INTERRELATION BETWEEN RESPIRATION, NET ASSIMILATION RATE, ORGANIC AND INORGANIC PHOSPHORUS UNDER PHOSPHORUS DEFICIENCY CONDITIONS

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ABSTRACT

The respiratory index of component organs of sugarcane variety Co 453 was determined under laboratory conditions at successive stages of the life cycle in relation to phosphorus deficiency, age of the plant and the nature of the respirable materials.

Respiratory index, in general, was high during the early stage and declined towards maturity. A critical limit of sucrose (1 mgm.), glucose (0.1 mgm.), fructose (0.1 mgm.), amino acids (40 mgm.), amides (10 mgm.) and organic phosphorus (0.4 mgm.) per 100 gm. plant material helped in maintaining a high respiration rate. Further increase, however, resulted in a fall in respiration.

The possibility of high respiration being associated with high sucrose/hexose (5 : 1), and low amino/amide (3 : 1) and organic/inorganic phosphorus (8 : 1) ratios was clearly indicated. An adequate sucrose/hexose, amino acids/amide nitrogen and organic/inorganic phosphorus appeared to be the principal factor in determining the relation between age and respiratory index.

High respiratory index of leaf was associated with its high insoluble nitrogen, total nitrogen and inorganic phosphorus content. Medium respiratory index of the roots was related to medium content of total soluble and insouble nitrogen and organic and inorganic phosphorus. Poor respiratory index of stem, on the other hand, showed some relation with low insoluble nitrogen, total nitrogen and inorganic phosphorus content.

Reasons for poor respiratory index of the stem in spite of rich respirable substrate, e.g. high sucrose, reducing sugars, amino acids, amides and organic phosphorus compounds have been discussed. Effects of phosphorus deficiency on respiration were generally insignificant.

High net assimilation rate of leaves during the early stage and relatively low N.A.R. under phosphorus deficiency were characteristically recorded. Absence of phosphorus interfered with further elaboration of amides and amino acids and thus resulted in poor protein content which was primarily responsible for low dry matter accumulation per unit area. The decline with age, on the other hand, was associated with poor chlorophyll content, reduced efficiency of leaves to absorb CO_2 during photosynthesis and the general decline in proteins which formed the bulk of the dry matter.

INTRODUCTION

Supply of phosphorus in the culture medium brings about characteristic variations in the uptake of phosphorus and its further elaboration into organic phosphorus compounds. The concentration of these organic and inorganic phosphorus compounds has been suggested very often to play an important part in the respiratory processes often resulting in a marked variation in the CO_2 output of the plant. Phosphorus deficiency has also been shown to bring about increase in the chlorophyll content and to alter the net assimilation rate (N.A.R.). Phosphorus deficiency effects on respiration and chlorophyll content have been reported earlier by Lal *et al.* (1951, 1952). It is the intention to trace in these pages the further interrelation, if any, between respiration, organic and inorganic phosphorus content, and N.A.R. of the plant.

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EXPERIMENTATION

The plant materials for these studies were secured from sugarcane (var. Co 453) grown under (A) complete nutrition, and (B) phosphorus deficiency conditions with the help of Hoagland's nutrient solutions as described earlier (Lal and Singh, 1957). Root, stem and leaf were carefully washed to remove dirt and adhering sand particles, chopped off separately and brought to the laboratory. The rate of respiration of these plant organs was determined by Blackman's continuous current method using $Ba(OH)_2$ as an absorbent of CO_2. The respiration measurements were taken on detached leaf, stem and root under a constant temperature of 30°C and in a CO_2 free stream of air. The rate of CO_2 output was finally expressed in mgm. of CO_2 per 100 gm. of the dry matter.

Net assimilation rate of the plant at successive stages of the life cycle was determined by the formula :—

$$\text{N.A.R.} = \frac{W_2 - W_1}{T_2 - T_1} \times \frac{\text{Log}_e L_2 - \text{Log}_e L_1}{L_2 - L_1} \times 1000$$

where W_2 and W_1 were the dry weights and L_2 and L_1 the leaf area at time intervals of T_2 and T_1, and expressed as grams of dry matter formed per 1000 sq. cms. of leaf area per day.

The inorganic phosphorus content was determined colorimetrically by the modified Truog and Meyer method (1929) as described by Bertramson (1942). Organic phosphorus was determined indirectly by subtracting the value of inorganic phosphorus from that of total phosphorus. All observations on respiration, N.A.R., inorganic and organic fractions were statistically examined to indicate the significance of the experimental data.

EXPERIMENTAL FINDINGS

A. *Respiratory Index :*

Respiratory index of sugarcane was found to vary to a certain extent with the plant parts, dificiency of phosphorus and with the age of the plant. Thus, in leaf, increase in age brought about marked improvement in the respiratory index which reached the highest level towards maturity. Phosphorus deficiency during early stages showed some increase in the leaf respiration but at later periods, the disparity between respiratory index of complete-nutrient and phosphorus-deficient plants was not so evident. In the stem, on the other hand, increases in age induced a marked decline in respiratory index reaching fairly low values towards maturity. This was true for both the phosphorus-deficient and complete-nutrient cultures. Barring the earliest stage of 45 days, when the complete-nutrient canes showed relatively high respiratory index of the stem in comparison to the phosphorus-deficient stem, at other stages the differences were not so characteristic. In so far as the roots were concerned, the general decline in the respiratory index of the root with age was evident, but the effect of phosphorus deficiency varied at successive samplings. During 45 and 135 days a tendency to increase respiratory index was particularly noted under phosphorus deficiency (Table IA).

Statistical analysis of the results, however, indicated the average response of the main effects and interactions to be insignificant (Table IB). The fall in the respiration rate with age also did not attain the significant level. Phosphorus deficiency too showed less marked variations in respiration. A general tendency of the leaf to exhibit higher respiration rate than that of the root which showed relatively high values in comparison to the stem, was observed (Table IC). The

TABLE I

Effect of phosphorus deficiency on the respiratory index of sugarcane (var. Co 453) under sand nutrient cultures

(mgm. of CO_2 per 100 gm. dry weight)

A. MAIN TABLE

Age in days	Treatments	Plant Parts			Average plant
		Leaf	Stem	Root	
	CN	9.4	43.9	27.8	27.03
45	–P	13.4	23.5	43.0	26.63
	Difference	–4.0	+20.4	–15.2	+0.40
	CN	22.3	16.6	40.1	26.33
90	–P	20.8	19.6	35.4	25.26
	Difference	+1.5	–3.0	+4.7	+1.07
	CN	36.2	8.6	9.7	18.16
135	–P	36.6	9.5	10.3	18.80
	Difference	–0.4	–0.7	–0.6	–0.64
	CN	38.7	2.4	7.6	16.23
225	–P	39.2	2.7	7.7	16.53
	Difference	–0.5	–0.3	–0.1	–0.30

B. ANALYSIS OF VARIANCE

Due to	D.F.	S.S.	M.S.S.	Ratio	F at 5%
Age	3	489.92	163.30	0.56	8.74
Treatments	1	0.11	0.11	0.00	24.40
Plant parts	2	512.17	256.08	0.88	19.41
Age × Treatments	3	2.57	0.85	0.00	8.74
Treatments × Plant parts	2	49.82	24.91	0.08	19.41
Error	12	3459.90	288.32		
Total	23	4514.49			

S.E. = ±16.98.

respiratory index, however, did not vary significantly with any of the conditions of the experiment (Table ID).

Net Assimilation Rate :

The N.A.R. of the plant was highest during the earliest stage of the life cycle and declined as age advanced. This was true of both the complete nutrient and phosphorus-deficient canes. The differences at later stages of the life cycle appeared less significant. A general tendency of lower N.A.R. under phosphorus deficiency was recorded (Table IIA). While this was true of sand nutrient cultures, the comparative data on soil cultures showed the useful effect of 60 ppm. of P_2O_5 in improving N.A.R. This was particularly noted during the first three stages of observation, indicating thereby the possibility of greater efficiency of the plant under 60 ppm. in the accumulation of dry matter (Table IIB).

TABLE I—(*Contd.*)

C. AGE × TREATMENTS INTERACTIONS

Treatments	Age in days				Mean of 12 values
	45	90	135	225	
CN	27.03	26.33	18.17	16.23	21.9418
–P	26.63	25.27	18.80	16.53	21.8083
Mean of 6 values	26.833	25.800	18.483	16.383	..

C.D. at 5% for means of 4 values = ±30.229
,, ,, ,, 6 ,, = ±21.349
,, ,, ,, 12 ,, = ±15.096

D. TREATMENTS × PLANT PARTS INTERACTIONS

Treatments	Plant Parts			Mean of 12 values
	Leaf	Stem	Root	
CN	26.650	17.875	21.300	21.9418
–P	27.500	13.825	24.100	21.8083
Mean of 8 values	27.075	15.850	22.700	

C.D. at 5% for means of 4 values = ±26.159
,, ,, ,, 8 ,, = ±18.499
,, ,, ,, 12 ,, = ±15.098

TABLE II

Effect of phosphorus deficiency on the average net assimilation rate of sugarcane plant (var. Co 453) per 1000 sq. cms. per day during successive stages of the life cycle under sand and soil nutrient cultures

A. SAND CULTURES

Treatments	Age in days				
	45	90	135	180	225
CN	1.57	0.48	0.47	0.15	0.31
–P	1.45	0.39	0.12	0.25	0.27

B. SOIL CULTURES

Age in days	Concentration of P_2O_5 in ppm. of soil				
	0	20	40	60	80
45	1.999	1.966	1.964	2.243	1.948
90	0.328	0.384	0.419	0.431	0.304
135	0.249	0.251	0.191	0.336	0.306
225	0.147	0.041	0.070	0.024	0.025

Inorganic and Organic Phosphorus :

The inorganic fraction of phosphorus showed slight variations with age, conditions of phosphorus deficiency and plant parts (Table IIIA). Taking the over-all plant part values into consideration, the inorganic phosphorus content did not vary significantly with age under both the conditions of nutrition (Table IIIB). The differences due to phosphorus deficiency or the plant part were equally insignificant (Table IIIC).

TABLE III

Effect of phosphorus deficiency on the inorganic phosphorus content of sugarcane (var. Co 453) under sand nutrient cultures

(gms. of P_2O_5 per 100 gm. dry matter)

A. MAIN TABLE

Age in days	Treatments	Plant Parts			Average (plant)
		Leaf	Stem	Root	
45	CN	0.0527	0.0811	0.0518	0.0619
	–P	0.0437	0.0705	0.0766	0.0636
	Difference	+0.0090	+0.0106	–0.0248	–0.0017
90	CN	0.0534	0.0488	0.0828	0.0617
	–P	0.0459	0.0260	0.1001	0.0573
	Difference	+0.0075	+0.0228	–0.0173	+0.0044
135	CN	0.0790	0.0570	0.0431	0.0597
	–P	0.0941	0.0511	0.0421	0.0624
	Difference	–0.0151	+0.0059	+0.0010	–0.0027
180	CN	0.1515	0.0287	0.0317	0.0706
	–P	0.1169	0.0258	0.0293	0.0573
	Difference	+0.0346	+0.0029	+0.0024	+0.0133
225	CN	0.0202	0.0483	0.0505	0.0397
	–P	0.0280	0.0549	0.0362	0.0397
	Difference	–0.0078	–0.0066	+0.0143	+0.0000

B. AGE × TREATMENTS INTERACTIONS

Treatments	Age in days					Mean of 15 values
	45	90	135	180	225	
CN	0.0619	0.0617	0.0597	0.0706	0.0397	0.0587
–P	0.0636	0.0575	0.0624	0.0573	0.0397	0.0560
Mean of 6 values	0.0627	0.0595	0.0610	0.0639	0.0396	

C.D. at 5% for means of 3 values = ±0.4673
,, ,, ,, 6 ,, = ±0.3300
,, ,, ,, 12 ,, = ±0.2088

TABLE III—(*Contd.*)

C. TREATMENTS × PLANT PARTS INTERACTIONS

Treatments	Plant Parts			Mean of 15 values
	Leaf	Stem	Root	
CN	0.0714	0.0528	0.0520	0.0587
–P	0.0657	0.0457	0.0569	0.0560
Mean of 10 values	0.0685	0.0492	0.0544	—

C.D. at 5% for means of 5 values = ±0.3615
,, ,, ,, 10 ,, = ±0.2603
,, ,, ,, 15 ,, = ±0.2088

The organic fraction of phosphorus showed a definite fall with age and varied characteristically with the factors under investigation (Table IVA). The age effect and effects of plant parts were found to be statistically significant. The significant interaction between age and treatments indicated that the effects of phosphorus deficiency on the organic phosphorus content of the plant varied markedly with age (Table IVB). The over-all plant part values indicated significant rise in the organic phosphorus content of the complete-nutrient plants at 135 days and a significant fall at later periods of the life cycle. Under phosphorus deficiency, highest organic phosphorus content at 90 days and a significant decline at 225 days were also noted. The over-all age values, however, did not show any significant reduction in organic phosphorus, although a tendency of such a nature was recorded (Table IV C). A significant rise in the organic phosphorus

TABLE IV

Effect of phosphorus deficiency on the organic phosphorus content of sugarcane (var. Co 453) under sand nutrient culture

(gms. of P_2O_5 per 100 gm. dry matter)

A. MAIN TABLE

Age in days	Treatments	Plant Parts			Average (plant)
		Leaf	Stem	Root	
45	CN	0.2759	0.4569	0.4846	0.4057
	–P	0.3277	0.5479	0.3970	0.4242
	Difference	–0.0518	–0.0910	+0.0876	–0.0185
90	CN	0.4558	0.3824	0.6181	0.4854
	–P	0.5452	0.5463	0.8706	0.6540
	Difference	–0.0894	–0.1639	–0.2525	–0.1686
135	CN	0.9108	0.4320	1.3217	0.8882
	–P	0.3964	0.3770	0.5359	0.4331
	Difference	+0.5244	+0.0550	–0.2142	+0.4551
180	CN	0.1152	0.2304	0.4551	0.2669
	–P	0.1472	0.3389	0.2992	0.2618
	Difference	–0.0320	–0.1088	+0.1559	+0.0051
225	CN	0.0892	0.1700	0.0729	0.1106
	–P	0.0471	0.0360	0.2754	0.1195
	Difference	+0.0421	+0.1340	–0.0227	–0.0089

TABLE IV—(*Contd.*)

B. ANALYSIS OF VARIANCE

Due to	D.F.	S.S.	M.S.S.	Ratio	F at 5%
Age	4	1.1837	0.2959	11.64	3.01
Treatments	1	0.0204	0.0204	0.80	24.60
Plant parts	2	0.2469	0.1234	4.85	3.63
Age × Treatments	4	0.3290	0.0820	3.22	3.01
Treatments × Plant parts	2	0.0303	0.0151	0.59	19.43
Error	16	0.4071	0.0254		
Total	29				

S.E. per = ±0.16.

C. AGE × TREATMENTS INTERACTIONS

Treatments	Age in days					Mean of 15 values
	45	90	135	180	225	
CN	0.4058	0.4854	0.8882	0.2669	0.1106	0.4313
–P	0.4242	0.6540	0.4364	0.2618	0.1195	0.3791
Mean of 6 values	0.4150	0.5697	0.6623	0.2643	0.1150	..

C.D. at 5% for means of 3 values = ±0.2771
,, ,, ,, 6 ,, = ±0.1967
,, ,, ,, 12 ,, = ±0.1237

D. TREATMENTS × PLANT PARTS INTERACTIONS

Treatments	Plant Parts			Mean of 15 values
	Leaf	Stem	Root	
CN	0.3694	0.3343	0.5904	0.4313
–P	0.2927	0.4756	0.4756	0.3791
Mean of 10 values	0.3311	0.5830	0.5330	..

C.D. at 5% for means of 5 values = ±0.2142
,, ,, ,, 10 ,, = ±0.1542
,, ,, ,, 15 ,, = ±0.1237

content of the stem and the root over that of the leaf was also recorded. It, therefore, became obvious that the organic phosphorus content varied most characteristically with the age and plant parts and showed more or less similar trend of variations with age as noted for respiration rate. The plant parts, however, showed differential response. Thus, the leaf showed highest respiration rate followed by root and stem, but the organic phosphorus content varied in the decreasing order, stem > root > leaf.

DISCUSSION

The data recorded in these pages indicate beyond doubt that leaves in general, showed a relatively higher rate of respiration than root or the stem, particularly during the second half of the life cycle. During early stages the roots showed higher respiratory index than the leaf. Such variations in the respiration rate of the component organs must necessarily be analysed in terms of the important changes in the concentrations of various respirable materials. Taking the plant as a whole, the decline in respiration with age depicted, in general, the low state of metabolic activity of growing plant towards maturity, in comparison to the early stages when growth, differentiation of tissues and other metabolic changes were taking place with rapidity. Attempts have, therefore, been made to correlate the rate of respiration at various stages of the life cycle under phosphorus deficiency and complete nutrition conditions with the changes taking place in the relative concentration of various organic fractions.

When the rates of respiration were plotted against the corresponding values of carbohydrates and other organic nitrogenous compounds (Fig. 1), the relationship between respiration and concentration of each of such fractions was characteristic. A general tendency of decrease in respiration with rise in sucrose, glucose, fructose and with increase in the ratios of amino/amide nitrogen, was evident. On the other hand, increase in amide, amino acids, organic phosphorus and rise in sucrose/hexose and organic/inorganic P ratios, caused increase in respiration.

At the critical limits of sucrose (1 mg.), glucose (0.1 mg.), fructose (0.1 mg.), amino acids (40 mgm.), amides (10 mgm.) and organic phosphorus (0.4 mgm.) per 100 gm., respiration was usually high. As this limit was raised, the rate of respiration did not increase but showed decline. It was equally important to note that the ratio of sucrose/hexose and amino acids/amides and organic/inorganic phosphorus, played an important rôle in regulating the intensity of CO_2 output. When the concentration of organic phosphorus was high relative to its inorganic component, a high ratio of organic/inorganic phosphorus resulted in a sharp rise in respiration. On the other hand, a low ratio of organic/inorganic phosphorus resulted in a fall in the respiration. Respiration also declined with increase in amino/amide ratio, reaching low value as the ratio 6 : 1 was reached. The greater the proportion of sucrose over hexose (high sucrose/hexose ratio) the higher were the rates of respiration of the tissues. It was also clear that glucose/fructose ratio did not appear to be as important as the other three ratios in regulating respiration.

What then caused a high respiration rate during early days and poor respiration rate at later periods ? The possibility of high respiration being related to high sucrose/hexose (5 : 1) and low amino/amide (3 : 1) ratio have been indicated. Another possible factor responsible for high rate of respiration, was the ratio of organic/inorganic phosphorus (8 : 1). One of the potent factors which led to high respiration during early stage, therefore, appeared to be an adequate sucrose/hexose, amino/amide nitrogen and organic/inorganic phosphorus ratios in the tissues.

The interrelation between the concentration of various organic fractions and the respiratory activity is also made clear from summarised results recorded in Table V for the component parts of sugarcane. Thus, the high rate of leaf respiration was mostly due to its high insoluble nitrogen, total nitrogen and inorganic phosphorus content. In contrast to the leaf, the roots showed medium respiration due to the medium values of total soluble and insoluble nitrogen, and medium amounts of inorganic and organic phosphorus present therein ; all sugar fractions, amide and 'rest' nitrogen were poorest in roots. In comparison to both the subterranean and the green chlorophyllous foliage, the stem showed the lowest respiration. Low respiratory index of the stem was recorded in spite of the fact that the respirable material was the richest as indicated by high sucrose, total reducing sugars, total sugars, amino acids, amides, total soluble nitrogen and organic phosphorus compounds. On the other hand, low respiratory index was related to the low insoluble nitrogen, total nitrogen and inorganic phosphorus content of this organ. The protein and inorganic phosphorus content in stem being low, the respiratory index showed a fall relative to that of the leaf and the root. Further, such storage tissues like that of stem, mostly consisted of non-living cells. The existence of a small proportion of actively metabolizing cells, and poor efficiency of such tissues to utilize the rich respirable material already present appeared to be equally important in reducing the respiratory index. There was yet another possibility of the accumulation of harmful and toxic substances in stem which inhibited the oxidation of the respirable materials to carbon dioxide stage. The

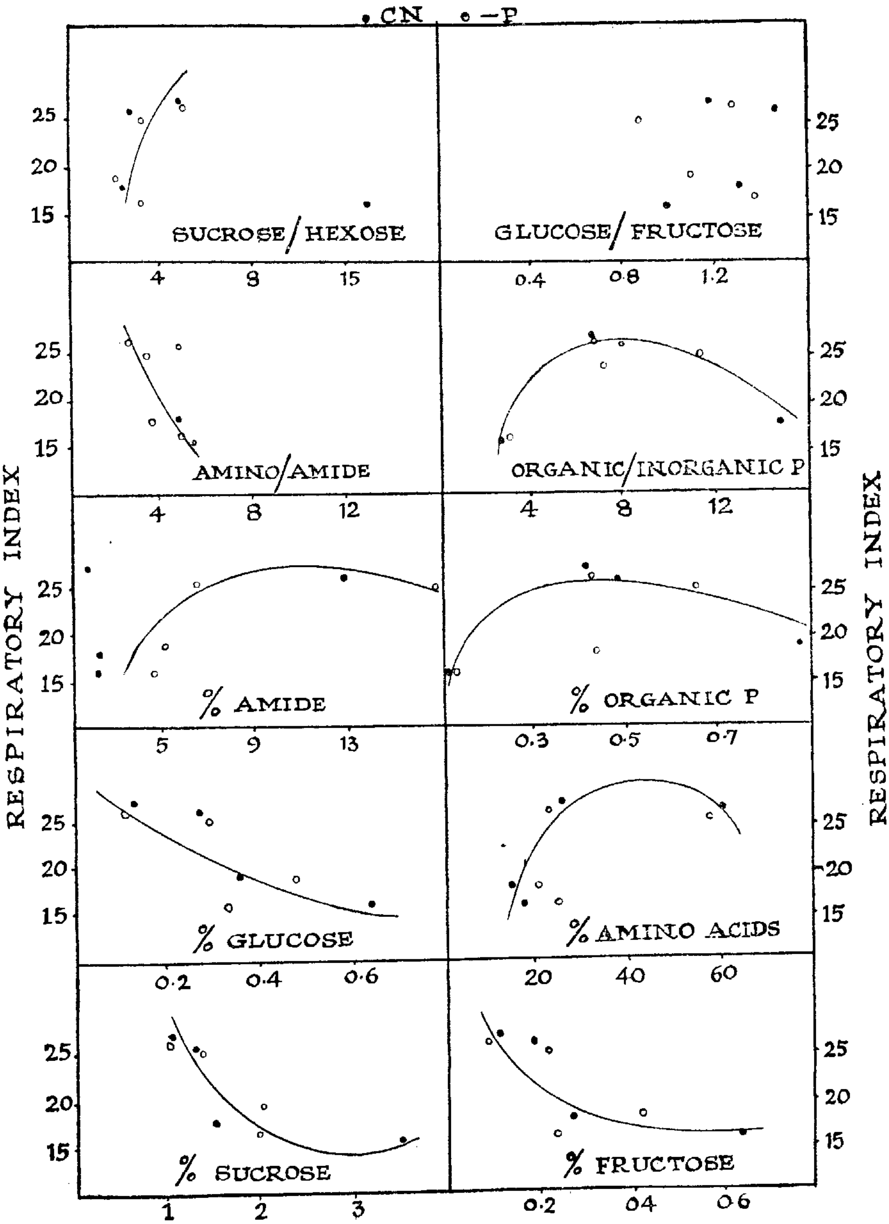

FIG. 1. Interrelation between respiration, organic and inorganic phosphorus and other fractions of nitrogen and sugars in canes grown under sand culture.

rich respirable materials present in the stem may also be converted into intermediate products such as organic acids, aldehydes and alcohol due to their restricted and incomplete oxidation caused by poor availability of oxygen, and partial narcotic effects of dissolved CO_2 and other intermediate products of partial anaerobiosis. Further work is needed to elucidate the nature of this age-respiration relationship with special reference to the aerobic and anaerobic oxidation of respirable materials.

So far as the effect of phosphorus deficiency on respiration rate was concerned, relatively lower respiratory index was associated with reduction in various sugar fractions and total insoluble nitrogen and the organic and inorganic content of phosphorus in tissues. The effects of deficiency of this element on the respiratory index were generally insignificant mainly on account of the fact that possible reduction caused by the low percentage of all sugar fractions, total insoluble nitrogen and organic and inorganic phosphorus were counterbalanced by the relatively high concentration of amino acids, amides and total soluble nitrogen in phosphorus deficient tissues. If the fall in carbohydrates indicated the possibility of low index of respiration, the high amides, amino acids and total soluble nitrogen showed the possibility of higher respiratory index. Both these effects seemed to result in maintaining a balance resulting in insignificant differences in respiratory index of the canes grown in complete-nutrient and phosphorus-deficient cultures. In an analysis of respiratory drifts in sugarcane, due consideration should, therefore, be given to the relative amounts of sugar, nitrogen and phosphorus fractions present in the tissues (Table V). The possible rôle of organic acids in the respiratory activity also needed careful investigation.

TABLE V

Order of response in component parts of sugarcane (var. Co 453) under phosphorus deficiency

Character	Order of Response	
	Plant parts	Nutrition
% Fructose	Stem > Leaf > Root	CN > −P
% Glucose	Stem > Leaf > Root	CN > −P
% Sucrose	Stem > Leaf > Root	CN > −P
% Reducing sugars	Stem > Leaf > Root	CN > −P
% Total sugars	Stem > Leaf > Root	CN > −P
% Nitrate	Root > Stem > Leaf	−P > CN
% Ammonia	Stem > Leaf > Root	CN > −P
% Amide	Stem > Leaf > Root	−P > CN
% 'Rest' nitrogen	Stem > Leaf > Root	−P > CN
% Total soluble nitrogen	Stem > Root > Leaf	−P > CN
% Total insoluble nitrogen	Leaf > Root > Stem	CN > −P
% Total nitrogen	Leaf > Root > Stem	−P > CN
Respiratory index	Leaf > Root > Stem	CN > −P
Inorganic phosphorus	Leaf > Root > Stem	CN > −P
Organic phosphorus	Stem > Root > Leaf	CN > −P

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