

SUGAR MOVEMENT TO ROOTS, MINERAL UPTAKE, AND THE GROWTH CYCLE OF THE COTTON PLANT¹

FRANK M. EATON AND HOWARD E. JOHAM

Comparative data are reported in this paper on the sugar concentrations in the fibrous roots (and other parts) of defruited and control cotton plants and the uptake by these plants of bromine, nitrogen, and potassium. The measurements were made 22 days after defruiting (21 days after the addition of bromine to the nutrient solution). The data are discussed in terms of the relation of sugar concentrations in fibrous roots to mineral uptake and the relation of mineral uptake to the growth cycle of the cotton plant.

The uptake of soil nutrients by the cotton plant, as shown by WHITE (27), CROWTHER (8, 9), DASTUR (10), OLSON and BLEDSOE (23), and others, proceeds at an increasing rate through the period of early growth and flowering but subsequently, as the number of bolls carried by the plants increases, the rate of uptake declines and actual losses of mineral elements from the above-ground portions of the plants may occur. It was suggested a number of years ago (8) that the observed reduction in nitrogen uptake during the fruiting period of cotton might be due to depressed root growth. The dominance of fruiting activity over vegetative development and root growth has been well established in cotton (12, 13, 19, 20) and it seems certain that the extension of roots into new soil zones and the development of new root surfaces would be important factors in solute uptake. The foregoing explanation, however, insufficiently accounts for all of the known facts. If, on the other hand, fruiting substantially reduces the concentration of sugars in the fibrous roots, the observed reduction in mineral uptake with fruiting can be more fully comprehended.

The necessity for an expenditure of energy for the accumulation of solutes against concentration differentials has been outlined by HOAGLAND (17) and more recent work with barley seedlings (5) adds assurance that sugars situated in the roots provide the primary respiratory fuel for mineral uptake. It has been shown (18, 20) that the developing cotton boll tends to have first call on labile carbohydrates. Irrespective of probabilities, however, it has not been established that the sugar concentrations in fibrous roots vary enough with fruiting to constitute a critical intermediate link between fruiting and the rate of mineral uptake. The responses of soybeans (3) and of tomatoes (2) to defoliation indicate that fruiting may alter the carbohydrate relations in the above-ground portions of plants without affecting materially the rate of mineral uptake. Two additional papers (24, 25) also pertain to the foregoing considerations.

In soybeans, AUSTIN (3) found the accumulation of some elements was depressed by defoliation; his data show, however, that defoliation had little

¹ Published with the approval of the Director as Technical Paper no. 841 of the Texas Agricultural Experiment Station.

effect on sucrose concentrations in stems and leaves and it substantially decreased reducing sugars and increased polysaccharides. In the tomato, HESTER (15) found no drop in mineral uptake with fruiting, and ARNON and HOAGLAND (2) concluded that deflorating tomato plants did not result in marked increases in potassium, calcium, magnesium, or phosphorus in above-ground vegetative organs. There were, however, higher concentrations of organic nitrogen and sugars in the stems and leaves.

Remarkable parallelisms are brought out by MILLER's data (22) between the levels of sugars in stems and leaves and the movement of minerals into the tops of wheat plants with heading. Relationships that seem to be quite direct have been reported likewise by COCHRAN (7) between depressed mineral accumulation and fruiting in pimiento and by CAROLUS (6) with the formation of tubers by potatoes. A decline in mineral uptake with advance in age has been found in tobacco by GRIZZARD, DAVIES, and KANGAS (14). ANDERSON, SWANBACK, and STREET (1) have assigned the loss of nitrogen and potassium from the leaves of topped tobacco plants to translocation to the suckers. In the majority of the foregoing papers causal mechanisms are not discussed and, except as mentioned, sugar determinations were not involved in the experimental work. MILLER (21) has made reference to relations between fruiting and the mineral uptake by additional plants.

Methods

Stoneville 2-B upland cotton was planted in the greenhouse in 3-gallon stone jars filled with river sand on March 18. Flowering started on May 10 at which time the plants were taken outdoors. They were supplied with a nutrient solution containing millimolar concentrations of salts as follows: 2 calcium nitrate, 2 magnesium sulphate, 3 potassium chloride, and 0.3 potassium dihydrogen phosphate; in addition 5 p.p.m. of boron, 0.5 p.p.m. of manganese, and 0.05 p.p.m. of zinc; iron was supplied as magnetite mixed with the sand. The use of the above solution was continued until June 1 except that on May 1, the 3 millimoles of potassium chloride were replaced with a like amount of potassium sulphate. Throughout the experiment the nutrient solution was supplied in sufficient excess to produce substantial drainage.

Sugars, after extracting the dried tissues with hot 80 per cent. alcohol, were determined by the WILDMAN and HANSEN (28) procedure except that in titration potassium permanganate oxidizing solution was employed with ortho-phenanthrolic indicator; starch was hydrolyzed in the residue from the sugar extraction with undiluted plant diastase (supplied by courtesy of Parke, Davis and Company); bromine was determined according to Hibbard (16), and nitrogen (including nitrate) by A. O. A. C. official methods (4). Potassium was determined by the chloroplatinate method outlined by St. JOHN and MIDGLEY (26).

Calendar

MAY 28

Eighteen jars were numbered and the heights of the plants measured. The plants were then divided into six groups of 3 plants each in such manner that the average height of the plants in each group would be approximately equal. Three groups were used for the defruited and 3 groups for the control treatment. The individual pots remained in their initial locations and their positions were therefore randomized as to treatment.

MAY 31

All bolls were removed from 3 sets of plants (defruited) and the large squares (floral buds) were subsequently removed before they flowered.

JUNE 1

Potassium bromide was substituted for potassium sulphate. The composition of the culture solution was otherwise altered at this time to give concentrations in millimoles per liter as follows: 8 $\text{Ca}(\text{NO}_3)_2$, 8 MgSO_4 , 12 KBr , and 1.2 KH_2PO_4 .

JUNE 22

Collection of samples. Material from the 3 plants of each group was combined. The order of sample collection was as follows:

12:30 P.M. C.S.T. Collected 4 sound main-stalk leaf blades (from the 11th to the 14th or 15th nodes) from each plant. These were weighed green and then dried for 2 hours at 80° C. under forced draft; drying was completed at 70° C.

1 to 2 P.M. Cut off the tops of all plants after removing the bolls from the control plants. These two fractions (bolls and combined leaves and stems) were weighed fresh and dried on the following day at 70° C.

2 to 4 P.M. The sand was washed from the pots and the roots rewashed in the laboratory under a jet. The fibrous and tap roots were separated and blotted, weighed fresh, and dried immediately in the same manner as the leaves.

Results

GROWTH OF CONTROL AND DEFRUITED PLANTS

During the 22 days following boll removal the defruited plants elongated at their terminal buds about twice as rapidly (table I) as the control plants. By the end of this period the fresh weight of fibrous roots of the defruited plants was double that of the control plants; lesser relative gains were found in the weights of the tap roots (included large laterals) and in the weights of the combined leaves and stems. The weights of tops plus roots (exclusive of bolls) at the end of the three-week period were, respectively, 503 and 799 grams for the control and defruited treatments; the weights of the bolls initially removed from the "defruited plants" were not recorded but had these weights been added to the final weights the results would indicate more

TABLE I

GROWTH AND FINAL FRESH WEIGHTS OF CONTROL AND DEFRUITED COTTON PLANTS.
EACH GROUP VALUE IS THE MEAN OF 3 PLANTS

TREATMENT	GROUP	HEIGHT				FINAL FRESH WEIGHT				
		INITIAL	INCREASE BY WEEKS			BOLLS	ROOTS		LEAVES AND STEMS	TOTAL
			1ST	2ND	3RD		FI-BROUS	TAP		
		<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>cm.</i>	<i>gm.</i>	<i>gm.</i>	<i>gm.</i>	<i>gm.</i>	<i>gm.</i>
Control	A	55.0	4.0	5.0	6.0	222	157	16.0	297	693
	B	56.0	6.0	6.0	5.0	195	142	17.0	299	655
	C	59.0	8.0	7.0	6.0	205	194	23.0	360	783
	Mean	56.7	6.0	6.0	5.7	207	164	18.7	319	710
Defruited	A	57.0	12.0	13.0	13.0	324	24.0	417	766
	B	58.0	11.0	13.0	12.0	363	30.0	492	885
	C	57.0	9.0	10.0	13.0	304	29.0	414	747
	Mean	57.3	10.7	12.0	12.7	330	27.7	441	799

definitely that the total dry matter accumulation by the defruited plants was greater during the experimental period than by the fruited plants (compare 12, 19).

BROMINE ACCUMULATION PER PLANT

The defruited plants accumulated almost twice as much bromine in the 3-week period as did the control plants (table II). The fraction of the total bromine found in the bolls was comparatively small; in terms of fresh weight the concentration of bromine in the bolls was approximately one third as great as in the corresponding main-stalk leaves.

CONCENTRATIONS OF BROMINE AND SUGARS IN FIBROUS ROOTS AND OTHER TISSUES

The sugar concentrations in the fibrous roots (table III) were increased

TABLE II

BROMINE ACCUMULATION IN ENTIRE PLANTS

TREATMENT	GROUP	MILLIGRAMS BROMINE PER PLANT				
		BOLLS	FIBROUS ROOTS	TAP ROOTS	LEAVES AND STEMS	ENTIRE PLANTS
		<i>mg.</i>	<i>mg.</i>	<i>mg.</i>	<i>mg.</i>	<i>mg.</i>
Control	A	68.3	231	18.7	685	1003
	B	77.3	347	27.4	749	1200
	C	63.6	367	45.4	1154	1630
	Mean	69.7	315	30.5	863	1278
Defruited	A	1003	40.0	1247	2290
	B	983	51.3	1615	2649
	C	791	49.0	1162	2003
	Mean	926	46.8	1341	2314

by defruiting approximately three fold but this difference did not meet the requirements of the 0.05 level of significance; starch concentrations found in the fibrous roots of the defruited plants were significantly higher than those found in the control plants. Corresponding to these differences in carbohydrate concentrations there was an increase of approximately sixty per cent. in the concentration of bromine in the fibrous roots of the defruited versus the control plants and this difference was highly significant. The concentrations of bromine found in the main-stalk leaves are correlated with the concentrations of sugar in the fibrous roots but they are not correlated with the concentrations of sugar in the leaves.

TABLE III

CONCENTRATIONS OF BROMINE AND CARBOHYDRATE IN FIBROUS ROOTS, TAP ROOTS, AND LEAVES OF CONTROL AND DEFRUITED COTTON PLANTS AND RESULTS OF ANALYSIS OF VARIANCE

TREATMENT	GROUP	MILLIGRAMS PER GRAM FRESH WEIGHT								
		FIBROUS ROOTS			TAP ROOTS			MAIN-STALK LEAVES		
		BROMINE	TOTAL SUGARS	STARCH	BROMINE	TOTAL SUGARS	STARCH	BROMINE	TOTAL SUGARS	STARCH
Control	A	1.60	0.078	1.95	1.17	5.11	13.7	0.95	3.11	13.6
	B	2.27	0.156	1.95	1.56	5.42	13.2	0.99	2.99	13.6
	C	1.65	0.073	1.94	2.01	4.86	13.7	1.70	2.61	12.5
	Mean	1.84	0.102	1.95	1.58	5.13	13.5	1.21	2.90	13.2
Defruited	A	3.03	0.245	2.12	1.58	13.10	33.7	2.10	3.53	12.7
	B	2.72	0.205	2.13	1.63	14.57	31.3	2.45	1.91	10.4
	C	3.01	0.451	2.26	1.89	14.66	25.5	1.84	3.33	12.8
	Mean	2.92	0.300	2.17	1.70	14.11	30.2	2.13	2.92	12.1
Mean difference		1.08	0.198	0.22	0.12	8.98	16.7	0.92	0.02	1.1
Required m.d. for sig. to 0.05		0.64	0.224	0.11	0.73	1.50	6.8	0.82	0.59	2.4

There was no difference in the concentrations of sugar or starch in the main-stalk leaves under the two treatments of this experiment. Samples collected earlier in the day in other experiments have shown higher carbohydrate concentrations in leaves from defruited plants than in those from fruited plants. MASKELL and MASON (18) likewise have found higher concentrations of both nitrogen and sucrose in the leaves, bark, and wood of defruited than of control cotton plants (average of 2 morning and 1 afternoon samples). In the control plants the sugars from the leaves presumably moved principally into the bolls, whereas in the defruited plants a part of the sugar that would otherwise have moved into the bolls was utilized in a greater growth of leaves and framework, but a relatively greater proportion of it was utilized in the extensive development of the fibrous roots.

ACCUMULATION OF NITROGEN AND POTASSIUM

Bromine was introduced in the culture solution as the test element on the day following defruiting whereas the other mineral elements of the nutrient solution were all present from the start. Analyses for the concentrations of total nitrogen and of potassium in the fibrous roots and in the main-stalk leaves were made out of general interest and these results, together with a recapitulation of the sugar and bromine data, are reported in table IV.

TABLE IV

CONCENTRATIONS OF SUGARS, BROMINE, TOTAL NITROGEN, AND POTASSIUM
IN FIBROUS ROOTS AND MAIN-STALK LEAVES

TREAT- MENT	GROUP	MILLIGRAMS PER GRAM FRESH WEIGHT							
		FIBROUS ROOTS				MAIN-STALK LEAVES			
		SUGARS	BRO- MINE	NITRO- GEN	POTAS- SIUM	SUGARS	BRO- MINE	NITRO- GEN	POTAS- SIUM
Control	A	<i>mg.</i> 0.078	<i>mg.</i> 1.60	<i>mg.</i> 1.26	<i>mg.</i> 0.57	<i>mg.</i> 3.11	<i>mg.</i> 0.95	<i>mg.</i> 5.87	<i>mg.</i> 2.36
	B	0.156	2.27	1.49	0.69	2.99	0.99	6.02	1.93
	C	0.073	1.65	1.63	0.64	2.61	1.70	6.40	2.25
	Mean	0.102	1.84	1.46	0.63	2.90	1.21	6.10	2.18
Defruited	A	0.245	3.03	1.75	0.92	3.53	2.10	5.73	1.80
	B	0.205	2.72	1.69	0.91	1.91	2.45	5.73	2.84
	C	0.451	3.01	1.94	0.90	3.33	1.84	5.78	2.73
	Mean	0.300	2.92	1.79	0.91	2.92	2.13	5.75	2.46
Mean difference		0.198	1.08	0.33	0.28	0.027	0.916	0.35	0.28
Required m.d. for sig. to 0.05		0.224	0.64	0.38	0.19	0.574	0.817	0.44	0.98

Higher concentrations of nitrogen and potassium, as well as of bromine, were found in the fibrous roots of the defruited plants. The increase in potassium was substantial but the difference in nitrogen lacked statistical significance. In the main-stalk leaves significant differences were found only in the instance of the bromine concentrations.

Discussion

Although there was no overlapping between treatments in the concentrations of sugar, bromine, nitrogen, or potassium in the fibrous roots, there was a marked variability within the treatments. If the observed increases in accumulation as reflected by the concentration of bromine, nitrogen, and potassium in the fibrous roots were actually produced by reason of the higher sugar concentrations, then the differences in accumulation should be directly correlated with the differences in sugar concentrations—irrespective of treatment. This aspect of the problem has been examined by calculating the coefficients of correlation between the concentrations of sugar and the concentrations of bromine, nitrogen, and potassium in the fibrous roots.

The values are as follows (a value of 0.811 is required for significance at 0.05): bromine, 0.844; nitrogen, 0.828; potassium, 0.781.

The fact that these coefficients of correlation are all positive and all high, with two of the three significant, provides additional evidence that the relationship between the level of sugars and the level of solute accumulation in the roots is a causal one. Significant correlations between sugars in the roots and minerals in the leaves were not found and in this experiment they were not necessarily to have been expected, since in terms of concentrations as differing from total accumulation the dilution effects associated with the more rapid growth of the defruited plants would parallel in direction the exhaustion effects resulting from the reduced uptake by the control plants.

It seems probable that above some relatively low concentration of labile carbohydrate in a root further increases would have little effect upon the rate of metabolic activity and in turn upon the rate of solute accumulation. It is worthy of note in this connection that there were like concentrations of bromine in the fibrous roots of the defruited A and C groups (table III) notwithstanding a nearly doubled concentration of sugar in the latter. Likewise there was no indication of a relationship between the sugar concentrations in the leaves, where sugars were much higher than in the fibrous roots, and the concentration of bromine in the leaves; and yet the uptake of bromine by leaf cells from the xylem vessels, or the retention of bromine by them, requires the expenditure of metabolic energy if the concentrations of labile ions in the leaf cells are greater than in the vessels.

It is useful to speculate on the indications afforded by the data with respect to the sugar concentrations in the active terminal regions of the fibrous roots under the two treatments. The sugar concentrations found in the masses of fibrous roots are probably excellent indices to the concentrations in their terminal regions but it is not to be assumed that the one is a direct measure of the other. The sugars in the tap roots (fraction included large laterals) were 50 times more concentrated than in the masses of fibrous roots under both treatments and yet it is reasonable to believe that at the points of attachment the concentrations in the fibrous roots tended to approach the concentrations in the tap roots. At the terminal ends of the fibrous roots the concentrations would of necessity, therefore, have been very much lower than the concentrations found for the masses as a whole; the values ranging from 0.0073 to 0.0451 per cent. (table IV) found for the concentrations of sugars in the masses of fibrous roots would suggest that the concentrations existing in the terminal regions of these roots must have been extremely low.

Observations that have been made on the growth reactions of the cotton plant are such as to indicate that the extent to which vegetative development is slowed down with the onset of fruiting is related not only to the degree of fruitfulness but also to the concentration of nutrients in the substrate. It seems reasonable that an interrelation between the two factors should exist since on theoretical grounds a greater expenditure of metabolic energy would

be required for the uptake of solutes from dilute than from concentrated substrates. The writers cannot recall ever having seen dormant terminal buds on cotton plants growing in sand cultures abundantly supplied with nutrients. Dormant buds are readily obtained, however, when the nitrate supply is sufficiently reduced. Plants growing on low-nitrogen soils in containers have been stimulated into improved growth and color either by the addition of nitrogen or by the removal of all previously set bolls; the two treatments appear to have similar effects, which is reasonable on the basis of metabolic consideration, since with an increased movement of sugar to the roots an increased uptake from the dilute substrate should follow. Renewed vegetative activity is almost always observed following the maturation of the first crop of bolls in the late summer.

Under field conditions the extension of roots into new soil zones makes available additional supplies of nutrients but in sand cultures this consequence of root growth would not exist. It is entirely possible, nonetheless, that with a greater number of roots the uptake of mineral elements might increase. Although neither of the foregoing considerations would seem to adequately account for the negligible, or even negative, uptake of soil nutrients by heavily fruited plants with depressed root development, the fact remains that in the present experiment the defruited plants developed greater root systems relative to the weight of their tops than did the control plants and that the defruited plants accumulated a greater weight of bromine. It seems reasonable to assign some part of the extra bromine uptake by the defruited plants to their extra roots but such an assignment in no way accounts for the higher *percentages* of bromine in the fibrous roots of the defruited plants; the higher percentages of bromine are most logically explained on the basis of the higher sugar concentrations. The concentrations of nutrients were made relatively high following defruiting in this experiment and the possibility was thereby avoided that lack of availability of any nutrient might have limited its uptake. On the basis of energy relationships it would seem that more outstanding differences would have resulted had the cultures been supplied with frequently replaced but very dilute solutions.

Although existing information leaves uncertain the manner of operation of many physiological relationships involved in the growth and fruiting of cotton, the finding of a direct relation between carbohydrate movement into the fibrous roots and mineral uptake makes possible a further projection of the cause and effect factors involved in the growth cycle. In undertaking to fit the foregoing findings into the existing information on this subject an omission is purposely made of all reference to the effects of drought. This omission may not be justified, particularly as it is known that there are substantial increases in the concentrations of carbohydrates in the cotton plant when the water supply is insufficient. The effect of drought on mineral uptake by cotton, however, has not been studied and many other physiological relationships are undoubtedly altered by high water tensions.

Limiting the present discussion to plants amply supplied with moisture, the physiological sequence of events, in accord with present information, would appear to be as follows: During the preflower and early flowering period photosynthetic products are rapidly converted into above-ground vegetative structures and root growth and there is an associated heavy uptake of soil nutrients. With flowering and the continued setting of bolls more and more of the carbohydrates and of the current and previously accumulated nitrogen (18) are moved to the bolls. The reduction in the movement of carbohydrates to the roots reduces mineral uptake and this reduction would in turn be expected to restrict growth. Accompanying the curtailed vegetative expansion, the effectiveness of the older leaves declines and the former upward trend in photosynthetic output (8) is flattened or reversed. By this stage many of the young bolls are shedding. The rates of shedding, flowering, and growth fluctuate some with changes in environmental conditions but the fluctuations are secondary to the broad trend of the cycle. Should the reciprocally depressing effects of reduced carbohydrates and reduced mineral uptake become sufficiently pronounced, the terminal bud of the plant becomes dormant and leaf and flower development ceases. With the maturation of the crop of bolls the cotton plant either dies (exceptional), as do annuals, or it resumes growth as do perennials—possibly depending upon the extent of its depletion.

In accord with the early conclusions of EWING (13) and MASON (19) there seems to be little room for doubt that much of the shedding of cotton bolls (exclusive of that caused by bud and boll insects) reflects a reduction in the number of bolls carried by the cotton plant to levels compatible with the plant's current ability to maintain boll growth. Daily graphs of shedding rates are typically characterized by major trends that are broken by successions of upward and downward variations. These marked variations in shedding suggest that the stimulus, whatever its nature, that gives rise to abscission may often cause the loss of more bolls than is necessary to reduce the boll load to a level compatible with the carrying capacity of the plant. Reductions below carrying capacity would account for the marked increases in flowering, boll setting, and growth that so often follow heavy shedding or that always follow the artificial removal of bolls. Likewise, it seems as logical to look for high shedding following a return to customary conditions after especially favorable weather as after unfavorable weather following customary conditions. Under environmental conditions sufficiently uniform as to avoid the waves of shedding and the subsequent momentary increases in growth and flowering rates, it seems probable that the interrelations between fruiting, mineral uptake, and growth would be even more clearly defined than they are under varying climatic conditions.

DASTUR and AHAD (10) working in the Punjab found maximum mineral uptake during the early flowering stages of both American and *desi* cottons. The *desi* cotton plants were more fruitful than the American and the authors noted that "As a rule the leaves of the *desi* plants get depleted of their

minerals more than the leaves of the American." The two varieties were alike as regards leaf nitrogen. Other than for the work just cited there is little basis for a conclusion on whether material differences exist in the rates of mineral uptake by highly determinate strains of cotton and strains that shed a greater proportion of their bolls and for a longer time continue to make vegetative growth. In those regions where diseases, insects, or climatic conditions are incompatible with late cotton, the early determinate strains are most popular but elsewhere the less determinate strains are usually found to be more productive. Under the latter conditions the artificial removal of all early flowers has resulted in higher yields (12); but in Mississippi (15), the removal of all squares (floral buds) during the first one to six weeks of the flowering period was without consistent effect on final yields and the larger plants were regarded as undesirable. The fact that yields were not depressed by square removal over long periods during the forepart of the flowering period strongly suggests that occasional bursts of shedding may be of minor significance.

Summary

The uptake of mineral elements has been shown by others to proceed rapidly in the cotton plant during its early growth period but to decline or become negligible with the setting of a large number of bolls. In this paper the effect of fruiting upon the sugar concentrations in the fibrous roots and in turn upon bromine uptake was studied by comparing fruited and defruited plants grown in sand cultures.

By the end of a period of three weeks, following the addition of bromine to the nutrient solution and the removal of flower buds and bolls, the concentration of sugar in the fibrous roots had tripled and the concentration of bromine had increased 60 per cent. over the control plants. The weight of bromine accumulated by entire defruited plants was double that found in the control plants. The fibrous roots of the defruited plants had a slightly higher concentration of nitrogen and a significantly higher concentration of potassium at the end of the experiment.

It appears that much of the decline in mineral uptake with heavy fruiting can be attributed to the reduced movement of carbohydrate to the roots.

The reduced vegetative expansion of the cotton plant that occurs during the period of heavy fruiting is undoubtedly due both to the utilization of carbohydrates by developing bolls and to the reduced mineral uptake. When these reciprocally depressing effects are sufficiently pronounced, vegetative growth becomes negligible. With the maturation of a crop of bolls the cotton plant either dies (exceptional) as do annuals, or it resumes growth as do perennials—possibly depending on the extent of its depletion.

BUREAU OF PLANT INDUSTRY, SOIL AND AGRICULTURAL ENGINEERING
AND THE TEXAS AGRICULTURAL EXPERIMENT STATION
COLLEGE STATION, TEXAS

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