

GENETIC ANALYSIS OF VARIABILITY AND INHERITANCE OF NITROGEN HARVEST INDEX IN WHEAT (*TRITICUM AESTIVUM* L.)

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Abstract

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Hybrid progeny of F₁ and F₂ generations were produced in diallel crosses (without reciprocals) of five genetically divergent wheat cultivars (Zitnica, Jugoslavija, Zelengora, NS Rana 2 and Nizija). The variability, mode of inheritance, gene effect, combining ability of parent cultivars and F₁ and F₂ hybrids for NHI were studied. The different mode of inheritance: partial dominance, dominance and overdominance for analyzed traits were established, with prevalence of overdominance, taking into account all crossing combinations. On the base of genetic components of variance analysis was estimated that non-additive gene action has higher impact than additive in the inheritance of NHI, with higher frequency of dominant alleles and positive interaction additive x dominant genetic effects. The average degree of dominance was positive and indicates overdominance as prevailing inheritance mode, considering all crossing combinations. Dominance i.e. overdominance as inheritance mode was recorded by regression analysis. The parents were divergent in terms of order of dominant and recessive alleles. The inter-alleles interaction was registered, too. Analysis of combining ability showed high significance of specific combining abilities in both of generations, while general combining abilities were significant only in F₂ generation, what confirm higher proportion of non – additive genetic variance. The relation genetic combining abilities/specific combining abilities was less than 1.

The best general combiner for NHI in both F₁ and F₂ generation was Zitnica cultivar. The highest values of specific combining abilities were obtained in combinations Zelengora x Nizija and Zitnica x NS Rana 2. The emphasized cultivars could be recommended for wheat breeding programmes as source of desirable properties.

Key words: inheritance, nitrogen harvest index, variability, wheat

Introduction

Yield levels and quality of produced grain play an important part in the successful and economic production and marketing of wheat. Traditionally, yield was economically the most important factor to the producer. However, as the end user became more demanding with regards to quality of the end product, linked to the possibility of exporting surplus production combined with higher quality standards required, the quality of produced grain became more important. Negative correlation among these two traits does not make possible simultaneous increase in the yield and in protein content. That is why breeders of wheat are forced to compromise between these characteristics (van Ginkel et al., 2001) So far, they have attached greater importance to yield.

Low soil nitrogen (N) availability is often the major nutrient factor limiting wheat productivity and obtain high grain yield, with satisfactory quality. Application of inorganic N fertilizer has become an important tool used to increase crop yields and grain quality in intensive agricultural systems (Andrews et al., 2004). However, large proportion of the applied N fertilizer is usually lost as a result of surface runoff, leaching, soil denitrification, volatilization and gaseous plant emission. Therefore, N management is essential for economic yield, optimum water utilization and to minimum pollution of the environment (Patel et al., 2004; Weinkauff, 2008). Because of these, there is a need to reduce the use of inorganic N fertilizer and search for wheat genotypes with greater N use efficiencies (NUE), either in a strict physiological sense (increased carbon(C) gain per unit N), or in an agronomic

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sense (increased dry matter or protein yield per unit plant N or per unit N applied and available to the crop) (Andrews et al., 2004). Thus, the efficiency of wheat cultivars in NUE could allow a reduction in N fertilizer use without a decrease in yield.

Genotypic specificity of wheat nitrogen nutrition efficiency presents reaction of plant to level of nitrogen supply, determined by general and cultivars specific genes from all three genomes of hexaploid wheat (Gamzikova, 1994). Therefore, the NUE of a crop is a function of the genetic constitution and the environment (climate, soil and management) in which it is grown, since all these factors control the rate of dry matter production. Hence, NUE is a complex term with many components and a great degree of compensation takes place among the components (Ladha et al., 2005).

Nitrogen harvest index (NHI), also known as translocation coefficient and reutilization efficiency, is indicator of genotype efficiency of nitrogen distribution between vegetative plant parts and grain. It represents the part of plant nitrogen used for protein synthesis. This indicator can be expressed as decrease of straw nitrogen in full maturity stage in relation to amount of nitrogen through period from anthesis to physiological maturity (postreutilized nitrogen). Ability of genotype to relocate nitrogen from vegetative parts to grain represents a base for grain protein increase, according to researches pointed out positive correlation of NHI and grain protein content (Saint Pierre et al., 2008; Bahrani et al., 2011). Pavlovic (1997), Rossela et al. (2004) and Nikolic et al. (2011) did not find any connection between these traits. Barraclough et al. (2010) stated that NHI could be used as a selective criterion for the increase in yield, which would not be followed by decrease in grain protein content. All these bring us to the conclusion that every increase in nitrogen harvest index does not have to be followed by increase in grain protein content i. e. NHI can have a positive effect on wheat grain yield.

Many researches showed that an important genotypic variation, under polygenes control, of nitrogen harvest index existed in wheat (Singh and Arora, 2001; Fageria and Baligar, 2003). The aim of this study is to estimate heritability of nitrogen harvest index and components of its genetic variability.

Materials and Methods

The five divergent winter wheat cultivars (*Triticum aestivum* ssp. *vulgare*) and hybrids produced in diallel crosses of Zitnica, Jugoslavija, Zelengora, NS Rana 2 and Nizija cultivars were analyzed. The parental genotypes, originating from the Serbia, Institute of Field and Vegetable Crops, Novi Sad, were chosen on the base of previous results about their di-

vergence of nitrogen use efficiency. Hybrid progenies of F_1 and F_2 generation were produced by method of diallel crosses (5×5 , without reciprocal). Seeds of F_1 and F_2 hybrids and parents were planted in randomized block system in three replications on the experimental field of Small Grains Research Center in Kragujevac (186 m.a.s.l.), Serbia. The soil type was smonitza in degradation (Vertisol). The chemical analyses were carried out in the Agrochemical Laboratory of the Center, indicating a moderate level of soil fertility and acidity.

The seeds were planted in 1m long rows, with distance between the rows 0.25 m and with 0.10 m space between each seed in row. The standard technology of scientific farming production of winter wheat, characteristic for region of Central Serbia, was applied. The plants in full maturity stage were used for analysis. The nitrogen was analyzed by use Kjeldahl methods. Nitrogen harvest index was determined according to Arduini et al. (2006), as ratio between N content in grain and total nitrogen content in above – ground plant part, multiplied by 100 and expressed with %.

The components of genetic variance were analyzed by method Hayman (1954) and Jinks (1954). Regression analysis was presented by points in scatter diagram (Mather and Jinks, 1971), while the combining abilities (general - GCA and specific - SCA) were analyzed according to Griffing (1956) method 2 mode I.

Results and Discussion

Analyzed parents cultivars displayed differences in the average value of nitrogen harvest index (Table 1). The lowest value of this parameter was noticed at NS Rana 2 (67.58%), while Zelengora cv. had the highest NHI (81.17%). The high values of NHI have not necessarily mean the highest values of grain protein content, but only part in total distribution of plant nitrogen, which is used in protein synthesis. Pavlovic (1997) found out that cv. NS Rana 2 has the highest grain protein content comparing with other tested cultivars.

The lowest value of NHI in F_1 generation was registered in cross combination Jugoslavija x Nizija (52.89%), and in combination Zelegora x Nizija (61.30%) in F_2 progeny. Combinations Zelengora x Nizija (74.92%) in F_1 generation and Zitnica x NS 2 (78.59%) in F_2 generation were distinguished by the highest values of studied trait (Table 1). It is evident that crossing of parents with higher degree of divergence provides superior progeny.

The models of inheritance for NHI are: over dominance, dominance and partial dominance, in both generations. Dominance, mainly, belongs to parents with lower values of NHI. This observation suggests a wide divergence of progeny and an important influence of external factors as in F_1 so in gen-

Table 1
Average values and inheritance mode of nitrogen harvest index (%) in wheat cultivars and hybrids

Cultivar	Zitnica	Jugoslavija	Zelengora	NS 2	Nizija	F ₁
Zitnica	77.25	62.51 ^{-od}	65.93 ^{-od}	68.48 ^{-pd}	64.83 ^{-od}	LSD
Jugoslavija	73.00 ^{-od}	78.3	63.98 ^{-od}	69.67 ^{-pd}	52.89 ^{-od}	0.05=12.19
Zelengora	75.00 ^{-od}	65.98 ^{-od}	81.17	67.80 ^{-d}	74.92 ^{-od}	0.01=16.44
NS 2	78.59 ^{-od}	69.09 ^{-pd}	66.86 ^{-d}	67.58	67.33 ^{-d}	
Nizija	75.86 ^{-od}	71.68 ^{-od}	61.30 ^{-od}	69.16 ^{-pd}	76.99	
F ₂	LSD 0.05=7.16 0.01=9.66					

eration of separate (Table 1). Distribution of nitrogen matter between vegetative and reproductive organs of wheat plant is in direct connection with distribution of entire dry matter. It is followed by relationship of NHI and grain harvest index (Pavlovic, 1997; Flood and Martin, 2001). The relatively low NHI values (60-80%) indicate wheat cultivars do not use nitrogen for formatting grain yield enough efficiently, leaving a significant part in vegetative plant parts to be lost irretrievably (Shahet al., 2009). It is a chance for wheat breeders to create genotypes with better translocation coefficient. Nikolic et al. (2011) recorded relation of genetic and environmental variance 76%: 24% in total variability of NHI. Significantly larger share of the total variation of genetic variance to the environment means less influence of environmental factors on the realized variation of trait, which in terms of selection and breeding is considered a very favorable ratio.

Genetic variance is a part of total variability of traits, whose components are presented in Table 2. Results of investigation point to higher value of dominant than additive component (H₁ and H₂ values are significantly higher than D values in both of tested generations). It, further, means that, taking into account all the crossing combinations, non-additive genetic factors are predominant in NHI inheritance in wheat hybrids. The positive interaction additive x dominant indicated that dominant genes have higher influence than recessive genes in the inheritance of NHI. The frequency of dominant genes (*u*) is higher than frequency of recessive (*v*) gene and distribution of dominant and recessive alleles in F₁ and F₂ generation are unequal (Table 2).

These results are in line with previous investigation (Pavlovic et al., 1998) about inheritance of many nitrogen use nutrition efficiency parameters. Average value of domination in F₁ and F₂ generation (ratio between additive and non-additive components) are similar and indicate that over dominance, as a mode of inheritance of NHI, prevail. Additive gene effect in F₁ generation of hybrids was lower but dominance played a more important role in the inheritance of NHI than addi-

tive variance (H₁ and H₂ are higher than value of parameter D). Also, in F₂ generation, non-additive gene have higher importance than additive (H₁ and H₂ are higher than value of parameter D). The positive interaction additive x dominant indicated that dominant genes have higher influence than recessive genes in the inheritance of NHI. That is confirmed by the ratio of number of dominant and recessive alleles ($K_d/K_r = 1.92$ in F₁ and $K_d/K_r = 2.28$ in F₂ generation) (Table 2).

Prevalence of dominant inheritance mode in both hybrid generations is confirmed by regression analysis. As it can be seen on Figure 1 and Figure 3, distance of expected regression line from limiting parabola is considerable. Although cross-section of expected line with the y-axis is above coordinate start in F₁ generation (Figure 2), distribution of points in third quadrant (Figure 2 and Figure 4) indicate overdominance as predominant mode of inheritance of NHI, taking into account all crossing combinations.

Table 2
Components of genetic variability of NHI in F₁ and F₂ hybrid generation

Components of variance	F ₁	F ₂
D	8.5812	20.17
H ₁	184.9	454.4
H ₂	161.07	312.07
F	25.07	74.71
E	17.7	6.12
H ₂ /H ₁	0.22	0.17
<i>u</i>	0.62	0.78
<i>v</i>	0.38	0.22
$\sqrt{\frac{H_1}{D}}$	4.64	4.75
K _d /K _r	1.92	2.28

In F_2 hybrid generation, expected regression line intersects the y - axes below coordinate start, which clearly indicates prevalence of overdominance mode of inheritance of NHI in wheat. Distribution of points in scatter diagram at graphic WrW' shows order of parents dominance. Cultivar Zelengora had most recessive alleles in F_1 and F_2 generations, while dominant alleles were presented, in larger number, in NS Rana 2, Nizija and Jugoslavija. Polygenes control of absorption and translocation of nitrogen in wheat plant was described in investigation of Austinet al. (1977) and Kisset al. (1983). Regression coefficient was considerably higher than 1 in F_1 and F_2 generation, $t = 22.85$ and $t = 3.88$ respectively. It indicates presence of interalleles interaction, that is confirmed by distribution of points at scatter diagram in relate to

theoretical regression line (Figures 1 and 2). Dominant alleles were more prevalent in cv. NS Rana 2, while recessive alleles for studied trait prevailed in Jugoslavija and Nizija (Figures 3 and 4).

Analysis of variance for combining ability for NHI displayed high significant values for specific combining abilities in F_1 and F_2 generations, but significant values for general combining abilities only in F_1 generation (Tables 3 and 4). Analysis of variance for combining ability showed that in both F_1 and F_2 generation, nonadditive (dominance and epistasis) gene effect played more important role in the inheritance of NHI ($GCA/SCA < 1$), that is in accordance with results of genetic variance components analysis and regression analysis of variability in progeny.

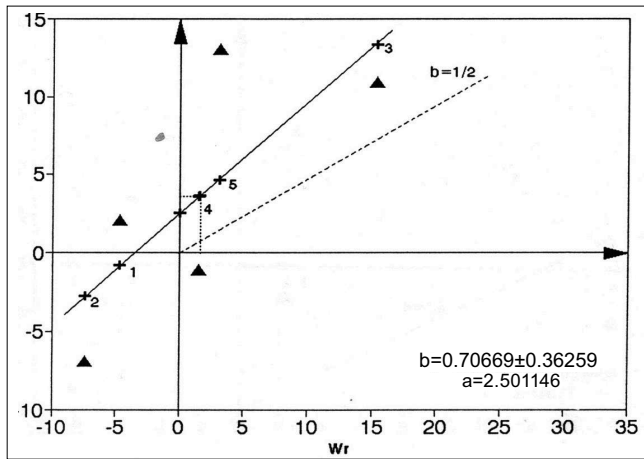


Fig. 1. Regression $VrWr$ analysis of nitrogen harvest index in wheat (P and F_1)

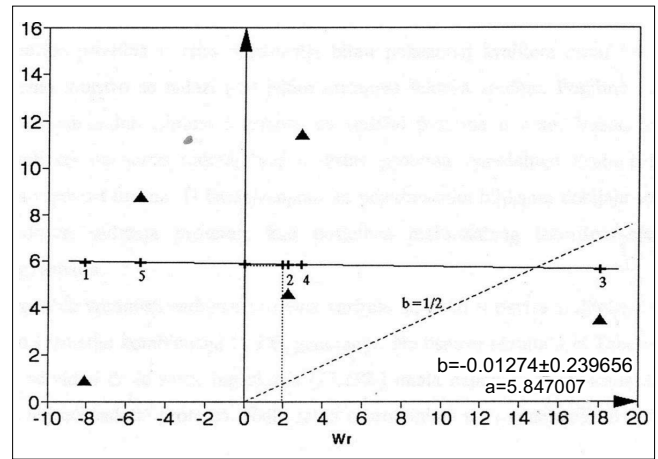


Fig. 3. Regression $VrWr$ analysis of nitrogen harvest index in wheat (P and F_2)

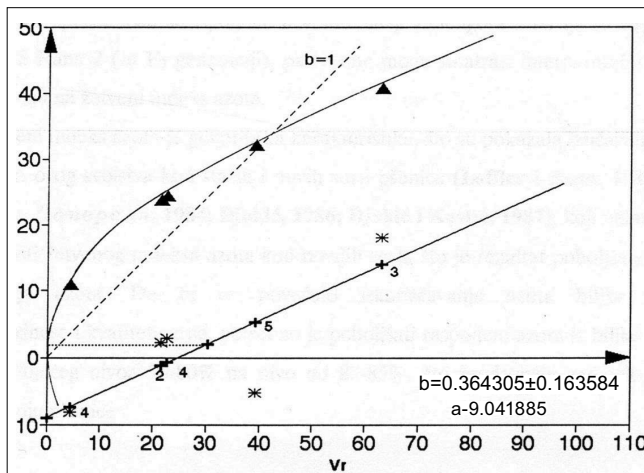


Fig. 2. Regression WrW analysis of nitrogen harvest index in wheat (P and F_1)

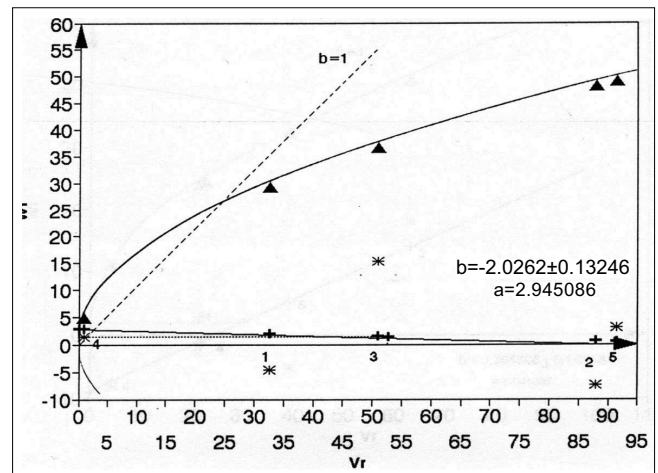


Fig. 4. Regression WrW analysis of nitrogen harvest index (P and F_2)

The best general combiners for NHI are cv. Zitnica (in F₁) and Zelengora (in F₂) generation (Table 5). However, Zitnica is the best general combiner for studied parameter and could be recommended as good parent in selecting and breeding programmes, considering all results. Zelengora represents good general combiner, too, interesting for breeding process for increasing NHI values in wheat.

The highest values of specific combining abilities were in combinations Zelengora x Nizija, (in F₁ generation) and Zitnica x NS rana 2 (in F₂ generation), so they could be con-

sidered as perspective in wheat breeding for HNI (Table 6). Such results are in accordance with fact that the best progeny are produced by crossing one parent with good and other with poor combining abilities.

Conclusion

Tested parental cultivars, used for diallel crosses, expressed significant differences in nitrogen harvest index values. The inheritance mode for NHI, in F₁ and F₂ hybrids,

Table 3
ANOVA of combining ability for NHI in F1 hybrid wheat

Source of variability	Df	SS	MS	F	Ft 0.05	Ft 0.01
GCA	4	75.47	18.87	1.07	3.2	5.1
SCA	10	124.28	12 428.40	702.17**	2.7	4
E	28		17.7			
GCA/SCA	0.0015					

Table 4
ANOVA of combining ability for NHI in F2 hybrid wheat

Source of variability	Df	SS	MS	F	Ft 0.05	Ft 0.01
GCA	4	109.43	27.36	4.47*	3.2	5.1
SCA	10	135 670	13 567	2218.3**	2.7	4
E	28		6.12			
GCA/SCA	0.002					

Table 5
GCA values for nitrogen harvest index in F1 and F2 generations

Cultivar	F1	F2	Rank1	Rank2
Zitnica	3.12	0.06	1	2
Jugoslavija	0.17	-1.46	2	5
Zelengora	-0.53	2.73	4	1
NS rana 2	-2.32	-1.06	5	4
Nizija	-0.44	-0.27	3	3
SE	1.56	5.03		
LSD 0.05	3.16	5.37		
LSD 0.01	4.22	7.18		

Table 6
SCA values for nitrogen harvest index in F1 and F2 generation

Combination	F ₁	F ₂
Zitnica x Jugoslavija	-5.4	-2.8
Zitnica x Zelengora	-6.17	-0.11
Zitnica x NS rana 2	0.17	5.27
Zitnica x Nizija	-4.26	0.67
Jugoslavija x Zelengora	-6.6	-6.26
Jugoslavija x NS rana 2	2.88	-1.27
Jugoslavija x Nizija	-14.69	-0.56
Zelengora x NS rana 2	-3.18	-2.8
Zelengora x Nizija	3.15	-10.24
NS rana 2 x Nizija	-0.65	-0.59
SE	5.03	2.96
LSD 0.05	10.16	5.97
LSD 0.01	13.58	7.98
LSD 0.01	13.58	7.98

were: over dominance, dominance and partial dominance, with prevailing of over dominance, taking into account all crossing combinations. Additive gene effect in both generations of hybrids was lower indicated that dominant genes have higher importance for inheritance of nitrogen harvest index. The positive interaction additive x dominant indicated that dominant genes have higher influence than recessive genes in the inheritance of NHI.

Regression analysis point to over dominance as prevalence mode of inheritance of NHI in wheat, considering all crossing combinations as well as presence of interalleles interaction. The various order of parental dominance was registered, that indicate genetic divergence of representation dominant and recessive alleles. Dominant alleles were more presented in NS rana 2 cultivar, while recessive alleles were more presented in Zelengora cv.

Analysis of combining ability showed high significance of SCA in both of generations, while GCA were significant only in F₂ generation, what confirm higher proportion of non – additive genetic variance.

The best general combiner for NHI in both F₁ and F₂ generation was Zitnica cultivar. The highest values of SCA were obtained in combinations Zelengora x Nizija and Zitnica x NS rana 2. The emphasized cultivars could be recommended for wheat breeding programmes as source of desirable properties.

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