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Effect of Fruits on Dormancy and Abscisic Acid Concentration in the Axillary Buds of *Phaseolus vulgaris* L.[1]

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IMRE A. TAMAS[2], JIM L. OZBUN[3], AND DONALD H. WALLACE
Department of Vegetable Crops, Cornell University, Ithaca, New York 14853

LOYD E. POWELL
Department of Pomology, Cornell University

CAROL J. ENGELS
Biology Department, Ithaca College, Ithaca, New York 14850

ABSTRACT

The mechanism regulating the growth of adult plants in two determinate bean (*Phaseolus vulgaris* L.) cultivars was investigated. "Redkloud" plants flowered, formed fruits, and ceased shoot growth earlier than "Redkote" plants. Redkloud attained a smaller plant size, compared to Redkote, by imposing dormancy on axillary buds at an earlier age. In both cultivars, cessation of bud growth coincided with maximum combined fruit length per plant. Removal of fruits caused resumption of axillary bud growth within 4 to 5 days. The amount of new growth induced by fruit removal depended on the cultivar and plant age. In fully developed Redkloud plants, where shoot growth had already ceased, total leaf and shoot number per plant nearly doubled within 2 weeks following fruit removal. A much smaller response was observed in the still growing Redkote plants. Fruits, therefore, are assumed to play a major role in the regulation of shoot growth and total plant size through the control of axillary bud dormancy. It seems that smaller plant size, earlier maturity, and earlier senescence of Redkloud, compared to Redkote, were the result of earlier flowering, and accomplished in part through the growth-inhibiting action of fruits.

The endogenous abscisic acid (ABA) concentration of axillary buds was higher in Redkloud than in Redkote. It increased with plant age in both cultivars. Five days after fruit removal the ABA level in bud tissue dropped to approximately 10 to 30% of the control level. When buds were treated with a solution of ABA containing 5 nanomoles of ABA per bud, growth was substantially inhibited. Fifteen days after ABA application the mean length of growing buds on intact and defruited plants was reduced by 40 and 62%, respectively, compared to the untreated controls. A role for ABA in axillary bud growth regulation was not firmly established, but these data suggest correlation between the growth potential of axillary buds and their ABA concentration.

Plant development involves an ordered sequence of events leading to the characteristic shape and size of each plant species. Each morphological variable, such as number or size of shoots, fruits, and other organs, tends to fall within a predictable range under a given environment. The mechanism determining the specific morphology of various plants is not well known. This paper and the companion article (19) suggest that fruits play a major role in plant development by inhibiting the growth of axillary buds and the development of other fruits as well. Related effects of fruits including the enhancement of senescence in leaves (8, 23) and apical meristems (10) have been reported.

ABA is known to occur (12) and undergo metabolism (24) in bean plants. Inasmuch as ABA has been found to affect growth in various species (2, 9) the present work also explored the relationship between axillary bud growth and endogenous ABA content in bean plants.

MATERIALS AND METHODS

Plant Material. Bean plants (*Phaseolus vulgaris* L. cv. Redkloud and cv. Redkote) were grown in pots containing a mixture of equal parts of peat and Vermiculite supplemented with mineral nutrients (1). The plants were fertilized weekly with a 0.24% (w/v) solution of a commercial fertilizer. Growth kinetics was determined with plants grown in a greenhouse during the long days of late summer and early fall. The plants used to study the effects of fruit removal, including hormone analysis, were grown in a controlled environment growth chamber at 28 C day and 22 C night temperature, and 60 to 70% RH. Daily illumination for 16 h by fluorescent tubes was supplemented by a small amount of incandescent light (48 50-w bulbs over an 8.8 m^2 area). Total intensity at the top of adult plants was about 5×10^4 ergs cm^{-2} s^{-1}. The timing of developmental events in the growth chamber was found to be similar to that in the greenhouse under the conditions given.

Growth Measurements. The number and/or length of stems, leaves, flowers, and fruits was determined on the same three greenhouse-grown plants at intervals. Total stem length per plant included the length of the central axis plus the axillary branches and their laterals. The reported number of flowers or fruits per plant included only those attached to the plant at the time of measurement. However, leaf number per plant included the abscised leaves, thus representing accumulated totals.

Fruit Removal. To study the effect of fruits on shoot growth (Fig. 2), growth chamber-grown plants were selected at varying ages from 23 to 49 days for Redkloud and 48 to 94 days for Redkote. All fruits (and flowers when present) were removed simultaneously from treated plants (two plants per age group for each cultivar) while an equal number of plants were left intact as controls. Leaf and shoot number per plant were determined at and 14 days after fruit removal. To study the effect of fruits on the

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[2] On leave from the Biology Department, Ithaca College, Ithaca, New York 14850.

[3] Present address: Department of Horticultural Science and Landscape Architecture, University of Minnesota, Saint Paul, Minnesota 55108.

endogenous ABA concentration in buds (Table I), plants were grown and fruits were removed as before. Five days after fruit removal, buds were harvested for analysis. All buds on a plant were used to form a sample.

ABA Extraction. Axillary buds up to about 10 mm in length were detached at the base. All buds from a plant were combined to form a sample (usual sample size varied from 30 to 200 mg dry weight per plant). The tissue was frozen over dry ice immediately upon harvesting, freeze-dried, and stored at −20 C in closed vials. Samples were ground in a Wiley mill, extracted at 0 C with 50 to 100 ml of 80% (v/v) methanol for 4 to 5 h and then again with 50 to 100 ml of methylene chloride overnight. The two extracts were passed through a Millipore filter (type HA, pore size 0.45 μm) and combined. The solvent was evaporated under reduced pressure at 25 to 30 C using a rotating evaporator. The dry residue was taken up in 25 ml of 1% (w/v) aqueous $NaHCO_3$ (pH 8.3), shaken with methylene chloride (3 × 25 ml), the organic phase was then discarded. The aqueous phase was adjusted to pH 2.5 with HCl, and again shaken with methylene chloride (3 × 25 ml). The combined organic phase was evaporated, the residue transferred in decane to a silica gel column made with hexane (14) and washed with 25 ml of 12% (v/v) ethyl acetate in hexane (solvents used for eluting columns were saturated with 0.5 M formic acid). The ABA-containing fraction was eluted with 25 ml of 18% (v/v) ethyl acetate (16, 18). The dry residue of this fraction was taken up in methanol for analysis by gas chromatography. Organic solvents, excepting decane, were double distilled.

Gas Chromatography. The samples were methylated with diazomethane (14) according to Schlenk and Gellerman (17), and dissolved in ethyl acetate. Routine quantitative analysis of ABA was done in a Barber Colman series 5000 gas chromatograph (18). The column (1.8 m × 4 mm i.d.) was packed with 1% GE XE-60 on a solid support of Varaport 30, 100 to 120 mesh. Argon was used as a carrier gas at a flow rate of 120 ml/min. The amount of ABA in the sample was measured with an electron capture detector. Injector, column, and detector temperatures were 220, 195, and 220 C, respectively. Detector response (integrated by peak area) was determined daily with the freshly prepared methyl ester of authentic *cis-trans*-ABA.

The presence of ABA in the samples was confirmed by comparing the mass spectrum of the methylated sample to that of the methyl ester of authentic ABA in a Finnigan 330 Quadruple GC-MS System.

ABA Application on Buds. Redkloud plants at the age of 52 days were defruited, and each axillary bud was treated with a 5-μl droplet of 1 mM ABA dissolved in 0.01% (v/v) Tween 80 (5 nmol ABA per bud). Buds on control plants received an equal volume of 0.01% Tween 80. Eight days after the start of the experiment, the application was repeated. A group of intact plants were similarly treated. Each treatment included three plants. The length and number of buds were determined at intervals.

Statistical Analysis. The effect of fruit removal on plant growth and ABA concentration was evaluated by analysis of variance using version 6.01 of the computer subprogram ANOVA of the Statistical Package for the Social Sciences (6).

RESULTS

Growth Kinetics. The growth of Redkloud and Redkote plants was monitored from germination to fruit maturity. The initial growth rates of the two cultivars (Fig. 1, A and B) were essentially identical up to about 40 days, as judged by total stem length and leaf number per plant (although some leaves abscised from older plants, Fig. 1B shows the accumulated number of leaves to reflect overall plant size; all other data in Fig. 1 show values existing on the date of observation). The central axis of both Redkloud and Redkote plants completed expansion in about 37 days at heights of 48 and 67 cm and mean node numbers of 7.3 and 7.7, respectively. After the age of 20 to 25 days, buds on the central axis began to grow and gave rise to axillary shoots.

In both cultivars up to five or six buds were present at a given axillary position. Of these, as many as three or four eventually developed into axillary shoots. Both Redkloud and Redkote were determinate in growth habit, bearing racemes at the end of all fully developed shoots. This limited the length of individual shoots, so sustained plant growth was from continuous formation of new shoots from axillary buds. Plants ceased to grow when the axillary buds remained dormant. This occurred at 45 days from planting in Redkloud and about 70 days in Redkote (Fig. 1, A and B).

On Redkloud plants, maximum number of flowers (Fig. 1C) and fruits (Fig. 1D) appeared about 3 weeks earlier than on Redkote. For both cultivars, attainment of maximal fruit number (Fig. 1D) and maximal combined fruit length on a plant (Fig. 1E) coincided with the cessation of shoot growth. Decline in fruit number was caused by large scale fruit abortion, about 80% in Redkloud (between the ages of 50 and 90 days) and 70% in Redkote (ages 70–110 days). Aborting fruits were characterized by the lack of seed development, flattening of pod walls, loss of green color, and eventual abscission. The frequency of abortion varied with the length and position of the fruit within the raceme. Compared to the viable fruits, those fruits that would likely abort were about half the size of the viable ones. The smaller fruits that most often aborted were positioned near the tip of racemes, while the larger ones near the base of racemes, *i.e.* close to the subtending leaf, were least likely to abort.

Some Redkloud buds resumed growth about 90 days after planting when the fruits were fully mature and dry (Fig. 1, A and B). This caused an increase in the number of flowers (Fig. 1C) and fruits (Fig. 1D), and a decline in the mean fruit length (Fig. 1F).

Effect of Fruit Removal on Shoot Growth. That cessation of shoot growth (Fig. 1, A and B) coincided with maximal fruit number (Fig. 1D) and maximal combined fruit length (Fig. 1E) suggested the possibility that fruits exercised control over axillary shoot (bud) growth. This was next explored by comparing the axillary shoot growth of intact and defruited plants. Fruit removal caused a dramatic resurgence of growth of Redkloud plants 35 days or older, in which shoot growth had already ceased. In these plants the number of leaves increased 70 to 80% more than in the intact controls during a 2-week period following fruit removal (Fig. 2A). Corresponding values for the increase in the number of axillary shoots were 80 to 120% over the control (Fig. 2B). The response to fruit removal was negligible in younger, rapidly growing Redkloud plants. Shoot growth in intact Redkote plants continued until about 70 days of age, and showed 20 to 70% increase (depending on age) upon fruit removal over the control (Fig. 2, C and D). The effect of fruit removal was highly significant, as shown by analysis of variance, on both leaf number ($F = 50.8$, $P = 0.001$) and shoot number ($F = 55.5$, $P = 0.001$). For leaf number, over 15% of the total variation was due to fruit removal (the correlation ratio [eta^2] was 0.154), and for shoot number it was over 21% ($eta^2 = 0.215$). There was no significant interaction at the 5% level between fruit removal on the one hand and age or cultivar on the other. The increase in leaf and shoot number resulted from the growth of an increased number of axillary buds in both cultivars.

Effect of Fruit Removal on ABA Concentration in Buds. The possibility that the fruit-controlled inhibition of axillary bud growth was mediated through ABA was tested by determining the ABA concentration in the axillary buds of both intact and defruited plants 5 days after fruit removal. The concentration of ABA in bud tissue of control plants was higher in Redkloud (4.4–10.5 μg/g dry weight) than in Redkote (1–6 μg/g dry weight), and it increased with age in both cultivars (Table I). Five days after fruit removal the buds of defruited plants showed a significant

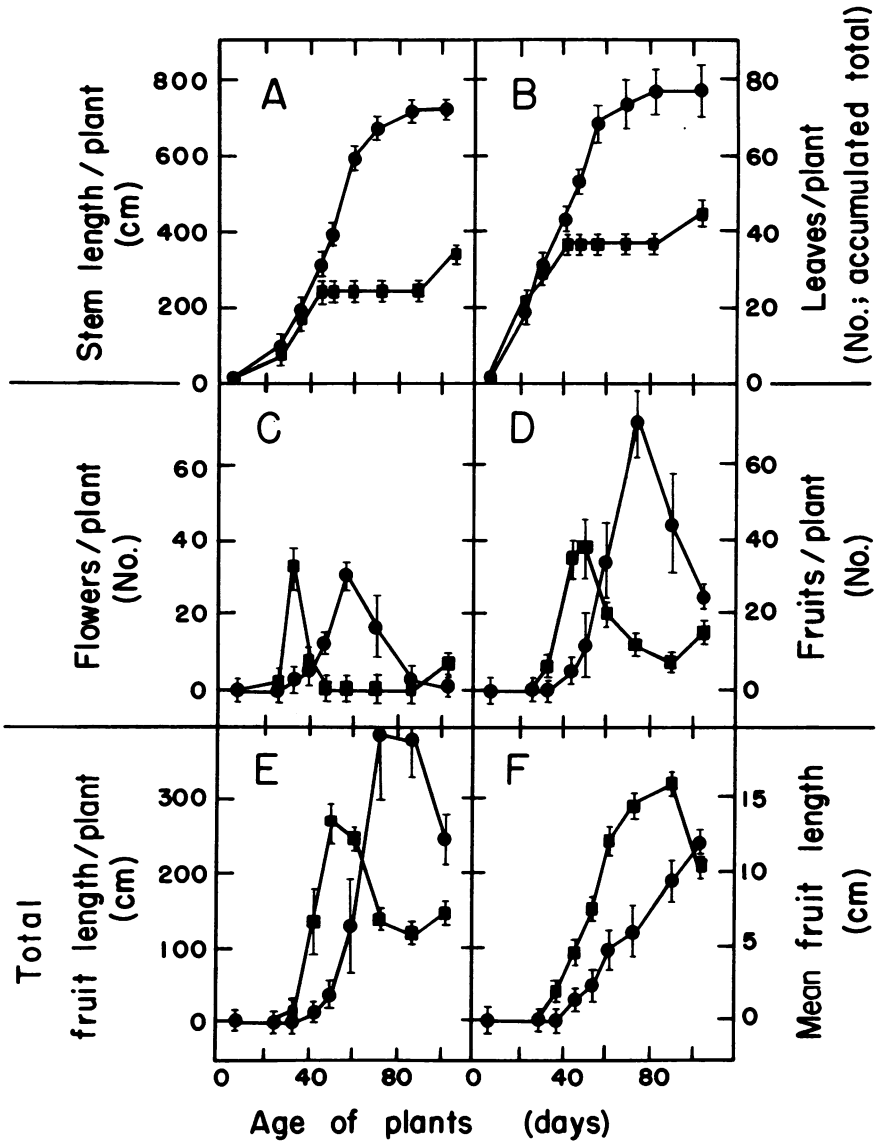

FIG. 1. Growth kinetics of Redkloud and Redkote cultivars. Plants of each cultivar were grown in the greenhouse and measured at intervals. Data points represent the mean obtained from three plants. A: total stem length per plant; B: accumulated total leaf number per plant; C: number of flowers per plant; D: number of fruits per plant; E: combined total length of all fruits on a plant; F: mean fruit length. In B, leaf number represents the accumulated total, including leaves already abscised. For all others, each data point shows the existing value on a given date. Error bars represent one standard error on each side of the mean. (■—■): Redkloud; (●—●): Redkote.

increase in size. Also, the concentration of ABA in the bud tissue of both cultivars dropped to approximately 10 to 30% of the control level. The effect of fruit removal on the ABA concentration in buds was highly significant ($F = 403.1$, $P = 0.001$). Over 35% of the total variation affecting ABA concentration was due to fruit removal ($eta^2 = 0.351$). Fruit removal also caused a small (about 15%) drop in the amount of ABA per bud, relative to that in the intact plants (Table I). Compared to the effect on ABA concentration, this change was much less significant ($F = 10.1$, $P = 0.034$).

Effect of ABA Application on Buds. When a solution of ABA was placed on the axillary buds of both defruited and intact plants, bud growth was inhibited (Fig. 3). Whereas the number of buds was not affected significantly ($F = 0.34$, $P = 0.999$), ABA application greatly decreased the length of buds, expressed as either mean bud length ($F = 22.2$, $P = 0.001$) or total bud length on a plant ($F = 32.0$, $P = 0.001$). There was relatively more inhibition of bud growth on defruited plants than on intact plants. Fifteen days after the initial ABA application on intact plants, the mean bud length of control and ABA-treated plants was 2.3 and 1.4 cm, respectively (Fig. 3E), representing about 40% inhibition by ABA. The corresponding values for defruited plants were 4.7 and 1.8 cm, respectively (Fig. 3F), giving about 62% inhibition. Similar differences were found between intact and defruited plants in the response of total bud length to ABA application (Fig. 3, C and D).

DISCUSSION

Fruits appeared to play a major role in regulating axillary shoot growth of two bean cultivars, Redkloud and Redkote. Because both cultivars had determinate growth, *i.e.* each main and axillary shoot terminated with a floral raceme, sustained growth required continued development of new shoots from axillary buds. However, during the development of fruits these axillary buds showed an increasing tendency to become dormant. Control of axillary bud growth by fruits is suggested in that in both cultivars bud growth repression coincided in time with maximal fruit number

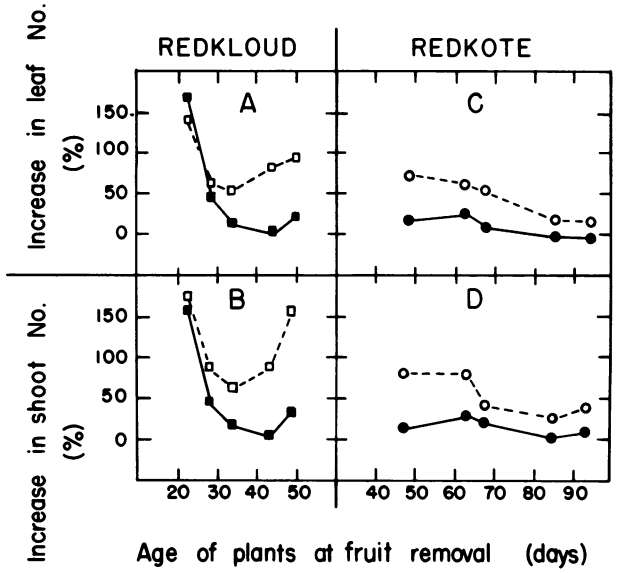

FIG. 2. Effect of fruit removal on shoot growth. Plants were grown in a controlled environment growth chamber. At varying ages, all fruits were removed simultaneously from certain plants. Other plants were left intact as controls. Leaf and shoot number per plant were determined just before and 14 days following fruit removal. Results are expressed as per cent increase in the measured variable 14 days after fruit removal. Each data point represents the mean obtained from two plants. A and C: increase in leaf number; B and D: increase in shoot number. (■——■): Redkloud, intact plants; (□——□): Redkloud, fruits removed; (●——●): Redkote, intact plants; (○- - -○): Redkote, fruits removed.

Table I. *Effect of Fruit Removal on the Endogenous ABA Concentration in Axillary Buds*

Plants were grown and fruits were removed as described under Figure 2. Five days after fruit removal, buds were harvested for analysis. All buds on a plant were used to form a sample. D: defruited plants; I: intact plants.

Cultivar	Plant Age at Harvest	Treatment	Mean Bud Dry Weight	ABA Concentration in Buds	ABA per bud
	days		*mg*	*μg ABA/g dry weight*	*ng ABA/bud*
Redkloud	43	D	10.8	0.45	4.9
	43	I	1.7	4.43	7.4
	48	D	6.9	2.72	18.8
	48	I	2.8	7.49	20.9
	53	D	7.7	1.93	14.8
	53	I	1.6	9.05	14.3
	63	D	9.7	0.82	8.0
	63	I	0.7	10.51	6.8
	68	D	5.2	1.82	9.5
	68	I	0.9	8.86	8.4
Redkote	64	D	7.6	0.26	2.0
	64	D	11.1	0.15	1.7
	64	I	3.0	0.99	3.0
	64	I	3.0	0.88	2.6
	70	D	12.3	0.11	1.3
	70	I	5.9	1.32	7.8
	70	I	9.8	0.75	7.4
	80	D	7.5	1.70	12.7
	80	I	3.6	4.60	16.7
	90	D	6.0	2.14	12.8
	90	D	5.0	3.22	16.3
	90	I	4.0	3.49	13.8
	97	D	5.0	2.01	10.1
	97	I	3.8	5.95	22.9

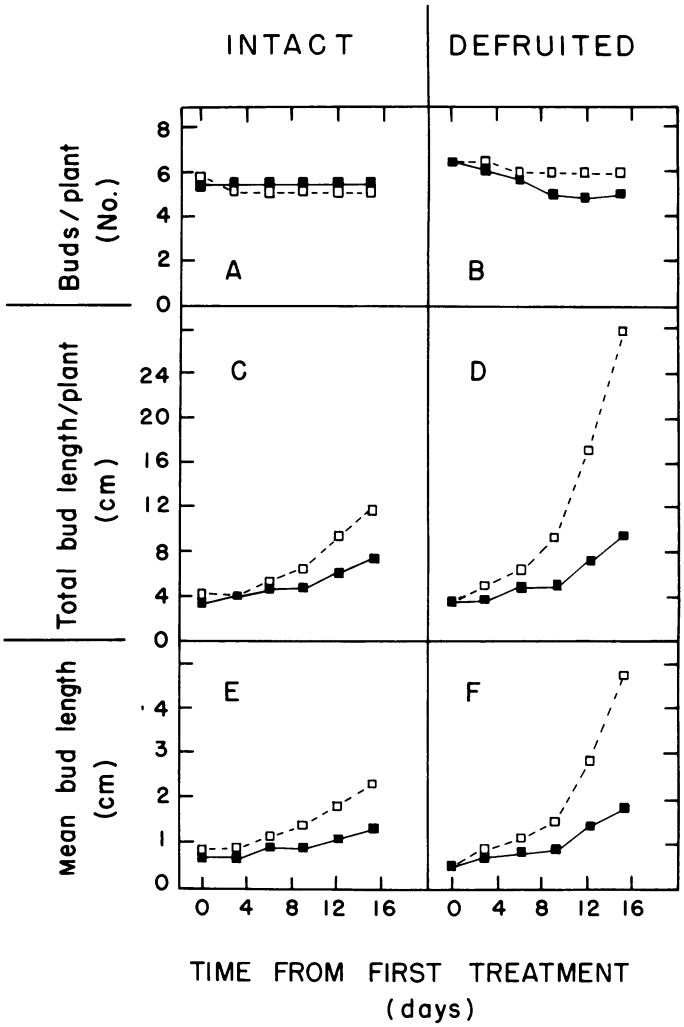

FIG. 3. Effect of ABA application on bud growth. Plants were grown in a growth chamber. Each axillary bud was treated with 5 nmol of ABA twice on both intact and defruited Redkloud plants. Data points represent the mean obtained from three plants. A, C, and E: intact plants; B, D, and F: defruited plants. (■——■): ABA treatment; (□- - -□): control. Day 0 represents the time of fruit removal and first ABA application. The second ABA application was given on day 8.

and maximal combined fruit length. Removal of fruits caused a 70 to 90% drop in the ABA concentration of buds and the resumption of bud development into growing axillary shoots. Fruits, therefore, appear to limit shoot growth by imposing dormancy on the axillary buds, in correlation with an increased ABA level in bud tissue. In Redkloud plants, repression of bud growth and accumulation of ABA in bud tissue occurred earlier than in Redkote, and there was a greater suppression of growth in Redkloud, matched by a higher ABA concentration in the buds. These results suggest that a relationship may exist between axillary bud inhibition and the ABA concentration in bud tissue. The fact that the lowered ABA concentration of buds in defruited plants coincided with bud growth suggests that the concentration decrease was due to a dilution of ABA by increased tissue volume. However, this cannot be known with certainty in the absence of data on ABA turnover in growing bud tissue. Although this work found only a modest drop in the amount of ABA per bud, the companion paper (19) showed a substantial decrease in the ABA content of young fruits, not resulting from dilution by growth, when older fruits were removed. Fruits appeared, therefore, to inhibit the development of axillary buds and other fruits, as well as to increase

actively the ABA content in affected fruits. It remains to be shown whether fruits could increase actively the ABA content of bud tissue as well.

The foregoing considerations suggest that lowered ABA concentration in bud tissue was not the initial stimulus causing the resumption of bud growth in defruited plants. However, the decreased inhibitor concentration was probably an important factor affecting continued bud growth. There is ample evidence that the growth-regulating effect of plant hormones, including ABA, is concentration-dependent. Moreover, results of this paper demonstrate that applied ABA is capable of inhibiting bud growth in the plants used here. Participation of ABA in correlative control of axillary bud growth is also suggested by data of Tucker and Mansfield (20) who found that the ABA concentration in axillary buds of *Xanthium* fell dramatically after they were released from the dominance of the apical meristem by decapitation. Application of synthetic ABA caused dormancy of actively growing seedlings of several woody species (2). Treatment with ABA also delayed budbreak in cuttings of *Acer rubrum* and *Fraxinus americana* (9). According to several reports, the ABA content was not well correlated with growth responses (15). Since regulation of bud growth may involve the interplay of two or more hormones (20), caution must be exercised in interpreting the relationship of growth with the level of a single substance.

The nature of the signal through which fruits control bud growth is not known. The ABA content of fruits in these experiments (data not given) did not show any relationship to their growth-suppressing effect on buds. Wareing and Seth (23) found, however, that the senescence-inducing effect of bean fruits on leaves was lessened by the excision of seeds, but was restored by an application of IAA to the deseeded pods. Since developing fruits usually produce significant amounts of IAA (5, 13, 21), it is conceivable that IAA serves as the correlative signal in the control of bud growth as well. Moreover, IAA is well known to perform that function in apical dominance (20). It is possible, therefore, that both the apical meristem and fruits control axillary bud growth through the same mechanism. Whereas in young plants the growing vegetative apex exerts a controlling influence, in mature plants fruits may become an important source of the correlative signal.

Results of an experiment on apical dominance in *Xanthium* suggested that IAA inhibited axillary bud growth by inducing ABA synthesis in bud tissue (20). Indeed, IAA was found to increase the level of an ABA-like inhibitor of pea stem sections (3). Whether fruits control axillary bud growth through a similar mechanism will be the subject of a subsequent communication.

Under long daylengths and moderately high temperatures, prevailing during these experiments, the two cultivars developed at different rates. In Redkloud, compared to Redkote, the various phases of development occurred earlier, including flowering, fruit set, cessation of axillary shoot growth, fruit maturity, and plant senescence. In addition, the size of Redkloud plants was substantially smaller. It seems likely that all of these characteristics of Redkloud resulted, directly or indirectly, from the early induction of flowering. Under short-day conditions, both flowering and maturation in Redkote plants occurred as early as in the photoperiod-insensitive Redkloud plants (4), suggesting that the timing of flowering might determine the progress of subsequent plant development. The phenomenon of axillary bud growth control by fruits, described in this work, helps to explain how the timing of flowering regulates not only fruit development, but shoot growth and final plant size as well. Since Redkloud plants completed flower and fruit formation and repressed axillary bud growth earlier than Redkote, they produced a smaller number of shoots and leaves. Fruits, therefore, directly affected the process of partitioning organic matter between reproductive and vegetative organs of the plant by altering their respective rates of development. Masaya (11) demonstrated that the effect of long daylength on the photoperiod-sensitive Redkote plants was to delay flowering and to increase the rate of development of shoots relative to fruits. In economically important species, the ratio of reproductive to total biomass may be expressed by the harvest index (the percentage of the plant's total weight represented by the weight of the useful product). The harvest index shows positive correlation with yield capacity in many species (22). Redkloud, the smaller of the two bean cultivars studied here, has a higher harvest index and, under long daylengths and moderately high temperatures, a greater yield capacity (7). The phenomenon of shoot growth control by fruits, therefore, may have a direct role in regulating yield capacity in these bean cultivars through its effect on plant size. Whether fruits in other species can also affect vegetative growth and yield capacity remains to be determined.

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