CHILEANJAR
CHILEAN JOURNAL of AGRICULTURAL RESEARCH

RESEARCH

INTERRELATIONSHIPS BETWEEN GRAIN NITROGEN CONTENT AND OTHER INDICATORS OF NITROGEN ACCUMULATION AND UTILIZATION EFFICIENCY IN WHEAT PLANTS

Olivera Nikolic[1*], Tomislav Zivanovic[2], Miodrag Jelic[3], and Ivica Djalovic[4]

The topic of N wheat nutrition was prevalent during the last decades of the 20th century for many reasons such as energy crises, profitability of small grain production, and ecosystem protection and preservation. The objective of this study was to determine the interrelationships between wheat (*Triticum aestivum* L.) grain N content and other indicators of N nutrition efficiency to better understand the N nutrition process in wheat plants. The experiment included 30 wheat cultivars and experimental lines from Serbia. Plant samples of each genotype were taken at anthesis and maturity. The following parameters related to N accumulation and translocation within the wheat plant were calculated: N content (at anthesis, grain, straw, and total at maturity), N harvest index (NHI), N reutilization (N reU), and N lost (-) or gained (N post-anthesis). Our results showed that N content in the aboveground part of the plant expressed very strong direct positive effects on N yield (phenotypic coefficient 3.78** to 9.34** and genotypic coefficient 1.43** to 2.32**), while its indirect effects varied. The influence of independent variables on grain N content has been changing from year to year in a negative way. Total N accumulation (N total) had the highest negative direct effect in the first year of the study (phenotypic coefficient -2.11**), N total in the second (phenotypic coefficient -2.78**), and N reutilization in the third (phenotypic coefficient -8.49**). Genotypic coefficients indicate that the most frequent strong direct negative effect was N reutilization (-0.47** and -0.99** in the first 2 yr of research, respectively). Nitrogen reutilization and its current assimilation are very important and related to grain N supply processes. Their interaction leads to the conclusion that forming N yield is a very complex mechanism and, as a result, grain yield and quality. The abovementioned parameters could be considered as important criteria in wheat breeding to improve production efficiency and reduce adverse impacts of N fertilizers on the ecosystem.

Key words: Interactions, nitrogen nutrition, path coefficients, *Triticum aestivum*.

Nitrogen is one of the main nutrients of the winter wheat crop. It is responsible for grain formatting and protein synthesis, i.e., the technological quality of grain. The topic of N wheat nutrition was prevalent during the last decades of the 20th century for many reasons. Fertilizers are an important percentage of direct crop costs and prices have escalated as a consequence of energy crises. This has caused the decrease in profitability of small grain production, including wheat. Among the fertilizer inputs used in wheat crops, N fertilizer normally affects production costs more than other inputs (Shrawat *et al*., 2008; Campillo *et al*., 2010). The excessive use of N fertilizers adapted to soil fertility conditions and plant needs also affects the decrease in profitability of wheat production (Zagal *et al*., 2003).

Using fertilizers is unavoidable in the wheat planting system to achieve a high grain yield. With an expanding world population, the challenge for the next decades will be to develop a highly productive agricultural sector while preserving the quality of the environment (Hirel *et al*., 2001; Patel *et al*., 2004; Shrawat *et al*., 2008; Weinkauf, 2008). One way to enhance productivity, maintain efficient production, and minimize environmental impact is to develop specific cropping strategies and select productive genotypes that can grow under low N conditions (Delmer, 2005). A multidisciplinary approach to breeding winter wheat that includes physiological indicators of N nutrition efficiency could help to achieve this goal (van Ginkee *et al*., 2001; Baker *et al*., 2004; Flowers *et al*., 2004; Zivanovic *et al*., 2006; Pathak *et al*., 2008). This approach to fertilization and mineral nutrition is appropriate in developing alternative forms of crop production such as organic and ecological (Knezevic *et al*., 2007; Murphy and Jones, 2007; Shrawat *et al*., 2008; Casagrande *et al*., 2009).

Increased N nutrition efficiency and absorption from soil reserves and applied fertilizers can be obtained

---

[1] EDUCONS University, Faculty of Ecological Agriculture, 35210 Svilajnac, Svetog Save 60, Serbia.
[*] Corresponding author (nikolicolivera69@yahoo.com).
[2] Belgrade University, Faculty of Agriculture Zemun, Nemanjina 6, 11080 Belgrade, Serbia.
[3] Prishtina University, Faculty of Agriculture Lesak, Kopaonicka bb, 38219 Leshak, Serbia.
[4] Institute of Field and Vegetable Crops, Novi Sad, Maksima Gorkog 30, 21000 Novi Sad, Serbia.
Received: 13 April 2011.
Accepted: 20 December 2011.

by increased mass or by the root system's absorbing capability. Given the natural environment needed for root system development, it is almost impossible to follow its formation and activity. We can make some indirect conclusions about the root system absorbing N more easily on the basis of some physiological parameters such as plant N accumulation at flowering, in the grain, in the straw, and total N.

Significant correlations between the accumulation of total N in a plant and grain yield, as well as all the indicators of N nutrition efficiency, were obtained in many research studies (Emam *et al*., 2009; Nikolic, 2009). Some results indicate interrelationships among all these parameters, especially N accumulated in wheat grain and grain protein content (Martre *et al*., 2003; Acreche and Slafer, 2009). Hence, it is easily concluded that the wheat plant N supply is important under several aspects (Öztürk, 2010). Sufficient amounts of N in the plant can overcome the negative correlation between wheat grain yield and protein content that is the principal obstacle in breeding wheat for both traits simultaneously. Better knowledge of the wheat plant N nutrition process, correlations of its efficiency indicators, and its relationship to grain yield and quality can significantly contribute to wheat breeding. Including these physiological parameters in classical wheat breeding programs can facilitate achieving well-adjusted wheat grain yields and adequate quality along with the need to rationalize production, reduce fertilizer use, and protect the ecosystem (van Ginkee *et al*., 2001). The obstacles to include physiology in wheat selection and breeding programs are related to the nature of physiological traits, the complexity of their interactions, and the sensitivity to external conditions as documented by site and year variability of the parameters (Asseng and Milroy, 2006; Váňová *et al*., 2006; Estrada-Campuzano *et al*., 2008).

The objective of this study was to determine the interrelationships between wheat grain N content and other indicators of N accumulation and utilization efficiency, i.e., N nutrition efficiency in order to better understand the N nutrition process in wheat plants.

MATERIALS AND METHODS

The study was carried out at the Small Grains Research Center in Kragujevac (186 m. a.s.l.) in Serbia during three consecutive seasons (2001-2002, 2002-2003, and 2003-2004). The soil type was smonitza in degradation (Vertisol). It is characterized by a heavy mechanical composition, instability, rough structure, and low porosity (Jelic, 1996). The chemical analyses were carried out in the Agrochemical Laboratory of the Center and indicated a moderate level of soil fertility and acidity (Table 1).

The mean temperatures and monthly rainfall during the wheat vegetation period (October-June) for the three seasons and the 30-yr mean (1970-2000) are shown in Table 2. Mean temperature was higher than the 30-yr mean in all of the 3 yr. The amount and distribution of rainfall varied considerably from year to year. The amount of rainfall was most suitable for plant growth in the third season. Rainfall (74.5 mm) during the germination period (October-November) in the first season was less than in the other two (97.00 and 111.8 mm) and the long-term mean (94.73 mm). Rainfall distribution during the rest of the vegetative period in the first season improved, but total rainfall was less than the long-term means.

Table 1. Chemical characterization of soil (0-20 cm) before establishing experiments (summer 2001).

Chemical characteristics	Summer 2001
Water pH	6.23
KCl pH	5.15
Total N, %	0.25
Available K, mg 100 g^{-1}	28.8
Available P, mg 100 g^{-1}	13.8
Organic matter, %	2.65

Table 2. Weather conditions during the three test growing seasons and long-term (30-yr) mean (LTM) for winter wheat.

	Mean monthly temperatures				Monthly rainfall			
Months	2001-2002	2002-2003	2003-2004	LTM	2001-2002	2002-2003	2003-2004	LTM
	°C				L			
October	13.8	12.2	10.6	11.40	10.4	65.5	83.2	47.53
November	4.6	9.7	8.9	5.90	64.1	31.5	28.6	47.20
December	-2.4	1.1	2.2	2.13	27.6	39.4	37.2	44.33
January	-0.1	0.7	-0.9	0.73	17.2	59.0	86.4	36.70
February	7.0	-2.4	3.0	2.42	20.1	19.7	59.5	35.77
March	8.9	5.8	7.1	6.43	26.0	2.8	21.3	41.57
April	10.8	10.8	12.8	11.22	63.7	37.2	52.3	50.77
May	18.4	19.9	14.5	16.24	38.6	42.3	50.3	65.43
June	21.6	23.3	19.8	19.40	57.2	47.7	61.4	81.27
	Seasonal mean				Total			
	9.18	9.01	8.67	8.43	324.9	345.1	483.2	624.43

The experiment included the following 30 wheat cultivars and experimental lines from Serbia's Small Grains Research Center, Kragujevac, and from the Institute of Field and Vegetable Crops, Novi Sad: Morava, Lepenica, Studenica, Takovcanka, Toplica, Srbijanka, KG 100, Lazarica, Bujna, Matica, Vizija, Pobeda, Rana 5, Evropa 90, Renesansa, Tiha, Mina, Prima, Kremna, Rusija, Pesma, KG-200/31, KG-253/4-1, KG-115/4, KG-165/2, KG-56/1, KG-100/97, Perla, KG-224/98, and KG-10.

The basic processing and pre-sowing soil preparation followed standard procedures. The experiment was a randomized complete block design with five replicates in 1.5 m long rows with 0.20 m spacing between rows. Manual sowing (200 grains per row and one genotype per row)) was done during the optimal winter wheat planting period for conditions in central Serbia (29 October 2001, 15 November 2002, and 06 November 2003). Before sowing in each season, NPK fertilizer (8:24:16) was applied at 300 kg ha^{-1}. At the tillering stage of each season, 8 g N row^{-1} (260 kg KAN ha^{-1}) was added.

Plant samples of each genotype were taken at anthesis (10 plants per replicate) and maturity (five plants per replicate). Samples were air-dried and the aboveground plant weight at anthesis (DM anthesis, g m^{-2}), grain yield (GY, g m^{-2}), straw weight at maturity (DM straw, g m^{-2}), and total aboveground biomass at maturity (BY, g m^{-2}) were measured. All dry vegetative samples and grain were first ground and plant N concentration was then determined by the standard macro-Kjeldahl procedure. Nitrogen content (at anthesis, grain, straw, and total at maturity) was calculated by multiplying N concentration by dry weight (g N m^{-2}). Moreover, the following parameters related to N accumulation and translocation in the wheat plant during grain filling were calculated according to Arduini *et al*. (2006) and Masoni *et al*. (2007):

N harvest index (NHI) = N grain/N content of aboveground parts at maturity (N total) (%) [1]

N reutilization (N reU) = N anthesis – N straw (g m^{-2}) [2]

N lost (-) or gained (N post-anthesis) = N content at maturity – N content at anthesis (g m^{-2}) [3]

The resulting data were statistically analyzed. Multiple regression "path" analysis (Wright, 1934; Ivanovic, 1984) was applied to determine the direct influence of N nutrition efficiency indicators (independent variables) on grain N content (dependent variable), as well as the indirect influence through other variables, standard errors of path coefficients, and significance testing.

In statistics, standardized coefficients are the estimates resulting from an analysis carried out on variables that have been standardized so that their variances are 1. This means that they refer to the expected change in the dependent variable per standard deviation increase in the predictor variable. Standardization of the coefficient is usually done to answer the question about which of the independent variables have a greater effect on the dependent variable in a multiple regression analysis when the variables are measured in different units. A path coefficient is a standardized regression coefficient. Standardized path coefficients were calculated by the inverse correlation matrix method (Edwards, 1979):

$$\left[R_{ij}\right] x \left[B_{yi}\right] = \left[R_{yi}\right] \Rightarrow \left[B_{yi}\right] = \left[R_{ij}\right]^{-1} x \left[R_{yi}\right]$$

where R_{ij}: symmetrical correlation matrix of independent variables; B_{yi}: standardized regression coefficient (path coefficient); R_{yi}: correlation coefficient of independent variables and dependent variable; and R^{-1}_{ij}: inverse matrix of R_{ij}.

The observed correlation can be decomposed into four parts: (1) Direct Effect (DE) due to the path from X to Y; (2) Indirect Effect (IE) due to paths through intermediate variables; (3) Unanalyzed (U) due to correlated exogenous variables; and (4) Spurious (S) due to third variable causes.

Not all correlations are composed of all four parts. Path analysis coefficients can be expressed in either of two metrics. The first metric is called unstandardized and employs the measurement scale of the original variables, whereas the second metric is identified as standardized. In fact, this is the result of a path analysis or regression performed on all variables that have been transformed into standardized variables (i.e., with means of 0 and standard deviations of 1.0). The path coefficients equal the standardized regression coefficients in standardized units and the purpose is to explain the proportions of variance and the correlations among variables.

RESULTS AND DISCUSSION

The correlation coefficient measures the mutual association between a pair of variables independently of other variables to be considered. Therefore, when more than two variables are involved, the correlations *per se* do not give the complete information about their relationships. Path coefficient analysis is particularly useful to study the cause and effect relationship because it simultaneously considers several variables in the data set to obtain the coefficients (Jedinski, 2001; Kashif and Khaliq, 2004).

Path coefficient analysis (Table 3) shows how the total contribution of N accumulation and utilization efficiency parameters to grain N content (N yield) was divided into direct and indirect contributions. Path correlation analysis revealed that plant N accumulation at anthesis (N anthesis) had the highest positive direct effect on grain N content in the first and third year (phenotypic coefficient 3.78** and 9.34**, respectively), or in the second and third year of the study (genotypic coefficient 1.43** and 2.32**, respectively). The influence of independent variables on grain N content has been changing from year to year in a negative way. Total N accumulation (N total) had the highest negative direct effect in the first year of the study (phenotypic coefficient -2.11**), N total in the second (phenotypic coefficient -2.78**), and N reutilization (N reU) in the third (phenotypic coefficient -8.49**). Genotypic coefficients indicate that the most frequent strong direct negative effect was N reutilization (-0.47** and -0.99** in the first and second year of research, respectively), while it was total N accumulation in the third season (-2.33).

Total N contribution at anthesis (genotypic coefficients) to grain N content varied from 0.30 to 0.87. Its partitioning points to the often negative impact via N reutilization were in all 3 yr. A very strong positive effect of accumulated plant N prior to anthesis to grain N content via total N accumulation (N total) in the first season (genotypic coefficients 0.91) indirectly points to a complex action mechanism of certain indicators and the need for synergy of a number of plant processes to the manifestation of desired effects on the dependent variable. It was also observed that out of the total contribution of 0.81 (phenotypic coefficient) by N anthesis to N yield in the first year, 3.78 was directly contributed, while the indirect influence via NHI (phenotypic coefficient 0.01) was negligible. On the contrary, negative indirect effects of N anthesis via N total accumulation (phenotypic coefficient

Table 3. Direct (boldface) and indirect effects of physiological parameters of N nutrition efficiency on grain N content in winter wheat t-test significance level: *P < 0.05; **P < 0.01.

					2001-2002					
Phenotypic coefficients						Genotypic coefficients				
Via	N anthesis	N total	NHI	N reU	N post-anthesis	Via	N anthesis	N total	NHI	N reU	N post-anthesis
N anthesis	**3.78****	3.25	0.08	3.55	1.10	N anthesis	**0.43****	0.34	-0.01	0.37	0.11
N total	-1.82	**-2.11****	0.04	-1.41	-1.54	N total	0.91	**1.14****	-0.26	0.72	0.79
NHI	0.01	-0.01	**0.71****	0.21	-0.14	NHI	0.00	-0.05	0.21**	0.04	-0.07
N reU	-1.55	-1.10	-0.48	**-1.65****	-0.02	N reU	-0.41	-0.29	-0.10	**-0.47****	0.01
N post-anthesis	0.38	0.96	-0.26	0.01	**1.31****	N post-anthesis	-0.06	-0.16	0.08	0.00	**-0.23****
Total	0.81	0.98	0.09	0.71	0.71	Total	0.87	0.98	-0.08	0.67	0.6
					2002-2003					
N anthesis	**-2.78****	-0.97	0.64	-2.56	1.03	N anthesis	**1.43****	0.20	-0.51	1.21	-0.84
N total	0.62	**1.78****	0.84	0.30	1.12	N total	0.06	**0.40****	0.09	-0.04	0.21
NHI	0.13	-0.26	**-0.55****	0.09	-0.26	NHI	-0.12	0.07	**0.33****	-0.10	0.10
N reU	2.17	0.40	-0.38	**2.36****	-1.27	N reU	-0.84	-0.22	0.30	**-0.99****	0.71
N post-anthesis	0.00	0.01	0.01	-0.01	**0.01**	N post-anthesis	-0.22	0.20	0.11	-0.27	**0.38****
Total	0.13	0.96	0.56	0.18	0.63	Total	0.30	0.96	0.31	-0.06	0.56
					2003-2004					
N anthesis	**9.34****	4.45	-3.45	4.44	1.77	N anthesis	**2.32****	1.60	-0.35	1.74	0.37
N total	-3.70	**-5.49****	1.96	-3.13	-3.70	N total	-1.61	**-2.33****	0.14	-0.84	-1.73
NHI	-0.33	-0.14	**4.70****	2.07	0.09	NHI	-0.06	-0.03	**0.43****	0.10	0.01
N reU	-7.13	-3.90	-3.74	**-8.49****	1.02	N reU	-0.19	-0.09	-0.06	-0.26	0.04
N post-anthesis	2.46	3.04	0.73	-4.40	**6.63****	N post-anthesis	0.33	1.51	0.04	-0.29	**2.04****
Total	0.63	0.96	0.21	0.50	0.82	Total	0.78	0.66	0.20	0.46	0.73

NHI: N harvest index; N reU: N reutilization; N post-anthesis: N lost (-) or gained.

-1.82) and N reutilization (phenotypic coefficient -1.55) to N yield were greater. This cannot explained if we bear in mind the generally positive relationships between all these parameters (Nikolic, 2009).

On the other hand, there are results showing that higher reutilization is usually followed by low grain protein content where higher N reutilization efficiency is used to increase grain yield (Hirzel *et al*., 2010). Although we take into consideration the indirect effects of N reutilization to grain N content via N accumulation at anthesis, we notice that the effect is almost positive and significantly high, except for the second year, and varied from 0.37 to 1.74 (genotypic coefficients) or from 3.55 to 4.44 (phenotypic coefficients). These results can be supported by previous research studies that emphasize that the bulk of grain N derived from N from vegetative organs accumulated in the development stages up to flowering to its mobilization and utilization processes (Stojkovic *et al*., 2003). Total contribution by N reutilization to grain N content was largely positive and ranged from 0.46 to 0.67 (genotypic coefficients) or from 0.18 to 0.71 (phenotypic coefficients). It was also recorded that N reutilization negatively and strongly affected grain N content via total N accumulation in the last season (genotypic coefficient -0.84). The processes of N reutilization and its post-anthesis accumulation are involved in N grain accumulation. The N post-anthesis accumulation only had a direct negative influence on N grain content (genotypic coefficient -0.23**) in the first year, but it was very weak. The highest direct effects of these parameters on N yield were recorded in the third season (genotypic coefficient 2.04**). Indirect effects of N post-anthesis accumulation were mostly negligible, except via total N accumulation (genotypic coefficients 0.79 and 1.73), N at anthesis (genotypic coefficient -0.84), and N reutilization (genotypic coefficient 0.71), a very interesting fact. The very strong positive synergy of N reutilization and N post-anthesis accumulation, as two very important N accumulation processes in wheat grain and with simple inverse correlations (Nikolic, 2009), suggests a very complex mechanism to form N yield and grain yield and quality and represents a significant foothold in wheat breeding. Mi *et al*. (2000) investigated the effect of applying N post-anthesis to N uptake and grain N content. They found that an additional N application during flowering could increase N uptake and grain N content, but the degree of increase differed among cultivars.

In a broader sense, term N utilization (NU) in a plant means its participation in the formation of grain yield and protein. Moll *et al*. (1982) defined NU efficiency (NUE) as grain production per unit of available N in the soil. These authors indicated that available soil N and total plant N are difficult to measure adequately. They established that NUE can be divided into the components of N uptake efficiency (plant N per unit of N fertilizer) and N utilization efficiency (grain yield per unit of plant N). The product of these two components is expressed as NUE (Moll *et al*., 1982; Ortiz-Monasterio *et al*., 1997; Dawson *et al*., 2008). The nitrogen harvest index (NHI) is usually used as a parameter for evaluating N utilization efficiency for protein synthesis. It represents a percentage of grain N in total plant N. Plant nitrogen utilization and increase in the yield is measured by the physiological N efficiency (PEN) parameter. Except for these parameters, N reutilization and N post-anthesis accumulation are also important indicators of wheat plant N nutrition efficiency. We dedicated special attention to N reutilization as the indicator of its utilization efficiency because this genotype characteristic is desirable in high temperature and limited N assimilation conditions during the generative period. Wheat grain is obtained up to one third from current N absorption and from vegetative organs; up to as much as 60-94% according to some research (Bebyakin and Kairgaliev, 2004; Barbottin *et al*., 2005).

Regardless of the genotypic and phenotypic coefficients, the highest total influence on N yield is total N in the mature plant (N total). Its values ranged from 0.66 to 0.98. The direct contribution of total N to grain N content was very often negative, but its positive effects via other parameters were significant (1.65, 3.25, and 4.45 via N at anthesis, or 1.51 and 3.04 via N post anthesis accumulation). Negative indirect influences were negligible. Total N in maturated plants is highly significant and there is frequently a strong relationship with accumulated N in the plant up to anthesis and N post-anthesis accumulation in wheat, but also in other plant species (Przulj and Momcilovic, 2001; Mariotti *et al*., 2003; Nikolic, 2009).

CONCLUSIONS

Nitrogen content in the aboveground part of the plant expressed very strong direct positive effects on grain N content (N yield) (phenotypic coefficient 3.78** to 9.34** and genotypic coefficient 1.43** to 2.32**), while its indirect effects varied. The direct effect of N reU on grain N was statistically significant and very often negative (phenotypic coefficient from -1.65** to -8.49** and genotypic coefficient from -0.26 to -0.99**), but the total contribution to grain N content by N reutilization was largely positive and ranged from 0.46 to 0.67 (genotypic coefficients) or from 0.18 to 0.71 (phenotypic coefficients). The indirect effects of N reutilization to grain N content via N accumulation at anthesis was almost positive and significantly high, except for the second year that varied from 0.37 to 1.74 (genotypic coefficients) or from 3.55 to 4.44 (phenotypic coefficients). The highest total influence on N yield was total N in mature plants (N total) with values that ranged from 0.66 to 0.98. The studied parameters have very complex relationships mostly with statistically significant effects on grain N content. The abovementioned parameters could be considered as an important pillar in wheat breeding for the increased yield and quality potential of genotypes through improved efficiency of N absorption and utilization. Further studies about many aspects are necessary to determine their interdependence and find possible uses as criteria in wheat breeding.

ACKNOWLEDGEMENTS

This paper is part of an investigation supported by the Ministry of Science and Technological Development (Government of Republic of Serbia), project 31054.

Relaciones entre el contenido de nitrógeno del grano y otros indicadores de acumulación y eficiencia de utilización de nitrógeno en plantas de trigo. La nutrición de N en trigo se ha vuelto un tema actual durante las últimas décadas del siglo pasado por muchas razones, como la crisis energética, rentabilidad de la producción de cereales de grano pequeño y la preservación y protección de los ecosistemas. El objetivo de este estudio fue determinar las interrelaciones entre el contenido de N del grano de trigo (*Triticum aestivum* L.) y otros indicadores de la eficiencia de nutrición del N para mejorar la comprensión del proceso de nutrición de N en la planta de trigo. Nuestros resultados mostraron que el contenido de N en parte aérea de la planta expresó efectos positivos directos muy fuertes sobre el rendimiento de N (coeficiente fenotípico 3,78** - 9,34** y coeficiente genotípico 1,43** - 2,32**), mientras que sus efectos indirectos variaron. La influencia de las variables independientes sobre el contenido de N del grano, en sentido negativo, ha ido cambiando de año en año. La acumulación de N total (N total) tuvo el mayor efecto negativo directo en el primer año (-2,11** coeficiente fenotípico), N total en el segundo año (-2,78** coeficiente fenotípico) y la reutilización de N en el tercer año de investigación (coeficiente fenotípico -8.49**). Coeficientes genotípicos indican que el efecto negativo directo frecuentemente más fuerte (en los primeros 2 años de investigación) tenía reutilización de N (-0,47** y -0,99**, respectivamente). Reutilización del N y su asimilación actual son procesos muy importantes y relacionados en el suministro de N del grano. Su interacción lleva a la conclusión de un mecanismo muy complejo de formación de rendimiento de N y, en consecuencia, del rendimiento y calidad del grano. Los parámetros mencionados podrían ser considerados como criterios importantes en el mejoramiento de trigo para mejorar la eficiencia de producción y para reducir los impactos adversos de fertilizantes nitrogenados en el ecosistema.

Palabras clave: *Triticum aestivum*, interacciones, nutrición de nitrógeno, coeficientes de trayectoria.

LITERATURE CITED

Acreche, M.M., and G.A. Slafer. 2009. Variation of grain nitrogen content in relation with grain yield in old and modern Spanish wheat grown under a wide range of agronomic conditions in a Mediterranean region. Journal of Agricultural Science 147:657-667.

Arduini, I., A. Masoni, L. Ercoli, and M. Mariotti. 2006. Grain yield, and dry matter and nitrogen accumulation and remobilization in durum wheat as affected by variety and seeding rate. European Journal of Agronomy 25:309-318.

Asseng, S., and S.P. Milroy. 2006. Simulation of environmental and genetic effects on grain protein concentration in wheat. European Journal of Agronomy 25:119-128.

Baker, D.A., D.L. Young, D.R. Huggins, and W.L. Pan. 2004. Economically optimal nitrogen fertilization for yield and protein in hard red spring wheat. Agronomy Journal 96:116-123.

Barbottin, A., C. Lecomte, C. Bouchard, and M.H. Jeuffroy. 2005. Nitrogen remobilization during grain filling in wheat: genotypic and environmental effects. Crop Science 45:1141-1150.

Bebyakin, V.M., and D.V. Kairgaliev. 2004. Content, distribution and reutilization of nitrogen in organs of spring soft wheat discriminated on protein content in corn. Sel'skohozâjstvenaâ biologiâ 5:68-75.

Campillo, R., C. Jobet, and P. Undurraga. 2010. Effects of nitrogen on productivity, grain quality and optimal nitrogen rates in winter wheat cv. Kumpa-INIA in Andisols of southern Chile. Chilean Journal of Agricultural Research 70:122-131.

Casagrande, M., C. David, M. Valantin-Morison, D. Makowski, and M.H. Jeuffroy. 2009. Factors limiting the grain protein content of organic winter wheat in south-eastern France: a mixed-model approach. Agronomy for Sustainable Development 29:565-574.

Dawson, J.C., D.R. Huggins, and S.S. Jones. 2008. Review. Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems. Field Crops Research 107:89-101.

Delmer, D. 2005. Agriculture in the developing world: connecting innovations in plant research to downstream applications. Proceedings of the National Academy of Sciences, USA 102:15739-15746.

Edwards, A.L. 1979. Multiple regression and the analysis of variance and covariance. p. 54-67. W.H. Freeman, San Francisco, California, USA.

Emam, Y., K.S. Salimi, and A. Shokoufa. 2009. Effect of nitrogen levels on grain yield and yield components of wheat (*Triticum aestivum* L.) under irrigation and rainfed conditions. Iranian Journal of Field Crop Research 7:323-334.

Estrada-Campuzano, G., D.J. Miralles, and G.A. Slafer. 2008. Genotypic variability and response to water stress of pre- and post-anthesis phases in triticale. European Journal of Agronomy 28:171-177.

Flowers, W., R. Weisz, R. Heiniger, D. Osmond, and C. Crozier. 2004. In-season optimization and site-specific nitrogen management for soft red winter wheat. Agronomy Journal 96:124-134.

Hirel, B., P. Bertin, I. Quilleré, W. Bourdoncle, C. Attagnant, and C. Dellay. 2001. Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. Plant Physiology 125:1258-1270.

Hirzel, J., I. Matus, and R. Madariaga. 2010. Effect of split nitrogen applications on durum wheat cultivars in volcanic soil. Chilean Journal of Agricultural Research 70:590-599.

Ivanovic, M. 1984. Primena metoda koeficijenta puta u geneticko – selekcionim istrazivanjima. Arhiv za poljoprivredne nauke 45:471-478.

Jedinski, S. 2001. Heritability and path-coefficient analysis of yield components in spring wheat. Grupy Problemowej Wodowli Pszency. Proceeding of Symposium, Zakopane, Poland. 218/219:203-209.

Jelic, M. 1996. Proucavanje mineralne ishrane psenice, gajene na lesiviranoj smonici. 121 p. Doctoral thesis. Faculty of Agriculture Zemun, Belgrade, Serbia.

Kashif, M., and I. Khaliq. 2004. Heritability, correlation and path coefficient analysis for some metric traits in wheat. International Journal of Agriculture & Biology 6:138-142.

Knezevic, D., A. Paunovic, M. Madic, and N. Djukic. 2007. Genetic analysis of nitrogen accumulation in four wheat cultivars and their hybrids. Cereal Research Communications 35:633-636.

Mariotti, M., I. Arduini, and L. Lulli. 2003. Traslocazione della biomassa nel frumento duro durante il grain-filling. p. 339-340. *In* Mori, M., and M. Fagnano (eds.) Proceedings of the XXXV Congress of the Italian Society of Agronomy, Napoli. 16-18 September. Imago Media, Caserta, Italy.

Martre, P., J.R. Porter, P.D. Jamieson, and E. Triboï. 2003. Modeling grain nitrogen accumulation and protein composition to understand the sink/source regulations of nitrogen remobilization for wheat. Plant Physiology 133:1959-1967.

Masoni, A., L. Ercoli, M. Mariotti, and I. Arduini. 2007. Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. European Journal of Agronomy 26:179-186.

Mi, G., L. Tang, F. Zhang, and J. Zhang. 2000. Is nitrogen after anthesis in wheat regulated by sink size? Field Crops Research 68:183-190.

Moll, R.H., E.J. Kamprath, and W.A. Jackson. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agronomy Journal 74:562-564.

Murphy, K., and S. Jones. 2007. Genetic assessment of the role of breeding wheat for organic systems. Wheat Production in Stressed Environments 12:217-222.

Nikolic, O. 2009. Geneticka divergentnost genotipova psenice za parameter efikasnosti ishrane azotom. 112 p. Doctoral thesis. Faculty of Agriculture Zemun, Belgrade, Serbia.

Ortiz-Monasterio, J.I., K.D. Sayre, S. Rajaram, and M. McMahon. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. Crop Science 37:898-904.

Öztürk, Ö. 2010. Effects of source and rate of nitrogen fertilizer on yield, yield components and quality of winter rapeseed (*Brassica napus* L.) Chilean Journal of Agricultural Research 70:132-141.

Patel, A.M., N. Augustine, and D.R. Patel. 2004. Nitrogen management for productivity of macaroni wheat (*Triticum durum*). Indian Journal of Agronomy 49:168-170.

Pathak, R.R., A. Ahmad, S. Lochab, and N. Raghuram. 2008. Molecular physiology of plant nitrogen use efficiency and biotechnological options for its enhancement. Current Science 94:1394-1403.

Przulj, N., and V. Momcilovic. 2001. Genetic variation for dry matter and nitrogen accumulation and translocation in two-rowed spring barley. II. Nitrogen translocation. European Journal of Agronomy 15:255-265.

Shrawat, A.K., R.T. Carroll, M. DePauw, G.J. Taylor, and A.G. Good. 2008. Genetic engineering of improved nitrogen use efficiency in rice by the tissue-specific expression of alanine aminotransferase. Plant Biotechnology Journal 6:722-732.

Stojkovic, S., D. Djokic, J. Stojanovic, and M. Biberdzic. 2003. Genotypic variations of some nitrogen utilization parameters in winter wheat. Plant Breeding and Seed Production 9:43-50.

van Ginkee, M., R. Ortiz-Monasterio, R. Trethowan, and E. Fernandez. 2001. Methodology for selecting segregating populations for improved N use efficiency in bread wheat. Wheat in a global environment. p. 611-620. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Váňová, M., S. Palík, J. Hajšlová, and I. Burešová. 2006. Grain quality and yield of spring barley in field trials under variable growing conditions. Plant Soil Environment 52:211-219.

Weinkauf, A.M. 2008. Improving wheat yield and grain nitrogen concentration through efficient use of nitrogen fertilizer. 71 p. Dissertation. South Dakota State University, Brookings, South Dakota, USA.

Wright, S. 1934. The methods of path coefficients. Annals of Mathematical Statistics 5:161-215.

Zagal, E., J. Hirzel, and I. Vidal. 2003. Evaluation of nitrogen-fertilizer recommendation for annual crops in soils of volcanic origin using a simulation model. Agricultura Técnica (Chile) 63:94-104.

Zivanovic, T., S. Vuckovic, S. Prodanovic, and G. Todorovic. 2006. Evaluation of inbred lines as sources of new alleles for improving elite maize hybrid. Cereal Research Communications 34(2-3):941-948.