Relative Importance of Uptake and Utilization Efficiency in Phosphorus Use Efficiency in a Red Oxisol: Following Moll's Insights.

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Introduction

The development of cultivars more efficient in the use of nutrients for grain production will be the second major research challenge in the XXI century, being overcome only by potable water supply USDA (2000). The efficiency of cultivated plants to use nitrogen, potassium and phosphorus was compared by Baligar and Fageria, 2001. The authors concluded that phosphorus had the lowest recover rate by plants among these three major macro nutrients.

A number of definitions of nutrient efficiency can be found in the literature (Good et al., 2004). Usually, these definitions deal with the ability of a genotype to produce grain per unit of available nutrient. A more accepted definition of an efficient genotype for a given nutrient is the one who is able to produce a maximum amount of grain with the smallest accumulation of this nutrient in the plant (Horst et al., 1974; Blair, 1993).

Breeding programs for P efficiency in plants have been much less frequent than breeding programs for other abiotic stresses such as aluminum tolerance. The main reason for that is the fact that phosphorus nutrition in the field is based on nutrient diffusion from soil to roots, which makes very difficult the development of screening procedures such as nutrient solution or green house evaluations that would mimic what happens in the field. The more reliable selection criterion for P efficiency is grain yield under contrasting P levels in the soil. Moll et al., 1982 proposed a methodology to evaluated nutrient use efficiency based on two components: the first one is the ability of the plant to get the nutrient from the soil (uptake efficiency) and the second is based on the capacity of the plant to produce grain per unit of nutrient absorbed (utilization efficiency). The majority of the studies on nutrient use efficiency deals only with means, while in a breeding program, both means and variances are important. Moll's paper gave a key contribution to the studies in nutrient use efficiency by proposing a methodology to use variances to determine the relative importance of the nutrient efficient components (uptake and utilization) in nutrient use efficiency. They applied the proposed methodology in a trial data of nine hybrids evaluated under two nitrogen levels. Their conclusions were that, for the group of genotypes studied, nitrogen use efficiency at the high level of N was mainly a function of uptake efficiency, and at the low level of N it was mainly due to utilization efficiency.

The methodology proposed by Moll et al., 1982 was used to study P efficiency in a group of 90 single cross hybrids from the EMBRAPA-Maize and Sorghum breeding program evaluated in a Red Oxissol under high and low P level. The goal of this work was to determine the relative importance of both P uptake and utilization in P use efficiency in this set of germplasm under high and low P in the soil.

Material and Methods:

Experimental conditions:

A group of 90 maize single cross hybrids was evaluated in a Red Oxissol in Sete Lagoas-MG under two P levels in 2000. Experimental design was a randomized complete block design with three replicates. The high P level area had 15 mg kg^{-1} of P from 0-20 cm and 2.6 mg kg^{-1} of P from 20-40 cm. The low P level area had 5 mg kg^{-1} of P from 0-20 cm and 1.3 mg kg^{-1} of P from 20-40 cm. P extractor used for soil analysis was Mehlich 1. Soil bulk density was 1. Plot size was 2.5 m long and 0.9 m between rows. Phosphorus available in the soil from 0-40 cm per plot was 7920 mg $plot^{-1}$ at high P level and 2831 mg $plot^{-1}$ at low P level. P availability in the soil (0-40 cm) per plant in each plot was obtained by dividing P in the soil (mg $plot^{-1}$) for number of plants per plot. The variables measured were: grain yield in grams $plant^{-1}$ (GY), straw yield (stalk, leaves, cobs and huskies) in grams $plant^{-1}$ (SY), % P in the grain (PG), % P in the straw (PS), P uptake efficiency (UPE), P utilization efficiency (UTE) and P use efficiency (USE). P absorbed in kernels and straw was calculated from yield x %P respectively. Total P uptake (mg $plant^{-1}$) was obtained by adding P in the kernels and straw.

Definitions and methodology

The key points from Moll's paper, adapted for P nutrition are:

a) Definitions of P efficiency:

P uptake efficiency =Total P in the plant (mg $plant^{-1}$) / P available in the soil (0-40 cm) in mg $plant^{-1}$.
P utilization efficiency = Grain weight (mg $plant^{-1}$) / Total P in the plant (mg $plant^{-1}$)
P use efficiency = P uptake x P utilization = Grain weight (mg $plant^{-1}$)/P available in soil (mg $plant^{-1}$)

b) Steps used to determine the relative importance of uptake and utilization in P use efficiency:

1) P use efficiency (Y) is a multiplicative relationship from uptake efficiency (X1) and utilization efficiency (X2). A data logarithm transformation was used to convert this relationship in an additive one or log(Y) = log(X1) + log (X2). The log transformation was done using the mean of each hybrid for each of the variables Y, X1 and X2, at low and high P in the soil.

2) The variables y, x1 and x2 were defined respectively as the deviation from the mean of Y, X1 and X2 ($y = Y - \mu$; $x_1 = X_1 - \mu$ and $x_2 = X_2 - \mu$)

3) The sum of squares of the log transformed P use efficiency (Σy^2) was decomposed into two sums of products: $\Sigma (x1 * y)$ and $\Sigma (x2 * y)$.

4) The relative importance of P uptake in P use efficiency is equal to $\Sigma (x1 * y) / \Sigma y^2$. In the same way, the relative importance of P utilization efficiency in P use efficiency is equal to $\Sigma (x2 * y) / \Sigma y^2$.

5) The relative importance of P uptake in P use efficiency ($\Sigma (x1 * y) / \Sigma y^2$) is a function of the product of the coefficient of correlation between P uptake ($x1$) and P use efficiency (y) or r_{x1y}, multiplied by the ratio of the standard deviation of $x1$ and **y** (S_{x1} / S_y). This can be written as

$\Sigma (x1 * y) / \Sigma y^2 = (r_{x1y})$ x (S_{x1} / S_y). In the same way the relative importance of P utilization in P use efficiency is a function of the product of the correlation between both, multiplied by their ratio of standard deviation or $\Sigma (x2 * y) / \Sigma y^2 = (r_{x2y})$ x (S_{x2} / S_y).

Statistical Analysis: A combined ANOVA using data from the high and low P environments was done for each variable using the software SAS. Broad sense heritability (HER) was calculated for each variable in each environment (HER= σ^2_g / σ^2_f where σ^2_g=(MSTreat-MSE)/r , σ^2_f = MSTreat/r and r=3) .

Results and Discussion:

The combined ANOVA for each variable showed that the effects of environment (two P level in the soil), genotypes (90 maize single crosses) and the interaction genotypes x environments were significant for grain yield (GY), straw yield (SY), P uptake efficiency (UPE) and P use efficiency (USE). For the variables % P in the grain (PG), % P in the straw (PS), and P utilization efficiency (UTE), the effects of environment and genotypes were significant but the interaction genotype x environment was not significant.

The means for GY (g $plant^{-1}$) under high and low P were 141.5 and 90.0 respectively, with a reduction of 36% in yield from the high to the low P environment. This reduction in yield across P levels has been considered adequate to discriminate genotypes in our breeding program for P use efficiency. The mean % of phosphorus in the grain (PG) at the high and low P level were 0.14 % and 0.10 % and in the straw (PS) these values were 0.05 % and 0.03 % corresponding to a reduction of P concentration across P levels of 29 % in the grain and 40 % in the straw.

P uptake efficiency measures the ability of the plant to absorb the available P in the soil. It is defined as the ratio between the total P in the plant (grain+straw) per unit of P available in the soil (in this study both were calculated in mg of P/plant). The mean value for P uptake efficiency at the high and low P level was 0.39 and 0.51. These values indicated that, from the P available in the soil from (0-40 cm), a mean of 39% was extracted by the plants in the high P soil and 51% in the low P soil. These values are probably overestimated according to P recovery trials in the literature (Baligar and Fageria, 2001). Two reasons could account for this fact. One is that the root system can go below 40 cm. Although, it should be remembered that it is well-known that the large fraction of the available P in Cerrado areas is in the layer of 0-20 cm. Another reason could be that the Red Oxisol used in this study has more than 60% of clay content and its capacity to supply P could probably be underestimated by the Mehlich 1 extractor. Also, Mehlich 1 does not account for the P organic fraction in the soil, which could be large in this Oxissol. In this case, the fraction of P available in the soil per plot (see Material and Methods) would be higher than 7920 mg $plot^{-1}$ at the high P level and 2831mg $plot^{-1}$ at the low P level. This fact could change the means of P uptake efficiency and P use efficiency but would not change anything in the variance estimations. P uptake efficiency increased by 31% from the high to the low P level in the soil.

P utilization efficiency measures the amount of grain produced (mg $plant^{-1}$) per unit of P absorbed by the plant (grains + straw), also in mg $plant^{-1}$. The mean value for P utilization efficiency at the high and low P level in the soil was 557 and 726 which indicates that for each mg of P absorbed by the plant at the low P level, the plant produced a mean of 726 mg of grain. P utilization efficiency increased by 30 % from the high to the low P level in the soil.

P use efficiency is the product of P uptake efficiency and P utilization efficiency. It measures the amount of grain produced (mg $plant^{-1}$) per unit of available P in the soil (mg $plant^{-1}$). The mean value for P use efficiency at the high and low P level in the soil was 208 and 368 which indicates that for each mg of P available in the soil at the low P level the 90 hybrids produced a mean of 368 mg of grain. As was discussed for P uptake efficiency, the values found for P use efficiency would also probably be overestimated due to the fact that the capacity of the soil used in this study to supply P could be underestimated by the Mehlich 1 extractor.

Broad sense heritability estimates for all variables in both environments ranged from 0.30 (%PS) to 0.71 (SY). These values are considered intermediate to high (Hallauer and Miranda Filho, 1998). This should be done to the fact that a single environment was used to obtain these estimations. It indicates that genetic variability is present for all studied variables.

The relative importance of the components of P efficiency (uptake and utilization) in P use efficiency was estimated using the methodology proposed by Moll et al., 1982. The hybrids sum of squares for P use efficiency under high and low P in the soil was 0.465 and 1.303 (Table 2). The decomposition of each of these sum of squares into the two sum of products shown that at high P, the value of 0.465 is a function of a sum of products due to P uptake efficiency of 0.419 and a sum of products due to P utilization efficiency of 0.046. This data shows that P uptake efficiency accounts for 90.1% of the variability observed in the 90 hybrids for P use efficiency and P utilization efficiency accounts for only 9.9% of this variability. In the same way, under low P in the soil, P uptake efficiency accounts for 92.9% of the variability observed for P use efficiency and P utilization efficiency accounts for only 7.1% of this variability. We can go one step further and try to understand way this happened, based on the correlation of each component of P use efficiency with this variable ($\boldsymbol{r_{x1y}}$ and $\boldsymbol{r_{x2y}}$) and also looking at the ratio of the variability observed between each component of P use efficiency (uptake and utilization), with P use efficiency ($\boldsymbol{S_{x1}} / \boldsymbol{S_y}$ and $\boldsymbol{S_{x2}} / \boldsymbol{S_y}$). For the low P level in the soil, the fact that P uptake efficiency explained 92.9% of the variability observed in P use efficiency is a function of the product of a high coefficient of correlation between these two variables (r=0.914) multiplied by an also large ratio of standard deviation between uptake and use efficiency ($S_{x1} / S_y = 1.017$) or 0.914x1.017= 0.929. On the other hand, the fact that P utilization efficiency at low P level in the soil explained only 7.1% of the variability observed in P use efficiency is a function of a low correlation between these two variables (r=0.169) and also a low variability for P utilization efficiency ($S_{x2} / S_y = 0.419$).

Similar trend is observed at high P level, where P uptake efficiency explained 90.1% of the variability observed in P use efficiency. This is a function of a still high coefficient of correlation between these two variables (r=0.701) multiplied by an also large ratio of standard deviation between uptake and use efficiency ($S_{x1} / S_y = 1.286$) or 0.701x1.286= 0.901. On the other hand, the fact that P utilization efficiency at high P level in the soil explained only 9.9% of the variability observed in P use efficiency is mainly a function of a low correlation between these two variables (r=0.107) while the variability for P utilization efficiency is not too low ($S_{x2} / S_y = 0.923$). These results differ from the ones reported for nitrogen (N) use efficiency in the paper of Moll et al., 1982, where uptake efficiency was more important at high N level and utilization efficiency was more important at the low N level. Two things should be taken into account when comparing nitrogen and phosphorus efficiency. The first is that a larger amount of N compared to P is required to produce a unit of dry matter in the plant. The second is that N is absorbed by mass flux while phosphorus is acquired by diffusion. This would imply that, if a low amount of N is available in the soil, a large investment of the plant to increase root system should not be as efficient as it could be in the case of P. In this case, at low level of N in the soil, remobilization within the plant could be a more efficient strategy, as found in Moll's study, while in the case of P, if a low amount is available in the soil, the strategy of increasing the size of the root system or changing its architecture should increase the soil volume exploited by the plant and allow it to increase P uptake. It also has to be noticed that, different types of germplasm, growing in different types of soil, could have different strategies to increase nutrient use efficiency.

Altogether, these data indicates that, for the set of germplasm represented by this 90 hybrids evaluated in a clay Red Oxissol, uptake efficiency is largely more important for P use efficiency than utilization efficiency. If this finding is confirmed in different sets of germplasm and based on more trials in this same soil, it will indicate that the research for P use efficiency in this type of soil should be concentrated in plant traits that can affect uptake, such as root system morphology, and other traits related to the ability of the plant to acquire P from the soil in a more efficient way. These results are also relevant to decide which traits should be more important to be scored in mapping populations to study P use efficiency in the same type of environment used in this work. Physiological studies using maize contrasting germplasm for P use efficiency developed at EMBRAPA-Maize and Sorghum and evaluated under high and low P level in this clay Red Oxisol, have shown that, the main difference between efficient and inefficient genotypes, is their ability to modulate root system morphology under P stress conditions (Brazil, 2003). This finding agrees with the results observed in this study and point out in the direction that, for these soil conditions, the main research efforts in improving P use efficiency should be devoted to traits related to increase P uptake efficiency.

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TABLE 1 : Combined analysis of variance for 90 single cross hybrids evaluated in two environments (LE with high- 15 $mg^* kg^{-1}$ P and low- 5 $mg^* kg^{-1}$ P). Traits evaluated were grain yield in gr/pl (GY), straw yield in gr/pl (SY), % P in the grain (PG), % P in the straw (PS), P uptake efficiency (UPE), P utilization efficiency (UTE) and P use efficiency (USE). Significance of the F test is shown close to each mean square. Means, % of reduction (-) or increase (+) in the mean from high to low P level, broad sense heritability (HER) and coefficient of variation (cv) are also shown. EMBRAPA-Maize and Sorghum, Sete Lagoas, 2006.

		Mean Squares						
Source	d.f.	**GY g plant^{-1}**	**SY g plant^{-1}**	**PG (%)**	**PS (%)**	**UPE (Pabs/Psoil)**	**UTE (Grain/Pabs)**	**USE (Grain/P soil)**
Environments	1	358262.8**	458790.1**	0.142431**	0.037834**	2.10332**	3838548.4**	3443537.3**
Genotypes	89	1963.3**	2992.8**	0.001426**	0.000177**	0.04906**	28338.2**	3443537.3**
Gen x Envir	89	789.1*	1109.1**	0.000893	0.000097	0.03250**	16608.4	12648.9**
Error	356	554.1	683.0	0.000689	0.000087	0.02219	13509.5	7795.2
Mean - High P		141.5	146.6	0.14	0.05	0.39	557	208
Mean - Low P		90.0	88.3	0.10	0.03	0.51	726	368
% reduction (-) or increase (+)		- 36	- 40	- 29	- 40	+ 31	+ 30	+ 77
HER-Low P		0.51	0.54	0.37	0.30	0.46	0.35	0.53
HER-High P		0.68	0.71	0.42	0.40	0.44	0.45	0.46
Cv-High P (%)		15.2	20.3	23.1	21.0	26.9	19.8	20.7
Cv-Low P (%)		28.1	24.8	18.4	24.8	35.1	16.7	31.8

- *, ** significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 2 : Contribution of sum of squares from each P efficiency component (uptake= x1 and utilization=x2) for the sum of squares for P use efficiency (y) at the high and low P environment. This contribution is determined by the fraction of hybrid sum of squares $\Sigma (x_i y) / \Sigma y^2$, where i=1 for P uptake efficiency and i=2 for P utilization efficiency. Each of this fraction is a function of the product of the coefficient of correlation between xi and y multiplied by the ratio of the standart deviation of xi and y.EMBRAPA-Maize and Sorghum, Sete Lagoas, 2006

P level / Trait	**Hybrid sum of squares**	**Fraction of hyb sum of squares** $\Sigma (x_i y) / \Sigma y^2$	r_{xiy}	(S_{xi}/ S_y).
HIGH P LEVEL				
P uptake efficiency (x1)	0.419	0.901	0.701	1.286
P utilization efficiency (x2)	0.046	0.099	0.107	0.923
P use efficiency (y)	0.465			
LOW P LEVEL				
P uptake efficiency	1.211	0.929	0.914	1.017
P utilization efficiency	0.092	0.071	0.169	0.419
P use efficiency (y)	1.303			