

RESPIRATION OF SUGARCANE IN RELATION TO ESSENTIAL PLANT NUTRIENTS

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I. INTRODUCTION

MITSCHERLICH and colleagues (quoted from Willcox, 1937) have shown that from the point of view of nutrient requirements, nitrogen element is the one that is required in maximum quantities followed by potash, phosphorus and other elements such as calcium, magnesium, sodium, silicon, iron, etc. Other workers have studied the effect of deficiency of essential elements on the respiratory activity of plant. Thus, Gregory and Richards (1929) and later on Richards (1932) studied the effect of manurial deficiency and observed that the curve of response exhibited a fall soon after the element became deficient. Similarly Lyon (1926, 1927) studied the effect of phosphatic deficiency on plant respiration. Hammer (1936) described the effect of nitrogen supply on the rate of metabolism in plants and showed a marked increase in the respiration rate on the application of nitrates to tomato and wheat plants. Arnon (1937) reported an increased rate of respiration even in the case of excised barley roots on the application of nitrates. Warbung and Negelani (Arnon, 1937) showed that the respiratory quotient of *Chlorella* increased following the absorption of nitrates. Nightingale, *et al.* (1931) observed the effect of calcium deficiency on nitrate absorption and on metabolism in tomato plants. Studies by Parija and Saran (1934) indicated that starved leaves exhibited an enhanced rate of respiration in a deficient environment.

Suzaki and Kenjo (1935, 1936, 1937), Kenjo (1938) and Saito and Kenjo (1939) published the results of their experiments on the effect of deficiency of nitrogen and phosphorus on leaf colour, growth of stalks and leaves, development of roots, sucrose content of juice, total ash content, etc. These experiments were performed in water cultures but the effect of nitrogen and phosphorus deficiency on respiration rate was not determined.

In the studies reported hereunder, an attempt was made to study the metabolic rate of excised shoots of plants raised in sand cultures deficient

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in nitrogen, potash and phosphorus and in the absence and presence of minor elements. Dry weight of plants was determined at the close of the experimental period to elucidate the interrelationship among the type of nutrient medium and respiratory process and growth of plants. And, therefrom, it was proposed to indicate the degree to which the various elements act as limiting factors in plant metabolism.

II. MATERIAL AND METHODS

The experiments were performed in glass jars measuring 24" × 18" × 10". These were filled with quartz sand that had been washed repeatedly to get rid of all extraneous matter. Equal weighed quantities of sand were put in each of the glass jars, enough of water being added to saturate the sand to its full capacity. Three one-eyed setts obtained from central three nodes of fully developed cane stalks were planted on 3-11-38 at 2½" depth in each of the glass jars. The setts were 2" in length and all weighed approximately equal, the range in the weights being 31.12 and 27.08 grammes. The germination of setts was duly recorded day after day. Most of the setts germinated within a week of the germination of the first sett in the experiment, but another week was allowed before the rest of the ungerminated setts were taken out. The pots were then so arranged (Table I) that the distribution of plants might as far as possible be equal with regard to date of germination.

TABLE I

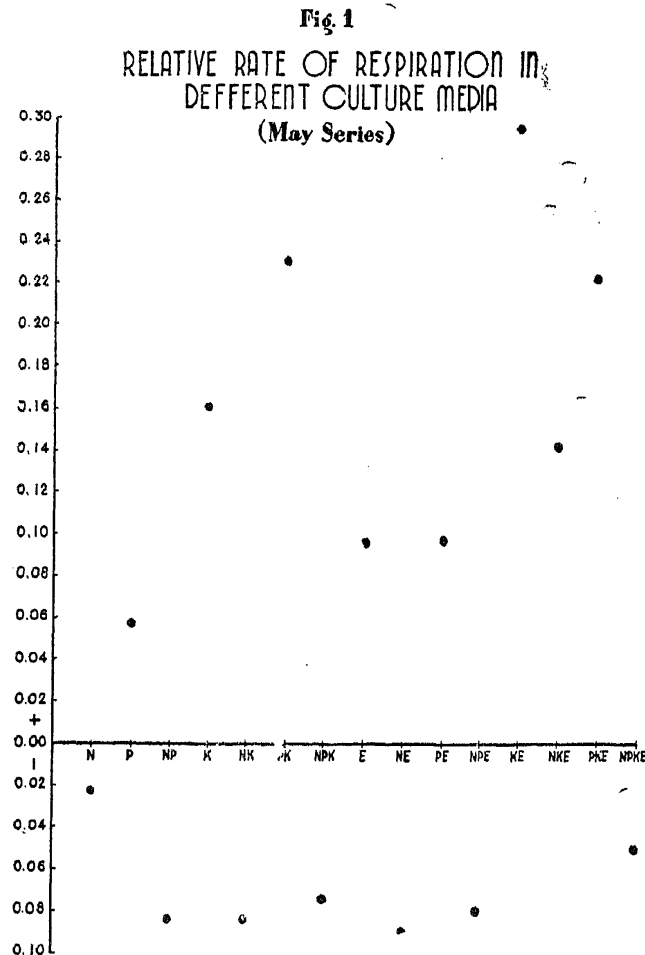
Showing the arrangement of pots for various nutrient treatments (Nov., 1938)

Sl. No.	Treatment	Reference	Pot No.	Date of germination			Pot No.	Date of germination			Pot No.	Date of germination		
				1	2	3		1	2	3		1	2	3
1	Control ..	A	26	18th	16th	16th	21	14th	18th	23rd	28	18th
2	N ..	B	13	21st	16th	15th	9	19th	20th	16th	35	16th	21st	25th
3	P ..	C	1	14th	13th	12th	2	19th	19th	15th	30	14th	23rd	25th
4	N P ..	D	7	14th	15th	14th	24	14th	16	23rd	20th	..
5	K ..	E	38	13th	16th	12th	41	25th	18th	17th	19	..	23rd	20th
6	N K ..	F	3	13th	17th	13th	32	19th	19th	19th	17	19th	20th	..
7	P K ..	G	4	14th	16th	14th	40	19th	26th	15th	44	20th	23rd	20th
8	N P K ..	H	10	20th	20th	16th	39	20th	46	18th	17th	17th
9	E ..	I	6	21st	19th	14th	14	..	21st	18th	37	14th
10	N ..	J	15	16th	21st	22nd	25	17th	43	18th	17th	15th
11	P ..	K	8	16th	14th	18th	31	..	17th	..	45	..	17th	17th
12	N P ..	L	11	21st	21st	17th	42	19th	17th	14th	47	14th	25th	26th
13	K E ..	M	5	16th	14th	19th	27	15th	21st	19th	29	26th
14	N K E ..	N	18	15th	14th	18th	33	18th	19th	20th	48	18th	21st	..
15	P K E ..	O	12	13th	14th	14th	23	17th	21st	21st	36	14th
16	N P K E ..	P	20	21st	19th	17th	22	17th	19th	15th	34	23rd	..	17th

Remarks.—E Treatment refers to combination of salts when salts other than N, P₂O₅ or K₂O were supplied.

After the rearrangement of pots the solutions containing the various nutrient salts were added. The culture media used was modified by Knop's solution as recommended by Shull and Loomis (1938), and balanced for sand culture work as suggested by McCall (1916). Various salts were replaced according to the scheme given by Shull and Loomis (*loc. cit.*) for excluding N, P_2O_5 or K_2O as the case may be from the full culture solution. But where only N, P_2O_5 or K_2O were to be applied separately or in combination, as shown in Table I, the same salts as used for the culture solution, were employed. For the control treatment, distilled water was used every time the solution was applied in the pots.

The plants were allowed to grow till the beginning of May when respiration studies on A and C plants were taken up. Excised shoots constituting the leaf tuft bearing two leaves below the standard (transverse mark) leaf



were used for the investigation. Method of gaseous exchange was employed for conducting respiration experiments. The apparatus described by Luthra and Cheema (1931) was used for the purpose with the slight modification as given by Khanna and Raheja (1938). This modification consisted in the use of a tower filled with pumice-stone saturated with concentrated

sulphuric acid to free the air of all moisture before entering the respiration chamber. From the CO_2 evolved, respiration rates were worked out on the basis of per gram fresh weight of material.

The one plant left over was allowed to grow till about middle of November. The respiration rates of excised shoots were worked out as above for each of the single plants in the pots. Almost simultaneously with the above determination, the respiration of whole plants were also determined. Besides measurements of length and maximum width of the last three fully matured leaves were also recorded. Further notes were taken on the leaf colour, nature of the leaf tuft and extent of the leaf tip drying.

III. EXPERIMENTAL RESULTS

The respiration data obtained during the month of May and November are presented below (Table II), while Fig. 1 in the text shows the relative rate of respiration of plants during May in the various cultural media (Table II).

The plotted points are the mean deviations from the control obtained by summing up all the values that are not asterisked in Table II minus the mean value for control and have been given (Table III, Column 11). It will be noticed that the respiratory activity of plants grown in culture media containing nitrogen salts except in the treatment N.K.E. is low (negative). On the other hand, the application of potassium salts increased, in general, the rate of respiration. P_2O_5 alone or in combination with K_2O increased the metabolic activity. Effect of E alone increased the respiration rate (Table III).

It will, however, be observed that the number of observations (Column 3, Table III) for each varied, and there were considerable variations in the respective values of the respiration rate of plants grown in culture media. To obviate the difficulty of unequal numbers, for working out the approximate analysis of variance, 'Effect Values' were derived by the method described in the appendix of the paper. These values have been graphed in Fig. 2.

It is observed that effect of nitrogen, potassium and E in the derived 'Effect Values' was also the same. Nitrogen in every case tended to decrease the rate of metabolism of the plant. The maximum effect of increasing the rate of respiration was indicated by potassium followed by E and least that of phosphorus.

The analysis of variance as worked out for the May series is given below (Table IV).

TABLE II

Showing respiration of plants during May and November

Sl. No.	Treatment	Pot No.	Rate of respiration in c.c. per hour per gram fresh weight		
			May A	May C	November B
1	Control	26	0.340	0.274	1.043
		21	0.390*	0.308*	..
		28	0.871*
		13	0.184	0.254	0.354
		9	0.169	0.178	0.941
2	N	35	0.331	0.589	1.024
		1	0.287	0.541	0.836*
		2	0.360	0.289	0.652
3	P	30	0.377	0.327	0.490
		7	0.200	0.127	0.608
		24	0.311	0.253	0.389
4	N. P.	16	0.836
		38	0.174	0.284	0.601
		41	1.011	0.404	1.383
5	K	19	..	0.449*	0.534*
		3	0.285	0.177	1.285
		32	0.223	0.210	0.831
6	N. K.	17	1.02*	..	0.680*
		4	0.651	0.153	1.430
		40	0.386	0.430	0.366
7	P. K.	44	1.342	0.269	0.384
		40	0.224	0.315	0.576
		10	0.247	0.141	0.322
8	N. P. K.	39
		37	0.367	0.629	1.121
		6	0.275	0.346	0.688
9	E	14	..	0.548*	2.680*
		43	0.200	0.319	1.656
		15	0.166	0.202	0.742
10	N. E.	25	0.387*
		8	0.181	0.628	0.904
		45	..	0.114*	1.800*
11	P. E.	31	0.721*
		42	0.314	0.324	0.331
		11	0.204*	..	1.150*
12	N. P. E.	47	0.146	0.220	0.252
		5	0.374	1.438	1.349
		27	0.233	0.361	1.165

TABLE II—(Contd.)

Sl. No.	Treatment	Pot No.	Rate of respiration in c.c. per hour per gram fresh weight		
			May A	May C	November B
13	K. E.	.. 29	1.283*
		18	0.499	0.275	0.761
		33	0.805	0.221	0.792
14	N. K. E.	.. 48	0.280*	..	0.522*
		12	0.423	0.542	1.660
		23	0.706	0.448	0.728
15	P. K. E.	.. 36	0.788*
		22	0.176*	0.133*	..
		20	0.359	0.144	1.724
16	N. P. K. E.	.. 34	..	0.195*	0.983*

* These figures were treated as abnormal and were, therefore, not used for interpretation of the data. It will be noticed that they relate to the data obtained with plants which were either one or two in a pot, *i.e.* all three plants were not there or else in the November series, the plant had dried and therefore the respiration data was omitted.

TABLE III

Showing rate of respiration of plants in the May series

Sl. No.	Treatments	No. of observations	Rate of respiration in c.c.						Mean value	Deviations from the control values	Derived effect values
			No. 1	No. 2	No. 3	No. 4	No. 5	No. 6			
1	2	3	4	5	6	7	8	9	10	11	12
1	Control ..	2	0.340	0.274	0.307
2	N. ..	6	0.184	0.254	0.167	0.178	0.331	0.589	0.284	-0.023	-1.506
3	P. ..	6	0.287	0.360	0.377	0.541	0.289	0.327	0.364	+0.057	-0.190
4	N. P. ..	4	0.200	0.127	0.311	0.253	0.223	-0.084	-0.304
5	K. ..	4	0.174	0.284	1.011	0.404	0.468	+0.161	+0.862
6	N. K. ..	4	0.285	0.177	0.223	0.210	0.224	-0.083	-0.456
7	P. K. ..	6	0.651	0.386	1.342	0.153	0.430	0.269	0.539	+0.232	-0.192
8	N. P. K. ..	4	0.226	0.315	0.247	0.141	0.232	-0.075	-0.074
9	E. ..	4	0.387	0.629	0.275	0.346	0.404	+0.097	+0.450
10	N. E. ..	4	0.200	0.319	0.166	0.202	0.222	-0.085	-0.076
11	P. E. ..	2	0.181	0.628	0.405	+0.098	-0.340
12	N. P. E. ..	4	0.314	0.224	0.146	0.220	0.226	-0.081	+0.058
13	K. E. ..	4	0.374	1.438	0.233	0.361	0.602	+0.295	+0.292
14	N. K. E. ..	4	0.499	0.275	0.805	0.221	0.450	+0.143	+0.318
15	P. K. E. ..	4	0.423	0.542	0.706	0.48	0.530	+0.223	-0.358
16	N. P. K. E. ..	2	0.359	0.144	0.252	-0.055	-0.184

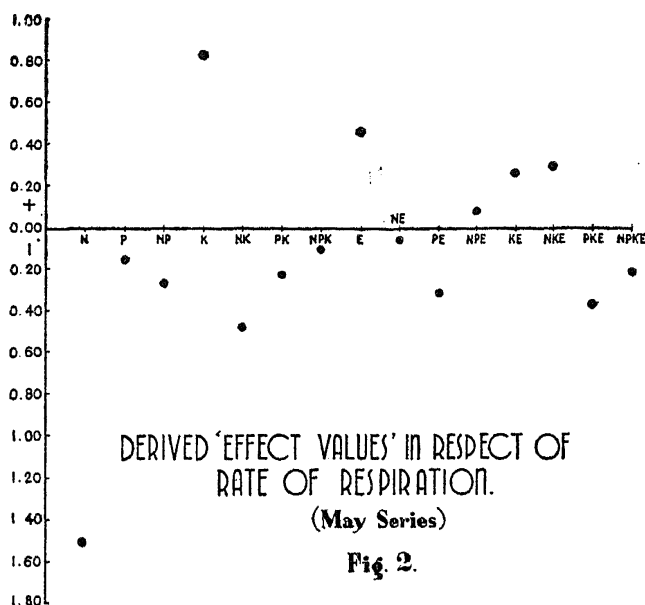


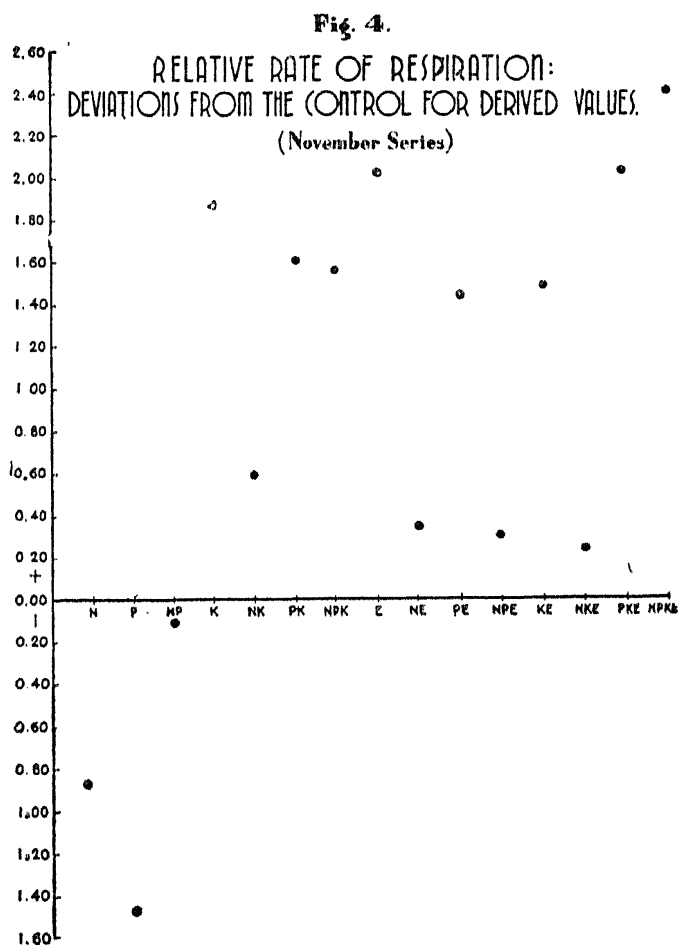
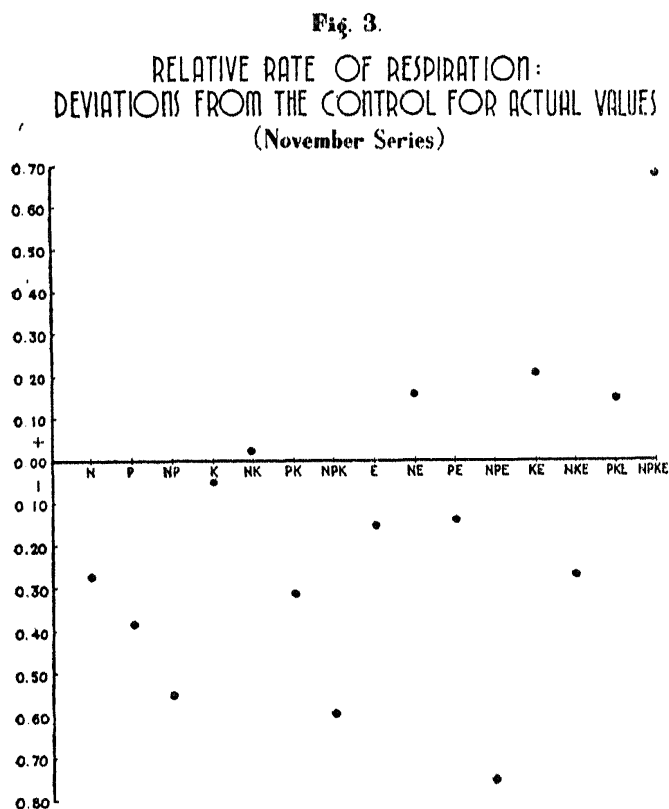
TABLE IV

Showing approximate analysis of variance of May series

Due to	D. F.	S. S.	M. S.	'F' values			
				Observed	Theoretical		
					P-0.20	P-0.05	P-0.01
N	.. 1	0.141752	0.141752	1.799	1.70	4.08	7.31
P	.. 1	0.002256	0.002256	0.029	do	do	do
K	.. 1	0.046443	0.046443	0.590	do	do	do
E	.. 1	0.012656	0.012656	0.161	do	do	do
N. P.	.. 1	0.005776	0.005776	0.073	do	do	do
N. K.	.. 1	0.012996	0.012996	0.164	do	do	do
N. E.	.. 1	0.000361	0.000361	0.005	do	do	do
P. K.	.. 1	0.002304	0.002304	0.029	do	do	do
P. E.	.. 1	0.007225	0.007225	0.092	do	do	do
K. E.	.. 1	0.005329	0.005329	0.068	do	do	do
N. P. K.	.. 1	0.000342	0.000342	0.004	do	do	do
N. P. E.	.. 1	0.000210	0.000210	0.003	do	do	do
N. K. E.	.. 1	0.006323	0.006323	0.080	do	do	do
P. K. E.	.. 1	0.008010	0.008010	0.102	do	do	do
N. P. K. E.	.. 1	0.002116	0.002116	0.027	do	do	do
Error	.. 48	3.781415	0.078779
Total	.. 63	4.035514

From this analysis, it is apparent that nitrogen effect referred to above was the highest though not significant. Since the variations in the respiration rate were very wide, the significance values were tested at 20% level of significance but no effect came out as significant. Wherever nitrogenous salt combined with any other salt or a combination of salts, the effect was to equalise the respiration rate to that of the control series. These interesting results have been discussed later in the text.

The supply of nutrients was continued upto the middle of July and later the plants were starved of their respective nutrient supply with a view to obtain wide differences in the rate of metabolism in various series (Parija and Saran, *loc. cit.*). The results of the respiratory studies conducted in November are given (Table V) in the text. It will be noticed that the number of plants taken up for investigation were different for the different series. Some of these plants had completely died out while others had to be discarded on grounds similar to those reported under the former studies. Fig. 3 illustrates the mean deviations in the respiratory activity from the



control series (Table V, Column 8). The respiratory activity was low when either nitrogen or phosphorus was applied and it was high when potash was given to the plants. The results were not found to exactly correspond with those stated above. Derived values (Fig. 4) were, therefore, worked out by the same method as given in the Appendix.

It is obvious that wherever potassium salt was supplied in nutrient culture media, the rate of katabolic process was high. Application of nitrogen in the form of calcium nitrate $[Ca(NO_3)_2]$, however, tended to decrease the rate of respiration except in the combinations N P K and N P K E. Effect of E (combination of minor elements) was to enhance the rate of respi-

TABLE V

Showing the rate of respiration of plants in the November series

Sl. No.	Treatments	No. of observations	Rate of respiration in c.c.			Mean value	Deviations from the control	Derived effect values	
			1	2	3				
I	2	3	4	5	6	7	8	9	
1	Control	..	1	1.043	1.043	..	14.439
2	N	..	3	0.354	0.941	1.024	0.773	-0.270	-0.901
3	P	..	3	0.836	0.652	0.490	0.659	-0.384	-1.545
4	N. P.	..	2	0.608	0.389	..	0.498	-0.545	-0.141
5	K.	..	2	0.601	1.383	..	0.992	-0.051	+1.915
6	N. K.	..	2	1.285	0.831	..	1.058	+0.015	+0.575
7	P. K.	..	3	1.430	0.366	0.384	0.727	-0.316	+1.567
8	N. P. K.	..	2	0.576	0.322	..	0.449	-0.594	+1.475
9	E	..	2	1.121	0.668	..	0.894	-0.149	+2.041
10	N. E.	..	2	1.656	0.742	..	1.199	+0.156	+0.385
11	P. E.	..	1	0.904	0.904	-0.139	+1.521
12	N. P. E.	..	2	0.331	..	0.252	0.292	-0.751	+0.329
13	K. E.	..	2	1.349	1.165	..	1.257	+0.214	+1.409
14	N. K. E.	..	2	0.761	0.792	..	0.776	-0.267	+0.137
15	P. K. E.	..	2	1.660	0.728	..	1.194	+0.151	+1.997
16	N.P.K.E.	..	1	1.724	1.724	+0.681	+2.381

TABLE VI

Showing approximate analysis of variance of November series

Due to	D. F.	S. S.	M. S.	' F ' values				
				Observed	Theoretical			
					P-0.20	P-0.05	P-0.01	
N	..	1	0.050738	0.050638	0.217	1.79	4.49	8.53
P	..	1	0.149189	0.149189	0.638	do	do	do
K	..	1	0.229201	0.229201	0.980	do	do	do
E	..	1	0.260355	0.260355	1.114	do	do	do
N. P.	..	1	0.001242	0.001242	0.005	do	do	do
N. K.	..	1	0.020664	0.020664	0.088	do	do	do
N. E.	..	1	0.009264	0.009264	0.039	do	do	do
P. K.	..	1	0.153468	0.153468	0.656	do	do	do
P. E.	..	1	0.144590	0.144590	0.618	do	do	do
K. E.	..	1	0.124080	0.124080	0.531	do	do	do
N. P. K.	..	1	0.135977	0.135977	0.581	do	do	do
N. P. E.	..	1	0.006765	0.006765	0.029	do	do	do
N. K. E.	..	1	0.001173	0.001173	0.005	do	do	do
P. K. E.	..	1	0.249251	0.249251	1.066	do	do	do
N. P. K. E.	..	1	0.354323	0.354323	1.516	do	do	do
Error	..	16	3.740210	0.233763
Total	..	31	5.630490

ration. Analysis of variance (Table VI) revealed that the variations were higher for E, P K E and N P K E. The effects for P K, N P K and K E were also fairly high. Though none of the effects is significant, it will be noticed in the above combinations that both in the absence and presence of E, the effect of K, P K and N P K was more or less similar. Evidently K being common to all, its effect on respiration was throughout very marked. These differences in the effect of nutrient salts on the rate of respiration of foliage have been discussed later in the text.

B. Dry weight data.—Dry weight studies were carried out for the November series and the results (Table VII) when arranged in descending order of yield were N K E, N P K E, N P K, N P E, N P, N, N E, P E, P K E, P, K E, N K, K, P K and E.

TABLE VII

Showing dry matter percentage of plants for the November series

Sl. No.	Treatments	Dry matter of plants (gm.)				Mean	Deviations from the control
		No. 1	No. 2	No. 3	Total		
1	Control ..	12.04	13.96*	23.60*	12.04	12.04	..
2	N ..	26.64	27.64	27.00	81.28	27.09	+15.05
3	P ..	13.79*	19.33	15.20	34.53	17.26	+ 5.22
4	N. P. ..	30.13	29.04	64.06*	64.17	32.09	+20.05
5	K ..	10.51	12.89	11.30*	23.40	11.70	- 0.34
6	N. K. ..	13.54	20.87*	14.64	28.18	14.09	+ 2.05
7	P. K. ..	12.96	10.24	10.62	33.82	11.27	- 0.77
8	N. P, K. ..	43.74	39.17	52.67*	82.91	41.46	+29.42
9	E ..	7.74	11.80*	10.19	17.93	8.97	- 3.07
10	N. E. ..	27.03	81.93*	23.94	50.97	25.49	+13.45
11	P. E. ..	19.58	31.61*	17.78*	19.58	19.58	+ 7.54
12	N. P. E. ..	36.90*	39.63	34.78	74.41	37.21	+25.17
13	K. E. ..	16.04	15.47	21.24*	31.51	15.76	+ 3.72
14	N. K. E. ..	44.61	45.13	55.58*	89.74	44.87	+32.83
15	P. K. E. ..	18.05	16.58	30.64*	34.63	17.32	+ 5.28
16	N. P. K. E. ..	43.69	43.99*	37.99*	43.69	43.61	+31.57

* Dry matter values for those plants of which the results of respiration were omitted have not been taken into consideration while working out the mean.

From the order stated above, it is evident that the application of nitrogen throughout was more effective than that of either phosphorus or potash in increasing the accumulation of dry matter in the plant. Except in the treatment N K E the combined effect of N P was much more than that of P or N alone. Effect of K, unless it was in combination with N P, was always to depress the yield factor. The relationship between the respiratory process and the yield factor has been discussed subsequently.

IV. DISCUSSION AND RESULTS

According to the fourth principle of agro-biology, a certain definite amount or intensity of growth factor produces a certain definite result (Willcox, 1930). In other words, the effect is a quantitative one. In an ensemble of growth factors also, the effect of any one of them is additive or cumulative. In the experiments reported above this has been clearly brought out in both the respiratory activity of plants carried out in May and that completed in November. At both the periods, the specific effect of nitrogen was to reduce the rate of respiration while addition of K, or E, except in combination with N P, was always to enhance the rate of respiration. It appears that nitrogen by virtue of its being a rapidly absorbed anion brings about more effective equilibrium in the rate of metabolism, that is to say, the accumulation of substances with nitrogen is higher and, therefore, the carbon dioxide output per unit of accumulated substance is low. No other substance reduces the respiratory quotient of the plant like nitrogen. In May series particularly, the effect of the presence of phosphorous salts, was to increase the rate of katabolic process. Combined with nitrogenous salts it was more effective in reducing the rate of respiration. Potassium salts in conjunction with N or P showed the least effect in reducing the rate of katabolism. But when all the big three—N, P and K combined, the effect was to reduce the rate of respiration. The combined effect of the salts other than those having nitrogen, phosphorus or potash was to enhance the breakdown of the metabolisable material and this was irrespective of the big three elements. The age of the plant did not matter in this respect because the specific effect was identical in both the May and the November series.

In the case of dry matter output, nitrogen in combination with the rest was most effective; the next in order being the combination of nitrogen and phosphorus. Effect of potash alone or in separate combination with nitrogen, phosphorus, nitrogen plus E, and phosphorus plus E was rather deleterious to the accumulation of dry matter.

From the results of the respiratory activity of plants and the accumulation of assimilated products, one may infer that potash is the first limiting factor of the three big ones, for it is the earliest to show its deleterious effect under the conditions of the experiment described above. The antagonism of salt exists so long as it does not combine with nitrogen and phosphorus but this is not less apparent because of the presence of high or low concentration of growth factors. This is clear from the similarity of the results in respect of respiration obtained from May series, when plants were maintained at the normal salt requirement, and from the November series, when the plants had been kept starved.

V. SUMMARY

Investigations on metabolic activity of plants were carried out in sand culture to study the specific influence of nitrogen, phosphorus, potash and combination of other minor elements, alone and in combination with one another. Respiration experiments were performed on plants grown upto November. The application of nutrient supply was stopped in mid-July when plants were starved with a view to study the antagonistic effect under normal and abnormal conditions of growth. The dry matter of plants harvested in November was also estimated. The results arrived at were as follows:

(i) Nitrogen decreased the rate of respiration. It was most effective in reducing the rate of respiration when it was applied in combination with all the other elements.

(ii) Effect of potash was just the opposite to that of nitrogen. It enhanced the rate of respiration unless it was present in combination with N P.

(iii) Phosphorus alone increased the rate of metabolism. But in combination with nitrogen it was very effective in reducing the rate of respiration and in combination with potash in keeping up a higher rate of respiration.

(iv) Effect of the combination of salts of the minor elements alone was to increase the rate of katabolic processes. In combination with nitrogen, phosphorus or potash, this effect was much less apparent.

(v) Nitrogen was most effective in the accumulation of dry matter; phosphorus was the next best while neither potash nor combination of other salts of minor elements effected any increase in the dry matter.

(vi) Potash has been shown as the first limiting factor as it is the earliest to show adverse effect on the respiratory process and it maintains its antagonism so long it does not combine with nitrogen and phosphorus together.

(vii) The antagonistic effect on respiratory process is maintained both under normal and abnormal conditions (starvation) of nutrient supply.

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