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# SECONDARY EFFECTS OF POTASSIUM AND NITROGEN NUTRITION OF RICE: CHANGE IN MICROBIAL ACTIVITY AND IRON REDUCTION IN THE RHIZOSPHERE

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## SUMMARY

In solution culture experiments with rice the effects of different potassium applications and of various nitrogen sources on some criteria of microbial activity were studied. The following results have been obtained:

The number of bacteria in the rhizosphere depends on the form of nitrogen available to the plants and the potassium nutritional state. With ammonium as a nitrogen source a greater number of bacteria is found in the rhizosphere than with nitrate. The interruption of potassium nutrition results in an increase in the total number of bacteria.

In accordance with the different bacterial colonisation, the oxygen content in the nutrient solution with nitrate remains higher than with ammonium nutrition. With an increase in bacterial number after K interruption, a corresponding depression of the oxygen content in the nutrient solution can be noted. This is due to the higher respiration rate of the roots and the bacteria adhering to them in K-deficient plants.

K deficiency consequently results in an increased concentration of reduced divalent iron in the nutrient solution.

From the above results it follows that optimum potassium nutrition makes an essential contribution towards counteracting highly reducing conditions in paddy soils.

## INTRODUCTION

In paddy cultivation, the oxygen is expelled from the soil by flooding. When due to microbial activity also the oxygen in the soil solution has been exhausted, reducing processes will occur. A certain 'optimum reduction zone' [24] or 'healthy reducing conditions' [9] are however regarded as being favourable because they are connected with the mobilisation of various nutrients. But more intense reducing processes leading to 'extreme reducing conditions' will, however, result in toxic concentrations of reduction products which give rise to the widespread physiological rice diseases. A steep increase in the concentration of reduced divalent iron has a particularly injurious effect on rice plants. Excessive uptake of divalent iron causes iron toxicity, known in Japan as 'Akagare type I', in India and Ceylon as 'Bronzing'. Micro-organisms play an essential part, both in oxygen consumption and reducing processes. That iron reduction in paddy soils is caused by bacteria has been detected by Kamura *et al.* [10]. Ottow [18 19 20 21] proved that manganese and iron reduction in gley soils is caused by facultatively anaerobic bacteria of the genera *Bacillus*, *Pseudomonas* and *Arthrobacter*, which predominantly also reduce nitrate, as well as by members of the *coli-aerogenes* group [22 23] and anaerobic nitrogen-fixing Clostridiae [21].

Several authors stated that iron toxicity can be prevented by abundant potassium dressings. Shibuya and Torii [25] already observed a positive effect of K application and supposed an antagonism between potassium and iron. These authors also mentioned that with high $Fe^{2+}$ concentrations sparingly soluble double salts are formed from $FeSO_4$ and $K_2SO_4$ so that the $Fe^{2+}$ concentration will be lowered. Recently, Tadano and Tanaka [26] found in several experiments that the plants well supplied with potassium absorbed less labelled $Fe^{2+}$—59 from a nutrient solution containing 300 ppm $Fe^{2+}$ than rice which had been given lesser amounts of K. In a pot experiment with acid sulphatic soil, the Fe content in the plants could be lowered by increasing K applications. Furthermore, in the K pots higher $E_h$ values in the soil were measured than in those without K. On the basis of these results, Tadano and Tanaka [26] indicate that potassium applications improve the 'iron excluding power' of rice plants.

It seems that so far only few investigations have been carried out dealing with the problem whether there exists a relation between the activity of rhizosphere bacteria and iron toxicity. Only McRae and Castro [13] suppose certain connections in this respect. They examined the root excretions of various rice varieties, being either susceptible or resistant to iron toxicity. These authors observed a higher excretion of carbohydrates in resistant plants. Microbiological investigations have, however, not been carried out but it can be assumed that in accordance with the higher excretion found in resistant strains a more intense microbial activity in the rhizosphere could have been expected.

In previous experiments on wheat the author found that, besides the well-known effect of potassium on plant growth and yield, potassium nutrition also exerts an influence on the number and activity of rhizosphere bacteria. With increasing K applications the number of bacteria decreases, particularly the number of those micro-organisms which decompose simple organic compounds. It could furthermore be observed that poor oxygen supply to the roots increases the number of rhizosphere micro-organisms. Low supply of both oxygen and potassium leads to considerable losses of nitrogen due to denitrification [27 28]. Oxygen deficiency and reducing conditions are also characteristic of paddy soils. Therefore investigations were carried out with a view to study the effect of varied potassium nutrition on microbial activity in the rhizosphere of rice.

## MATERIAL AND METHODS

### *Cultivation of the plants*

The experiments were carried out in nutrient solution in order to cover only the micro-organisms adhering to the roots and to exclude possible influences from the soil environment. Rice of the French cultivar Cigalon was seeded in petri dishes to germinate. After three days the seedlings, seven each per vessel, were placed on a coarse-meshed net attached to beakers with a content of 500 ml. Algal growth in the vessels could be prevented by covering the beakers with dark lids provided with holes through which the plants could grow. During the warm summer months (July and August) the plants were grown in the open air and afterwards in the greenhouse with additional illumination. Water was replenished when necessary.

### *Nutrient solution*

Nitrogen was given to one half of the vessels as nitrate and to the other half in the ammonium form. At the start of the experiment, each nitrogen treatment was further subdivided into two K treatments ($K_1$ and $K_2$). After 52 days the potassium supply to one half of the $K_2$ plants was discontinued ($K_{(2)0}$). The composition and the initial concentration of the nutrient solution is indicated below.

Iron reduction was investigated only in the $NH_4$ treatment because $NO_3$ retards the decrease of the redox potential [32] and thus prevents $Fe^{3+}$ reduction.

Six times during the growing period one half of the above amounts of nutrients (except $Fe_2O_3$) was added to the vessels. From the third nutrient application on $K_2SO_4$ was replaced by equivalent amounts of KCl in order to

$NO_3$ nutrient solution

| | |
|---|---|
| $Ca(NO_3)_2 \cdot H_2O$ | 4 m$M$/l |
| $Ca(H_2PO_4)_2 \cdot H_2O$ | 0.5 m$M$/l |
| $MgCl_2 \cdot 6\,H_2O$ | 1 m$M$/l |
| Fe–EDTA | 50 mg/l |
| A–Z solution (Hoagland) | 1 ml/l |
| $K_1$ $K_2SO_4$ | 0.5 m$M$/l |
| $K_2$ $K_2SO_4$ | 2 m$M$/l |

$NH_4$ nutrient solution

| | |
|---|---|
| $(NH_4)_2SO_4$ | 3 m$M$/l |
| $(NH_4)_2HPO_4$ | 1 m$M$/l |
| $MgCl_2 \cdot 6\,H_2O$ | 1 m$M$/l |
| $CaCl_2$ | 2 m$M$/l |
| Fe–EDTA | 50 mg/l |
| A–Z solution (Hoagland) | 1 ml/l |
| $K_1$ $K_2SO_4$ | 0.5 m$M$/l |
| $K_2$ $K_2SO_4$ | 2 m$M$/l |
| $Fe_2O_3$ | 2 m$M$/l |

prevent a further accumulation of sulphate in the nutrient solution. Moreover, to the $NH_4$ solution then $CaCO_3$ was given instead of $CaCl_2$ to counteract a pH depression. For this reason and also as a preventive measure for avoiding higher sulphate concentrations $(NH_4)_2SO_4$ was replaced by equivalent amounts of ammonia water, beginning with the third nutrient application.

### *Physico-chemical measurements*

Oxygen. The measurement of the oxygen content of the nutrient solution was carried out by means of an oxygen electrode (Rank Brothers, England). 50 ml of the nutrient solution were transferred with a pipette from the bottom of the vessels to small flasks from which the air had been expelled by nitrogen. Then 5 ml were pipetted from these flasks into the measuring chamber of the oxygen electrode where the $O_2$ content was determined.

Iron. Determination of divalent iron in the nutrient solution was carried out with 2,2' bipyridine by means of photometry [17].

### *Determination of bacterial number*

Before harvesting, 2.5 g root fresh matter was taken from each beaker and cut into small pieces. Then the joint root matter from four replications was put into a one-liter flask, 500 ml water and 30 g sand were added and the mixture was shaken for 30 min. The total number of bacteria was determined according to the plate-count method [28].

### *Measurements of respiration*

The oxygen consumption of excised roots was assessed according to the Warburg method at 25°C. For this determination 500 mg root fresh matter and 10 ml 0.1 $M$ tricin buffer (pH 7) were added to 90 ml Warburg flasks. The respiration quotients were calculated from the $O_2$ consumption for the first 30 min only because later on the difference between the individual treatments diminished.

## RESULTS

The oxygen contents of the nutrient solutions, measured at different intervals after K interruption, are listed in Table 1.

TABLE 1

Oxygen content of the nutrient solutions (mg $O_2/l$)

| Treatments | | Age of the plants in days | | |
|---|---|---|---|---|
| | | 76 | 82 | 83 |
| $NH_4$ | $K_{(2)0}$ | 0.5 | | 0.9 |
| | $K_2$ | 8.6 | | 3.7 |
| | $K_1$ | 17.0 | | 10.7 |
| $NO_3$ | $K_{(2)0}$ | 10.6 | 13.6 | |
| | $K_2$ | 16.3 | 20.6 | |
| | $K_1$ | 13.5 | 19.1 | |

The oxygen contents of the nutrient solutions containing nitrate were always higher than those observed in the ammonium solutions. Considerable differences could also be stated between the various K treatments. The $K_1$ plants, which already at the start of the experiment had received less potassium, showed marked depressions in growth although no visible symptoms of potassium deficiency could be detected. Due to the lower amount of root matter in these vessels (Table 5), the oxygen content of the nutrient solution did not fall off as sharply as in the other treatments. The influence of varied potassium applications on the oxygen content in the root environment can therefore only be assessed from a comparison between the $K_2$ and the $K_{(2)o}$ vessels in which the amount of root matter was nearly the same (Table 5). The lowest oxygen content was found in the $K_{(2)o}$ nutrient solutions (Table 1). A remarkable influence of the nitrogen source on the oxygen content of the $K_2$ and $K_{(2)o}$ variants could be noted. The $O_2$ content in the $NO_3$ treatments was always considerably higher than in the $NH_4$ treatments.

With decreasing oxygen content the concentration of divalent iron increased. As a matter of fact, the Fe(II) content was highest in the $K_{(2)o}$ treatment (Table 2). It can be seen that the concentration of divalent iron in the nutrient solution was more than doubled after the interruption of potassium supply, but it was still far from causing iron toxicity.

In Table 3 the respiration quotients $Q_{O_2}$ of the roots are given.

The results show that the heavy loss of oxygen after K interruption is connected with the increased oxygen consumption of the

TABLE 2

Content of divalent iron in the nutrient solution in ppm

| Treatments | Age of the plants in days | | | |
|---|---|---|---|---|
| | 55 | 76 | 82 | 83 |
| $NH_4$ $K_{(2)0}$ | 3.0 | 10.6 | 4.0 | 4.9 |
| $K_2$ | 2.3 | 2.4 | 1.8 | 1.4 |
| $K_1$ | 1.0 | 1.0 | 0.5 | 0.2 |

TABLE 3

Respiration quotients $Q_{O_2}$ ($\mu$l $O_2$ consumption g root fresh matter/h)

| Treatments | $NO_3$ | $NH_4$ |
|---|---|---|
| $K_{(2)0}$ | 0.324 | 0.166 |
| $K_2$ | 0.301 | 0.127 |
| $K_1$ | 0.411 | 0.159 |

roots and the micro-organisms adhering to them. The $O_2$ consumption of the nitrate treatments was determined 28 days, that of the ammonium treatments 31 days after K interruption, respectively. The high oxygen consumption of the nitrate-treated roots, which was more than twice as high as that of the roots of the ammonium treatments, is somewhat spectacular. The lowest respiration quotients could be established for the plants supplied with the highest rate of potassium. Both the plants which from the start had received lower K applications as well as those with interrupted K nutrition showed increased root respiration.

TABLE 4

Total number of bacteria per gram of root fresh matter

| | $NH_4$ treatments $\times 10^6$ | $NO_3$ treatments $\times 10^6$ |
|---|---|---|
| $K_{(2)0}$ | 2036 | 988 |
| $K_2$ | 1686 | 896 |
| $K_1$ | 1244 | 622 |

From the differences between bacterial populations on the roots in the nitrate and ammonium treatments (Table 4) it can be deducted that the contribution of bacteria to total respiration is much lower with nitrate than with ammonium nutrition. The number of bacteria was determined 36 and 37 days, respectively, after K interruption. The total number of bacteria in the ammonium treatments was considerably higher than with nitrate supply. K interruption resulted in an increase in total number of bacteria. The $K_1$ treatment showed the lowest bacterial colonisation. This fact will later be discussed in detail. The dry matter weight of those plants which from the start of the experiment had received smaller K applications was considerably lower than that of the other plants. Slighter differences could be noted between the plants continuously supplied with higher rates of K and those with interrupted K nutrition (Table 5).

TABLE 5

Dry matter weight of plants in grams per pot at the end of the experiment

| | Treatments | Shoot | Root |
|---|---|---|---|
| $NH_4$ | $K_1$ | 8.5 | 1.7 |
| | $K_{(2)0}$ | 11.0 | 3.6 |
| | $K_2$ | 12.0 | 3.9 |
| $NO_3$ | $K_1$ | 7.7 | 2.4 |
| | $K_{(2)0}$ | 12.6 | 3.5 |
| | $K_2$ | 17.8 | 3.5 |

In order to be able to assess the influence exerted by the interruption of K supply on the decrease of oxygen content and the increase of iron(II) content, as well as bacterial number, it was indispensable that the volume of nutrient solution per unit quantity of root material was practically constant. Under natural conditions in the soil, in contrast to solution culture, the influence of the roots is much more restricted to their immediate environment. It can therefore be assumed that under such conditions poor potassium nutrition from the start would result in similar effects as a later interruption of K supply in solution culture experiments the more so as the diffusion of oxygen in the soil solution proceeds rather slowly.

## DISCUSSION

The experiments on rice confirmed earlier results obtained in experiments on wheat [27] [28], *viz* that with poor potassium supply to the plants more bacteria are present in the rizosphere than with optimum K nutrition. Root respiration (roots and micro-organisms on the root surface) is also more intense in plants poorly supplied with potassium. According to results obtained from still unpublished experiments with sterile wheat plants, increasing K applications also lower the oxygen consumption of sterile roots. Several authors stated that potassium deficiency results in increased respiration of nonsterile roots, *e.g.* in rice [3], taro plants, beans and barley [14 15]. The greater intensity of respiration with K deficiency is connected with the higher content of respiration substrate in these plants. Okamoto and Oji [16] among others found higher contents of total sugar, reducing sugars, soluble nitrogen and amino nitrogen in roots of sweet potato plants deficient in potassium (further references to literature see Trolldenier [27]), which is due to the inhibited synthesis of cell constituents of higher molecular weight [5]. The higher content of such substances in the roots of K-deficient plants results in increased root exudation as could be stated in beans cultivated under sterile conditions after assimilation of $C^{14}O_2$ by the shoots and measurement of the concentration of $C^{14}$ bound in organic compounds in the nutrient solution [29]. The increased root exudation of K-deficient plants furnishes an explanation for the greater intensity of microbial life in the rhizosphere since exudates are the basic food for such organisms.

Rice differs from many other plants by the fact that its roots are largely independent of the oxygen present in the environmental medium. Oxygen supply is secured from intracellular air spaces of shoots and surface roots [1]. Under certain conditions the roots even excrete oxygen, but according to Kalpage [17] oxygen consumption by rice roots can also surpass the oxygen supply from the aboveground plant parts to the roots. Whether the oxygen transport within the plant depends in a certain way on the nutritional state needs further investigation. Only then it will be possible to state whether the observation that plants poorly supplied with K 'cause more reduction of the root zone' [2] is not only related with the increased respiration of roots and micro-organisms, as has been found in the present experiments, but possibly also with the poorer oxygen transport within the plant. The part played by micro-organisms and roots in the lowering of the oxygen content in the nutrient solution can only be assessed by comparative experiments with plants grown under sterile conditions. From the lower bacterial colonisation of the plants supplied with nitrate and their higher respiration quotient, in comparison with the ammonium-treated plants, it can, however, be concluded that the source of nitrogen plays a decisive part in this respect. The relatively low bacterial colonisation with nitrate nutrition agrees well with the high oxygen content of the nutrient solution. In contrast thereto, the oxygen consumption by the roots in the Warburg experiment was rather high. This apparent inconsistency can possibly be ascribed to the fact that the high oxygen requirements for the energy-consuming nitrate assimilation in the roots under normal conditions is covered by transport from the aboveground plant parts and not by the root environment, whereas the excised roots in the experiment were dependent on the oxygen supply from the Warburg vessels. This assumption is supported by results of Vlamis and Davis [30 31], which indicate that intact rice plants absorb nutrients from solutions through which nitrogen is being passed whilst excised roots assimilate the nutrients only in the presence of oxygen in the solution. Roots supplied with nitrate need a corresponding amount of hydrogen donators for nitrate reduction. As carbohydrates take over this function, the consumption of these compounds in the $NO_3$ plants is higher than that with $NH_4$ nutrition. Therefore it is possible that the excretion of carbohydrates by $NO_3$ plants is lower than that of $NH_4$ plants. This might be the reason for the smaller number of bacteria on the roots and the higher oxygen content in the nutrient solution. On the other hand, the oxygen content of the root environment also exerts a certain influence on the number of bacteria. According to Grineva [6], root exudation is increased during short periods of anaerobiosis. This might be due to the increase in the content of organic compounds of low molecular weight in the roots. As a matter of fact van der Heide *et al.* [7] found a higher sugar content in barley roots when grown in nutrient solution through which nitrogen was passed than with the passage of air. This is in accordance with the results of own experiments on wheat [28], which showed a higher bacterial colonisation of the roots in unaerated pots. The close interrelationship between oxygen content of the nutrient solution and bacterial number is clearly seen in the $K_1$ plants. Due to their smaller amount of root matter the oxygen in the nutrient solution was not so rapidly exhausted. It is possible that in spite of the poor K nutritional state of these plants less exudates had been excreted than by the $K_2$ plants. Only thus their low bacterial colonisation can be explained.

The heavy decrease of oxygen after the interruption of K nutrition gives rise to anaerobic processes and a lowering of the redox potential. Numerous micro-organisms replace the lacking molecular oxygen by chemically bound oxygen as terminal electron acceptor. $NO_3$, $MnO_2$, $Fe(OH)_3$ and $SO_4$ are utilized in decreasing order of the standard redox potential of the corresponding redox systems [24]. That micro-organisms play an essential part in the lowering of the potential was shown by Karbach [11] who incubated a watersaturated soil with and without addition of toluene. Only in the soil, in which the micro-organisms had been inactivated by the addition of toluene, the redox potential was not lowered. In accordance with the heavier decrease of the oxygen content in the nutrient solutions with K interruption, the concentration of divalent iron was 2 to 4 times higher than with optimum K nutrition. As already mentioned, iron reduction is especially brought about by denitrifiers and anaerobic nitrogen fixers. Previous experiments on wheat showed that the number of individuals of both groups increased when potassium is in short supply.

It can be assumed that the relatively low $Fe^{2+}$ concentrations measured in this experiment are related with the structure of the supplied trivalent iron. Ottow [18] in his investigations on the reduction of various iron compounds by bacteria, stated that even with pure cultures the addition of $\alpha - Fe_2O_3$ (hematite), which was also used in the above experiments, did not raise the concentration in the nutrient solution beyond 1–20 ppm. Through addition of iron (III) phosphate andhydrated $Fe_2O_3$ ($Fe(OH)_3$), however, up to 84 ppm $Fe^{2+}$ could be found in the nutrient solution. The occurance of detrimental reduction processes in the rhizosphere has also been observed by other authors. Investigations by Dommergues *et al.* [4] [8] with saline soils indicate that the reduction of sulphate to $H_2S$, being extraordinarily toxic to plants, is caused by rhizosphere organisms.

The author's results appear to be in contradiction with the conclusions of McRae and Castro [13]. As mentioned above, the latter found in exudates of resistant varieties larger amounts of carbohydrates than in susceptible ones. It was therefore assumed that sufficient exudation of carbohydrates or amino acids by the roots 'support a population of aerobes in the rhizosphere, and such organisms could be important in oxidizing some of the toxic products of soil reduction'. However, it should be taken into account that higher metabolic activity of aerobes is accompanied by higher oxygen consumption, so that further oxidation will scarcely occur. The experimental data presented by the author on the other hand suggest less root exudation and less microbial activity in the rhizosphere of healthy plants. As the occurence of physiological rice disorders undoubtedly depends on several ecological factors not yet fully elucidated, it is to be expected that with increasing knowledge the obvious discrepancy can be explained. Anyhow, the present experiments reveal the impact of the nutritional status of the plant on the activity of the rhizosphere organisms regarding their possible part in physiological rice disorders. The results may be summarized as follows:

Insufficient potassium nutrition gives rise to larger excretion of organic compounds, thus allowing high bacterial activity accompanied by rapid oxygen consumption, later on reduction processes, such as iron reduction, take place, and with increasing concentrations of toxic reduction products finally nutritional disorders will be encouraged.

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