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BIOCHEMICAL AND NUTRITIONAL STUDIES ON POTASSIUM[1]

I. Effects of Potassium on the Respiration of Higher Plants

By

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I. Introduction

The extensive and prolonged investigations on the effects of potassium in green plants have been carried on in recent years from the standpoint of agronomy. But the true functions of potassium through an interest in the biochemical and enzymological properties relating metabolic process are not yet fully solved.

We have attempted to clarify the functions of potassium in the metabolism of higher plants and at first a good deal of attention was devoted to investigate the fundamental phenomena concerning the metabolic- especially respiratory-process. The authors wish to report the results obtained concerning respiration in relation to potassium as part 1.

Generally speaking, the physiological functions of potassium upon the green plants, so far as we know from the previous publications, could be summarized as follows, namely (1) effect on carbohydrate metabolism or formation, breaking down and translocation of starch(1～10), (2) effect on the nitrogen metabolism and the synthesis of protein in green plants, (11～15), (3) control and regulation of activities of various essential mineral nutrients(16～21), (4) neutralizing the physiologically important organic acids (22, 23), (5) as activator of various enzymes, (7～9), (6) promoting the growth of young meristem (24), (7) adjusting the stomatal movement (25), and so on.

Among previous investigations, some of important ones on respiration are as follows. In 1920 J. Stoklasa(26) pointed out that the potato and the cucumber plants cultured in a medium supplied with a heavy amount of potassium showed a higher evolution of carbon dioxide, compared with the same plants raised under potash deficient conditions. These results are not in accord with the modern idea of respiration in relation to potassium.

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Afterwards, F. G. Gregory and F. J. Richards(27) observed that the barley plant which showed slight symptoms of potassium deficiency evolved more carbon dioxide than the barley plant supplied with rich potassium. Then F. J. Richards presumed that the increase of the amino acid content in the potassium deficient plant may be the cause of the respiration rise. Also the rise of oxygen respiration and the depression of anaerobic respiration through the addition of potassium was observed by G. Rohde (28), and he presumed this respiration promoting effect may depend upon the activation of respiratory enzyme through the iron containing pigment as cytochromes.

H. Scheffer(17) et al made experiments on the relation between the carbon dioxide evolution and the intake of potassium using yeast and they concluded that potassium was taken in and sodium was given off by yeast cells according to the rise of their respiration.

At the first step of our research, we assumed that among the respiration in the glycolysis process, potassium may combine with 3-phospho-glyceric acid and other organic phosphate esters. Relating to Krebs cycle potassium may form soluble salts with physiologically important hydroxyorganic acids, but sodium, on the contrary, may give difficult soluble salts with these acids under the same conditions. So fundamental experiments on the effect of potassium were carried on by the authors.

Materials and methods

From our preliminary experiments, certain differences in the effect of potassium, between the respiration of monocotyledonous and dicotyledonous plants were observed, so the seedlings of many species were adopted for the estimation of the rate of respiration in relation to the potassium supply.

Tomatoes, rice plants (Nôrin 16) and barley (Aizu 4) were raised by the water culture method supplied with the following nutrients solutions under strictly regulated conditions for ten to twentyfive days, until their top length attained about 10–15 centimeters.

Table 1. Composition of the nutrient solution

$(NH_4)_2SO_4$, $NaNO_3$	N	50 ppm
$Na_2HPO_4 \cdot 12H_2O$	P_2O_5	30 "
KCl	K_2O	10 "
$CaCl_2$	CaO	40 "
$MgCl_2 \cdot 6H_2O$	MgO	30 "
Fe-citrate	Fe_2O_3	3 "
minor elements	Mn 0.5, Cu 0.02, Zn 0.05, B 0.5, Mo 0.05.	

Respiration intensity was measured precisely by means of Warburg's manometer, using as many samples as possible of evenly grown seedlings.

Our measurement was carried on at 24°C in complete darkness to avoid trace of photosynthesis. Experimental results were expressed as O_2 uptake cmm/mg of dry weight/minutes or O_2 uptake cmm/g of green weight/minutes. The potassium content was estimated by flame photometer after ashing at 550°C and extracting with dilute hydrochloric acid.

Experiments and results

(1) *Effect of the form of nitrogen on the respiration in relation to potassium*

From our preliminary experiments it was observed that the form of nitrogen supplied during the culture period seriously affects the potassium status of green plants.

Barley seedlings were cultured for 48 hours with and without potassium. Each plot had two sections, one supplied with NO_3-nitrogen and the other with NH_4-nitrogen. After 48 hours, ten seedlings were taken out and excess water was blotted off by filter paper. The respiration intensity was measured as to separated roots and tops. The result obtained is shown in Table 2.

Table 2. N, K nutrient status and respiration (barley seedling)

Treatment (48 hours.)		Respiration intensity*	
		Roots	Tops
NO_3-N (50 ppm)	+K (K_2O 50 ppm)	1.4	1.0
	−K	1.6	1.1
NH_4-N (〃)	+K (K_2O 50 ppm)	2.3	0.8
	−K	3.3	1.1

* Respiration intensity : O_2cmm/mg dry weight/30min

From this result the following may be concluded.

1. The potassium defficient plants showed higher respiration per unit weight in both NH_4-nitrogen and NO_3-nitrogen plots than those of potassium enriched plants.
2. The oxygen uptake per unit weight of the roots is higher than that of the tops in both NH_4-nitrogen and NO_3-nitrogen plots.
3. The respiration of the roots of the plants supplied with NH_4-nitrogen is always more active than that of the roots of the plants supplied with NO_3-nitrogen, in both potassium deficient and sufficient treatments.

(2) *Effect of nitrogen, potassium and glucose supply on the respiration of seedlings.*

Considering the result of experiment(1), special attention must be payed to the supply of respiration substrate as glucose. Culture methods for seedlings are just the same as those of the aforementioned experiment, but in addition, 0.9% of glucose was given as substrate at the time of measurements. The result obtained was as follows.

Table 3. N, K, glucose nutrient and respiration (barley seedling)
Respiration intensity: O_2 cmm/mg dry weight)/30 min

Treatment		hrs.	0	24	72
Roots	glucose (0.9%) NO_3-N (50 ppm)	+K (50 ppm)	3.7	4.7	2.9
		−K	"	5.2	3.7
Tops	glucose (0.9%) NO_3-N (50 ppm)	+K (")	2.5	1.0	1.7
		−K	"	1.1	1.9

The same tendencies were observed in this experiment notwithstanding the addition of substrate, so it may be concluded that the effect of the preliminary supply of potassium does not depend upon the mere increase of photosynthesis or accumulation of respiration substrate.

(3) *Effect of concentration of supplied potassium and sodium on the respiration.*

From the result of experiment(1), the effect of the coexisting monovalent cations may be hardly overlooked, so the interaction of potassium and sodium on respiration was examined. The respiration intensity of the whole plants of rice seedlings was measured, with the addition of various amounts of potassium and sodium in the manometer vessel (Table 4, 5).

Table 4. Respiration in regard to potassium concentration (rice plant seedlings)
Respiration intensity: O_2 cmm/g green weight/15 min

K_2O concentration in nutrient solution (p. p. m.)	Respir. intensity after 20 hrs.
200	0.8
50	0.9
5	1.1
2	1.2
0	1.2

From these results, it may be concluded that the decrease of the concentration of potassium in the culture solution brought a severe rise of respiration, nevertheless the supply of sodium had no distinct influence on the respiration between the concentration of 0–1500 p. p. m., sodium supply over 1500 p. p. m. gives rise of respiration.

Table 5. Respiration in regard to sodium concentration (rice plant seedlings)
Respiration intensity : O_2 cmm/g (green weight)/15 min

Na_2O concentration in nutrient (%) (NaCl)	hrs. 0	5	8	23
1.5	1.0	1.52	2.33	3.15
0.5	"	1.36	2.25	2.91
0.3	"	1.09	2.22	1.83
0.15	"	1.00	2.22	1.67
0.1	"	1.01	2.22	1.66
0.025	"	1.00	2.21	1.67
0.005	"	1.01	2.22	1.68
0.00025	"	0.99	2.18	1.65
0	"	1.00	2.21	1.67

(4) *The intake of potassium in relation to the respiration.*

The barley seedlings were placed in the manometer vessel with a potassium (190 p. p. m.) and glucose (0.01%) supply, and the oxygen uptake was measured, simultaniously the potassium concentration of the outer solution was estimated. The results obtained are indicated in Table 6 and Figure 1.

Table 6. Intake of potassium and respiration (barley seedling)

hrs.	0.5		1.5	4	15	17	17.5
Respiration intensity	6.2	glucose addition	6.5	8.6	8.0	6.4	5.7
K_2O concentration	190		182.5 ±0.1	180.0 ±0.2	182.5 ±1.0	185.0 ±0.6	190.0 ±0.2

Respiration intensity : O_2 cmm/g (green weight)/20 min.
K_2O concentration : p. p. m. in the outer solution

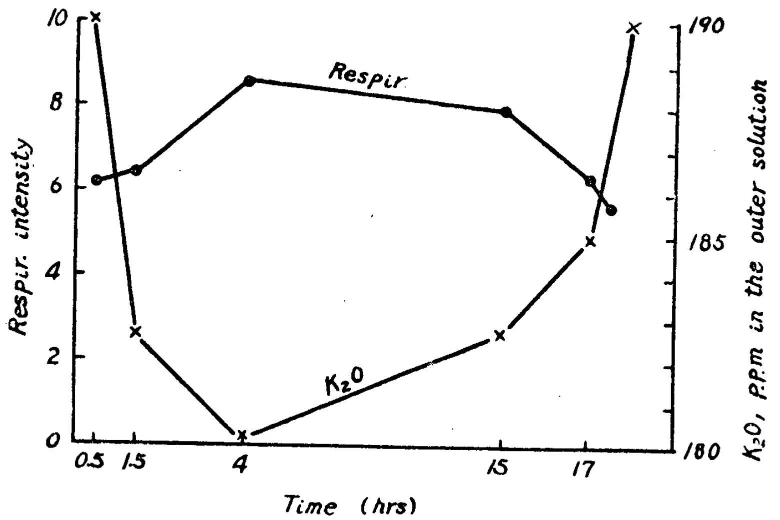

Fig. 1.

The result obtained was extremely important. The respiration of barley was greatly increased by the addition of glucose and the concentration of potassium in the outer solution decreased rapidly. In the lapse of time, the respiration decreased according to the consumption of the substrate, then potassium ion came out from the plant tissues. This result is partly in accord with that of Scheffer et al (17).

(5) *Effect of iron addition on the respiration in relation to potassium.*

According to G. Rohde(28), iron addition might bring a rise of respiration of the plant, so authors examined the effect of iron. Experimental plans are shown in Table 7. At this experiment 0.9% of glucose was added to make clear the changes in the respiration intensity. Tomato plants were adopted for this experiment. The total volume of solution added to each manometor vessel was 2 ml.

From this experiment it was shown that the dicotyledonous plant as tomato also behaves commonly as the monocotyledonous plants.

Potassium deficient tomatoes showed a higher oxygen uptake than those supplied with proper amounts of potassium. We could not observe the activating effect of the iron supplement relating with potassium on the respiration in many cases of our treatments.

Table 7. Potassium, iron nutrient and respiration (tomato seedling)

Treatments (after 3 hours) { a, 0.9% glucose, 0.2 ml. + water, 1.8 ml.
b, 0.9% glucose, 0.2 ml. + 0.9% KCl, 0.2 ml + water, 1.6 ml.

" { a′, 0.9% glucose, 0.2 ml. + 0.9% KCl, 0.2 ml + 0.1% $FeCl_3$, 0.2 ml. + water 1.4 ml.
b′, 0.9% glucose, 0.2 ml. + 0.1% $FeCl_3$, 0.2 ml + water 1.6 ml.
c′, " + 0.9%KCl, 0.2 ml. + water, 1.6 ml.

Respiration intensity: O_2 cmm/g green weight/20 min.

hrs.	Initial period*			Treatments	Experimental period					
	0	1	3		4	5	10	12	21	23
a	0.55	0.78	0.80	glucose	1.30	1.70	1.40	1.00	0.90	0.61
b	0.55	0.83	0.83	glucose + K	1.00	1.25	1.08	0.75	0.75	0.60
a′	1.07	1.60	1.60	glucose + K + Fe	1.86	2.00	1.78	1.60	1.50	1.40
b′	1.01	1.56	1.60	glucose + Fe	1.77	2.07	1.70	1.50	1.30	1.10
c′	1.05	1.58	1.58	glucose + K	1.76	1.96	1.80	1.61	1.49	1.41

* The treatments were adopted after the 3 hours' initial period.

Discussion

Numerous investigations have long been pursued on the relation between the form of nitrogen supplied and potassium. It was confirmed by Takahashi (19) that potassium and ammonium ions behave competitively at the intake of ions by tobacco roots, as they are both monovalent cations, so the absorption of potassium is seriously depressed by the absorption of ammonium ion.

He also observed that potassium deficient symptoms could be seen on ammonium supplied tobacco plants, more distinctly than on those supplied with nitrate.

From our experiment (1), the authors found that the respiration of the ammonium supplied plant is far higher than that of the nitrate supplied plant. We could not say with certainty that this increase of the respiration might depend upon the interferance of intake of potassium ion by ammonium ion or that the action of oxygen derived from nitrate may act as hydrogen acceptor in the respiration process and economize the oxygen uptake from the outside.

The content of potassium in the roots is generally lower than that of the tops in rice plant and barley (1).

According to the modern idea of ion absorption by roots, the energy consumed during intake is derived from the active respiration. Since the roots has particular physiological roles such as ion absorption, the respiration of the root must be kept in a highly active state, on the contrary, from our experiments potassium is able to suppress the respiration of the plant tissues.

Therefore it might be considered that the lower content of potassium inside of the root has the meaning of controling the respiration and absorption of ions by the root.

The result of our experiment(3) showed that the concentration of potassium from 0 to 200 p. p. m, which is commonly used in solution culture and could be found in soil solution, can seriously affect the respiration. From this fact, it may be concluded that the potassium may concern directly with the respiratory process, because it brings the change of oxygen uptake within the range of the normal concentration of environment, while on the contrary, sodium might have no direct connection, as it has no effects on oxygen uptake within the condition of normal environment. The authors would conclude that the rise of oxygen uptake by the higher concentration of sodium depends upon the expulsion or replacement of potassium by sodium, which, as a result causes the respiration increase. This expulsion or replacement of potassium from tissue by high concentration of sodium is alrerdy observed by many research workers; namely for chlorella by J. T. Scott(16), for alfalfa by J. T. Cope(21) and for frog muscle by Stainbach(18).

The above assumed direct concern with the respiratory process was also clearly shown in experiment(4). It may be very important that potassium can easily enter in the root and again come out according to the respiration intensity or the supply of substrate from the leaves. These results partly accord with those of Scheffer in relation to the potassium, sodium and glucose supply in yeast cells.

It is very difficult to suggest the action of iron from our experiment, but the respiration might not be intensified by mere addition of iron which has been taken to be activated by potassium, as potassium itself checks the respiration of tissue.

From the experiment(4) it is very interesting that the increase of oxygen uptake caused by the addition of glucose for barley root brings rapid intake of potassium, but according to the former experiments(1), (2), and (3), respiration intensity should be suppressed by the absorbed potassium, so it may be said that the amount of potassium inside of the tissue is able to regulate the excessive consumption of substrate in the respiratory process.

Now we would suggest that potassium takes part in the regulation or control of respiration by means of direct connection with the repiratory process itself.

Summary

(1) The effects of the potassium supply on the respiration of tomatoes, rice plants and barley seedlings in relation to other factors were fully investigated.

(2) All plants in potassium starved condition, showed markedly increase in respiration intensity, and the effect on respiration appeares rapidly by the slight changes of potassium status in environment.

(3) Sodium seems to have no direct connection with the respiratory process.

(4) At the time of increase in respiration intensity caused by the addition of glucose, potassium is taken in and the decrease of respiration caused by the consumption of substrate brings excretion of part of the absorbed potassium.

(5) Respiration is not intensified by the iron, which has been thought to be activated by potassium.

(6) It may be suggested that potassium regulates the respiratory process through direct connection.

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