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Introduction

The term „Nitrogen fertilizing efficiency“ (nutrition) implies the effect of N unit from fertilizer and soil on forming yield. „Nitrogen utilization efficiency“ is referred to as „agrochemical N efficiency“ and „utilization efficiency“ in the East and West European literature, respectively. Both N fertilizing efficiency and N nutrition efficiency could be used as appropriate terms. These investigations comprise three groups of issues, which also represent the stages of investigations.

1. Studying of possible physiological parameters determining the level of N nutrition efficiency of wheat, as well as N agrochemical efficiency in wheat.

2. The choice of the most suitable physiological parameters for a successful selection towards an increased N nutrition efficiency and their application in the selection process, as well as finding out these traits in the hybrid progeny at earlier phases of plant growth and development.

3. The study of the genetic basis for controlling individual parameters of N nutrition efficiency in wheat for establishing and developing donors, gene bearers with expressed traits for an improved N nutrition efficiency.

These considerations present an elaborated concept of V o s e, 1963; E p s e t i n, 1972; S a r i ć, 1983; Gabelman and Gerlof, 1983; Clark, 1983, 1989; K l i m a š e v s k i, 1985, on breeding varieties which will take up and utilize mineral elements from fertilizer and soil more efficiently. In this study, one of the possible approaches as a solution to these problems has been brought up.

As being interdisciplinary by their nature, the present studies should rely on the achievements in physiology, agrochemistry, genetics and selection. They also should be an impetus to new and more up-to-date issues than the existing ones, so they should be initiated within these sciences.

Not only is theoretical significance implied in these studies, but they are also concerned with practical issues. Although fertilization is considered to be the most efficient cultural practice for increasing yield and improving quality, at the same time it is the biggest item in the wheat production costs, often amounting to more than a half of production value. Hence, a problem arises of profitability of applying fertilizers in wheat. With the onset of energy crisis, this problem has become more and more manifest. A way-out is to increase fertilizing efficiency, i.e. to accomplish higher yields with the existing fertilizer amounts on the one hand, or to achieve current yields with lower fertilizer amounts, on the other. In addition to economical, these studies should alleviate some ecological problems concerned with fertilizer application. They aim at avoiding losses of applied fertilizers and reducing soil and water contamination by means of the improved N uptake from fertilizers.

However, many scientists point out that investigations aimed at applying of reduced N amounts in wheat production are not promising. This is reinforced by the fact that in 1 tonne of grain yield with adequate straw amount, 25 kg of nitrogen could be accumulated so that almost no substantial profitability can be expected. This only applies to N utilisation in the plant. It means that N should

be actively used in the plant so that per each 25kg of accumulated N, 1 tonne of grain yield could be obtained. For achieving this N accumulation, wheat should be fertilized with 50kg N/ha or only 30kg N/ha at N uptake of 50% and 80%, respectively. It should also be emphasized that 1 tonne of wheat yield could be obtained when lower N amount applied than 25kg N/ha, that is 20kg N/ha or even 15kg N/ha. Concurrently with this, it has been shown that N depleted per unit yield largely varied due to a genotype. All this suggests the possibility of a more profitable fertilizer application depending not only on growing system, but also on genotype.

The physiological basis for breeding varieties efficient in N nutrition with moderate requirements for N fertilizer was analyzed in this study.

Nitrogen fertilization (nutrition) efficiency of wheat (agrochemical efficiency)

Nitrogen fertilization efficiency of wheat represents the effect of available N forms in soil on yield. This efficiency is determined by yield per available N unit in the soil. Fertilization efficiency represents the effect of N fertilization of wheat on grain yield. This efficiency is measured by increase in yield per N fertilizer unit. It is also known as „agrochemical or agronomical efficiency“ (Fischer R.A., 1981; Novoa, Loomis, 1981; Crasswell, Godwin, 1984; Đokić, 1988). The varieties with improved N nutrition efficiency are also known as those with small N input (Danbroth, Bassam, 1983), or with an increased agrochemical efficiency (Klimiševski, 1974; Gamzikova, 1974; Novoa, Loomis, 1981), or with better N economy (Austin et. al. 1977).

Nitrogen nutrition efficiency of wheat represents the adaptation of the variety to utilize N from external medium in forming yield, that is the strength of the plant response to the uptake of N from external medium and its utilization in the plant.

Aiming at limiting the choice of parameters of N nutrition efficiency, a question was raised of how fertilization could affect the increase in yield. This effect can be achieved when the plant takes up N from external medium translocating it to the shoot in the form of low-molecular compounds. These substances are further transformed to adequate organic compounds subsequently affecting speed and volume of the processes occurring in the shoots, in which the assimilates for filling grains have been formed. Therefore, the effect of N on yield (ENf) will depend on N uptake efficiency (NUpE) and on NUtE in forming the assimilates for filling grains. The NUpE is calculated by the ratio between N that has been taken up and used from the fertilizer:

$$(NUpE = \frac{T-upN}{Nf}), \text{ and that of N utilisation by the ratio between grain yield N}$$

and N accumulation in the plant: ($NUtE = \frac{Yg}{AN}$). So, the N fertilizing efficiency presents their product, (M o l l e t a l., 1972; N o v o a, L o o m i s, 1981; C r a s w e l l, G o d w i n, 1984), as follows:

$$NFE = NUpE \times NUtE = \frac{AN}{Nf} \times \frac{Yg}{AN} = \frac{Yg}{Nf}.$$

NFE of wheat is dependent on soil climatic conditions, variety, N amounts and other factors. Marked tendency is that with increase in N amount, the decrease in NFE occurred (Tab. 1). if NFE is increased from 20-35 kg of grains/kg of N nutrient at either high or low N amounts applied, the same yield will be obtained using only 75 kg N/ha instead of 120 kg.

Table 1 - NFE - kg of grains/kg of N nutrient
(Kostić, Đokić, 1981)

doses of N kg/ha	kg of grains/kg of fertilizer	% of variations	x
40-63	22-48	2.18	35
80-126	18-39	2.16	28
120-150	15-25	1.66	20

In general, two ways exist to increase N nutrition efficiency of wheat aiming at lower costs for wheat fertilization, the agrotechnical and selection genetic one. The former way suggests that growing system should be somewhat changed to provide conditions for improved N uptake and utilisation from fertilizer and soil, hence N amounts required for wheat fertilizing would be reduced. The latter way comprises breeding new genotypes of wheat able to take up and use N more efficiently. This way is by far the cheaper, including only costs for cultivar breeding, compared with constant and extremely high costs for additional cultural and amelioration procedures, soil improvement required by the first approach.

Nitrogen uptake efficiency

The efficiency of adoption reflects the activity of the root system, as an absorption organ. It represents the ability of the root system to absorb nitrogen, and to convey its greater portion either in inorganic or organic form to the above-ground part.

Two ways are suggested for measuring N adoption efficiency. The first is based on N fertilisation adoption percent, or on its aggregate amounts available in soil. Thus, adoption efficiency can be expressed by comparing the varieties different in optimum N fertilisation proportions. The N adoption efficiency (absorption) is calculated through the following formula:

$$\text{EAN} = \frac{\text{increase in N amounts in plant depending on fertilisation}}{\text{used N amounts in the form of fertilizer}} \quad \text{or}$$

$$\text{EAN} = \frac{\text{total N amounts in the plant}}{\text{total amounts of available N in soil}}$$

Further, NUpE from fertilizer is presented by N accumulated in the plant so that the varieties evenly fertilized with N fertilizer amounts can be compared. Hence, the differences between varieties in N accumulation in the plant will at the same time represent the differences in NUpE.

Nitrogen accumulation is the product derived from dry matter (DM) of the plant and N contained in it: $A = \%N \times DM$. So accumulated N can be expressed per unit area and per individual plant.

Productive traits of wheat varieties are often compared on the basis of yield per unit area, being the basic criterion of productivity. Both plant mass and their number per unit area can extremely vary among varieties, which need not necessarily affect the differences between varieties in yields per unit area. Thus, it is preferable to present N accumulation in a crop per unit area.

For comparing the hybrid progeny from thin sowing, primary stems are better to analyze than entire plants. Primary stems from thin sowing better reflect the differences in N accumulation among the varieties from thick sowing than the entire plants. The plants from thick sowing struggle for nutritional space as much as secondary stems do for primary stems in thin sowing.

However, little has been done on N accumulation in high yielding new varieties so far. Little attention has been paid to the root mass and its activity. As a consequence, higher yields of new varieties were associated with lower N concentration in the grain and lower content of proteins.

Nitrogen uptake amounted to about 50% according to the results in Table 2. This percent is somewhat lower in large-scale production, about 40%, ranging from 30-50%, (Jagodin et al., 1989). Nevertheless, it is possible to improve N uptake as it extremely varies within a variety as much as among them, Table 2 and Table 3 respectively. This lies in the fact that plant takes up N more efficiently at lower N amounts rather than at higher ones.

Tab. 2 - NUpE from fertilizer

% of adoption	% of varitation	method	Literature	Note
24-50	2.88	isotopic	Deržavin, Sedova 1979.	145 assays
43		isotopic	Hauk 1981.	289 assays
12-70	5.83	isotopic	Korenkov, Borisova 1980.	165 assays
26-51	1.96	difference	Žeravica 1971.	
58-70	1.20	difference	Kostić et al 1994.	120 kg N/ha
51-69	1.29	difference	Kostić et al 1994.	150 kg N/ha
89, 67, 56	1.33, 1.20	difference	Đokić, Lomović 1990.	30,60,90
56, 53, 49	1.06, 1.08	difference	Đokić, Lomović 1990	120, 150
				180 kg N/ha
90		difference	Spiertz, Wan der haar 1978.	
44-60	1.36	difference	Gasser, Iordanou 1967.	
58-69	1.19	difference	Gasser, Iordanou 1967.	
33-90	2.73	isotopic	Hamid 1972.	
28-38	1.36	isotopic	Pushman, Bingham 1976.	

Tab. 3 NUpE dependent on genotype

Accumulated N mg/plant	% of variation	Literature
25-34	1.36	Kostić, Đokić, 1988.
44-68	1.55	Đokić, 1989.
21-28	1.33	Đokić et al, 1994.
29-51	1.76	Đokić et al, 1995.

If N uptake from fertilizer increases from 50% to 75%, then the common amount of 120kg N/ha can be reduced to 80kg N/ha. Simultaneously, NUpE from soil reserves will increase. About half of N from these reserves is accumulated by wheat in our conditions.

The more N applied, the more N accumulated in the plant, but this increase is not proportional to the N amounts applied. Nitrogen uptake was observed to be lower per fertilizer N unit. What brought about the decrease in NUpE from fertilizer when N amount increased? It should be stressed that N amount when somewhat changed resulted in almost no change in root mass. The increased N uptake from higher N amounts was the consequence of accelerated root absorption. Nitrogen was increasingly absorbed by the root per root unit mass and unit area within unit time, while N uptake was lower per unit of applied N. Therefore, the N absorption rate (N applied per unit time) had to be matched with increase in fertilizer amount, that is the root permeability had to be higher to allow NUpE. Unfortunately, this has not been attained yet with the existing varieties.

Nitrogen accumulation in the plant as a criterion of N uptake efficiency

N accumulation in the plant can be the criterion of NUpE when growing conditions allow the same N availability and N fertilizer, respectively. NUpE is determined through dividing accumulated N amount in the plant by the amounts of added or available N, being even in each variety. Therefore, the varieties will be ranked the same in terms of N accumulation and N uptake from fertilizer, respectively. However, this is not analogous to the varieties, varying in optimum N content, when grown in adequately available N. For computing the NUpE, N amounts accumulated in the plant are divided by those of N utilised, differing from variety to variety. Thus the varieties with similar values of N accumulation in the plant can considerably vary in the NUpE from fertilizer. As a consequence, high NUpE from fertilizer might be followed by low N accumulation in the plant and vice versa.

N will be evenly accumulated at abundant N nutrition in some of genotypes and at scarce N nutrition in the others. NUpE will be higher at scarce N nutrition. This can be exemplified by equal increase in N accumulation in the plant of 60kg N/ha obtained using 120kg N/ha in one variety, and 150kg N/ha in the other when the NUpE from fertilizer amounts to 50% and to 40%, respectively.

The N accumulation in the plant is primarily the criterion of cultivar productivity. In the up-to-date, high yielding cultivars, the N utilization in the plant is likely to vary much less than N accumulation if N nutrient is adequately applied. In terms of these two parameters, the yield will depend more on the one varying more, which is N accumulation in this case.

Nitrogen utilization efficiency

NUtE in the plant is characterized by the shoot activity to transport N acquired into processes of synthesis in order to accelerate these processes and plant productivity. The NUtE is likely to depend on the plant ability to affect the rate of N cycling and re-utilisation (recycling) in the plant.

NUtE in the plant is also known as physiological efficiency. It means that N plays a direct and active part in activating photosynthetic processes, in which organic matter is formed. This efficiency is measured by assimilate amount formed for filling grains per plant N unit:

$$EUtE = \frac{Y_g}{AN} .$$

Selection of wheat has been improved in terms of increasing N efficiency in forming assimilates for filling grains, also resulting in higher yields. However, as the increase in N physiological efficiency represents the increase in grain yield per plant N unit, at the same time it represents the decrease in N amount per grain yield unit and lower N content in grain.

As evident from the results in Tables 4 and 5, the NUtE in the plant can considerably vary subject to N nutrition and the genotype. Lower values (the first

in the column) of NUtE were obtained at higher, and higher (the second in the column) at lower N fertilizer amounts applied (Table 4).

Tab. 4 - NUtE in the plant

kg of grains/kgN	% of variation	literature
37 - 49	1.32	Osipova 1964.
34 - 37	1.09	Morozova 1965.
37 - 48	1.30	Žeravica 1971.
41 - 49	1.20	Turčin, Gladiš 1977.
42 - 61	1.45	Marković et al 1978.
32 - 42	1.31	Gluhinski et al 1978.
32 - 46	1.44	Đokić, Lomović 1990.
30 - 60	2.00	Đokić, Kostić 1992.
35 - 52	1.49	Đokić, Kostić 1994.
18 - 42	2.33	Potapov 1969.

The current level of the NUtE in the plant amounts to about 30-40kg of grains per kg of N contained in the plant. However, on unfertilized plots or those fertilized with small N amounts, the NUtE was found to amount to 50-60kg of grains per kg of N in the plant, (Đ o k i ć, K o s t i ć, 1990). If the NUtE is increased from 40 to 50kg of grains per kg of N in the plant, the yield of 5 tonnes will be obtained using only 100kg N/ha instead of 120kg N/ha. In this case, the part of accumulation of 40kg N/ha to be provided from fertilizer could be achieved using 80kg N/ha and 60kg N/ha at N utilisation of 50% and 70%, respectively.

In addition, significant differences were observed among varieties in N physiological efficiency. According to our studies, the NUtE in the plant amounted to 39-61g of grains per gram of N in the plant, (K o s t i ć, Đ o k i ć, 1988; Đ o k i ć, 1989; Đ o k i ć et al., 1994). It indicates that abundant reserves exist for utilizing N more efficiently by means of selection.

Tab. 5 - NUtE in the plant dependent on the genotype

kg of grains/kgN	% of variation	literature
37 - 45	1.22	Kostić, Đokić 1988.
33 - 43	1.30	Đokić 1989.
39 - 50	1.28	Đokić et al 1994.
34 - 46	1.36	Đokić et al 1995.
28 - 44	1.57	Klimaševski 1991.

Nitrogen utilization efficiency and quality of grain

The increase in NUtE in the plant is interesting from the point of view of increase in profitability and productivity, but is accompanied by decrease in yield quality. In other words, the increase in NUtE represents the increase in yield per N unit, but prevalently lower N and protein content will affect the nutritive, feed and technological quality of grain and flour.

A question arises to what extent it is reasonable to increase the NUtE in the plant, since it is accompanied by reduced N concentration in the grain. Only after consideration of some regular patterns of change in yield and protein content in grain subject to N fertilization, can certain conclusions be drawn.

In the initial stage, yield and protein content in the grain had simultaneously been rising affected by N, while later only protein content continued to rise (Figure 1). These lowest N amounts providing the maximum yield might present the optimum ones, because it is their effect on which both basic traits of grain, i.e. its quality and quantity, are dependent.

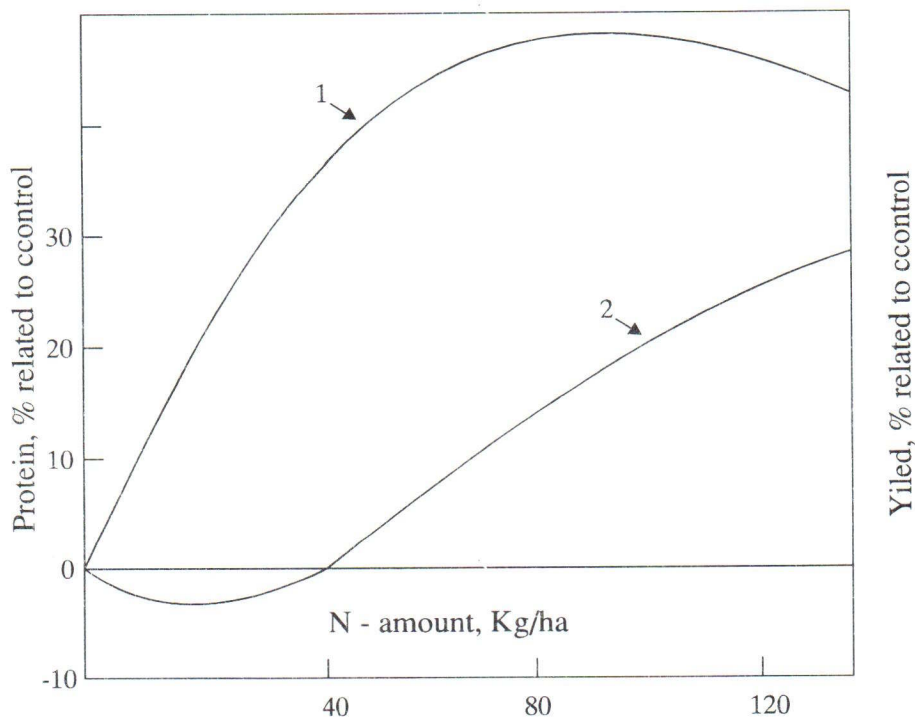


Fig. 1. – Grain Yield of wheat (1) and protein content in grain (2) affected by rising N amounts (Pavlov, 1979)

Initially, the NUtE in the plant had dropped less rapidly until the yield reached optimum values, to have continued to drop more rapidly later. On the other hand, this dependence indicates that maximum NUtE in the plant can be achieved at initial points of the rising segment of the curve, presenting the dependence of yields on N amounts. However, in these conditions, genotype exhibited no potential for yield. Therefore, the NFE in different varieties should be determined when optimum N amounts are applied.

To make progress in this sense, we should focus on breeding genotypes able to reach their maximum yields at lower N content in the grain. In wheat varieties represented in our production, the maximum yield is obtained with about 2% of N content in the grain. When growing conditions are controlled and soil irrigated, the yields can be optimized using N of 1.7%, and lower than that. According to some data, the maximum yield can be obtained with protein content of 8.8% (8.3-9.1%), (Goos et al., 1985) or higher than that, (Penk, 1975; Thompson et al., 1975; Glenn et al., 1985; Đokić, Lomović, 1990), (Table 6). So, it is possible to increase yield at the expense of N utilisation in the plant at constant N accumulation in the plant. Considerable reserves allow N content to be decreased in the grain. It was found that N content could be reduced even up to 1.4% either on fertilized or irrigated soil (Marković et al., 1978; Đokić, Kostić, 1992).

Table 6 - Content of proteins for obtaining optimum grain yield

literature	% of proteins	variations
Goos et al 1972.	11.5	11.1 - 12.0
Thompson et al 1975.	13.0	
Penk 1975.	14.0	
Glenn et al 1980.	8.8	8.3 - 9.1
Đokić, Lomović 1991.	11.0	

It was established that at N content of 1.4% and its harvest index of 80%, the yield of 5t/ha could be obtained using 90 kg of N accumulation in the plant and only 30 kg of N from fertilizer. Provided that N accumulation amounts to 125kg N/ha, the yield of 7.2 t/ha with 1.4% of N will be attainable instead of 5 t/ha with 2% of N. At present, this low N percent in the grain occurs either on irrigated soil, or with scarce N nutrition, leading to extremely low yields. Therefore, the main problem is to get the same NUtE either at intensive or scarce fertilization, i.e. to obtain high yields as a result of increased N utilisation in the plant.

That selection of wheat is promising may be exemplified by malting barley, the maximum yields of which have been achieved with N content in the grain, lower by 10-20% than that in wheat.

It should be pointed out, however, that lower protein content leads to the lower glue content, and consequently the technological quality of grain and bread and their nutritive and feed value deteriorates, too. A question arises whether bread of good quality can be produced from the crop with so low protein content, and what minimum protein content can provide bread of good quality.

The technological quality of grain and flour were found to depend not only on glue content, but also on its physical characteristics. In the varieties with prevalently good physical characteristics of the glue, protein content can be reduced to 9-10% without affecting the quality of bread. In those with poor characteristics of glue, the yield could be noticeably increased at the expense of reduced protein content in the grain. These varieties would be used as forage. In wheat selection this possibility has not yet been taken into account, so that wheat could not compete with maize as a crop for producing forage.

The relationship between NUPE and NUTE

Within a variety, the increase in N accumulation in the plant results in decrease in N utilization for forming yield. The yield increases and subsequently stagnates and declines. Within a variety, increased N amounts first optimize yields at low accumulation and high utilization of N, while later these yields occur at high accumulation and low utilization of N. For higher profitability, the maximum yields are preferable at lower accumulation, but at higher NUt E in the plant for lower requirements for N fertilizer.

According to the analyses, N accumulation was observed to be higher in more recent and more productive varieties than in the older ones. However, these higher yields were accompanied by somewhat lower N content in the plant, grain and higher NUTE in the plant. Dry matter was accumulated at higher rate than N. This led to reduction in N concentration in the plant, which led to slowing down of organic matter synthesis. Therefore, the lack of N accumulation appears to be a limiting factor of productivity in wheat selection. It seems difficult to obtain the genotypes with the N accumulation that could radically increase yield without reducing N content in the grain. Therefore, more attention should be paid in future to development and activity of the root system, which might provide higher N accumulation in the plant.

NFE and fertilization profitability

The higher N amount results in the lower N uptake and utilization in the plant, hence lower NFE. Initially, N affects yield increase, which reaches its peaks and then drops. Therefore, the highest NFE is achieved at the lowest N amount, but resulting in low yields, failing to cover fertilization costs. A question arises which fertilization efficiency enables the best fertilizing profitability. Roughly speaking, wheat fertilization will be profitable if 50% of the yield increased by means of fertilization cover fertilization costs, and if the other 50% cover transport and distribution. When the energy crisis intensified, fertilization costs considerably rose with no increase in yields to cover fertilization costs.

NFE of wheat and productivity

The rank of varieties grown under the same conditions is the same in terms of NFE and yield. When computing the NFE, productivity as a product of

accumulated and used N in the plant is divided by evenly applied N in each variety for yield determination. Therefore, varieties are ranked in NFE as much as in yield. If the results are obtained when different N amounts are applied, or in soils different in N availability, the yields will be divided by various N amounts applied. Hence, the varieties with the same productivity are likely to considerably vary in NFE and vice versa. It means that the varieties with either high or low NFE exist among low and high productive ones.

Division of genotypes of wheat according to NFE

As reported by S a r i ć (1984), based on N concentration in the plant and organic matter production, all the varieties of wheat can be divided into four groups:

- high N concentration and high production of organic matter;
- high N concentration and low production of organic matter;
- low N concentration and high production of organic matter;
- low N concentration and low production of organic matter.

Based on this division, let us consider the characterization of wheat variety groups according to NFE. As N content in the plant is negatively correlated with NUtE, the groups with high N concentration in the plant will be characterized by low NUtE and vice versa. We could also indirectly draw conclusions on the differences in N accumulation in the plant between individual groups. The group with high organic matter production and high N concentration will be characterized by high N accumulation in the plant. The group with high organic matter production and low N concentration and the one with low organic matter production and high N concentration will be characterized by average N accumulation. Finally, the group with low organic matter production and low N concentration will be characterized by low N accumulation in the plant.

However, the above characteristics are not indicative of the NUpE from fertilizer and soil. The characteristics of individual groups differing in production of organic matter and in the necessary concentrations of mineral nutrients in the plant for achieving this productivity are here under consideration, and not the amounts of available N, which should be provided for obtaining these concentrations in the plant.

As NFE is dependent on NUpE and NUtE, four combinations can be singled out ranging from low to high values of these parameters:

- high NUpE and high NUtE in the plant, (Up2Ut2) - high NFE;
- high NUpE and low NUtE in the plant, (Up2Ut1) - average NFE;
- low NUpE and high NUtE in the plant (Up1Ut1) - average NFE;
- low NUpE and NUtE in the plant (Up1Ut1) - low NFE.

The genotypes of the first group will be characterized by high yield if high NUpE from fertilizer and soil is associated with high N accumulation in the plant, and by low protein content in the grain due to high NUtE in the plant. This

is the characteristic of modern high yielding varieties of wheat. Although the genotypes of the second group have high N accumulation in the plant as those of the first group, they will be characterized by average yield due to low NUtE with increased content of proteins. These are traits of modern varieties of wheat, having increased protein content.

Low NUpE in the genotypes of the third and fourth group is usually accompanied by low N accumulation in the plant. Hence, they are not characterized by high, but by an average or low yield dependent on how efficiently accumulated N has been used. Low yield and high protein content are prevalent in the fourth group due to low NUtE. The fourth group have traits intrinsic to relatively old varieties of wheat with increased protein content.

Provided that NUpE is substituted with its accumulation, four combinations of genotypes will be obtained, varying in the degree of N accumulation and NUtE in the plant. They also vary in yields and protein content in the grain. They have the following characteristics:

- high N accumulation and utilization efficiency in the plant - high yields and low content of proteins;
- high N accumulation and its low utilization efficiency in the plant - high or average yields, high content of proteins in the grain.
- low N accumulation and its high utilization efficiency in the plant - average or low yields, low content of proteins;
- low N accumulation and its low utilization efficiency in the plant - low yields and high protein content in the grain.

From the wheat selection point of view, the division of varieties could be interesting in terms of the degree of:

- N accumulation in the plant,
- NUtE in the plant.

This division is accounted for by the degree of yield determined by the product of the above two parameters and by improvement of either one or of the other parameter, inducing increase in yield.

G a m z i k o v a (1994), singled out two types of varieties, being agrochemically efficient:

- for low levels of nutrient availability in soil,
- for optimum or and/or high levels of nutrition.

The physiological biochemical traits of the former group of varieties appear to be low concentration of nutrients in the plant and a high rate of organic matter synthesis. The varieties able to efficiently use the environmental conditions, the sun energy, water and soil fertility, as well as to take up P from less readily available forms in soil and to increase symbiotic nitrogen fixation, belong to the above group.

The traits of the latter group appear to be high concentration of nutrients in the plant and high rate of organic matter synthesis. Its varieties are able to exhibit their productive traits at abundant fertilizer amounts. Moreover, they have great potential for N accumulation. Hence, N could be economically and more efficiently used through the increase in biomass and grains, highly rich in proteins. The analyses showed that N mostly accumulated in the varieties, having the best

grain yield and reduced protein content in the grain (T a k e d a, F r e y, 1978; K r a m e r, 1979) Therefore, based on these varieties, yield increase is only possible with increasing N accumulation in the plant provided that the existing NUtE is maintained, that is to say the current level of proteins in grain. So, two options are proposed to increase N accumulation in the plant: either by means of greater N supply from fertilizer and soil or N greater uptake at the existing N availability. From the selection efficiency point of view, the latter possibility is more interesting.

On the other hand, yield increase is highly promising at higher NUtE in the plant. As a consequence, protein content could be largely reduced in the grain, hence its quality could deteriorate when processed and used as food. Moreover, the increase in NUtE could result in the reduction of its concentration in the plant to the extent when it could become a limiting factor in forming assimilates for grain filling.

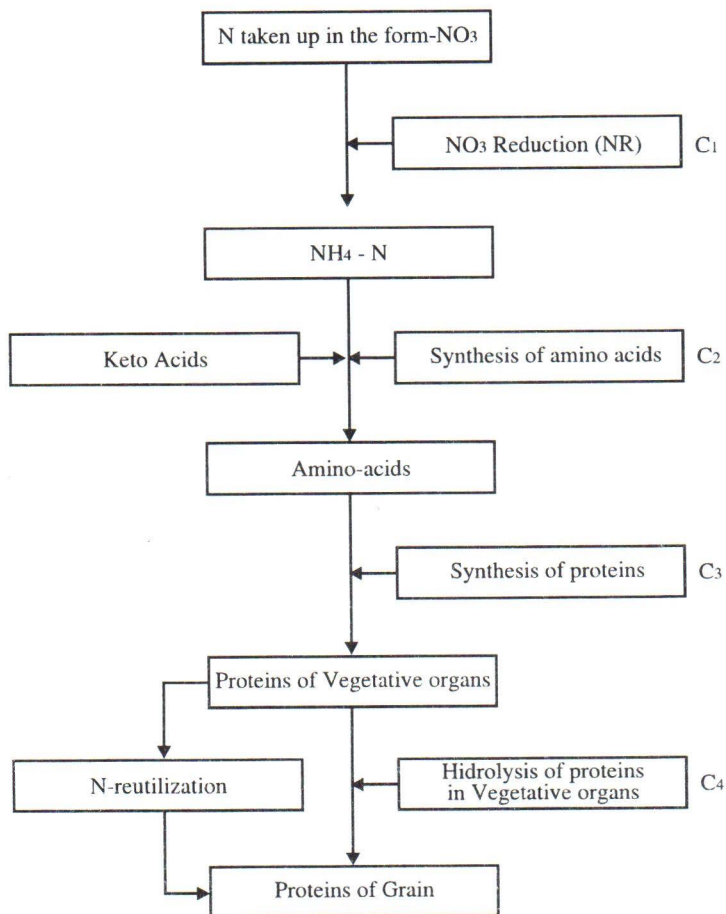
Other parameters as criteria of NFE

In addition to the above two parameters, immediately affecting and determining the level of NFE, the others also exist, affecting NFE through their indirect effect on each of the two. Being complex (integrated) parameters, the NUpE and NUtE are dependent on more simple ones. So, they are derived from the action of simple parameters. Some of them can affect both basic ones. The other parameters are, as follows:

- biological yield, grain yield and harvest index;
- development and activity of the root system;
- N concentration in the plant and individual organs;
- total N accumulation in the plant and that before and after fertilization ;
- N harvest index;
- nitrate reduction efficiency in the plant;
- N re-utilization efficiency of vegetative organs.

Biological yield, grain yield and harvest index: Higher values of biological and grain yield at equal N availability at the same time represent higher NFE. Similarly, higher values of grain harvest index at similar biological yield at equal N availability represent higher NFE.

Development and activity of the root system: The varieties of enlarged mass, stronger and extended activity of the root system are characterized by higher uptake of N available in soil, followed by its higher accumulation in the plant and higher NUpE. In these varieties, better water supply may be expected, which will favour N utilization in the plant. The activity of the root system was found to be more important for nutritive efficiency of mineral substances than the root mass, and the same holds true for active absorption surface share compared with entire surface (K l i m a š e v s k i j, 1990). The development of the root system may be assessed through dry matter content through the root mass share in the total plant mass.

N taken up in the form-NO₃

Scheme of N-metabolism in wheat

N concentration in the plant, grain and straw: High N concentration in the plant indicates that only few assimilates were formed per plant N unit, i.e. that NUtE proved low. If the NUtE in the plant is expressed by the quantities of biological yield per plant N unit, then it is equal to the reverse value of N concentration in the plant, as can be seen from the following ratio:

$$\text{NUtE} = \frac{\text{Yb}}{\text{AN}} ; \%N = \frac{\text{AN}}{\text{Yb}} \Rightarrow \text{NUtE} = \frac{1}{\%N}$$

However, N concentration in the plant can also be the criterion of its uptake from fertilizer, being presented as:

$$\text{NUpE} = \frac{\text{Yb} \times \%N}{\text{Nf}}, \text{ and of N accumulation, AN} = \text{Yb} \times \%N$$

provided that varieties do not essentially vary in biological yield (Yb). The differences among varieties in N concentration will represent the differences in N accumulation.

Furthermore, the increased N concentrations in the grain and straw also point to rather low utilisation of N from the plant in forming yield and to low NFE. The N concentration in the grain is negatively correlated with yields (Kram er, 1979; Pavlov, 1984; Đokić, Kostić, 1995). The genotypes with lower yield, grown in similar conditions, exhibit lower NFE and NUtE in the plant and grain. However, the selection for lower N concentration in the grain aiming at increase in NFE and overall productivity can result in poorer grain quality as a raw material for food industry and forage.

Low N concentrations in the straw also point to better NFE and NUtE in the plant, (Kostić, Đokić, 1991). Straw content was observed to vary, depending on the variety and nutritional level, from 0.20 to 0.60. When N concentration in the straw falls from maximum to minimum value in the straw, the yield of 7.5 t/ha, based on the difference in N amount of 30 kg, can be increased by 1.2 t/ha, (1 tonne of grains with an adequate straw quantity amounting to 24 kg/ha).

N accumulation in the plant: From the formula of NUpE, $(\frac{\text{AN}}{\text{Nf}})$, it

can be seen that NUpE from fertilizer will be higher with higher N accumulation in the plant. This accumulation provides the activity of the vegetative organs, in which the assimilates for grain filling have been formed. One portion of N from the vegetative organs is transported into grain as required for forming and filling grains. Simultaneously, N concentration diminishes in vegetative organs, which can cause decrease in intensity and duration of the activity of these organs. Therefore, the improved N uptake from the soil in this period can extend the activity of vegetative organs and enhance yield per fertilizer N unit, i.e. to increase the NFE.

The nitrogen harvest index (NHI): NHI can be used as a criterion when judging the nitrogen utilisation in the plant. This dependence can be expressed by the following ratio:

$$\text{NUtE} = \frac{\text{Yg}}{\text{AN}} = \frac{\%N}{\text{AN}} = \frac{1}{\%N} \frac{\text{Ng}}{\text{AN}} = \frac{\text{NHI}}{\%N}$$

The less varying N concentration in the grain, the higher positive correlation between NUtE and NHI.

Nitrate reduction efficiency in the plant: The effect of N on the plant practically means its uptake by the plant and further transforming to adequate organic forms. Both N uptake and accumulation in the plant are dependent on the rate of N participation in plant metabolism. NO₃-N is the basic form of N uptake

in natural conditions. This form should first be reduced to ammonium form to take part in plant metabolism. The first phase of this process, i.e. nitrate reduction to nitrites is under control of enzymes, nitrate reductase (Scheme c1). This is a key reaction and at the same time a limiting factor for both N uptake and utilisation in the plant. Therefore, the nitrate reductase activity is frequently suggested as the criterion of productivity. Johnson et al., (1976), found a highly positive correlation, ($r=0.90$) between the nitrate reductase activity and genotype productivity. However, the other researchers could not claim this with certainty, (Pavlov, Grabovskaja, 1978; Voronova et al., 1978). The nitrate reductase activity appears to be a necessary, but not the only condition required for high productivity. The other limiting factors for nitrogen metabolism exist in the plant, too.

N re-utilisation efficiency: Up to the fertilization stage, greater portion of N from wheat crop had been accumulated followed by N redistribution during reproductive stage. Large portion of nitrogen matter of vegetative organs was observed to flow into grain. This process is known as re-utilisation (Scheme c4). Its extent would depend on enzyme activity, performing the hydrolysis of the vegetative organ proteins and transporting the hydrolysis products into grain. Moreover, this process will be responsible for yield and NFE. Hence, the enzyme activity of the hydrolysis of the vegetative organ proteins appeared as the second limiting factor for metabolism and N utilization in the plant. At low re-utilisation of nitrogen from vegetative organs, great amounts of N from plant remain unused in the straw.

It is known that differences among varieties in re-utilisation efficiency do not always overlap with those in nitrate reductase activity. This is one of the major reasons for the nitrate reductase activity not always showing a high correlation with productivity and NUtE in the plant.

As evident from the scheme (c1 and c4), these processes are independent in terms of space and time. Their activity is determined by metabolic systems, which are not interrelated, but are under control of different genetic mechanisms (Šumnij et al., 1981; Gamzikova, 1994).

Assessment of variety efficiency

The differences among varieties in nitrogen nutrition efficiency are basically the differences in yield per fertilizer N unit or per N available in soil. This is the simplest way to assess the NFE. The varieties can further be assessed according to NUtE and NUtE in the plant. In this regard, the varieties can be fertilized with different N amounts, being adequate for each variety, hence these amounts of N will neither inhibit yield nor exceed the optimum amounts. Insofar as the varieties are not essentially different in demands for N and other characteristics, the investigations can proceed using equal N amounts, being somewhat lower than the optimum ones. In that case, the ranking of plants in terms of yield will overlap with that in terms of NFE. In addition, for testing varieties in NUtE, it is better to apply low and medium N amounts, and for studying NUtE medium and higher ones.

For a rapid screening of selection material immediately before sowing, the experiments could be conducted for 25 days, using lower N than the optimum. Promising genotypes should primarily be selected based on N accumulation, followed by NUtE in the plant and N overall efficiency. NUtE can reliably be assessed based on N uptake and its use in the sprouts emerging from grain in crops grown in sand, in quartz sand with no nutritive solutions (Đ o k i ć et al., 1994 a). Therefore, even more nitrogen was observed in sprouts than in grain, as well might be attributed to asimbiotic nitrogen fixation in the root isosphere.

On the other hand, the N nutrition efficiency can be assessed on the basis of relative lagging behind of yield or dry matter when N nutrition is, but scarce. The varieties, the yield of which is lagging behind when inadequate N amounts applied rather than adequate ones, are characterized by higher NUpE and NUtE, respectively. The so-called index of N efficiency is frequently used to measure NFE. This index represents the quotient of yield product of one genotype when N applied at two levels, (N1 and N2) and of X yield mean value for each genotype studied:

$$\text{NFI}_{\text{NE}} = \frac{Y_g(N1) \times Y_g(N2)}{Y_g(N1) \times Y_g(N2)}$$

The varieties with the above index being higher than one are considered efficient in N nutrition. This approach is often used in other studies, too.

Selection for yield

From N nutrition point of view, yield represents the product of N accumulation and utilization in the plant: $Y_g = AN \times \text{NUtE}$.

So, yield is not a simple magnitude, but a resultant of the two parameters, the values of which may extremely vary. Yield appears to be invariable either when high N accumulation is correlated with low utilization and vice versa, or in the case of mean values of both parameters. So far, N uptake from fertilizer and its use in the plant have shown sufficient degree of variability towards a successful selection for productivity and fertilizing efficiency by uniting peaks of both parameters into a new genotype. These parameters can be as easily determined and followed in terms of inheritance within selection process. However, when selection brings about reduced variability between the two parameters up to the level which can hinder good selection, the possibilities should be investigated for increasing this variability. Other parameters described above could be used for this purpose.

Based on our more recent results (Đ o k i ć et al., 1995), by uniting the peak of N accumulation of 51 mg on primary stem in one variety, (Jawa), and that of N utilisation of 46 g of grains per N g in the other (Partizanka), into a new genotype, (genotype X), the yield of 2.29g could be obtained, being by about 23% higher than that in the better yielding parent (scheme).

$$Y = AN \times \text{NUtE} = 51 \times 45 = 2.29\text{g}$$

Based on the same data, the NUtE in the plant would be increased to 50.6g of grains per N g, (genotype X1) when harvest index peak, (Skopljanka) and the minimum value of N concentration (CT-745) amount to 91% and 1.8%, respectively

$$\text{NUtE} = \text{HI} / \% \text{Ng} = 91 / 1.8 = 50.6$$

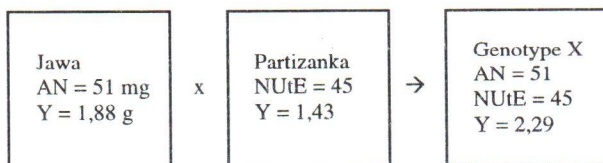
Combining thus increased NUtE in the plant (scheme, genotype X1) with N accumulation peak of 51g, the yield of 2.59g on primary stem will be obtained (genotype X2), being by 44% higher than that in the better yielding parent.

$$Y = \text{AN} \times \text{NUtE} = 51 \times 50.6 = 2.59\text{g}$$

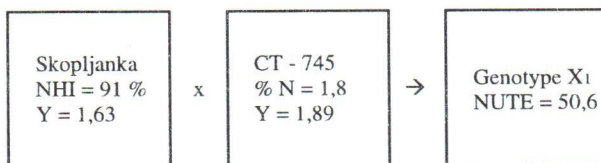
Mention should be made of the fact that uniting the peaks of N accumulation and utilisation in the plant into a new genotype might be rather difficult due to a negative correlation between these two parameters. The same holds true for the peaks of the NUPE and NUtE if the high NUPE is accompanied by high N accumulation. Therefore, it is desirable to obtain the genotypes with no peaks, but increased and balanced values of the two parameters.

Combination of wheat N nutrition parameters in selection process

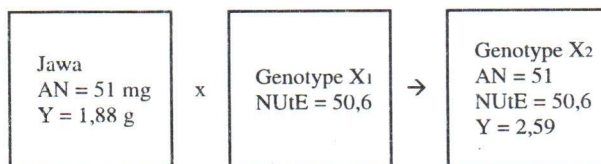
Combining parameters of wheat nutrition with N
in selection process



$$Y = \text{AN} \times \text{NUtE} = 51 \times 45 = 2,29 \text{ g}$$



$$\text{NUtE} = \text{NHI} / \% \text{Ng} = 91 \times 1,8 = 50,6$$



$$Y = \text{AN} \times \text{NUtE} = 51 \times 50,6 = 2,59 \text{ g}$$

Strategy of selection process for breeding varieties efficient in N nutrition

1. For selection of parental pairs, the studies will involve high yielding varieties represented in our production and worldwide.

2. The studies will be organized as field trials using three N amounts of 90, 120 and 150kg N/ha and control (without N added). These N amounts most often represent the optimum ones for individual groups of varieties in our soil - climatic conditions.

3. The selection of the varieties for inclusion in the selection process will proceed in two phases:

a) In the first phase, the most productive varieties from each group will be singled out with adequately chosen N amount. The selection will proceed on the basis of biological yield, harvest index of spike and yield per plant and primary stem spike. At the same time, these varieties will be characterized by the highest N fertilization (nutrition) efficiency.

b) In so selected material, the analyses will be made of N uptake and accumulation from fertilizer and soil and N accumulation in the plant.

4. On the basis of the above two parameters, all the varieties will be divided into three groups, as follows:

- with high N uptake and accumulation efficiency
- with high N utilisation efficiency in the plant
- with average values of the two parameters

At similar yields, growing conditions, and similar N amounts, the increased, average and decreased content of proteins will occur in the first, second and third group of genotypes, respectively.

The varieties fertilized with different N amounts will be divided into groups according to the NUpE from fertilizer, while the division within a group will be based on the level of N accumulation in the plant.

5. The varieties for hybridization will be selected to enable crossing the varieties with the highest NUpE and accumulation with those of the highest NUtE in the plant.

6. Individual selection from the hybrid progeny will start from the F2 generation in the manner as in selection (3 and 4); first, according to productivity, and second according to the parameters of N uptake and utilization in the plant.

7. The lines will be developed from the third group genotypes and selection will proceed towards breeding new varieties. The first and second group genotypes, as gene sources for increased N uptake and utilisation in the plant will be used for further hybridization.

Genetic control and inheritance of N nutrition of wheat

As already mentioned, NUpE and NUtE parameters are complex values of the integrated processes as the result of the activity of more simple parameters, each provided with its own system of genetic control. Therefore, a question arises whether and how the two systems are tied up in entities, representing genetic mechanisms controlling both complex parameters. As being separated in terms of

time and space and substantially different in their physiology, it is assumed that these processes are under control of two independent genetic systems. One is responsible for N uptake from fertilizer and soil, and the other for N utilization in the plant. However, little work has been done on these systems so far. Moreover, the absence of clear concepts about genetic mechanisms for controlling N nutrition makes it difficult to use and manage these processes in selection work towards increased N nutrition efficiency.

Table 7 - Identification and localization of genes controlling the processes of mineral nutrition in the plant

Gene Type	control of the process	literature
ys	Controls Fe adoption by maize	Beadle 1929.
fe	Disruption of the reduction $\text{Fe}^{3+} \rightarrow \text{Fe}^{2+}$ in soybean roots	Weiss 1943.
btl	Inhibition of Cu transport from the root to above ground tomato organs	Wall, Andruss 1962.
np	Soybean susceptibility to high P- feeding level	Bernard, Hawel 1964.
ke	Efficiency of K - feeding with beans	Shea et al 1967.
nia	Inhibition of NRA in tobacco	Muller et al 1978. 1983.
nar 1 - 4	Revelation of NRA in barley	Kleinhofs et al 1978. Tokarev, Šumni 1978. Godovikova 1985.
nr ₁	Regulation of nitrates assimilaition in soyban	Nelson et al 1984.
Fe ₁ Fe ₂	Wheat adaptivity to Fe deficiency	Majstrenko, Godovikova 1989.
genes of the ninth chromosome	Accumulation of Ca and P in maize hybrids	Naismith et al 1974.
genes of the longer arm in ninth chromosome	Accumulation of M11 in maize leaf	Naismith et al 1987.
5R chromosome in rye	Resistance to Cu deficiency in substitution lines of wheat	Graham et al 1987.
5A chromosome in winter wheat	N - feeding improvement in spring cultivar Saratovskaja 29	Gamzikova 1994.

Testing the genetic control and mineral nutrition inheritance dates from the recent years. Except for the first works of B e a d l e (1929) relating to genet-

ic control examined in chlorotic streak on maize mutants and those of Harwey (1939) on hereditary uptake of ammonium and nitric nitrogen, the first more systematic and comprehensive investigations in this field appeared as late as the twenties of this century (Tab.7). These examinations are mostly related to the studies of genetic control on nitrogen uptake and metabolism in wheat crop (Tab.8). The above stated studies first occurred in the U.S. (O. Sullivan et al. 1974; Gerloff 1976; Gabelman 1977; Eirlich, Hageman 1973; Deckart et al. 1982), then in the Soviet Union (Tokarev, Šumnić 1977, 1982; Gamzikova et al. 1984; Gamzikova, Kalašnjik 1988; Gamzikova et al. 1988-1989, 1990-1991; Godovikova 1985; et al. Majstrenko et al. 1986), in Germany (Mettin et al. 1980), Hungary (Kiss et al. 1983; Kiss, Balint 1988), Bulgaria (Bočev, Ganeva 1984) and Yugoslavia (Mihaljev, Kastori 1983).

Table. 8 - Genetic control inheritance of NUpE and NUtE in wheat,
(Gamzikova, 1994)

result	literature
High heritability of NR activity	Eirlich, Hageman, 1973.
Inheritance of N harvest index	Austin et al, 1997.
Share of chromosomes of 2,4 and 6 homologous in controlling adoption and transport of N	Mettin et al, 1980.
Intermediary inheritance of N accumulation in kernel	Galterio et al, 1983.
Polygenic control of N adoption and translocation in plant	Kiss et al, 1983.
Predominant share of additive variability in controlling N-content in tip leaf	Mihaljev, Kastori 1983.
Positive effect of cytoplasm on N adoption and concentration in kernel	Bochev et al, 1983.
Expression of awn genes affected y n-feeding	Bočev, Ganeva 1984.
Genetic control of utilization N, soil, fertiliser	Gamzikova i dr., 1984.
Identification of chromosomes determining the response to N-feeding level	Gamzikova i dr., 1984.
Establishing the correlation of 5A with response to N-feeding level	Majstrenko i dr., 1986.
Intermediary inheritance of N-utilisation trait in crops	Kiss, Balint 1988.
Genetic systems of N-utilisation control, and response to N-feeding level	Gamzikova, Kalašnjik 1988.
Identification of chromosomes determining N-accumulation and distribution in the plant	Gamzikova i dr., 1988.
Additive effect of genes controlling harvest-index of N	Sajfulin i dr., 1989.
Pleotropic effect of Rht gene on N adoption and utilisation from soil and fertiliser	Gamzikova, 1990. Gamzikova i dr., 1989., 1991.

The present study on the wheat variety Chinese Spring has shown that in the control of adoption and distribution of nitrogen in the wheat crop at least seven chromosomes are included (Balint et al. 1983; Kiss et al. 1983; Kiss, Balint 1988). It is also pointed at the significance of aggregate genes of cytoplasm in nitrogen adoption in the crops and at nitrogen concentration in grain as well as at the fact that cytoplasm largely modifies the effect of the genes of nucleus on adoption of mineral nutrients.

According to Gamzikova (1994), nitrogen nutrition of wheat is controlled by a complex system of additively dominant genes. The genes with particularly pronounced effect on nitrogen adoption and metabolism process have been identified. They belong to genomes of all the three groups of wheat ploidy.

Substitution of chromosomes with soft wheat crops proved fairly efficient approach to nitrogen nutrition upgrading. Gamzikova (1994) obtained the best efficiency, when 5A chromosome of winter varieties was entered in genotypic medium of the spring variety Saratovskaja 29, and somewhat lesser effect in the case of 5A, 1D and 7D chromosomes intrinsic to the spring variety Janetckis Probat. Better effect resulted not only from the property of the chromosome entered, but also from its interaction with genotype of the variety being acceptor. On the basis of the analyses it may be concluded that from the selection standpoint, genetic sources are important to enhanced and extended activity of the root system, which would presumably contribute to greater adoption of nitrogen from the soil and fertilizer, as well as to the gene sources to improve the activity, i.e. nitrogen-in-plant utilisation. Such studies would cement the ideas on the so-called physiological-genetic methods of the varieties as to be efficient owing to N nutrition.

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FIZIOLOŠKE OSNOVE SELEKCIJE PŠENICE NA EFIKASNOST ISHRANE AZOTOM

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Rezime

U radu se na osnovu sopstvenih i ispitivanja drugih autora analizira-ju fiziološke osnove ishrane pšenice azotom u cilju stvaranja sorata efikasnih u usvajanju i iskorišćavanju azota. Efikasnost đubrenja, (ishrane), azotom definiše se kao aktivnost jedinice azota đubriva, ili pristupačnog azota zemljišta u formiranju prinosa. Efikasnost ishrane pšenice azotom, (EFN), zavisi od njegovog usvajanja iz đubriva, (AN), i njegovog iskorišćavanja u biljci, (UN) u formiranju prinosa. Efikasnost usvajanja azota iz đubriva meri se odnosom usvojenog i upotrebljenog azota, (EAN = AN/Nf), a efikasnost iskorišćavanja količinama prinosa po jedinici azota biljke, (EUN = Yg/AN). Efikasnost đubrenja azotom predstavlja njihov proizvod:

$$EDN = EA \times EU = \frac{AN}{ND} \times \frac{Yg}{AN} = \frac{Yg}{Nd}$$

Efikasnost đubrenja azotom meri se povećanjem prinosa zrna pod uticajem đubrenja po jedinici azota đubriva.

Prema veličini ova dva parametra sve sorte pšenice su podeljene u četiri grupe:

1. Visoka efikasnost usvajanja i visoka efikasnost iskorišćavanja azota - visoka efikasnost ishrane azotom
2. Visoka efikasnost usvajanja i niska efikasnost iskorišćavanja azota - osrednja efikasnost ishrane azotom
3. Niska efikasnost usvajanja i visoka efikasnost iskorišćavanja - osrednja efikasnost ishrane azotom
4. Niska efikasnost usvajanja i niska efikasnost iskorišćavanja azota - niska efikasnost ishrane azotom

Osim ova dva analizirani su i drugi mogući parametri za efikasnost ishrane azotom, kao što su: biološki prinos, prinos zrna i žetveni indeks; razvijenost i aktivnost korenovog sistema; koncentracija azota u biljci i zrnu i slami; akumulacija azota u biljci u periodu pre i posle oplodnje; žetveni indeks azota; efikasnost redukcije nitrata u biljci; efikasnost reutilizacije azota u biljci.

Ispitivanja su pokazala da efikasnost usvajanja i iskorišćavanja azota u biljci ispoljavaju znatna modifikaciona i genotipska variranja što daje osnove za poboljšanje efikasnosti ishrane azotom. Efikasnost usvajanja azota iz đubriva varirala je 10 do 90%, a efikasnost iskorišćavanja od 30 do 60kg zrna na kg azota biljke. Ako bi smo usvajanje azota iz đubriva povećali od 50 na 75%, a njegovo iskorišćavanje u biljci od 40 na 50kg zrna azota biljke, onda bi smo uobičajene kličine azota za pšenicu od oko 120kg N/ha smanjili na polovinu. Za ostvarivanje takvih poboljšanja u efikasnosti ishrane azotom postoje agrotehnički i selekcionogenetički putevi pri čemu se prednost daje selekcionogenetičkim.