EFFECTS OF POTASSIUM ON CHLOROPHYLL, ACIDITY, ASCORBIC ACID, AND CARBOHYDRATES OF *ANANAS COMOSUS* (L.) MERR.[1]

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(WITH THREE FIGURES)

Introduction

A study concerned with the effects of iron on chlorophyll, acidity, ascorbic acid, and carbohydrate fractions of *Ananas comosus* was reported in a previous publication (**35**). Also, the effects of different amounts of potassium on growth and ash constituents of the same plants were reported in a former paper of this series (**36**). This study is concerned with the effects of potassium on chlorophyll, acidity, ascorbic acid, and different carbohydrate fractions of the same plants.

The literature pertaining to the effects of potassium on chlorophyll emphasizes the fact that potassium deficiency may cause chlorophyll breakdown with the subsequent development of brown spots and leaf necrosis comparable to those observed in *A. comosus*. WALL (**46**) has recognized in tomatoes two types of potassium deficiency symptoms: the first stage marked by a stunted, hard, yellow plant was associated with a high carbohydrate content; and the second, in which the carbohydrate content had greatly diminished, the plant began to grow, turned green, became soft, and at the same time the lower leaves commenced to die progressively up the stem. RICHARDS and TEMPLEMAN (**31**) claim that symptoms of potassium deficiency in barley may either be a light yellow color of leaves associated with succulence and rapid death of the leaves or a dark green associated with white or brown spots on the leaves. According to ROHDE (**32**), leaves of plants adequately supplied with potassium are yellowish green, while those deficient in potassium are deep green and contain more chlorophyll. No yellow color was observed in the leaves of *A. comosus* supplied with the low amounts of potassium indicated in this study, but instead a deep green color with a few brown spots and leaf tip necrosis was extensive in old leaves.

Our information pertaining to the effects of potassium on ascorbic acid is meager. However, ascorbic acid and total carboxylic acid reserves were closely associated with the chlorophyllose tissues of the plant (**35, 37, 39**). Comparable relationships between ascorbic acid and chlorophyllose tissues were shown by GIROUD (**6, 7, 8**) for other plants. Ascorbic acid, according to GUHA and GHOSH (**11**), is synthesized in *Phaseolus mungo* from mannose by an enzyme at pH 5.8 but not at 7.4. Ascorbic acid in the fruit of *A. sativus*, a synonym of *A. comosus* (L.) Merr., described as a reducing factor first by SZENT-GYÖRGYI (**42**), was reported to occur in fair concentrations

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corresponding to that in the turnip. STOTZ *et al.* (**41**) consider the function of ascorbic acid in plant tissues comparable to that of cytochrome in animal tissues because both substances are rapidly reduced and oxidized by physiological respiratory systems. SZENT-GYÖRGYI (**43**) observed that tissues of cabbage leaves containing ascorbic acid were able to remove oxygen from the atmophere by means of the enzyme, ascorbic acid oxidase (hexoxidase), whereas those lacking ascorbic acid were unable to do so. His explanation was that "ascorbic acid plays an important part in the respiration of plants by connecting, as hydrogen carrier, the system in which the molecular oxygen enters into reaction." JAMES *et al.* (**21**) have observed that in the presence of ascorbic acid and atmospheric oxygen barley plant sap oxidized lactic acid to pyruvic acid.

The information pertaining to the effects of potassium on carbohydrate enzymes and carbohydrates is relatively extensive but not in perfect agreement on all points. VULQUIN and LISBONNE (**45**) state that diastase *in vitro* completely separated from neutral salts becomes inactive and resumes its activity only upon the addition of potassium and other metals. The viewpoint of KENDALL and SHERMAN (**23**) is that diastase accelerates the condensing as well as the hydrolytic reaction in carbohydrates. The studies of MASKELL (**25**) and JAMES (**19**) suggest that both condensing and hydrolytic reactions which may be designated as hexose-starch and starch-hexose reactions are dependent upon temperature, concentration of hexose, and concentration of enzyme. Fluctuations in the amount of starch in the leaves are not reflected in the velocity of starch-sugar reaction because starch is only slightly soluble and constitutes, therefore, a saturated solution. Any effect of potassium upon the rates of the reaction should be through the concentration of hexose or enzyme—a reduced hexose concentration during a period of darkness might lead to a faster disappearance of starch than during a period of light. Translocation of sugars is from high to low concentrations in the opinion of MASON and MASKELL (**26**). Diastase activity was increased by potassium in potato leaves (**19**), in bean leaves (**18**), and in Lemna (**48**) but was decreased in sugar cane (**12**) and sugar beets (**5**). HOAGLAND (**17**) claims that the activity of the various diastases may be modified in one direction or the other by a deficiency of potassium.

Plants supplied with small amounts of potassium contained in their leaves higher concentrations of reducing sugars than those with high potassium (**12, 22, 27, 28, 29, 42**). In totally potassium-deficient plants the amounts of reducing sugars were low (**9, 12, 16**) and according to GREGORY *et al.* (**9, 10**) they were due to low assimilation rate, high respiration, high protein synthesis, and excessive meristematic activity. High reducing sugar values in low-potassium plants are usually accompanied by low values in disaccharides (**12**) and polysaccharides, but the findings of WATSON (**47**) and RICHARDS (**30**) and RICHARDS and TEMPLEMAN (**31**) are in disagreement with HARTT (**12**) and those of the authors as reported below. Correlation between amounts of starch in the leaves and potassium supplied to the roots

was obtained in *Pisum sativum* by DAY and COMBONI (**4**) and JAMES (**19**), although starch accumulation in leaves is transient according to DAVIS as cited by HOAGLAND (**18**). Also, high starch in the stem correlated with a high potassium supply to the roots as shown in this and other studies (**22, 25, 27, 28, 29**). The low starch values obtained by WHITE (**48**) in the totally potassium-deficient cultures of Lemna may fall in the category characterized by GREGORY as due to a low assimilation rate, high respiration, high protein synthesis, and excessive meristematic activity. RUSSELL (**33**) claims correlation between the amounts of potassium supplied to roots and of fructosan polysaccharides in barley. According to HASTINGS (**13**), quoted by BARRON (**1**), the synthesis of glycogen in rat liver is increased fourfold if the slices are suspended in a solution containing potassium and magnesium at concentrations found in the intracellular fluid in the presence of glucose.

Methods

Techniques for the culture and sectioning of the plants and methods for the chemical analysis of the tissues and for the statistical treatment of the data are the same as those reported in previous publications (**35, 36, 37**).

Synoptical expressions replacing certain often repeated appellations in the text have been introduced for designating the different series. Thus the nitrate-nitrogen series is designated by N-n and the ammonium-nitrogen by A-n.

Results

DRY MATTER

Dry matter values, reported in table I as milligrams per gram of fresh weight, were higher in the leaves of the Low-K than High-K cultures in both nitrogen series, whereas in the stem similar values were higher in the High-K than Low-K cultures. The data in figure 2 and in table III show that the differences in dry matter between leaves and stem had resulted from a greater sugar content in the leaves of the Low-K cultures and a higher starch content in the stem of the High-K cultures. Total dry matter values per plant, reported in table VII, were higher in the High-K than Low-K cultures. Hemicelluloses, or celluloses plus lignin, although important items in dry matter, varied less with respect to amounts of potassium in the cultures than either sugars or starches.

TITRABLE ACIDITY

Titrable acidity, reported as milligrams of citric acid per gram of fresh tissue in table I and depicted in figure 1, was higher in the High-K than in the Low-K cultures. It was mostly restricted to the chlorophyllose sections of the leaves; the non-chlorophyllose sections of the leaves, or the stem and roots contain very low values as reported, also, in previous studies (**35**).

It is possible that the accumulation of greater amounts of organic acids in the Low-K cultures of the N-n than A-n series might have been favored by the higher calcium content of the plants, in accordance with the views of

various investigators (**3, 36, 38, 40**). However, later unpublished data suggest that diurnal changes and growth rates are concerned more directly with tissue acidity than other factors.

Ascorbic acid

Ascorbic acid values, reported in table II, were, with a few exceptions, higher for the Low-K than High-K cultures in the N-n series, but in the A-n

TABLE I

Effects of 205 vs. 4 mg. of potassium per liter of nutrient solution supplied with equal amounts of nitrate- or ammonium-nitrogen on the dry matter* and titrable acidity, reported as citric acid† in different sections of one-year-old *Ananas comosus* (L.) Merr.

Plant sections	Nitrate-N				Ammonium-N			
	High K		Low K		High K		Low K	
	Citric acid	Dry matter	Citric acid	Dry matter	Citric acid	Dry matter	Citric acid	Dry matter
	mg.	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*
Leaves:								
Old (B) 1+2 (base)	23.9	134	0.7	138	30.0	126	18.3	142
3	78.8	122	7.0	128	70.3	124	52.3	134
4	113.0	130	97.0	152	114.0	135	85.2	157
5 (tip)	102.0	150	100.0	160	113.5	164	79.0	170
Mature (C) 1 (base)	23.2	112	22.0	118	34.8	112	16.1	118
2	73.8	122	68.0	122	47.2	108	22.2	118
3	123.0	125	114.5	140	137.7	117	75.7	148
4	152.0	126	151.0	165	158.7	141	101.3	170
5 (tip)	161.0	155	140.0	179	172.3	173	102.3	178
Active (D) 1 (base)	19.8	96	33.0	97	30.0	87	16.2	99
2	43.2	118	43.6	117	51.4	113	21.8	119
3	146.6	118	139.0	138	112.4	120	70.7	144
4	208.5	144	159.0	157	228.5	140	113.6	169
5 (tip)	227.0	159	173.5	177	212.3	172	130.5	184
Young (E) 1 (base)	30.2	86	31.7	87	38.5	83	18.6	86
2	38.0	100	48.6	105	43.0	105	23.2	112
3	179.0	125	154.0	125	138.0	130	65.7	137
4+5 (tip)	255.0	151	188.0	163	186.5	169	104.3	165
Stem:								
Base	15.1	212	28.5	158	31.6	184	22.7	154
Middle	31.6	203	36.5	140	31.9	160	33.4	144
Apex	50.4	127	47.5	122	52.8	110	36.3	124
Roots	8.7	149	11.5	166	8.7	149	7.3	137

* Milligrams per gram of fresh tissue.
† Milligrams per gram of dry tissue.

series they were higher for the High-K than Low-K cultures. The significance of the reversal of ascorbic acid values with respect to amounts of potassium and different kinds of inorganic nitrogen is not obvious at this time and cannot be explained. Ascorbic acid concentrations were very high in the chlorophyllose sections of the leaves in contrast to those in the non-chlorophyllose sections. However, such concentrations were not directly proportional to those of chlorophyll in different leaves of the same plant or in

similar leaves of different plants. Ascorbic acid and titrable acidity values correlated, being simultaneously either high or low in the same sections, although the values of the latter were consistently many times higher than those of the former.

CHLOROPHYLL AND CAROTENOIDS

Chlorophyll values varied in similar leaf sections of different cultures, as shown in table II. Chlorophyll differences between High-K and Low-K cultures in the N-n series in favor of the former cultures were statistically significant (odds 277 : 1). Also, similar differences in the A-n series but in favor of the Low-K cultures were statistically significant (odds 207 : 1). The

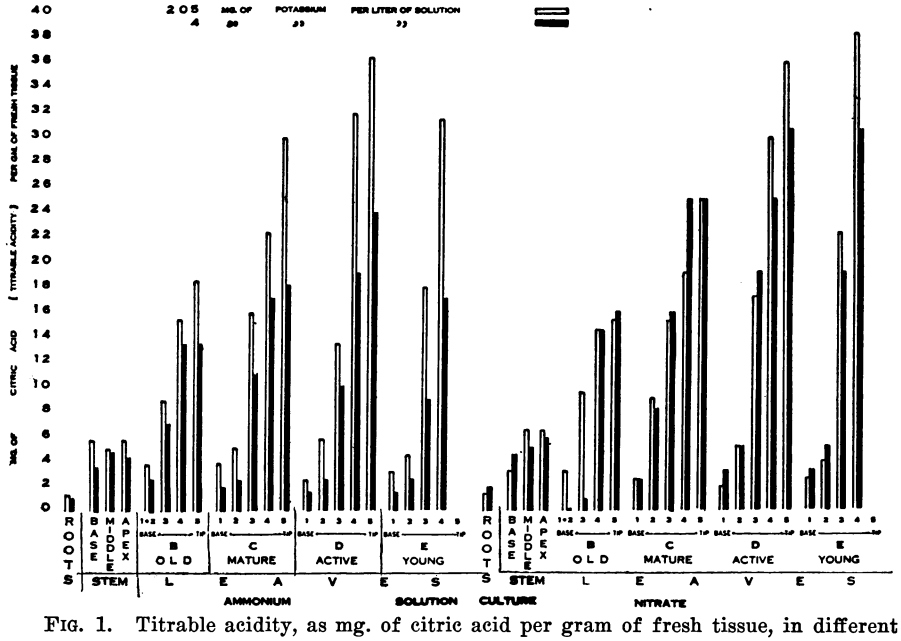

FIG. 1. Titrable acidity, as mg. of citric acid per gram of fresh tissue, in different sections of *A. comosus* grown in cultures supplied with 205 or 4 mg. of potassium per liter and with equal amounts of nitrate- or ammonium-nitrogen.

difference of the means of the chlorophyll content of the Low-K cultures between N-n and A-n series, in favor of the latter series, was statistically significant (odds 9999 : 1), but that of the High-K cultures lacked statistical significance.

The amounts of carotenoids and chlorophyll correlated in all leaf sections. The difference of the means between High-K and Low-K cultures in the N-n series, in favor of the High-K cultures (odds 64 : 1) was statistically significant; but in the A-n series, it was in favor of the Low-K cultures (odds 2500 : 1). A similar difference of the carotenoids of the Low-K cultures between N-n and A-n series, in favor of the A-n series (odds 9999 : 1) was statistically significant, but that of the High-K cultures lacked statistical significance (odds 3 : 1).

TABLE II

EFFECTS OF 205 VS. 4 MG. OF POTASSIUM PER LITER OF NUTRIENT SOLUTION SUPPLIED WITH EQUAL AMOUNTS OF NITRATE- OR AMMONIUM-NITROGEN ON CHLOROPHYLL, CAROTENOIDS, AND ASCORBIC ACID (MG. PER GRAM OF DRY TISSUE) IN DIFFERENT SECTIONS OF ONE-YEAR-OLD *Ananas comosus* (L.) MERR.

PLANT SECTIONS	NITRATE-N						AMMONIUM-N					
	HIGH-K			LOW-K			HIGH-K			LOW-K		
	CHLOROPHYLL	CAROTENOID	ASCORBIC ACID	CHLOROPHYLL	CAROTENOID	ASCORBIC ACID	CHLOROPHYLL	CAROTENOID	ASCORBIC ACID	CHLOROPHYLL	CAROTENOID	ASCORBIC ACID
	mg.	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*
Leaves:												
Old (B) 1+2 (base)	1.61	0.187	0.2	1.49	0.174	0.2	1.51	0.151	0.3	1.36	0.169	0.2
3	4.90	0.753	2.7	3.10	0.446	5.9	4.15	0.540	2.7	4.40	0.641	1.9
4	4.57	0.761	8.5	4.17	0.618	15.7	5.19	0.800	18.3	4.77	0.704	6.7
5 (tip)	4.57	0.734	10.0	3.65	0.562	14.1	4.25	0.740	18.1	5.76	0.820	14.9
Mature (C) 1 (base)	.....	.....	0.1	.....	.....	0.2	.....	.....	0.1	.....	.....	0.3
2	1.63	0.188	1.1	1.94	0.213	0.3	2.06	0.250	0.6	2.13	0.245	0.5
3	4.21	0.608	7.4	3.67	0.550	11.0	3.70	0.488	9.9	5.16	0.682	3.8
4	3.90*	0.648	12.3	3.70	0.563	22.7	4.43	0.690	26.5	5.32	0.777	10.2
5 (tip)	4.71	0.807	11.3	3.71	0.537	13.8	5.49	0.787	31.3	5.38	0.878	13.2
Active (D) 1 (base)	.....	.....	0.1	.....	.....	0.2	.....	.....	0.5	.....	.....	0.3
2	1.61	0.161	0.1	1.22	0.137	0.2	1.92	0.097	0.4	1.45	0.151	0.3
3	3.63	0.475	0.9	3.59	0.428	2.5	3.72	0.433	1.6	4.77	0.610	0.2
4	4.55	0.656	30.6	3.52	0.705	25.9	4.12	0.614	41.6	4.73	0.752	10.6
5 (tip)	4.28	0.598	38.8	3.83	0.668	42.1	4.57	0.755	57.3	5.25	0.887	36.4
Young (E) 1 (base)	.....	.....	0.1	.....	.....	0.2	.....	.....	0.1	.....	.....	0.4
2	1.32	0.110	0.1	1.58	0.143	0.2	1.49	0.143	0.1	1.83	0.205	0.3
3	2.73	0.288	0.2	2.58	0.296	0.2	2.83	0.331	0.5	3.29	0.496	0.2
4+5 (tip)	3.81	0.570	12.9	3.58	0.490	20.6	2.71	0.415	25.3	3.94	0.643	8.3

* Doubtful.

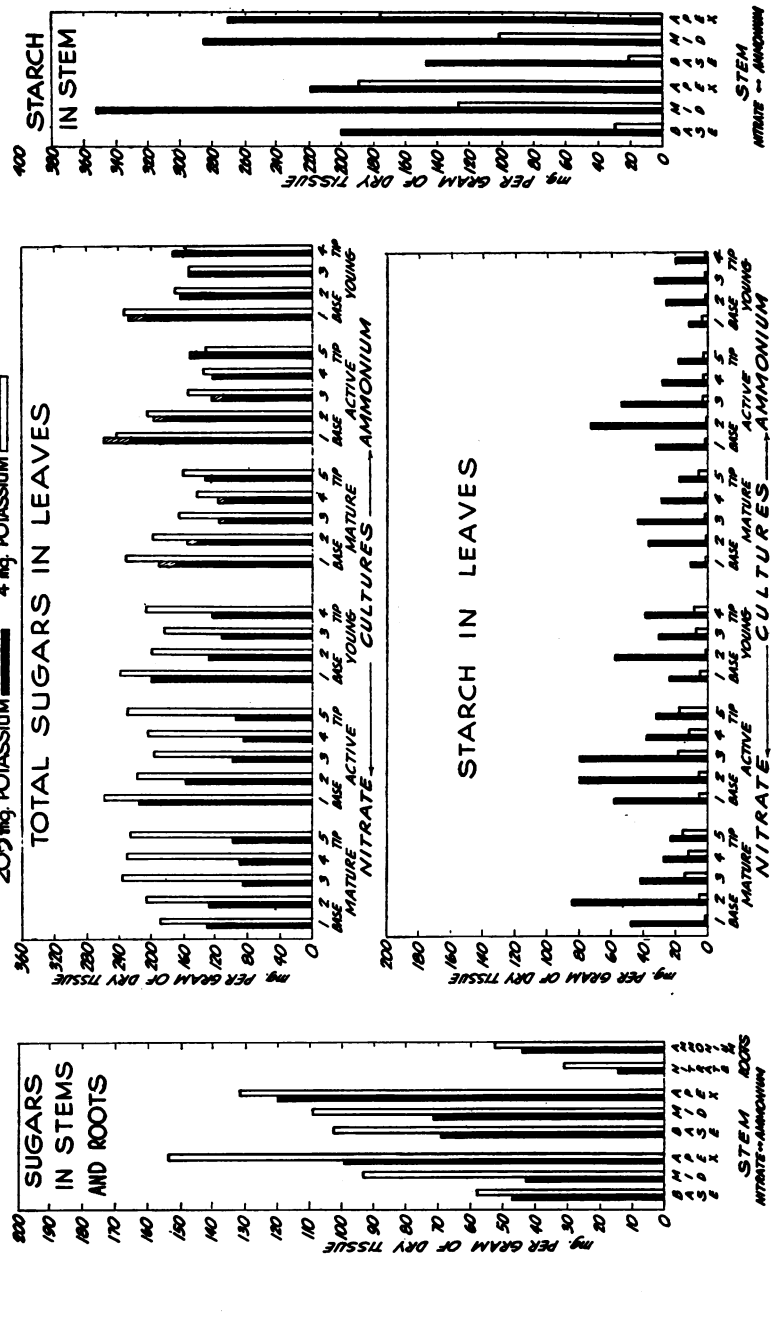

FIG. 2. Total sugars or starch, as mg. per gram of dry tissue, in different sections of *A. comosus* grown in cultures supplied with 305 or 4 mg. of potassium per liter and with equal amounts of nitrate- or ammonium-nitrogen.

The fact that chlorophyll and carotenoid values were higher in the High-K cultures of the N-n series and in the Low-K cultures of the A-n series contradicts any possible effects of potassium on the chlorophyll and carotenoid content of the leaves. Other factors possibly associated with the relations of potassium to nitrate or ammonium assimilation might have been responsible for such differences as indicated in the above results.

Sugars

Total sugar values, depicted in figure 2, as per mil of fresh weight, were, with a few exceptions, greater in the Low-K than High-K cultures in both series. Comparison of total sugar values of the leaves of the High-K cultures shows that they were greater in the A-n than N-n series, but those of the Low-K cultures were reversed. Reducing sugar values, in table III, were greater for the Low-K than High-K cultures in both series, indicating that potassium supplied in insufficient amounts to the Low-K cultures re-

TABLE III

Effects of 205 vs. 4 mg. of potassium per liter of nutrient solution supplied with equal amounts of nitrogen either as nitrate or ammonium on the amounts of reducing sugars* and sucrose*

Plant sections	N-n series				A-n series			
	High K		Low K		High K		Low K	
	Reducing sugars	Sucrose	Reducing sugars	Sucrose	Reducing sugars	Sucrose	Reducing sugars	Sucrose
	mg.	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*	*mg.*
Leaves:								
Old (B) 1+2 (base)	87.5	23.2	144.0	21.0	94.0	30.0	109.5	30.0
3	98.7	37.7	184.0	31.0	117.5	35.5	142.0	33.0
4	94.4	33.9	195.0	31.0	100.0	40.0	142.0	35.0
5 (tip)	86.0	38.0	181.0	33.0	111.0	44.0	156.0	44.0
Mature (C) 1 (base)	107.0	23.0	164.0	23.7	161.0	30.0	203.0	30.0
2	96.0	32.0	189.0	16.0	126.4	28.6	175.0	25.0
3	51.2	35.3	201.0	35.0	79.0	37.0	130.0	37.0
4	48.6	41.4	192.5	37.5	73.3	44.7	110.0	35.0
5 (tip)	55.0	42.0	182.5	44.5	89.0	45.0	117.0	44.0
Active (D) 1 (base)	195.0	20.0	238.0	21.0	239.3	20.7	225.0	19.0
2	136.0	22.0	199.0	18.0	176.0	22.0	187.0	19.0
3	70.0	29.0	171.3	24.7	89.3	34.2	119.0	36.0
4	45.8	40.2	174.4	30.6	79.1	44.4	98.5	36.0
5 (tip)	56.5	38.5	190.0	38.0	108.0	44.0	94.2	37.8
Young (E) 1 (base)	170.0	32.0	209.0	30.0	197.5	30.5	205.0	29.0
2	110.0	19.0	186.0	12.0	143.0	20.0	149.0	21.0
3	88.0	26.0	163.0	20.0	126.0	28.0	132.0	22.0
4+5 (tip)	83.0	42.0	177.0	30.0	130.5	42.5	130.0	27.0
Stem:								
Base	19.6	27.4	40.3	17.7	46.1	22.9	80.0	22.0
Middle	12.8	30.2	63.0	30.0	46.4	25.0	84.0	25.0
Apex	56.3	41.7	105.7	47.3	76.3	43.7	84.0	47.6
Roots	2.7	12.0	8.4	22.3	23.6	20.0	28.1	23.8

* Milligrams per gram of dry tissue.

sulted in accumulations of variable magnitudes of total and reducing sugars in both leaves and stem. Comparison of the difference of reducing sugars as percentage of total sugars between Low-K and High-K cultures (table IV) shows that such differences increased progressively in the N-n series from the basal (no. 1) to the terminal (no. 5) sections of the leaves and from the apical to the basal sections of the stem. In the A-n series similar differences between High-K and Low-K cultures were not as great as in the N-n series indicating that the rate of conversion of reducing sugars to more complex carbohydrate compounds had possibly been retarded either by the primary products of ammonium assimilation or by Cl ions present in the solution cultures of High-K cultures in the A-n series.

TABLE IV

DIFFERENCE BETWEEN LOW-K AND HIGH-K CULTURES IN REDUCING SUGARS AS PERCENTAGE OF TOTAL $\frac{\text{R.S. (LOW-K)} \times 100}{\text{T.S. (LOW-K)}} - \frac{\text{R.S. (HIGH-K)} \times 100}{\text{T.S. (HIGH-K)}}$ IN DIFFERENT PLANT SECTIONS*

SERIES	LEAVES						STEM	
	SECTIONS	OLD	MATURE	ACTIVE	YOUNG	AVERAGE	SECTIONS	
		%	%	%	%	%		%
N-n	1	8.3	4.9	1.2	3.3	4.4	Base	27.5
	2	.....	17.1	5.9	8.8	10.6	Middle	37.8
	3	13.1	26.1	16.8	12.0	17.0	Apex	11.6
	4	13.0	29.8	31.6	19.1	23.4	.....	.....
	5	15.3	23.7	23.8	.....	20.9	Roots	7.8
A-n	1	4.2	2.9	0.0	0.9	2.0	Base	11.8
	2	.....	7.2	1.8	0.0	3.0	Middle	12.0
	3	4.2	9.8	4.3	4.0	5.6	Apex	0.7
	4	8.5	13.7	9.2	7.5	9.7	.....	.....
	5	6.4	6.2	0.3	.....	3.25	.....	.....

* R.S. = Reducing Sugars; T.S. = Total Sugars.

Sucrose values (table III) were, with a few minor exceptions, greater in the High-K than in the Low-K cultures. In table V, mean sucrose values as percentage of total sugars in the N-n series were 27.1 and 53.4 per cent. respectively, for the leaves and stem of the High-K cultures; those of the Low-K cultures were 12.9 per cent. for the leaves and 31.0 per cent. for the stem. Similar values in the A-n series were 23.5 per cent. for the leaves and 35.0 per cent. for the stem of the High-K cultures and for the Low-K cultures leaf values were 18.45 and stem values 27.0 per cent. They indicate that in the N-n series sucrose synthesis from reducing sugars was 2.10 and 1.72 times greater for the leaves and stem, respectively, in the High-K than Low-K cultures. A similar synthesis in the A-n series was 1.27 and 1.30 times greater for the leaves and stem, respectively, in the High-K than Low-K cultures. Considering the chlorophyllose sections (nos. 3–5) alone in the N-n series, sucrose values were from 2.0 to 3.2 times greater in the High-K than in the Low-K cultures. These values, being much higher for the chlo-

rophyllose sections than for the entire leaf, suggest the possibility of a greater rate of sucrose synthesis from reducing sugars in the chlorophyllose than in the non-chlorophyllose sections. On the basis of this assumption accumulations in the basal leaf sections or in the stem may indicate sucrose translocation but not synthesis in situ. Comparison in table III of the

TABLE V

SUCROSE AS PERCENTAGE OF TOTAL SUGARS AND STARCH AS PERCENTAGE OF TOTAL AVAILABLE CARBOHYDRATES (SUGARS PLUS STARCHES) IN DIFFERENT SECTIONS OF ONE-YEAR-OLD *Ananas comosus* GROWN IN SOLUTION CULTURES CONTAINING EQUAL AMOUNTS OF NITROGEN FROM NITRATE OR AMMONIUM SALTS BUT EITHER 205 OR 4 MG. OF POTASSIUM PER LITER OF SOLUTION

PLANT SECTIONS	SUCROSE				STARCH			
	N-N		A-N		N-N		A-N	
	HIGH-K	LOW-K	HIGH-K	LOW-K	HIGH-K	LOW-K	HIGH-K	LOW-K
	%	%	%	%	%	%	%	%
Leaves:								
Old (B) 1+2 (base)	19.8	12.7	24.2	21.6	13.1	1.5	6.9	0.4
3	27.6	14.8	23.2	18.9	16.6	5.0	11.7	1.9
4	26.4	13.7	28.6	19.8	9.3	4.0	11.0	1.6
5 (tip)	14.5	15.4	28.3	22.0	7.2	5.0	5.7	1.6
Mature (C) 1 (base)	17.7	12.6	15.7	12.9	25.0	0.8	5.2	0.3
2	25.0	7.8	18.4	12.5	37.0	2.4	17.8	0.4
3	40.8	14.8	31.9	22.2	30.5	5.2	26.0	1.9
4	46.0	16.3	37.9	24.0	21.7	4.3	18.1	1.5
5 (tip)	43.3	19.6	33.6	27.3	17.3	5.9	10.8	3.4
Active (D) 1 (base)	9.3	8.1	8.0	7.8	19.7	1.8	10.3	0.7
2	13.9	8.3	11.1	9.2	31.3	2.1	25.0	0.3
3	29.3	12.6	27.7	23.1	41.8	7.7	28.6	2.3
4	46.8	14.9	35.9	26.7	28.1	5.1	16.5	1.6
5 (tip)	40.6	16.7	29.0	27.9	23.3	6.1	9.7	1.8
Young (E) 1 (base)	15.8	12.5	13.4	12.4	9.4	1.7	4.5	1.5
2	14.7	6.1	12.3	12.3	35.2	0.5	13.1	0.5
3	22.8	10.9	18.2	14.3	19.1	3.4	16.2	0.9
4 (tip)	33.6	14.5	24.5	17.2	21.9	3.4	9.4	1.0
Stem:								
Base	57.5	30.8	33.4	21.6	79.4	30.6	65.8	16.0
Middle	70.0	32.3	35.1	23.0	88.3	55.2	78.4	45.8
Apex	32.2	30.9	36.4	36.3	66.8	76.4	67.0	83.0
Roots	82.0	73.0	46.0	45.8	28.8	16.2	.....	.....

effects of different kinds of inorganic nitrogen on the polymerization of reducing sugars show that such effects were greater in the High-K than Low-K cultures and were more effective in the N-n than in the A-n series. Ammonium ions supplied to the A-n series tended to retard the rate of conversion of reducing sugars to starch whereas nitrate-N, regardless of amounts supplied, interfered little or none with such processes. Sucrose, reported in table V as percentage of total sugars, was higher in the High-K than Low-K cultures in both nitrogen type series, indicating that synthesis of this disaccharide was promoted more by high than low amounts of potassium.

STARCH

Starch, more than any other organic constituent of the tissues, was affected by the amounts of potassium in the solution cultures. Being a reserve carbohydrate it accumulated in the stem from 10 to 20 times more than in the leaves, as depicted in figure 2.

Starch depositions in the leaves do not present the same gradients as inorganic salts; the former are restricted to sections irrespective of polar orientation whereas the latter, influenced by the transpiration stream, tend to increase gradually from the basal to the terminal sections. Starch depositions in the active (D) leaves of High-K cultures were greatest in the tissues of relatively low photosynthetic and growth activity, as in the transitional (no. 2) and low chlorophyllose (no. 3) sections; in the Low-K cultures, the low chlorophyllose (no. 3) contained more starch than the transitional (no. 2) or other sections. In other leaves, with different rates of growth and metabolic activity, starch accumulations were also found in other leaf sections besides the transitional (no. 2). The above comparisons, indicating that the starch content of the transitional (no. 2) section was affected more by the potassium content in the cultures than other sections, suggest its possible use as an index of plant responses to potassium treatments. The information so far available, indicating that ammonium ions supplied to solution cultures decrease more than nitrate ions the rate of starch synthesis and accumulation in such sections, suggests that interpretations of data on starch findings should consider any inter-relationships as might exist between K, NH_4, or NO_3 ions.

The starch content of different stem sections varied; it was higher in the medial than apical sections of the High-K cultures and lower in the medial than apical sections of the Low-K cultures. The basal stem sections in all cultures contained lower amounts of starch than others. Starch as percentage of total available carbohydrates (sugars plus starches), reported in table V, was from 3 to 30 times higher in the mature (C) and active (D) leaves of the High-K than Low-K cultures in the N-n series. Differences in stem starch values for the different sections between High-K and Low-K cultures (table VI) increased in favor of the former cultures as follows: in the apical, 35 per cent. ($16 + 54 \div 2 = 35$); in the medial, 179 per cent. ($177 + 180 \div 2 = 179$); and in the basal sections, 600 per cent.

Starch deposition differences in the Low-K cultures between apical and medial stem sections, in favor of the former sections, were 49 and 72 per cent., respectively, for the N-n and A-n series; those between apical and basal sections, not shown in table VI, also in favor of the former, were 552 and 773 per cent., respectively; those between medial and basal sections, in favor of the former, were 340 and 385 per cent., respectively. Similar differences in the High-K cultures between apical and medial stem sections, in favor of the latter, were 61 and 6 per cent., respectively, for the N-n and A-n cultures; those between the apical and basal sections, not shown in table VI, also in favor of the former, were 9.6 and 83.7 per cent., respectively; and those be-

tween the medial and basal sections, in favor of the former, were 76 and 94 per cent., respectively. Hence the gradients of starch deposition from the apical to the basal sections decreased 552.0 and 9.5 per cent., respectively, for the Low-K and High-K cultures, which indicates that the rate of starch deposition was 58.1; i.e., (552.0 ÷ 9.5) times lower in the Low-K than High-K cultures. In the A-n series similar gradients, also decreasing from the apical to the basal sections, were lower, 733.0 and 83.7 per cent., respectively, for the Low-K and High-K cultures, indicating that the rate of starch depo-

TABLE VI

COMPARATIVE ANALYSES OF THE PERCENTAGE DIFFERENCES IN STARCH IN STEM SECTIONS BETWEEN HIGH- AND LOW-POTASSIUM CULTURES, BETWEEN NITRATE- AND AMMONIUM-NITROGEN SERIES, OR BETWEEN MEDIAL- AND APICAL- OR BASAL-SECTIONS

ITEM NO.	COMPARISON	STEM SECTIONS	CULTURES	SERIES	DIFFERENCE MG./GM.	PERCENTAGE
1	H-K vs. L-K	Apical	H-K,* L-K†	N-n	219–189 = 30	16
2	H-K vs. L-K	Medial	H-K, L-K	N-n	352–127 = 225	177
3	H-K vs. L-K	Basal	H-K, L-K	N-n	200– 29 = 171	600
4	H-K vs. L-K	Apical	H-K, L-K	A-n	270–175 = 95	54
5	H-K vs. L-K	Medial	H-K, L-K	A-n	285–102 = 183	180
6	H-K vs. L-K	Basal	H-K, L-K	A-n	147– 21 = 126	600
7	N-n vs. A-n	Apical	H-K	N-n, A-n	219–270 = 51	– 23
8	N-n vs. A-n	Medial	H-K	N-n, A-n	352–285 = 67	24
9	N-n vs. A-n	Basal	H-K	N-n, A-n	200–147 = 53	26
10	N-n vs. A-n	Apical	L-K	N-n, A-n	189–175 = 14	8
11	N-n vs. A-n	Medial	L-K	N-n, A-n	127–102 = 25	25
12	N-n vs. A-n	Basal	L-K	N-n, A-n	28– 21 = 7	33
13	Med. vs. Ap.	Med.-Ap.	H-K	N-n	352–219 = 133	61
14	Med. vs. Bas.	Med.-Bas.	H-K	N-n	352–200 = 152	76
15	Med. vs. Ap.	Med.-Ap.	L-K	N-n	127–189 = –62	– 49
16	Med. vs. Bas.	Med.-Bas.	L-K	N-n	127– 29 = 98	340
17	Med. vs. Ap.	Med.-Ap.	H-K	A-n	285–270 = 15	6
18	Med. vs. Bas.	Med.-Bas.	H-K	A-n	285–147 = 138	94
19	Med. vs. Ap.	Med.-Ap.	L-K	A-n	102–175 = –73	– 72
20	Med. vs. Bas.	Med.-Bas.	L-K	A-n	102– 21 = 81	385

* H-K = high-potassium cultures.
† L-K = low-potassium cultures.

sition was 8.76; i.e., (733.0 ÷ 83.7) times lower in the Low-K than High-K cultures.

Stem starch values reported as percentage of dry matter in table VII were 27.18 and 11.72, respectively, for the High-K and Low-K cultures in the N-n series while in the A-n series they were 23.45 and 8.8 per cent., respectively, for the High-K and Low-K cultures, indicating 2.32 and 2.66 times more starch in the High-K than Low-K cultures for the N-n and A-n series, respectively.

The comparisons of starch deposits in sections 2 and 3 of the leaves between High-K and Low-K cultures bear out approximately the same relations as those of the stem.

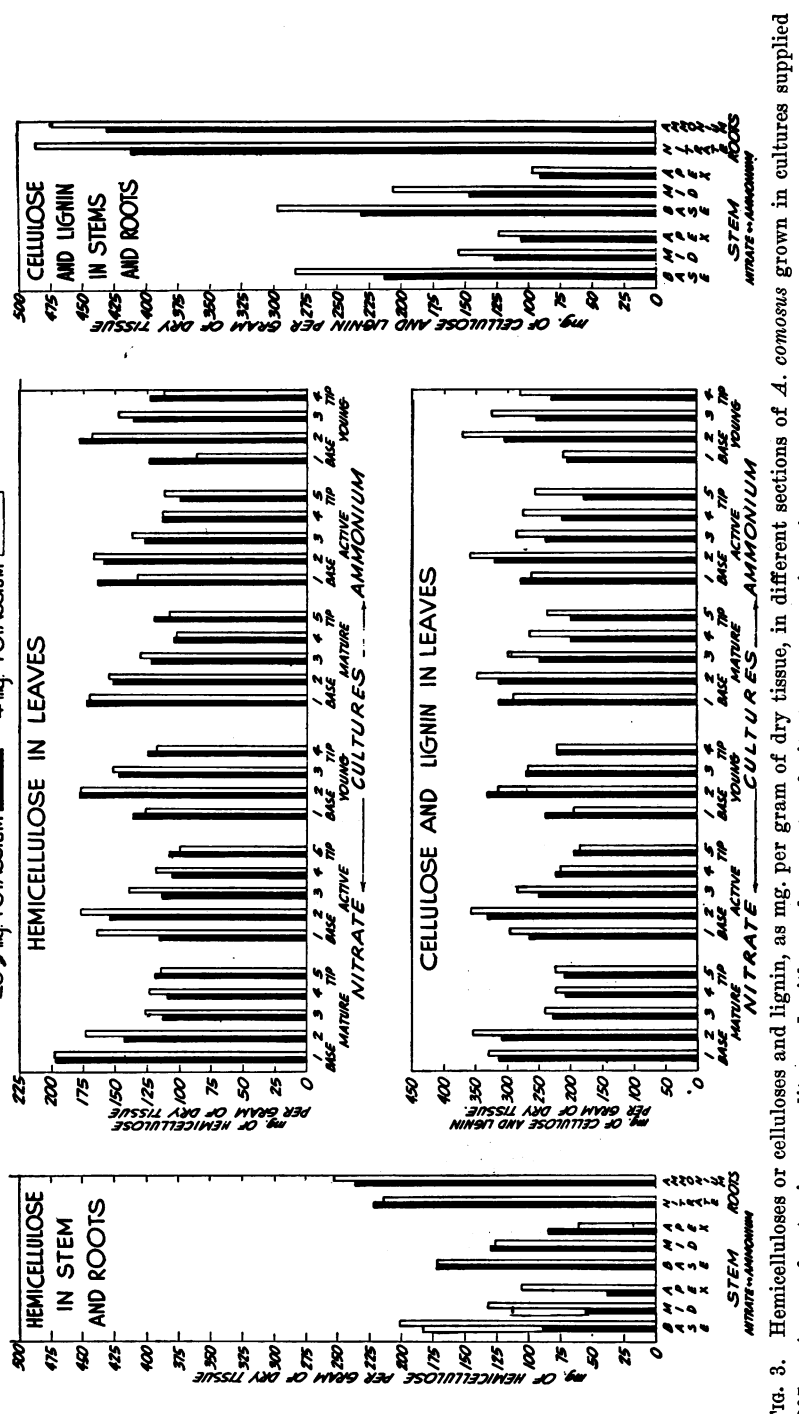

FIG. 3. Hemicelluloses or celluloses and lignin, as mg. per gram of dry tissue, in different sections of *A. comosus* grown in cultures supplied with 205 or 4 mg. of potassium per liter and with equal amounts of nitrate- or ammonium-nitrogen.

TABLE VII

TOTAL AMOUNTS IN GRAMS OF OBSERVED DRY MATTER (D.M.) AND RECOVERED DRY MATTER IN GRAMS OR PERCENTAGE, DETERMINED BY ANALYSIS AS CELLULOSE-LIGNIN, HEMICELLULOSE, SUGAR, STARCH, CITRIC ACID, ASCORBIC ACID, CHLOROPHYLLOSE PIGMENTS, ORGANIC NITROGEN (× 6.25), AND ASH PER PLANT OF ONE-YEAR-OLD *Ananas comosus* GROWN IN SOLUTION CULTURES WITH 205 OR 4 MILLIGRAMS OF POTASSIUM PER LITER AND WITH EQUAL AMOUNTS OF NITROGEN EITHER AS NITRATE OF AMMONIUM

Substances	Nitrate series								Ammonium series							
	High-K				Low-K				High-K				Low-K			
	Plant	Leaves	Stem	Roots	Plant	Leaves	Stem	Roots	Plant	Leaves	Stem	Roots	Plant	Leaves	Stem	Roots
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Cellulose-lignin	129.3	100.7	8.3	20.3	104.5	79.8	4.4	20.3	123.0	102.6	7.8	12.6	99.5	75.9	3.6	20.0
Hemicellulose	66.6	52.7	6.9	10.4	56.1	42.6	3.2	10.3	68.7	55.2	6.5	7.0	45.8	32.9	2.2	10.7
Sugar	51.6	47.4	3.5	0.7	71.1	67.2	2.4	1.5	71.1	65.5	4.3	1.3	45.3	43.4	1.9	.....
Starch	32.9	17.0	15.8	0.1	6.2	3.4	2.8	+*	24.0	12.3	11.7	+	2.2	0.7	1.5	.....
Citric acid	57.1	54.9	1.9	0.3	37.9	36.4	0.9	0.6	57.3	55.1	1.9	0.3	20.3	19.8	0.5	.....
Ascorbic acid	4.7	4.7	.....	.....	3.4	3.4	.....	.....	7.6	7.6	.....	.....	2.1	2.1	.....	.....
Chloroph. pigments	1.5	1.5	.....	.....	1.0	1.0	.....	.....	1.5	1.5	.....	.....	1.1	1.1	.....	.....
Org.-N (× 6.25)	36.9	31.9	3.8	1.2	31.9	26.2	2.6	3.1	40.0	35.0	3.1	1.9	38.8	34.4	2.5	1.9
Ash	59.6	52.0	5.5	2.1	18.7	14.3	3.1	1.3	45.8	39.7	4.8	1.3	14.2	11.6	1.4	1.2
Recovered D.M.	440.2	362.8	45.7	35.1	330.8	274.3	19.4	37.1	439.0	374.5	40.1	24.4	269.3	221.9	13.6	33.8
Observed D.M.	511.4	406.3	58.1	47.0	386.7	314.8	23.9	48.0	504.0	424.7	49.9	29.3	320.0	261.0	17.0	42.0
Not recovered D.M.	71.2	43.5	12.4	11.9	55.9	40.5	4.5	10.9	65.0	50.2	9.8	4.9	50.7	39.1	3.4	8.2
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
Cellulose-lignin	25.25	26.35	14.28	43.25	27.08	25.40	18.40	42.30	24.42	24.20	15.63	43.00	31.10	29.08	21.05	47.65
Hemicellulose	13.04	13.00	11.88	22.15	14.08	13.55	13.38	21.70	13.64	13.00	13.03	23.90	14.30	12.62	12.94	25.50
Sugar	10.10	11.67	6.02	1.50	18.36	21.30	10.05	3.13	14.10	15.42	8.82	4.44	14.20	16.62	11.18	.....
Starch	6.44	4.19	27.18	0.20	1.60	1.08	11.72	+	3.77	2.90	23.45	+	0.69	0.27	8.80	.....
Citric acid	11.17	13.52	3.27	0.64	9.80	11.56	3.77	1.25	11.37	12.95	3.81	1.03	6.35	7.59	2.90	.....
Ascorbic acid	0.92	1.16	.....	.....	0.88	1.08	.....	.....	1.51	1.79	.....	.....	0.66	0.80	.....	.....
Chloroph. pigments	0.29	0.37	.....	.....	0.26	0.32	.....	.....	0.30	0.35	.....	.....	0.37	0.42	.....	.....
Org.-N (× 6.25)	7.24	7.89	6.54	2.55	8.27	8.33	10.88	6.46	7.94	8.24	6.22	6.50	12.12	13.18	14.70	4.53
Ash	11.67	12.80	9.47	4.47	4.84	4.54	12.97	2.71	9.10	9.34	9.62	4.44	4.44	4.45	8.24	2.86
Recovered D.M.	86.12	90.95	78.64	74.76	85.17	86.86	81.17	77.55	86.15	88.19	80.58	83.31	84.23	85.03	79.81	80.54
Fresh weight (gm.)	3859	3210	335	314	2741	2280	173	288	3869	3330	342	197	2250	1820	120	310

* + = traces (not measurable).

Hemicelluloses

Hemicellulose values reported as milligrams per gram of dry tissue in figure 3 differed slightly between Low-K and High-K cultures. Differences in the hemicellulose content of the leaves between different cultures in the same series were small and insignificant. Thus the pattern for the hemicellulose distribution in different cultures did not conform in all respects to that for sugars depicted in figure 2. Certain small differences appearing in the data were possibly caused by the different sources of nitrogen rather than by the amounts of potassium in the cultures. Therefore, the physiological processes involved in hemicellulose deposition may differ from those of starch. Former studies (**35**) have also suggested that hemicelluloses in *A. comosus* do not represent reserves of readily available carbohydrates, as sugars or starch, but that they are allied more to structural substances and are comparable in this respect to celluloses and lignin.

The data in table VII, reporting hemicellulose as percentage of dry matter as well as total amounts per plant, show that the percentage values were approximately the same in both leaves and stem but in the roots they were almost twice as great as in the former organs. The percentage of hemicellulose content of the dry matter of the leaves, stem, and roots in the different cultures was relatively uniform for the specific organ regardless of great differences in the amounts of potassium and kinds of inorganic nitrogen between different cultures.

Cellulose-lignin

The combined weights of these compounds (fig. 3) were, with minor exceptions of certain sections, significantly greater for the Low-K than High-K cultures in the A-n series, but in the N-n series similar differences lacked statistical significance. The cellulose-lignin distribution was comparable to that of hemicelluloses in the different cultures. The data in table VII, reporting cellulose-lignin as percentage of dry matter as well as total amounts per plant, show that percentage cellulose-lignin values in the stem were approximately one-half as great as in the leaves and those in the leaves one-half as great as in the roots. The higher cellulose-lignin values in the leaves and roots than in the stem are directly related to the lignocellulose values of the fibrovascular system which occupies a much greater volume and area in the former than latter organs.

Discussion

Understanding of the physiological function of potassium in carbohydrate synthesis is beclouded by the lack of harmony in the results of different investigators. Hibbard and Grigsby (**16**) have summarized their studies with the statement that: "Any attempt to prove that any particular element aids directly or indirectly in the synthesis of carbohydrates or proteins, is instrumental in interrupting hydrolysis or condensation of starch, or affects the regulation of the translocation of inorganic or of elaborated foodstuffs will lead one now only into a cul-de sac." This statement, taking into con-

sideration the disharmonious conclusions of various workers, expresses without exaggeration the approximate state of our information on the physiological functions of potassium. SCHMALFUSS (**34**) remarks that potassium acts indirectly on proteins and carbohydrates; its primary function in the life processes of the plant must be sought in the colloidal activity of K-ions.

The absence of organic compounds containing potassium in plant tissues and the almost complete recovery of this element from the sap of plants in ionic state suggest that it plays an indirect rôle in most biological processes in the cell.

The data in table VII, reporting total amounts per plant of cellulose-lignin, hemicellulose, starch, citric acid, ascorbic acid, chlorophyllose pigments, organic-N, and ash as well as values of the same as percentage of dry matter, show certain inter-relationships which deserve further comment. The cellulose-lignin and hemicellulose fractions as percentage of dry or fresh matter were highest in the roots; the former being almost twice as great as the latter. Cellulose-lignin values as percentage of dry matter were almost half as great in the leaves as in the roots but twice as great as in the stem, but those of hemicellulose were approximately the same in both leaves and stem. Except for the differences mentioned in the cellulose-lignin and hemicellulose fractions which may be classified as organogenic, other differences resulting from cultural treatments were relatively absent. Therefore, it may be assumed that hemicelluloses and lignocellulose substances are components of structural units and undergo little or no change in metabolic processes requiring energy from carbohydrates. Sugar, starch, and organic acids, however, either carboxylic or amino acids, being intermediate products of metabolism and subject to further oxidation or reduction, vary greatly in different organs because of variations in the physiological function and metabolism of such organs. Differences in cultural treatments, as High-K vs. Low-K or NO_3 ions vs. NH_4 ions affecting the tempo or course of metabolic processes, change greatly the relative content of the tissues in sugar, starch, or organic acids but not in hemicellulose or ligno-cellulose substances.

Titrable acidity, in agreement with the findings of other investigators who have observed that tissue acidity may be increased by increasing the concentration of the nitrate salts of Na, K, or Ca, was higher in the High-K than Low-K cultures. However, it was suggested by certain unpublished studies that, owing to the great fluctuations in acidity between day and night samples, between samples collected during cloudy or sunny weather, or between plants of a different rate of growth and vigor, the differences between High-K and Low-K cultures might have been influenced, at least in part, by these climatic and physiological factors as well as the amounts of potassium in the cultures.

The data on ascorbic acid suggest that the amounts of potassium within the limits of this study did not influence the ascorbic content of the tissues. If mannose serves as the primary substance for the synthesis of ascorbic acid, according to GUHA and GHOSH (**11**), then information pertaining to the rôle

of potassium on mannose synthesis might have explained the behavior of the plants towards the ascorbic acid content of the tissues. The results on chlorophyll and carotenoids were inconsistent and indecisive on account of the more dominating rôle exerted by the different sources of nitrogen rather than by potassium.

In view of the transient nature of starch in the leaves, it is advisable to employ, for critical studies, other organs of the plant with food storage parenchymatous tissues (fruits, stem, tubers, etc.) where starch accumulations or depletions are exaggerated. The gradients of starch distribution in the stem of *A. comosus* as reported in table VI may be explained as follows:

The differences in the starch values of the stem between the High-K and Low-K cultures, being relatively small in the apical regions but becoming greater in the medial and basal sections, suggest that starch deposition under conditions of restricted starch synthesis, as in the Low-K cultures, was limited only to the tissues of the apical sections and that as these tissues advanced in age and their position was taken by new ones the amount of starch they received was progressively reduced. This condition was brought about either by a restricted sugar translocation or by a reversal in the ratio of synthesizing to hydrolyzing starch enzymes. The lower amounts of starch in the High-K cultures of the A-n than N-n series should be attributed to a lower rate of sugar polymerization in the former series. The higher amounts of starch in the medial than in the apical sections of the High-K cultures may indicate a greater differentiation in the relative amounts of storage tissue in the former sections on account of inherent differences in the chronological age and physiological maturity of the tissues. The lower starch content in the basal than in the medial stem sections of the High-K cultures should be attributed also to differences in the relative amounts of starch storage tissue which in the basal sections decreased on account of a greater hemicellulose and cellulose-lignin content. The higher starch content in the apical than the medial or basal stem sections of the Low-K cultures should be attributed to a gradually decreasing rate of conversion of sugar to starch and deposition of the latter from the apical to the basal sections. The changes in the rate of conversion of sugar to starch were induced, in the opinion of the authors, by enzymes operating differently under conditions of insufficient amounts of potassium.

LISSYZIN's (**24**) interpretation of the mechanism of starch formation from sucrose follows the scheme: sucrose $\rightleftharpoons$ monose $\rightleftharpoons$ dextrins $\rightleftharpoons$ starch, which shows that no direct transformation of sucrose into starch takes place and also that hydrolysis of starch to sucrose proceeds through monose formation as the intermediate stage. Phosphorylation is apparently the key and lock in various phases of carbohydrate metabolism. BARRON (**1**), explaining the mechanism of carbohydrate breakdown and polymerization in plants as demonstrated by JAMES and HANES, says: "The existence of the first phase, carbohydrate $\rightarrow$ pyruvate has been shown by JAMES *et al.* (**19**)

in the metabolism of barley when pyruvic acid was formed by barley sap from glucose in the presence of adenylic acid and the necessity of phosphorylation for carbohydrate breakdown demonstrated by the ratio of O_2 formation to inorganic P disappearance. The importance of phosphorylation for carbohydrate metabolism by plants has been corroborated by HANES (**14, 15**) on the breakdown and synthesis of starch by phosphorylase, quite similar to CORI'S phosphorylase, but isolated from potato and pea seeds." The rôle of potassium or of nitrogen either as nitrate or ammonium in phosphorylase activity has not been adequately studied to offer a concrete explanation of the findings. It may be assumed, however, on the basis of the data herein presented, that cultural treatments with nitrogen or potassium, affecting protoplasmic activity and, in turn, the course of enzymatic reactions, may accelerate or retard the mechanism of starch synthesis and its deposition in different organs.

Tissue hydration often associated with the physiological functions of potassium by various investigators shows little or insufficient evidence in its favor. Although the higher water content in the stem of the Low-K cultures might have interfered with the condensation of sugars and their conversion into starches, this argument does not apply to the leaves where high sugars were associated with a lower water content.

The data suggest that the better plant growth obtained with adequate than with deficient amounts of potassium may be caused by a better synthesis, polymerization, and assimilation of readily available carbohydrates and other vitally essential substances.

Summary

1. The amounts of chlorophyll and carotenoid pigments in the leaves were not affected by the amounts of potassium in the cultures. Certain differences encountered were probably due to the different kinds of nitrogen in the culture, as the effects of ammonium versus nitrate nitrogen were more pronounced on the chlorophyll content of the leaves than those of high versus low potassium.

2. Titrable acidity values reported as citric acid were greater, except in a few cases, in the high- than in the low-potassium cultures. Ascorbic acid values were greater in the low-potassium cultures of the nitrate-nitrogen series but smaller in the corresponding cultures of the ammonium-nitrogen series, indicating that ascorbic acid was affected more by the relations between nitrate versus ammonium nitrogen than by high versus low potassium.

3. Total sugar values were greater in the low- than in the high-potassium cultures, indicating a low rate of polymerization of sugars to starch or other complex carbohydrates in the former cultures. Sucrose as percentage of total sugars was greater in the high- than low-potassium cultures and was more abundant in the chlorophyllose than non-chlorophyllose tissues of the leaves.

4. Starch values were greater in the high- than in the low-potassium cultures, indicating a higher rate of synthesis in the former cultures, pre-

sumably from sugars. Starch depositions were greatest in the transitional and low chlorophyllose sections of the leaves and medial stem sections.

5. Hemicelluloses and celluloses plus lignin were slightly higher in the low- than in the high-potassium cultures.

6. These data emphasize that adequate amounts of potassium in the nutrient solution and consequently in plant tissues are essential for the condensation of reducing sugars to sucrose and starch.

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