

U EFFECT OF LIGHT INTENSITY, NITROGEN SUPPLY, AND
FRUITING ON CARBOHYDRATE UTILIZATION
BY THE COTTON PLANT¹

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(WITH EIGHT FIGURES)

The objects of the present investigation were to determine the effects of light intensity and nitrogen supply upon the accumulation of carbohydrates in the cotton plant and in turn upon the utilization of carbohydrates in growth and fruiting activities.

In some measure at least the American upland cotton plant differs from many agricultural plants in that from an early stage in its development, the vegetative and reproductive phases of growth proceed simultaneously; with the production of fruiting branches a non-fruitful condition can exist only as a result of the casting-off of floral buds and bolls during the course of their development. Fruiting branches usually arise from all but the lowest five to eight nodes of the main stalks, of the upland cotton plant, and from each of the nodes of these fruiting branches (fig. 1) there is subtended a floral bud and a leaf; these appear at the same time. The fruiting branches of the cotton plant are sometimes designated as sympodia but in this connection see the discussion of their morphology by Cook (5).

The investigation was developed by means of two sand culture experiments. The first was conducted at a relatively low average light intensity of about 900 or 1,000 foot candles at midday and the second under light intensities averaging about 9,000 or 10,000 foot candles at midday. In both experiments four nitrate concentrations were employed—a nitrogen-deficient level, two intermediate levels, and a toxically high level. Each experiment included two series of plants: (1) fruited plants, and (2) plants from which all floral buds were removed before they flowered. The latter plants were included to aid in differentiating between the effects of treatment and the effects of fruiting upon growth and upon carbohydrate accumulation and utilization.

The low-light experiment was conducted under muslin shades in a greenhouse during the winter and the high-light experiment under free exposure outdoors during the summer. Other than for a lowering of the position of the first fruiting branches in medium and late varieties (23), but not in early varieties, evidence is lacking of photoperiodism in American upland cottons. More definite effects of photoperiodism in a number of other cottons (23) have, however, been recognized. Given adequate light intensities and suitable temperatures, American upland cottons develop fruiting branches and bolls in a characteristic manner during either winter or summer.

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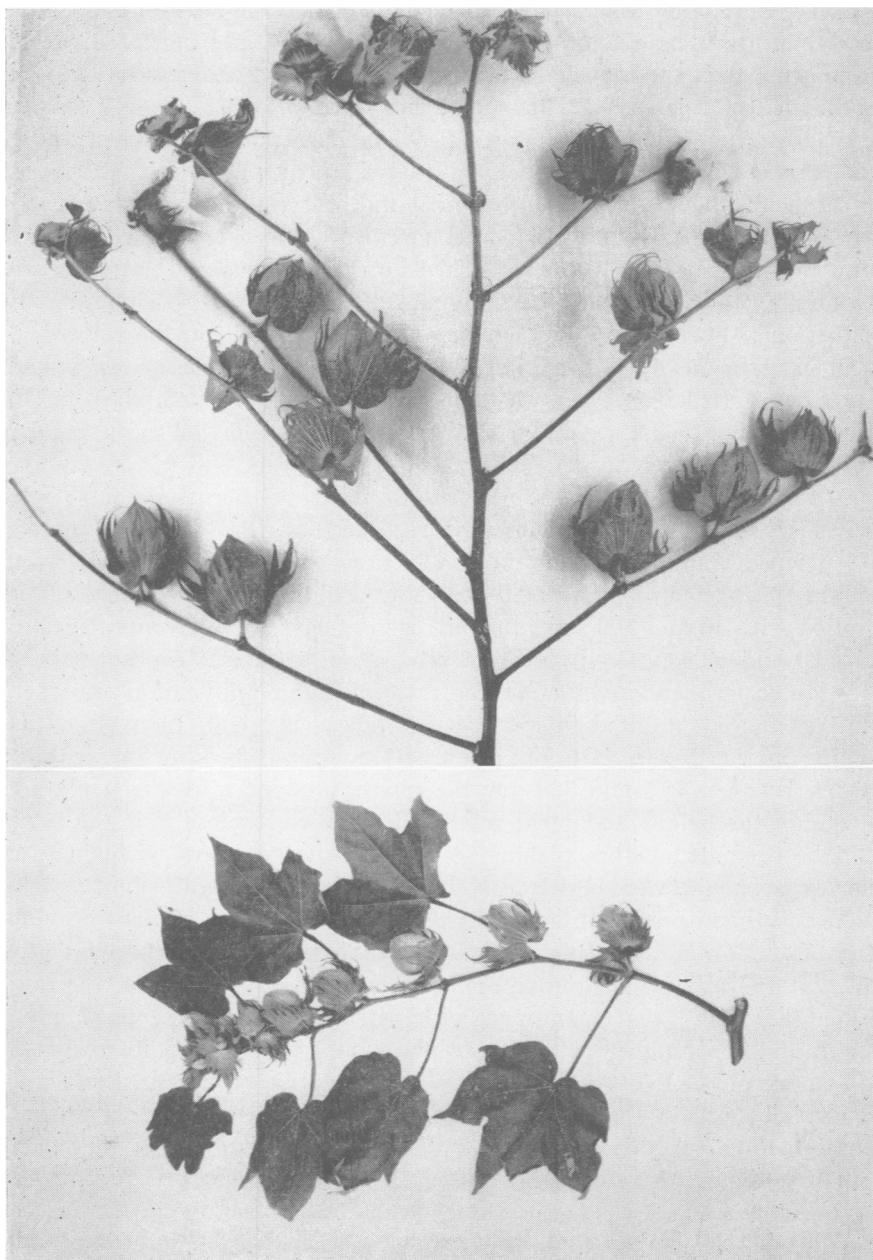


FIG. 1. Above: Upper portion of a cotton plant with leaves removed showing fruiting branches with bolls, vacant nodes (from which floral buds or young bolls had shed) and flowers and floral buds near the ends of the upper branches. Below: A single fruiting branch with a boll, or floral bud, at each node.

Investigations by others have shown that growth, flowering, and cotton production are increased up to certain points by the addition of nitrogen, phosphorus, and potassium, but that the addition of fertilizers has no outstanding effect upon fruitfulness in terms of the percentage of the bolls shed. HARLAND (17) working with Sea Island cotton in the West Indies found this to be the case and concluded that the principal loss in St. Vincent was occasioned by shedding due to fungal and bacterial diseases complicated by heavy rainfall. EWING (15), working with cottons of varied boll sizes, found the mean percentage of bolls shed by three varieties of cotton grown on a fertile valley soil to be 55.3 and on a hill soil 55.5; notwithstanding the production of over three times as many flowers and bolls on the valley soil. In an experiment by NELSON and WARE (30), in which greater growth responses resulted from nitrogen than from phosphate or potassium fertilization, shedding took place under all treatments in proportion to the number of blooms. The percentages of blooms shed were quite uniform in the five-year averages and largely independent of the fertilizer treatments; relatively high shedding percentages were recorded in a dry year. WADLEIGH (34), considering the effects both of nitrogen and of "physiological drought," reported 48.3 and 50.0 per cent. shedding by greenhouse plants supplied with 10 and 100 p.p.m. of nitrogen at low osmotic concentrations, and 46.0 and 58.5 per cent., respectively, at high osmotic concentrations.²

In an experiment involving three rates of water application and three of nitrogen that resulted in marked differences in yield, CROWTHER (7), working in the Sudan with Egyptian cotton, found shedding percentages varying between 30.5 and 39.8 for the nine treatments. Between plats in the Sudan the height and yield relationships were so close that the latter could be predicted before picking started. Between years, yields (9) in other experiments, were closely correlated in the Sudan with plant weight, height and the nitrogen content of leaves at various stages of plant development. Correlation failures in the Sudan area are noted in a paper on cotton in Egypt (8) as having been traced to pest damage. In Egypt, the same author (7) found that manuring with nitrogen usually increased plant growth and the number of bolls per plant, and that phosphate increased the amount of seed cotton per boll. The correlations found in the Sudan did not hold well in Egypt (8) because of shedding attributed to environmental factors. Additional data on the effects of nitrogen on the cotton plant, together with references to other literature, have been reported in

² Since this manuscript was prepared for publication, WADLEIGH (Arkansas Agr. Exp. Sta. Bul. 446, 1944) has published results on the responses of the cotton plant to variations in nitrogen supply over the non-toxic range; the plants were grown in a greenhouse during the summer. His paper deals extensively with nitrogen utilization and the work is extended to effects on fiber and seed.

Recent data by J. H. TURNER, JR. (Jour. Amer. Soc. Agron. 35: 688-698, 1944) are also pertinent. Under conditions of marked deficiency, the addition of potassium increased leaf retention, boll sizes, and the percentage of flowers that developed into bolls. These effects were most marked in years of high fruitfulness. Small-bolled varieties produced more flowers and shed less, but also yielded less, than did large-bolled varieties.

papers by ARMSTRONG and ALBERT (2), BROWN and POPE (5), HOLLEY, DULIN, and PICKET (19), and DASTUR (10).

The literature on the effects of light intensities on cotton is less extensive than that on nitrogen. EWING (15) in two seasons found no relation between shedding and cloudy weather but thought that there might have been a relation in a succeeding summer when his light recorder was not in operation. MASON (27), working in the West Indies, observed that during the later stages of plant development augmented shedding rates followed dark humid days during which there was generally much rain. He further observed, in keeping with his belief that carbohydrate availability was involved, that the removal of all leaves was followed by the dropping of most of the young fruit. DUNLAP (11), in similar connection, found that subjecting plants to light intensities of about 50 f.c. for a number of days caused shedding. Short fruiting branches were obtained by BERKLEY (3) in a winter experiment in a Missouri greenhouse under varied lengths of day. Cotton plants grown during the summer by KNIGHT (22) under the heavy shade provided by two layers of Hessian cloth had short fruiting branches which produced no flowers; under a single layer of white cloth the plant height was greater, but the numbers of main-stalk nodes and of fruiting nodes were fewer than those of freely exposed control plants and the yield was about half. Data on relations between light quality and fruitfulness are not available, but THARP (32) obtained a more rapid growth of young cotton plants in a cellulose-acetate-covered house than in a glass-covered house.

Plan and methods

The four nitrogen concentrations employed in the experiments were 1 (or as noted later, 0.5), 4, 16, and 64 milliequivalents of nitrate per liter of nutrient solution. Twenty-one Stoneville 2B cotton plants, each in a four-gallon jar filled with river sand, were grown at each nitrate level. Of these 21 plants, 14 were allowed to fruit and 7 were debudded. The concentrations in m.e./l. of nitrate and of the other nutrient-solution constituents added to tap water were as follows:

SOLUTION DESIGNATION	Ca	Mg	K	NO ₃	SO ₄	Cl	HPO ₄
1	2	4	3.3	1	4	4	0.3
4	4	4	3.3	4	4	3	0.3
16	16	4	3.3	16	4	3	0.3
64	64	4	3.3	64	4	3	0.3

The tap water contained (m.e./l.) Ca, 0.2; Mg, 0.1; Na, 2.2; HCO₃, 1.6; SO₄, 0.2; and Cl, 0.7. Magnetite was added to the sand as a source of iron at the rate of 0.2 per cent. Boron, manganese, and zinc were added to the nutrient solutions at the rate of 5.0, 0.5, and 0.05 p.p.m., respectively. The concentration of nitrate supplied to the low-nitrate plants in the low-light experiment was reduced from 1.0 to 0.5 m.e./l. during the first week of

flowering. This change was made because up to time of flowering the 1-m.e. plants under low light elongated as rapidly as did the 4-m.e. plants. The solution with 4 m.e. of nitrate was used for all plants prior to the start of differential treatments (see calendar, table I).

The nutrient solutions were added to the sand cultures in units of 2 liters with sufficient frequency to produce copious drainage. It was the general intention that from each two-liter addition there should be between 25 and 50 per cent. of drainage from the jars supporting the larger plants, with a proportionately greater amount of drainage from the jars supporting the smaller plants; the same amount of new solution was supplied to the jars under all treatments. Because of the uptake of nitrogen in excess of water by the plants growing in low-nitrate solutions and of water in excess of nitrate by the plants in the higher nitrate solutions, the nitrate concentrations in the drainage solutions departed substantially from the nitrate concentrations in the solutions applied. It is not implied, therefore, that the concentrations designated for the new solutions were those actually presented to the plant roots. Near the end of the low-light experiment, solutions displaced from representative pots in each treatment, following the addition of 2 liters of new solution after 24 hours' use of the old, had the following nitrate concentrations (m.e./l.):

FRUITED PLANTS				
Nitrate in solution applied	0.5	4.0	16.0	64.0
Nitrate in drainage solution	0.0	8.0	36.8	94.6
Percentage of solution recovered	65.0	28.0	37.0	64.0
DEBUDDED PLANTS				
Nitrate in solution applied	0.5	4.0	16.0	64.0
Nitrate in drainage solution	0.0	9.1	37.2	101.7
Percentage of solution recovered	57.0	39.0	30.0	36.0

The low-light intensities during the winter in the greenhouse experiment were obtained by the use of muslin shades suspended from rings strung on overhead wires. The shades were used on bright days, but on cloudy days they were drawn back. On cloudy days, without the shades, the daily light intensities at the tops of the plants customarily varied between 300 and 800 f.c. at midday. On bright days under the shades the light intensity at different positions in the greenhouse varied between 700 and 1,500 f.c.; this variation on bright days was caused principally by the partial shadow cast on one of the benches by overhead ventilators. The variation between the benches was equalized to some extent by shifting the pots so that each occupied 3 different positions during the flowering period; one shift in the position of the pots was made prior to flowering. The high-light experiment was conducted outdoors during the summer under free exposure. The outdoor light intensity on a horizontal plane varied from about 9,000 to 11,000 f.c. on bright days at midday. On cloudy days, of which there were relatively few during the fruiting period, the midday intensity probably did not fall below 3,000 f.c. A value between 900 and 1,000 f.c. during the low-

light experiment and between 9,000 and 10,000 f.c. during the high-light experiment would probably approach with sufficient accuracy the average midday light intensities during the respective flowering periods. A Weston photometer was used for the light intensity measurements.

Recognizing that plant development and boll development would be slower during short days in the greenhouse than outdoors in the summer, an effort was made to compensate roughly for the difference in the number of hours per day available for photosynthesis by extending the duration of the winter experiment (table I). The ratio of day lengths during the fruit-

TABLE I

CALENDARS FOR THE LOW-LIGHT AND HIGH-LIGHT EXPERIMENTS

PERIOD OR TREATMENT	LOW LIGHT				HIGH LIGHT			
	DATE	DAY LENGTH	ELAPSED TIME	INTERVAL	DATE	DAY LENGTH	ELAPSED TIME	INTERVAL
Planted	Oct. 20	<i>hours</i> 11.3	<i>days</i>	<i>days</i>	Apr. 8	<i>hours</i> 12.7	<i>days</i>	<i>days</i>
Diff. nitrate treatments started* ...	Nov. 18	10.5	29	29	May 6†	13.5	28	23
First flowers	Dec. 27	10.1	68	37	May 30	14.0	52	24
Cropped	Feb. 16	11.1	119	51	July 9	14.1	92	40

Cropping procedure: 10 A.M. C.S.T.‡ Duplicate samples of sound mainstalk leaf blades were collected from 12th to 16th nodes of each plant.
11 A.M. to 1 P.M. Cut and weighed bolls and tops of plants.
1 P.M.§ The roots of all plants were pulled out, washed free from sand, and the root bark was then separated for duplicate samples.

* Started using shades to reduce light intensity in low-light experiment on December 1.

† Plants removed from greenhouse to free exposure outdoors.

‡ At 10:30 A.M. the day had advanced about 34 per cent. beyond sunrise on February 16 and 38 per cent. beyond on July 9.

§ At 1:30 P.M. the day had advanced about 61 per cent. beyond sunrise on February 16 and 60 per cent. beyond on July 9.

ing periods in the two experiments was (winter/summer) $10.6/14.1 = 0.75$; the ratio of the periods allowed for fruiting was (summer/winter) $40/51 = 0.78$; and the ratio of the observed lengths of the periods from planting to first flowers was (winter/summer) $52/68 = 0.76$. The mean temperatures during the fruiting periods were similar; in the summer experiment the mean maximum was 90.7° , the mean minimum 71.9° , and the average mean daily temperature 81.3° F. The greenhouse thermostat in the winter experiment was set at 80° and there were substantial plus and minus departures from this that varied with the exterior temperature and radiation.

The time of cropping in the respective experiments was selected to coincide as nearly as possible with the probable approaching end of the period of weight increase of the first bolls set. As shown in figure 2, the daily rate of dry-weight increase of a cotton boll, although not linear, is substantial

from about the fifth day after flowering to about ten days prior to opening. Inasmuch as boll development was slower in the low-light greenhouse experiment than in the high-light experiment, the same average rate of carbohydrate movement to each boll per day did not occur under the two sets of conditions. With this qualification in mind, the number of developing bolls per unit of plant weight has certain advantages in a nutritional interpretation over shedding percentages which take as their basis the total number of buds or the number of flowers. All of the bolls of both experiments were still green when the plants were cropped and no data on the mature bolls were secured.

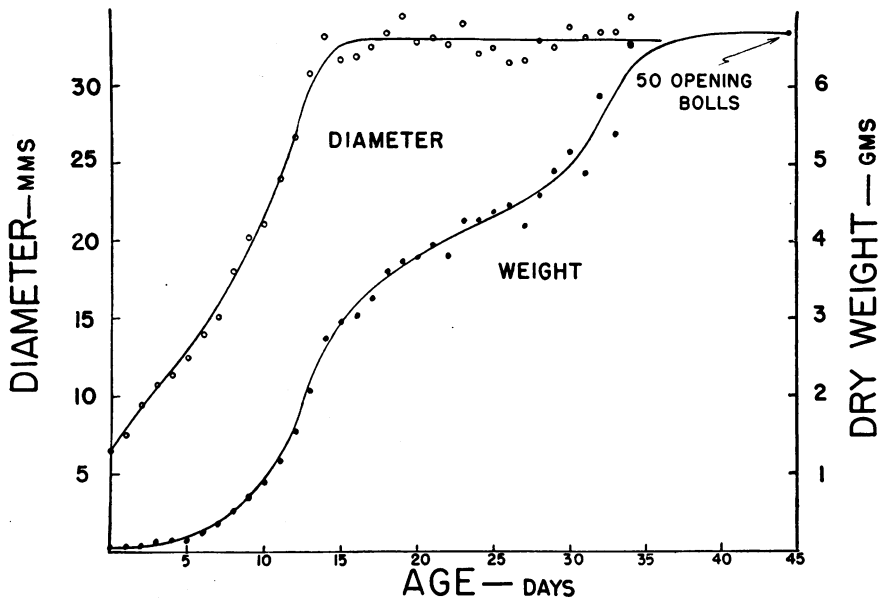


FIG. 2. The diameters and dry weights of Acala cotton bolls by days from flowering to maturity at Sacaton, Arizona, in 1926. The final 50 bolls (ages 42 to 46 days) were removed from the plants on September 20 and the others (4 to 20 bolls for each mean) were removed on August 26.

The fresh-leaf and root-bark samples were placed in, and the sugars extracted with, hot 80 per cent. alcohol (including water of the samples); neutral lead acetate and sodium oxalate were used in clarifying and deleading. Analyses for sucrose were made on solutions which had been inverted with hydrochloric acid for 24 hours at room temperatures. After gelatinizing 2-gram samples of the residues from the alcohol extraction, starch was determined by treating with 20 ml. of a 0.5 per cent. solution of undiluted diastase (supplied by courtesy of Parke, Davis and Company) for one hour at 55° C., again heating to boiling, cooling to 55° C., and re-treating with diastase, as before, for one hour or longer if the material still showed color with iodine solution. After cooling, the supernatant liquid was centrifuged from the residue and the latter washed three times. The solution was then

made to volume and hydrolyzed with acid for dextrose determination. The residue after the hydrolysis and extraction of starch was refluxed with 2 per cent. hydrochloric acid for 2.5 hours and the sugars reported as hemicellulose. The sugar determinations were made according to the method

TABLE II

GROWTH AND FRUITING OF COTTON PLANTS AS INFLUENCED BY LIGHT INTENSITY AND BY NITRATE SUPPLY. ALL VALUES ARE AVERAGES PER PLANT

LOW LIGHT												
TREATMENT AND NITRATE SUPPLY	HEIGHT	MAIN-STALK NODES	FRUITING BRANCH NODES*		FRESH WEIGHTS			FLOWERS		DEVELOPING BOLLS		
			TOTAL	ON CENTRAL BRANCHES†	STEMS AND LEAVES	BOLLS	TAP ROOTS	TOTAL	SHED	TOTAL	PER 100 GRAMS OF STEMS AND LEAVES	
<i>m.e./l.</i>	<i>cm.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>gm.</i>	<i>gm.</i>	<i>gm.</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>no.</i>	
Fruited												
1 (0.5)	70	18.7	1.6	128	117	11.8	6.9‡	17‡	5.7	4.46	
4	91	23.7	2.6	319	153	22.2	12.5‡	9‡	11.4	3.47	
16	95	23.9	2.6	328	150	21.6	12.5‡	10‡	11.2	3.36	
64	79	22.1	2.6	239	142	14.6	10.9‡	12‡	9.6	4.09	
Debudded												
1 (0.5)	123	23.6	25	2.7	197	17.6	
4	121	25.3	42	4.3	417	30.1	
16	116	26.0	46	4.2	443	29.2	
64	113	25.5	43	4.1	350	18.2	
HIGH LIGHT												
Fruited												
1	60	17.4	14	1.6	107	170	10.4	13.1	46	7.2	6.75	
4	91	21.9	52	5.3	382	458	28.1	33.7	35	22.9	6.42	
16	92	21.4	58	4.6	367	468	29.1	33.7	35	22.9	6.43	
64	81	20.0	38	4.0	252	370	22.0	32.3	43	18.4	7.58	
Debudded												
1	86	19.9	48	3.7	158	20.9	
4	113	23.4	107	4.5	555	46.6	
16	108	23.4	118	5.3	566	53.8	
64	102	21.9	104	5.4	445	41.8	

* Fruiting-branch nodes include all of those producing flowers or squares with a bract width of 15 mm. or more. There was a heavy shedding of very small squares by the fruited plants under low light but square shedding by the debudded plants under low light and by all plants under high light was negligible. Nodes counted on the fruited plants under low light were based on the size of the subtended leaves.

† Fruiting branches subtended by the 10th, 12th, and 14th main-stalk nodes.

‡ These values are so largely influenced by the heavy shedding of floral buds (see note above) that they have little significance.

of WILDMAN and HANSEN (35) except that in titration, potassium permanganate and ortho-phenanthroline indicator were used. By the foregoing procedure the division between "starch" and "hemicellulose" is drawn on the basis of diastatic activity.

It is well known that diastase is generic in its action since it includes

a number of enzymes which are capable of attacking starch, dextrin, and like substances. To add undue specificity to "starch" values in plant nutrition and thereby exclude from consideration closely related carbohydrates

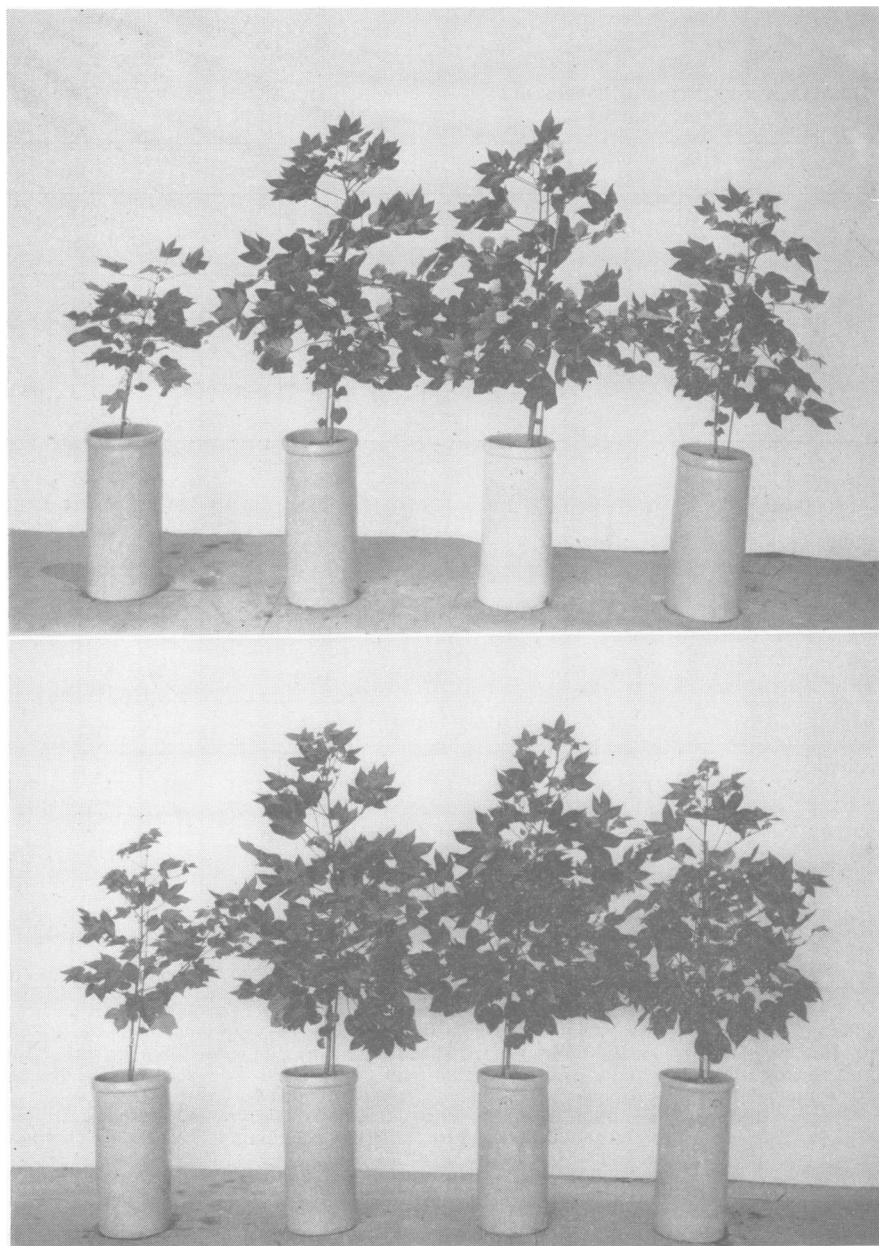


FIG. 3. Fruited (above) and debudded (below) cotton plants of average height at the end of the high-light experiment. Left to right: 1, 4, 16, and 64 m.e./l. of nitrate in nutrient solution.

is often undesirable and it is also undesirable to include these other compounds as "hemicellulose" since in such event the significance of the latter fraction is reduced.

Experimental procedure

PLANT DEVELOPMENT AND FRUITING

In both the high- and the low-light intensity experiments the vegetative development of the cotton plants (fig. 3) and the number of bolls they produced were reduced both by the low and by the high concentrations of nitrate (table II). In terms of relative fruitfulness, however, the plants on the solutions of very low and very high nitrate were slightly more productive than the plants growing on the substrates with intermediate nitrate;

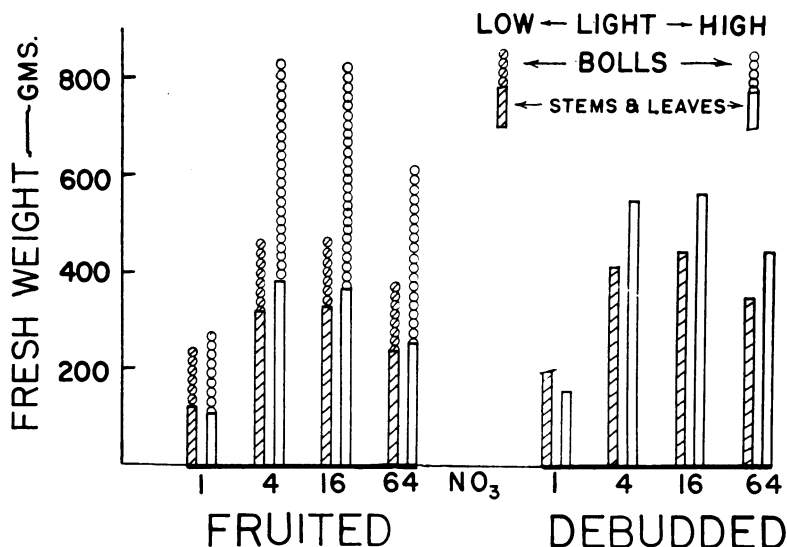


FIG. 4. Fresh weights of stems and leaves, and of bolls in the low-light and high-light experiments.

i.e., they produced more bolls per 100 grams of fresh weight of stems and leaves. These differences in relative fruitfulness were statistically significant in the low-light but not in the high-light experiment.

Under the high-light intensity the plants were markedly more fruitful than under low light, but high light did not result in a corresponding increase in the weight of stems and leaves (fig. 4). The average number of bolls per plant under low light (all nitrate levels) was 9.2 and under high light 17.9, whereas the average fresh weight of stems and leaves under low light was 253 grams and under high light 277 grams. Low light thus curtailed fruiting to a far greater extent than it did vegetative development. The fresh weight of bolls averaged 51 per cent. of the fresh weight of stems and leaves under low light and 132 per cent. under high light.

The heights of the plants and the number of main-stalk nodes were not

affected very much by light intensities, but light had a notable effect upon the number of nodes developed by the fruiting branches. Of the debudded plants those under high light developed twice as many fruiting-branch nodes as did those under low light. Similarly, except at the low nitrogen level, the fruited plants under the high light had many more nodes on their central fruiting branches than did those under low light. It appears accordingly that low-light intensity (or possibly the reduced carbohydrates associated with the low light) has effects on the development of fruiting branches that are distinct from its effects on the development of the main stalk.

There was a negligible amount of shedding of floral buds by both the fruited and the debudded plants under high light, but the shedding of floral buds was a prominent feature in the reactions of the fruited plants, but not of the debudded plants, under low light. The buds were removed from the debudded plants when they had involueral bract widths of about 15 mm., whereas the buds shed from the low-light fruited plants were customarily very small; usually they had bract widths between 2 and 5 mm.

The effects of nitrate supply and the effect of fruiting upon the growth of the cotton plant are shown by the diagrams in figure 5; these data are all from the high-light experiment. Favorable nitrate supplies, like the removal of floral buds, resulted in an increased number of both main-stalk and fruiting-branch nodes. Only nodes bearing squares with a bract width of about 15 mm. were counted and for this reason no squares are shown terminating the branches of the debudded plants. All of the higher branches of the debudded plants were actively growing and producing squares, however, at the end of the experiment.

The diagrams (fig. 5) bring out a salient difference in the effects upon growth of the deficient and toxic concentrations of nitrate. At the time of cropping none of the terminal buds of the main stalks of the low-nitrogen plants were active and few fruiting branches were terminated by squares. The high-nitrate plants, on the other hand, were still growing at the end of the experiment but at a slower rate than the plants in the intermediate concentrations; all of the terminal buds of the high-nitrate plants were active at this time and nearly all of the upper branches were still forming leaves and squares. Nitrogen deficiency, in other words, prevented vegetative expansion as these plants set the last of their bolls, whereas an excess of nitrate only slowed development.

High nitrate reduced the fresh weight of both fruited and debudded plants, under both light intensities, out of proportion to its effect on the number of main-stalk and fruiting-branch nodes; the morphological differentiation of parts by the high-nitrate plants was thus more rapid than was growth as measured either by internode length or weight of plant. In high nitrate, as in low nitrate, it was not only plant height that was reduced, but also the diameters of the main stalks and branches and the area of the leaves. CROWTHER (7) has dealt with the effects of nitrogen and of water on growth and differentiation in cotton over the non-toxic ranges of nitrogen

supply. He concluded that differences in internode lengths, which are correlated with yield, imply critical variation in water supply, whereas node numbers depend upon the amount of nitrogen. Data presented in

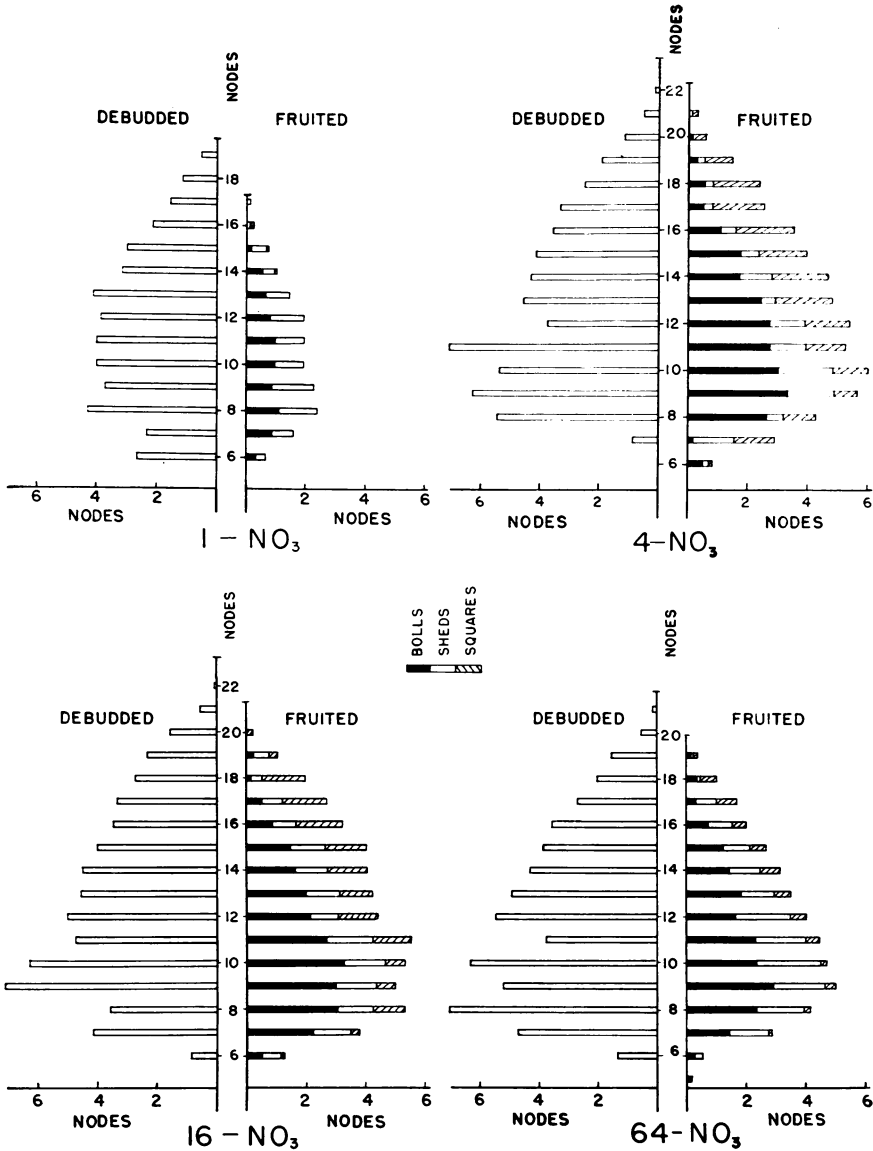


FIG. 5. Number of main-stalk and fruiting-branch nodes and number of bolls, sheds, and squares (floral buds) per fruiting branch at the four nitrate levels in the high-light experiment. See illustrations of the fruiting branches of cotton, fig. 1.

another paper (13) have shown that water movement to cotton leaves is probably not impaired by saline substrates, but that with saline substrates the water in the xylem vessels is continuously under tension.

The high-nitrate concentration was more toxic to the fruited than to the debudded plants. Under low light the weight of stems and leaves of the fruited plants supplied with 64 m.e./l. of nitrate was 28 per cent. below the mean of the two intermediate concentrations (4 and 16 m.e.), whereas the weight of the stems and leaves of the debudded plants was reduced by only 19 per cent. The corresponding growth depressions in the high-light experiment were 33 per cent. for the fruited plants and 21 per cent. for the debudded plants.

TABLE III

CARBOHYDRATE AND NITROGEN ACCUMULATION IN LEAVES OF FRUITED AND DEBUDED COTTON PLANTS AT FOUR NITROGEN LEVELS AND UNDER LOW- AND HIGH-LIGHT INTENSITIES. ALL VALUES AS PERCENTAGE OF FRESH WEIGHT

LOW LIGHT								
TREATMENT AND NITRATE IN CULTURE SOLUTION	MOIS- TURE	CARBOHYDRATES					NITROGEN	
		REDUC- ING SUGARS	SU- CROSE	STARCH	SUM	HEMI- CELLU- LOSE	NO ₃	TOTAL
<i>m.e./l.</i>	%	%	%	%	%	%	%	%
Fruited								
1 (or 0.5)	0.08	0.21	0.26	0.53	1.28	0.006	0.44
4	0.03	0.17	0.23	0.43	1.10	0.078	0.48
16	0.04	0.18	0.24	0.46	1.04	0.091	0.53
64	0.06	0.21	0.25	0.52	1.08	0.099	0.63
Debudded								
1 (0.5)	0.10	0.23	0.41	0.74	1.52	0.004	0.45
4	0.05	0.18	0.24	0.47	1.17	0.078	0.50
16	0.09	0.18	0.26	0.53	1.24	0.096	0.55
64	0.08	0.20	0.26	0.54	1.19	0.108	0.67
HIGH LIGHT								
Fruited								
1	78.0	0.15	0.26	1.21	1.62	2.77	0.57
4	76.5	0.13	0.28	1.34	1.75	2.65	0.64
16	75.2	0.13	0.33	1.59	2.05	2.83	0.65
64	72.6	0.18	0.31	1.78	2.27	2.83	0.75
Debudded								
1	76.4	0.20	0.25	1.79	2.24	3.39	0.51
4	76.1	0.14	0.34	1.54	2.04	2.59	0.69
16	73.4	0.15	0.43	2.04	2.62	3.01	0.76
64	70.9	0.16	0.37	2.82	3.35	4.00	0.84

In both of the experiments all vegetative branches were removed just before the appearance of the first flowers, but vegetative branches which appeared later were not disturbed. The appearance and growth of new vegetative branches became a prominent feature of the subsequent growth of the high-light debudded plants but in the other three treatments their growth was negligible. The debudded plants supplied with 1, 4, 16, and 64 m.e. of nitrate in the high-light experiment developed, respectively, an average of 1.6, 9.4, 10.4, and 8.0 vegetative branches per plant from their main-stalk nodes and 0, 14.1, 13.8, and 10.6 vegetative branches from fruiting-branch nodes. The counts of vegetative branches included those that had two or more leaves.

CARBOHYDRATE AND NITROGEN ACCUMULATION

A factorial summary of the carbohydrate and nitrogen accumulation data is presented in figure 6 and the detailed effects of the individual treatments are presented in tables III and IV. In the factorial summary the bars corresponding to each level of nitrate supply are the means of the 8 values representing the concentrations found in the leaf and root tissues of the fruited and debudded plants at low- and high-light intensities. Simi-

TABLE IV

CARBOHYDRATE AND NITROGEN ACCUMULATION IN ROOT BARK OF FRUITED AND DEBUDED COTTON PLANTS AT FOUR NITROGEN LEVELS AND UNDER LOW- AND HIGH-LIGHT INTENSITIES. ALL VALUES AS PERCENTAGE OF FRESH WEIGHT

LOW LIGHT								
TREATMENT AND NITRATE IN CULTURE SOLUTION	MOISTURE	CARBOHYDRATES					NITROGEN	
		REDUCING SUGARS	SUCROSE	STARCH	SUM	HEMI-CELLULOSE	NO ₃	TOTAL
<i>m.e./l.</i>	%	%	%	%	%	%	%	%
Fruited								
1 (0.5)	0.23	0.41	0.54	1.18	2.24	0.028	0.11
4	0.20	0.58	0.38	1.16	2.21	0.090	0.18
16	0.21	0.63	0.37	1.21	2.06	0.117	0.21
64	0.21	0.57	0.32	1.10	2.22	0.128	0.33
Debudded								
1 (0.5)	0.42	1.62	2.01	4.05	2.61	0.006	0.14
4	0.31	1.32	0.52	2.15	2.32	0.073	0.20
16	0.41	1.46	0.50	2.37	2.23	0.102	0.25
64	0.34	1.30	0.56	2.20	2.24	0.117	0.43
HIGH LIGHT								
Fruited								
1	80.8	0.13	0.25	1.51	1.89	2.59	0.13
4	82.5	0.27	0.44	1.09	1.80	2.79	0.16
16	79.4	0.48	1.06	1.37	2.91	3.19	0.20
64	77.9	0.67	1.07	1.65	3.39	3.12	0.23
Debudded								
1	77.6	0.82	2.43	2.77	6.02	2.96	0.13
4	77.9	0.71	1.89	1.81	4.41	3.19	0.27
16	73.8	0.68	2.28	3.90	6.86	3.48	0.35
64	70.9	0.70	2.16	5.61	8.47	3.94	0.45

larly, the overall effect of fruiting on accumulation of carbohydrate and nitrogen is represented by the respective means of the 16 values for the concentrations found in the leaves and root bark at the four nitrate levels under low and high light. The effects of light intensity and of tissue sampled (leaves and root bark) are likewise shown as the mean of sixteen values. The factorial summaries serve the worthwhile purpose of orientation as regards trends under varied conditions but a consideration of the detailed results remains necessary for effects of interactions.

SUGARS AND STARCH.—On the basis of the factorial summary (fig. 6), deficient nitrogen resulted in an added accumulation of reducing sugars,

sucrose, and starch. By reference to tables III and IV, however, it is to be observed that this effect, although pronounced in the debudded plants, was minor or in some instances reversed in the fruited plants.

With increasing concentrations of nitrate above 4 m.e./l. successive increases are shown in the factorial summary for the concentration of reducing sugars, sucrose, and starch. This effect was minor, or in some instances reversed, in both the fruited and debudded plants under low light; it usually occurred in the fruited plants under high light, and was consistent

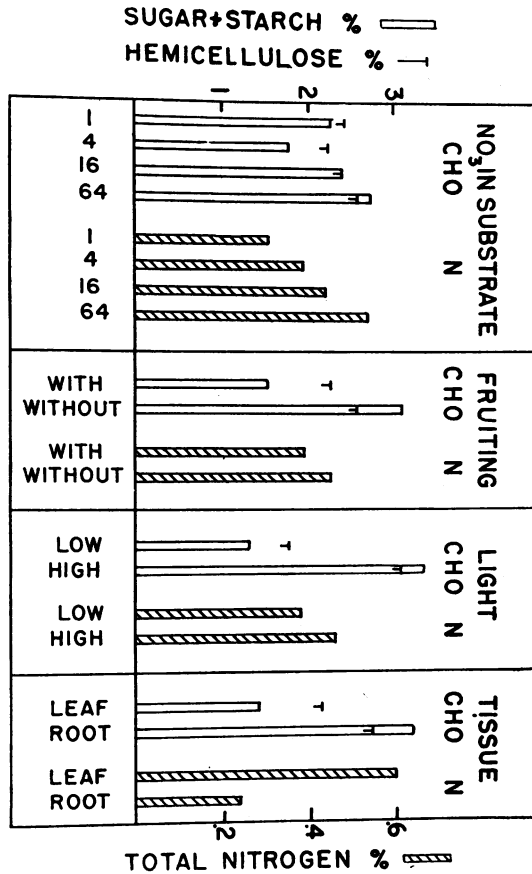


FIG. 6. Factorial summary of effects of nitrate supply, fruiting, light, and tissue sampled on the accumulation of sugars plus starch, hemicellulose, and nitrogen.

except for sucrose in the debudded plants under high light. The effect of high nitrate on sucrose is at variance with its effect on reducing sugars and starch; sucrose tended to decrease rather than to increase in the 64 m.e./l. concentration relative to 16 m.e./l.

Debudding resulted in greater increases in carbohydrates in the root bark than in the leaves. The small additional accumulation of carbohydrates that is observable in the leaves of the debudded, as compared with the

fruited plants, probably reflects the utilization of carbohydrates by the bolls; the utilization of carbohydrates by the bolls would reduce carbohydrate in the phloem and thereby possibly promote a more rapid movement out of the leaves. The most outstanding effect of debudding was the increase in sucrose in the root bark. This increase in sucrose concentration in the root bark accords well with the conclusion of MASON and MASKELL (28) that carbohydrate movement into the cotton boll occurs primarily as sucrose. In the present experiments, debudding resulted in the sucrose that otherwise would have gone into the bolls moving on to the root bark and the increase in sucrose in the root bark of the debudded plants exceeded the increases in reducing sugars and starch.

HEMICELLULOSE

In the leaves, figure 7, hemicellulose tended to change as starch changed and its concentration exceeded that of starch. High light caused a large increase in both fractions and in the debudded plants both of these fractions were markedly influenced by nitrate supply.

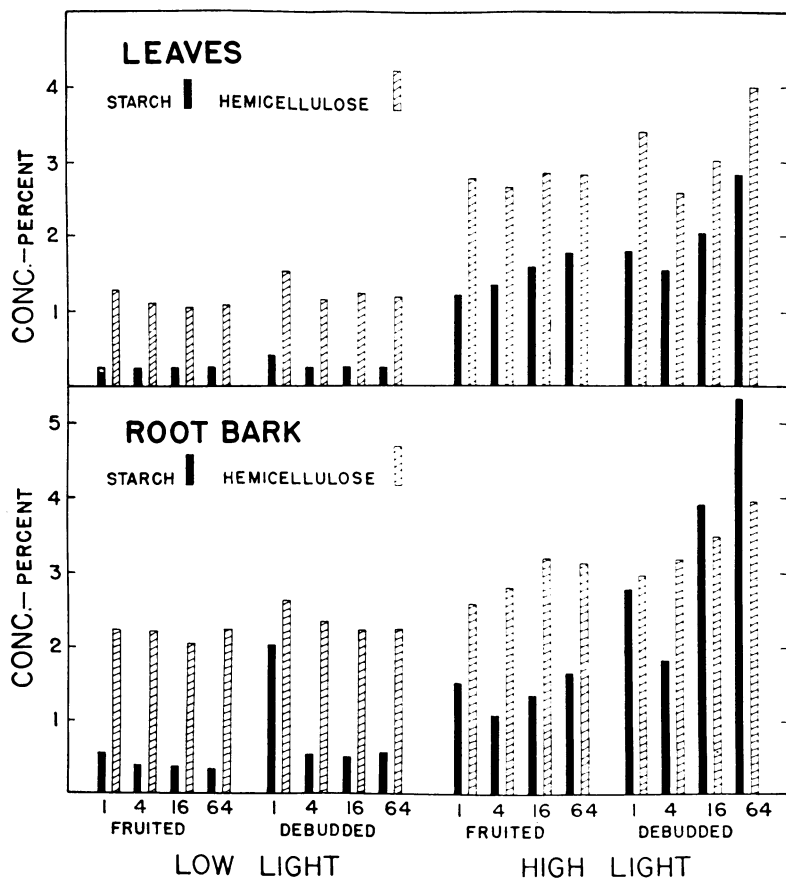


FIG. 7. Accumulation of starch and hemicellulose in leaves and root bark.

In the root bark, starch was increased when nitrogen was deficient whereas hemicellulose showed little variation.

Debudding resulted in large increases in the concentrations of starch found in the root bark but had only a minor effect on the concentrations of hemicellulose. This is difficult to understand for the reason that a substantial movement of the sugars responsible for hemicellulose formation presumably takes place to the fruiting structures.

NITROGEN

A general correlation extends throughout the data between the concentration of nitrate supplied in the substrate and the concentrations of nitrogen found in the leaves and in the root bark. The 1, 4, 16, and 64 m.e./l. concentrations of nitrate (in the solutions as applied) resulted respectively in average concentrations of 0.49, 0.58, 0.62, and 0.72 per cent. total nitrogen in the leaves and 0.13, 0.20, 0.25, and 0.36 per cent. total nitrogen in the root bark. Each four-fold increase in the concentration of the nitrate in the solution applied resulted in small increases within the plant and these successive increases in the plants were of similar magnitude. The entire 64-fold increase in the nitrate concentration of the culture solution failed to double the nitrogen content of the leaves or to quadruple root bark concentrations.

Both the debudding and the use of high light were accompanied by added sugar and starch accumulations in the root bark, and with these added carbohydrate accumulations, there were increases in the concentrations of nitrogen. This result is in accord with other results (14) wherein direct correlations were shown between sugars in the fibrous roots of cotton and the accumulation of bromine, potassium, and nitrogen. In that work, as in the present, there is a substantial basis for the conclusion that the extent of nitrogen uptake is influenced by and may be directly dependent upon the extent to which carbohydrates are moved into the fibrous roots.

Nitrate accumulation within the plants was measured only in the low-light experiment. In the leaves the ratios of nitrate to total nitrogen averaged about 1 to 6, but in the root bark the proportion of nitrate was much greater.

Discussion

CARBOHYDRATE ACCUMULATION AND UTILIZATION

Substantial uncertainty must always accompany any attempt to interpret the significance of data on carbohydrate accumulation. The concentrations found within a tissue at time of sampling represents at best only a fluctuating balance between the rate of input, whether from photosynthesis or by translocation from other tissues, and the rates of export and utilization; the latter may be by respiration or by the elaboration of the carbohydrates into organic acids, nitrogenous compounds, cellulose, etc. The tissues selected for sampling may or may not be representative of the plant as a whole. Assuming that the tissues are representative, however, a greater accumulation in one set of plants than in another can mean either that the treat-

ment imposed favored a higher rate of photosynthesis or that some constituent or condition limited utilization. This, as is well known, is a way of saying that the extent of accumulation finds significance largely in the light of the inferences that are drawn with respect to the probable effects of the variables under investigation. If these inferences fit the findings, or the departures can be explained, the investigator is led to believe that some advance has been made toward an understanding of causes and effects.

TABLE V

RECAPITULATION OF VEGETATIVE GROWTH AND FRUITING, AND OF CARBOHYDRATE AND TOTAL NITROGEN ACCUMULATION

LOW LIGHT							
NITRATE IN NUTRIENT SOLUTION	FRESH WEIGHT		BOLLS		AVERAGES OF LEAVES AND ROOT BARK		
	STEMS AND LEAVES	BOLLS	PER PLANT	PER 100 GRAMS STEMS AND LEAVES	SUGARS PLUS STARCH	TOTAL NITROGEN	CARBOHYDRATE/NITROGEN RATIO
<i>m.c./l.</i>	<i>gm.</i>	<i>gm.</i>	<i>no.</i>	<i>no.</i>	%	%	
Fruited							
1 (0.5)	128	117	5.7	4.5	0.85	0.29	2.93
4	319	153	11.4	3.8	0.80	0.33	2.42
16	328	150	11.2	3.4	0.84	0.37	2.27
64	239	142	9.6	4.1	0.81	0.48	1.69
Debudded							
1 (0.5)	197	2.40	0.30	8.00
4	417	1.31	0.35	3.74
16	443	1.45	0.40	3.62
64	350	1.37	0.55	2.49
HIGH LIGHT							
Fruited							
1	107	170	7.2	6.8	1.76	0.35	3.03
4	382	458	22.9	6.4	1.78	0.40	4.45
16	367	468	22.9	6.4	2.48	0.43	5.76
64	252	370	18.4	7.6	2.83	0.49	5.77
Debudded							
1	158	4.13	0.51	8.10
4	555	3.23	0.69	4.68
16	566	4.74	0.76	6.23
64	445	5.91	0.84	7.03

In the present work a greater accumulation of sugars and of the compounds grouped as starch was found to result from the use of high-light intensities than low-light intensities and further accumulation resulted when the plants were debudded. A somewhat greater accumulation was found also in the plants on nutrient solutions that were deficient in nitrate and again in those that were supplied with an excess of nitrate than in those supplied with the intermediate concentrations. The tendency toward an accumulation of carbohydrate with deficient nitrogen has long been recognized (24) and the accumulation with an excess of nitrate may be similar in cause with the accumulation found to be associated with an excess of

chloride and sulfate salts (16). In both instances, table V, such accumulation of carbohydrate was associated with depressed growth; i.e., the responsible factors depressed utilization more than they did photosynthesis.

From the standpoint of the main interests that prompted the present investigation the effects of nitrogen supply has proven to be of lesser significance than the effects of light and of debudding. This is the case for the reason that the data have reaffirmed, in accord with the evidence from other sources, that variation in nitrogen supply, in conjunction with abundant supplies of other nutritional elements, does not greatly alter the relative fruitfulness of the cotton plant. Over the range of 1 to 64 m.e. of nitrate, the partition in carbohydrate utilization between vegetative development and fruiting remained essentially unchanged; per unit of fresh weight of leaves and stems the number of bolls produced was not affected to any outstanding degree. This lack of any pronounced effect of nitrogen on relative fruitfulness was found to be the case both under the diverse conditions represented by light intensities of 1,000 f.c. associated with short winter days in a greenhouse and by those represented by intensities of 10,000 f.c. in mid-summer out-of-doors.

Turning to the effect of light, it seems evident (table V) that the mid-day light intensities of about 1,000 f.c. were insufficient for the manufacture of enough carbohydrate to satisfy the growth capacities of the plants. Recalling that the duration of the low-light experiment was extended roughly in proportion to the reduction in day length, it was found at time of cropping that the weights of stems and leaves produced under low light were essentially equal to the weights of stems and leaves under high light. This was not the case, however, with weights of bolls. The weight of bolls produced by the high-light plants was 2.5 times as great as the weight produced by the low-light plants. In other words, the entire growth curtailment under low light was represented by the curtailment of fruiting activities. Or, conversely, the extra photosynthetic product produced under high light was utilized principally in boll production.

The average carbohydrate concentrations (sugar plus starch) were 2.7 times greater (average of leaves and root bark at all nitrate levels) under high light than under low light, and high light increased the weight of bolls by 2.5 times. The close similarity in these values is of course coincidental, but to follow an interpretation that might be placed on some of the research by MASON, MASKELL, and PHILLIS (26, 28, 29) the increased carbohydrate concentrations within the high-light plants could be construed as having brought about an enhanced rate of movement of carbohydrates, along descending sucrose gradients, into the reproductive structures. This explanation, however, does not seem to be wholly adequate, especially when it is remembered that the potentials for movement into the vegetative buds and roots were similarly increased.

Debudding under both low and high light resulted in marked increases in vegetative development and also increased carbohydrate concentrations.

In no instance, however, did the stems and leaves of the debudded plants weigh as much as the stems and leaves plus the bolls of the fruited plants; notwithstanding the greater leaf area for photosynthetic activity of the former. In other words the *increase* in carbohydrate utilization in the vegetative parts of the debudded plants did not compensate for the utilization that took place in the bolls of the fruited plants. The fact, nevertheless, that vegetative growth was increased by bud removal leaves no doubt that the growing bolls did curtail vegetative expansion. It is probable that the carbohydrate utilization by the bolls was an important, if not the only cause, of the lesser vegetative growth of the fruited plants.

Under low light the weight of the vegetative growth of the fruited plants exceeded the weight of bolls whereas under high light this situation was reversed. The utilization partition between vegetative and reproductive activities was thus in favor of the reproductive under high light and in favor of the vegetative under low light. Or, stated otherwise, some part of the dominance of reproductive activities that existed under high light was lost under low light. Additional consideration will be given to the light factor after a further consideration of carbohydrate utilization by the bolls.

EFFECT OF LIGHT ON CARBOHYDRATE UTILIZATION BY BOLLS

The idea has been prevalent in the literature for many years that the number of bolls retained by a cotton plant is a function of the number it can "nourish" or "support." The availability of water and of the essential elements being assumed ample, the carbohydrate supply has customarily been regarded as a chief limiting factor in boll production. The present data afford an opportunity, possibly an especially favorable one, for further examining this hypothesis. As a means of simplifying the discussion, attention will be restricted to the plants supplied with 4 and 16 m.e. of nitrate under low and high light. The growth and sugar and starch data from these plants have been brought together in table VI.

As a first consideration, it may be observed, table VI, that under low light the fruited 4- and 16-m.e. plants had about the same fresh weights, set about the same number of bolls, and had essentially equal concentrations of sugars and starch in their leaves; the concentrations in the root bark were higher than in the leaves, but between the 4- and 16-m.e. treatments there is no indication of a significant difference in any of these measurements. It would be reasonable to conclude that the carbohydrate supply limited the fruiting of these low-light plants and that it also limited their vegetative growth; such a conclusion is supported by the fact that the debudded plants had substantially higher concentrations of carbohydrates in their root barks than did the fruited plants and that they made substantially more vegetative growth and produced many more floral buds.

Similarly, under high light, and again comparing the 4- and 16-m.e. fruited plants, there was little difference between these treatments in fresh weight, or in the number of bolls that were set; both groups of plants shed

TABLE VI
 RECAPITULATION OF GROWTH AND CARBOHYDRATE DATA FOR STUDY OF FACTORS INFLUENCING CARBOHYDRATE UTILIZATION BY BOLLS

TREATMENT	FRESH WEIGHT				BOLLS		CARBOHYDRATES											
	LEAVES PLUS STEMS	TAP ROOTS	BOLLS	PER 100 GRAMS STEMS PLUS LEAVES	PER PLANT	no.	LEAVES				ROOT BARK				SUM			
							REDUCING SUGARS	SUCROSE	STARCH	SUM	REDUCING SUGARS	SUCROSE	STARCH	SUM				
gm.	gm.	gm.	no.	no.	no.	%	%	%	%	%	%	%	%	%	%	%		
LOW LIGHT																		
Fruited	319	22.2	153	3.8	11.4	no.	0.03	0.17	0.23	0.43	0.20	0.58	0.38	1.16				
16 m.e. NO ₃	328	21.6	150	3.4	11.2	no.	0.04	0.18	0.24	0.46	0.21	0.63	0.37	1.21				
Debudded	417	30.1	0.05	0.18	0.24	0.47	0.31	1.32	0.52	2.15				
16 m.e. NO ₃	443	29.2	0.09	0.18	0.26	0.53	0.41	1.46	0.50	2.37				
HIGH LIGHT																		
Fruited	382	28.1	458	6.4	22.9	no.	0.13	0.28	1.34	1.75	0.27	0.44	1.09	1.80				
16 m.e. NO ₃	367	29.1	468	6.4	22.9	no.	0.13	0.33	1.59	2.05	0.48	1.06	1.37	2.91				
Debudded	555	46.6	0.14	0.34	1.54	2.04	0.71	1.89	1.81	4.41				
16 m.e. NO ₃	556	53.8	0.15	0.43	2.04	2.62	0.68	2.28	3.90	6.86				

35 per cent. of their bolls. Likewise, there was only a suggestion of a difference in the sugar or starch concentrations in the leaves between the two nitrate levels. There were, however, relatively large differences between these two nitrate levels in the sugar and starch concentrations in the root bark of both the fruited and debudded plants; i.e., more carbohydrate was passed on to the root bark by the 16-m.e. plants than by the 4-m.e. plants, indicating that the effects of light intensity on carbohydrate accumulation are not independent of substrate characteristics. Under high light, as under low light, the carbohydrate supply can be construed as having limited growth and boll production for with the floral buds removed, the plants accumulated more carbohydrate, made more vegetative growth, and developed more floral buds than did the fruited plants.

These high-light plants set twice as many bolls per plant and almost twice as many bolls per 100 grams of fresh stems and leaves as did the low-light plants and they had an average of 2.6 times as high carbohydrate concentrations in their leaves and root bark as did the low-light plants. A critical question is introduced by this observation. If carbohydrate supply limited the fruitfulness of the high-light plants, why were the carbohydrates in the high-light plants not reduced to the levels found in the low-light plants before the carbohydrate supply became the limiting factor? Evidence that the carbohydrates found in the high-light plants were not unusual is provided by the similarity with the concentrations found in plants of comparable development growing in the field.

EFFECT OF LIGHT ON FRUITING DOMINANCE

Before singling light out as the dominant influence that altered fruitfulness and the level of carbohydrate accumulation between the winter and summer experiments some further attention to length of day and temperature is desirable.

As noted in the introduction, KONSTANTINOV (23), though finding length of day to alter the fruiting activities of some but not all of the perennial arborescent cottons, particularly those from equatorial regions, and to a slight extent varieties of Egyptian and of medium and late uplands, concluded that the early upland cottons, as well as wild forms from Mexico and elsewhere, were without length of day reactions. When length of day reactions were found, the basic change consisted in a lowering of the position of the first fruiting branches. Lengths of day ranging from 6 to 14 hours were arranged by covering the plants with plywood boxes.

Although the mean temperatures of the summer and winter experiments were similar and it has seemed doubtful that the small and unavoidable differences could have contributed to the greater fruitfulness of the high-light plants, it is known that temperature has a notable effect on the fruiting of the cotton plant. An experiment was conducted in 1922 (12) near San Diego, California, where the midday summer temperatures are rarely in excess of 80° or 85° F. and the cotton plant sets few bolls and develops a pre-

dominance of vegetative branches. Using a 13-hour day, Durango cotton plants subjected to nightly temperature of 90° F. fruited well and developed no vegetative branches; whereas plants subjected to an uncontrolled nightly temperature averaging about 65° F. (also a 13-hour day), set no bolls and developed many vegetative branches.

There are fairly direct indications from other sources that light intensity, independently of air temperature or length of day, has notable effects on the relative fruitfulness of cotton. In 1935, KNIGHT (22) reported on the effects of shade on the development of an American upland cotton grown in field plots under full exposure and under the shade provided by a single layer of white cloth. The shade increased the height of the plants from 55 to 60 cm. but reduced the number of bolls per plant from 10 to about 5, the yield per plot from 20.8 to 7.2 pounds, and the number of fruiting branch nodes per plant from 63 to 44. KNIGHT undertook these experiments in the Sudan hoping that he might thereby account for the non-fruitful growth of cotton in an area to the south that was characterized by much cloudy weather, but he makes no statement of his conclusion.

If light intensity is, as it seems, one of the critical factors determining the dominance of fruiting activities in cotton over vegetative growth and, in association therewith, the levels at which the carbohydrate concentrations in the plant are maintained, the subject possesses a substantial physiological significance. The data at hand are not sufficiently extensive to justify much theoretical discussion but a number of questions are nevertheless involved. Prominent among these is whether high light in favoring boll growth at the expense of vegetative expansion is responsible for the formation, or inhibition, of some hormone that differentially determines the kind of growth activity that predominates, or whether the light affects directly, according to degree of exposure, the enzymes that are responsible for carbohydrate utilization. The fact that hormone activities may be local, like enzymatic activities, adds to the difficulties involved in a decision. It is nevertheless desirable to consider the fact that the meristematic tissues of the vegetative structures are more extensively exposed to light than are the floral buds and the contents of the boll. The involucrel bracts that enclose the floral bud effectively protect it from direct light and following anthesis the massive structure of the boll likewise derives from the bracts a substantial measure of protection. This question is obviously complex but measurements made by KEARNEY (20) would seem to have some bearing on the subject. He found that developing Pima cotton bolls, which are protected by especially prominent involucrel bracts, were caused to shed in larger numbers and the bolls that were retained to be smaller when mature, when the involucrel bracts were cut away at or before anthesis than when they were left intact.

NUTRITIONAL FACTORS AND HORMONES IN RELATION TO THE DEVELOPMENT OF VEGETATIVE BRANCHES AND THE SHEDDING OF FLORAL BUDS AND BOLLS

The vegetative branches of the cotton plant, which closely resemble in their morphology (5, 6) the main stalk, develop under favorable conditions

from the axils of the leaves of the main stalk, of other vegetative branches, and of the fruiting branches. Fruiting branches may also arise from any of these positions even though, like the vegetative branches, their development may be limited to a single internode.

COOK and MEADE (6) have pointed out: "Weather that is dry enough to retard the growth of plants also discourages the formation of limbs and vegetative branches while humid conditions favor the production of both." In the present investigation vegetative branches were produced to an appreciable extent only by the debudded plants supplied with 4 m.e./l., or more, of nitrate under high light. These plants had higher concentrations of carbohydrate and nitrogen than the plants under other treatments and, on the basis of this evidence, it would be reasonable to assign high carbohydrate and nitrogen supply, together with favorable moisture conditions, as causes for their development and growth.

Following methods used by HITCHCOCK and ZIMMERMAN (18) in their experiments with tomato plants, the writers have secured evidence that hormone as well as nutritional factors may be involved in the development of vegetative branches. When black cloth bags were placed over the terminal 4 or 5 inches of cotton plants growing in the field during the summer no measurable increase in branch formation resulted, but when the same bags were used on potted plants growing in the full light within a greenhouse during the winter the responses were clear cut and unmistakable. The extensive development of vegetative branches that followed the application of the bags in the greenhouse experiment is illustrated in figure 8. The cloth used for the bags was not entirely opaque and when stretched over the cell of a photometer and exposed directly toward the sun it transmitted 600 f.c. of light. Too much light for this response may have passed through the cloth under the summer conditions, but other explanations for the lack of response during the summer are not excluded. As mentioned in the previous section, the development of fruiting branches has been found in other investigations (12) to be repressed and the formation of vegetative branches to be greatly stimulated when day temperatures were mostly below 80° F., but temperatures of 90° F. provided during the night reversed this behavior.

The present information does not permit of any well defined application of observation, or theory, to relations between hormone activity and the shedding of cotton bolls, but some of the marked differences between cottons in the extent to which shedding occurs, would seem to preclude the possibility that in all cases this shedding can be attributed solely to nutritional relations. As previously noted the 4- and 16-m.e. plants under high light produced like numbers of bolls, and shed like numbers and yet the concentration of sugars in the root bark of the latter (also the 64-m.e. plants) was substantially higher than in the 4-m.e. plants. It has been noted (6) that certain Asiatic cottons have not been fruitful when introduced into the United States and such cottons have been found to be more fruitful when exposed to short days (23) than to long days. Heritable differences (21) in

shedding rates have been recorded and many hybrid plants have been observed to be unproductive. Nutritional relationships are indicated, on the other hand, by the well known fact that large balled upland cottons shed more but produce more seed cotton than does the small balled Pima Egyptian cotton which retains a greater proportion of its bolls. EWING (16) has likewise recorded differences in the rates of shedding among upland cottons with different boll sizes.



FIG. 8. Stimulation of vegetative branch formation by capping terminal growth with black cloth bag. At left, capped plant with 4 branches (av. of 6 plants, 2.7); at right, control plant with 1 short branch (av. of 6 plants, 0.7). All leaves except those on the vegetative branches have been removed.

In direct accord with the carbohydrate concentrations found in the plant tissues there was an extensive shedding of very small floral buds by the fruited plants at all nitrate levels under low light, whereas the shedding of floral buds was negligible from the debudded plants (buds removed when much larger) under low light, and from both the fruited and debudded plants under high light. The fact that the debudded plants under low light

did not shed their buds goes far to eliminate the possibility that such shedding was a hormone or length-of-day response characteristic of a specific set of external conditions. Specific effects of high or low nitrogen supplies are likewise eliminated, since the low-light fruited plants shed their squares extensively at all nitrate levels. On the basis of the foregoing correlation between carbohydrate levels and square shedding a reasonable nutritional explanation is afforded, but additional causes under other conditions are not eliminated and an extensive shedding of floral buds sometimes occurs in the field (1, 25). Following the initiation of abscission floral buds usually remain in place until they have turned brown and been disengaged by the enlargement of the pedicel sockets.

In endeavoring to account for the intermediary mechanism between nutritional factors, or hormone activities, and the shedding of floral buds and bolls of cotton, it is worth while to remember that with the development of fruiting branches a non-fruitful condition can exist only as the result of abscission. A final question must exist accordingly as to whether the stimulus responsible for the behavior of the cells in the abscission layers acts by preventing this separation or stimulates these cells into separation.

CARBOHYDRATE-NITROGEN RATIOS³

It has seemed to the writers that the concept of carbohydrate/nitrogen ratios, wherein the actual magnitudes of the contributing values are lost sight of, is a matter quite apart from the significance of carbohydrate and nitrogen concentrations considered as such, either alone or in conjunction with one another. The latter relations have aided an interpretation of the foregoing experiments but it has not been possible to derive much benefit from the ratios of these two variables. As pointed out by others in the past, there has been some confusion in the interpretation of carbohydrate and nitrogen data due to difficulties in differentiating between causes and effects.

Whether attention is directed to the carbohydrate/nitrogen ratios that may be calculated separately for leaves and root bark or to the averages of these concentrations from which the ratios in table V are computed, the results show that these ratios were influenced to nearly as great an extent by fruiting itself as by any of the treatments that altered fruitfulness. Observations repeated in many experiments with cotton prompt the belief that all of the debudded plants, irrespective of their carbohydrate-nitrogen

³ When this manuscript was returned by the editor for the authors' review it carried the following signed comment along the margin of the first paragraph under the above heading: "I have never been able to see, nor do I now see, value in a C/N ratio as a possible means of expressing a causative factor concerned with flowering of plants, despite the fact that I am supposed to be one of the proponents of the idea. Hence I agree here. Even to decide the meaning of the presence of C and N is very difficult and to establish such a simple ratio seems impossible to me. The most one may hope for is to determine the possible interrelations of the carbohydrate and nitrogenous constituents of plants and the possible meaning of such relations in reference to the vegetative, reproductive, or fruiting status."—E. J. KRAUS. This statement is repeated here with DR. KRAUS' approval hoping thereby to clear up a misconception and otherwise serve a useful purpose.

ratios, would have promptly set bolls if the debudding had been stopped at any time, and, likewise, that the removal of previously set bolls from any of the fruited plants would have been followed by the setting of new bolls to replace them.

It is true that the carbohydrate/nitrogen ratios of the fruited plants were substantially lower under low light than under high light and that the latter plants were most productive. On the other hand, through the four nitrate concentrations supplied to the fruited plants of the low-light experiment the trend of the ratios was consistently downward, whereas in the high-light experiment this trend was upward, and yet in both experiments the relative fruitfulness of the plants supplied either with low or high nitrate was somewhat greater than that of the plants supplied with intermediate concentrations. Some of the dominance of fruiting activities over vegetative growth that was found under high light was lost under low light but this reduction in fruiting dominance was not materially altered by nitrogen supply.

Had the investigation been extended to include measurements of potassium and phosphorus accumulation, a further insight might have been gained, as pointed to by others, on the relation of nitrate supply to the accumulation of these elements and the effects of phosphorus, in particular, on carbohydrate transformations.

NITROGEN SUPPLY AND FRUITFULNESS UNDER FIELD CONDITIONS

The general accord between vegetative growth and fruitfulness of cotton under varied nitrate supply as found by many investigators, as well as in the present experiments, raises a point of significance in regard to the cause of the non-fruitful cotton plants that have sometimes been observed on rich moist soils. These non-productive, rank-growing plants have been referred to variously as "he cotton," "bull cotton," and "cotton gone to weeds." Although the growth of such plants is sometimes regarded as being due to an overabundance of nitrogen, direct evidence seems to be lacking that nitrogen supply is in itself the cause. If excessive nitrogen can be an immediate cause of non-fruitfulness in cotton it would seem that someone would have observed it in connection with the hundreds of nitrogen fertilization experiments that have been conducted in the cotton producing regions. Insofar as the writers could determine from their search of the literature, no such observation has ever been recorded and there was no evidence of such a relationship in the present experiments. An experimental demonstration that a non-fruitful growth of cotton can be brought about, under conditions otherwise suitable for boll setting, by any arrangement of nitrogen supply or of carbohydrate/nitrogen ratios would attract great interest. In the absence of a conclusive demonstration of this character it is more reasonable to look for the cause of marked unfruitfulness in other directions. A rank growth can occur only with an abundant nitrogen supply but that does not mean that extra nitrogen is in itself a cause of nonfruitfulness.

It is extensively believed that cotton stimulated in heavy vegetative

growth by abundant supplies of nitrogen suffers more severely from drought than when growth has been retarded. On the other hand, determinant strains of cotton have been observed by DR. J. W. NEELY at Stoneville, Mississippi, to be less able to withstand mid-summer drought than ranker growing less-determinant strains planted nearby. It seems probable that the latter cottons, by reason of the greater root development that is associated with fewer early-season bolls, more fully occupied the deeper zones of the alluvial soil and thereby obtained moisture that was not available to the determinant cottons.

A rank but unproductive growth of cotton can in some instances be attributed to the activities of the flea hopper, *Psallus seriatus* Reut. This bud-destroying insect is of special interest in the present connection for the reason that it destroys the floral buds while they are very small (31) leaving no evidence of the insect activity except for the vegetative condition of the plants. It has been pointed out (33) that succulent cotton growing on rich moist soil is especially attractive to flea hoppers and the destruction of the floral buds would contribute directly to an increased vegetative expansion of the plant. The flea-hopper suggestion does not exclude other explanations. In their study of the shedding of floral buds associated with wet soils, ALBERT and ARMSTRONG (1) called attention to a similarity of the resulting plants to flea-hopper injured plants but emphasized that this insect had not been found to be present.

The plants of the present experiments were supplied with what were regarded as ample concentrations of potassium, phosphorus, boron, etc. There is a possibility that a non-fruitful condition might result from abundant nitrogen in the presence of limiting concentrations of other of the essential elements. Something of this character has been observed in the instance of boron but otherwise no very concrete evidence that such is the case has been found in the literature. In the instance of boron deficiency, however, the shedding of floral buds was associated with a marked shortening of the length of the fruiting branches.

Summary

The foregoing work has shown that the level of nitrate supply to the cotton plant has, in itself, no outstanding effect upon fruitfulness relative to plant size. An increase in nitrate from a low level resulted in an increase in vegetative growth and in an increased number of bolls. A toxically high concentration of nitrate reduced growth and reduced the number of bolls. These relations were found to exist both in an experiment conducted in the greenhouse during the short days of winter under muslin shades (midday light intensity about 1,000 foot candles) and during long summer days under free exposure outdoors (midday light intensity about 10,000 foot candles). The plants were grown in sand cultures supplied with nutrient solutions in sufficient excess to produce 25 to 50 per cent. of drainage.

The nitrate was supplied in nutrient solutions in concentrations of 1, 4,

16, and 64 m.e. per liter (14, 56, 224, and 396 p.p.m. of nitrogen). At both light intensities the plants on low nitrate (1 m.e.) were less than half as large as those on 4 and 16 m.e. of nitrate, and the plants on high nitrate (64 m.e.) were about 75 per cent. as large. In both experiments the relative fruitfulness values (number of bolls per 100 grams of fresh weight of stems and leaves) for the 1- and 64-m.e. plants were actually a little higher than the values for the plants supplied with 4 and 16 m.e. Under low light these values were 4.46, 3.47, 3.36, and 4.09; and under high light 6.75, 6.42, 6.43, and 7.58 for the four respective nitrate levels. Relative to their fresh weights the 1- and 64-m.e. plants differentiated more nodes and flower buds than did the 4- and 16-m.e. plants and their shedding percentages were higher.

At the respective nitrate levels, the fresh weight of stems and leaves in the low-light experiment were nearly the same as the corresponding weights under high light, but the high-light plants were far more fruitful. The mean number of bolls per plant at the 4 nitrate levels in the winter experiment were respectively 5.7, 11.4, 11.2, and 9.6 and in the summer experiment 7.2, 22.9, 22.9, and 18.4. Fruiting activities thus exercised a much greater dominance over vegetative growth under high light than under low light. The mean temperatures in the two experiments were similar. It has been shown by others that relative length of day has little, or no, effect upon the fruiting of American upland cottons.

Each of the experiments included two series of plants: (1) fruited plants and (2) plants from which all floral buds were removed as these attained a bract width of about 15 mm. The debudded plants were included to aid a differentiation between the effects of treatment and effects of fruiting upon growth and upon carbohydrate accumulation and utilization.

Debudding resulted in an increased number of main stalk and fruiting branch nodes, and resulted in a large increase in the weight of stems and leaves. This increase in weight of stems and leaves was much less in the low-light experiment than in the high-light experiment which is in accord with the lower weight of bolls in the low- than in the high-light experiment.

High nitrate was more toxic to the fruited than to the debudded plants.

On the basis of a factorial summary, carbohydrate concentrations were lowest in plants supplied with 4 m.e. of nitrate, lower in fruited than in debudded plants, lower under low light than under high light, and lower in the leaves than in the root bark. The interactions between treatments altered some of the foregoing effects.

Shedding of very small floral buds was a prominent feature in the growth of the fruited plants under low light (all nitrate levels) but bud shedding from fruited plants under high light was negligible, and it was also negligible from the debudded plants (buds removed when much larger) under both light intensities. Square shedding thus occurred only from the plants with the lowest carbohydrate concentrations.

The 64-fold increase in the nitrogen-concentration in the substrate tended

to double the nitrogen content of the leaves and quadruple the concentration in the root bark.

Higher nitrogen concentrations were found in the debudded than in the fruited plants and also under high light than under low light. This is in accord with the extent of carbohydrate accumulation in the root bark and it is in agreement with results previously reported that supported a metabolic explanation of the seasonal trend of nitrogen levels in the cotton plant.

The data on fruitfulness and on carbohydrate and nitrogen accumulation afford little or no basis for attaching any special significance to carbohydrate/nitrogen ratios in the cotton plant. Fruiting itself had effects on this ratio as great as the nitrate supply. The actual magnitudes of the carbohydrate and nitrogen concentrations, however, were both informative.

In both experiments it appeared that limited carbohydrate supply was responsible for much of the boll shedding. However, the high-light plants contained sugar and starch concentrations (average of leaves and root bark of fruited and debudded plants at all nitrate levels) 2.7 times as high as the low-light plants. The fact that carbohydrate concentrations were not reduced in the high-light plants to the levels found in the low-light plants before shedding occurred is interpreted as indicating that high light sets in motion some factor that depresses carbohydrate utilization. Fruiting activity had a greater dominance over vegetative growth under high light than under low light.

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