Brazilian maize landraces variability under high and low phosphorus inputs

Leandro Teodoski Spolaor[1], Gabriel Cipolaro Guirado[2], Carlos Alberto Scapim[2], Mauricio Carlos Kuki[2], Filipe Augusto Bengosi Bertagna[2], Josué Maldonado Ferreira[1], Claudemir Zucareli[1], and Leandro Simões Azeredo Gonçalves[1]*

[1]Agronomy Department, Universidade Estadual de Londrina (UEL), Rodovida Celso Garcia Cid, Km 380, Londrina, PR 86051-900, Brazil.
[2]Agronomy Department, Universidade Estadual de Maringá (UEM), Av. Colombo, 5790, Maringá, PR 87020-900.
Corresponding author: Leandro Simões Azeredo Gonçalves Address: Londrina, Paraná, Brazil, Phone number: 55+ (43) 33715988
E-mail: leandrosag@uel.br

Abstract

Landraces are considered important sources of abiotic stress tolerance. Among the different abiotic stresses, phosphorous (P) deficiency is considered one of the limiting factors in tropical and subtropical soils. Thus, the aim of the present work is to evaluate and compare P acquisition and use efficiency in landraces and improved varieties of maize in Brazil and classify varieties based on their performance (yield) under low (efficient versus inefficient) and high (responsive versus non-responsive) P supplementation. It also investigates the relationship among variables in regards to P use efficiency (PUE) and agronomic traits and evaluates genetic diversity among varieties. Thirteen landraces varieties and five improved varieties were evaluated in two P-contrasting experiments (with and without P application during sowing) in two counties (Londrina and Maringá), Paraná, Brazil. There was a wide genetic variability among the varieties for the agronomic and P efficiency traits. P acquisition efficiency (PAE) showed high correlation with PUE and grain yield (GY). On the other hand, no correlation was detected between PUE and GY for P use internal efficiency (PUTE). In the experiment without P at sowing, the improved variety ST0509 showed high values for PUE and GY, whereas, among the landraces, the varieties Amarelão, Caiano and Caiano 2 stood out, being considered promising varieties for future PUE breeding programs.

KeyWords *abiotic stress; phosphorous use efficiency; plant breeding.*

Introduction

Phosphorous (P) deficiency is one of the key limiting factors in tropical and subtropical soils, since most of these soils show low natural availability and high capacity to adsorb and fix this nutrient (Sanchez and Salinas, 1981). The alternative adopted to minimize this problem is the use of correctors and phosphate fertilizers (predominantly of phosphate rocks), adapting soil to plant (Veneklaas et al., 2012). However, recent estimates show that the price of phosphate fertilizers will increase in the next decades, since the most easily explored P reserves will be depleted still in this century (Cordell et al., 2009; Scholz et al., 2013).

With the increase of the world's population and the decline of phosphate rocks sources, there will be an increasing need to improve phosphate efficiency in the plant and in the whole production scale and use (Rose et al., 2013). At the plant level, phosphorous use efficiency (PUE) has been defined as the relationship between grain production per unit of nutrients available for the plant (Moll et al., 1981). This index is determined by the plants capacity to acquire nutrients from the soil (P acquisition efficiency - PAE) and the internal metabolic processes of this nutrient inside the plant (P internal use efficiency – PUTE) (Veneklass et al., 2012; Mendes et al., 2015).

A high number of mechanisms has been related to the increase in PAE, including the morphology, physiology and/or biochemistry of the root system, association with microorganisms (bacteria and mycorryza) and the production of root exudates, such as organic anions and phosphatase enzymes (Wang et al., 2010; Santos et al., 2015). PUTE is attributed mainly to efficiency in recycling, translocation and P use stored in plants under low nutrient availability conditions (Veneklaas et al., 2012; van de Wiel et al., 2016).

PUE genotypic variations have been identified in several works related to maize crop (Parentoni and Souza Júnior, 2008; DoVale et al., 2013; Mendes et al., 2014; Santos et al., 2015; Zhang et al., 2014a), allowing the selection of desirable alleles to increase low P tolerance. By mapping QTLs related to phosphorous use efficiency, Mendes et al. (2014) verified that approximately 80% of the QTLs mapped for PAE co-located with those for PUE, showing that P acquisition efficiency is the key determinant of PUE in tropical maize, corroborating with the results obtained by Parentoni and Souza Júnior (2008) and Bayuelo-Jiménez and Ochoa-Cadavid (2014).

In regards to abiotic stresses, several studies have been conducted to identify and use maize landraces as tolerance sources in case of water deficit (Hayano-Kanashiro et al., 2009; Prasanna, 2012; Meseka et al., 2015), cold (Peter et al., 2009; Rodríguez et al., 2010), and aluminum toxicity (Carvalho et al., 2004; Coelho et al., 2016). They can also be used for low nutrients adaptation (Machado et al., 2001; Ferro et al., 2007; Bayuelo-Jiménez and Ochoa-Cadavid, 2014).

When evaluating PUE of 20 maize landraces originating from Purepecha Plateau, Mexico, Bayuelo-Jiménez and Ochoa-Cadavid (2014) verified a wide genetic variability among landraces for PAE and PUTE in P deficient soils and that this variability can be applied to future breeding programs. In Brazil, Machado et al. (2001) evaluated ten maize varieties (landraces and improved) in regards to absorption efficiency, translocation and P use under nutrient solution and in the field, and verified that two landraces (Caiano de Sobrália and Carioca) showed grain yield and P efficiency rates similar to the best improved varieties.

The aim of this study is to evaluate and compare the acquisition and utilization of P efficiency in maize landraces and improved varieties in Brazil and classify these varieties based on their performance (yield) under low (efficient versus inefficient) and high (responsive and non responsive) P supplementation. It also investigates the relationship among variables related to PUE and agronomic traits and evaluates the genetic diversity among the varieties.

Materials and Methods

Genetic material and experimental site

The study evaluated 18 maize varieties, being 13 landraces (Branco Antigo, Caiano, Aztecão, Maia, Palha Roxa, Amarelão, Carioca, Branco Gelinski, Cunha, 14 variedades, Planalto, Caiano 2 and Amarelão 2) and five improved varieties (AL 30, ST0509, ST2109, ST1309 and ST0504). Two P contrasting experiments (with and without P application at sowing were conducted in two counties (Londrina – 23°20'S e 51°12'W, and Maringá – 23°25'S e 51°57'W) in the Paraná state, Brazil. Soils are characterized as Red Latosol Eutrophic and Oxisoil for the Londrina and Maringá environments, respectively.

Experimental design

Experiments were sown during the 2014/2015 crops, using randomized blocks design in a factorial scheme, being the experimental unit constituted of two lines of 5m, with spacing between plants and lines of 0.90 x 0.20m, respectively, resulting in a stand estimated at 55.555 plants/ha^{-1}.

To characterize the experiments in the environments, layers of soil samples of 0-20cm were taken for chemical analysis (Table S1). Sowing fertilization for the P experiment was done with the application of 400 Kg ha^{-1} of formulated 8-28-16 (32 Kg ha^{-1} of N, 112 Kg ha^{-1} of P2O5 and 64 Kg ha^{-1} of K2O). Under P absence condition, sowing fertilization was done with the application of 66 Kg ha^{-1} of urea and 150 Kg ha^{-1} of formulated 00-00-20 (64 Kg ha^{-1} of K2O). Coverage fertilization was conducted in two experiments, with plants at the V6 stadium and the application of 200 Kg ha^{-1} of urea. The other crop treatments were conducted as recommended by the crop, following technical recommendations for maize crops. Data regarding rain and maximum and minimum temperature means, observed during the experimental period, were obtained from Instituto Agronômico do Paraná (IAPAR) weather stations, in Paraná, Brazil (Figure S1).

Agronomic and P efficiency traits

The following agronomic traits were analyzed: *i*) plant height (m) (PH), *ii*) first corn ear insertion height (m) (EH), *iii*) number of ears per plant (NE), and *iv*) grains yield (Kg ha^{-1}) (GY), corrected for 13% humidity standard. For the experiments without P, five plants, representing each plot, were cut (at harvest time) and dried in an air ventilation chamber at 65°C (up to a constant weight) to determine the percentage of grain dry matter and stubble. Later, grain and stubble phosphorous content was measured by the spectophotometric molybdenum blue test. Based on the data, this study estimated *v*) grain phosphorous content (PG, Kg Kg^{-1}), *vi*) P use rate (PUR, equals the grain dry matter by P unit in the grains expressed in expressed in Kg Kg^{-1}) and *vii*) crop index (PHI, equals the P unit in the grains per P unit in the shoot). To determine P use efficiency the following efficiency rates were adopted: *viii*) acquisition (PAE), *ix*) internal use (PUTE), and *x*) P use (PUE) proposed by Moll et al. (1981). These traits were obtained as follows: PAE = Pt/P applied (kg of P in the plant at maturity per Kg of fertilizer P applied); PUTE: GY/Pt (kg of grain dry matter produced per kg of P in the plant); and PUE: multiplying of PAE and PUTE.

Statistical analysis

Agronomic and phosphorous efficiency data were submitted to an individual analysis of variance (by experiment) and later verified the homogeneity of the residual variances through the Pearson and Hartley test (1956), analyzed jointly. The statistical model adopted for the agronomic data joint analysis was the following: $Y_{ijkm} = \mu + G_i + E_j + L_k + GE_{ij} + GL_{ik} + ELjk + GEL_{ijk} + (B/L)E_{jkm} + e_{ijkm}$, where Y_{ijkm} is the plot average phenotypic value, μ is the experiments' general average , G*i* the i-th genotype fixed effect (i = 1, 2, ..., 18), E_j the j-th experiment fixed effect (j = 1, 2), L_k the k-th location fixed effect (k = 1, 2), GE_{ij} the i-th genotype with the j-th experiment interaction effect, GL_{ik} the i-th genotype with the k-th location interaction effect, EL_{ik} the j-th experiment with the k-th location interaction effect, GEL_{ik} the i-th genotype with the j-th experiment and the k-th location triple interaction effect, $(B/L)E_{jkm}$ effect of the k-th block inside the k-th location with the j-th experiment and e_{ijkm}: the random error. The statistical model adopted for the P efficiency data during the joint analysis was: $Y_{ikm} = \mu + G_i + L_k + GL_{ik} + B/L_{jkm} + e_{ijkm}$, where Y_{ijkm} is the plot average phenotypic value, μ the experiments' general value, Gi the i-th genotype fixed effect (i = 1, 2, ..., 18), the k-th location fixed effect L_k (k = 1, 2), GL the i-th genotype interaction with the k-th location, B/Lkm the effect of the k-th block inside of the k-th location and eikm: the random error. Posteriorly, data were submitted to the Scoot-Knott clustering analysis (1974).

The methodology proposed by Fageria and Kluthcouski (1980) was used to differentiate genotypes regarding use efficiency and response to phosphorous application. Nutrient use is defined by the grains yield average in the low level, while the response to the use of the nutrient is obtained by the difference between grains yield in the two levels divided by the difference between P dosages. Data from the experiments without P at sowing were also submitted to the Pearson's correlation analysis and the UPMGA hierarchical clustering (Unweighted Pair Group Method using Arithmetic averages) based on the average normalized Euclidean distance. All analyses were conducted by the R program (http://www/r-project.org).

Results

The joint analysis of variance of the agronomical data showed significant differences for genotypes sources of variation for most agronomic traits, except for NE (Table S2). On the other hand, for the experiments was observed significant effect only for GY. GY mean value was 3281.91 Kg ha^{-1} for the experiment with the absence of P during sowing, while with P was 4002.28 Kg ha^{-1}, an yield increase by 18%.

Differences were not detected for location, considering that the average GY was 3698.50 and 3581.59 Kg ha^{-1} in the Londrina and Maringá environments, respectively. As for interactions, only GY were significant for genotypes x experiments (GE) and genotypes x location (GL), showing different genotypes performance before experiments and locations variations. The coefficient of variation (CVs) varied from 13.89 (EH) to 19.04 (NE).

Most traits related to phosphorous efficiency were significant for genotypes and locations variation sources, except for PG for genotypes and PHI for locations (Table S3). PUE mean values were from 160.91 to 66.27 Kg Kg^{-1} for the Londrina and Maringá environments, respectively. For the GL interaction, only PUE and PHI were significant. CVs (%) varied from 6.24 (PHI) to 30.19 (PAE).

In experiments without P at sowing, variety ST0509 obtained higher GY in both locations, followed by

Table 1. Mean clustering by the Scott-Knott test (P < 0.05) for three agronomic traits in 18 maize varieties evaluated during experiments with and without phosphorous, at sowing, in Londrina and Maringá environments, Paraná, Brazil.

Genotypes[2/]	GY[1/]				PH	EH
	Londrina		Maringá			
	With P at sowing	Without P at sowing	With P at sowing	Without P at sowing		
Branco Antigo	3059.86 Ac	2515.75 Ab	3261.60 Ad	3817.68 Ab	2.70 b	1.70 b
Caiano	4817.83 Aa	3851.19 Aa	3590.84 Ad	3980.41 Ab	2.93 a	1.72 b
Aztecão	4116.08 Ab	2816.12 Bb	3761.03 Ac	4510.80 Ab	2.70 b	1.73 b
Maia	4409.25 Ab	3174.37 Bb	2553.31 Ae	3053.96 Ac	3.15 a	1.94 a
Palha Roxa	4159.45 Ab	3421.38 Aa	4168.11 Ac	2850.06 Bc	2.66 b	1.70 b
Amarelão	4991.44 Aa	4295.69 Aa	4935.07 Ab	4323.98 Ab	2.80 b	1.87 a
Carioca	5239.87 Aa	2386.69 Bb	4531.08 Ab	2820.74 Bc	2.55 b	1.54 b
Branco Gelinski	3841.95 Ab	2024.86 Bc	2770.23 Ae	2382.66 Ad	2.48 c	1.61 b
Cunha	2164.43 Ac	1438.54 Ac	3043.95 Ad	1706.35 Be	2.28 c	1.34 d
14 variedades	3242.87 Ac	2645.73 Ab	3862.67 Ac	3471.04 Ac	2.42 c	1.49 c
Planalto	3989.70 Ab	2725.04 Bb	3903.62 Ac	3303.04 Ac	2.18 c	1.21 d
Caiano 2	4997.35 Aa	4638.90 Aa	3996.02 Ac	4414.59 Ab	2.58 b	1.60 b
Amarelão 2	2314.36 Ac	1428.52 Ac	2254.44 Ae	1160.83 Be	2.17 c	1.21 d
AL30	3247.17 Ac	2666.30 Ab	4543.38 Ab	3315.33 Bc	2.10 c	1.22 d
ST0509	5159.45 Aa	5207.98 Aa	6126.28 Aa	6719.51 Aa	2.32 c	1.33 d
ST2109	5414.70 Aa	4208.69 Ba	3556.69 Ad	2165.67 Bd	2.46 c	1.48 c
ST1309	4705.31 Aa	3946.78 Aa	4677.14 Ab	3505.12 Bc	2.18 c	1.28 d
ST0409	5682.46 Aa	4199.96 Ba	3208.32 Ad	3091.67 Ac	2.32 c	1.34 d

[1/]GY: Grain Yield (Kg ha-1), PH: plant height (m) and EH: ear height (m).
[2/]Means followed by the same upper and lower case letters, horizontally and vertically, respectively, constitute a statistically homogeneous group

Caiano2, Amarelão and Caiano (Table 1). In the Londrina environment, the Aztecão, Maia, Carioca, Branco Gelinski, Planalto, ST2109 and ST0504 varieties showed a GY increase when P was added to sowing, while for Maringá environment this increase was obtained in the Palha Roxa, Carioca, Cunha, Amarelão 2, AL30, ST2109 and ST1309 varieties. As for PH and EH, the lowest values were verified for the Cunha, Planalto, Amarelão 2, AL30, ST0509, ST1309 and ST0504 varieties.
The index proposed by Fageria and Kluthcouski (1980) is in agreement with the Scott and Knott clustering (1974) for the classification of efficient and responsive varieties (Figure 1). In the Londrina environment, to PUE, determined by PAE and PUTE, the highest values were observed for ST0509 and Caiano 2 (264.97 and 236.01 Kg Kg^{-1}, respectively) in Londrina. the highest value for the Maringá environment was shown by ST0509 (153.05 Kg Kg^{-1}), followed by Amarelão, Aztecão, Caiano, Caiano2, ST1309, ST0504, Banco Antigo, Palha Roxa and Maia.
The Scott and Knott cluster analysis (1974) showed no differences among the varieties for the PUR variable. Values varied from 324.10 (Palha Roxa) to 512.16 Kg Kg^{-1} (ST0509). The PHI varied from 0.601 to 0.872 Kg Kg^{-1} and 0.667 to 0.880 Kg Kg^{-1} in Londrina and Maringá, respectively. The varieties Aztecão and Cunha

Figure 1. *Use efficiency and response to the application of phosphorous in maize varieties by the Fageria e Kluthcouski (1980) methodology in Londrina (a) and Maringá (b) environments. I: efficient and responsive cultivars, II: non-efficient but responsive, III: non-efficient and non- responsive, and IV: efficient but non-responsive.*

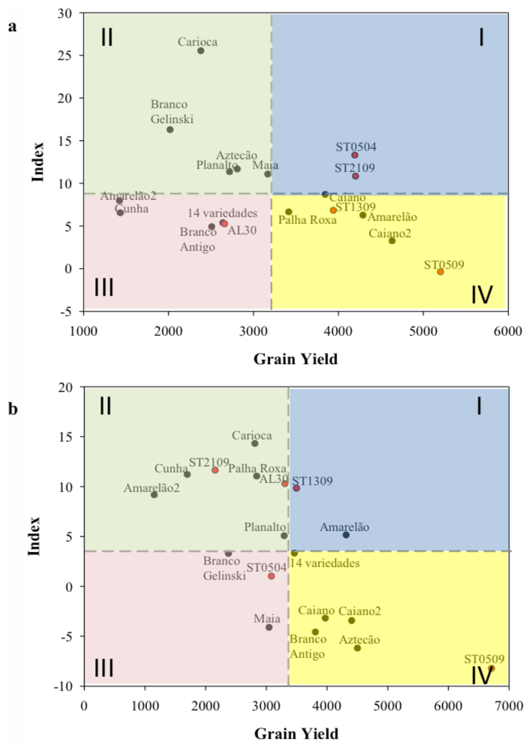
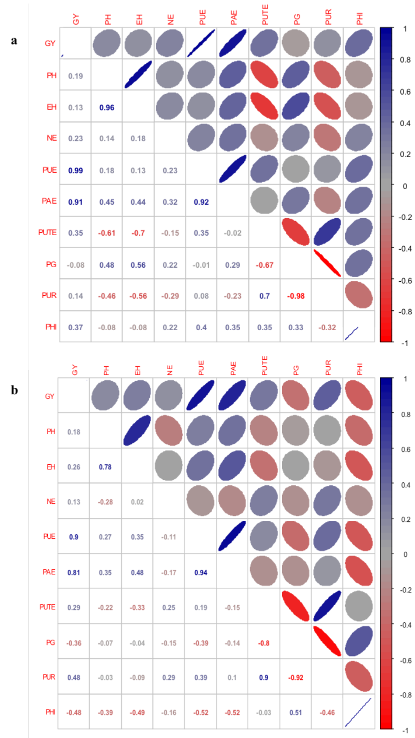


Figure 2. *Pearson correlation between agronomic and phosphate efficiency variables in 18 maize varieties evaluated in experiments without phosphorous, in sowings carried out in Londrina and Maringá environments, Paraná, Brazil.*



ST0504 and ST2109 were classified as efficient and responsive, while Caiano, Palha Roxa, ST1309, Amarelão, Caiano2 and ST0509 were classified as efficient but non-responsive. In regards to the Maringá environment, ST1309 and Amarelão varieties were considered efficient and responsive and Caiano, Caiano2, Branco Antigo, Aztecão and ST0509 efficient but non-responsive.
Two groups of PAE were formed by Scott and Knott (1974), with 11 varieties allocated in the group with higher value (from 0.365 to 0.541 Kg Kg^{-1}) (Table 2). There was no group separation for PUTE. In regards (Londrina) and Caiano, Caiano 2 and ST0509 (Maringá) showed the lowest values.
The correlation between the Londrina and Maringá variables is shown in Figure 2. There was a high correlation between GY and PUE (0.99** and 0.90**, respectively, in the two environments) and PAE (0.91** and 0.81**, respectively), while no correlation was detected for PUTE. PUE was highly correlated with PAE in both locations (0.92** and 0.94**, respectively) and correlated negatively with PHI in the Maringá environment (-0.52*).
Being the PG trait the inverse of the PUR, and, as the

Table 2. Means clustering by the Scott-Knott test (P < 0.05) for five traits related to phosphorous efficiency in 18 maize varieties evaluated in experiments without phosphorous, at sowing, in Londrina and Maringá environments, Paraná, Brazil.

Genotypes	PAE	PUTE	PUE		PUR	PHI	
			Londrina	Maringá		Londrina	Maringá
Branco Antigo	0.365 a	269.49 a	127.99 Ac	71.29 Bb	351.72 a	0.775 Aa	0.758 Ab
Caiano	0.541 a	262.27 a	195.94 Ab	91.92 Bb	371.20 a	0.745 Aa	0.667 Ac
Aztecão	0.441 a	254.90 a	127.38 Ac	94.12 Ab	384.22 a	0.707 Bb	0.821 Aa
Maia	0.434 a	268.16 a	161.50 Ac	69.16 Bb	337.89 a	0.793 Aa	0.793 Aa
Palha Roxa	0.437 a	266.31 a	174.07 Ab	70.78 Bb	324.10 a	0.815 Aa	0.835 Aa
Amarelão	0.523 a	292.66 a	218.55 Ab	96.13 Bb	351.94 a	0.840 Aa	0.825 Aa
Carioca	0.279 b	282.92 a	121.43 Ac	42.48 Bc	360.22 a	0.781 Aa	0.802 Aa
Branco Gelinski	0.260 b	302.39 a	117.17 Ac	45.04 Bc	348.39 a	0.808 Aa	0.833 Aa
Cunha	0.173 b	260.43 a	73.19 Ad	23.48 Bc	377.82 a	0.601 Bc	0.863 Aa
14 variedades	0.309 b	314.37 a	134.61 Ac	60.77 Bc	391.95 a	0.802 Aa	0.814 Aa
Planalto	0.240 b	357.86 a	138.64 Ac	37.35 Bc	419.93 a	0.856 Aa	0.844 Aa
Caiano 2	0.518 a	317.52 a	236.01 Aa	89.27 Bb	396.79 a	0.840 Aa	0.765 Ab
Amarelão 2	0.116 b	319.09 a	63.61 Ad	15.59 Ac	415.19 a	0.803 Aa	0.852 Aa
AL30	0.277 b	277.90 a	135.65 Ac	26.93 Bc	338.56 a	0.796 Aa	0.873 Aa
ST 0509	0.540 a	385.88 a	264.97 Aa	153.05 Ba	512.16 a	0.759 Aa	0.770 Ab
ST 2109	0.393 a	296.27 a	203.20 Ab	49.04 Bc	378.73 a	0.816 Aa	0.831 Aa
ST 1309	0.432 a	320.89 a	200.80 Ab	81.15 Bb	379.05 a	0.872 Aa	0.846 Aa
ST 0409	0.457 a	287.94 a	201.67 Ab	75.36 Bb	372.74 a	0.787 Ba	0.880 Aa

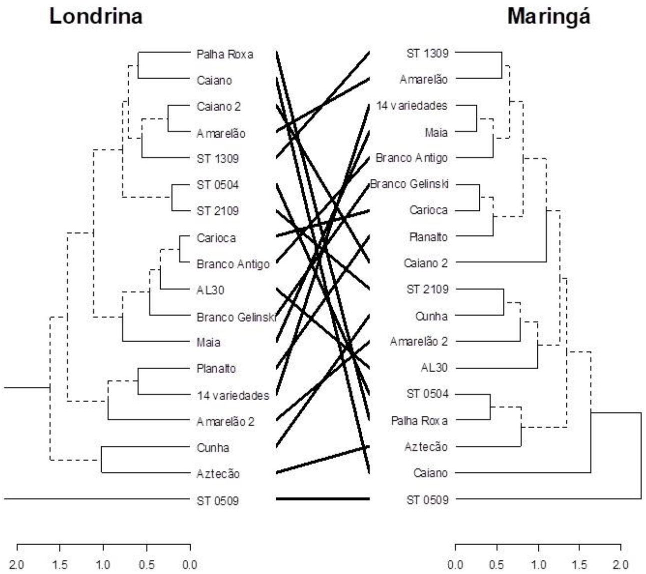
[1] PAE: P acquisition efficiency (Kg Kg^{-1}), PUTE: P internal use efficiency (Kg Kg^{-1}), PUE: P use efficiency (Kg Kg^{-1}), PUR: P use rate (Kg Kg^{-1}) and PHI: P harvest index (Kg Kg^{-1}). [2/] Means followed by the same upper and lower case letters, horizontally and vertically, respectively, constitute a statistically homogeneous group

latter is one of the components of the PUTE variable, high and negative correlations were observed between PG and PUTE (-0.67** and -0.80** for the Londrina and Maringá environments, respectively). These correlations were also found between PG and PUR (-0.98** and -0.92** for the Londrina and Maringá environments, respectively) (Figure 2). The PHI variable, in the Maringá environment, was correlated negatively to GY, EH, PUE, PAE and PUR (-0.48*, -0.49*, -0.52*, -0.52* and -0.46*, respectively) and positively to PG (0.51).

The UPGMA hierarchical cluster analysis showed different dissimilarity patterns between the matrixes generated in the Londrina and Maringá environments (Figure 3). However, both dendrograms allocate, in isolation, genotype ST0509, in which this variety shows high grain yield associated with P use efficiency.

Using the R package NbClust in the Londrina environment, five was considered an optimum number of groups. Seven varieties (Palha Roxa, Caiano, Caiano 2, Amarelão, ST1309, ST0504, ST2109) were allocated to Group I and showed higher GY, PUE and PAE when compared to groups II, III and IV. Group II (Carioca, Branco Antigo, AL30, Branco Gelinski and Maia) showed intermediate values for most of the analyzed

Figure 3. *Genetic dissimilarity dendrogram among 18 maize varieties by UPGMA based on the dissimilarity matrix of agronomic and phosphorous efficiency variables.*



variables, while groups III (Planalto, 14 variedades and Amarelão2) and group IV (Cunha and Aztecão) showed the lowest values for GY, PUE and PAE. Group III showed the highest values for PUTE.

In the Maringá environment, five was also the optimum number of groups by the NbClust package (Figure 3). Groups I (ST1309, Amarelão, 14 variedades, Maia, Branco Antigo, Branco Gelinski, Carioca, Planalto, Caiano2) and III (ST0504, Palha Roxa and Aztecão) showed intermediate values for GY, PUE, PAE for most of the assessed varieties. On the other hand, group II (ST2109, Cunha, Amarelão2, AL 30) obtained the lowest values for GY, PH, EH, PUE, PAE PUE and PAE. Group I showed the highest values for the PUTE variable. The Caiano variety, allocated to group IV, obtained the lowest PHI value

Discussion

Phosphorous is one of the nutrients most used in maize production around the world and the main mineral for maize development in the Brazilian Cerrado. Most soils in these regions show low pH, high Al content, low nutrients availability and high phosphorous sorption. So, research aiming at developing plants with greater soil phosphate absorption and at increasing productivity or biomass per absorbed P unit become essential for maintaining sustainability in these agricultural systems.

This study observed high genetic variability among varieties for agronomic traits and P efficiency. Such response constitutes a key element for breeding programs for the selection of efficient and responsive varieties to P supplement.

The addition of P to sowing promoted an average increase of 18% in GY, being 24% in the Londrina environment and 11% in the Maringá environment. By assessing 36 maize commercial cultivars under low and high P availability, Coimbra et al. (2014) observed an average GY of 3380.49 and 4773.64 Kg ha^{-1}, respectively, with an increase by 30%. Bayuelo-Jiménez and Ochoa-Cadavid (2014) conducted three PUE experiments and verified that only one experiment showed differences in P application, promoting an increase by 12% in GY (2570 and 2930 Kg ha^{-1} for low and high P, respectively). The increase differences observed for GY may be related to the P level in the soil, which showed higher values for the Maringá environment.

PUTE showed a variation from 254.90 to 385.88 Kg Kg^{-1}. These values are in agreement with those verified by Parentoni and Souza Júnior (2008), who reported an average value of 298 Kg Kg^{-1} in 48 tropical maize genotypes. According to van de Wiel et al. (2016), there is a variety of metabolic changes involved in PUTE, attributed mainly to recycling efficiency, translocation and P use stored in plants under low nutrient availability. PUTE was decomposed into two components, use rate (PUR) and harvest index (PHI). PUR showed high correlation with PUTE (0.7** and 0.9** in environments in Londrina and Maringá, respectively), while an association with PUTE was not observed for PHI. Parentoni and Souza Júnior (2008) corroborates with these results in which they verified that the PUR component was more important than the PHI to explain the variability observed in PUTE. On the other hand, Bayuelo-Jiménez and Ochoa-Cadavid (2014) verified that the harvest indexes were the most important in explaining PUTE variability. These differences indicate the importance of soil type and the influence on the relative importance of PAE versus PUTE.

PUR is calculated by dividing grain yield by the amount of phosphorous in the grain. In this case, the higher the P concentration in the grains, the lower the PUTE, which can be observed in the correlation between PG and PUTE (-0.67** and -0.8** in the Londrina and Maringá environments, respectively). In this context, selection strategies to increase PUTE in maize in Oxisols must focus in reducing P concentration in the grains (Parentoni and Souza Júnior, 2008).

The present work shows a high correlation between PAE and PUE and GY. On the other hand, a correlation between PUE and GY was not detected. PUE increase can be obtained through a PAE and/or PUTE increase (Veneklaas et al., 2012). However, according to several works, PAE is the key determining factor of PUE (Parentoni and Souza Júnior, 2008; Wang et al., 2010; Mendes et al., 2015). Parentoni and Souza Júnior et al. (2008), evaluating the relative importance of PAE and PUTE over the EUP, verified that PAE was almost twice more important than PUTE in the variability observed in PUE, in environments with low P availability, and three times more important in those with high availability. Mendes et al. (2015) verified that approximately 80% of the QTLs mapped for PAE co-located with those for PUE. A correlation between PUTE and PAE in the two environments was not observed, indicating that the two variables are independent.

According to Wang et al. (2010), the most important characteristics in P acquisition are those related to the roots morphology and architecture. The roots architecture has high plasticity in response to the development under low P conditions, and plants adapted to these conditions have more adventitious roots, less root diameter, more superficial roots, aerenchyma, more dispersed lateral roots, greater biomass and denser and longer root hair (van de Wiel et al., 2016). Besides alterations in the root system, other mechanisms are also considered important for a better P acquisition such as the association with microorganisms (mycorryza and bacteria) and the production of root exudates such as organic anions and phosphatase enzymes (Wang et al., 2010; Santos et al., 2015).

Mechanisms for the activation of root system alterations in response to low P availability depend on changes in the localized P concentration, transportation and / or sensitivity to growth regulators. During this process, several genes are activated, triggering changes in the molecular, physiological and cellular processes, promoting greater plant adaptation to environments with low P availability (Ha and Tran, 2013; Niu et al., 2013; Zhang et al., 2014b).

In this paper genetic variability for efficiency and responsiveness was observed in 18 maize varieties. By the UPGMA cluster analysis, ST0509 was isolated in the two environments, with high values for PUE and GY, in the experiment without P at sowing. Varieties allocated to group I also obtained high values for PUE and GY in the Londrina environment. However, when analyzed in the Maringá environments, these varieties were allocated in different groups, with the Amarelão, Caiano and Caiano 2 varieties showing high PUE and GY values. Bayuelo-Jiménez and Ochoa-Cadavid (2014) also verified a wide variability for efficiency and responsiveness among local maize varieties originated from Purepecha Plateau, Mexico, indicating that this variability can be applied to future breeding programs for P use efficiency.

In conclusion, the present study showed an important genotypic variability for GY and PUE for genotypes assessed under low P conditions. As in other works on maize crops, PUE differences were attributed mainly to PAE and not to PUTE. PUTE showed low variability and low correlation with GY, and was correlated negatively to the P concentration in the grains. This research emphasizes the need for studies comparing different maize landraces under low P concentrations, since the variability observed in PUE offers a selection opportunity for plant breeding programs.

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