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Effect of Older Fruits on Abortion and Abscisic Acid Concentration of Younger Fruits in *Phaseolus vulgaris* L.[1]

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ABSTRACT

In two cultivars of bean (*Phaseolus vulgaris* L., Redkloud and Redkote) the older fruits growing at the base of racemes aborted less frequently than the younger ones above them. When older fruits at the base of racemes were removed, the abortion rate of the younger ones was reduced and their abscisic acid (ABA) concentration was lowered. Thirteen days after fruit removal, 36 to 45% of the younger fruits remained viable on treated plants while less than 12% of the younger fruits were viable on control plants. On these intact controls the ABA concentration of young fruits was at least twice that of defruited plants. A similar difference was found when the ABA content was expressed on a per fruit basis, suggesting a direct regulatory influence of older fruits over the ABA content of younger fruits.

Premature fruit abscission, often of a large percentage of fruits on a plant, is a common phenomenon that has been reported for a number of plant species including apples (9), beans (15), and cotton (4, 8). In beans, abscission appears to be the last step in the process of fruit abortion, which is characterized by cessation of seed development, flattening of pod walls, and loss of green color (15). Events leading to fruit abortion may include a decrease in the concentration of auxins (9) and an increase in the concentration of ethylene and ABA (4, 8). However, neither the regulation of these hormonal changes within a fruit nor the coordination of fruit abortion with over-all plant development is well understood.

In the companion article, fruits were shown to inhibit the growth of axillary buds of bean plants (15). The present report describes the competitive inhibition of young fruits by adjacent older fruits of bean plants.

MATERIALS AND METHODS

Bean plants (*Phaseolus vulgaris* L. cv. Redkloud and cv. Redkote) were grown in a controlled environment growth chamber. The conditions of plant growth and methods of ABA analysis were described in the companion paper (15). The effect of older fruits on the abortion rate and ABA content of the younger ones was tested as follows. Fruits within each raceme were classified into categories of "older" (those at the base of the raceme), "younger" (those in the upper part of the raceme), and "aborting" (those showing premature loss of green color and lack of developing seeds). Fruits were tagged and measured, followed by the removal of older fruits from all racemes of treated plants on day 0. Control plants were left intact. After 13 days each category of fruits was counted and measured. Fruits retained their original classification regardless of size, except newly yellowing fruits were included in the aborting category. Following measurement, fruits were harvested and their ABA content determined (15). All fruits belonging to a category on a plant were used to form a sample. Fruit number per sample was generally between 10 and 20. Growth measurements (Table I) represent the mean obtained from two plants. Statistical analysis was performed using the same procedure as previously described (15).

RESULTS

Effect of Older Fruits on the Growth and Abortion of Younger Fruits. The relative age of developing bean fruits within a raceme affected their rate of abortion: older fruits at the base of the raceme aborted less frequently than the younger ones above them. When the older fruits were removed from each raceme, the abortion rate of the younger fruits greatly decreased in both cultivars (Table I). On treated plants (older fruits removed), 36 to 45% of the younger fruits remained viable, while on controls the number was below 12%. Only 18 to 33% of the older fruits aborted on control plants. The effect of older fruit removal was highly significant, as shown by analysis of variance, on the number of viable younger fruits ($F = 45.5$, $P = 0.001$). Over 82% of the total variation in young fruit number was due to treatment (the correlation ratio [eta^2] was 0.821). As expected, fewer aborting fruits were observed on treated plants ($F = 7.03$, $P = 0.037$; eta$^2 = 0.20$). Although removal of the older fruits caused some increase in the length of the younger fruits and decrease in the length of aborting fruits compared to the controls (Table I), these changes were statistically not significant ($F = 2.99$, $P = 0.133$ for younger fruits; $F = 0.92$, $P = 0.999$ for aborting fruits). Similarly, when fruit size was expressed on a dry weight basis (Table II), the change in the size of younger fruits upon the removal of older fruits was not significant ($F = 3.66$, $P = 0.103$).

Effect of Older Fruits on the ABA Concentration of Younger Fruits. To test the effect of competition among fruits on their ABA concentration, all categories of fruits in Table I were harvested for ABA analysis 13 days after the removal of older fruits from treated plants. All fruits showing symptoms of abortion were included in the aborting category regardless of original classification. As shown in Table II, the average ABA concentration of younger fruits, not including any aborting fruits, was at least two times higher in control plants than in treated ones for both cultivars ($F = 333$, $P = 0.001$; eta$^2 = 0.21$). A highly significant difference was also found when the ABA content of younger fruits was expressed on a per fruit basis ($F = 1924$, $P = 0.001$; eta$^2 = 0.20$). In intact controls, the average ABA concentration of younger fruits was at least twice that of older fruits. The ABA concentration of aborting fruits (data not shown) varied between very wide limits and showed no consistent relationship with treatment or plant age.

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Table I. *Effect of Older Fruits on Growth and Abortion of Younger Fruits*

Fruits within each raceme were classified into categories of "older" (those at the base of the raceme), "younger" (those in the upper part of the raceme), and "aborting" (those showing premature loss of green color and lack of developing seeds). Fruits were tagged and measured, followed by the removal of older fruits from treated plants (day 0). Control plants were left intact. After 13 days (day 13) each category of fruits was counted and measured. Fruits retained their original classification regardless of size, except that newly yellowing fruits were included in the aborting category. I: intact plants; D: defruited plants (older fruits removed). Data represent the mean obtained from two plants.

Cultivar	Plant Age on Day 13	Treatment	Day	No. of Fruits/Plant			Mean Fruit Length		
				Older	Younger	Aborting	Older	Younger	Aborting
	days							*cm*	
Redkloud	52	I	0	28	36	6	8.8	3.0	2.3
	52	I	13	22	4	14	13.3	13.1	8.5
	52	D	0	25	35	2	10.9	3.0	1.5
	52	D	13	–[a]	13	6	–[a]	15.1	4.8
	62	I	0	22	18	12	14.2	7.9	6.6
	62	I	13	18	1	18	14.7	9.5	10.0
	62	D	0	24	14	13	13.5	7.3	7.9
	62	D	13	–[a]	5	12	–[a]	12.6	9.5
Redkote	63	I	0	36	54	4	11.6	3.6	3.4
	63	I	13	24	5	30	13.6	10.1	8.0
	63	D	0	37	55	7	11.5	3.5	3.7
	63	D	13	–[a]	25	14	–[a]	12.4	6.1
	69	I	0	24	7	13	12.9	6.1	6.8
	69	I	13	16	0[b]	16	13.2	–[b]	12.1
	69	D	0	18	9	10	13.3	6.8	8.8
	69	D	13	–[a]	4	13	–[a]	11.6	7.7

[a] Fruits removed (see under "Materials and Methods").

[b] All fruits aborted.

Table II. *Effect of Older Fruits on ABA Concentration of Younger Fruits*

Plants were the same as those described in Table I. On day 13, fruits were harvested and analyzed for ABA. I: intact plants; D: defruited plants (older fruits removed). Data represent the ABA concentration of individual samples formed from all fruits belonging to a category on a plant. There were two plants in each age/treatment group.

Cultivar	Plant Age on Day 13	Treatment	Younger Fruit Mean Dry Weight	ABA Concentration of Fruits		ABA per Younger Fruits
				Older	Younger	
	days		*g*	*ng ABA/g dry weight*		*ng ABA/fruit*
Redkloud	52	I	0.55	289	443	243
	52	I	0.97	338	520	507
	52	D	0.88	–[a]	135	119
	52	D	0.83	–[a]	84	70
	62	I	0.70	595	18,700	14,400
	62	I	–[b]	357	–[b]	–[b]
	62	D	0.90	–[a]	1,960	1,760
	62	D	1.09	–[a]	1,840	2,020
Redkote	63	I	0.30	178	276	39
	63	I	0.69	105	419	289
	63	D	0.86	–[a]	210	181
	63	D	0.62	–[a]	110	68
	69	I	–[b]	97	–[b]	–[b]
	69	I	–[b]	68	–[b]	–[b]
	69	D	0.93	–[a]	806	753
	69	D	1.00	–[a]	870	866

[a] Fruits removed (see under "Materials and Methods").

[b] All fruits aborted.

DISCUSSION

There was much premature senescence among bean fruits, leading to the abortion of many fruits at all stages of development. Aborting fruits were characterized by cessation of seed development, flattening of pod walls, and loss of green color, followed by eventual abscission. Premature senescence was especially prevalent among the relatively younger fruits growing in the upper part of individual racemes. First formed fruits at the base of racemes aborted much less frequently. Upon the removal of these older fruits, the incidence of abortion among the younger fruits was greatly reduced. Competition thus exists among developing fruits, and older fruits can cause premature senescence and abscission of younger fruits.

Competition by fruits could affect earlier stages of reproductive development as well. Van Steveninck (16) noted on lupine plants that flowers in the lower whorls of a raceme set more fruits than those toward the apical part of the raceme. Removal of the older, more basally located fruits from the raceme increased fruit set of subsequently opening flowers. The well known phenomenon of alternate bearing among stone and pome fruits seems to depend on the inhibition of flower-bud differentiation by developing fruits (2). Competition by fruits could, therefore, affect all stages of reproductive development, and may be a significant cause of such widespread phenomena as failure of flower formation, flower abscission, and early fruit drop.

The mechanism through which fruits control the development of other parts of the plant is not known. The senescence of the apex in peas (3) and the leaves of soybeans (7) is thought to be promoted by an as yet unidentified "senescence factor" or "senescence signal" released by fruits. Wareing and Seth (17) were able to replace the senescence-inducing effect of bean fruits on leaves with an application of IAA to the deseeded pods. In peas, GA_3 applied to the apex under senescence-inducing conditions prevented senescence (3). In this work, the presence of older fruits increased the incidence of premature senescence and the ABA concentration of younger fruits on bean plants. In the companion article (15), fruits were found to contribute to axillary bud dormancy and increased ABA concentration in bud tissue. When the fruits were removed, bud growth resumed and the ABA concentration in the buds declined. Whereas in buds the decline in ABA concentration was apparently the result of dilution by increased tissue volume, in fruits the amount of ABA per fruit also decreased when older fruits were removed. The older fruits, therefore, seemed to have a direct controlling influence over the ABA content of younger fruits, suggesting in turn an active regulatory role for ABA in this correlative interaction. Since younger fruits collected for ABA analysis did not include aborting fruits, the higher ABA concentration in younger fruits of intact plants was not the consequence of senescence but perhaps a reflection of conditions preceding fruit abortion.

There are numerous reports suggesting a role for ABA in fruit and seed development. ABA concentration increased just prior to or during the maturation of orange fruits (14) and wheat grains (12) and the senescence of soybean pods (13). The external application of ABA enhanced the maturation and the resulting abscission of sour cherry fruits (18). ABA was also shown to stimulate ethylene production in various tissues (5, 6, 10). Thus, ABA may enhance senescence either directly or through the agency of ethylene (6, 10). The promotion by older fruits of young fruit senescence may be the result of increased ABA concentration in the younger fruits. The increase in the ABA content of presenescent fruits could merely be a consequence of the action of senescence-controlling factors, such as ethylene (1, 11). Further work is necessary to clarify the role of ABA in fruit senescence.

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