EFFECTS OF EXFLORATION ON PLANT METABOLISM

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(WITH TEN FIGURES)

Introduction

The practical importance of the proper balance between the vegetative and reproductive processes in fruit crops has stimulated many horticultural investigations seeking to improve our practical control of these functions. Owing to the slow growth, large stature, and perennial habit of fruit trees as well as their delayed response to experimental manipulation, it has been difficult to secure comprehensive data directly. Consequently considerable work has been done on short-lived annuals, like tomatoes, the development of which is known to be comparable to that of fruit trees.

Use of herbaceous plants in horticultural studies has incidentally provided a considerable amount of agronomic data, and hence it has been natural for the agronomist to extend such investigations in his own field to important herbaceous crops not previously investigated. The existing extensive literature implies that an inverse quantitative relation exists between the reproductive and vegetative processes, growth usually tending to diminish as the size of the fruit crop increases (**4, 5, 7, 13, 14, 21, 22, 23**). It should be noted, however, that structural features of the plant in part determine the relationship between vegetative and reproductive processes. In plants of the determinate habit, the inflorescence utilizes all the apical meristem and hence arrests elongation. According to many investigators, the indeterminate habit, on the other hand, presumably permits stem elongation to continue until the developing fruits begin to monopolize the food supply. The fact that fruiting obviously interferes with elongation in crop plants of the indeterminate growth habit has led to the inference that all plants of this type behave similarly (**26**). It is difficult, however, to see how this interpretation would apply to indeterminate plants which normally set only a small quantity of fruit. Moreover, the rosette vegetative phase of certain long day plants such as spinach suggests that the photoperiod may be as important as reproduction in suppression of stem growth.

In short day plants exhibiting arrested elongation under short day conditions, it is not apparent whether the response is due to fruiting or only to the shorter day length. Although the statement has been made (**2**) that "the reproductive phase of growth apparently curtails the vegetative phase" in the soy bean, a preliminary investigation by the writer dis-

closed that exfloration of the soy bean, an indeterminate short day plant, did not result in increased growth. The present investigation was consequently undertaken to discover why exflorated soy bean plants did not behave like more typical species such as the tomato, which continue vegetative development indefinitely if exflorated.

Methods

Initial exfloration experiments with soy bean plants grown in the greenhouse seemed to indicate that the vegetative development was not influenced by continued removal of flowers. To determine whether this lack of response to exfloration might have been due to unfavorable conditions in the greenhouse, the experiment was repeated during successive seasons on plants grown out-of-doors. The results being entirely confirmatory, a more intensive investigation was undertaken. Data presented here are for two crops of plants, one grown in the summer of 1931 and another in the summer of 1932. Ito San soy beans were grown out-of-doors in well inoculated soil and all flowers were removed from one series of plants but left to develop on the control series. All plants were watered during periods of dry weather. Material was harvested for chemical analyses at frequent intervals, 20-gm. samples being preserved in alcohol for carbohydrate determinations and larger samples dried in an oven at 100° C. for dry weight, total nitrogen, and ash determinations.

Total organic nitrogen not modified to include nitrates was determined on samples of the dried material. The material preserved in alcohol was extracted several times with 80 per cent. alcohol (37), reducing sugars being determined on aliquots of the clarified extract and expressed as dextrose. Aliquots of the same extract were hydrolyzed with hydrochloric acid for the determination of total sugars, which are also expressed as dextrose. The residue from the alcoholic extraction was hydrolyzed by boiling for 2.5 hours with dilute hydrochloric acid under a reflux condenser. Reducing sugars were then determined and expressed as polysaccharides (20).

Samples of the dried material were ashed, dissolved in hydrochloric acid, and made up to volume for mineral analyses. Calcium was precipitated as oxalate and titrated with potassium permanganate. Phosphorus was determined colorimetrically by a modification of the Bell-Doisy colorimetric method (3). Magnesium was precipitated from the filtrate of the calcium determinations as magnesium ammonium phosphate and the phosphate content of the precipitate determined by the same method as used for phosphorus. Potassium was precipitated as potassium cobaltinitrite and weighed directly in Gooch crucibles.

Material for the 1931 crop was harvested when flowering began and a month later when the fruits had reached almost their full size. The samples designated as "leaves" represent composite samples of all the leaves on the plants. The stems were divided equally into upper and lower halves and are referred to as "upper stems" and "lower stems." Harvesting of the 1932 crop was begun when the plants were still very small and the data are more comprehensive, but unfortunately the plants were badly damaged by winds before the last harvest and their weights are not available. The "tips of stems" represent 2 to 3 inches of the tips of the stems.

FIG. 1. Similarity in appearance of mature exflorated and fruiting soy bean plant.

Data and discussion

Growth of normal Ito San soy bean plants proceeded rapidly for some time after flowering began, the check in the growth rate seeming to coincide with the enlargement of the fruits. The stem tips of rapidly growing plants were large and blunt, but as the plants reached maturity these tips became more and more slender and the new internodes became shorter until they finally ceased to grow.

Continuous removal of flowers, however, did not increase either height or diameter of the stems or size of the leaves. Growth stopped at the same time in the exflorated and the control plants. There was a slight wrinkling of the leaves of some of the exflorated plants. The similarity in appearance of the exflorated and control plants was striking (fig. 1). The ana-

TABLE I

ANALYSES OF 1931 ITO SAN SOY BEANS; PERCENTAGES IN TERMS OF DRY WEIGHT

| | JULY 3, 1931 | | | AUGUST 7, 1931 | | | | | | |
| | BLOOMING | | | EXPLORATED | | | CONTROLS | | | |
	LEAVES	UPPER STEM	LOWER STEM	LEAVES	UPPER STEM	LOWER STEM	LEAVES	UPPER STEM	LOWER STEM	FRUITS
	%	%	%	%	%	%	%	%	%	%
Percentage dry weight	22.20	12.15	15.09	30.80	27.71	29.03	30.90	24.77	27.15	27.05
Total nitrogen	4.36	3.00	1.49	4.04	1.60	1.50	3.95	1.52	1.20	3.63
Reducing sugars	1.34	2.58	2.04	1.23	2.79	1.97	1.02	4.37	4.37	2.10
Total sugars	4.34	5.90	5.53	3.25	4.90	3.73	2.82	6.58	6.21	4.92
Polysaccharides	17.43	15.81	16.44	17.65	22.42	26.44	12.49	16.18	18.18	21.92
Total carbohydrates	21.77	21.71	21.97	20.90	27.32	30.17	15.31	22.76	24.39	26.84
Calcium	1.43	1.28	1.11	1.72	1.14	0.92	1.95	0.93	0.79	0.82
Magnesium	0.26	0.28	0.28	0.26	0.27	0.34	0.28	0.27	0.34	0.27
Phosphorus	0.43	0.36	0.35	0.29	0.27	0.27	0.28	0.21	0.28	0.43
Potassium	2.53	4.39	3.62	1.57	1.78	1.50	1.35	1.87	1.28	2.32

lytical data for 1931 are given in percentages of dry weight (table I) and in grams per plant (table II), and are illustrated graphically (figs. 2–5).

TABLE II

SOY BEANS, ABSOLUTE WEIGHTS OF CONSTITUENTS IN GRAMS PER PLANT

	JULY 3	AUGUST 7		
	BLOOMING	EXFLORATED	CONTROLS (STEMS AND LEAVES)	CONTROLS (PLUS FRUITS)
	gm.	*gm.*	*gm.*	*gm.*
Fresh weight	134.00	269.00	257.00	364.00
Dry weight	24.00	79.50	73.00	101.80
Nitrogen	0.795	2.23	1.94	3.03
Reducing sugars	0.439	1.44	1.97	2.54
Total sugars	1.21	3.01	3.36	4.79
Polysaccharides	4.03	16.73	10.83	17.15
Total carbohydrates	5.24	19.74	14.19	21.94
Calcium	0.314	1.10	1.03	1.23
Magnesium	0.065	0.222	0.212	0.295
Phosphorus	0.096	0.222	0.190	0.326
Potassium	0.785	1.28	1.07	1.78
C/N ratio	6.58	8.85	7.32	7.24
Moisture / Potassium	140.20	148.00	172.00	147.40

It has been shown by MURNEEK (**23, 25**) that fruit production limits the growth of tomato plants and that defruiting or exfloration greatly increases the size of the plants so treated. Experimental exfloration has no such stimulating effect on the growth of the soy bean. This is a photoperiodic plant in which short day length apparently not only induces flowering but inhibits stem elongation as well. However, a shorter day seems to be necessary to affect the growth rate than to initiate flower formation, because growth continues for some time after flowering begins, long enough in fact to treble the dry weight of the stems and leaves, observations which are also confirmed by the work of other investigators. GARNER and ALLARD (**9**) found that Biloxi soy beans in a ten-hour day stopped growing as soon as flowering began, but under the influence of a 13-hour day they tended toward an everbearing habit so that growth and fruiting proceeded simultaneously. OWEN (**30**) observed that sterile soy bean plants became but little larger than those which set fruits, and that microchemical tests indicated the presence of an abundance of starch in the stems of these sterile plants.

NIGHTINGALE (**27**) believes that in *Salvia* assimilation of nitrogen is limited by a short photoperiod, and as a result carbohydrates accumulate in

the plants which then become fruitful because of the increase in the C/N ratio. Accumulation of carbohydrates in the stems of exflorated soy bean plants (figs. 6, 7) cannot be explained in this way because the soy bean is not limited in its ability to absorb nitrogen under short day conditions. This is evident from the data which show that about 36 per cent. more nitrogen is assimilated by the controls than by the exflorated plants under short day conditions during which fruiting normally occurs. Movement of
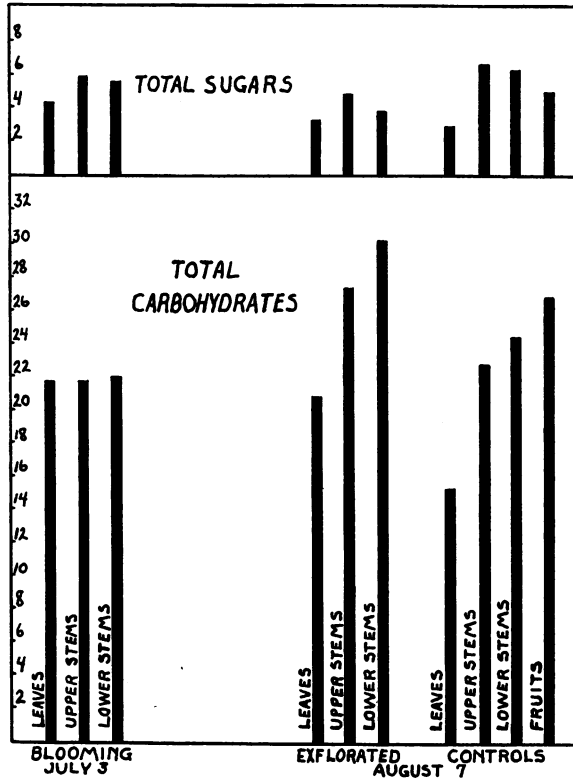
FIG. 2. Composition of soy beans; percentages in terms of dry weight.

nitrogen from the stems and leaves does not account for all of the nitrogen in the fruits. The analytical data not only show that the vegetative reserve is maintained but that more is taken in to supply the demands of the developing fruits. This interpretation agrees with the observation made by WEBSTER (39) that nitrogen in the soy bean is not massed in one part of the plant at the expense of any other part. Further confirmation of this condition is found in the data of BORST and THATCHER (2), which show that the absolute amount of nitrogen increases faster in the seeds than it decreases in the stems. GINSBURG and SHIVE (12) have also found that the

nitrogen content of normal soy beans was not appreciably altered by increasing the nitrogen concentration of the culture solution.

Data given in this report also indicate that nitrogen was not accumulated in exflorated plants, being but little higher than in the vegetative parts of control plants. On the other hand, the percentages of nitrogen were almost as high in the stems and leaves of exflorated and control plants as in flowering plants which were still vegetatively active. If lack of nitrogen assimilation had been the limiting factor in the growth of exflorated
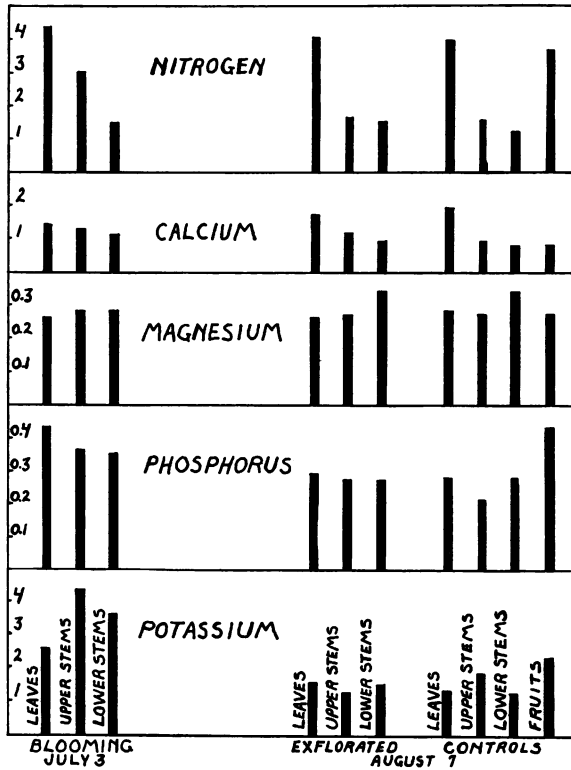

FIG. 3. Composition of soy beans; percentages in terms of dry weight.

plants, their nitrogen content should have been very low. Consequently, it may safely be concluded that the short day conditions which induce the reproductive phase do not entail nitrogen shortage, as suggested by NIGHT-INGALE for *Salvia*; and further, there is no experimental evidence to substantiate the hitherto commonly accepted inference that the nitrogen demand of fruiting soy beans is so great as to deplete all reserves and thereby interfere with growth.

It is also to be noted that there was a slow rate of potassium intake after flowering as compared with the increase in dry weight and nitrogen, and this was coupled with decreased succulence of the tissues. These conditions are significant and probably important factors in the cessation of growth. NIGHTINGALE, SCHERMERHORN, and ROBBINS (29) found that potassium deficiency caused an early setting of fruit, lack of growth, accumulation of carbohydrates, and a low proportion of meristematic tissue in the tomato.
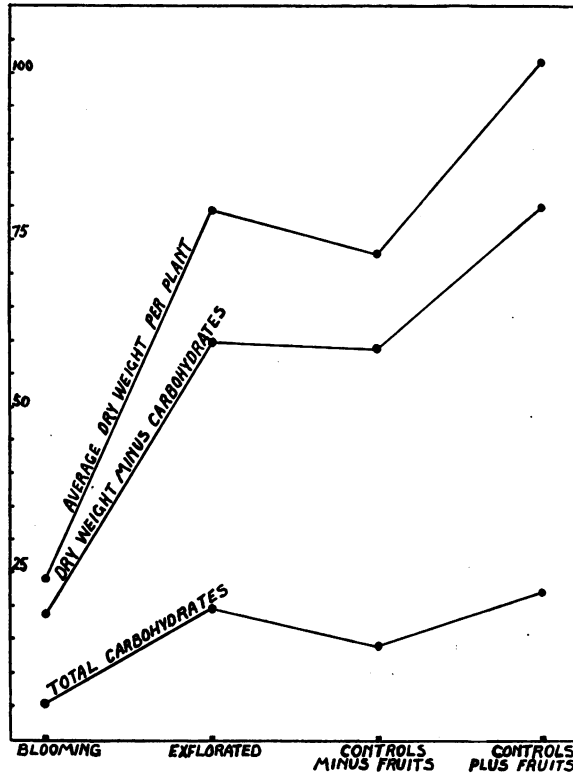

FIG. 4.   Composition of soy beans; absolute weights in grams per plant.

They concluded that growth was limited because potassium is essential for synthesis of organic nitrogen from nitrates. In the case of the soy bean, however, a different interpretation is more plausible, namely, that potassium deficiency limited nitrogen assimilation only indirectly because the mechanism of cell division and growth was inhibited. The plant still had the ability to assimilate nitrogen if it could be utilized by some growing part of the plant. The controls assimilated nitrogen to supply the developing fruits, although potassium was at the same low level in the vegetative parts of the controls as in the exflorated plants. In the soy bean, therefore,

potassium must be essential for the later stages of protein synthesis, *i.e.*, probably for the condensation of amino acids. Hence potassium deficiency interferes with the formation of new protoplasm and limits meristematic activity in the stems.

As in the case of nitrogen, neither calcium, magnesium, potassium, nor phosphorus accumulated in the exflorated plants and yet the development of fruits did not deplete the reserves in the controls. This means that prac-
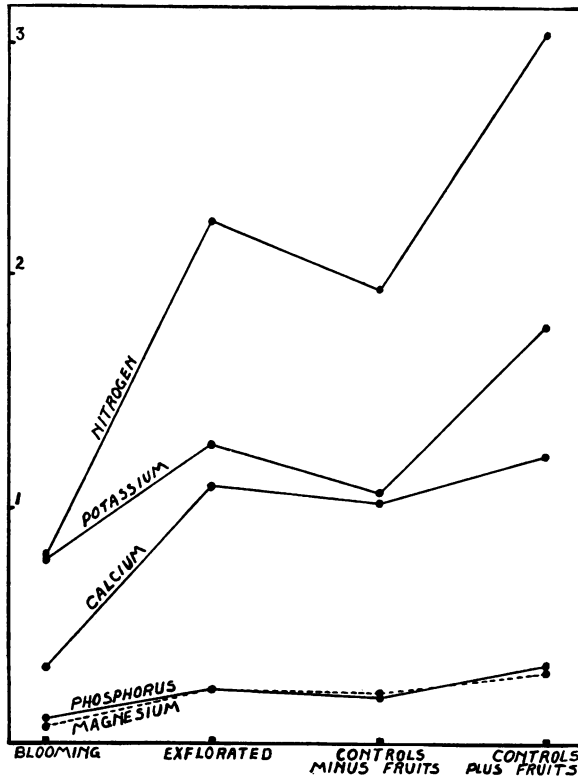

FIG. 5. Composition of soy beans; absolute weights in grams per plant.

tically the only substances stored in excess in the soy bean are carbohydrates; and that the plant, although inactive meristematically, still has the ability to take in nitrogen and minerals so that fruiting never becomes the exhaustive process which it is in some other plants (**23, 24**).

Arguments for and against the idea of balance between carbohydrates and nitrogen as the controlling factor in growth and reproduction of plants (**1, 6, 16, 18, 19, 28, 31, 32**) must consider the behavior of photoperiodic plants (**8, 9, 10, 11**). As already mentioned, *Salvia,* a short day plant, seems to be limited in its ability to assimilate nitrogen by a short day and
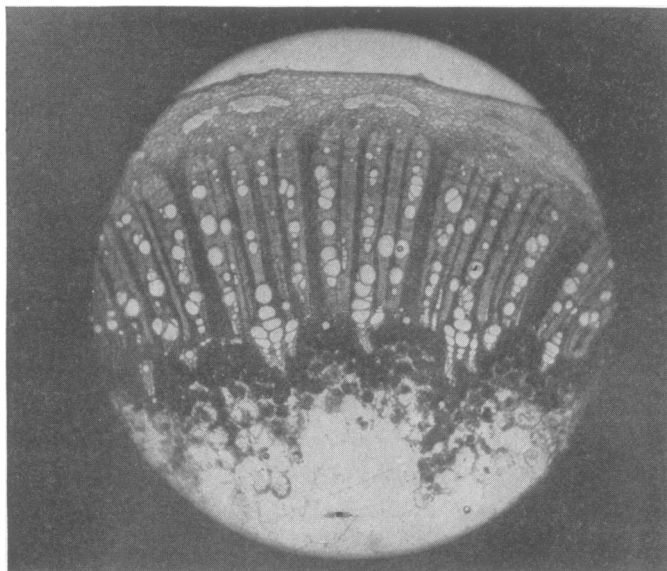
FIG. 6. Cross section of stem of exflorated soy bean plant stained with **iodine to** show storage of starch in medullary rays and pith.
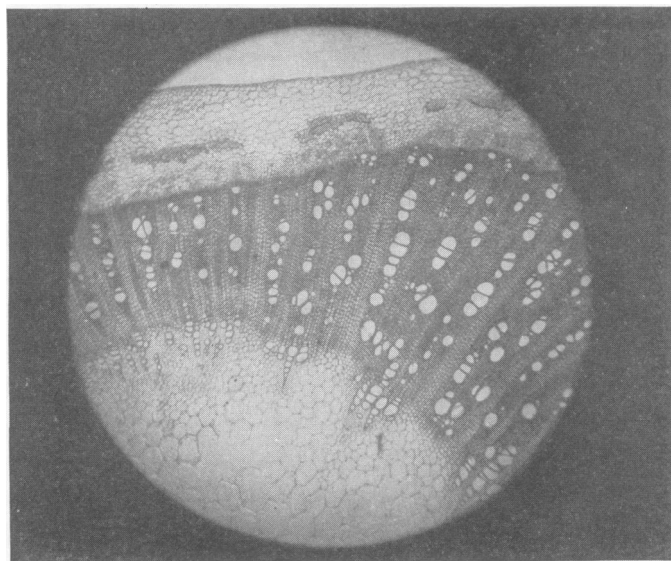

FIG. 7. Cross section of stem of normal control soy bean plant showing **practically** no starch (*cf*. fig. 6).

TABLE III

ANALYSIS OF 1932 ITO SAN SOY BEANS; PERCENTAGES IN TERMS OF DRY WEIGHT

DATE	PLANT PART	DRY WEIGHT	TOTAL NITROGEN	REDUCING SUGARS	TOTAL SUGARS	POLYSAC-CHARIDES	CALCIUM	MAGNE-SIUM	PHOS-PHORUS	POTAS-SIUM
		%	%	%	%	%	%	%	%	%
June 6	Leaves	14.45	5.20	2.67	4.16	11.34	2.12	0.377	0.440	2.29
	Tip of stem	9.04	4.20	6.30	8.70	12.49	1.32	0.296	0.611	5.08
	Upper stem	9.38	3.20	4.47	5.78	15.09	2.14	0.377	0.296	3.65
	Lower stem	15.26	2.02	2.23	2.67	16.62	1.58	0.285	0.212	1.89
June 21	Leaves	17.77	4.56	3.27	4.13	12.89	2.02	0.356	0.378	1.76
	Tip of stem	8.58	3.76	7.91	8.57	16.54	1.05	0.235	0.621	5.70
	Upper stem	11.01	2.31	6.00	6.43	15.89	1.31	0.248	0.290	4.10
	Lower stem	17.16	1.67	3.50	3.89	17.51	1.07	0.249	0.242	2.58
July 10; blooming	Leaves	15.00	4.99	4.40	5.42	16.12	1.28	0.215	0.467	2.60
	Tip of stem	8.94	3.17	7.60	10.78	16.41	1.23	0.237	0.592	5.01
	Upper stem	10.92	2.01	6.88	8.80	21.07	1.27	0.260	0.304	4.35
	Lower stem	17.88	1.11	4.36	5.68	18.44	0.95	0.243	0.242	2.18
August 18; exflorated	Leaves	28.96	3.35	1.85	3.77	22.65	1.88	0.313	0.266	1.06
	Tip of stem	23.54	2.20	3.21	5.31	21.43	1.49	0.297	0.347	1.42
	Upper stem	27.29	1.78	2.12	4.03	24.53	0.96	0.323	0.279	0.89
	Lower stem	31.78	1.38	1.62	3.36	20.91	0.80	0.352	0.315	0.72
August 18; controls	Leaves	25.83	3.91	2.28	4.33	16.55	2.31	0.425	0.278	0.83
	Tip of stem	22.19	2.39	3.92	5.18	17.18	1.26	0.315	0.273	1.05
	Upper stem	23.56	1.68	4.03	5.39	18.27	1.04	0.394	0.310	0.81
	Lower stem	30.97	0.66	2.89	4.57	18.93	0.61	0.256	0.186	0.32
	Fruits	20.62	3.95	4.27	7.09	22.24	1.02	0.261	0.502	1.34

TABLE IV
Soy beans, average total percentages per plant

TIME SAMPLED	PERCENTAGES			
June 6, seedlings (dry wt. per plant 1.30 gm.)	Dry weight	12.94	Calcium	2.01
	Total sugars	4.46	Magnesium	0.362
	Polysaccharides	12.30	Phosphorus	0.416
	Total nitrogen	4.62	Potassium	2.56
June 21, vegetative (dry wt. per plant 7.61 gm.)	Dry weight	15.79	Calcium	1.72
	Total sugars	4.56	Magnesium	0.318
	Polysaccharides	14.24	Phosphorus	0.356
	Total nitrogen	3.81	Potassium	2.36
July 10, blooming (dry wt. per plant 21.57 gm.)	Dry weight	14.18	Calcium	1.19
	Total sugars	6.34	Magnesium	0.231
	Polysaccharides	17.65	Phosphorus	0.384
	Total nitrogen	3.35	Potassium	2.92
August 18, exflorated	Dry weight	28.80	Calcium	1.47
	Total sugars	3.82	Magnesium	0.322
	Polysaccharides	22.54	Phosphorus	0.282
	Total nitrogen	2.61	Potassium	0.98
August 18, controls (minus fruits)	Dry weight	25.84	Calcium	1.65
	Total sugars	4.65	Magnesium	0.379
	Polysaccharides	17.40	Phosphorus	0.267
	Total nitrogen	2.73	Potassium	0.744
August 18, controls (plus fruits)	Dry weight	24.68	Calcium	1.54
	Total sugars	5.11	Magnesium	0.358
	Polysaccharides	18.30	Phosphorus	0.352
	Total nitrogen	2.96	Potassium	0.855

flowering accompanies the subsequent accumulation of carbohydrates. The experimental evidence for this conclusion, however, is very meager. In some long day plants the greatest accumulation of carbohydrates occurs under short day conditions, but flowering is initiated only by long days (**35, 36**).

From the results of ringing and defoliating experiments, HARVEY (**16**) claims that the vegetative responses of apple shoots are very definitely controlled by the ratio of carbohydrates to nitrogen. ROBERTS (**33**) and THOMAS (**34**) suggest that accumulation of carbohydrates interferes with nitrogen metabolism and retards growth. On the other hand, a high ratio of carbohydrates to nitrogen seems to be the result of inhibited or retarded growth and not the cause of it in many cases. HARTWELL (**15**) found that
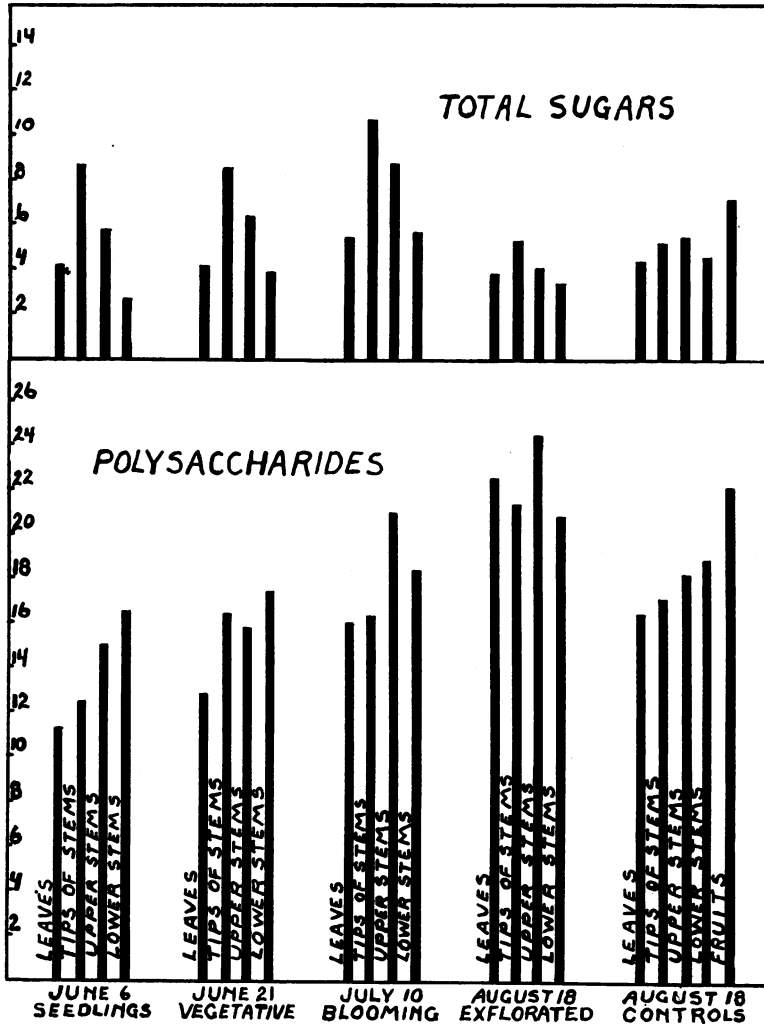
FIG. 8. Composition of soy beans; percentages in terms of dry weight.

accumulation of starch seemed to be correlated in general with conditions which caused a retardation of growth. If high carbohydrates limit growth, we still lack convincing experimental data to explain why long days stimulate growth in plants which have become high in carbohydrates under the influence of short days. This happens in some long day plants (35, 36), and GARNER and ALLARD (8, 9) have rejuvenated soy beans and other short day plants after they had begun to set fruits by subjecting them to long days.
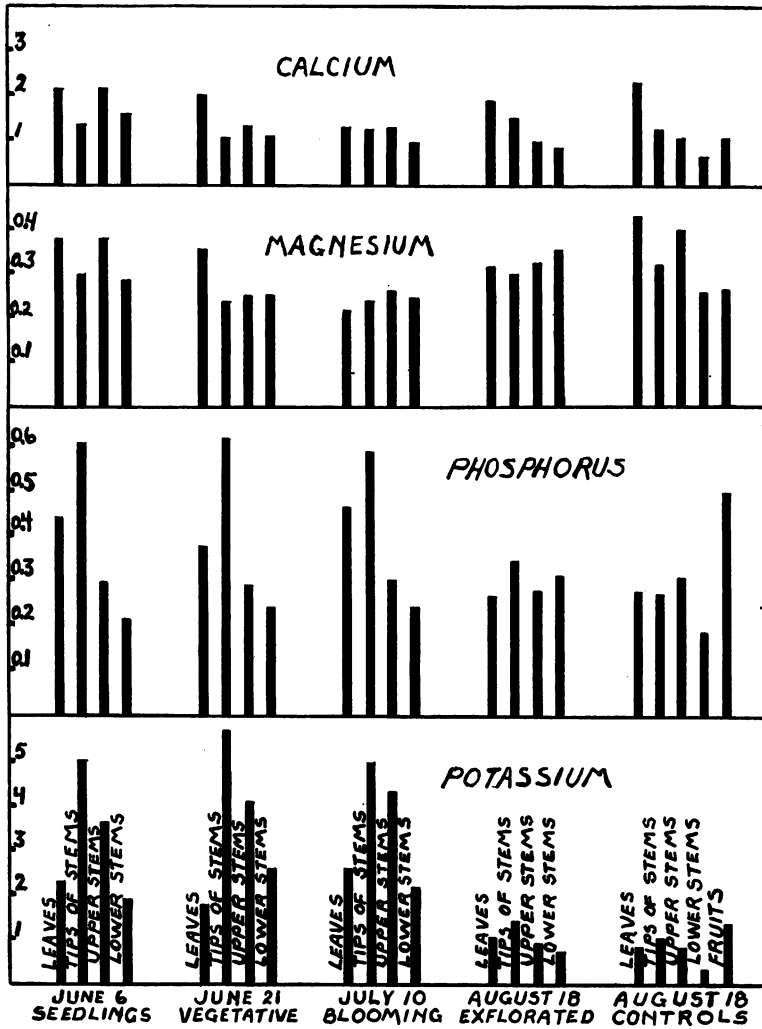
FIG. 9.   Composition of soy beans; percentages in terms of dry weight.

The data for 1932 (tables III and IV and figs. 8–10) are given in full, although this involves some duplication, because they cover a full life cycle and because they represent a more detailed analysis of the plants than do those for 1931.   These data disclose a high potassium content associated with high moisture content during the period of rapid growth, but nitrogen was not much higher in vegetative than in mature plants.   Cessation of growth could hardly be attributed to a shortage of nitrogen, but the short-age of potassium probably had something to do with the decrease in mois-
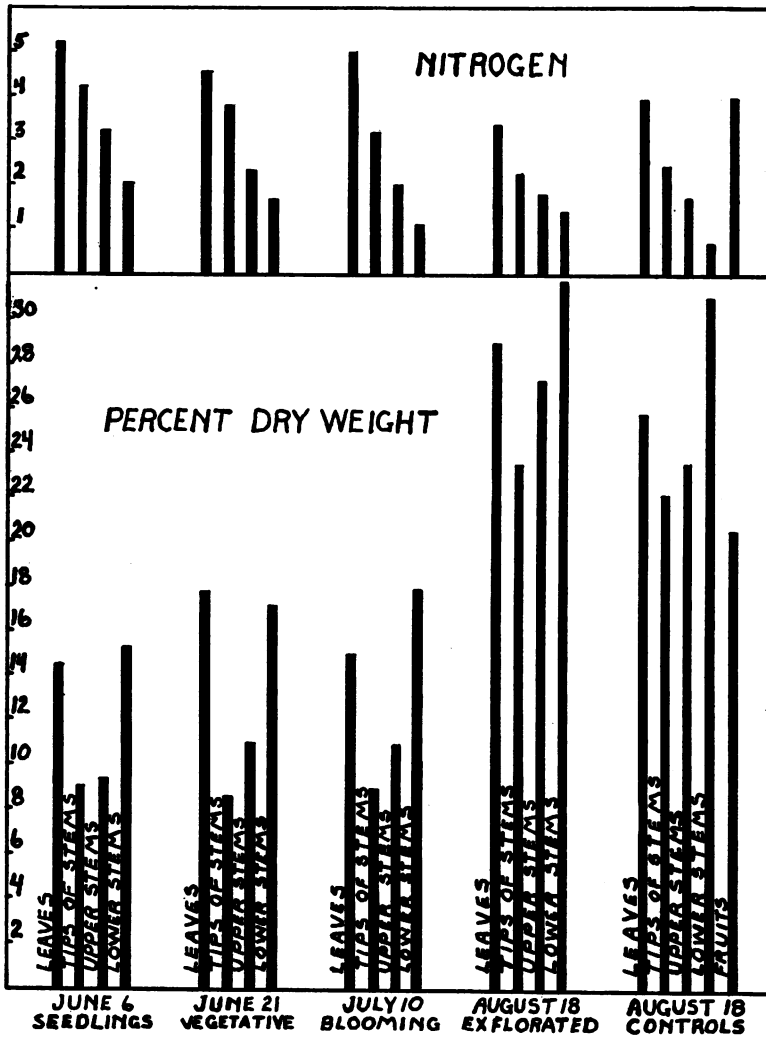
FIG. 10. Composition of soy beans; percentages of nitrogen in terms of dry weight and percentage dry weight in terms of fresh weight.

ture content and the retarded growth. Physiological dryness of tissues seems to be characteristic of plants deficient in potassium (36, 38). The appearance and behavior of exflorated soy bean plants are similar to those described by JANSSEN and BARTHOLOMEW (17) for tomato plants grown in a medium lacking in potassium. The percentages of phosphorus are highest in regions of rapid growth, stem tips of vegetative plants and fruits of control plants, but it does not decrease in other parts of the plant so much as does potassium when the plant stops growing.

Decreases in the percentages of potassium and moisture in the stems and leaves of mature soy bean plants are not due to fruiting since they are not prevented by exfloration. Likewise exfloration does not prevent cessation of growth. It seems likely then that the moisture, potassium, and to a less extent the phosphorus contents of the tissues are in some way related to nitrogen metabolism and the growth of new tissues. Whether these represent causes or only conditions accompanying particular growth responses cannot be stated with certainty.

In conclusion it may be stated that although growth of the soy bean plant normally stops at about the time that the fruits develop, plants from which the flowers are removed do not grow any larger than such normal plants. Hence cessation of growth is not due to fruiting, since it is not prevented by exfloration. Neither is it to be explained as a result of limited ability of the plant to absorb nitrogen. The best available explanation at present seems to be that the meristematic regions of the stem become inactive or dormant owing apparently to the decrease in day length, and the cessation of nitrogen absorption and the accumulation of carbohydrates are due to lack of growth. The exact mechanism of the action of the photoperiod is unknown, but in the soy bean it is related in some way to the moisture and potassium contents of the tissues. Exflorated soy bean plants show many of the symptoms of potassium starvation.

Summary

1. In normal soy bean plants growth stopped at about the time that the fruits developed, which would suggest that fruit development was responsible for the cessation of growth.

2. Exfloration did not increase the vegetative development, growth ceasing simultaneously in exflorated and control plants.

3. The soy bean is a photoperiodic plant and apparently the shortening of the day length not only initiates the reproductive phase but also curtails the vegetative processes.

4. A shorter day is required to inhibit growth in the soy bean than is necessary to initiate flowering.

5. There was an abnormal accumulation of carbohydrates in exflorated plants.

6. Nitrogen did not accumulate in exflorated plants, but on the other hand it was not depleted in control plants by the development of fruits.

7. Neither calcium, magnesium, phosphorus, nor potassium was depleted in control plants by the development of fruits.

8. As the plants ceased to grow there was an increase in the percentage of dry weight, or in other words a decrease in moisture content, in both exflorated and control plants.

9. This decrease in moisture content and cessation of growth were associated with a marked decrease in the percentages of potassium in all parts of the stems and the leaves. Phosphorus decreased in the stem tips when the stems ceased to elongate.

10. The behavior of exflorated soy bean plants resembles the responses of some other plants to potassium starvation, and the suggestion is therefore made that the length of day may affect vegetative growth through its influence on the concentration of potassium in the tissues of the plant.

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