C). Measurements were made on sunny days during the summer (7/1986). Light intensity was 1800-2000 $\mu\text{E m}^{-2} \text{sec}^{-1}$ in the field and 1200-1500 $\mu\text{E m}^{-2} \text{sec}^{-1}$ in the phytotron. Each variety was measured 3 times (on different days), with 5 replicates each time. Young fully grown second trifoliolate leaves were used. In the phytotron plants were grown at 27/17°C. Plants from 32/27°C were exposed to this temperature for 1 week before photosynthesis measurement.

Varieties	CO ₂ uptake ($\mu\text{M CO}_2/\text{m}^2/\text{sec}$)						
	Field		Phytotron				P
		%	27/17°C	%	32/27°C	%	
LEGACY	26.0	100	23.9	100	22.7	100	NS
SUPERGLOSS WATERFALL	23.5	90	-	-	-	-	
SUPERGLOSS TORY	22.9	88	-	-	-	-	
BBL-47	21.0	81	17.9	75	18.4	81	NS
EARLY GALATIN	20.9	80	17.2	72	16.7	74	NS
PURPLE QUEEN	20.2	78	-	-	-	-	
PURPLE ROUGE	20.1	77	-	-	-	-	
PI-271998	18.0	69	16.6	69	16.3	73	NS
TENDERETTE	17.0	65	13.7	57	15.5	68	0.05
LSD (5%)	1.8				1.2		

The possibility that temperature during growth affects bean tolerance to higher temperatures (acclimation to 42°C) was examined in greater detail in BBL-47 and PI-271998. Plants were grown at 22/17°C. At the age of 20 days half of them were exposed for 7 days to 32/27°C, before CO₂-uptake measurements were carried out at 25°C, 35°C and 42°C in a custom-designed gas-exchange system (Armstrong Co.)².

Under 42°C both varieties exhibited a great reduction in net-photosynthesis (Table 33). However, this reduction was smaller if plants were previously exposed to 32/27°C. Thus, both varieties possess a potential for HT acclimation. This potential for acclimation was significantly ($P=0.001$) greater in PI-271998 compared to BBL-47. Similar results were found in St. Paul by membrane stability tests, and Photosynthesis-Chl. fluorescence measurements. On the other hand, PI-271998 also exhibited higher rates of net-photosynthesis than BBL-47 in all temperature treatments (Table 33).

Dark-respiration was increased by higher temperatures (Table 34). This increase may cause a larger deficiency in photosynthates, particularly in meristematic regions, leading to lower pod and seed set. However, dark-respiration was significantly ($P=0.01$) lower in BBL-47, the variety in which the reproductive processes were more affected by 32/27°C, compared to PI-271998. Furthermore, both varieties exhibited the same relative increase in dark-respiration by HT (about 30%). On the other hand, temperatures at which plants were grown (22/17°C vs. 32/27°C) did not affect dark-respiration rates at 20°C or 30°C.

Thus, no clear relationship can be established between the HT effects on dark-respiration and the decrease in yield.

2) We thank Dr. A. Schwartz for these measurements.

Table 33 : Effects of temperature during growth (22/17°C vs. 32/27°C) on rate of photosynthesis under different temperatures.

GROWTH TEMPERATURE	rate ($\mu\text{mole CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$)					
	PI-271998			BBL-47		
	25°C	35°C	42°C	25°C	35°C	42°C
22/17°C	16 a	16 a	10 b	12 a	11 a	2 b
32/27°C	16 a	16 a	12 b	12 a	13 a	9 b
Significance	NS	NS	*	NS	NS	***

* P=0.05; *** P=0.001 - indicates differences between growth temperatures.

Different letters indicate significant (P=0.001) differences in rate between temperatures within each variety. At each temperature treatment net photosynthesis of PI-271998 was significantly (P=0.001) greater than in BBL-47.

Table 34 : Effects of temperature during growth (22/17°C vs. 32/27°C) on dark respiration rate at 20°C and 30°C.

GROWTH TEMPERATURE	rate ($\mu\text{mole CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$)					
	PI-271998			BBL-47		
	20°C	30°C	P	20°C	30°C	P
22/17°C	0.30	0.80	0.01	0.20	0.64	0.01
32/27°C	0.33	0.91	0.01	0.21	0.55	0.01
P	NS	NS		NS	NS	

Discussion and Conclusions

One of the main goals of the project was the evaluation of different screening approaches to survey bean germplasm collection for higher HT tolerance and/or acclimation potential to HT.

Two main approaches were used:

- a) Exposure to HT (32/27°C in the phytotron; 27°C at night in the greenhouse) at different stages of reproductive development. In this approach we examined HT tolerance of different developmental processes involved in the determination of pod and seed set: micro- and macrosporogenesis, pollination, fertilization, early embryo and seed growth, flower and pod abscission.
- b) Determination of heat acclimation potential (HAP): defined as increased membrane stability to HT (50°C) of leaf cells due to previous plant exposure to 37°C for 24 hours.

Although a complex of factors interact in the field and determine yield, we expected a correlation to be found between HT tolerance and/or acclimation as determined by the above approaches, and germplasm performance under HT in the field (summer trials).

Relationship between HT effects at anthesis and summer yield decrease

In snap-beans, exposure to 5 days of 32/27°C at sporogenesis in the phytotron resulted in flowers with non-viable pollen and parthenocarpic pod development in the 11 accessions examined (Table 9). Thus, this stage is very sensitive to HT and inadequate for screening purposes.

Pollination and fertilization were less affected if plants were exposed to HT just before anthesis. Nevertheless, pod and seed set were reduced. Extent of reduction varied between varieties (Table 23).

However, no correlation was found between the relative (%) yield reduction in the phytotron (32/27°C vs. 22/17°C) and in the field (summer vs. spring) (Fig. 28). On the other hand a significant correlation ($r=0.775$; $P=0.02$) was found between the relative reduction due to six nights of 27°C at anthesis in the greenhouse, and the summer reduction in the field (Table 23, Fig. 29). At this stage it is difficult to define the causes for the different quantitative responses to HT in the phytotron and the greenhouse. In the phytotron the average relative reduction in yield (gr pods/plant) was larger than in the greenhouse (-39% vs. -29%; averages compare same varieties). Average summer decrease in the field was even lower (-24%). It seems that in the phytotron other yield constraints were acting besides HT resulting in lower pod and seed set. In the phytotron plants were grown in smaller pots than in the greenhouse. Thus, plants were smaller, produced fewer pods and had smaller root systems, even under 22/17°C. On the other hand, plants in the greenhouse reached a similar biomass and pod production as in the field. In the greenhouse, the improved water and mineral uptake, and/or a better endogenous hormonal balance due to the larger root systems, might have resulted in a larger pod set and in a reduction of the negative effect of HT.

Although plant development in the greenhouse was more or less similar to that in the field, work in the phytotron was essential for a definite and clear identification of the reproductive stages affected by HT. On the other hand, screening for HT tolerance under greenhouse conditions (greater pots, etc.) seems to be a more realistic approach, although temperature control is less exact than in the phytotron. This conclusion is further supported by the fact that a good correlation was found between yield stability (b) in the field trials and the relative (%) reduction of yield (FW pods/plant) by high night temperature (27°C) under greenhouse conditions ($r=0.832$; $P=0.01$) (Fig. 30). Snap-bean varieties showing lower yield reduction by HT at night were those with the highest yield stability in the field (lower b). On the other hand, no correlation was found between b and

Fig. 28: Relationship between relative (%) yield reduction by HT in the phytotron (FW pods/plant) and by the summer conditions in the field (FW pods/m²).

Fig. 29: Relationship between relative (%) yield reduction by HT in the greenhouse (FW pods/plant) and by the summer conditions in the field ($r=0.775$; $P=0.02$).

Fig. 30: Relationship between relative (%) yield reduction by HT in the greenhouse (FW pods/plant) and yield stability (b) in the field ($r=0.832$; $P=0.01$).

the relative reduction in yield after exposure to 32/27°C at anthesis in the phytotron.

Two basic assumptions were behind the idea of screening for HT tolerance at the anthesis stage:

a) Anthesis and early pod development are usually assumed to be very sensitive stages to stress conditions. Thus, processes like pollination, fertilization, and early embryo and seed development are probably the factors limiting pod and seed set under HT.

b) Higher HT tolerance of reproductive processes is probably correlated with a higher HT tolerance of other processes affecting yield (photosynthesis, growth, etc.).

In the phytotron photosynthesis (Table 32) and growth (Kigel and Ofir, unpublished) were unaffected by exposure to 32/27°C. The main processes negatively affected by 27°C at night were pollen development, anther dehiscence, pollen tube growth and fertilization (Tables 9 and 10). Due to the obligatory self-pollination of bean flowers, lack of fertilization results in pod abscission or pod abortion, as observed in the phytotron. In the field, however, pods/m² of most snap-bean varieties (Fig. 14, see 1987-88 trials), and dry-bean accessions (Fig. 22), was unaffected or even increased during the summer. Furthermore, seed set/pod was unaffected by the summer conditions in snap-bean (Fig. 15), or slightly reduced only in some accessions of dry-bean (Fig. 23). Thus, although high night temperature reduces pod and seed set under controlled conditions, lack of pollination or fertilization, pod abscission or abortion do not seem to be the main factors limiting bean production under ample irrigation in Israeli summer conditions. Nevertheless, the significant correlation between yield reduction in the greenhouse by high night temperature (in the absence of other limiting factors) and the summer performance in the field may indicate that higher HT tolerance of reproductive processes correlates with a larger tolerance of other processes determining yield in the field.

Relationship between HAP and summer yield decrease

In the second approach the main assumption was that yield of germplasm exhibiting higher HAP will be less affected by HT conditions. However, no correlation was found between HAP and relative yield reduction by exposure to 32/27°C at anthesis in the phytotron, or exposure to 27°C at night during anthesis in the greenhouse (Table 23), or with the summer yield reduction in the field trials in snap or dry-bean accessions (Fig. 31). Furthermore, HAP and summer yields were not correlated.

Fig. 31: Relationship between HAP and relative (%) yield reduction in the field by summer conditions, in snap-bean and dry-bean accessions [dry-bean accessions examined in 1987-88 () or only in 1988 (■)].

Snap-bean varieties with higher HAP tend to have a larger yield stability (b) in the field, but the correlation was quite low ($r=0.5$, $P=0.10$). On the other hand, dry-bean accessions with higher HAP tend to show lower stability (higher b). Thus, the relationship between HAP and yield stability in the field is also weak and inconclusive.

The lack of correlation between HAP and the effect of HT under controlled conditions is difficult to explain. One possible explanation is that the great sensitivity of pollen development to $32/27^{\circ}\text{C}$ (or 27°C at night) is not related to membrane stability. Thus, HT tolerance or acclimation processes occurring at the leaf, or at the photosynthesis levels, are not necessarily associated with higher tolerance or acclimation of reproductive processes.

Another possibility is that HAP is affected by plant growth conditions (light intensity, thermo- or photoperiod, mineral nutrition, etc). In this case, bean genotypes may differ in their HAP responses to the growth conditions. Thus, the lack of correlation between HAP, as determined in St. Paul, and yield reduction, as determined in Israel, may have resulted from the different conditions under which the plants were grown.

General conclusions

Yield reduction by hot weather is undoubtedly due to an accumulation of effects on a variety of developmental and physiological processes that determine yield. These processes probably differ in their tolerance and/or acclimation capacity to HT. In the phytotron (Tables 7A and 7B) and in the field (Figs. 13, 14 and 15, Table 29), yield components (pods/plant; seeds/pod; seed size) were differentially affected by HT or summer conditions. Moreover, HAP and yield reduction were not correlated. On the other hand, bean genotypes may differ in the processes that limit their yield under HT,

precluding generalizations about a main controlling process affected by heat.

Analysis of our field data in relation to the spring and summer climatic conditions support the possibility that HT per se is not the main limiting factor for bean production (at least under the Israeli summer conditions). No correlation was found between the average maximal temperature during flowering and early pod development and yield of snap- or dry-bean (Tables 15 and 17). Furthermore, the exceptional hot and dry weather in the spring of 1988 (Fig. 10) did not result in a strong reduction of yield, probably due to the ample irrigation supplied (Table 16).

The lack of correlation between HAP (as measured in St. Paul) and field results further supports the conclusion that HT is not the main yield constraint in the field, provided that plants are well irrigated. In fact, summer yields in our trials increased from year to year with irrigation improvement (Tables 15 and 16). According to current research in Israel (Kigel, Ofir, Schwartz), bean plants are very sensitive to water stress. They lose turgor rapidly, and stomatal conductance decreases at relatively high leaf relative water content and moderate soil water deficits. Thus, under low water availability, HT may reduce yield indirectly, by increasing water loss and reducing net photosynthesis and growth. Furthermore, water stress may be critical at the stage of seed filling (unpublished).

An overall evaluation of our findings suggest that HT per se will not represent the main constraint for growing bean in warmer seasons or regions, provided that associated biotic factors (plant diseases, pests) and plant water stress (water availability) are avoided. Our field results suggest that under warm climatic conditions water stress limits yield much more than HT alone. Thus, future work must be addressed towards a better understanding of the water stress effects on yield limiting processes, specifically those related to reproductive development. Nevertheless, increased heat tolerance and/or acclimation to HT may increase yield performance under water

stress. The genotypic differences in specific responses to HT, and to summer conditions in general that we found in this project indicate that heat tolerance and/or acclimation can be improved in bean through breeding programs.

Our field results indicate that an important criterion in the evaluation of bean genotype performance under HT and/or water stress in the field will be their yield stability, as measured over a wide range of environmental conditions. Under certain conditions, a better strategy of production will be to grow varieties showing a high stability under adverse conditions, instead of varieties with high yields under optimal conditions. A better understanding of the relationships between the processes determining yield stability and tolerance or acclimation to heat and drought conditions is necessary for the breeding of bean genotypes showing better adaptability to HT and water stress.

Description of Cooperation

Cooperation on the evaluation of germplasm screening methodology and on acquisition of germplasm from other world sources and breeding programs were key elements beyond the project-designed cooperation with Dr. Kigel. Thus, Dr. Wallerstein of the Volcani Institute worked with us to provide new methodology utilizing leaf ethylene evolution which was used in for progeny evaluation in the breeding phase. In addition, germplasm was obtained from the International Center for Tropical Agriculture (CIAT), Cali, Colombia, as well as from numerous bean breeding programs both public and private.

Evaluation of Research Achievements

This project has succeeded in identifying germplasm of common bean (*P.vulgaris*) having greater heat acclimation potential and heat tolerance. This genetic material thus is a resource for bean breeders and physiologists who may be interested in developing improved cultivars or in investigating the nature of heat stress tolerance and heat acclimation potential in an important world food crop.

Information was provided on the inheritance of tolerance and research comparing the efficacy of selection methods was initiated. This research is continuing and additional funds have been secured to make this possible. Thus, the groundwork toward practical outcome, the development of improved cultivars, has been established.

In retrospect, the project might have placed more emphasis on the evaluation of heat stress at the pod setting stage, rather than only on dry yield at the end of the bean life cycle, as a means of focusing more on the split set phenomenon so important in snap bean production.