Genetic control of grain yield and nitrogen use efficiency in tropical maize

Leandro Vagno de Souza[1], Glauco Vieira Miranda[2], João Carlos Cardoso Galvão[2], Fernando Roberto Eckert[2], Éder Eduardo Mantovani[2], Rodrigo Oliveira Lima[2] and Lauro José Moreira Guimarães[3]

[1]Empresa de Pesquisa Agropecuária de Minas Gerais, Centro Tecnológico Triângulo e Alto Paranaíba, Caixa Postal 351, CEP 38001-970 Uberaba, MG, Brazil. E-mail: souzalv@hotmail.com [2]Universidade Federal de Viçosa, Departamento de Fitotecnia, CEP 36570-000 Viçosa, MG, Brazil. E-mail: glaucovmiranda@ufv.br, jgalvao@ufv.br, fernandoagro2001@yahoo.com.br, dumantovani@yahoo.com.br, rlimaagro@yahoo.com.br [3]Embrapa Milho e Sorgo, Caixa Postal 285, CEP 35701-970 Sete Lagoas, MG, Brazil. E-mail: lauro@cnpms.embrapa.br

Abstract – The objectives of this work were to study the genetic control of grain yield (GY) and nitrogen (N) use efficiency (NUE, grain yield/N applied) and its primary components, N uptake efficiency (NUpE, N uptake/N applied) and N utilization efficiency (NUtE, grain yield/N uptake), in maize grown in environments with high and low N availability. Experiments with 31 maize genotypes (28 hybrid crosses and three controls) were carried out in soils with high and low N rates, in the southeast of the state of Minas Gerais, Brazil. There was a reduction of 23.2% in average GY for maize grown in soil with low N, in comparison to that obtained with high N. There were 26.5, 199 and 400% increases in NUtE, NUpE, and NUE, respectively, for maize grown with low N. The general combining ability (GCA) and specific combining ability (SCA) were significant for GY, NUE and NUpE for maize grown in high N soil. Only GCA was significant for NUpE for maize grown in low N soil. The GCA and SCA for NUtE were not significant in either environment. Additive and non-additive genetic effects are responsible for the genetic control of NUE and GY for maize grown in soils with high N availability, although additive effects are more important.

Index terms: *Zea mays*, abiotic stress, absorption efficiency, combining ability, commercial hybrids, utilization efficiency.

Controle genético da produção de grão e da eficiência de uso do nitrogênio em milho tropical

Resumo – O objetivo deste trabalho foi estudar o controle genético da produtividade de grãos (PG) e da eficiência no uso de nitrogênio (EUN, produção de grãos/N aplicado) e seus componentes primários – eficiência de absorção (EAbN, N absorvido/N aplicado) e utilização (EUtN, produção de grãos/N absorvido) –, em milho cultivado em ambientes com alta e baixa disponibilidade de nitrogênio. Trinta e um genótipos de milho (28 cruzamentos entre híbridos comerciais e três testemunhas) foram avaliados em solos com alta e baixa doses de aplicação de N. Houve redução de 23,2% na média de PG em milho cultivado em solo com baixo teor de N, em relação à obtida com alto N. Com baixo teor de N no solo, observaram-se aumentos de 26,5, 199 e 400% em EUtN, EAbN, e EUN, respectivamente. Em milho cultivado em solo com alto teor de N, as capacidades geral (CGC) e específica (CEC) de combinação foram significativas em PG, EUN e EAbN. Em milho de solos com baixo teor de N, apenas a CGC, na EAbN, foi significativa. A CGC e a CEC não foram significativas, em nenhum dos ambientes, na EUtN. Efeitos genéticos aditivos e não aditivos são responsáveis pelo controle genético da EUN e PG, em milho cultivado em solos com elevada disponibilidade de N, mas os efeitos aditivos são mais importantes.

Termos para indexação: *Zea mays*, estresse abiótico, eficiência de absorção, capacidade de combinação, híbridos comerciais, eficiência de utilização.

Introduction

Current levels of maize production (*Zea mays* L.) will not be sufficient to support the demand for this cereal in the coming decades (Bänziger et al., 2004), with serious risks to global food security due to the extensive use of maize in food, biofuel and feed.

Worldwide, about 100 million hectares are planted with maize, and the cultivation of this cereal in tropical developing countries represents approximately 50% of the total planting. In these regions, cultivation is usually done under low N availability, as a result of low natural soil fertility, low investment in nitrogenous fertilizers and production instability due to the occurrence of drought (Monneveux et al., 2005).

Data for 2005 (USDA, 2005) show that more than five million megagrams of N are required for maize crop in the USA each year. This equates to an investment of over 15.9 million dollars a year. In general, cultivars developed by breeding programs are highly productive and respond to applications of N, but have low efficiency in the use of this nutrient (O'Neill et al., 2004). The development of maize cultivars with greater N use efficiency would make a great contribution to plant breeding for sustainable agriculture (Presterl et al., 2002).

Moll et al. (1982) defined N use efficiency (NUE) as the weight of the grains, divided by the amount of N applied to soil. They defined two primary components of use efficiency, known as N uptake efficiency (NUpE) and N utilization efficiency (NUtE). The NUpE is obtained by the total amount of N in the mature plant, divided by the amount of N applied to soil. The variable NUtE is obtained by the ratio between grain weight and the total amount of N in the mature plant. From these two primary components, NUE can be obtained by the product of NUpE and NUtE. Parentoni & Souza Junior (2008) made use of this methodology for assessing phosphorus use efficiency in 28 maize genotypes grown in environments with high and low P availability.

Hirel & Gallais (2004) found that alleles responsible for the genetic control of N efficiency are expressed in accordance with the degree of N availability. Several reports in the literature described the use of diallel crosses to study the genetic control and determination of heterotic groups (Lee et al., 2005; Melani & Carena, 2005; Pswarayi & Vivek, 2007; Miranda et al., 2008). Through diallel analysis, it is possible to determine the additive and nonadditive effects in the genetic control of a particular characteristic. According to Sprague & Tatum (1942), these effects are related to the general combining ability and specific combining ability, respectively.

An understanding of the processes associated with NUE, especially in relation to its primary components (uptake and utilization efficiency), are among the most important factors in determining strategies for the management and development of cultivars in breeding programs with the aim of improving nutrient use efficiency (Uribelarrea et al., 2007).

The objectives of this work were to study the genetic control of grain yield and N use efficiency and its primary components (uptake and utilization efficiency), in maize grown in environments with high and low N availability.

Materials and Methods

A complete diallel between eight commercial maize cultivars, from different institutions, was obtained in 2003 (Table 1). These cultivars were selected based on previous work, which found different levels of performance, in environments with high or low N availability. In the summer of 2003, these crosses were evaluated at Estação Experimental de Coimbra, MG, Brazil (20°50'30"S and 42°48'30"W, at the altitude 720 m), in an Argissolo Vermelho-Amarelo distrófico (Arenic Hapludult) (Embrapa, 2006).

The experimental design was a randomized blocks, with two replicates. The plot was formed by two rows of 5 m in length, spaced at 0.80 m, with a productive area of 8 m^2. The hybrid combinations and controls were evaluated in two environments, with different rates of N application. The conventional system was used to prepare the soil.

In the environment with high N availability (high N), N fertilizer was applied in accordance with a grain yield of over 8,000 kg ha^{-1} (150 kg ha^{-1} N). In the environment with low N availability (low N), 30 kg ha^{-1} of N was applied, according to recommendations of Ribeiro et al. (1999). The other cultural practices were conducted according to technical recommendations for maize cultivation (Galvão & Miranda, 2004).

The grain yield was corrected to 13% humidity and expressed in kilograms per hectare. The N use efficiency (NUE) and its primary components – N utilization efficiency (NUtE) and N uptake efficiency (NUpE) – were calculated according to Moll et al. (1982). For each N availability, efficiencies were obtained as follows: NUpE = N in plant/N applied (kg kg^{-1}); NUtE = grain yield/N in plant (kg kg^{-1}, kg of grain per kg of N extracted); NUE = NUpE x NUtE (kg kg^{-1}).

Table 1. Characteristics of maize cultivars in the diallel utilized.

Cultivar	Obtainer	Type[1]	Cycle	Type of grain
AG 1051	Monsanto/Agroceres	DH	Semi-early	Dent
AG 122	Monsanto/Agroceres	DH	Early	Semi-dent
BR 106	Embrapa	COP	Semi-early	Semi-dent
DKB 747	Monsanto/Dekalb	DH	Early	Flint
DKB- 901	Monsanto/Dekalb	SH	Early	Dent
DKB-333B	Monsanto/Dekalb	SH	Semi-early	Semi-flint
P 3041	Pioneer	TH	Early	Flint
XB 7012	Semeali	TH	Early	Flint

[1]DH, double hybrid; SH, simple hybrid; TH, triple-cross hybrid; COP, cultivar open-pollinated.

To estimate N levels and content in plants, five plants per plot were collected at the physiological maturity, and grains were separated. Then a sample of 1,000 g was dried at 70°C to constant weight, to obtain the dry mass branch (DMB). The same procedure was adopted for the grain mass. Analyses were performed in the Laboratory of Plant Nutrition, of the Department of Crop Science of the Universidade Federal de Viçosa.

The t test was used for multiple comparisons with significance set at 5% probability. The methodology to estimate the effects of general and specific combining abilities was that proposed by Griffing (1956), method 4, for hybrid combinations only. Diallel analyses were conducted in each environment, and the model used was: $Y_{ij} = \mu + G_j + S_{ij} + \bar{\varepsilon}ij$, in which: Y_{ij} is the effect of the overall average; G_i and G_j are the overall effects of general combining ability (GCA), associated with the i^{th} and j^{th} genitor; and S_{ij} is the effect of specific combining ability (SCA), between parents i and j. In this model, Y_{ij} and $\bar{\varepsilon}_{ij}$. are the average and the random error associated with the average ij, respectively.

All the statistical analyses were performed using the GENES program, Windows version (Cruz, 2005).

Results and Discussion

The grain yield (GY) means in high and low N environments were 10,121 and 7,766 kg ha^{-1}, respectively (Table 2), with 23.2% reduction in average GY between environments (with variation from 28.4 to 41.6%). Presterl et al. (2003) found that the relative difference between GY ranged from 14.5 to 55.4%, when comparing data from 21 maize trials carried out with inbred lines, under conditions of high and

Table 2. Means of grain yield (GY, kg ha^{-1}), nitrogen uptake efficiency (NUpE, N uptake/N applied), nitrogen utilization efficiency (NUtE, grain yield/N uptake), nitrogen use efficiency (NUE, grain yield/N applied), in high and low N, and stress effect (SE, %), in GY, caused by N deficiency.

Treatament	High N				SE	Low N			
	GY	NUpE	NUtE	NUE		GY	NUpE	NUtE	NUE
AG 1051 x DKB 901	13,316	2.00	45	89	35.8	8,544	6.33	45	285
AG 1051 x XB 7012	9,999	1.74	42	67	16.4	8,355	5.97	45	279
AG 1051 x DKB 333	8,894	2.02	30	59	26.4	6,549	5.17	43	218
AG 1051 x P 3041	8,335	1.93	30	56	1.4	8,217	6.79	40	274
AG 1051 x BR 106	9,937	1.82	39	66	23.3	7,626	5.61	46	255
AG 1051 x DKB 747	10,852	1.89	39	73	26.0	8,034	4.77	57	268
AG 1051 x AG 122	11,908	2.16	37	79	32.4	8,046	7.83	35	268
DKB 901 x XB 7012	5,912	1.37	29	40	3.1	5,727	4.01	48	191
DKB 901 x DKB 333	10,027	2.07	33	67	16.5	8,373	7.39	39	280
DKB 901 x P 3041	9,649	1.98	35	65	26.5	7,096	5.59	42	237
DKB 901 x BR 106	8,437	1.44	41	56	31.4	5,786	4.37	45	193
DKB 901 x DKB 747	8,675	1.72	34	58	14.0	7,462	5.19	48	249
DKB 901 x AG 122	5,934	1.10	37	40	-28.4	7,618	5.92	45	254
XB 7012 x DKB 333	9,458	2.27	28	63	-15.4	10,912	9.58	41	364
XB 7012 x P 3041	10,984	1.98	38	73	23.9	8,359	6.37	44	279
XB 7012 x BR 106	10,505	1.89	38	70	30.7	7,278	6.06	41	243
XB 7012 x DKB 747	10,326	2.15	32	69	41.6	6,029	4.82	42	201
XB 7012 x AG 122	10,723	2.03	36	72	36.6	6,797	5.86	40	227
DKB 333 x P 3041	12,184	4.14	20	81	14.4	10,435	8.42	41	348
DKB 333 x BR 106	9,178	2.98	21	61	38.2	5,668	7.43	26	189
DKB 333 x DKB 747	10,140	2.09	34	68	25.2	7,581	5.69	45	253
DKB 333 x AG 122	10,112	2.30	30	68	16.7	8,426	6.23	46	281
P 3041 x BR 106	10,193	1.88	37	68	5.2	9,667	7.08	47	323
P 3041 x DKB 747	10,584	2.05	35	71	34.0	6,986	5.80	41	233
P 3041 x AG 122	11,537	2.33	33	77	28.8	8,217	6.02	48	274
BR 106 x DKB 747	10,579	2.17	33	71	26.4	7,789	5.99	44	260
BR 106 x AG 122	8,380	2.30	25	56	21.2	6,606	5.84	37	220
DKB 747 x AG 122	11,527	3.05	27	77	34.6	7,543	5.81	43	252
DKB 747	9,987	1.66	42	67	26.7	7,321	5.26	47	244
DKB 333	10,034	1.73	40	67	32.3	6,797	5.76	39	227
P 3041	15,466	2.30	46	103	29.5	10,903	9.88	38	364
Mean	10,121	2.08	34	67	23.3	7,766	6.22	43	259
$LSD_{0.05}$(1)	2,496	0.84	17	17		3,296	2.91	14	110
CV (%)	12	20	25	12		21	23	16	21

(1)Least significant difference at 5% probability.

low N availability. Liu et al. (2008) observed reductions of 22.35 and 30.28%, in the average GY of maize hybrids between environments with high or low N availability at two sites. Ferro et al. (2007) observed a 21% relative difference between GY in high and low N. These values are within the range proposed by Bolaños & Edmeades (1996) as characteristic of N deficient environment. These authors suggested that the average obtained under abiotic stress conditions is between 20 and 30% lower than that achieved by the same genetic group in an equivalent environment free from stress. Despite the 23.2% reduction caused by N stress, high average GY was found in both environments, demonstrating the high productive potential and the adaptation of hybrid combinations and controls used, and enabling the identification and selection of superior genotypes.

Among the controls, the triple-cross hybrid P 3041 was the most prominent, with an average GY of 15,466 kg ha^{-1} in high N, which was similar to the hybrid combination AG 1051 x DKB 901. In the low N, P 3041 was similar to other hybrid combinations that produced more than 7,616 kg ha^{-1}, a value not reached by other controls (Table 2). Miranda et al. (2005) evaluated maize cultivars in the Southeast of Minas Gerais State, Brazil, and obtained similar results for the hybrid P 3041, which exceeded the average grain yield of 15 early cultivars evaluated over two years and at three sites.

The NUE in high N showed an overall average of 67 kg kg^{-1} (Table 2), with range from 39.5 to 103 kg kg^{-1} (kg of grain per kg of N applied), and a CV of 12%. In low N, the average was 259 kg kg^{-1} and NUE ranged from 189 to 364 kg kg^{-1}, with a CV of 21%. In high N, the NUE for the triple-cross hybrid P 3041 surpassed all the other treatments statistically, except for the hybrid combination AG 1051 x DKB 901. However, in the low N, the NUE of P 3041 was not different from the hybrid combinations with averages of more than 254 kg kg^{-1} (Table 2). In experiments with maize hybrid in low and high N, Akintoye et al. (1999) found NUE of 55 and 25 kg kg^{-1} (kg of grain per kg of N applied), respectively. These authors used the average of four N levels and three sites, and found an average NUE that varied from 39.8 to 30.4 kg kg^{-1}. The superiority of the NUE values found in the present study was due to higher average GY observed in both environments, which demonstrates the high genetic potential of the hybrid combinations and controls.

The average NUtE in high and low N was 34 and 43 kg kg^{-1} (kg of grain per kg of N in the plant), respectively. In the high N, treatments with average superior to 29 kg kg^{-1} did not differ statistically. Therefore, no differences were found among the controls, and only five hybrid combinations were overtaken by controls (Table 2). In low N, treatments in which NUtE averaged more than 43 kg kg^{-1} did not differ from each other. This group consisted of 16 hybrid combinations and the hybrid DKB 747. Similar results were observed by Worku et al. (2007), in the evaluations of cultivars and maize hybrids in high and low N, in which they found a NUtE average of 36 kg kg^{-1}in high N and 54 kg kg^{-1} in low N.

In high N, the average NUpE was 2.08 (plant N/N applied, kg kg^{-1}). In this environment, the hybrid combination DKB 333 x P 3041 showed the highest NUpE average, equal to 4.14 kg kg^{-1}. With low N, NUpE average was 6.22 kg kg^{-1}, with a range from 4.01 to 9.88 kg kg^{-1}. In this environment, P 3041 showed the highest average, although not statistically different from every treatment with averages of more than 6.97 kg kg^{-1} (Table 2).

The averages of the primary components of NUE were higher in low N than in high N. This is consistent with the results obtained by Uribelarrea et al. (2007); they evaluated maize hybrids in six doses of N and found that NUE, NUtE and NUpE were negatively associated with N availability. Parentoni & Souza Junior (2008) also observed lower values of P use efficiency, P acquisition efficiency and P utilization efficiency in high P availability, compared to low availability, in 28 maize genotypes.

It was observed that the average NUE in low N was approximately four times higher than that obtained in high N. This result can be explained by the difference between the primary components of NUE between environments. For NUtE, there was the increase of 26.5% in low N, in relation to high N. The NUpE increased by 199% in low N, which indicates that NUpE is important for increasing NUE during stress. Parentoni & Souza Junior (2008) also observed that the efficiency of absorption is a key component of P use efficiency, in environments with low availability of this nutrient.

The general (GCA) and specific (SCA) combining ability of grain yield were significant in high N, but nonsignificant in low N (Table 3). The effects of GCA and SCA for NUE, in high N, were significant (Table 3). These results contrast with those of Medici et al. (2004), who found significant effects of GCA and SCA on grain yield and NUE, in high and low N, when evaluating 15 maize hybrids derived from diallel crosses between the inbred lines of cultivars AG 302 and AG 311.

For NUtE in both environments, the effect of genotypes (hybrid combinations) was not significant and there was no evidence of genetic variability in this feature. This can be explained by the fact that modern maize cultivars have been selected according to their average GY, in experiments in which they are given high N doses, a condition that, according to Uribelarrea et al. (2007), can lead to the lack of genetic variability for the utilization of N or remobilization from the grains.

These results show that additive and nonadditive genetic effects are responsible for genetic control of GY, NUpE and NUE in high N. Therefore, different methods for obtaining new varieties can be exploited for the selection of parents. But the increased importance of additive genetic effects in relation to nonadditive ones shows that the additive effects should be prioritized, which is verified by the relationship between the square mean GCA and SCA, in which the square sum of GCA was 2.6, 7.9 and 2.5 times greater than the square sum of SCA for GY, NUpE and NUE, respectively.

As for NUpE, there were significant effects for both GCA and SCA in high N, but only of GCA in low N. Therefore, in low N, an alternative approach to selection and development of cultivars would be to exploit the genes related to the GCA of NUpE. Despite the unimportance of nonadditive and additive genetic effects for GY and NUE, in low N, the selection for increasing NUpE is expected to also increase the average GY and NUE in this environment, due to the genetic correlation between GY and NUpE (0.95) and NUpE and NUE (1.00). The correlation between NUpE and GY was similar to that found by Presterl et al. (2002), who evaluated inbred maize lines and hybrids in three levels of N and found that, in low N, NUpE was significantly correlated with GY.

Table 3. Mean squares of grain yield (GY), nitrogen uptake efficiency (NUpE), nitrogen utilization efficiency (NUtE), and nitrogen use efficiency (NUE), in high and low N.

Source of variation[(1)]	DF	GY	NUpE	NUtE	NUE
			High N		
Hybrids combinations	27	5,369,182**	0.6329**	66.79^{ns}	237.08**
GCA	20	5,011,415**	1.1986**	126.95^{ns}	216.64*
SCA	7	5,494,400**	0.4348**	45.73^{ns}	244.23**
Error	30	1,493,614	0.1696	70.21	67.83
SQ GCA / SQ SCA		2.6	7.9	-	2.5
			Low N		
Hybrids combinations	27	3,257,215^{ns}	28,869^{ns}	57.31^{ns}	3,624^{ns}
GCA	20	3,524,572^{ns}	47,698*	62.95^{ns}	3,914^{ns}
SCA	7	3,163,639^{ns}	22,278^{ns}	55.34^{ns}	3,522^{ns}
Error	30	2,604,678	20,392	44.06	2,892

[(1)]GCA, general combining ability; SCA, specific combining ability. ^{ns}Non-significant. * and **Significant by F test, at 5 and 1% probability.

In high N, the cultivars DKB 333, P 3041, DKB 747 and AG 122 showed GCA positive estimates for GY, NUpE and NUE. Cultivar AG 1051 showed a GCA positive estimate for GY and NUE (Table 4).

Figure 1 shows the GCA estimates for NUpE obtained under high and low N availability. The x-axis plots GCA for NUpE, in high N, and the y-axis give the estimates of GCA at low N. In quadrant 1, cultivars AG 122, P 3041 and DKB 333 show GCA positive estimates in both environments, indicating the potential to be used as a source of germplasm, both for the environment with low and high availability of N. Hybrid DKB 747 had only a positive estimate in the absence of stress. Estimates for other cultivars were negative in both environments, which indicates the lack of potential as parents for increasing the frequency of alleles favorable for NUpE.

In high N, 13, 14 and 15 hybrid combinations were identified with SCA considered positive for NUpE, GY and NUE, respectively (Tables 5 and 6). The hybrid combinations which showed SCA positive estimates

Table 4. Estimates of general combining ability of maize cultivars for grain yield (GY), nitrogen uptake efficiency (NUpE), and nitrogen use efficiency (NUE), in high N.

Genitor	GY	NUpE	NUE
AG 1051	611.69	-0.19	4.04
DKB 901	-1,270.15	-0.50	-8.29
XB 7012	-277.48	-0.21	-1.88
DKB 333	70.27	0.53	0.46
P 3041	649.19	0.26	4.29
BR 106	-393.81	-0.04	-2.63
DKB 747	518.69	0.07	3.46
AG 122	91.60	0.09	0.54

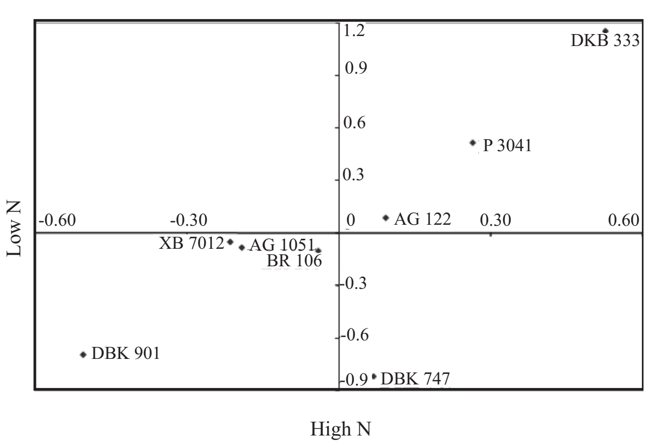

Figure 1. Estimates of general combining ability and general nitrogen uptake efficiency, in high and low N.

Table 5. Estimates of specific combining ability of maize cultivars for grain yield (diagonal above) and for nitrogen uptake efficiency (diagonal below), in high N.

	AG 1051	DKB 901	XB 7012	DKB 333	P 3041	BR 106	DKB 747	AG 122
AG 1051		4,035.98	-273.69	-1,726.94	-2,864.36	-219.86	-216.86	1,265.73
DKB 901	0.60		-2,479.36	1,288.39	331.48	161.98	-512.02	-2,826.44
XB 7012	0.05	-0.01		-273.77	673.31	1,237.31	145.81	970.39
DKB 333	-0.42	-0.05	-0.14		1,525.56	-436.94	-387.44	11.14
P 3041	-0.24	0.12	-0.17	1.25		-0.86	-522.86	857.73
BR 106	-0.05	-0.12	0.04	0.39	-0.45		515.14	-1,256.77
DKB 747	-0.09	0.06	0.19	-0.60	-0.38	0.04		978.23
AG 122	0.16	-0.59	0.05	-0.42	-0.13	0.14	0.79	

Table 6. Estimates of specific combining ability of maize cultivars for nitrogen use efficiency, in high N.

	AG 1051	DKB 901	XB 7012	DKB 33	P 3041	BR 106	DKB 747	AG 122
AG 1051		27.07	-1.85	-11.68	-19.01	-1.60	-1.18	8.24
DKB 901			-16.51	8.65	2.32	0.74	-3.35	-18.93
XB 7012				-1.76	4.40	8.32	0.74	6.65
DKB 333					10.07	-3.01	-2.60	0.32
P 3041						0.15	-3.43	5.49
BR 106							3.49	-8.10
DKB 747								6.32
AG 122								

for GY, NUpE and NUE were: AG 1051 x AG 122, AG 1051 x DKB 901, BR 106 x DKB 747, DKB 333 x P 3041, DKB 747 x AG 122, DKB 901 x P 3041, XB 7012 x AG 122, XB 7012 x BR 106, XB 7012 x DKB 747.

Conclusions

1. Additive and nonadditive genetic effects are responsible for genetic control of N use efficiency and grain yield, in high N availability, and the additive effects are more important.
2. For all the genotypes studied, the N uptake efficiency has additive genetic control in high and low N availability.
3. Cultivars DKB 333, AG 122, and P 3041 showed good potential for their use as parents to increase the allele frequency for N uptake efficiency, in high and low N availability.
4. Cultivars DKB 333, P 3041, AG 122 and DKB 747 presented the same allele frequency for grain yield, N uptake efficiency and N use efficiency, in environments with high N availability.

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