



Genetic responses of traits relationship to components of nitrogen and phosphorus use efficiency in maize

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ABSTRACT. This study had three objectives: i) to observe maize inbred lines response to nitrogen (N) and phosphorus (P) acquisition as well as their utilization efficiencies and traits of root morphology in contrasting levels of these nutrients, ii) to study the relationship between root morphology and nutrient use efficiencies for both nutrients, and iii) to identify contrasting parents with components N and P use efficiency for an inheritance study. We evaluated 15 inbred lines in two experiments conducted in contrasting conditions of N and P. We evaluated the shoot, root traits and nutritional efficiencies and observed the genetic variability for most traits. Selection can be practiced for most of these traits in specific environments. Under conditions of nutritional stress, average and heritability estimates were of lesser magnitude. In this study, the shoot and root morphology traits were shown to be associated with the acquisition efficiency of both N and P in all of the environments that were evaluated.

Keywords: *Zea mays*, acquisition and utilization efficiencies, root morphology, abiotic stress, REML/BLUP.

Respostas genéticas de caracteres relacionados aos componentes da eficiência no uso de nitrogênio e fósforo em milho

RESUMO. Esse estudo teve três objetivos: i) observar a resposta de linhagens de milho quanto às eficiências de absorção e de utilização de N e P e de caracteres de morfologia de raiz em níveis contrastantes destes nutrientes; ii) estudar as relações entre caracteres de morfologia de raiz e as eficiências nutricionais para ambos os nutrientes e iii) identificar genitores contrastantes quanto aos componentes da eficiência no uso de N e P para estudo de herança. Foram avaliadas 15 linhagens de milho em dois experimentos conduzidos em condições contrastantes de N e P. Avaliou-se parte aérea, caracteres de raiz e eficiências nutricionais e observou-se variabilidade genética para a maioria dos caracteres avaliados. A seleção pode ser praticada para a maioria destes caracteres em ambientes específicos. Em condições de estresse nutricional, as médias e herdabilidades apresentaram estimativas de menor magnitude. Nesse estudo, os caracteres parte aérea e morfologia de raiz apresentaram elevada associação com a eficiência de absorção, tanto para N como para P, em todos os ambientes avaliados.

Palavras-chave: *Zea mays*, eficiências de absorção e de utilização, morfologia radicular, estresse abiótico, REML/BLUP.

Introduction

Considering the current scenario of global climate change and that the major advances in agriculture have been designed for favorable environments during the "Green Revolution", the performance of crops under adverse conditions in marginal environments remains a subject of constant discussion. However, the use of fertilizers in agriculture, together with an improvement in crop systems, provides an adequate food supply for human and animal consumption.

The production of nitrogen (N) fertilizers by the Haber-Bosch process was one of the most important inventions of the 20th century enabling food supplies

to world production (SMIL, 1999). However, with the high cost of fertilizers, declining natural resources, and the expectation that the world population will reach 10 billion people by the mid-21st century, an increase of approximately 43% of the world's current population (FEDOROFF et al., 2010), the future challenge will be to accommodate the population's necessities through the development of a high agriculture productivity while preserving environmental quality. Thus, the effective utilization of genetic plant resources will be needed to answer the challenge.

Research of plant species or genotypes that are able to absorb and assimilate nutrients efficiently is

extremely important (SOUZA et al., 2008). Genetic variability exists in the capture of soil nutrients proven by genotypes that are increasingly responsive to high amounts of fertilizers, especially N and phosphorus (P), which are limiting factors to agricultural production (TILMAN et al., 2002). This responsive research has been accompanied by decreased nutritional efficiency, contributing to increased pollution in many regions (CUI et al., 2009).

Phosphorus is a limiting nutrient in many regions of the world, especially in the highly weathered soils of the tropics, while N has not yet been invested in by developing country producers because of its high price (HIREL et al., 2007). Thus, it is necessary to adopt different genotypes when subjected to minimum nutrients to maintain satisfactory production.

Many definitions and methodologies exist that describe the calculation of the nutritional efficiency of a crop. However, researchers have recently adopted a more plausible definition specifically; is the ability of a given genotype to produce biomass or grains under certain nutritional supplementation (PARENTONI; SOUZA JUNIOR, 2008; WHANG et al., 2010). Nutrient use efficiency is composed of the acquisition efficiency (AE) and the internal utilization efficiency (UtE). Acquisition efficiency is defined as the ability of a genotype to acquire specific nutrients from the soil; the UtE refers to the ability of this genotype to produce biomass or grain using the absorbed nutrient. Thus, greater N use efficiency (NUE) and P (PUE) can be achieved by increasing the AE and UtE (CHEN et al., 2009; PRESTERL et al., 2002).

Several biochemical and physiological traits are involved in increasing UtE in plants. For example, in P acquisition the most important traits are morphology and root architecture, because P availability is unevenly distributed throughout the soil profile (WHANG et al., 2010). Root architecture, defined as the space configuration of the root system (LYNCH; BROWN, 2001), determines the extent explored through the soil profile. As a result of seeking to adapt to adverse conditions, the root architecture genetics may suffer changes. For example, low moisture stress can increase root system depth and lateral root formation (CHUN et al., 2005). Under conditions of low P availability, the changes occur in the upper root layers, providing increased nutrient acquisition (HAMMER et al., 2009).

Genotypic variation in the extension of lateral roots and thrust can lead to the selection of genotypes that are more efficient in nutrients acquisition. The identification of quantitative trait loci (QTL) in the initial stage of maize to root traits, including extension of lateral and axial root under water stress (RUTA et al., 2010), response to low P and N availability (GALLAIS; HIREL, 2004; ZHU et al., 2005) revealed the importance of studying root morphology at an early

stage to predict the performance of genotypes in later stages. Thus, early evaluation or indirect selection using correlated traits are of great interest in plant improvement under abiotic stress because they accelerate the process of selection by immediately discarding less promising genotypes, thus concentrating on potentially accessible resources.

The objectives of this study were as follows: i) Identify differential behavior of maize inbred lines for nutrient acquisition efficiency, nutrient utilization and traits of root morphology in contrasting N and P environments, ii) Study the relationship between the traits of root morphology and the acquisition efficiency and utilization efficiency of N and P in contrasting levels and, iii) Identify contrasting parents with components N and P use efficiency for an inheritance study.

Material and methods

Plant material and experimental design

We used 15 maize inbred lines from the *Programa Milho*[®], Federal University of Viçosa - UFV, Minas Gerais State, Brazil. These inbred lines were evaluated in two experiments with contrasting conditions of N (Experiment 1) and P (Experiment 2). The experiments were performed in a randomized block design in a factorial structure in triplicate. The plot was one plant per pot.

Growth conditions

The experiments were conducted in the greenhouse of the Crop Science Department, UFV, Minas Gerais State, Brazil (20°45'14"S, 42°52'53"W) in October 2009. The day to night average temperature was 33 to 25°C. The seeds were sterilized for 1 minute in a 0.5% solution of sodium hypochlorite (NaOCl) and then washed with deionized water. The seeds were pre-germinated in a box with individual cells for germination, three seeds per inbred line. Soon after emergence, seeds were transplanted. One seedling from each inbred line was transplanted in cylindrical PVC pots 4 dm³ in size (10 cm diameter x 50 cm height). The substrate for Experiment 1 was prepared by sand and vermiculite mixing at a ratio of 1:1, previously describe by Walk et al. (2006). For experiment 2, a mixed of 50% sand, 37.5% vermiculite and 12.5% soil with very low P was used. The soil was used to absorb the phosphorus and to prevent it from being readily available to the plant.

From the seventh day after seedling emergence, the nutrient solution was replenished every 2 days. In Experiment 1, the solution used contained (in mmol L⁻¹): 2.0 Ca(NO₃)₂, 0.75 K₂SO₄, 0.65 MgSO₄, 0.1 KCl, 0.25 KH₂PO₄, 1.0 x 10⁻³ H₃BO₃, 1.0 MnSO₄ x 10⁻³, 1.0 x 10⁻⁴ CuSO₄, 1.0 x 10⁻³ ZnSO₄, 5.0 x 10⁻⁶

$(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$, 0.1 Fe-EDTA and one of two N levels, low N (LN) or high N (HN), describe previously by Chun et al. (2005). The LN solution contained 0.2 mmol L⁻¹ Ca (NO₃)₂, (i.e., 10 times less and Ca was offset by CaCl₂). For Experiment 2, P was added in the form of triple superphosphate. For the low P condition (LP), 20 mg dm⁻³ was added; 104 mg dm⁻³ of P was added for the high P (HP). The other nutrients were supplied by the nutrient solution without phosphorus addition containing 1.0M Ca(NO₃)₂·4H₂O, 1.0 M MgSO₄·7H₂O, 0.5M K₂SO₄, 0.32 mM CuSO₄·5H₂O, 46.0 mM H₃BO₃, 0.073 mM $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$, 9.1 mM MnCl₂·4H₂O, 0.76 mM ZnSO₄·7H₂O and 38.0 mM Fe-EDTA.

The seedlings were harvested at the vegetative stage when 4 leaves were completely expanded (V4), 25 days after sowing. The seedling shoots were separated from the root system, packaged in paper bags and dried in a circulating forced air oven at 60°C for 72 hours.

Measurements of root and shoot traits and nutritional efficiencies

The N and P shoot dry weights (SDW_N and SDW_P, respectively) were determined after drying for 72 hours at 60°C.

The root system was evaluated by image analysis using the software WinRhizo Pro 2009a (Basic, Reg, Pro & Arabidopsis for Root Measurement) coupled to an Epson Perfection V700/V750 scanner equipped with additional light (TPU), with a resolution of 400 dpi, as described by Bouma et al. (2000). The lateral and axial root lengths were extracted from the all class of diameter (d), obtained by WinRhizo as lateral root length (LLAT) with diameter less than or equal to 0.5mm and axial root length (LAXI) with diameter greater than 0.5mm, according Trachsel et al. (2009). We also evaluated for the two components of nitrogen and phosphorus use efficiency as proposed by Hirel et al. (2007): i) acquisition efficiency (AE) – NAE or PAE = N or P in the plant/N or P applied, ii) utilization efficiency (UtE) – NUtE or PUtE = SDW/N or P in the plant.

Statistical analyses

Because some data were not normally distributed, data transformation was performed. For the variables NAE, NUtE, PAE and PUtE that represented ratio values expressed between zero and one, transformations were performed using the follow equation $\sqrt{x+0.5}$. For the variables LLAT and LAXI that demonstrated positive asymmetry, the transformation equation that was used $\log(x+1)$.

From these data, statistical analyses were performed using the equations of mixed models, as

described by Bernardo (2002):

$$y = Xr + Zg + Wi + e$$

where:

y is the vector of phenotypic data; r is the vector of repetition effects within the environments (fixed); g is the vector of genotypic effects (random), where $g \sim N(0, G)$ being $G = A\sigma_g^2$; i is the vector of the effects of genotype interaction x environment (random), and e the error vector, being that $e \sim N(0, R)$ and $R = I\sigma_e^2$. The letters X, Z and W are incidence matrices that relate the effects of r, g and i to vector y, respectively.

In the focus of mixed models, G refers to the genetic covariance matrix between the inbred lines, being denoted by $A\sigma_g^2$. In this study, the coefficient of coancestry (A) was disregarded and, consequently, the matrix G was assumed as $A\sigma_g^2$, i.e., A=I. Thus, σ_g^2 equals the genetic variance between the inbred lines and the corresponding vector \hat{g} corresponds to the predictions of the genotypic values of inbred lines.

To obtain the above solutions, the components of genetic and non-genetic variance were assumed as unknown and were estimated by restricted maximum verisimilitude (DF-REML). The predicted responses to the selection were conducted by making the average breeding values of selected inbred lines for each environment. Based on the predicted genotypic values of the inbred lines, the genetic correlations among the traits studied were estimated using the Pearson coefficient. The selection gains were obtained by the average genotypic values of selected inbred lines. All tests were performed using the computer statistical package Statistical Analysis System (SAS) version 9.1 (SAS, 2003).

Results and discussion

The genotypes differed significantly by analysis of deviance for the majority of the traits evaluated, with the exception PUtE (Table 1). Differential genotypic behaviors were observed when subjected to conditions of low and high N and P, evidenced by the significant effect of genotype-by-environment interactions; the exception was for root traits in the high N environment. Therefore, evaluated in this way, the environments were contrasted sufficiently to identify the variability between genotypes.

Table 1. Values of verisimilitude (LRT) of deviance analysis, estimates of genotypic variance ($A\sigma_g^2$), the variance of genotype-by-environment interaction (σ_{ge}^2), residual variance (σ_e^2), broad sense heritability (h_g^2), overall average and coefficient of variation (CV%) of shoot dry matter of N (SDWN) and P (SDWP), N acquisition efficiency (NAE) and P (PAE), N utilization efficiency (NUtE) and P (PUtE), lateral root length in the environment of N (LLAT N) and P (LLAT P), axial root length in the environment of N (LAXI N) and P (LAXI P) from 15 maize inbred lines, Viçosa, Minas Gerais State, Brazil.

Effect	SDW _N	SDW _P	NAE	PAE	NUtE	PUtE	L _{LAT} N	L _{LAT} P	L _{AXI} N	L _{AXI} P
Genotype ¹	45.6***	35.27***	18.13***	5.63**	3.02*	0.93 ^{NS}	23.97***	30.51***	22.05***	35.79***
G x E ¹	8.23**	39.91***	5.5**	10.35***	2.79*	11.35***	0 ^{NS}	50.28***	0.01 ^{NS}	20.78***
σ_g^2	0.053	0.035	4x10 ⁻⁴	1x10 ⁻⁵	3.4x10 ⁻³	0.023	0.015	6x10 ⁻³	0.019	5.2x10 ⁻³
σ_{ge}^2	0.019	0.053	4x10 ⁻⁴	1x10 ⁻⁵	0.016	2.556	1x10 ⁻⁴	0.013	4x10 ⁻⁴	4.8x10 ⁻³
σ_e^2	0.028	0.018	8x10 ⁻⁴	1x10 ⁻⁵	0.052	3.814	0.023	3x10 ⁻³	0.026	3.2x10 ⁻³
h_g^2	0.79	0.55	0.58	0.07	0.17	0.01	0.82	0.44	0.80	0.64
Mean	0.83	1.17	0.81	0.72	3.51	23.27	3.74	3.43	3.26	2.85
CV%	20.27	11.35	3.39	0.34	6.50	8.39	3.79	1.63	4.98	2.00

¹Values of LRT; Significant at ***p = 0.01, **p = 0.05, * p = 0.10 and ^{NS} non-significant at test χ^2 .

The traits of shoot dry matter and root morphology for both P and N environments presented medium to high magnitudes of heritability. The broad sense heritability of medium to high magnitude for the majority of traits indicated that direct or indirect selection enables selection with satisfactory gains. However, PAE, NUtE and, PUtE showed low magnitude coefficients of heritability. Thus, for these traits that suffer high environmental influence - because they depend on the expression of many enzymes (as in the case of N use) and specific element nutrition carries, multiple progenies or replicates should be used to soften the residue effect of the heritability problem.

The significant differences observed between inbred lines indicated genetic variability allowing the selection of possible genetic gains with hybrid combinations. The significant difference observed between stress and no stress, for both N and P, indicated that they were adequate in simulating contrasting environments. As different behaviors were observed inbred lines according to the environments, indicated by the significant genotype-by-environment interaction, selection for specific environments was practicable for most traits. The exceptions to this selection ability were LLATN and LAXIN. Trachsel et al. (2009), by mapping QTLs for lateral and axial root growth of tropical maize, identified that genotype selection, based in these same traits, may be only performed with nutrient availability. However, despite the genetic variability for each N availability condition, the results indicated that the genotype performances for LLAT and LAXI were similar in those two conditions because the interaction G x E is not significant. Thus, selection could be based on performance of only one nutrient level.

For almost all traits evaluated, the highest general average values were observed in the experiment with N compared to P; the only exception was for PUtE.

This result demonstrated that more N than P is required to produce biomass in maize seedlings.

Considering the relationship between the traits studied, the presence of a significant and positive relationship between LLAT and LAXI and both low and high N and P was observed (Table 2). Moreover, both low and high N and P also had a significant positive correlation between AE with LLAT and LAXI. UtE did not significantly correlate with any radical morphological trait for both levels of N and P; however, UEt correlated negatively with AE in the LP condition. The SDW presented significant correlated with high magnitude with radical morphological traits and AE in high and low N and P, with the exception of the trait LLAT in HP.

Correlations among these same traits were observed previously by Trachsel et al. (2009) in tropical maize. According to that study, this significant correlation between the types of roots occurred by hierarchical dependence among them, i.e., the extent of axial length increases the points of emergence of lateral roots. Hodge et al. (2009) reported that extension of the root system is genetically controlled, but the growth rate of axial and lateral roots is modulated by environmental conditions. This was observed by Zhang et al. (2007) in Arabidopsis, which when subjected to high N availability inhibited the development of lateral root tissue while under low availability the opposite effect was observed.

Hund et al. (2009) also worked with maize inbred lines and demonstrated that under high nutrient availability, the plants invest in the largest axial root preferentially over the lateral roots. However, this relationship was not observed in our study. Under both high and low availability of N and P, only the AE were correlated significantly and positively with the types of roots.

Table 2. Genotypic correlations between shoot dry matter (SDW), acquisition efficiencies (AE), utilization (UtE), lateral (LLAT) and axial root length (LAXI), in high (HN) and low (LN) N (lower diagonal) and high (HP) and low (LP) P (higher diagonal) from 15 maize inbred lines, Viçosa, Minas Gerais State, Brazil.

	AE		UtE		L _{LAT}		L _{AXI}		
	LP	HP	LP	HP	LP	HP	LP	HP	
AE	0.68**	0.87**	0.24 ^{ns}	0.16 ^{ns}	0.63**	0.33 ^{ns}	0.72**	0.58*	SDW
UtE	0.92**	0.97**	-0.52*	-0.35 ^{ns}	0.58*	0.56*	0.60*	0.72**	AE
L _{LAT}	0.46 ^{ns}	0.42 ^{ns}	0.13 ^{ns}	0.25 ^{ns}	-0.10 ^{ns}	-0.46 ^{ns}	0.00 ^{ns}	-0.33 ^{ns}	UtE
L _{AXI}	0.80**	0.81**	0.80**	0.87**	0.17 ^{ns}	0.21 ^{ns}	0.72**	0.82**	L _{LAT}
	0.79**	0.84**	0.81**	0.88**	0.15 ^{ns}	0.22 ^{ns}	0.90**	0.90**	
	LN	HN	LN	HN	LN	HN	LN	HN	
	SDW		AE		UtE		L _{LAT}		

Significant at **p = 0.01, *p = 0.05, ^{ns} non-significant at test t.

The significant correlation between LLAT and NAE in LN conditions indicates that the lateral roots have an important role in N acquisition, with a trait that can be used for early indirect selection. This was also observed by Lazof et al. (1992) in maize, where nitrate acquisition by lateral roots was 1.5 times greater than in the axial roots. The elongation of lateral roots requires less biomass per root unit than axial roots. According to Forde and Lorenzo (2001) smaller diameter roots explore the soil volume more intensively. In contrast, the correlation between the types of roots and the efficiency of utilization were not significant in both conditions of nutrient availability, both for N and P. Thus, the radical traits showed no important role in P and N utilization and in this way are not suitable for indirect selection of more efficient genotypes. Therefore, the roots only have significance for the acquisition of N and P and are not related to the incorporation of these nutrients in the plant mass, which is instead performed by internal mechanisms of the plant, such as enzyme activity and specific carriers.

According to Liu et al. (2004), axial roots determine root architecture, defined as the space configuration of the root system, and they allow a better geometric development. Plants with fewer angles in the root system in relation to the soil surface have better handling of mainly P in surface soil and, consequently, are more tolerant to low nutrient supplementation (RUBIO et al., 2003). It was also observed in present study for HP condition that there was a significant and negative relation between AE and UtE, demonstrating that plants that absorb a readily are not necessarily tolerant or efficient because they cannot utilize all the absorbed nutrients.

The genotypic values of inbred lines for AE and UtE, in both experiments (N and P) are shown in Figure 1, with QI and QII in the right and left upper quadrants and QIII and QIV in the lower left and lower right quadrants, respectively.

QI is characterized by the high genotype value of the components of use efficiency of N and P, with the inverse observed in QIII. It was observed that some inbred lines had very contrasting performance in the studied environments. For example, the inbred line L8 presented positive genotypic values for the components of use efficiency in the majority of environments evaluated, except PUE in HP, while the L3 line presented negative genotypic values for almost all environments, except for HN.

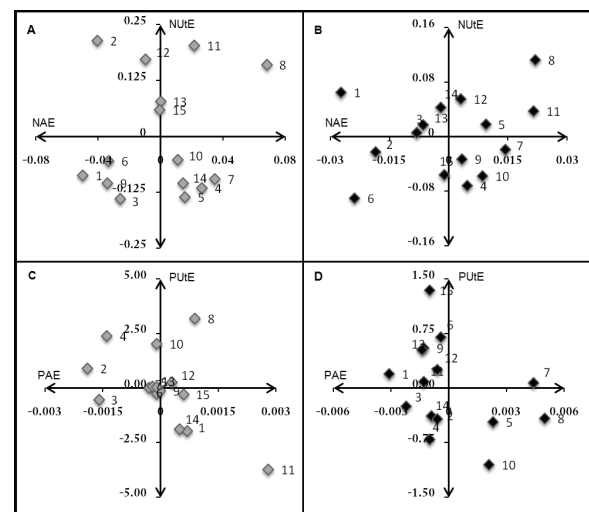


Figure 1. Genotypic values between N utilization efficiency (NUtE) and N acquisition efficiency (NAE) in LN (A) and HN (B), P utilization efficiency (PUtE) and P acquisition efficiency (PAE) in LP (C) and HP (D) from 15 maize inbred lines, Viçosa, Minas Gerais State, Brazil.

Gain estimates with selection were obtained by genotypic values of the inbred line considered to be superior. For this, we simulated the 20% selection of the superior inbred line for each of the traits evaluated in N and P environments (Table 3). It was observed that it is possible to gain with selection for all the traits studied; the predicted gains with direct selection were superior to indirect gains for all traits in all environments considered. However, for some of these traits, situations existed where the indirect gains were

equal to or similar to the direct gains. This can be observed for the AE in all environments for the SDW in HN and LP when selected indirectly by SDW in LN. Additionally, NUtE in low and high N presented satisfactory gains with indirect selection by AE at low P.

The trait that provided the greatest gains with indirect selection was SDW in LN (12.05%). However, the trait that generated positive gains with selection for all traits was the SDW in HP. Moreover, this presented indirect gains at satisfactory levels (10.49%).

Considering the experimental accuracy, all the traits presented good accuracy in the estimates of genotypic values. This indicated that few repetitions were necessary for the assessment of genotypes. However the same was not observed for the SDW, because a higher number of observations were required than what were used in this study. Considering the coefficient of coancestry among genotypes, an attempt was made to minimize the effects of uncontrolled factors in the experiment.

In most environments, the same inbred lines were higher for AE and UtE, observed for both N and P. This indicated that these inbred lines can be used in the formation of more efficient N and P use in synthetic or hybrid combinations. This strong relationship between the genotypes performance indicated that the mechanisms that control AE and UtE for N and P may be pleiotropic or epistatic. This may occur due to the dependence of metabolic pathways on ATP in the acquisition and internal transport of N in the plant, which requires considerable energy availability. Thus, plants more efficient in the use of N must also be the same for P.

To achieve increases in the UE of a particular nutrient, it is necessary to increase its components. Thus, to increase the nutrient use efficiency, the inbred lines L8 and L11 presented themselves as the most promising, with similar performance in LN and HN. For PUE in the LP, the inbred line L8 distinguished itself again. The L7 line also presented

higher genotypic values for components of PUE in HP conditions; the genetic potential of these inbred lines for efficient N and P use is clear. Moreover, based on the dispersion of genotypes in the graphs, it reiterates the lack of relationship between AE and UtE in all N and P environments.

Considering the results of selection gains, it was possible to obtain significant gains through direct selection; however, using indirect selection, it was possible to distinguish SDW that provided satisfactory gains in two environments. In HP, SDW provided gains with all traits, albeit reduced. Additionally, in LN, SDW provided the largest selection gains with selection, but also generated negative gains, especially for the trait of UtE in LP and HP. According to Whang et al. (2010), when the availability of a particular nutrient is limiting, AE is more important than UtE, although the effect of the latter trait has been neglected in some studies. According to Corrales et al. (2007), higher PUE in maize occurs because of major increases in PAE in relation to PUtE in LP. Similar results were found by Parentoni and Souza Junior (2008) under LP and HP. Thus, the SDW in LN conditions should be the trait used in improvement programs aimed at selecting plants efficient in the use of both N and P.

For that this to occur, the genes that are being screened for controlling the trait should be the same in both environments and/or be strongly linked. Moreover, genetic variation and, heritability in the environment for indirect selection, needs to be greater than in the environment of direct selection. In breeding for nutritional use efficiency is common and was observed in this study. Thus, under stress, there is a decrease in phenotypic variety and heritability as well, making it harder to select because the different genotypes tend to have similar results. Although there are significant genotype-by-environment interactions, genetic gains for nutrient use efficiency under low availability can be obtained by selecting the most efficient in ideal farming situations.

Table 3. Estimates of direct gains (diagonal) and indirect with selection (%) for the traits, shoot dry matter (SDW), acquisition efficiency (AE) and utilization efficiency (UtE) in high and low N and P for 15 maize inbred lines, Viçosa, Minas Gerais State, Brazil.

Trait	LN			HN			LP			HP			Mean	
	AE	UtE	SDW	AE	UtE	SDW	AE	UtE	SDW	AE	UtE	SDW		
LN	AE	5.30	-0.48	27.34	1.68	0.20	24.65	-0.03	8.06	7.55	0.39	-1.52	32.57	8.81
	UtE	-1.14	5.61	6.51	0.25	0.66	13.07	0.06	-3.72	-3.04	-0.13	-0.07	-12.17	0.49
	SDW	5.11	2.54	36.78	2.36	1.24	47.10	0.16	-0.71	12.98	0.38	-0.37	36.97	12.05
HN	AE	5.11	2.54	36.78	2.36	1.24	47.10	0.16	-0.71	12.98	0.38	-0.37	36.97	12.05
	UtE	0.37	2.34	9.83	-0.09	2.20	7.14	0.09	2.12	12.69	0.06	0.04	6.40	3.60
	SDW	4.33	2.17	32.84	2.16	1.59	47.29	0.16	-0.78	12.06	0.28	-1.15	20.78	10.14
LP	AE	1.65	2.62	19.27	0.66	2.04	20.71	0.20	-3.62	12.41	0.03	-0.20	-0.15	4.64
	UtE	4.33	-0.07	23.12	1.44	-0.17	19.98	-0.03	10.86	10.21	0.28	-3.13	8.98	6.32
	SDW	2.86	2.67	23.11	1.38	1.04	28.87	0.05	7.84	15.92	0.30	-1.75	19.92	8.52
HP	AE	4.86	-0.66	26.60	1.87	1.05	35.40	0.02	4.66	10.07	0.54	-1.17	49.25	11.04
	UtE	-2.77	-0.94	-16.13	-0.88	-1.71	-19.19	0.02	-0.97	2.12	-0.13	3.71	10.24	-2.22
	SDW	4.20	1.19	25.78	1.44	0.34	23.45	0.06	4.25	13.02	0.39	1.43	50.31	10.49

Conclusion

Maize inbred lines exhibit differential behavior on the components of nitrogen and phosphorus use efficiency. The lengths of axial and lateral roots showed a strong association with nitrogen and phosphorus acquisition and utilization efficiency, independent of the availability of these nutrients. Inbred lines 8, 11, 3 and 12 showed contrasting performance to components N and P use efficiency and thus can be used to study inheritance.

References

- BERNARDO, R. **Breeding for quantitative traits in plants**. Woodbury: Stemma Press, 2002.
- BOUMA, T. J.; NIELSEN, K. L.; KOUTSTAAL, B. Sample preparation and scanning protocol for computerised analysis of root length and diameter. **Plant and Soil**, v. 218, n. 1-2, p. 185-196, 2000.
- CHEN, J. Y.; XU, L.; CAI, Y. L.; XU, J. Identification of QTLs for phosphorus utilization efficiency in maize (*Zea mays* L.) across P levels. **Euphytica**, v. 167, n. 2, p. 245-252, 2009.
- CHUN, L.; MI, G. H.; LI, J. S.; CHEN, F. J.; ZHANG, F. S. Genetic analysis of maize root characteristics in response to low nitrogen stress. **Plant and Soil**, v. 276, n. 2, p. 369-382, 2005.
- CORRALES, I.; AMENÓS, M.; POSCHENRIEDER, C.; BARCELÓ, J. Phosphorus efficiency and root exudates in two contrasting tropical maize varieties. **Journal of Plant Nutrition**, v. 30, n. 6, p. 887-900, 2007.
- CUI, Z. L.; ZHANG, F. S.; MI, G. H.; CHEN, F. J.; LI, F.; CHEN, X. P.; LI, J. L.; SHI, L. F. Interaction between genotypic difference and nitrogen management strategy in determining nitrogen use efficiency of summer maize. **Plant and Soil**, v. 317, n. 1-2, p. 267-276, 2009.
- FEDOROFF, N. V.; BATTISTI, D. S.; BEACHY, R. N.; COOPER, P. J. M.; FISCHHOFF, D. A.; HODGES, C. N.; KNAUF, V. C.; LOBELL, D.; MAZUR, B. J.; MOLDEN, D.; REYNOLDS, M. P.; RONALD, P. C.; ROSEGRANT, M. W.; SANCHEZ, P. A.; VONSHAK, A.; ZHU, J. K. Radically rethinking agriculture for the 21st century. **Science**, v. 327, n. 5967, p. 833-834, 2010.
- FORDE, B. G.; LORENZO, H. The nutritional control of root development. **Plant and Soil**, v. 232, n. 1-2, p. 51-68, 2001.
- GALLAIS, A.; HIREL, B. An approach to the genetics of nitrogen use efficiency in maize. **Journal of Experimental Botany**, v. 55, n. 396, p. 295-306, 2004.
- HAMMER, G. L.; DONG, Z. S.; MCLEAN, G.; DOHERTY, A.; MESSINA, C.; SCHUSLER, J.; ZINSELMEIER, C.; PASZKIEWICZ, S.; COOPER, M. Can changes in canopy and/or root system architecture explain historical maize yield trends in the US Corn Belt? **Crop Science**, v. 49, n. 1, p. 299-312, 2009.
- HIREL, B.; LE GOUIS, J.; NEY, B.; GALLAIS, A. The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. **Journal of Experimental Botany**, v. 58, n. 9, p. 2369-2387, 2007.
- HODGE, A.; BERTA, G.; DOUSSAN, C.; MERCHAN, F.; CRESPI, M. Plant root growth, architecture and function. **Plant and Soil**, v. 321, n. 1-2, p. 153-187, 2009.
- HUND, A.; TRACHSEL, S.; STAMP, P. Growth of axile and lateral roots of maize: I development of a phenotyping platform. **Plant and Soil**, v. 325, n.1-2, p. 335-349, 2009.
- LAZOF, D. B.; RUFTY, T. W.; REDINBAUGH, M. G. Localization of nitrate absorption and translocation within morphological regions of the corn root. **Plant Physiology**, v. 100, n. 3, p. 1251-1258, 1992.
- LIU, Y.; MI, G. H.; CHEN, F. J.; ZHANG, J. H.; ZHANG, F. S. Rhizosphere effect and root growth of two maize (*Zea mays* L.) genotypes with contrasting P efficiency at low P availability. **Plant Science**, v. 167, n. 2, p. 217-223, 2004.
- LYNCH, J. P.; BROWN, K. M. Topsoil foraging - an architectural adaptation of plants to low phosphorus availability. **Plant and Soil**, v. 237, n. 2, p. 225-237, 2001.
- PARENTONI, S. N.; SOUZA JUNIOR, C. L. Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes. **Pesquisa Agropecuária Brasileira**, v. 43, n. 7, p. 893-901, 2008.
- PRESTERL, T.; GROH, S.; LANDBECK, M.; SEITZ, G.; SCHMIDT, W.; GEIGER, H. H. Nitrogen uptake and utilization efficiency of European maize hybrids developed under conditions of low and high nitrogen input. **Plant Breeding**, v. 121, n. 6, p. 480-486, 2002.
- RUBIO, G.; LIAO, H.; YAN, X. L.; LYNCH, J. P. Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. **Crop Science**, v. 43, n. 2, p. 598-607, 2003.
- RUTA, N.; LIEDGENS, M.; FRACHEBOUD, Y.; STAMP, P.; HUND, A. QTLs for the elongation of axile and lateral roots of maize in response to low water potential. **Theoretical and Applied Genetics**, v. 120, n. 3, p. 621-631, 2010.
- SAS Institute. **SAS/STAT software versão 9.1**. Cary: SAS 2003. (CD-ROM).
- SMIL, V. Detonator of the population explosion. **Nature**, v. 400, n. 6743, p. 415, 1999.
- SOUZA, L. V.; MIRANDA, G. V.; GALVÃO, J. C. C.; ECKERT, F. R.; MANTOVANI, E. E.; LIMA, R. O.; GUIMARÃES, L. J. M. Genetic control of grain yield and nitrogen use efficiency in tropical maize. **Pesquisa Agropecuária Brasileira**, v. 43, n. 11, p. 1517-1523, 2008.
- TILMAN, D.; CASSMAN, K. G.; MATSON, P. A.; NAYLOR, R.; POLASKY, S. Agricultural sustainability and intensive production practices. **Nature**, v. 418, n. 6898, p. 671-677, 2002.
- TRACHSEL, S.; MESSMER, R.; STAMP, P.; HUND, A. Mapping of QTLs for lateral and axile root growth of

tropical maize. **Theoretical and Applied Genetics**, v. 119, n. 8, p. 1413-1424, 2009.

WHANG, X.; SHEN, J.; LIAO, H. Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops? **Plant Science**, v. 179, n. 4, p. 302-306, 2010.

WALK, T. C.; JARAMILLO, R.; LYNCH, J. P. Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. **Plant and Soil**, v. 279, n. 1-2, p. 347-366, 2006.

ZHANG, L. X.; LI, S. X.; ZHANG, H.; LIANG, Z. S. Nitrogen rates and water stress effects on production, lipid peroxidation and antioxidative enzyme activities in two maize (*Zea mays* L.) genotypes. **Journal of Agronomy and Crop Science**, v. 193, n. 6, p. 387-397, 2007.

ZHU, J. M.; KAEPLER, S. M.; LYNCH, J. P. Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. **Theoretical and Applied Genetics**, v. 111, n. 4, p. 688-695, 2005.

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