AD 673767

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DATE: 6 July 1965

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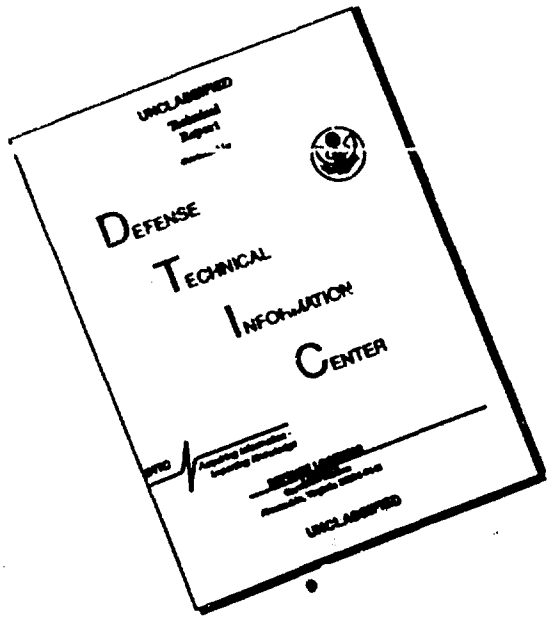

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PHYSIOLOGY AND NITROGEN NUTRITION OF ROOT SYSTEM IN RICE

- USSR -

[Following is a translation of an article by N. S. Petinov and N. N. Kharanyan in the Russian-language journal Agrokhimiya (Agrochemistry), No 5, 1964, pages 144-160.]

In recent years, many studies dealing with the physiology of rice have been carried out, revealing characteristics of the vital processes of this valuable agricultural plant.

Of considerable interest are problems dealing with the nitrogen nutrition of rice plants, which is one of the chief factors governing its harvest yield.

A review of studies in this area and experimental data of the present authors can expand and deepen investigations of this important problem aimed at control of physiological processes.

Considered in this article are the following areas: 1) physico-chemical conditions of inundated soil on which rice is grown; 2) morphological structure and chemical composition of the root system; 3) physiology of the nitrogen nutrition of rice; 4) specifics of nitrogen metabolism and the mechanism of detoxification of ammonia.

1. Physicochemical Conditions of Inundated Soil of Rice Fields

Physicochemical conditions of inundated soil greatly affect absorption by the plant of nitrogen and other mineral elements.

Studying in detail oxidation-reduction processes occurring in the soils, Neunylov [1] showed that at the surface of the root and in a thin layer of soil about it there is established a strongly oxidized medium compared to the strongly reduced medium of the rest of the soil bulk. The difference in electrical potentials between root surface and the soil in contact with it is 0.5-0.8 volts. This high potential is maintained by rice roots and affords opposition to the harmful effect of products of anaerobic decay and is utilized also by reduced compounds. The lower the oxidation-reduction potential of the soil, the more energetically do processes of ammonification take place. Strongly pronouned processes of reduction occur in the soil of rice fields: salts of nitrous acid are reduced to molecular nitrogen, sulfuric acid salts to hydrogen sulfide, cellulose and carbohydrates -- to hydrogen and methane.

In one of the recent studies on oxidation-reduction reactions of rice field soil [2] it was shown that the high-yield rice fields of Japan are mosaic in structure with regard to the OV-potential (Eh). Plots of soil with a high OV-potential have a positive effect on the absorptive activity of roots, while plots with low Eh result in a decreased absorption of nutrients.

Rice roots require the presence of oxygen in the rhizosphere, which protects them from the toxic effect of reduced compounds like hydrogen sulfide, methane, etc. Oxidation by roots of surrounding soil in which reducing processes predominate is an adaptive reaction characteristic of rice. Free iron and manganese, which can be present in the soils of rice field in abundance play the same role [3]. The presence of a thin layer of iron oxide covering rice roots has an effect on their oxidative processes.

Percolation of water through the soil vertically downward also promotes better supply of oxygen dissolved in water to the roots. Study of the effect of water permeation rate through rice field soils on the nature of the development of the root system [4] has shown that percolation intensifies the surface development of the root system, the intensity of its respiration and the activity of its oxidative reactions. On deluvial soils, relatively poorly drained, containing a large content of organic matter, percolation of water has a greater effect than on well-drained, fertile soils. This effect is expressed in increased dry weight of plants and grain yield. Also demonstrated is the accelerated formation of root hairs in the soaking of water. The OV-potential in soils with

percolation and without it is the same.

Mituo and Janatori [5] determined the chemical analysis of the root system of rice grown on well and on poorly drained soils. It was found that plants grown on well-drained soils have a higher phosphorus and protein nitrogen content. The iron content in roots is usually higher in plants grown on well-drained soils. Aeroating the water keeps the thin surface of soil in an oxidized state, characterized by an OV-potential of 350 millivolts. It contains the following oxidized product: nitrates, sulfates, and ferric ions. Immediately under this layer, the OV-potential is reduced. Here, there are still present products in the reduced state.

Agrotechnical investigations of rice field soils of the Kuban' [6, 7] have shown that a severe drop in the nitrate content and an increase in ammonia nitrogen occurs due to reduction processes on going in the soil of the inundated rate field. The amount of ammonia nitrogen increases sharply by the time seedlings appear, as a result of high activation of ammonifying bacteria and weak development of plants not wholly absorbing the reserve of accumulated ammonia nitrogen. By the tillering phase, the soil content of ammonia nitrogen is reduced, while in the tasselling phase, it is again increased. These investigations have shown that the accumulation of ammonia salts in rice field soil reaches its maximum during the tillering-tasseling period.

Nitrogen nutrition of rice plants is primarily determined by the dynamics of ammonia nitrogen in the soil, the nitrate forms of nitrogen being only of secondary importance. Under the layer of water, the organic matter decomposes with the formation of ammonia, which is readily absorbed by the soil. Nitrification of ammonia nitrogen occurs in the oxidized layer of soil under the action of autotrophic microorganisms. Nitrate and nitrite nitrogen forming in the oxidized zone is denitrified, passing through the reduced layer [8]. Investigations [9] have also shown that immediately after inundation of the field with water, the amount of ammonia nitrogen and Fe^{++} ions in it rises sharply, while the OV-potential is simultaneously appreciably reduced. Nitrates disappear in the reduced layer, ferric is reduced to ferra and sulfuric to hydrogen sulfide -- all this promotes increased soil pH.

The thickness of the layer of water influences nitrogen absorption. Experiments conducted (Ghosh [10]) in order to establish water layer values for intensity of growth and

absorption of nitrogen revealed that the content of dry substance and nitrogen in rice roots is reduced with increase in thickness of water layer.

2. Morphological Structure and Chemical Composition of Rice Root System

Under normal conditions, the root system of the rice plant is fairly compact, and its roots propagate horizontally. In two week old plants, two types of roots are readily distinguished: 1) long soft, light chestnut, highly branched, and 2) relatively short, thick, unbranched, with white, waxy surface. In six weeks after planting, the white roots begin to branch and become weak and soft. The number of these white roots in fifteen day old plants begins to increase and continues increasing until flowering. During the plant maturation period, the root system of the rice plant is represented by thin, branched, and soft roots [11].

The anatomical structure of the rice root system has been studied in detail by Yerygin and Yrabchun [12] and Ryabchun [13]. It has been established in this research that the integumental tissues of the roots in the absorption zone are well separated, the pericycle and the lignifying cells of the lignin parenchyma which surrounds vessels of the prot- and metaxylema are differentiated in the central cylinder of the root in this area. In the zone of aerenchyma emergence formed due to breakdown of unspecialized bark cells lignifying the sclerenchymatous sheath isolate the bark from the surrounding environment.

When the root attains a length of 1-2 cm, mechanical elements begin to form successfully -- connective cells and the sclerenchyma. With increasing separation from the apex, the strength of the mechanical elements of the root weaken. At a distance of 10-15 cm from the root apex, the layer of the epidermal cells proves to be almost wholly degraded, and the role of the integumental tissue is played by the exoderm. Still further from the root apex, exodermal cells can also be degraded, and the function of the integumental tissue begins to be carried out by the sclerenchyma.

When the root obtains a length of about 30 cm, the aerenchyma emerges at different sites of the internal root at a distance of 1-5 cm from the embryonic zone. With separation from the root tip the surviving cells of the inner bark become fewer and fewer and the central cylinder can

communicate in this case with the soil only through side rootlets.

Investigation of the layered distribution of the rice root system [14] has shown that 82% of the root lies within the upper 4 cm of soil. Rice plants, in contrast to other grasses, develop "respiratory" roots, which form a thin, highly branched network and spread horizontally into the uppermost layers of soil. These roots differ from normal, deep-lying roots by their physiological functions as well: they are adapted to absorb oxygen and to advance it throughout the root system. Such roots appear in the tillering phase and function until ripening of grain. Also interesting is the fact, discovered by Jamada and Iyema [15] in studying the qualitative composition of the internal atmosphere of rice plants, that diurnal variations in gas composition at the base of the root are found to be related to the intensity of solar radiation, soil temperature, and also, as the authors suggest, periodicity of cellular division. Jamada, Joshio, and others [16], using data on oxygen content in the medium surrounding the root system with limitation of light and removal of some of the use, and also the respiratory rates of these roots and taking into account the relationship between absorption of oxygen and its tension, had calculated the amount of oxygen borne from the above-surface portions of the plant. It was found that 1 cm^2 of root cross section received about 0.8 ml of oxygen per hour.

Direct determination of oxygen in rice roots made by Raalte [17] has shown that at the base of the roots aerenchyma air contains 9-14% oxygen, and the apex -- the youngest portion of the root -- several times less, which is accounted for by the more energetic use of oxygen in the process of respiration, associated in its turn with growth processes. The author regard the main oxygen source to be the above-surface portion of the plant. Oxygen present in the water in a gaseous state is absorbed on a lesser scale. Upper layers or rice root cells are permeable to it. According to the date of Raalte [18], roots of two month old rice plants daily liberate 1-3 mg of oxygen.

As follows from data of the studies of Mitsui [19], liberation of oxygen by rice roots is associated, on the one hand, with root metabolic activity, in particular with absorption of nitrogen, phosphorus, and potassium, and on the other -- with the liberation of energy. Using the fact of the very high content of acetic acid, at 50.7% (with 28.7% organic acids of the Krebs cycle), the author suggests the possibility of the existence of an ionic pathway of energy

liberation -- the pathway of "glycolic acid." When energy is liberated in this way, hydrogen peroxide is accumulated, which in the presence of peroxidase and catalase is readily decomposed into water and oxygen. Glycolic acid oxidase vigorously oxidizes glycolic acid to glyoxylic. Thus, the "glycolic acid pathway" is, in the author's view, the most probable source of liberation of oxygen by roots. Therefore, some of the hydrogen liberated in the rhizosphere, is produced in the roots themselves which is in opposition to the view of certain authors that the oxygen source in the roots is only the above-surface portion of the plant.

The activity of catalase in rice roots is considerably less than in leaf blades and the leaf sheath [20]. Activity of peroxidase in early developmental phases is especially high in the roots and low in leaves. At later developmental phases this ratio is reversed. These facts afford the conclusion that the pathway of hydrogen peroxide decomposition in shoots and roots is dissimilar in early developmental phases of plants.

Soldatenkov and Chao Hsien-Tuang [21] regard transport of oxygen in plant sap as possible based on correlations typical of movement of assimilates, in which case the participation of the OV-system and, in particular, ascorbic acid, polyphenols, and also the appropriate enzyme -- is assumed. Following reduction in roots, these compounds under anaerobic conditions can be advanced in the opposite direction in leaves, where they are oxidized by air oxygen and in the oxidized state return to roots, where they are again reduced. The protective action of leaves on the root system deprived of oxygen consists in supplying it with atmospheric oxygen through a conductive system.

Usually, a healthy rice root is elastic and is entirely, with the exception of the tip, covered by a reddish-brown film of ferric oxide. If hydrogen sulfide overcomes the oxidizing capacity of rice roots, sometimes with a deficiency of active iron in rice soil, the residue of ferric oxide in the microsoil cannot protect the roots from the evolving hydrogen sulfide, then the soluble sulfide or hydrogen sulfide begins to penetrate within the root cells.

The investigations of Mori [22] were undertaken to study the action of respiratory inhibitors on the growth of rice roots. Used as an inhibitor was a solution saturated with hydrogen sulfide, which was added to the cultivated plant. Young roots or tissues of high metabolic activity.

Oxygen intensifying oxidative processes engenders conditions for fuller utilization of organic acids, thus promoting utilization of ammonia and its further participation in the synthesis of amides and other nitrogenous organic compounds. Therefore, under ammonia nitrogen conditions the increase in oxygen concentration in the root zone must improve plant development [23].

Baba and Katsumi [24] note that in the phase of maximum tillering a great number of new roots appear, starch present in abundance in tissues of the rootcap being expended in their formation. Here also phosphorylase is present in large amounts. The expenditure of starch in growth processes also has been confirmed by the fact that the more intensive appearance of new roots with the rapid phosphorolysis of starch and inhibited in the case of slow phosphorolysis [25]. The young roots are marked by high respiratory intensity, exhibit high activity of cytochromoxidase and are characterized by rapid absorption of nitrogen, phosphorus, and potassium, the absorption maximun occurring in the tillering phase.

To study the mechanism of absorption of water and salts by the rice root system Okhaima [26] used plants in which old and young roots were divided into two groups. Upon removal of old roots, the young roots began to more energetically absorb water and the mineral salts, while when only the old roots were left, only water absorption was intensified. The meristem of rice roots is characterized by high content of compounds and enzymes playing a large role in metabolism of protein-bound potassium, organic phosphorus and iron, acidic and alkalin phosphatase, dehydrogenase, etc. The energy supply in this portion of the root is low, accounted for by its rapid utilization [27].

Using histochemical methods of investigation, Kawata and Ishihara [28] established that in the meristem of the rice root tip two types of cells are present: one type with high and one with low RNA content. Cells rich in RNA grow slowly and bear root hairs. Cells poor in RNA, in contrast, grow rapidly and do not form root hairs. The RNA maximum is bound in growing root hairs. In cells with root hairs RNA is retained longer than in other cells of the epidermis. Chemical analysis of an embryonic rice root 1 cm in length showed that nitrogen, phosphorus, and sugar decrease in content from the root tip to the base. The highest content values are located in a 5-millimeter segment of the root tip. The content of hemicellulose and cellulose, in contrast,

incre se from .oot tip .o base. The content of physiologically active compounds is reduced and the content of compounds constituting the cellular membrane is increased [29] -- with age.

Using roots of 9-12-day old rice plants, Joshida and Takahashi [30] studied respiration, inhibition and distribution of enzymatic activity in different portions of the root from the tip to the base. Respiratory intensity (QO_2) of a segment less than 10 mm from the tip (meristematic zone) proved to be higher than in a zone 20-50 mm from the tip (elongation zone). Here, respiratory intensities almost half as high as in the meristematic zone, while in the zone above 50 mm (differentiation zone) -- still less. This ratio changes when nitrogen is used. QO_2 (N) in the meristematic zone is relatively low and a maximum QO_2(N) is noted in the elongation zone. In the differentiation zone, QO_2(N) is as low as QO_2. From this fact follows the conclusion that the meristematic zone shows highest respiratory activity. The respiratory coefficient decreases from the meristematic zone to the zones of elongation and differentiation. Respiration in the meristematic zone is inhibited by azide, while in the elongation zone, by 8-oxyquinoline. This opposing response of different zones to inhibitors leads to the conclusion that respiration in the meristematic zone proceeds through cytochromoxidase, and in the elongation zone through ascorbinoxidase. Determination of peroxidase and succindehydrogenase showed that the activity of the first is lower in the root tip and increases considerably in a direction toward the base, while the activity of the latter, in contrast, is localized at the root tip, and its contents decreases in a baseward direction. Thus, the activity of peroxidase can be an indicator of "senility," while that of succindehydrogenase -- of the "youth" of rice root tissues.

Also interesting is the characteristic that the activity of catalase in rice roots in early developmental phases of the plant is lower than in the leaf blades and leaf sheaths, while peroxidase activity in roots is higher [20]. In latent developmental phases, this ratio is reversed. These facts afford the conclusion that the decomposition pathway of hydrogen peroxide formed in metabolism in shoots and roots differs in early stages of rice plant development.

In our study [31] it is shown that the oxidation-reduction potential of rice roots averages six times higher than that of leaves, which points to the predominance of oxidative reactions in the former and of reducing reactions in

the latter. Of interest is the fact that a reciprocal relationship exists between the values of the leaf and root OV-potential (Table 1).

TABLE 1

Interrelationship Between OV-Potential of Rice Roots and Leaves (in millivolts)

a) Объект исследования	b) Начало кущения 27.VI	c) Кущение 4.VII	d) Трубкование		g) Перед выбрасыванием метелки 31.VII
			e) 10.VII	f) 24.VII	
h) Корни	220	140	85	170	205
i) Листья	85	55	110	115	80

[Legend]: a) material of investigation; b) onset of tillering, 27 June; c) tillering, 4 July; d) shooting; e) 10 July; f) 24 July; g) before tasseling, 31 July; h) roots; i) leaves.

TABLE 2

Interrelationship Between Respiratory Intensity of Rice Roots and Leaves (in microliters of O_2 per gram of dry weight per hour)

a) Варианты опыта	b) Объект исследования	c) Кущение		f) Трубкование 25.VII	g) Выбрасывание метелки 1.VIII	h) Формирование зерна 8.VIII
		d) 27.VI	e) 5.VII			
i) Без удобрений	m) Корни	45,8	31,1	—	—	—
	n) Листья	100,8	116,0			
j) Азот	Корни	70,2	50,1	46,0	6,6	3,7
	Листья	120,0	148,4	42,4	58,4	110,4
k) Фосфор	Корни	45,8	36,1	24,7	19,7	23,4
	Листья	122,2	140,8	97,1	132,0	112,7
l) Азот + фосфор	Корни	36,7	—	30,7	12,8	11,2
	Листья	127,3		45,1	96,5	109,5

[Legend]: a) experimental variant; b) material of investigations; c) tillering; d) 27 June; e) 5 July; f) shooting, 25 July; g) tasseling, 1 August; h) grain formation 8 August; i) without fertilizers; j) nitrogen; k) phosphorus; l) nitrogen plus phosphorus; m) roots; n) leaves.

Roots regulate the oxidation-reduction state of leaves, maintaining it at a specific optimum level [32], by exchange

of life activity products of these organs. It can be assumed that due to intensified oxidative reactions in roots, the reactions in leaves are weakened, and vice-versa.

Comparative study of the respiratory intensity of roots and leaves of the rice plant by the present authors revealed that with increased leaf respiratory intensity, the intensity of root respiration is reduced (Table 2). All these facts point to the existence in rice plants of an intimate interrelationship between respiration and oxidation-reduction reactions occurring in leaves and roots.

Takashashi and Joshida [33] have noted that the concentrations in organic nutrients in roots is usually lower than in the above-surface portion in all developmental phases however an exception is represented by iron, whose concentration in the roots is considerably higher than in the above-ground portion. The concentration of nitrogen, phosphorus, and magnesium varies in the roots parallel to changes in the above-surface portion.

3. Physiology of Nitrogen Nutrition of the Rice Plant

A fairly large number of studies have dealt with problems of the physiology of rice nitrogen nutrition. Their main emphasis has been the study of the effect of different nitrogen doses on the content of organic and inorganic components of the rice plans by developmental phases and by individual organs in order to determine the best time for applying nitrogen top dressing and dosages to be used, as well as specific details of the nitrogen metabolism.

It has been found that in the rice plant as well as in other plants, processes associated with the absorption of ions of mineral salts and other vital processes depend on oxygen absorption [34]. However, these are data which indicate that when rice roots are placed under anaerobic or almost anaerobic conditions, plants can absorb nutritive salts and continue to grow satisfactorily. Zsoldas [35] has established that in the rice plant, in contrast to barley, absorption of nitrate and phosphate ions under anaerobic conditions is not inhibited and aeration does not yield a positive effect, however, with removal of the above-portion of the plant aeration begins to play a positive role in absorption of the nutrient elements, for when the above-surface portion is removed uptake of oxygen is halted. Anaerobiosis

can also indirectly injure rice plants due to accumulation of toxic substances in direct proximity to the roots.

In the total absence of oxygen, rice shoots liberate 150% more carbon dioxide than in air, while under these same conditions wheat shoots liberate only 57% more [14]. It is suggested that in this case, energy promoting growth processes is formed anaerobically and can be used more effectively than energy involved in respiration.

The adaptivity of the rice plant to anaerobiosis evidently is not associated with special properties of its reductional enzymatic systems [36]. The biological adaptiveness of rice shoots to reduced oxygen concentration as accounted for, in the view of the authors, by the increased activity of metal-containing systems of the cytochrome-cytochromoxidase type, which can under these conditions bind the amount of air oxygen required for normal life activity.

Takamashi and Janagisawa [3] believed that there are two groups of ions: one group (ammonium, nitrates, phosphates, and potassium) are absorbed metabolically and enter into intimate relationships with the biological organization of the root, thus opposing the possibility of diffusion from the root into the surrounding medium which is poor in these ions; and those in the second group (silicon, calcium, and magnesium) are absorbed mechanically, and for their absorption, the concentration of the external medium must be higher than a specific level with respect to ions of this group.

The views expressed by these authors are inaccurate and contradict the widely accepted viewpoint. In many investigations conducted in recent years, it has been shown that absorption of mineral substances by a plant is an active physiological process, which is directly associated with the life activity of the root system and the above-surface organs of the plants, and only the initial stage of absorption of cations and anions of mineral salts occurs through physicochemical adsorption. This was especially pointedly shown in the monograph of Kolosov [37].

In a work of Jamada and Ota [38] an analysis is made of the interrelationship between respiration of rice roots and their absorption of nitrogen. It has been established that the intensity of root respiration (calculated per unit dry substance) varies with age and with the physiological condition of the plant. The highest intensity of root respiration has been noted in the tillering phase, then it is

gradually reduced as the tasselling period is approached. The intensity of nitrogen absorption day by day is fully in agreement with the value of root respiration and reaches the maximum also during this period, after which it begins dropping. In other words, the increasing intensity of root respiration involves increased intensity of nitrogen absorption, while with a decrease in respiratory intensity the opposite situation prevails. However, with increased respiratory intensity, no corresponding equal increase in nitrogen absorption occurs. The reason for this is that in the latter developmental phases, the amount of nitrogen in the soil is reduced and, moreover, the capacity for nitrogen absorption is considerably diminished in the growing plant.

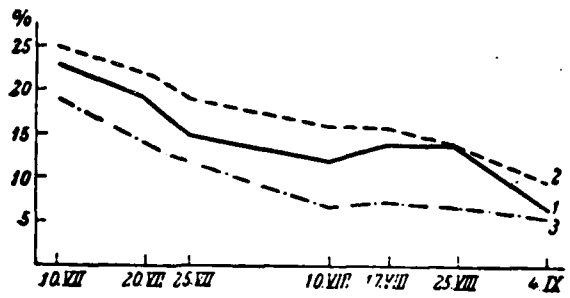

Fig. 1. Effective absorbent surface of root systems of the rice plant (in per cent of total adsorbing surface)

1 -- $N_{60}P_{60}$ kg/hectare; 2 -- $N_{120}P_{120}$ kg/hectare; 3 -- $N_{240}P_{240}$ kg/hectare, 10 July -- tillering, 20 July and 25 July -- shooting, 10 August -- flowering, 17 August -- formation of grain, 25 August -- milky ripeness, 4 September -- waxy ripeness.

The oxidative properties of rice roots predominating during the first plant developmental period promote intensive absorption of ammonia salts. With the flowering phase, reduction reactions promoting absorption of nitrate nitrogen [39] begin to predominate in rice roots. The altering nature of OV-properties of rice roots has also been noted in the study [40].

A very important fact is the existence of a direct relationship between root pH and root capacity for exchange of

mineral salt ions. With increase in pH, this capacity usually is reduced [41].

Our experiments [42, 43] conducted during 1957-1960 under field conditions at the Azovskiy Test Field of the Donskiy Zonal Institute of Agriculture and at the Kuban' Experimental Rice Station with the Rice Varieties Dubovskiy 129 and Krasnoarmeyskiy 313, grown under inundation conditions, and in growing experiments conducted in Moscow in 1961, established that the highest effective absorbing surface of the rice root system occurs in the phases of tillering and shooting (Figure 1). In this same period, respiratory processes proceed most intensively in roots, that is, the necessary conditions for intensive absorption of mineral nutrition elements are produced (Figure 2).

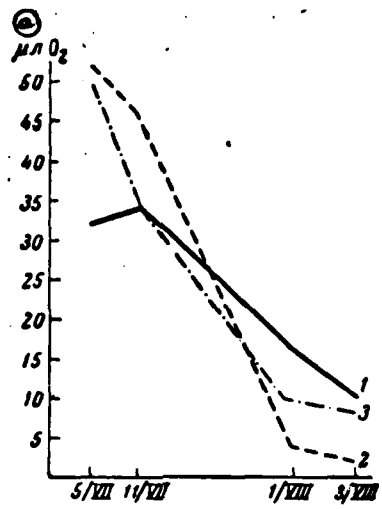

Fig. 2. Intensity of rice root respiration (in microliters of O_2 per gram of moist weight per hour)

1 -- without fertilizer; 2 -- N_{240} kg/hectare; 3 -- $N_{160}P_{120}$ kg/hectare, 5 July -- tillering, 11 July -- shooting, 1 August -- tasseling, 8 August -- grain formation.

[Legend]: a) microliters.

It was also shown that excess nitrogen-phosphorus nutrition ($N_{240}P_{240}$ kg/hectare in the form of ammonium sulfate and superphosphate) considerably reduce the value of the effective absorbing surface of the root system. The total adsorbing and effective absorbing surface of the rice root system was best developed with a moderate dose of nitrogen-phosphorus fertilizers ($N_{20}P_{20}$ kg/hectare).

It is important to notice that high ammonium sulfate doses produced a rise in root respiratory intensity during early developmental phases of rice plants (tillering, shooting), while in later phases root respiration of these plants proved to be inhibited.

The data we obtained (Figure 3) also points out that with excess nitrogen-phosphorus nutrition, the OV-potential of roots shifted toward the side of reduction reactions, and the pH value of roots in this case rose sharply, which reduced the absorbing capacity of the roots.

Takahashi et al [44] has given a clear picture of the content of organic and inorganic components of rice plants supplied with different amounts of nitrogen by developmental phases. It is shown that in the tillering phase, the products of photosynthesis in combination with inorganic substances absorbed by the roots are converted into proteins, which are then utilized by the plant to form shoots and roots. During this period, owing to the abundance of nitrogen, the leaf area is substantially increased, which in its turn intensifies formation of carbohydrates to the degree that later the roots are incapable of absorbing the corresponding amount of nitrogen and its relative quantity is reduced, which inhibits tillering, and plants enter the shooting phase. During this phase, absorption of nitrogen is considerably reduced, however, the ratio of different organic nitrogen fractions remains balanced. In the tasselling phase, the nitrogen content in the plant is severely reduced. Also altered is a relative amount of nitrogenous compounds; the amount of ammonia and amide nitrogen rises and the protein nitrogen content is reduced.

The intensity of nitrogen absorption by the rice plant reaches a maximum in two periods: in total tillering and in the tasselling period, [45]. Using nitrogen labeled ammonium sulfate, Singh, Kumazawa, and Mitsui [46] investigated the rate of formation of nonprotein and protein nitrogen and relationship between them in the tasselling phase. With the aid of N^{15} it was possible to show that the incoming nitrogen

is readily incorporated into nonprotein compounds in all parts of the plant. NH_4^+ absorbed by the roots is rapidly transported to the young leaves in the form of ammonia or amino acids, while only a small portion of it enters old leaves. In the latter, decay processes predominate over synthetic processes, therefore conversion of nonprotein nitrogen into synthetic processes, therefore conversion of nonprotein nitrogen into protein here is very weak. Using N^{15}, these authors also established that the rate of incorporation of incoming nitrogen into root metabolism is higher than in the remaining portions of the rice plant. Seasonal variations in nitrogen content in rice roots depend chiefly on the content of soluble nitrogen fractions. The content of total nitrogen remains constant, during all developmental phases [47]. Variations in content of solute nitrogen, in its turn, depends on the content of amine nitrogen. The results of the experiments of these authors afford grounds for suggesting that the initial synthesis of different amino acids occurs in the roots. During the period when the plants are supplied with nitrogen through the nutrient medium, in rice roots the ammoniacal nitrogen content is higher than in the shoots. Accumulation of ammoniacal nitrogen in roots is probably due to active penetration and not to passive diffusion, and serves as a source of amino acid synthesis.

Tanaka, Patnaik, and Abichandani [47] studied the effect of four nitrogen levels: 1) deficiency -- (10 mg/liter); 2) normal (20-40 mg/liter); 3) abundant (60 mg/liter); 4) excess (60 mg/liter) [sic] -- on accumulation of dry substance and grain yield. It was found that the deficiency of nitrogen utilization for grain formation is high up to a concentration of 40 mg/liter. Higher nitrogen doses result in inhibited protein synthesis, where a large amount of solut and nonprotein nitrogen is formed, which unfavorably affects grain formation.

A dynamic equilibrium exists between synthesis of protein from absorbed nitrogen and its decomposition. If synthetic process are more energetic, adsorbed nitrogen is rapidly converted into protein compounds, which promotes a higher grain yield.

Thus, Sibuya [49] has shown that the absorption of ammonia salts leads to intensified synthesis of nitrogen compounds, somewhat retarding photosynthesis and root formation due to the intensified ATP [adenosinetriphosphate] requirement in the synthesis of these compounds.

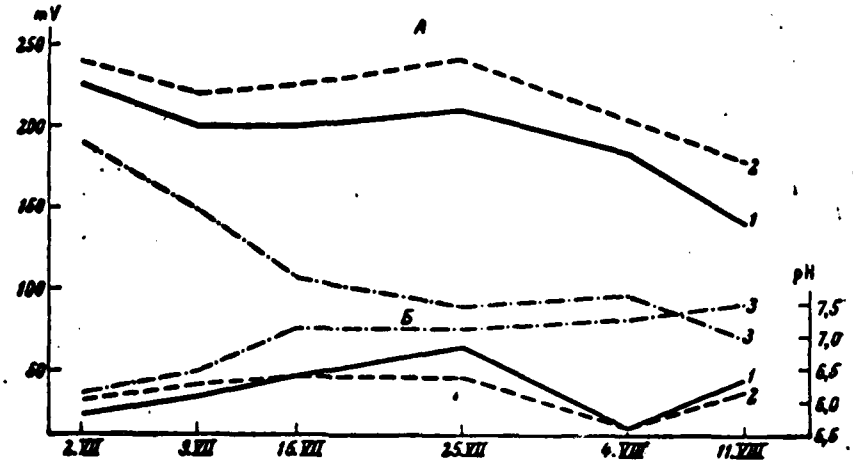

Fig. 3. Oxidation-reduction potential (A) and pH (B) of rice roots

1 -- $N_{60}P_{60}$ kg/hectare; 2 -- $N_{120}P_{120}$ kg/hectare; 3 -- $N_{240}P_{240}$ kg/hectare. 2 July, 9 July, and 15 July -- tillering, 25 July and 4 August -- shooting, 11 August -- flowering.

As the result of experiments conducted by Ishizuka and Tanaka [50] in order to find the optimum nitrogen dosage for wet-grown rice, three categories of conditions have been established: 1) inadequate nitrogen nutrition -- up to 5 mg of nitrogen per liter; 2) normal -- 5-60 mg per liter; 3) excess -- above 60 mg. The best conditions for maximum rice yield are produced in the transition from normal to excess nutrition. The factor of increased nitrogen content in the grain approximates the optimal conditions of nitrogen nutrition.

In a large study on absorption of nutrient elements by rice plants Mitsui and Kamazawa [51] have show that when there is a nitrogen or phosphorus deficiency, the intensity of root respiration is reduced, while it rises for potassium deficiency. The latter is accounted for by the increased requirement of degrading products of metabolism. The authors proposed the existence of two pathways for organic acid metabolism. One of these -- the tricarboxylic acid cycle and the other is the pathway of glycolic acid oxidation. Acetic acid

accumulating in large amounts can serve as the starting reagent for both pathways. At each phase of oxidation in the glycolic acid pathway one mole of hydrogen peroxide is liberated, which can be used in the oxidation of the rhizosphere in the same form or degraded under the action of catalase into oxygen and water.

There are indications [52] that when there is a nitrogen, phosphorus, and potassium deficiency, the total organic acid content is reduced from 80 to 24 milliequivalents/100 grams. Acetic, glycolic, fumaric, succinic, oxalic, malic, aconitic, citric, isocitric, tartaric and lactic acids have been detected in organic acid fractions, while the proportion of acetic acid accounts for 40-80% of the total organic acid contents.

Temperature of soil and nutrient solution also affects absorption of nutrients and nitrogen metabolism of rice plants. Baba, Takahashi, and Iwata [53] have noted that when the temperature of cultural solutions shifts above or below the optimal (30°) absorption of nutrients in water is worsened, the content of ammoniacal, amide and solute nitrogen is increased, and the content of protein nitrogen decreased.

Hirose and Goto [54], investigating two-week old rice shoots as to their capacity to absorb urea and ammonium ions, established that absorption of ammonia increases wit' increased nitrogen content in the nutrient solution to 0.002% and further increase in NH_4^+ content in the medium does not bring about increased absorption as far as 0.008% conten.. At higher concentrations, the value of NA_4^+ absorption is reduced. Intensity of urea absorption increases with its increased content in the nutrient medium to as high as an 0.025% concentration. The authors proposed that the mechanism of urea absorption is a simple diffusional process in contrast to the process NH_4^+ absorption, which occurs through formation of complexes of ammonia carriers.

4. Specifics of Nitrogen Metabolism in the Rice Plant and Mechanism of Ammonia Detoxification

Rice plants grown under inundation conditions are marked up specific details of nitrogen metabolism. For example, alanine can be accumulated in amounts of 50-60% of total free amino acid content. It is believed that the transport of nitrogen in the rice plant occurs chiefly in the form of alanine, pyruvic acid being its source of synthesis. It is of interest that the specific accumulation of

alanine is observed when rice is cultivated without inundation [55]. Kretovich and Kasparek [56] have shown that alanine is one of the most important compounds, in the form of which ammonia salts entering the plant are assimilated and converted into organic form. As also true of the previous author, the authors just cited have arrived at the conclusion of the exceptionally high capacity of rice plants for alenine synthesis from pyruvic acid. Noteworthy is the energetic participation of γ-aminobutyric acid in the process of reamination. The synthesis of alenine from sodium pyruvate is accompanied in the rice plant by appreciable consumption of γ-aminobutyric acid and asparagine.

Mitsui and Hirata [57] have found that Krebs cycle acids increase absorption of NH_4^+ and phosphorus. Acetate and glycolate at a concentration of $3 \cdot 10^{-3}$ mole considerably stimulate adsorption of potassium and only slight change or in fact inhibit absorption of NH_4^+ - N and phosphorus. Under these conditions, acetate and glycolate as proposed, are metaboliz d by another pathway than the Krebs cycle. Asparagine, as well as alanine, can be the transport form of nitrogen [46]. In addition, based on its content in the plant, the necessity of nitrogen top feeding can be quite precisely determined, since its amount is in close agreement with nitrogen nutrition of the rice plant [58] and depends on the NH_4^+ content and oxygen pressure in the surrounding medium [55].

Using as nitrogen sources amino acids and the amides: aspartate, glutamate, glycine, valine, leucine, asparagine, and glutamine, and, investigating their assimilation and transport, Saio et al [59] succeeded in showing that all these compounds are better utilized than NH_4-N at a concentration of 0.0004%. Alanine and glutamine appear first in the sap of the plach. Shimoda [60] holds that valine, leucine, and phenyl-alanine are almost wholly unabsorbed by rice plants, while methionine acts toxically. Whatever nitrogen source is used, the bleeding sap [pasoka] is always rich in alanine, glycine, asparagine, and glutamine. L- and d- alanine, d-lysine and glycine are absorbed more intensively. Asparagine and glutamine are contained in large amounts in the bleeding sap, as well aspargic and glutamic acids.

Mitsui, Kumazawa [61], Mitsui, Nodzawa [62], and Ozaki, Tai [63] have shown that with intensified nitrogen nutrition the content of the free amino acids especially alanine, valine, arginine, and asparagine, are increased to a greater extent than other amino acids, and that of glutamic and aspargic

acids considerably less than, for example, valine, alanine, etc. Sometimes the former are not found at all. The authors account for this by the fact that these amino acids are energetically utilized in reamination reactions. The formation of arginine has been noted in the inhibition of protein compound synthesis, in this case being suggested that argenine is one of the forms of nitrogen accumulation. It is emphasized that what importance from the viewpoint of root physiology is played by the decrease or increase in free amino acid content is as still very unclear.

Study of the assimilation of ammoniacal nitrogen of rice plants over brief intervals of time following the use of N^{50} (1 and 6 hours) has shown that in one hour (N^{15} is detected only in the nonprotein fraction of roots and leaves, in 6 hours -- in the protein. The concentration of N^{15} of ammoniacal nitrogen in protein hydrolysates was higher than in protein, which pointed to the possibility of its ready incorporation in protein molecules [64].

Based on experiments conducted in sterile cultures, Chakaraborty and Sen Gupta [65] have concluded that rice plants under conditions of nitrogen starvation are capable of absorbing molecular nitrogen from the atmosphere.

A relatively small number of studies have dealt with the effect of high nitrogen doses on metabolism and morphology of the root system.

The study of the effect of nitrogen nutrition level on absorption of nutrients by rice plants has shown that excess absorption of nitrogen at early stages inhibits its further uptake, which is due to the reduced absorptive capacity of roots and leads to poor nutrition of plants in later developmental phases. Excess nitrogen doses adversely affect root system development. Roots become short, thin, fibrous, their root hairs are totally lacking [40, 48].

The results of experiments on the different concentrations of ammoniacal nitrogen in rice plants [66] have shown that in comparison with controlled plants, the ratio of roots/shoots at increased concentrations varies considerably in favor of the shoots. With increased ammonium ion concentration, in the nutrient medium, the content of free ammonium ions both in roots and in shoots rises. It is important to note that the NH_4^+ content is considerably higher in roots than in shoots. Except for toxic doses, increases nitrogen doses beneficially affects shoot growth, while root growth

is attenuated. The author accounts for the different action of high nitrogen doses on root and shoots by the high NH_4^+ content in roots. In addition, only a small portion of the NH_4^+ absorbed by roots reaches the shoots. The author believes that the borderline between the toxic action of increased doses of ammonium sulfate depends on the physiological condition of the plant -- intensity of photosynthesis, respiration, and absorption of nutrients.

Varga and Zsoldos [67] have suggested that ammonia affects functions of enzymes associated with compounds controlling growth. Measurement of the activity of oxidase of indolylacetic acid and the action of ammonia on it has shown that the latter inhibits its activity. With increase in ammonium concentration abnormal accumulation of auxins in root tissues occurs, which results in inhibited root growth.

Also of much interest and importance is the fact that change in OV-reactions occurring in rice roots subjected to nitrogen deficiency [68]. The reducing capacity (with respect to H_2S formation) reaches a peak in the earing period and is observed only for a nitrogen deficiency. Roots experiencing nitrogen deficiency are almost marked by high capacity to reduction of nitrates and a weak capacity to oxidation of esculin. It is shown that with a decrease in nitrogen content at the stem base, less than 1% root growth is held up. In this case, the nitrogen content in the roots themselves is 1.5%. If the nitrogen content at the stembase is greater than 1.5%, it is utilized chiefly in the formation of new roots.

Also unique are the pathways of ammonia detoxification in the rice plant. Several studies have dealt with the toxic effect of ammonia given excess nitrogen nutrition of rice plants, including those of Malavolta [69] and Zsoldos [70, 71]. The former found substantial accumulation of ammonia in 4-week old rice plants supplied with ammonia nitrogen. Abnormal accumulation of ammonia was not accompanied by increased asparagine and glutamine content, which suggested to the author that the usual mechanism of ammonia detoxification by formation of amide is inoperative at this developmental stage. Confirmation of this was the fact that the same plants a week later had a still higher ammonia content, but with a considerably higher amide fraction. This result led the author to propose the hypothesis that one of the modes of ammonia detoxification in rice plants is the reoxidation of reduced forms of nitrogen.

In order to elucidate the utilization and detoxification of ammonia by plant tissues Zsoldos [70] studied the effect of different doses of ammonia fertilizers on nitrogen metabolism of rice plants. The author estimated the uptake, binding, and transformation of ammonia from the content of different amino acids in individual plant organs. He found that peptides are accumulated in the largest amount, followed by asparagine and glutamine. This suggested the hypothesis that the primary ammonia acceptor are the peptides, while asparagine and glutamine appear in the reamination process. Along with an increase in ammonia concentration in the external solution, the alanine and asparagine content in the stem is increased. In a following study Zsaldos [71] showed that increasing nitrogen doses first of all inhibit root growth. For example, when excess nitrogen doses are applied, the dry weight of roots is reduced by one-third. At very high nitrogen doses, further accumulation of alanine is halted, and in this case the deterimental effect of ammonia on root systems is clearly evidenced. An inverse proportional relationship has been observed between content in roots of free alanine and ammonia.

Studying the effect of nitrogen doses on the mechanism of ammonia detoxification in rice, Yerygin and Aleshin [72] have noted that detoxification in rice stem proceeds through the amides and arginine. Alanine, aspargic, and glutamic acid represent only auxiliary assistance in this mechanism. The mechanism of ammonia detoxification in rice roots is, however, associated with alanine formation.

Conclusions

1. Oxidation by rice roots of surrounding soil and which reducing processes predominate is an adaptive reaction characteristic of rice plants. Evolution of oxygen by rice roots is associated with the absorption of nitrogen, phosphorus, and potassium.

2. Rice plants in contrast to other grasses develop "respiratory" roots, which spread horizontally in the uppermost layers of soil. These roots are adapted for absorption of oxygen and its transport through the root system.

3. Nitrogen nutrition of rice plants is chiefly determined by the dynamics of ammoniacal nitrogen in soil, since building up a layer of water leads to leaching of the nitrate nitrogen.

4. The highest value of effective absorbing surface of rice root system is shown in the tillering and shooting phases. During this period, processes of respiration proceed most intensively in roots, that is, conditions are established for intensified absorption of mineral nutrition elements. With excess nitrogen-phosphorus nutrition, the development of the effective absorbing surface of the root system is inhibited. In this situation, the oxidation-reduction potential of roots is shifted toward the side of reduction reactions, while their pH values rise sharply, also reducing the absorbing capacity.

5. The oxidation-reduction potential or rice roots averages six times higher than that of leaves, which evidences the predominance of oxidative reactions in the former and of reduction in the latter. A reciprocal relationship exists between values of oxidation-reduction potential of leaves and roots. Here, roots regulate the oxidation-reduction state of leaves, maintaining it at some specific optimal level.

6. There is a reciprocal relationship between pH values of roots and their capacity for exchange of mineral salt ions. With increase in pH values, this capacity is usually reduced.

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Received 16 May 1964

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