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Review

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NITROGEN ASSIMILATION IN MAIZE

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A review of the nitrogen assimilation in maize is given, with special emphasis on the differential uptake and metabolic strategies employed for the incorporation of the nitrate and ammonium. The data presented show that for optimum growth and development maize requires both forms of nitrogen to be present in the soil. Under stress conditions (low temperatures, drought or low pH and aluminium toxic soils) such different uptake and metabolic pathways express themselves in a differential response, making it possible to alleviate some of the unfavourable effects of stress conditions by feeding maize plants in the field with an appropriate nitrogen fertiliser mixture. In the future, breeding of plants with specific nitrogen assimilation pathways, as a way to battle non-optimal environmental conditions, could be envisaged.

Key words: nitrogen assimilation, photosynthesis, nitrate, ammonium, ion uptake by roots, *Zea mays* L.

Ključne reči: asimilacija azota, fotosinteza, nitrat, amonijum, usvajanje jona od korena, *Zea mays* L.

INTRODUCTION

Among the mineral nutrients nitrogen is unique in that the plant can take it up as the positively charged ammonium ion (NH_4^+) and /or the negatively charged nitrate ion (NO_3^-). Both nitrogen forms are available in the soil to a smaller or greater extent. Whilst ammonium can be produced in the soil as an intermediate of the urea metabolism and the degradation and oxidation of other organic matter, nitrate is the dominant form of soil nitrogen available to plants under default (normal) conditions. This is due to the fact that under natural conditions ammonium is quickly converted to nitrate as the result of the ubiquitous distribution of soil micro-organisms, capable of metabolic utilisation of the free energy contained in the process of ammonia oxidation. However, in agronomy practice, mankind has devised ways of supplying ammonium to the agriculturally important plants, altering the NO_3^-/NH_4^+ ratio and keeping it far from the natural equilibrium.

Nitrogen assimilation involves the uptake of nitrogen from the soil by the root system, the metabolic conversion of the absorbed nitrate form in the root and/or the shoot, transport to the shoot, and its incorporation into different organic forms in the cell metabolism. Most plants can use either nitrate or ammonium as a source of nitrogen. However, the degree of effectiveness of these forms on plant growth and nutrient uptake when both sources of nitrogen are available is dependent on plant species and $NH_4^+ : NO_3^-$ ratio (Errebhi & Wilcox, 1990). Maize plants require both nitrogen forms for maximal growth (Schrader et al., 1972). If the source of nitrogen is nitrate, it may be reduced in the root or transported to the shoot where it can be processed.

Maize is the plant with which contemporary breeding in the last 70 years has achieved the greatest results, the average yield of grain increasing more than 500% from the yield achieved for centuries before. Of course, such yields are possible only when high energy input agronomy practice is applied, and adequate water, light and high temperatures are available. The photosynthetic process, as far as it is known, is the same amongst the ancient varieties selected by nature in different environments and the new hybrid varieties of maize being planted throughout the conr belt region of the world. It is common knowledge that the ancient varieties are not capable of utilising extra fertiliser (especially nitrogen) when provided to such plants, as opposed to the selected and improved hybrids, capable of utilising up to 200 kg of fertiliser per hectare per year, resulting in such a spectacular increase in growth, yield and utilisation of the efficient C_4 type of photosynthetic process. However, no consistent physiological, biochemical or molecular biology explantation has been offered to explain what is known as „*good recombination characteristics*" and „*heterosis*" amongst the breders. The logical explantation would be that the new varieties of maize have an altered nitrogen assimilation pathway, capable of taking up and transforming the nitrogen provided by human endeavour, when sufficient energy is available, but this has yet to be proved.

AMMONIUM AND NITRATE UPTAKE BY THE ROOT

Ammonium uptake systems, defined as energy-dependent and carrier-mediated in algae, fungi and bacteria (Kleiner, 1981), in higher plants are relatively less studied. In rice roots ammonium influx is biphasic and mediated by two discrete transport systems (Wang et al., 1993). At low ammonium concentrations (below 1mM) influx is mediated by saturable high affinity transport system with high Q_{10} and significant sensitivity to metabolic inhibitors. At higher concentrations ammonium influx shows a linear response due to low-affinity transport system, being much less responsive to metabolic inhibitors and temperature. Mechanism of high-affinity transport which appears to be an active process in roots of rice (W a n g et al., 1994) is unknown. The effects of CCCR, ATPase inhibitor (DES) and respiratory inhibitors (KCN + SHAM) confirm the dependence of these processes on metabolic energy and indicate the involvement of H* transport (direct or indirect). It was suggested (W a n g et al., 1994) that passive entry of ammonium might occur in the low-affinity transport system (specific channel for NH_4^+ or a shared cation channel).

The uptake of NO_3^- appears to be mediated by at least two distinct systems in higher plants. The first is an inducible high-affinity active transport system, which has a low K_m for NO_3^-, shows Michaelis-Menten saturation kinetics, is sensitive to metabolic inhibitors and regulated according to the plant nitrogen status. Nitrate induced pH dependent transient depolarisation of membrane potential, followed by a repolarisation, and observed on different plant objects (U l r i c h, 1987), was explained by the operation of a NO_3^-/H^+ symport mechanism with excess protons, and subsequent stimulation of proton pump. In maize roots a similar electrical response, which displayed nitrate-inducibility, pH dependence, as well as sensitivity to plasma membrane ATPase inhibitors, was closely correlated to nitrate uptake characteristics (M c C l u r e et al., 1990a, b). The second transport system is a constitutive, low-affinity transport system, operating at higher NO_3^- concentrations, with linear kinetics and lower sensitivity to metabolic inhibitors. Although it has some characteristics that would be expected of a passive, channel mediated transport system, recent results suggest that this system might also be active (K i n g et al., 1992).

The plant plasma membranes contain redox systems involved in trans-plasma membrane electron transport from internal electron donors, such as NAD(P)H, to specific electron acceptors, often accompanied by proton extrusion from the cell. A possible involvement of constitutive plasma membrane-bound nitrate reductase in redox activities in membrane was indicated by immunological correlation between nitrate reduction activity and reduction of extracellular electron acceptors (J o n e s & M o r e l, 1988). They proposed a model in which plasma membrane-bound nitrate reductase reduces extracellular electron acceptor and intracellular nitrate and also acts as a trans-plasma membrane proton pump.

Since it was proposed that such a nitrate reductase could be also responsible for nitrate transport across plasma membranes (B u t z & J a c k s o n, 1977), the hypothesis was supported or disputed by different authors. Experiments with barley genotypes lacking the nitrate reductase gene demonstrated the independence of nitrate uptake and nitrate reductase activity (W a r n e r & H u f f a k e r, 1989). On the other hand, the existence of nitrate reductase activity localised in the plasma membrane, in addition to soluble cytoplasmic nitrate reductase, in different plant objects including barley and maize root (W a r d et al., 1989), and inhibition of nitrate uptake and plasma membrane-bound nitrate reductase of barley roots by same antibodies (W a r d et al., 1988), indicates a possible relationship between NO_3^- transport and NO_3^- reduction in the plasma membrane. This plasma membrane-bound nitrate reductase activity in maize roots exhibited two different activities (NADH and NADPH-dependent), both being constitutive and insensitive to ammonium, contrary to the soluble cytoplasmic nitrate reductase with low constitutive activity (D e M a r c o et al., 1994).

METABOLIC CONVERSION OF NITROGEN FORMS AND ROOT-SHOOT INTERACTIONS

Nitrogen taken up from the soil can be stored in the root, incorporated into organic molecules in the root, or transported to the shoot and there stored or incorporated into organic matter. The process of nitrogen incorporation into organic matter is among the most energy-intensive processes in plant. All of the organic forms of nitrogen must be derived from NH_4^+. Conversion of one molecule of NH_4^+ to glutamate requires two electrons and one ATP. In the case of nitrate serving as the nitrogen source, it must be first converted to NH_4^+. This reduction of nitrate to ammonium is a two reaction step, NO_3^- reduction to NO_2^- requiring two electrons and catalysis by nitrate reductase (NR EC 1.6.6.1 and 2), and NO_2^- reduction to NH_4^+ requiring six electrons and catalysis by nitrite reductase (NiR EC 1.7.99.3). Thus, the uptake and incorporation of nitrate by plants is a much more energy-demanding and costly process. Therefore, plants expend less energy for NH_4^+ assimilation. Enzymes required for nitrate reduction and for the assimilation of ammonium ion are found both in the root and shoot (Oaks & Hirel, 1985).

When ammonium is the source of nitrogen, it is incorporated into the amide nitrogen of glutamine, glutamine then being exported to other parts of the plant (Oaks, 1992). In such a case the nitrate uptake system(s), and the nitrate and nitrite reductases, with their high energy demands, would be bypassed. When nitrate is the dominant ion taken up by the plant, the plant root responses to such an increase of environmental NO_3^- are the induction of enhaced NO_3^- uptake system(s) and induction of enzymatic activities to catalyse the reduction of NO_3^- to NH_4^+ (Jackson et al., 1986; Larson & Ingemarsson, 1989). Also, increased availability of NO_3^- induces the system for the assimilation of reduced nitrogen, the transport of NO_3^- to the shoot, proliferation of the root system, changes root to shoot ratios and enhances root respiration (Granato & Raper, 1989; Bloom et al., 1992).

In the case of nitrate reduction occurring in the leaf, the whole process is linked directly to the photosynthetic assimilation process. It was shown that C_4 plants (amongst which is maize) have the enzymes of nitrogen reduction and amination distributed between the two types of photosynthetic cells and chloroplasts, the high energy demand components (reductases) being localised in the mesophyll cell (Moore & Black, 1979). Maize has been known for a long time to be an *efficient nitrogen utilising species*. Such a characteristic was based on the capability of maize to achieve a greater total dry weight to nitrogen ratio, when compared to other agriculturally important plants. It was only with the discovery of the C_4 pathway, when it was shown that the most prominent leaf enzyme, ribulose bisphosphate carboxylase/oxygenase (in C_3 plants accounting for 50% of the leaf protein), due to the efficient functioning of the photosynthetic process of such plants can be reduced in quantity, thus altering the total dry weight/nitrogen ratio (Hatch, Osmond & Slatyer, 1971) that an explantation for such greater efficiency was offered. The energy for nitrate reduction in nonchlorophyllous tissues comes from oxidation of carbohydrates or organic acids.

Under conditions of limited external nitrate concentrations (without ammonium present), higher nitrate reductase is detected in maize leaf than in root tissue (Oaks & Hirel, 1985), but with increasing nitrate concentrations the component of nitrate becoming reduced in roots also increases. Thus the proportion of nitrate reduced in maize roots was shown to be about 37% of the total nitrate taken up (Van Benishchem et al., 1989), the remainder being reduced in the shoot tissue. Other authors have shown that the partitioning of nitrate assimilation between root and shoot and relative concentrations of nitrate and reduced nitrogen in xylem sap, in maize plants, showed substantial proportion of nitrate assimilation in the shoot (up to 90%) (Andrews, 1986). Our results (Hadži-Tašković Šukalović & Baoguo, 1996) demonstrated that changes of NO_3^- concentration in nutrient solution from 2.5 mM to 10.9 mM increased the specific activity of the nitrate reductase for 170% in root and 50% in leaf tissue of 15 days old maize. The ratio of leaf to root nitrate reductase activity being 5.7 in low NO_3^- solution and decreasing to 3.2 in high NO_3^- solution. This suggests that growth of plants in high nitrate concentrations alters the proportion of nitrate reduced in the shoot by enhancing the root capacity to reduce NO_3^-. Such observations could be explained by a metabolic shift to a different mechanisms for the uptake of nitrate ions.

Nitrogen from ammonium is processed primarily in the roots (Lewis, 1986). When ammonium is the available source of nitrogen, it is incorporated into glutamine in the root mainly in a reaction mediated by glutamine synthetase (GS EC 6.3.1.2). Glutamine is the dominant form of transport to the other parts of the plant. Synthesis of glutamine requires glutamate, ammonium and ATP in a reaction with GS. This reaction takes place in root tissue under normal conditions, assuming that glutamate is generated from glutamine and 2-oxoglutarate, an intermediate of TCA cycle in a reaction mediated by glutamate synthase, (GOGAT EC 1.4.7.1) as discovered by Lea and Mifflin (1974). As a result of this NH_4^+ - induced metabolic activity in the root, which could deprive other tissues of carbon skeletons and energy resources required for growth under high NH_4^+ conditions and thereby result in NH_4^+ toxicity. On the basis of organic nitrogen transported to the shoot, it was suggested that the GS/GOGAT system alone may not be sufficient to assimilate NH_4^+ in roots (Handa et al., 1984) and glutamate dehydrogenase (GDH EC 1.4.1.2) activity in maize roots has been reported with NH_4^+ assimilation (Handa et al., 1985; Oaks et al., 1980), expecially when high NH_4^+ concentration is available for plant growth. Aminating function of GDH which uses 2-oxoglutarate, NH_4^+ and NADH in high ammonia conditions is considered to be involved in tissue detoxification. Recent results have shown that ammonium isomerization of GDH molecule occurs with high NH_4^+ concentration (above 5 mM) to form the hexameric structure of enzyme (Osuji & Madu, 1995). This is a critical reaction step in the synthesis of glutamate. Many authors reported the amination function of GDH for numerous plant tissues (Yamaya & Oaks, 1987; Zhang-Qiang et al., 1992; Osuji & Cuero, 1992). Our unpublished results (Hadži-Tašković Šukalović & Vuletić) on maize root mitochondria isolated from 15-days old plants grown on 10.9 mM NO_3^- $\pm$ 7.2 mM NH_4^+ demonsrated also an amination role of GDH induced by high NH_4^+ level present in nutrient solution. Increased GDH activity indicate that mitochondria could be the place of glutamate synthesis and therefore, may be involved in detoxification of excess of NH_4^+. As the result of the requirement of carbon skeleton and energy for NH_4^+ assimilation and biosynthetic purposes, mitochondria exhibited intensified TCA cycle activity and also increased phosphorilative and non-phosphorilative activity which could provide a mechanism for the turn-over of the TCA cycle. Glutamate synthesis in mitochondria by GDH would function as an amino donor in transaminations inside mitochondria to provide aspartate (in a reaction with oxaloacetate) or alanine (in reaction with pyruvate), as well as for the formation of glutamine in a reaction with GS outside mitochondria (Oaks, 1992).

Uptake of NO_3^- in maize is not inhibited in the presence of NH_4^+, but assimilation of NO_3^- into organic nitrogen is retarded by NH_4^+. When both nitrogen forms are absorbed, NH_4^+ is used preferentially for synthesis of amino acids and protein (Schrader et al., 1972). Assimilation of nitrate or ammonium is dependent on carbohydrate metabolism. In root tissue, a significant provision of carbon required for amino and organic acids synthesis is derived from phosphoenolpyruvate (PEP) carboxylation (Arnozis et al., 1988; Cramer et al., 1993). The requirements of NH_4^+ assimilation cannot be fully satisfied by the endogenous supply of 2-oxoglutarate because of the intensified amino acid synthesis, and therefore higher rates of dark fixation of dissolved inorganic carbon provides the carbon skeleton for both, amino acid and organic acid synthesis. In nitrate assimilating plants, the products of PEP carboxylation are preferentially diverted to organic acid synthesis. According to Cramer et al. (1993), the capacity of plants to assimilate NH_4^+, especially under limiting supply of respiratory 2-oxoglutarate, is determined by the capacity of such plants to provide the necessary carbon skeleton in the roots. A balanced ammonium-nitrate assimilation may induce a desirable organic acid content in plant tissue.

NITROGEN ASSIMILATION IN STRESS CONDITIONS

Instead of internal control, the uptake and assimilation of two nitrogen containing ions in maize are regulated also by external conditions. Concentration of nitrogen, pH, temperature and light all influence nitrogen uptake, transport to the shoot and assimilation (Jackson & Volk, 1992).

Nitrate assimilation is more affected than NH_4^+ assimilation in all stress conditions, independent of the stress origin. Many studies indicate that the leaf nitrate reductase is an extremely susceptible enzyme to environmental changes. Decreased leaf nitrate reductase activity was reported in the conditions of low light intensity (Li & Oaks, 1995), high temperature and drought (Amos & Scholl, 1977), low temperature (Bakker & Van Hasselt, 1982; Hadži-Tašković Šukalović & Zarić, 1991), or aluminium toxicity stress (Hadži-Tašković Šukalović et al., 1993). Hadži-Tašković Šukalović & Baoguo, (1996) reported a strong negative effect of aluminium on the maize leaf NADH-nitrate reductase activity. The reduction of activity was dependent on the maize genotype analysed. In some cases, more than 70% of enzyme specific activity was lowered during aluminium stress. An opposite effect was detected in roots. NADH-nitrate reductase specific activity was slightly decreased or even stimulated. Therefore, it was evident that aluminium stress changed proportions for nitrate reduction between shoots and roots. The same authors demonstrated that bifunctional NAD(P)H-nitrate reductase activity was significantly elevated in roots, suggesting that this enzyme plays a more important role in NO_3^- assimilation under aluminium stress and therefore in aluminium tolerance.

Low temperatures decrease the NO_3^- transport to the shoot and increase the NO_3^- concentration in the root tissue (Kafkafi, 1990), but aluminium stress limits the NO_3^- uptake (Durieux et al., 1995) and decrease NO_3^- concentration in maize roots (Hadži-Tašković Šukalović & Baoguo, 1996; Mihailović et al., 1995). Under unfavourable external conditions, NH_4^+ is a better source of nitrogen, because it is quickly metabolised in the root tissue, and translocation of metabolites to the shoot is less affected by root temperature. It is in this context that the activity of enzymes involved in the incorporation of NH_4^+ to organic compounds are not affected, or even stimulated in different stress conditions.

Miranda-Ham & Loyola-Vargas (1994) reported the resistance of maize root glutamine synthetase during water and salt stress. Hadži-Tašković Šukalović et al. (1990) found that aluminium stress did not affect the GS activity, but even increased GDH activity in roots of many maize inbred lines subjected to stress. In order to survive unfavourable conditions, many plants absorb more NH_4^+ than nitrate (Shaviv, 1990).

CONCLUSIONS

According to Kafkafi (1990) NH_4^+ can serve as a good source of nitrogen as long as sugar reserves and supply are available in the root, and opposite, the conditions when high consumption of sugart takes part in the root, NO_3^- is a better source of nitrogen for the plant. The adaptability of maize plant to change the proportion of NO_3^- or NH_4^+ rates of uptake under stress conditions, gives a mechanism for improvement of crop yield by adequate supply of appropriate nitrogen nutient.

It is obvious from the data presented that maize plants have a versatile and adaptable nitrogen uptake and metabolism system. Under conditions of stress, or through human endeavour and varying fertiliser application, when different forms of nitrogen are supplied to plants, its cellular mechanisms are capable of performing a switch and metabolic adaptation so as to be able to take up as much nitrogen as possible.

The importance of studying nitrogen assimilation Olsen (1986) emphasised with words: „*Controlled nitrogen (ammonium-nitrate) nutrition is the largest and most significant laboratory proven potential for increased crop growth that has not been demonstrated on a field scale*". We would like to add the word „*yet*".

REFERENCES

Amos, J.A., & Scholl, R.L. (1977): Effect of growth temperature on leaf nitrate reductase, glutamine synthetase and NADH-glutamate dehydrogenase of juvenile maize genotypes. – Crop Sci. *17*: 445-448.

Arnozis, P.A., Nelemans, J.A. & Findenegg, G.R. (1988): Phosphoenolpyruvate carboxylase activity in plants grown with either NO_3^- or NH_4^+ as inorganic nitrogen source. – J. Plant Physiol. *132*: 23-27.

Andrews, M. (1986): The partitioning of nitrate assimilation between root and shoot of higher plants. – Plant Cell Environ. *9*: 511-519.

Bakker, N. & Van Hasselt, P.R. (1982): Photooxidative inhibition of nitrate reductase during chilling. – Physiol. Plant. *54*: 414-418.

Bloom, A.J., Sukrapanna, S.S. & Warner, R.L. (1992): Root respiration associated with ammonium and nitrate absorption and assimilation by barley. – Plant Physiol. *99*: 1294-1301.

Butz, R.G. & Jackson, W.A. (1977): A mechanism for nitrate transport and reduction – Phytochem. *13*: 409-417.

Cramer, M.D., Lewis, O.A.M. & Lips, S.H. (1993): Inorganic carbon fixation and metabolism in maize roots as afected by nitrate and ammonium nutrition. – Physiol. Plant. *89*: 632-639.

De Marco, A., Jia, C., Fischer-Schliebs, E., Varanini, Z. & Lütge, U. (1994): Evidence for two different nitrate-reducing activities at the plasma membrane in roots of *Zea mays* L. – Planta *194*: 557-564.

Durieux, R.P., Bartlett, R.J. & Magdoff, F.R. (1995): Separate mechanisms of aluminium toxicity for nitrate uptake and root elongation. – Plant and Soil *172*: 229-234.

Errebhi, M. & Wilcox, G.E. (1990): Plant species response to ammonium-nitrate concentration ratios. – J. Plant Nutr. *13:* 1017-1029.

Granato, J.C. & Raper, C.D. (1989): Proliferation of maize *(Zea mays* L.) roots in response to localized supply of nitrate. – J. Exp. Bot. *40:* 263-275.

Hadži-Tašković Šukalović, V., Lazić-Jančić, V., Vuletić, M. & Denić, M. (1990): The effect of aluminium on the nitrogen assimilation enzyme activities in maizie. – Arch. Sci. Biol. *42:* 155-165.

Hadži-Tašković Šukalović, V. & Zarić, Lj. (1991): Study of effect of low temperature on some nitrogen assimilation enzymes in the maize leaf. – J. Sci. Agric. Res. *52:* 133-142.

Hadži-Tašković Šukalović, V., Lazić-Jančić, V. & Vuletić, M. (1993): Effect of aluminium on nitrate reductase activity in maize genotypes differing in Al-tolerance. – Proced. II Simpozium on chemistry and the environment, 9-13 June, Vrnjačka Banja.

Hadži-Tašković Šukalović, V. & Baoguo, L (1996): NADH and NAD(P)H nitrate reductase activities of maize exposed to aluminium stress. – Plant Physiol. & Biochem. (Special issue): 157.

Handa, S., Waren, H.L., Huber, D.M. & Tsai, L.Y. (1984): Nitrogen nutrition on seedling development of normal and opaque-2 genotypes of corn. – Canad. J. Plant Sci. *64:* 885-894.

Handa, S., Waren, H.L., Huber, D.M. & Tsai, L.Y. (1985): Nitrogen nutrition and N-assimilation in maize seedlings. – Canad. J. Plant Sci. *65:* 87-93.

Hatch, M.D., Osmond, C.B. & Slatyer, R.O. Eds. (1971): Photosynthesis and Photorespiration. – Wiley Interscinece, New York.

Jackson, W.A. & Volk, R.J. (1992): Nitrate and ammonium uptake by maize: Adaptation during relief from nitrogen suppression. – New Phytol. *122:* 439-446.

Jackson, W.A., Pan, W.L., Moll, R.H. & Kamprath, E.J. (1986): Uptake, translocation and reduction of nitrate. *In* Biochemical Basis of Plant Breeding. Vol. 2 (C. Neyra, ed.), pp. 73-108. – CRC Press, Boca Raton.

Kafkafi, U. (1990): Root temperature, concentration and the ratio NO_3^-/NH_4^+ effect on plant development. – J. Plant Nutr. *13:* 1291-1306.

King, B.J., Siddiqi, M.Y. & Glass, A.D.M. (1992): Studies of the uptake of nitrate in barley. V. Estimation of root cytoplasmic nitrate concentration using nitrate reductase activity-implications for nitrate influx. – Plant Physiol. *99:* 1582-1589.

Klainer, D. (1981): The transport of NH_3 and NH_4^+ across biological membranes. – Biochim. Biophys. Acta *639:* 41-52.

Lambers, H., Simpson, R.J., Beitharz, V.C. & Dalling, M.J. (1982): Growth and translocation of C and N in wheat *(Triticum aestivum)* grown with split root system. – Physiol. Plant. *56:* 421-429.

Larson, C.M. & Jngemarsson, B. (1989): Molecular aspects of nitrate uptake in higher plants. *In* Molecular and Genetic Aspects of Nitrate Assimilation (eds. Y.R. Kinghorn and J.L. Wray). – Oxford Scinece Publishers, New York.

Lea, P.J. & Miflin, B.J. (1974): Alternative route for nitrogen assimilation in higher plants. – Nature (Lond.) *251:* 614-616.

Lewis, O.A.U. (1986): Plants and Nitrogen. Edward Arnold, London.

Li, X-Z. & Oaks, A. (1995): The effect of light on nitrate and nitrite reductases in *Zea mays.* – Plant Sci. *109:* 115-118.

McClure, P.R., Kochian, L.V., Spanswick, R.M. & Staff, J.E. (1990): Evidence for cotransport of nitrate and protons in maize roots. I. Effects of nitrate on membrane potential. – Plant Physiol. *93:* 281-289.

McClure, P.R., Kochian, L.V., Spanswick, R.M. & Staff, J.E. (1990): Evidence for cotransport of nitrate and protons in maize roots. II. Measurement of NO_3^- and H^+ fluxes with ion-selective microelectrodes. – Plant Physiol. *93:* 290-294.

Mihailović, N., Hadži-Tašković Šukalović, V., Vučinić, Ž. & Bogdanović, M. (1995): Response of nitrate concentration and assimilation in maize leaves to the presence of aluminium and different ion forms of nitrogen. – Proceedings of the I Regional Symposium „Chemistry and the environment", 25-29. September, 1995, Vrnjačka Banja.

Miranda-Ham, M.L. & Loyola-Vargas, V.M. (1994): Glutamate dehydrogenase and glutamine synthtase activities in maize under water and salt stress. – Fyton *56:* 7-15.

Moore, R. & Black, C.C. (1979): Nitrogen assimilation pathways in leaf mesophyll and bundle sheath cells of C_4 photosynthesis plants formulated from comparative studies with *Digitaria sanguinalis* (L.). – Platn Physiol. *64:* 309-313.

Oaks, A., Stulen, J., Jones, K., Winspear, M.J., Misra, S. & Boessel, J.L. (1980): Enzymes of nitrogen assimilation in maize roots. – Planta *148:* 477-484.

Oaks, A. & Hirel, B. (1985): Nitrogen metabolism in roots. – Ann. Rev. Plant Physiol. *36:* 345-365.

Oaks, A. (1992): A re-evaluation of nitrogen assimilation in roots. – Bio Science *42:* 103-111.

Olsen, S.R. (1986): Using soil and fertilizer chemistry to improve corn productivity. – Potash and Phosphate Institute, Maximum Yield Corn Research Roundtable, November 1985, St. Louis, Mo.

Osuji, G.O. & Cuero, R.C. (1992): Regulation of ammonium ion salvage and enhancement of the storage protien contents of corn, sweet potato, and yam tuber by N-(carboxymethyl)chitosan application. – Agric. Food. Chem. *40:* 724-734.

Osuji, G.O. & Madu, C.W. (1995): Ammonium ion-dependent isomerization of glutamate dehydrogenase in relation to glutamate synthesis in maize. – Phytochem. *39:* 495-503.

Schrader, L.E., Domska, D., Jung, P.E. & Petterson, L.A. (1972): Uptake and assimilation of ammonium-N and nitrate-N and their influence on the growth of corn (*Zea mays* L.). – Agron. J. *64:* 690-695.

Shavir, A., Hazan, O., Neumann, P.M. & Hagin, J. (1990): Increasing salt tolerance of wheat by mixed ammonium nitrate nutrition. – J. Plant Nutr. *13:* 1227-1239.

Ullrich, W.R. (1987): Nitrate and ammonium uptake in green algae and higher plants: mechanisms and relationship with nitrate metabolism. *In* Inorganic Nitrogen Metabolism (Eds. W.R. Ullrich, P.J. Aparicio, P.J. Syrett, F. Castillo). – Springer-Verlag, Berlin Heildelberg.

Van Bensichem, M.L., Nelemans, J.A. & Hinnen, M.G.J. (1989): Nitrogen cycling in plant species differing in root reduction of nitrate. – Colloq. on plant nutrition, Wageningen.

Wang, M.Y., Siddiqi, M.Y., Ruth, T.J. & Glass, A.D.M. (1993): Ammonium uptake by rice roots. II. Kinetics of $^{13}NH_4^+$ influx across the plasmalemma. – Plant. Physiol. *103:* 1259-1267.

Wang, M.Y., Glass, A.D.M., Shaff, J.E. & Kochian, L.V. (1994): Ammonium uptake by rice roots. III. Electrophysiology. – Plant Physiol. *104:* 899-906.

Ward, M.R., Tischner, R. & Huffaker, R.C. (1988): Inhibition of nitrate transport by anti-nitrate reductase IgG fragments and the identification of plasma membrane associated nitrate reductase in roots of barley seedlings. – Plant Physiol. *88:* 1141-1145.

Ward, M.R., Grimes, H.D. & Huffaker, R.C. (1989): Latent nitrate reductase activity is associated with plasma membrane of corn roots. – Planta *177:* 470-475.

Warner, R.L. & Huffaker, R.C. (1989): Nitrate transport is independent of NADH and NAD(P)H nitrate reductases in barley seedlings. – Plant Physiol. *91:* 947-953.

Yamaya, J. & Oaks, A. (1987): Synthesis of glutamate by mitochondria. – An anaplerotic funciton for glutamate dehydrogenase. – Physiol. Plant *70:* 749-756.

Zhang-Qiang, S., Jolivet, J. & Dizengremel, P. (1992): Effect de l'alimentation azotée sur le matabolisme du feuilles de Soja. – C.R. Acad. Sci. (Paris). Ser. III, *314:* 565-571.

Rezime

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Daje se pregled mehanizama asimilacije azota (sa posebnim osvrtom na kukuruz), razmatrajući različite puteve usvajanja i metaboličkih transformacija za ugradnju nitritnog i amonijačnog jona. Podaci pokazuju da je za optimalan rast i razvoj kukuruza poželjno prisustvo obe forme azota u zemlištu. U uslovima stresa (niska temperatura, suša ili niski *pH* i aluminijum toksična zemljišta) takvi različiti putevi usvajanja i metabolizma azota nalaze ekspresiju u različitim odgovorima biljke, omogućavajući da se neki od štetnih efekata stresa uklone prihranom biljaka kukuruza u polju odgovarajućom kombinacijom azotnih formi pri đubrenju. U budućnosti, selekcija biljaka sa specifičnim putevima asimilacije azota bi mogla da se pokaže kao jedan od pristupa borbe protiv neoptimalnih uslova spoljašnje sredine.