ORIGINAL ARTICLE

Characterization of Ethiopian chickpea (*Cicer arietinum* L.) germplasm accessions for phosphorus uptake and use efficiency II. Interrelationships of characters and gains from selection

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ABSTRACT

The efficient use of phosphorus fertilizer in an environmentally friendly and sustainable ways is preferred because of cost and ecological concerns. An experiment was conducted with 155 chickpea genotypes in 2009/10 at two locations (Ambo and Ginchi) in Ethiopia to study interrelationships, broad-sense heritability and genetic gains from selection for attributes of phosphorus-uptake and use efficiency and other agronomic characters on which data were collected. Significant positive correlations were observed between characters of plant tissue phosphorus contents (r = 0.22-0.85), between plant tissue phosphorus contents and phosphorus yields (r = 0.22-0.99), between plant tissue phosphorus yields (r = 0.23-0.89) and parameters of phosphorus-uptake and -use efficiency in a number of cases. Grain yield and some of its components showed significant positive correlations (r = 0.70-0.99) with phosphorus yield efficiency. Broad-sense heritability values ranged from 60-93% and genetic advance values ranged from 4-62% in the absence of phosphorus. The corresponding broad-sense heritability and genetic advance values in the presence of phosphorus ranged from 59-93% and 4-79%, respectively. Selection among the Ethiopian chickpea gene pool for most of the traits studied would be expected to be effective, indicating the need for the initiation of a planned breeding program for improving phosphorus uptake and use efficiency.

Key words: Broad sense heritability, correlation coefficients, genetic gain from selection, P uptake efficiency and P use efficiency

INTRODUCTION

The continued use of high fertilizer input accelerated depletions of the non-renewable raw materials and energy resources required for fertilizer production (FAO, 1984; Bøckman, 1997; Syers *et al*., 2008). The harmful effect of fertilizers as pollutants of ground and/or surface water is an issue of great concern, particularly in developed counties (Isfan *et al*., 1995; Roy, 1995; Beem and Smith, 1997; Quinones *et al*., 1997; Sharpley *et al*., 2003). Generally nutrient deficiency problems can be overcome through development and use of cultivars efficient in nitrogen fixation in legumes, integrated plant nutrition systems (use of organic and inorganic fertilizers) and use of nutrient use efficient genotypes (Sanginga *et al*., 2000; Ahmad *et al*., 2001; Gill *et al*., 2005; Syers *et al*., 2008).

Chickpea produces extensive roots and substantial quantities of organic acids that solubilize phosphorus from the soil (Alloush *et al*., 2000; Veneklaas *et al*., 2003; Gahoonia *et al*., 2007). However, a number of researchers have found that nutrient uptake and use efficiencies are associated, among other factors, with the crop genotypes (Beebe *et al*., 2006; Ogoke *et al*., 2006; Srinivasarao *et al*., 2006).

Limited information is available on genetics of phosphorus use efficiency in legumes. Nutrient uptake and use efficiencies were found to be associated particularly with root growth and development in many crops, including haricot bean (Beebe *et al*., 2006), soybean (Ogoke *et al*., 2006), chickpea (Srinivasarao *et al*., 2006) and white clover (Blair and Godwin, 1991), indicating that genes regulating root growth and development could be manipulated to improve nutrient uptake and use efficiencies. Vesterager *et al*. (2006) also reported mechanisms of phosphorus uptake and use efficiencies in pigeonpea and cowpea, which included the release of some organic acids. The association with various fungi, particularly vesicular arbuscular micorrhizal fungi (VAM), facilitates uptake of nutrients, including phosphorus, by legumes (Miyasaka and Habte, 2001).

Crop adaptation to a marginal, nutrient deficient environment may be achieved via genetic modifications in structure and/or function of crop plants, which could improve their ability to survive and reproduce under such stresses (Kramer, 1980). Studies of different legumes, including chickpea, have shown existence of genetic variability for traits related to phosphorus use efficiency (Aráujo *et al*., 1998; Krasilnikoff *et al*., 2003; Walley *et al*., 2005; Srinivasarao *et al*., 2006; Vesterager *et al*., 2006).

Ethiopia, as the secondary center of genetic diversity for many legume crops including chickpea, owns an immense wealth of genetic diversity for many legumes (Hagedorn, 1984; Mekibeb *et al*., 1991). For effective utilization in breeding programs of these germplasm, however, genetic studies showing selection criteria and the possible progresses that can be made through future breeding activities should make an integral part of collection and conservation programs (Carvalho, 2004). Such studies not only unveil the magnitude of genetic variability available in the germplasm for conservation but also enable the determination of useful genes (Arumuganathan and Earle, 1991; Hayward and Breese, 1993).

Screening and selection would generate promising genotypes only if the source germplasm is genetically variable. Crossing is also likely to produce higher heterosis, desirable genetic recombination and segregation in progenies when it is made between genetically diverse parents (Singh, 2002). Ethiopia, with a chickpea germplasm holding of over 1155 (Tanto and Tefera, 2006), owns an immense wealth of genetic diversity for many legumes (Hagedorn, 1984; Hailu *et al*., 1991). Nevertheless, limited information is available on the extent and pattern of trait interrelationships and genetic variability, particularly for attributes of phosphorus uptake and use efficiencies, in these germplasm, as most of them have not yet been systematically characterized and evaluated (Tanto and Tefera, 2006). The objectives of this study were to determine trait interrelationships, examine the level of broad sense heritability and genetic gains from selection for phosphorus uptake and use efficiencies and other agronomic traits.

MATERIALS AND METHODS

Plant materials

One hundred fifty five chickpea genotypes, including 139 collections from different geographical regions of Ethiopia, 5 improved genotypes from ICRISAT, 8 commercial cultivars released in Ethiopia and three genetically non-nodulating references received from ICRISAT and ICARDA, constituted materials for the study.

The test environments

The experiment was conducted under field conditions at two locations (Ginchi and Ambo) in central part of Ethiopia for one year during the main cropping season of 2009/10 (September to January). The two locations are characterized by Vertisol soils (Dibabe et al., 2001) and assumed to represent the major chickpea production areas in Ethiopia. Climatic data of the two locations during the growing period were taken from Ambo and Holetta Research Centers as presented in Figures 1a and b.

Phosphorus application and experimental layout

The experiment was laid down in a randomized complete block design with 2 replications. Each block was divided into two adjacent sub-blocks to accommodate both the phosphorus fertilized and unfertilized plots. The sub-blocks were separated 1.5 m apart. Whole set of genotypes were planted separately in alternating adjacent sub-blocks with and without phosphorus in side-by-side pairs. Undamaged clean seeds of each genotype selected to a reasonably uniform size by hand sorting were planted on the seedbeds. Plot size was 1 row 4m long. One sub-block in each block received basal application of phosphorus in the form of triple supper phosphate (TSP) containing 46% P_2O_5 in water soluble form at the recommended rate (calculated as 20 gm for a single row of 4 meters) and not to the other sub-block. The accessions were assigned to plots at random within each sub-block.

As a source of nitrogen, all genotypes were inoculated with an effective isolate of *Rhizobium* for chickpea, CP EAL 004, originally isolated by the National Soil Laboratory from a collection of Ada'a District of East Shewa Zone, Ethiopia. The isolate was found to be efficient in nodulation and symbiotic nitrogen fixation in previous studies (Hailemariam and Tsige, 2006). The inoculum was received at the concentration of approximately 10^9 cells gm^{-1} of peat carrier. The concentration and purity of the inoculum was confirmed in the Soil Microbiology Laboratory at Holetta Research Center immediately before planting. Seeds of all genotypes were coated with the inoculant at the rate of approximately 2 gm of inoculum for 80 seeds using 40% gum Arabic as an adhesive. All other crop management practices were applied uniformly to all treatments as required so that the test genotypes could express their genetic potentials for the traits under consideration.

Data collection

Data were collected either on plot basis or from randomly selected five plants mostly based on the descriptor developed by IBPGR, ICRISAT and ICARDA (1993). Data were recorded on phosphorus related traits which include: shoot P content (SPC, g 5 $plants^{-1}$), grain P content (GPC, g 5 $plants^{-1}$), biomass P content (BMPC, g 5 $plants^{-1}$), shoot P yield (SPY, mg 5 $plants^{-1}$), grain P yield (GPY, mg 5 $plants^{-1}$), biomass P yield (BMPY, mg 5 $plants^{-1}$), phosphorus harvest index (PHI), apparent use of P from fertilizer and soil (APUfs, %), apparent use of P from fertilizer (APUf, %), apparent use of P from soil (APUs, %), phosphorus yield efficiency (PYE, GY P $applied^{-1}$), phosphorus physiological efficiency (PPE, GY P in $plant^{-1}$), days to 50% flowering (DTF), days to 90% maturity (DTM), grain filling period (GFP), No. of pods (NP, 5 $plants^{-1}$), No. of seeds (NS, 5 $plants^{-1}$), shoot dry matter weight (SDMW, g 5 $plants^{-1}$), total biomass weight (BMWT, g 5 $plants^{-1}$), harvest index (HI), grain production efficiency (GPE, g 5 $plants^{-1}$), biomass production rate (BPR, %), economic growth rate (EGR, %), thousand seed weight (TSW, g) and grain yield (YLD, g 5 $plants^{-1}$).

Shoot and grain phosphorus analysis

Representative shoot and grain samples were collected at 90% physiological maturity and oven-dried to constant moisture at 70°C for 18 hours and ground to pass through 1 mm size mesh sieve. The determination of phosphorus content was made using the wet digestion technique (AOAC, 1970) at Holetta and Debre Zeit Soil Science Research Laboratories. Phosphorus uptake and use efficiency was estimated by a combination of the difference, balance and partial factor productivity methods (Cassman *et al*., 1998) following Syers *et al*. (2008) (equation 1).

The phosphorus harvest index (PHI), i.e. the ratio of the amount of the element in the grain relative to the amount of the element in the total above-ground biomass of the plant, was estimated as:

$$\mathrm{PHI} = \frac{\text{Grain P yield}}{\text{Biomass P yield}}$$

Relative reductions of phosphorus related and agronomic characters in phosphorus untreated plants relative to the respective phosphorus treated plants were calculated to evaluate the sensitivities of the characters to phosphorus unavailability at both locations (Pimratch *et al*., 2008) as:

$$\text{Relative reduction} = 1 - \left(\frac{\text{performance without P}}{\text{Performance with P}}\right)$$

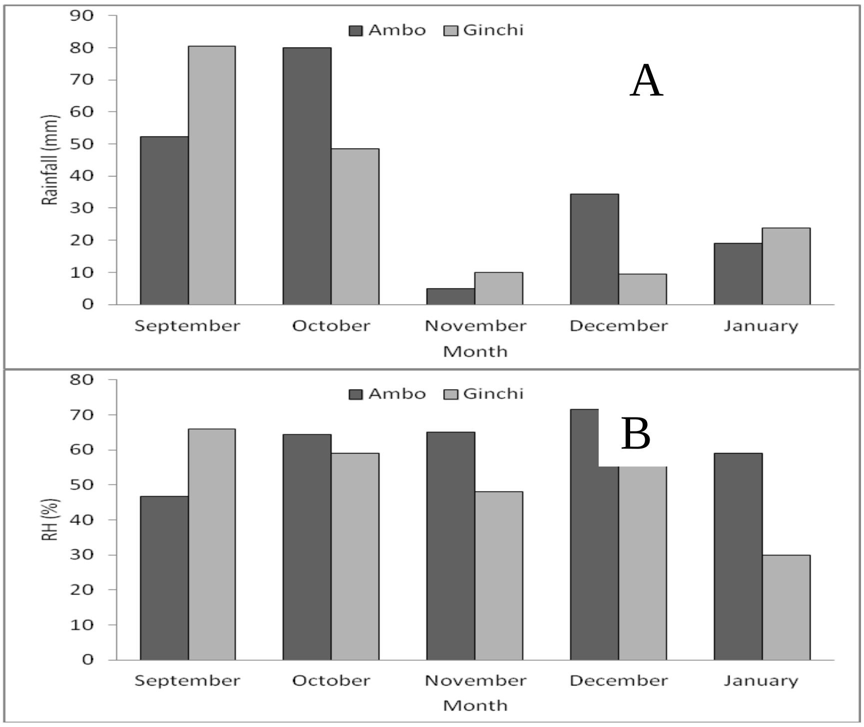

Figure 1a. Rainfall (mm) and relative humidity (%) at (A) Ambo and (B) Ginchi during the growing season

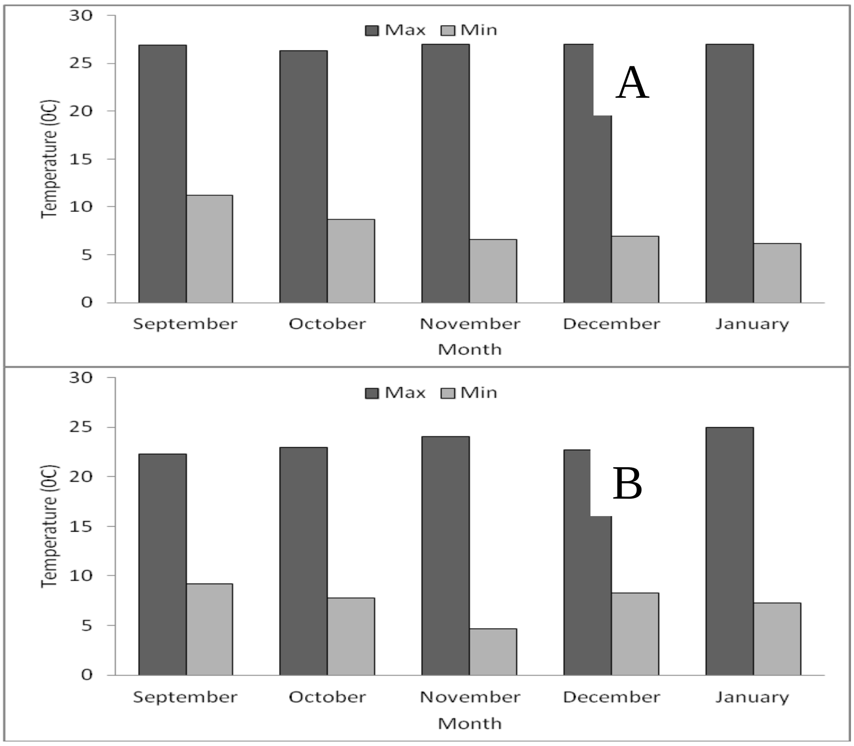

Figure 1b. Maximum and minimum temperatures (oC) at (A) Ambo and (B) Ginchi during the growing season

The apparent use of P from fertilizer and soil sources (APUfs %) =

$$\frac{Biomass\ uptake\ of\ P\ in\ treated\ plants\ (g/5\ plants)\ X\ 100}{P\ applied\ to\ treated\ plants\ (g/5\ plants)}$$

The apparent use of P from fertilizer (APUf %) =

$$\frac{[Biomass\ uptake\ of\ P\ in\ treated\ plants - Biomass\ uptake\ of\ P\ in\ untreated\ plants]\ X\ 100}{P\ applied\ to\ treated\ plants}$$

The apparent use of P from soil (APUs %) = APUfs – APUf

Phosphorus yield efficiency (PYE) =

$$\frac{Grain\ yield\ of\ treated\ plants\ (g/5\ plants)}{P\ applied\ to\ treated\ plants\ (g/5\ plants)}$$

Phosphorus physiological efficiency (PYE) =

$$\frac{Grain\ yield\ in\ treated\ plants\ (g/5\ plants)}{P\ in\ treated\ plants\ (g/5\ plants)}$$

Plant phosphorus yields were obtained by multiplying their tissue phosphorus concentration by dry matter yield as follows:

$$Grain\ P\ yield = Grain\ P\ content \times grain\ yield$$

$$Shoot\ P\ yield = Shoot\ P\ content \times shoot\ yield$$

$$Biomass\ P\ yield = Grain\ P\ yield \times shoot\ P\ yield$$

Equation 1. Phosphorus uptake and use efficiency was estimated by a combination of the difference, balance and partial factor productivity methods following the above equations.

Statistical analysis

Frequency distribution was used to reveal the magnitude and pattern of distribution of variation in selected traits. To compare selected subsets of the 5% best genotypes within the whole population, the former were sorted based on rank orders and their means were independently computed for each character. Mean performances of the 5% best selected genotypes and the base population (considering the whole set of genotypes as a base population), were calculated and the significance of the differences was determined by use of the t-test as:

$$t = \frac{\overline{X} - \mu}{\sigma/\sqrt{n}}$$

where $\overline{X}$ is mean of selected genotypes, μ is mean of the base population, σ is the standard deviation calculated for the base population and n is the number of genotypes selected from the base population.

Partitioning of the total variance into components attributable to genotype (σ_g^2), location (σ_l^2) and genotype by location interaction (σ_{gl}^2) effects and error variance (σ_e^2) was performed by equating various observed mean squares to their expected mean squares (Table 1) (see Singh and Chaudhary 1985):

$\sigma_g^2 = [(\sigma_e^2 + R\sigma_{gl}^2 + RL\sigma_g^2) - (\sigma_e^2 + R\sigma_{gl}^2)]/RL = (MS3\text{-}MS4)/RL$

$\sigma_e^2 = MS5$

$\sigma_{gl}^2 = [(\sigma_e^2 + R\sigma_{gl}^2) - (\sigma_e^2)]/R = (MS4\text{-}MS5)/R$

where MS3 = mean square of genotypes, MS4 = mean square of genotype by location, MS5 = mean square of error, R = number of replication and L = number of location (Table 1).

Broad sense heritability (h^2), defined as the proportion of the total variability that is attributable to genetic causes or the ratio of the genetic variance to the total phenotypic variance, was calculated as:

$h^2 = \sigma_g^2 / [\sigma_g^2 + \sigma_{gl}^2/L + \sigma_e^2/RL] \times 100$

The expected genetic advance (GA), which represents the difference between the mean genotypic values of the selected population divided by the mean genotypic value of the original population, was calculated, assuming a selection intensity of 5%, as:

$GA = K.\ \sigma_P.\ h^2$

$$\text{GA as \% of mean} = \frac{\mathbf{GA}}{\overline{X}} \times 100$$

where K = the selection differential (K = 2.06 at 5% selection intensity) and σ_P = phenotypic standard deviation (Singh and Chaudhary, 1985).

Correlation coefficients between pairs of characters were estimated using the standard formula as:

$r = Cov_{(xy)} / sqrt[\sigma_x^2 + \sigma_y^2]$

where $Cov_{(xy)}$= co-variance of traits x and y, σ_x^2 = variance of x and σ_y^2 = variance of y.

RESULTS AND DISCUSSION

Relationships between phosphorus characters

There were significant ($P \leq 0.01$) positive associations between characters of plant tissue (shoot, seed and biomass) phosphorus contents (r = 0.22-0.85), and phosphorus yields (i.e. shoot P yield, grain P yield and biomass P yield) (r = 0.22-0.99), and between characters of plant tissue phosphorus yields themselves (r = 0.23-0.89). Phosphorus harvest index was also associated positively with grain phosphorus content and with grain phosphorus yields but showed negative association with shoot phosphorus content and shoot phosphorus yield. The association between phosphorus harvest index and biomass phosphorus content was negative (r = -0.18) when phosphorus was not applied and positive (r = 0.64) when phosphorus was applied (Table 2a). This may indicate that the proportional allocation of phosphorus to grain was increased with the external application of phosphorus in the form of fertilizer.

Phosphorus harvest index was not associated with biomass phosphorus yield both in the absence and presence of phosphorus. Therefore, selection for more plant tissue phosphorus contents would increase total phosphorus yields whereas selection for better grain phosphorus content and grain phosphorus yield would result in genotypes with better phosphorus harvest index (i.e. genotypes that mobilize and partition more phosphorus into their seeds). On the other hand, selection for shoot phosphorus content and shoot phosphorus yield could result in genotypes that mobilize and partition less phosphorus into their seeds (Beebe *et al*., 2006; Liao *et al*., 2008).

Table 1. Skeleton of combined ANOVA used in calculation of components of variation for symbiotic and agronomic characters in 155 chickpea genotypes

Source of variation	Degree of Freedom	Mean Square (MS)	Expected Mean Square (EMS)
Locations	L –1	MS1	$\sigma_e^2 + G\sigma_r^2 + GRL\sigma_l^2$
Replications /location	L(R -1)	MS2	$\sigma_e^2 + G\sigma_r^2$
Genotypes	G –1	MS3	$\sigma_e^2 + R\sigma_{gl}^2 + RL\sigma_g^2$
Genotype x Location	(G –1)(L -1)	MS4	$\sigma_e^2 + R\sigma_{gl}^2$
Error	L (G -1)(R –1)	MS5	σ_e^2

There were significant positive correlation coefficients (r = 0.29-0.96) between apparent uptakes of phosphorus from both soil and fertilizer and plant tissue phosphorus contents. Phosphorus yield efficiency was also increased with increased plant tissue phosphorus contents and phosphorus yields. Phosphorus physiological efficiency showed significant positive association with grain phosphorus content (r = 0.32) and grain phosphorus yield (r = 0.31), significant negative association with shoot (r = -0.39) and biomass (r = -0.23) phosphorus contents and with shoot biomass yield (r = -0.39) but not significantly associated with biomass phosphorus yield (r = 0.02), indicating that the higher the grain phosphorus content and phosphorus yields the higher would be the phosphorus physiological efficiency.

Both fertilizer and soil apparent phosphorus uptake efficiencies were not associated with phosphorus harvest index, indicating the possibility for simultaneous selection for these traits, whereas phosphorus yield and physiological efficiencies showed strong positive associations with phosphorus harvest index (r = 0.50 and 0.65, respectively). Phosphorus physiological efficiency was not improved by increased phosphorus apparent uptakes both from the soil and fertilizer whereas phosphorus yield efficiency was improved in both cases (Table 2a). Therefore, phosphorus yield efficiency could help as a better indicator of phosphorus use efficient genotypes than phosphorus physiological efficiency that requires destructive sampling.

Relationships between agronomic characters

A number of agronomic components including pod and seed number, shoot and biomass dry weight and physiological components, including grain production efficiency, and biomass production and economic growth rates showed highly significant positive correlation coefficients with each other and with grain yield in all the cases. Grain yield was positively associated with grain filling period, number of pods and seeds, shoot and biomass dry weight, harvest index, grain production efficiency and biomass and economic growth rates.

It was observed that the earlier the days to flowering and maturity, the better the grain yield. This result was obtained under moisture stressed condition when the genotypes were grown with residual moisture. In another environment, where there is adequate moisture for longer growing period, it may be possible that late maturing genotypes more efficiently exploit the moisture resource and perform better than early genotypes. For instance, in winter grown chickpea, where moisture use efficiency was better (Singh, 1990), late maturing varieties gave better yields than early maturing varieties because of their phenological advantages (Özdemir and Kardavut, 2003). Therefore, the importance of improvement in phenological traits may depend on the environment as selection for a long growing duration may also result in yield increments under the moisture rich environments (Keneni *et al*., 2006).

Seed size and grain harvest index were either negatively or non-significantly correlated with most of the traits with only a few exceptions. Seed size, for instance, showed significant positive association only with days to flowering and maturity both under phosphorus fertilized and unfertilized conditions and with shoot dry matter weight and economic growth rate under phosphorus fertilized condition. Seed size was negatively correlated with grain filling period but non-significantly with grain yield. Grain harvest index showed a consistent and significant positive association with grain filling period, grain production efficiency, economic growth rate and grain yield with and without phosphorus application. Improvement of seed size through selection among this gene pool could, therefore, result in a negative selection for traits like pod and seed numbers because of compensatory growth but it may not have any adverse effect on grain yield (Table 2b).

Relationships between phosphorus and agronomic characters

Days to flowering and maturity revealed significant ($P \leq 0.01$) negative correlation coefficients with grain phosphorus content, phosphorus yield and phosphorus harvest index; positive correlation coefficients with shoot phosphorus content and phosphorus yield, no association with apparent use of phosphorus both from the soil and fertilizer and significant negative association with phosphorus yield (r = -0.34) and phosphorus physiological (r = -0.39) efficiencies. Neenu *et al*. (2014) and Badini *et al*. (2015) also observed that phenological development is delayed with increased level of phosphorus. On the other hand, grain filling period was positively associated with both phosphorus yield and physiological efficiencies. This may be an indication that genotypes with the faster developmental switch to reproductive growth earlier in the growing season had better comparative advantage to mobilize and more efficiently use the available phosphorus for reproductive growth. On the other hand, genotypes that lagged behind at flowering might have invested more resources at vegetative growth and exposed relatively a longer part of their reproductive growth to an end-of-season moisture stress.

Under both fertilized and unfertilized conditions, grain harvest index showed significant positive associations with grain phosphorus content, grain phosphorus yield, phosphorus harvest index and phosphorus yield and physiological efficiencies. On the contrary, grain harvest index showed significant negative associations with shoot phosphorus content and shoot phosphorus yield but no significant associations were observed with biomass phosphorus content and phosphorus yield. Increments in number of pods and seeds, shoot and biomass weight, grain production efficiency, biomass and economic growth rates and grain yield generally increased plant tissue phosphorus contents and phosphorus use efficiency parameters in general in most cases. Seed size did not have a strong association with parameters of plant tissue phosphorus contents, tissue phosphorus yields, and phosphorus harvest index and phosphorus use efficiency except in a few cases when phosphorus was applied from an external source.

A number of agronomic and physiological traits including number of pods and seeds, shoot and biomass dry weight, grain production efficiency, biomass and economic growth rates, and grain yield were positively associated with both phosphorus yield and physiological efficiencies but more strongly with the former (Table 2c). Note also that all phosphorus related characters including plant tissue (shoot, grain and biomass) phosphorus contents and phosphorus yields, phosphorus harvest index and attributes of phosphorus uptake and use efficiencies, namely apparent use of phosphorus fertilizer and soil sources, apparent use of phosphorus from fertilizer, apparent use of phosphorus from soil and phosphorus physiological efficiency were positively correlated with phosphorus yield efficiency, with no exception (Table 2a). The need to perform destructive plant tissue (grain and foliage) analysis, which requires additional labor, time and expense, would complicate breeding for higher tissue (shoot, grain and biomass) phosphorus contents, which is, fortunately, not required to calculate phosphorus yield efficiency. This study also indicated that improvement in phosphorus content and use efficiency could be achieved through indirect selection for better grain yield and a number of its agronomic and physiological determinants. Economic growth and biomass production rates, grain production efficiency, and shoot and biomass dry weight, showed significant positive correlation coefficients, ranging from r = 0.70 to 0.99, with phosphorus yield efficiency (Table 2c).

From this study, we understood that growing chickpea with and without phosphorus resulted only in changes of magnitude but not of the direction of correlation coefficients between characters with only a few exceptions. Similar results were reported by Sinebo (2002) who observed a similar pattern of trait association in barley grown with and without nitrogen and phosphorus fertilizers in Ethiopia.

Theoretically, the genetic expression of different traits and the extent and pattern of their relationship with each other may vary with changes in the test environment (Lawes *et al.*, 1983), including soil fertility levels (Banziger *et al.*, 1997). In the present case, fortunately, the same selection criteria can serve to improve phosphorus use efficiency and grain yield both in the presence and absence of phosphorus, indicating that the same sets of genes control each trait under both condition or there is no independent genetic control between the two traits with and without phosphorus (Falconer, 1989).

Genetic variation and expected gains from selection

Broad sense heritability and genetic advance from selection for phosphorus related and agronomic traits in the absence and presence of phosphorus are given in Figures 2a and b. In the absence of phosphorus fertilizer, broad sense heritability values ranged from 60 to 93% whereas genetic advance values ranged from 4 to 62%. The corresponding broadsense heritability and genetic advance values in the presence of phosphorus fertilizer ranged from 59 to 93% and from 4 to 79%, respectively.

Heritability and genetic advance values did not show a definite trend with the presence or absence of phosphorus. From the available literature, the magnitudes of heritability and genetic advance values under favorable and unfavorable environments also do not appear to follow a simple trend. Some researchers have shown that favorable environments had higher estimates of heritability and genetic advance values than unfavorable environments (Singh, 2002; Simmonds, 1991; Banziger and Edmeades, 1997), as heritability and genetic advance values may be concealed because of a greater genotype by environment under unfavorable conditions (Rosielle and Hamblin, 1981). On the contrary, other reports indicated that there was no interrelationship between the type of the environment (yield level) and the magnitude of heritability and genetic advance values (Ceccarelli and Grando, 1996). The magnitude of heritability and genetic advance values had been rather affected by the nature of the genetic material under consideration than the test environment (Ceccarelli and Grando, 1996).

Table 2a. Correlation coefficients (r) between plant tissue phosphorus contents, phosphorus yields and phosphorus use efficiency traits in 155 chickpea genotypes grown on Vertisol with residual moisture in the absence and presence of phosphorus fertilizer in Ethiopia

Characters	P level	Characters[1]											
		GPC	SPC	BMPC	GPY	SPY	BMPY	PHI	APUfs	APUf	APUs	PYE	PPE
GPC	P_0	1.00	0.36**	0.85**	0.99**	0.36**	0.88**	0.31**	---	---	---	---	---
	P_1	1.00	0.22**	0.70**	0.99**	0.22**	0.84**	0.52**	0.68**	0.39**	0.31**	0.87**	0.32**
SPC	P_0		1.00	0.78**	0.37**	0.99**	0.78**	-0.75**	---	---	---	---	---
	P_1		1.00	0.59**	0.23**	0.99**	0.71**	-0.68**	0.58**	0.32**	0.29**	0.17*	-0.39**
BMPC	P_0			1.00	0.85**	0.78**	0.97**	-0.18*	---	---	---	---	---
	P_1			1.00	0.71**	0.59**	0.83**	0.64**	0.96**	0.56**	0.44**	0.56**	-0.23**
GPY	P_0				1.00	0.37**	0.89**	0.31**	---	---	---	---	---
	P_1				1.00	0.23**	0.85**	0.51**	0.68**	0.39**	0.31**	0.87**	0.31**
SPY	P_0					1.00	0.76**	-0.72**	---	---	---	---	---
	P_1					1.00	0.71**	-0.68**	0.58**	0.32**	0.29**	0.30**	-0.39**
BMPY	P_0						1.00	-0.15	---	---	---	---	---
	P_1						1.00	-0.01	0.81**	0.46**	0.38**	0.72**	0.02
PHI	P_0							1.00	---	---	---	---	---
	P_1							1.00	-0.06	0.01	-0.07	0.50**	0.65**
APUfs	P_0								1.00	---	---	---	---
	P_1								1.00	0.56**	0.47**	0.57**	-0.22**
APUf	P_0									1.00	---	---	---
	P_1									1.00	-0.46**	0.39**	-0.02
APUs	P_0										1.00	---	---
	P_1										1.00	0.20**	-0.22**
PYE	P_0											1.00	---
	P_1											1.00	0.60**
PPE	P_0												1.00
	P_1												1.00

[1]GPC=grain P content, SPC = shoot P content, BMPC=biomass P content, GPY=grain P yield, SPY=shoot P yield, BMPY=biomass P yield, PHI=phosphorus harvest index, APUfs=apparent use of P from fertilizer and soil, APUf=apparent use of P from fertilizer, APUs=apparent use of P from soil, PYE=phosphorus yield efficiency, PPE=phosphorus physiological efficiency

Table 2b. Correlation coefficients (r) between agronomic traits in 155 chickpea genotypes grown on Vertisol with residual moisture in the absence and presence of phosphorus fertilizer in Ethiopia

Characters	P level	Characters[2]												
		DTF	DTM	GFP	NP	NS	SDMW	BMWT	HI	GPE	BPR	EGR	TSW	YLD
DTF	P_0	1.00	0.55**	-0.82**	-0.30**	-0.33**	-0.02	-0.16	-0.54**	-0.63**	-0.18*	-0.20*	0.21*	-0.40**
	P_1	1.00	0.52**	-0.83**	-0.32**	-0.34**	-0.06	-0.15	-0.42**	-0.63**	-0.18*	-0.21*	0.18*	-0.34**
DTM	P_0		1.00	0.03	-0.12	-0.06	-0.07	-0.16	-0.34**	-0.29**	-0.23*	-0.33**	-0.06	-0.30**
	P_1		1.00	0.05	-0.04	-0.03	0.05	0.01	-0.31**	-0.18**	-0.11	-0.19*	-0.03	-0.17*
GFP	P_0			1.00	0.27**	0.35**	-0.02	0.09	0.41**	0.55**	0.06	0.01	-0.29**	0.27**
	P_1			1.00	0.34**	0.38**	0.11	0.17*	0.28**	0.62**	0.14	-0.01	-0.23**	0.29**
NP	P_0				1.00	0.83**	0.61**	0.66**	0.09	0.63**	0.66**	0.60**	-0.53**	0.65**
	P_1				1.00	0.79**	0.55**	0.56**	0.12	0.57**	0.58**	0.50**	-0.45**	0.56**
NS	P_0					1.00	0.54**	0.60**	0.12	0.62**	0.58**	0.54**	-0.65**	0.62**
	P_1					1.00	0.47**	0.53**	0.27**	0.63**	0.53**	0.52**	-0.59**	0.62**
SDMW	P_0						1.00	0.97**	-0.21*	0.64**	0.96**	0.81**	0.04	0.77**
	P_1						1.00	0.74**	-0.23*	0.58**	0.96**	0.70**	0.17*	0.69**
BMWT	P_0							1.00	-0.01	0.79**	0.98**	0.91**	0.02	0.90**
	P_1							1.00	0.12	0.70**	0.74**	0.78**	0.12	0.80**
HI	P_0								1.00	0.47**	-0.06	0.27**	-0.09	0.37**
	P_1								1.00	0.52**	-0.07	0.41**	-0.12	0.49**
GPE	P_0									1.00	0.76**	0.83**	-0.08	0.95**
	P_1									1.00	0.69**	0.75**	-0.01	0.92**
BPR	P_0										1.00	0.90**	0.05	0.88**
	P_1										1.00	0.79**	0.16	0.80**
EGR	P_0											1.00	0.08	0.96**
	P_1											1.00	0.18*	0.95**
TSW	P_0												1.00	-0.06
	P_1												1.00	0.10
YLD	P_0													1.00
	P_1													1.00

[2]DTF=days to 50% flowering, DTM=days to 90% maturity, GFP=grain filling period, NP=No. of pods, NS=No. of seeds, SDMW=shoot dry matter weight, BMWT=total biomass weight, HI=harvest index, GPE=grain production efficiency, BPR=biomass production rate, EGR=economic growth rate, TSW=thousand seed weight, and YLD=grain yield.

Table 2c. Correlation coefficients (r) between plant tissue phosphorus contents, phosphorus yields and phosphorus use efficiency with agronomic traits in 155 chickpea genotypes grown on Vertisol with residual moisture in the absence and presence of phosphorus fertilizer in Ethiopia

Characters	P level	Characters[3]											
		GPC	SPC	BMPC	GPY	SPY	BMPY	PHI	APUfs	APUf	APUs	PYE	PPE
DTF	P_0	-0.38**	0.38**	-0.01	-0.36**	0.38**	-0.06	-0.60**	---	---	---	---	---
	P_1	-0.32**	0.27**	-0.01	-0.31**	0.27**	-0.08	-0.47**	-0.01	-0.01	0.02	-0.34**	-0.39**
DTM	P_0	0.22**	0.27**	0.01	-0.21**	0.27**	-0.02	-0.36**	---	---	---	---	---
	P_1	-0.11	0.30**	0.15	-0.11	0.30**	0.08	-0.37**	0.16	0.02	0.15	-0.17*	-0.29**
GFP	P_0	0.29**	-0.27**	0.02	0.29**	-0.27**	0.07	0.47**	---	---	---	---	---
	P_1	0.30**	-0.12**	0.11	0.29**	-0.12	0.15	0.30**	0.11	0.03	0.08	0.29**	0.26**
NP	P_0	0.60**	0.20*	0.54**	0.61**	0.20*	0.52**	0.22**	---	---	---	---	---
	P_1	0.46**	0.15	0.39**	0.46**	0.15	0.42**	0.23**	0.38**	0.27**	0.01	0.56**	0.34**
NS	P_0	0.56**	0.05	0.44**	0.56**	0.05	0.42**	0.31**	---	---	---	---	---
	P_1	0.51**	0.07	0.34**	0.51**	0.07	0.41**	0.33**	0.30**	0.20**	0.10	0.62**	0.45**
SDMW	P_0	0.71**	0.57**	0.86**	0.72**	0.57**	0.79**	-0.08	---	---	---	---	---
	P_1	0.58**	0.57**	0.56**	0.58**	0.57**	0.73**	-0.05	0.58**	0.45**	0.14	0.70**	0.22**
BMWT	P_0	0.82**	0.48**	0.85**	0.82**	0.48**	0.82**	0.09	---	---	---	---	---
	P_1	0.65**	0.33**	0.80**	0.30**	0.33**	0.65**	0.16	0.80**	0.55**	0.27**	0.80**	0.22**
HI	P_0	0.30**	-0.29**	-0.09	0.30**	-0.29**	0.07	0.56**	---	---	---	---	---
	P_1	0.46**	-0.48**	-0.02	0.45**	-0.48**	0.07	0.78**	-0.01	-0.05	0.04	0.49**	0.55**
GPE	P_0	0.85**	0.10	0.59**	0.85**	0.10	0.65**	0.50**	---	---	---	---	---
	P_1	0.82**	0.07	0.48**	0.81**	0.06	0.62**	0.54**	0.49**	0.30**	0.20*	0.92**	0.58**
BPR	P_0	0.80**	0.44**	0.82**	0.80**	0.44**	0.78**	0.12	---	---	---	---	---
	P_1	0.67**	0.48**	0.55**	0.67**	0.48**	0.74**	0.10	0.55**	0.43**	0.14	0.80**	0.36**
EGR	P_0	0.85**	0.31**	0.71**	0.85**	0.31**	0.75**	0.28**	---	---	---	---	---
	P_1	0.81**	0.23**	0.56**	0.81**	0.22**	0.42**	0.42**	0.57**	0.42**	0.16	0.95**	0.53**
TSW	P_0	-0.03	0.13	0.02	-0.04	0.13	0.04	-0.14	---	---	---	---	---
	P_1	0.12	0.17*	0.12	0.11	0.17*	0.17*	-0.09	0.15	0.08	0.09	0.10	-0.05
YLD	P_0	0.89**	0.24**	0.70**	0.89**	0.24**	0.74**	0.39**	---	---	---	---	---
	P_1	0.87**	0.17*	0.56**	0.87**	0.17*	0.72**	0.50**	0.57**	0.39**	0.19*	0.99**	0.59**

[3]For explanation of abbreviations refer to Table 2 a and b above

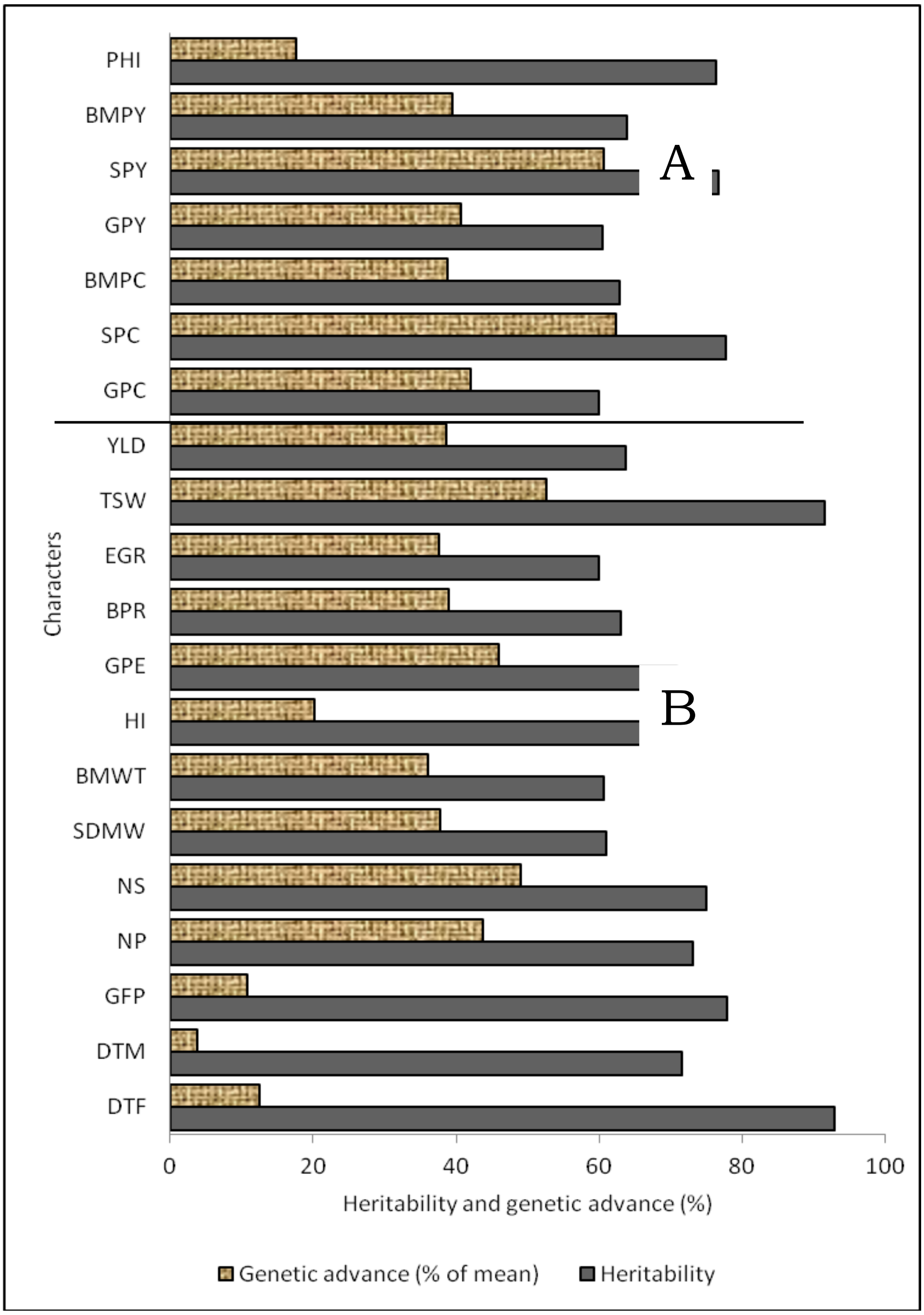

Figure 2a. Estimates of broad-sense heritability (h^2) and expected genetic advance (GA) from selection in 155 chickpea genotypes grown without phosphorus fertilizer for phosphorus and agronomic characters (for explanation of abbreviations refer to Table 2 a and b above).

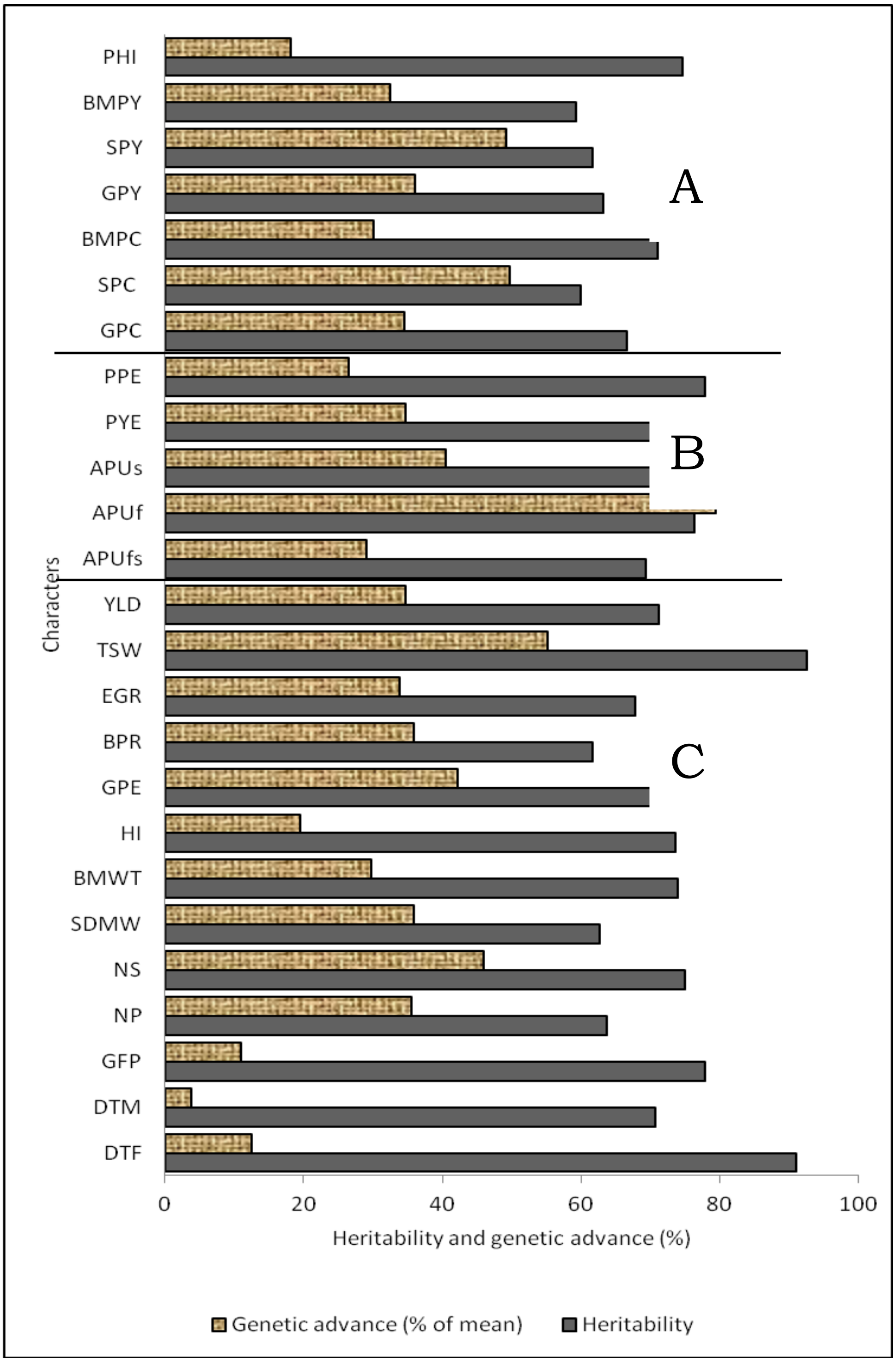

Figure 2b. Estimates of broad-sense heritability (h^2) and expected genetic advance (GA) from selection in 155 chickpea genotypes grown with phosphorus fertilizer for phosphorus and agronomic characters (for explanation of abbreviations refer to Table 2 a and b above).

Selection within the present gene pool for most of the traits appeared to be effective both in the presence and absence of phosphorus as they mostly showed favorable interrelationships and medium to high broad sense heritability values, indicating that the phenotype reflected the genotype (Singh, 2002).

Selection for a trait with high heritability (80% or more) should be fairly easy as there would be a close correspondence between genotype and phenotype, but selection could be difficult or virtually impractical for a trait with low heritability, say less than 40% because of concealment by the environment of genotypic effects (Singh, 2002).

Linear regressions were fitted between heritability and expected genetic gain values of traits calculated from the same genotypes grown in the presence and absence of phosphorus. There was a strong positive association between heritability values of the same traits calculated from the same genotypes grown with and without phosphorus fertilizer ($R^2 = 0.4548$). Association between genetic advance values of the same traits calculated from the same genotypes grown with and without phosphorus fertilizer was rather stronger ($R^2 = 0.9469$) (Figure 3). This may indicate existence of similar pattern of heritability and genetic gains from selection with and without phosphorus, as the traits may not be sensitive to such changes and genotype by management interaction effects were minimal.

The t-test showed highly significant differences between means of the selected subsets of the 5% best genotypes ($\overline{X}$) and the population parameters (μ) for plant tissue phosphorus content, phosphorus yields, phosphorus harvest index, phosphorus use efficiency and agronomic characters under both fertilized and unfertilized conditions (Table 3). Comparison of the mean performance for respective characters of selected subsets of the 5% best genotypes with the mean performance of the whole population revealed possibilities for different levels of improvement through selection.

The least change of 13% was observed in P harvest index both with and without phosphorus. The highest difference of 90% and 108% was observed for seed size without and with phosphorus, respectively (Table 4), indicating that the selected genotypes were not true representatives of the population and that almost all characters effectively responded to phenotypic selection (Singh, 2001).

Comparison of the top 5% genotypes with a recently released variety Natoli resulted in comparative advantages of 51-72% and 7-18% for biomass phosphorus content in the absence and present of phosphorus, respectively. Similarly, the best 5% genotypes resulted in comparative advantages of 48 to 75% and 16 to 23%, respectively, for biomass phosphorus yield in the absence and present of phosphorus. The difference for phosphorus harvest index ranged from 17 to 28% and 14 to 22%, and for biomass dry weight ranged from 42 to 59% and 1 to 14 % in the absence and presence of phosphorus, respectively. The comparative advantages of the best genotypes ranged from 5 to 14% for apparent use of phosphorus fertilizer and soil sources, 30 to 46% for apparent use of phosphorus from soil, 12 to 39% for apparent use of phosphorus from fertilizer, 14 to 32% for phosphorus yield efficiency and 23 to 32% for phosphorus physiological efficiency. According to Syers *et al*. (2008), 25% of the added phosphorus fertilizer may be taken up by the crop and the remainder of the phosphorus must come from soil sources.

A released variety, Habru, and a genotype introduced from ICRISAT, ICC 4918, were found to be among the best 5% for apparent use of phosphorus fertilizer and phosphorus yield efficiency. However, desirable characters were found to be distributed among different genotypes and a single genotype combining desirable attributes may be of rare occurrence. The utilization of these germplasm in the efforts underway to develop efficient genotypes needs a series of multiple crossing to bring the desirable traits into a single genetic background.

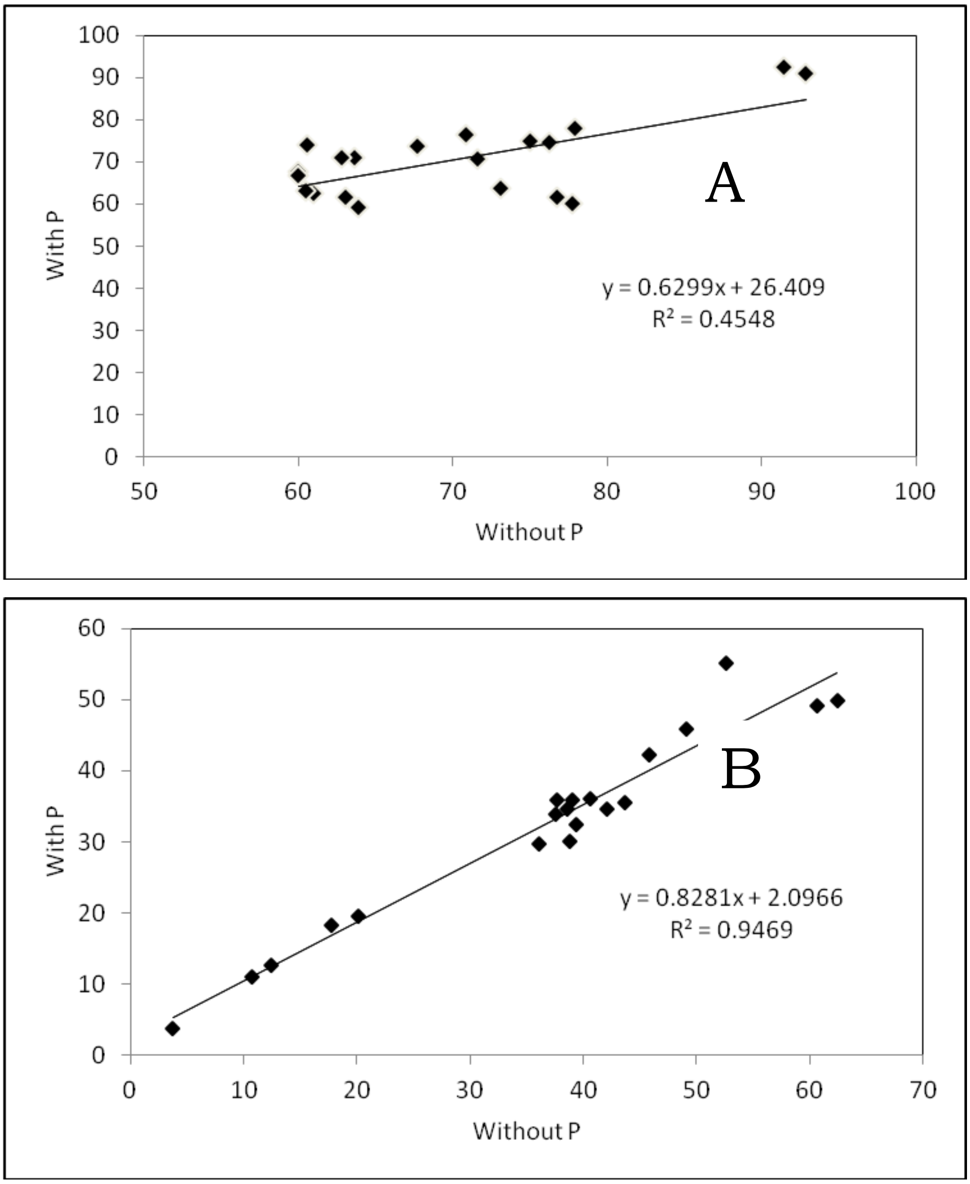

Figure 3. Interelationship between (A) heritability and (B) genetic advance from selection values of in 155 chickpea genotypes grown without and with phosphorus fertilizer showing a strong association between genetic parameters of traits calculated in the two environments

Table 3. Comparison of the mean performances of selected subsets ($\overline{X}$) of the 5% best accessions for symbiotic and agronomic characters with the average performances of the whole population (μ) of 155 chickpea genotypes

Characters[4]	Without phosphorus					With phosphorus				
	Mean of selected genotypes ($\overline{X}$)	Population parameter (μ)	Change through selection ($\overline{X}$-μ)	Change as % of population parameter (μ)	t	Mean of selected genotypes ($\overline{X}$)	Population parameter (μ)	Change through selection ($\overline{X}$-μ)	Change as % of population parameter (μ)	t
Plant tissue phosphorus contents and yields										
SPC	0.137	0.076	0.061	80.26	7.95**	0.187	0.123	0.064	52.03	6.65**
GPC	0.240	0.168	0.072	42.86	6.67**	0.296	0.224	0.072	32.14	5.58**
BMPC	0.874	0.612	0.262	42.81	6.90**	1.076	0.828	0.248	29.95	6.03**
SPY	136.538	76.305	60.233	78.94	7.86**	186.738	123.369	63.369	51.37	6.58**
GPY	240.188	168.089	72.099	42.89	6.69**	295.750	223.395	72.355	32.39	5.63**
BMPY	351.350	244.393	106.957	43.76	6.96**	444.888	346.761	98.127	28.30	5.53**
PHI	0.779	0.686	0.093	13.56	4.72**	0.729	0.644	0.085	13.20	4.47**
Phosphorus uptake and use efficiency										
APUfs	---	---	---	---	---	83.59	65.749	17.841	27.14	5.75**
APUf	---	---	---	---	---	39.74	23.151	16.589	71.66	5.58**
APUs	---	---	---	---	---	59.59	42.574	17.016	39.97	5.86**
PYE	---	---	---	---	---	60.13	45.797	14.333	31.30	5.53**
PPE	---	---	---	---	---	83.03	68.519	14.511	21.18	4.79**
Agronomic characters										
NP	483.05	343.11	139.940	40.79	5.70**	538.09	408.40	129.69	31.76	5.58**
NS	538.18	387.52	150.660	38.88	4.81**	621.90	455.35	166.55	36.58	4.82**
SDMW	136.39	94.25	42.140	44.71	7.50**	160.24	117.48	42.76	36.40	6.38**
BMWT	199.68	142.53	57.150	40.10	7.07**	217.10	167.85	49.25	29.34	6.00**
HI	42.71	35.68	7.030	19.70	6.08**	40.90	34.63	6.27	18.11	5.65**
GPE	70.19	49.59	20.600	41.54	5.56**	80.82	59.04	21.78	36.89	5.26**
BPR	174.08	119.45	54.630	45.73	7.37**	200.68	147.19	53.49	36.34	6.38**
EGR	117.41	84.37	33.040	39.16	6.61**	130.85	100.02	30.83	30.82	5.63**
TSW	220.38	115.65	104.730	90.56	9.99**	220.288	111.95	108.34	96.78	10.63**
YLD	66.08	48.21	17.870	37.07	6.04**	75.16	57.25	17.91	31.28	5.53**

[4]For explanation of abbreviations refer to Table 2 a and b above; ** = highly significant ($P \leq 0.01$)

Table 4. Comparison of mean performances of 5% of the genotypes selected for better performances for attributes of phosphorus use efficiency as compared to Natoli, a recently released variety

Without phosphorus			With phosphorus		
Biomass phosphorus content (g/5 plants)					
	Performance			Performance	
Genotype	Mean	%over Natoli	Genotype	Mean	%over Natoli
209093	0.940	71.69	41066	1.135	17.92
209096	0.935	70.78	41215	1.112	15.53
207657	0.930	69.86	41103	1.092	13.45
207734	0.858	56.62	41275	1.072	11.38
41274	0.840	53.42	41015	1.070	11.17
41284	0.835	52.51	207763	1.058	9.92
41066	0.833	52.05	41053	1.038	7.84
ICC 19180	0.825	50.68	41274	1.033	7.32
Mean	0.875	59.70	Mean	1.076	11.82
Natoli	0.548	---	Natoli	0.963	---
Biomass phosphorus yield (mg/5 plants)					
209093	390	75.09	41275	462	23.25
207657	385	72.85	207763	455	21.25
209096	363	63.02	Habru	447	19.25
41066	339	52.15	207645	445	18.50
41274	336	50.63	41111	440	17.38
41111	336	50.63	207734	438	16.74
41015	332	49.01	ICC 4918	436	16.32
231328	330	48.20	41015	436	16.16
Mean	351	57.70	Mean	445	18.61
Natoli	223	---	Natoli	375	---
Phosphorus harvest index					
209089	0.825	27.91	207742	0.758	21.69
41298	0.785	21.71	41115	0.740	18.88
ICC 4918	0.780	20.93	209097	0.730	17.27
41160	0.780	20.93	207761	0.728	16.87
41311	0.775	20.16	207658	0.723	16.06
207744	0.773	19.77	41312	0.723	16.06
41296	0.760	17.83	207150	0.723	16.06
41274	0.758	17.44	207659	0.713	14.46
Mean	0.780	20.84	Mean	0.730	17.17
Natoli	0.645	---	Natoli	0.623	---
Biomass dry weight (g/5 plants)					
41284	215	59.08	41053	234	14.01
207734	213	57.82	207763	223	8.32
41274	208	53.82	41049	220	7.20
41272	194	43.51	41019	217	5.55
209093	193	42.99	41274	215	4.62
ICC 19180	193	42.70	Habru	211	2.58
207657	193	42.70	41215	209	1.90
209096	191	41.51	41275	208	0.97
Mean	200	48.02	Mean	217	5.64
Natoli	135	---	Natoli	206	---

CONCLUSIONS

It was revealed that selection for better grain yield and a number of its agronomic and physiological determinants, particularly economic growth and biomass production rates, grain production efficiency, and shoot and biomass dry weight could help to develop chickpea varieties with better phosphorus yield efficiency without any need to perform destructive plant tissue analysis. Fortunately, selection based on the combination of the same component characters can also simultaneously improve grain yield.

Seed size was negatively correlated not with grain yield but with most of the traits determinant to grain yield. Being highly economic trait, more care and more precise evaluation of more germplasm (particularly introductions or their cross derivatives) may help to improve seed size. In cases when economically important traits are negatively associated with other traits of economic importance, the breeder must set minimum standards for one trait while selecting for the other or simultaneous selection from among broader genetic bases to improve both traits could be a better strategy.

Existence of adequate levels of heritable variation was revealed for most of the phosphorus related and agronomic traits studied. Future breeding should exploit the heritable variability available in Ethiopian chickpea gene pool for attributes of both phosphorus use efficiency and grain yield. Genetic enhancement of the accessions selected in this study to increase the frequency of best performing genes through further intra accession selections would be expected to result in more promising lines.

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