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Flower and Pod Abscission Due to Heat Stress in Beans

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Abstract. The effect of high temperature on abscission of bean (*Phaseolus vulgaris* L.) flowers and pods was studied under growth chamber and greenhouse conditions. Experiments investigated stages at which flowers are sensitive to heat stress, the period when reproductive structures abscise, and sensitivity of male and female flower parts to heat stress. Heat treatments (2 days at 35C, 10 hours per day) were applied through flower ontogeny, from 8 days before anthesis until anthesis. The flower bud stages were defined by correlating the pedicel length with days to reach anthesis. The prefertilization period showing highest sensitivity to heat stress extended from \approx 6 days before anthesis to anthesis. We found that 82% of heat-stressed structures abscised as small pods (< 2 cm in length), even when the stress was applied at various flower bud stages. Reciprocal crosses made with pollen from heated plants or on heattreated flowers indicated that pollen was more affected by heat stress than by female structures.

Binkley (1932) and Ahmadi (1956) reported bean yield reductions due to abscission of reproductive structures during dry and hot weather. Dickson and Boettger (1984b) suggested that bean yield losses sometimes attributed to drought are more likely to be caused by high temperatures (> 30C) in midsummer. Iwami (1951) reported a high negative correlation between percentage pod set and temperature in beans. Davis (1945) found that blossom abscission increased by $\approx 2\%$ for each degree above 24C.

The negative effect of high temperature on pod set is documented; however, the physiological basis for this flower loss is still unclear. Ahmadi (1956), Inoue and Suzuki (1959), and Dickson and Boettger (1984a) indicate that decreased pod set at high temperatures is related to pollen injury, but Halterlein et al. (1980) reported that a constant 35C actually increased pollen production and did not decrease the number of pollen tubes reaching the base of the style.

Research has concentrated on the effect of heat on open flow-

ers or flower buds close to anthesis (Ormrod et al., 1967; Inoue and Suzuki, 1959) and has not determined if high temperatures given to flower buds earlier in ontogeny could adversely affect their ability to set. The present work investigates the effect of heat treatments given at various times during flower ontogeny on abscission, and determines the relative sensitivity of male and female flower parts to heat-induced flower abscission.

Materials and Methods

Bean plants were grown in 1-liter nursery cans in an artificial soil composed of equal proportions of vermiculite and peat. Pots were watered as needed and fertilized twice weekly with soluble fertilizer supplying 0.32 g N, 0.08 g P, and 0.15 g K per pot through the watering system. Plants were exposed to 35C during 10 hr of a 14-hr photoperiod. For the remainder of the day, plants were at 20C. Photon flux in growth chambers and greenhouses was measured at plant level using a Lambda Instruments Model 185 radiation meter with a quantum sensor (LI-COR, Inc., Lincoln, Neb.). Light level in the growth chamber experiments was 230 μ mol·s⁻¹·m⁻² unless noted otherwise.

Relation of flower ontogeny to pedicel length (Expt. 1). Seven pots each of the cultivars Majestic (Rogers Bros.), Bush Blue Lake 47 ('BBL 47', Asgrow) and ARS 5Bp-7. (M. Silbernagel, Presser, Wash.) were grown in a growth chamber at 22/20C day/night with a 14-hr photoperiod. The pedicel length of the lowest three floral nodes on the terminal inflorescence was mea-

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sured daily, starting when the pedicel was first visible, until anthesis.

Heat sensitivity of flower stages (Expt. 2). This experiment tested the effect of high temperature duration and stage of flower development susceptible to heat. Three 'BBL-47' plants per treatment were started in a greenhouse with 20 to 26C maxima. Treatments (35C) were applied for 1, 2, or 3 days when the second floral node of the terminal inflorescence was 8, 6, 4, 2, or 0 days before anthesis. In addition, a high temperature control (35/20C, day/night) remained in the high temperature chamber from 8 days before to 3 days after anthesis. A low temperature control (26/20C) stayed in the greenhouse throughout.

The number of flower buds at each of the three flower nodes was determined before each treatment was applied, and the number of scars of abscised flowers at the floral nodes studied was recorded 18 days after anthesis. The experiment had a completely random design with factorial combination of treatments (3 durations \times 5 times to anthesis) plus two added controls (Federer, 1955). Analysis of variance was calculated on arcsin-transformed percent abscission data.

Comparison of cultivars (Expt. 3). This experiment had a purpose similar to Expt. 2 and compared 'Majestic', 'BBL-47', and 'ARS 5Bp-7'. Plants were grown in a 22/20C growth chamber with 14-hr photoperiod before and after heat treatment. Three plants per cultivar per treatment were exposed in a growth chamber to 35C for 2 days for 10 hr each day at 4, 2, or 0 days before anthesis of the terminal inflorescence. A control remained at 22/20C for the duration. Abscission at the first three nodes of the terminal inflorescence was recorded 18 days after anthesis of the controls. The experimental design and statistical analysis were similar to Expt. 2. Analysis of variance was calculated from the arcsin-transformed data.

Age of buds (Expt. 4). 'Majestic' and 'BBL-47' plants were grown in a greenhouse with 20 to 25C maxima for the first 20 days, then transferred to a 22/20C growth chamber with 420 μ mol·.s⁻¹m⁻² photon flux and 14-hr photoperiod. Heat treatments (35C for 10 hr each day) of 2 days' duration were imposed at 8, 6, 4, 2, or 0 days to anthesis of node two on the terminal inflorescence. The control plants remained at 22/20C. There were five plants per treatment for each cultivar.

Total abscission, number of pods, and a daily record of abscission on the three lowest nodes of the terminal inflorescence were kept until 20 days after anthesis. The abscised structures were classified as follows: Flower buds from differentiation to ≈ 2 days before anthesis, flowers near or at anthesis, pods <2

Table 1. Pedicel length for the different stages of flower development for the three cultivars studied in Expt. 1. Each number represents a mean of seven plants.

Days to	Pedicel length (mm) ^{z,y}		
anthesis	BBL-47	ARS 5Bp-7	Majestic
8	0.85 ± 0.14	0.83 ± 0.21	0.80 ± 0.22
7	0.93 ± 0.19	1.33 ± 0.27	1.16 ± 0.29
6	1.46 ± 0.44	2.18 ± 0.25	1.62 ± 0.14
5	2.38 ± 0.46	2.83 ± 0.29	1.88 ± 0.52
4	3.46 ± 0.39	3.69 ± 0.30	2.69 ± 0.35
3	4.50 ± 0.39	4.77 ± 0.59	3.63 ± 0.34
2	5.89 ± 0.78	6.45 ± 0.41	4.26 ± 0.32
1	8.59 ± 0.58	8.63 ± 0.43	6.88 ± 0.75
Anthesis	10.32 ± 0.81	10.10 ± 0.51	9.68 ± 0.57

'Overall relation of pedicel length (y) and days to anthesis (x) is given by In y = 2.365 + 0.313x (r = 0.985).

^yMean \pm s D.

cm, pods from 2 to 4 cm long, and pods >4 cm. The experimental design and statistical analysis were similar to Expt. 2.

Sensitivity of male and female flower parts (Expt. 5). The heat-sensitive cultivar Majestic was planted in May 1987 to determine whether male or female flower structures were more susceptible to heat stress. Eighteen plants were greenhouse-grown under maxima of 26 to 33C, with maximum photon flux of 880 to 1020 µmol·s⁻¹·m⁻². Another eighteen plants were exposed for 2 days to 35C (10 $hr \cdot day^{-1}$) in a growth chamber when first flower buds were near anthesis. A few younger buds were also tagged on each plant at the time of heat treatment and used in crossing 1 day before anthesis. Nine heat-treated plants were used as a source of pollen, and nine as females. For crossing, flowers were emasculated 1 day before anthesis and pollinated with pollen from a newly opened flower. Pollen was always taken from a different plant than that used for the female. A total of 214 crosses was made. While making the crosses, priority was given to the lower flowers on floral nodes; other flowers on the same node were removed to avoid competition. The crossing pattern of the treatments was as follows: 1) Female at normal temperatures \times male heat-treated (NTO \times HTP); 2) Female heat-treated \times male at normal temperatures (HTO \times NTP); 3) female and male both at normal temperatures (NTO \times NTP); and 4) self-pollinated at normal temperatures.

Results and Discussion

'Majestic' and 'BBL-47' flowered 32 days after planting, and the line ARS 5Bp-7 at 34 days (Expt. 1). The first flowers to open on the terminal inflorescence were those at the first floral node, and then flower opening progressed acropetally. The first three floral nodes were chosen for most trials reported here

Table 2. Percent abscission at the lowest three nodes of the main stem terminal inflorescence as influenced by heat treatment at various times before an thesis in Expts. 2 and 3. Values are averages for 1-, 2-, and 3-day heat durations in Expt. 2.

	Abscission (%) ^z			
Heat treatment		Expt. 3		
start	Expt. 2			ARS
(days to anthesis)	BBL 47	BBL 47	Majestic	5Bp-7
8 or more	53 (47)			
7 to 6	75 (60)			
5 to 4	96 (78)	52 (46)	81 (64)	30 (33)
3 to 2	83 (66)	56 (48)	63 (52)	48 (44)
1 to 0	89 (71)	85 (67)	67 (55)	81 (64)
lsd 0.05 ^y	(10)	. ,	(14)	. ,
Control low temp.	37 ` ´	26	41	26
Control high temp.	82			
Statistical significanc	e (Expt. 2)	Statistical	significance ((Expt. 3)
Time to anthesis*	**x	Time to	anthesis**	
Heat duration ^{NS}		Cultivar*		
Time \times duration ^{NS}		Time \times cultivar*		
Control low temp. vs. all		Control low temp. vs. all other		
other treatments***		treatn	nents***	
Control high temp	o. vs. all			
other treatments	5 ^{NS}			

^{*}Arcsin-transformed values in parenthesis.

 3 LSD value for separation of time to anthesis effects (in column) in Expt. 2; interaction LSD (time × cultivar) in Expt. 3.

Neither linear nor quadratic components of the sum of squares for time to anthesis were significant.

^{SS...,...} Nonsignificant or significant at P = 0.05, 0.01, or 0.001, respectively.

Table 3. Percent abscission at floral nodes 1, 2, and 3 on terminal inflorescence for two bean cultivars heat-treated (35C for 10 hr·day⁻¹) for 2 days, beginning at various times to anthesis (Expt. 4).

	Abscission (%) ^{y,x}			
Heat treatment	Floral node 1		Floral	Floral
(days) ^z	BBL 47	Majestic	node 2 ^w	node 3 ^w
8 DB			3 (10)	20 (27)
6 DB	17 (24)	80 (63)	23 (29)	32 (34)
4 DB	70 (57)	73 (59)	86 (68)	82 (65)
2 DB •	73 (59)	83 (66)	97 (80)	88 (70)
Anthesis	77 (61)		90 (72)	90 (72)
1–2 DA	33 (35)	30 (33)		
Control	0 ` ´	0 ` ´	0	0
Statistical significance ^v				
Cultivar	*		NS	NS
Time to anthesis	* * *		***	* * *
Cultivar × time	NS		NS	NS
Control vs. all other			* * *	***
treatments	* * *			
$LSD_{0.05}$ time to				
anthesis	(19)	(13)	(17)	
LSD _{0.05} cultivar	(1	2)	<u> </u>	

^zDB = days before anthesis; DA = days after anthesis.

^vDashed line = no buds at this stage.

^{*}Arcsin-transformed values in parenthesis.

"Average of two cultivars.

'The analysis of variance and LSDS were calculated on arcsin-transformed data.

^{NS....} Nonsignificant or significant at P = 0.05 or 0.001, respectively.

because there was only 2 days' difference between opening of flowers at nodes one and two, and 4 days between nodes one and three in the three cultivars. Flowers within a floral node opened almost simultaneously. This pattern facilitated the application of the heat treatment in subsequent trials. Subhadrabandhu et al. (1978) reported that the first flower to open has a higher probability of setting than flowers that open later on; this ensures that the abscission observed was due to the treatments instead of competition among flowers and fruits.

About 9 days elapsed from the stage at which the flower pedicel could be measured until anthesis (Table 1). There was a close positive relation between the natural log of pedicel length (y) and flower bud age (x) [ln y = 2.365 + 0.313x, r = 0.985]. This relation was used to estimate days to anthesis in all subsequent experiments. Differences among cultivars in the pedicel length-bud age relation were small.

Heat treatment significantly increased flower abscission in Expt. 2 (Table 2). Buds fewer than 6 days before anthesis were more susceptible to high temperature than were younger reproductive tissue. Durations of heat from 1 to 3 days produced no differences in the amount of abscission, averaging 79% (data not shown). The 11-day heat treatment of the high temperature control resulted in 82% abscission, not significantly different from heat duration of 1 to 3 days.

In Expt. 3, overall abscission was reduced compared to Expt. 2 (Table 2), perhaps because plants were transferred from one growth chamber to another for the heat treatment, rather than from greenhouse to growth chamber, as in Expt. 2. Cultivars BBL 47 and ARS 5Bp-7 had the highest percent abscission for flowers close to anthesis, while 'Majestic' was also highly susceptible at 5 to 4 days before anthesis. This difference resulted in a significant time × cultivar interaction. Overall, 'Majestic'

Table 4. Reproductive structure abscission, induced by 2-day heat treatment (35C for 10 hr·day⁻¹), as related to developmental stage of flower at time of abscission. Abscission was averaged across treatments for all 60 plants (Expt. 4).

	Abscission
Development stage of flower	(%)
Flower buds from differentiation to 2 days before a	nthesis 4
Flower near to or at anthesis	8
Pods <2 cm	82
Pods from 2-4 cm	6
Pods >4 cm	0

Table 5. Percent abscission of manually pollinated bean flowers differentially heat-treated (35C for 10 hr) for 2 days at various times before anthesis.

Heat treatment	Abscission (%)		
(days to anthesis)	$\overline{\text{NTO} \times \text{HTP}}$	$NTO \times NTP$	HTO \times NTP
7–10	76 ± 4^{y}		60 ± 22
36	98 ± 5	•	54 ± 32
Control, manual		40	
Control, self-poll.		18	

Pollinations were made with normal- (NTP) or high-temperature pollen (HTP), onto normal- (NTO) or high-temperature ovaries (HTO). Mean \pm s.E.

lost more flowers than the other two cultivars. The reported tolerance of 'ARS 5Bp-7' to high temperatures (Weaver et al., 1985) was not evident in this experiment.

The results of Expt. 4 confirm that buds fewer than 4 days from anthesis are more susceptible to abscission than are younger buds (Table 3). These age effects were apparent in buds at all nodes on the terminal inflorescence. Cultivar differences were significant only at the lowest node, where 'Majestic' was more susceptible to abscission than 'BBL 47'. Subjecting plants with small pods to the 2-day heat treatment resulted in very little abscission of these structures (Table 3).

Although heat was imposed at several stages of flower development in Expt. 4, 82% of the reproductive structures were shed when pods were <2 cm in length, i.e., between 2 and 5 days after anthesis (Table 4). Izquierdo and Hosfield (1981) also reported that 64% to 82% of the reproductive structures abscised by field-grown beans were pods shorter than 1 cm. His and our results strengthen the view that heat treatment caused a malfunction of male or female flower parts, expressed as abscission after lack of seed set.

The results of Expt. 5 again indicate that heat treatment close to anthesis reduces fruit set (Table 5). Heat had a greater adverse effect on male than on female flower parts. When exposed to 35C for 2-day periods starting 6 to 3 days before anthesis, pollen from hand-treated plants caused 98% abscission of flowers on plants grown at normal temperature (Table 5). In the reciprocal cross, 54% abscised. This result appears to contradict those of Weaver et al. (1985), who showed that a 2-day exposure to 35 or 41C starting at 6 days before anthesis had no effect on percent viable pollen grains, as measured by pollen stainability. The discrepancy between stainability and function, and use of the resistant cultivar ARS 5Bp-7, rather than the susceptible 'Majestic', may explain these differences. In agreement with our results, heat stress just before anthesis sharply reduced pollen viability in the work of Weaver et al. (1985). Inoue and Suzuki (1959), Farlow et al. (1979), and Dickson and Boettger (1984a)

also found that male flower parts were more susceptible to heat than the female parts.

The foregoing experiments indicate that bean flowers become sensitive to heat stress by ≈ 6 days before anthesis and retain that sensitivity into the anthesis period. Anatomical studies appear to confirm that preanthesis heat stress has little adverse effect on the developing embryo sac (Ormrod et al., 1967). The effect of heat on pollen development has so far not been reported in bean. In tomato (*Lycopersicon esculentum* Mill.), Iwahori (1965) found that heat disrupted the meiosis stage of both microsporogenesis and megaspore formation. The tomato flower buds reached this stage at 9 to 5 days before anthesis. In contrast to the present results, tomato flowers were less susceptible to damage when exposed to heat in the last 4 days before anthesis. Further work is needed with bean to trace the effects of heat stress and to explore the anatomical and physiological basis for differences among cultivars.

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