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Characterization of Ethiopian chickpea (*Cicer arietinum* L.) germplasm accessions for phosphorus uptake and use efficiency I. Performance evaluation

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ABSTRACT

Breeding chickpea (*Cicer arietinum* L.) genotypes with better phosphorus use efficiency has a considerable economic and ecological significance. One hundred fifty-five chickpea genotypes were evaluated with and without phosphorus fertilizer in 2009/10 at Ambo and Ginchi, Ethiopia. A randomized complete block design with 2 replications was employed. Data on tissue phosphorus contents, phosphorus uptake and use efficiency and agronomic parameters were collected. Analysis of variance showed significant differences among the genotypes, locations, phosphorus levels and genotype by location interaction effects. The application of phosphorus improved a number of characters with a few exceptions. Yield increments of 15% and 17% were recorded at Ambo and Ginchi, respectively. Acc. Nos. 207763 (33%), 207742 (26%) and 207563 (19%) were three of the best genotypes for yield response to phosphorus application. Genotype by phosphorus level and phosphorus by location interaction effects were non-significant except in a few cases while their three way interaction effects were entirely non-significant. The result suggests possibilities for identification of chickpea genotypes superior to the varieties released so far and justifies the need for the initiation of a planned breeding program to exploit the wealth of genetic variation available among these genotypes in order to improve P use efficiency and reduce dependency on commercial fertilizers.

Key words: *Cicer arietinum*, germplasm accession, P efficient genotypes, P responder genotypes, P uptake efficiency, P use efficiency

INTRODUCTION

Phosphorus is among the most important yield-limiting elements required by legume crops in considerable amounts. Phosphorus deficiency problems can be overcome through development and use of integrated plant nutrition systems that includes nutrient efficient genotypes (Sanginga *et al*., 2000; Ahmad *et al*., 2001; Gill *et al*., 2005).

The breeding of nutrient use efficient cultivars based on minimizing the intensive use of fertilizers along with genotypes that are able to mobilize the limiting nutrient in greater amounts is getting wide acceptance particularly in marginal areas where resource-poor farmers insist not to apply adequate amount of fertilizers (Daoui *et al*., 2012). For the majority of those less favored group of farmers dwelling under marginal situations, there is no doubt that varieties that can give reasonable yields with minimal level of commercial fertilizers are more preferable than high yielding varieties based on high investments for fertilizer inputs (Keneni, 2007).

Nutrient use efficient genotypes are defined in slightly different ways. Some consider them as genotypes that are able to mobilize the limiting nutrients in greater amounts (acquisition efficiency) and then better use the absorbed nutrients for yield formation (use efficiency) (Bowen and Zapata, 1991; Gahoonia and Nielsen, 1996; Ascher *et al*., 2001; Beebe *et al*., 2006; Liao *et al*., 2008). Others consider them simply as genotypes that are able to yield better under nutrient deficient conditions (Gunes *et al*., 2006). Still others describe them as genotypes which have high yield at both high and low soil fertility levels as opposed to nutrient use inefficient genotypes which have high yield only at high soil fertility levels but greatly reduced yield at low fertility levels (Ransom *et al*., 1993). Basically most of the definitions are based on yield per unit of nutrient input or yield per plant tissue content of nutrient (White *et al*., 2005). Additional definitions encompassing biochemical aspects have also been suggested (Römer and Schenk, 1998; Ahmad *et al*., 2001; Fageria *et al*., 2008). Nutrient use efficiency is also described in different ways. Soil scientists generally equate it with the percentage of the applied nutrient utilized by the crop, agronomists with the amount of the produce per unit of applied fertilizer and physiologists with yield per weight of fertilizer absorbed by the crop (Bowen and Zapata, 1991; Fageria et al., 2008). A combined definition as the ratio of shoot dry matter or seed yield at deficient nutrient supply to that obtained under adequate nutrient supply was also suggested (Gunes *et al*., 2006).

Many studies showed that legumes may enhance nutrient use efficiency of associated or subsequently grown cereals (Jemo *et al*., 2006; Vesterager *et al*., 2007; Kirkegaard *et al*., 2008) by producing exudates that solubilize soil nutrients including fixed forms of phosphorus (Ascher *et al*., 2001; Ali *et al*., 2002; Ojo *et al*., 2006; Vesterager *et al*., 2006; Fageria *et al*., 2008). For instance, white lupine (*Lupinus albus*) improved phosphorus uptake for wheat (*Triticum aestivum*) (Gardner and Boundy, 1983), pigeon pea (*Cajanus cajan*) for sorghum (*Sorghum bicolor*) (Ae *et al*., 1990), faba bean (*Vicia faba*), cowpea (*Vigna unguiculata*) and groundnut (*Arachis hypogaea*) for maize (*Zea mays*) (Li *et al*., 2003a; Vesterager *et al*., 2007; Waddington *et al*., 2007) and soybean (*Glycine max*), chickpea and faba bean for wheat (Herridge *et al*., 2000; Li *et al*., 2003b; Rao *et al*., 2004; Fan *et al*., 2006). Some reports also indicated that growing legumes after cereals with only residual nutrients enabled harvesting full yields of both crops (Bahl and Pasricha, 1998; Ahlawat *et al*., 2007). In Ethiopia, yield of wheat grown after faba bean was substantially increased but it was stated as the result of symbiotic nitrogen fixation (Gorfu, 1998).

Chickpea (*Cicer arietinum* L.) was reported to produce extensive roots and substantial quantities of organic acids and can solubilize and utilize particularly phosphorus from the soil (Alloush *et al*., 2000; Veneklaas *et al*., 2003; Gahoonia *et al*., 2007). A number of authors found that nutrient use efficiency is associated with root growth and development in many legume crops including haricot bean (*Phaseolus vulgaris*) (Beebe *et al*., 2006), soybean (Ogoke *et al*., 2006), chickpea (Srinivasarao *et al*., 2006) and white clover (Blair and Godwin, 1991). On the other hand, Vesterager *et al*. (2006) reported mechanisms of phosphorus uptake and use efficiency in pigeon pea and cowpea involving the release of some organic acids.

Phosphorus deficiency may cause yield losses of 0–45% in chickpea (Ali *et al*., 2002). However, studies on different legumes including chickpea showed existence of genetic diversity for traits related to phosphorus efficiency (Aráujo *et al*., 1998; Krasilnikoff *et al*., 2003; Walley *et al*., 2005; Srinivasarao *et al*., 2006; Vesterager *et al*., 2006). Genetic manipulation of genes regulating parameters of phosphorus use efficiency (Ojo *et al*., 2006) and root growth and development also resulted in improved phosphorus uptake and use efficiency in some legumes (White *et al*., 2005; Beebe *et al*., 2006), Ogoke *et al*., 2006; Srinivasarao *et al*., 2006).

Breeding successes have also been reported in some cases like the release of two improved soybean varieties with potentials of doubling yield without additional inputs (McKnight Foundation, 2008). The same source also reported the identification of promising haricot bean varieties for release to farmers in tropical and sub-tropical parts of China and Africa. In addition, few reports indicated existence of cultivars with multiple-nutrient use efficiency (Bassam, 1998) and those that can combine desirable traits of both deficiency tolerance and nutrient use efficiency (G´orny, 2001).

Ethiopia, with chickpea germplasm holding of over 1155 (Tanto and Tefera, 2006), owns an immense wealth of genetic diversity for many legumes (Hagedorn, 1984; Mekibeb *et al*., 1991). Nevertheless, limited information is available on the status of phosphorus uptake and use efficiency in these chickpea germplasm accessions. This study was, therefore, designed to assess the performance of Ethiopian chickpea germplasm accessions and identify source of desirable genotypes for phosphorus uptake and use efficiency.

MATERIALS AND METHODS

Plant materials

In this study, a total of 155 chickpeas were evaluated. They include 139 accessions from different geographical regions of Ethiopia kindly provided by the Ethiopian Institute of Biodiversity Conservation (IBC), 5 improved genotypes provided by ICRISAT, 8 originally introduced commercial cultivars released in Ethiopia and three genetically non-nodulating genotypes received from ICRISAT and ICARDA. These chickpeas, called hereafter as “genotypes” for experimental purpose, are described in Table 1. The map of the areas of collection of the Ethiopian accessions is also given elsewhere (Keneni *et al*., 2012).

All genotypes were rejuvenated during 2008/2009 under the same condition at Ginchi to minimize initial variation due to difference in seed age and indigenous seed phosphorus content (Liao *et al*., 2008).

The test environment

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. Chickpea is mostly grown on Vertisol soils with residual moisture 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. Soil samples from both locations were collected from the rhizosphere (top 20 cm) for physico-chemical characterization (Table 2).

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.

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) as follows:

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:

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

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

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

Table 1. Description of the test genotypes

Geographical origin	No of Genotypes	Name of genotypes (serial numbers in bracket stand for designation in this study)
Arsi	13	Acc. No. 231327 (1), Acc. No. 231328 (2), Acc. No. 209093 (3), Acc. No. 208829 (4), Acc. No. 209094 (5), Acc. No. 209092 (6), Acc. No. 209096 (7), Acc. No. 209097 (8), Acc. No. 209098 (9), Acc. No. 41002 (10), Acc. No. 207761 (11), Acc. No. 207763 (12), Acc. No. 207764 (13)
East Gojam	13	Acc. No. 41268 (14), Acc. No. 41026 (15), Acc. No. 41074 (16), Acc. No. 41075 (17), Acc. No. 41073 (18), Acc. No. 41076 (19), Acc. No. 41021 (20), Acc. No. 41027 (21), Acc. No. 41222 (22), Acc. No. 207734 (23), Acc. No. 41103 (24), Acc. No. 41320 (25), Acc. No. 41029 (26)
West Gojam	13	Acc. No. 41015 (27), Acc. No. 41271 (28), Acc. No. 41272 (29), Acc. No. 41276 (30), Acc. No. 207745 (31), Acc. No. 41275 (32), Acc. No. 41277 (33), Acc. No. 207743 (34), Acc. No. 207744 (35), Acc. No. 41273 (36), Acc. No. 41274 (37), Acc. No. 207741 (38), Acc. No. 207742 (39)
North Gonder	13	Acc. No. 41316 (40), Acc. No. 41298 (41), Acc. No. 41311 (42), Acc. No. 41313 (43), Acc. No. 41280 (44), Acc. No. 41312 (45), Acc. No. 41315 (46), Acc. No. 41308 (47), Acc. No. 41299 (48), Acc. No. 41046 (49), Acc. No. 41047 (50), Acc. No. 41304 (51), Acc. No. 41303 (52)
South Gonder	12	Acc. No. 41295 (53), Acc. No. 41296 (54), Acc. No. 41289 (55), Acc. No. 41290 (56), Acc. No. 41284 (57), Acc. No. 41291 (58), Acc. No. 41297 (59), Acc. No. 41293 (60), Acc. No. 41019 (61), Acc. No. 41048 (62), Acc. No. 41049 (63), Acc. No. 41053 (64)
West Harargie	11	Acc. No. 41054 (65), Acc. No. 41052 (66), Acc. No. 209082 (67), Acc. No. 209083 (68), Acc. No. 209084 (69), Acc. No. 209091 (70), Acc. No. 209087 (71), Acc. No. 209088 (72), Acc. No. 209089 (73), Acc. No. 209090 (74), Acc. No. 209081 (75)
East Shewa	13	Acc. No. 41159 (76), Acc. No. 41160 (77), Acc. No. 41161 (78), Acc. No. 207661 (79), Acc. No. 207667 (80), Acc. No. 207666 (81), Acc. No. 41141 (82), Acc. No. 207665 (83), Acc. No. 41134 (84), Acc. No. 41128 (85), Acc. No. 41168 (86), Acc. No. 41129 (87), Acc. No. 41130 (88)
North Shewa	13	Acc. No. 41110 (89), Acc. No. 207657 (90), Acc. No. 41111 (91), Acc. No. 41106 (92), Acc. No. 207658 (93), Acc. No. 41142 (94), Acc. No. 41207 (95), Acc. No. 41215 (96), Acc. No. 41216 (97), Acc. No. 41066 (98), Acc. No. 41011 (99), Acc. No. 41007 (100), Acc. No. 41008 (101)
West Shewa	13	Acc. No. 41186 (102), Acc. No. 209035 (103), Acc. No. 41176 (104), Acc. No. 41175 (105), Acc. No. 41174 (106), Acc. No. 209027 (107), Acc. No. 41170 (108), Acc. No. 41171 (109), Acc. No. 41185 (110), Acc. No. 209036 (111), Acc. No. 41190 (112), Acc. No. 41195 (113), Acc. No. 41197 (114)
Tigray	12	Acc. No. 207150 (115), Acc. No. 207151 (116), Acc. No. 207563 (117), Acc. No. 207564 (118), Acc. No. 207894 (119), Acc. No. 207895 (120), Acc. No. 213224 (121), Acc. No. 219797 (122), Acc. No. 219799 (123), Acc. No. 219800 (124), Acc. No. 219803 (125), Acc. No. 221696 (126)
South Wello	13	Acc. No. 41114 (127), Acc. No. 212589 (128), Acc. No. 41113 (129), Acc. No. 207659 (130), Acc. No. 207660 (131), Acc. No. 41115 (132), Acc. No. 225878 (133), Acc. No. 225873 (134), Acc. No. 225874 (135), Acc. No. 225877 (136), Acc. No. 207645 (137), Acc. No. 207646 (138), Acc. No. 225876 (139)
ICRISAT	5	ICC 5003 (140), ICC 4918 (141), ICC 4948 (142), ICC 4973 (143), ICC 15996 (144)
National releases	8	Shasho (ICCV 93512) (145), Arerti (FLIP 89-84C) (146), Worku (DZ-10-16-2) (147), Akaki (DZ-10-9-2) (148), Ejere (FLIP-97–263 C) (149), Teji (FLI 97–266 C)(150), Habru (FLIP 88-42c)(151), Natoli (ICCX-910112-6)(152)
Non-nodulating checks	3	ICC 19180 (153), ICC 19181 (154), PM 233 (155)

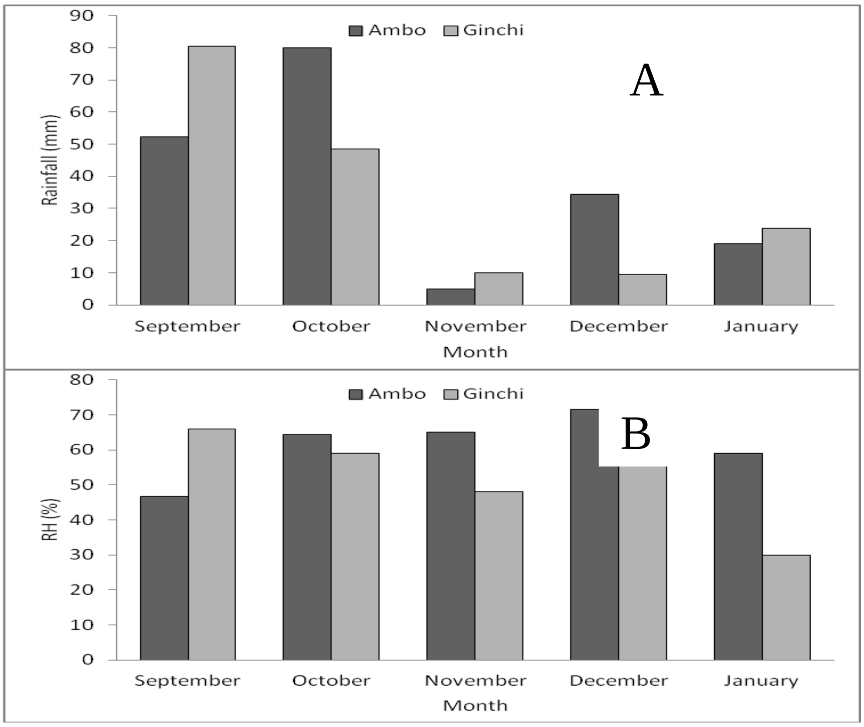

Figure 1a.Rainfall (mm) and relative humidity (%) at (A) Ambo and (B) Ginchi during the growing season

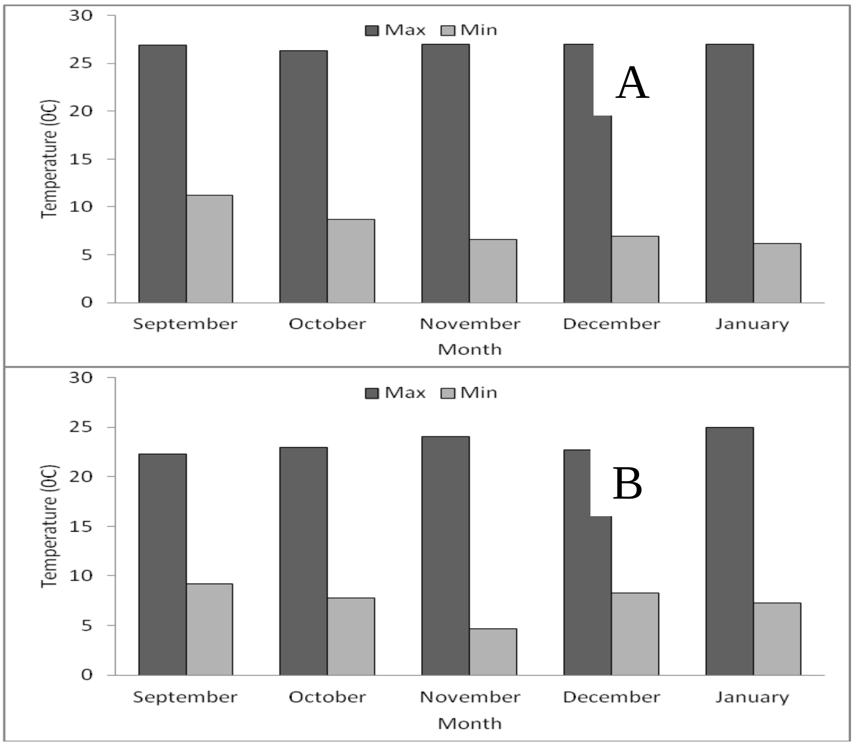

Figure 1b. Maximum and minimum temperatures (oC) at (A) Ambo and (B) Ginchi during the growing season

Table 2. Description of the test locations for geographical position and physico-chemical properties of the soils

Parameter	Source of soil	
	Ambo	Ginchi
Latitude	09° 00′ N	09° 00′ N
Longitude	37° 22′ E	38° 10′ E
Altitude (m.a.s.l.)	2225	2200
Mean annual rainfall (mm)	1000	1110
% Clay	70.00	65.83
% Silt	15.00	20.42
% Sand	15.00	13.75
Organic C (%)	1.53 (low)	1.30 (low)
N (%)	0.103 (low)	0.103 (low)
C/N ratio	14.85 (high)	12.62 (high)
P (ppm*)	18.07 (high)	4.49 (low)
K (Meq/100 gm soil)	2.438 (high)	2.485 (high)
Ca (Meq/100 mg soil)	59.03 (high)	39.62 (high)
Mg (Meq/100 mg soil)	11.20 (high)	9.00 (high)
Na (Meq/100 mg soil)	0.70 (high)	0.61 (high)
So_4 S (ppm)	5.23 (optimum)	5.62 (optimum)
Fe (ppm)	27.73 (high)	51.50 (high)
pH (1:1 H_2O)	7.23 (optimum)	6.18 (optimum)
EC (μS)**	650.00 (high)	547.33 (high)

*ppm = parts per million; **μS = micro siemens

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:

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

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:

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

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}).

Statistical Analysis

The SAS computer package (SAS Institute, 1996) was used to test for presence of outliers and normality of residuals. Separate and pooled analysis of variance were conducted to quantify the total variation among the genotypes using the following model of analysis of variance:

$$Y_{ijkm} = \mu + (b/l)_{ik} + g_j + l_k + p_m + (gl)_{jk} + (gp)_{jm} + (pl)_{km} + (gpl)_{jkm} + e_{ijk}$$

where Y_{ijkm} = phenotypic observation on genotype j in block i (at location k and phosphorus level m) (i = 1…B, j = 1…G, k = 1…L and p = 1…P) and G, L, P and B = number of genotypes, location, block and phosphorus level, respectively, μ = grand mean, $(b/l)_{ik}$ = the effect of block i (within location k), g_j = the effect of genotype j, l_k = the effect of location k, p_m = the effect of phosphorus level m, $(gl)_{jk}$ = the interaction effect between genotype j and location k,

$(gp)_{jm}$ = the interaction effect between genotype j and phosphorus level m, $(pl)_{km}$ = the interaction effect between phosphorus level m and location k, $(gpl)_{jkm}$ = the interaction effect between genotype j, phosphorus level m and location k, and e_{ijkm} = the residual or effects of random error.

Existence of significant difference among the genotypes, locations, phosphorus level and their interaction were determined using the F-test. Mean separation was done using Dunkan's Multiple Range Test (DMRT) at 1% or 5% probability levels following Gomez and Gomez (1984). Two criteria were used to categorize the genotypes into four phosphorus efficiency groups: biomass and grain yields under phosphorus fertilized and unfertilized conditions.

The genotypes were grouped into four categories using the method initially suggested by Gerloff (1977) and later applied by many others (e.g. Ortiz-Monasterio *et al.*, 2001; Gunes *et al.*, 2006). The categories include: (i) inefficient, non-responder; (ii) efficient, non- responder; (iii) inefficient, responder; and (iv) efficient, responder. This method assumes phosphorus responsiveness as the capacity to produce more yield as a result of more phosphorus uptake when the supply of the latter is increased (Ahmad *et al.*, 2001). An efficient cultivar has higher mean performance than the other cultivars under low nutrient supply, while a responder cultivar has higher mean performance under high nutrient supply. We scattered the genotypes using performances in the absence and presence of phosphorus fertilizer. Then, in order to categorize the genotypes into efficient, non-efficient and responder, non-responder groups, we used the mean performances in the absence and presence of phosphorus fertilizer as the cutting points (Gunes *et al.*, 2006).

RESULTS AND DISCUSSION

The crop season and test locations

The two locations received more or less similar amount of rainfall with different pattern of distribution but Ambo was more humid than Ginchi (Figures 1a and b). It was witnessed that more or less the weather variables recorded did not deviate much from the long-term trends at both locations (data not shown), indicated that the present findings could be reproducible in other seasons. The physicochemical properties of the soils from the two test locations, Ambo and Ginchi, showed equal level of low nitrogen contents (0.103%) but high levels of K, Ca, Mg, Na and Fe (Jones, 2003) with variable amounts. The levels of exchangeable cations were also high with pH values more or less closer to neutral. The level of soil phosphorus was high at Ambo and low at Ginchi (Table 2). Similar results were reported from previous analysis of soils from the same locations (Dibabe *et al.*, 2001).

Performances of the genotypes

Significant differences ($P \leq 0.01$) were observed among the genotypes for all characters evaluated in this study (Table 3). The comparison of test genotypes with variety Natoli, a recent release in 2007, showed the existence of a number of superior landraces. For instance, a number of landraces outperformed Natoli for characters of plant tissue phosphorus contents, phosphorus yields, phosphorus uptake and use efficiency and for other agronomic characters including grain yield as indicated in Figures 2a and b.

However, no landrace was superior or even comparable to the released varieties in general and Natoli in particular for seed size. This is related to the special attention recently given to breeding large-seeded chickpea varieties in response to the market demand (Keneni *et al.*, 2011). The comparison of the whole set of genotypes for parameters of phosphorus uptake and use efficiency also showed existence of better genotypes to the released varieties including Natoli (Appendix 1). This indicated the possibilities for developing better varieties for phosphorus use efficiency to the released ones in using chickpea landraces collected from Ethiopia as source materials.

The location effects were also significant in a number of cases but non-significant for apparent use of phosphorus from fertilizer, phosphorus yield efficiency, number of seeds, biomass and economic growth rates, seed size and grain yield. Likewise, many characters significantly varied ($P \leq 0.01$) between the two phosphorus levels with the exception of phenological characters (i.e. days to flowering and maturity and grain filling period), biomass and seed size (Table 3). Genotype by location interaction effects also revealed significant differences ($0.01 \geq P \leq 0.05$) for all characters except grain phosphorus content, apparent use of phosphorus from soil and fertilizer, phosphorus yield and phosphorus physiological efficiency and harvest index.

High levels of G × E interaction effects normally hinder progress from crop breeding and complicate the task of plant breeding as a whole (Ceccarelli and Grando, 1996). Where spatial variability is great even within a short distance as in Ethiopia (EMA, 1988), genotype by location interaction effects, or the differential response of genotypes at different locations, will also be expected to be high (Falconer, 1989).

Table 3. Combined analysis of variance (across locations and phosphorus levels) for phosphorus-use efficiency and agronomic performance of 155 chickpea genotypes tested at two locations in Ethiopia

Character	Mean square[1]							CV (%)
	L	G	P	L × G	G × P	L × P	L × G × P	
Phosphorus contents and yields								
Shoot P content (SPC, g/5 plants)	**	**	**	**	NS	*	NS	22.04
Grain P content (GPC, g/5 plants)	**	**	**	NS	**	NS	NS	28.29
Biomass P content (BMPC, g/5 plants)	**	**	**	**	NS	NS	NS	25.04
Shoot P yield (SPY, mg/5 plants)	**	**	**	**	NS	*	NS	27.47
Grain P yield (GPY, mg/5 plants)	**	**	**	**	**	NS	NS	24.31
Biomass P yield (BMPY, mg/5 plants)	**	**	**	**	NS	NS	NS	21.24
Phosphorus harvest index	**	**	**	*	NS	NS	NS	11.53
Phosphorus uptake and use efficiency								
Apparent use of P from fertilizer and soil (APUfs, %)	**	**	---	*	---	---	---	19.86
Apparent use of P from fertilizer (APUf, %)	NS	**	---	NS	---	---	---	24.95
Apparent use of P from soil (APUs, %)	**	**	---	NS	---	---	---	21.91
Phosphorus yield efficiency (PYE, GY/P applied)	NS	**	---	NS	---	---	---	24.95
Phosphorus physiological efficiency (PPE, GY/P in plant)	**	**	---	NS	---	---	---	15.98
Agronomic characters								
Days to 50% flowering (DTF)	**	**	NS	**	NS	NS	NS	3.92
Days to 90% maturity (DTM)	**	**	NS	**	NS	NS	NS	2.95
Grain filling period (GFP)	**	**	NS	**	NS	NS	NS	6.89
No of pods (NP, 5 plants^{-1})	**	**	**	**	NS	NS	NS	21.58
No of seeds (NS, 5 plants^{-1})	NS	**	**	**	NS	NS	NS	23.35
Shoot dry matter weight (SDMW, g 5 plants^{-1})	**	**	**	*	NS	NS	NS	24.61
Total biomass weight (BMWT, g 5 plants^{-1})	**	**	**	*	NS	NS	NS	21.04
Harvest index (HI)	**	**	NS	NS	NS	NS	NS	16.03
Grain production efficiency (GPE, g 5 plants^{-1})	**	**	**	**	NS	NS	NS	22.37
Biomass production rate (BPR, %)	**	**	**	**	NS	NS	NS	20.68
Economic growth rate (EGR, %)	NS	**	**	*	NS	NS	NS	21.12
Thousand seed weight (TSW, g)	NS	**	NS	*	NS	NS	NS	18.43
Grain yield (YLD, g 5 plants^{-1})	NS	**	**	*	NS	NS	NS	24.95

[1] L = location, G = genotype, P = phosphorus level; **=highly significant ($P \leq 0.01$), * = significant ($P \leq 0.05$) and NS = non-significant ($P > 0.05$)

Legume crops are also known to be more liable to the impacts of high genotype by environment interaction effects than other crops like cereals (Hawtin *et al*., 1988) and, therefore, the existence of significant genotype by location interaction effects for a number of quantitative characters measured in this study cannot be unexpected.

The genotype by phosphorus and phosphorus by location interaction effects were significant only in two cases each, i.e. for shoot phosphorus content and phosphorus yield, and grain phosphorus content and phosphorus yield, respectively. However, even this limited number of significant genotype by phosphorus level interaction effects observed in this study could be still manageable in breeding programs as the interactions were mostly a "non cross-over" type. That is, despite the existence of significant interaction effects, most of the genotypes more or less consistently maintained their relative rank orders with changes in phosphorus level (data not shown). When genotypes perform consistently across locations, breeders are able to effectively evaluate germplasm with a minimum cost in a few locations for ultimate use of the resulting varieties across wider geographic areas. However, with high genotype by location interaction effects, genotypes selected for superior performance under one set of environmental conditions may perform poorly under different environmental conditions (Singh, 1990; Romagosa *et al*., 1996; Ceccarelli, 1997). Therefore, it could be implicated that selection of better performing genotypes at one location may not enable the identification of genotypes that can repeat nearly the same performances at another location. However, separate evaluations with and without phosphorus fertilizer may not be necessarily needed at this level as evaluation under any one of the two may serve to identify appropriate genotypes for both conditions.

The slightly larger coefficients of variation (CV) values (> 20%) in many traits may be related to the production of the chickpea genotypes on residual moisture where the crop was highly stressed or a sample based estimation of mean performances from only five plants grown on small plots or the combined effects of the two.

The role of phosphorus in genotypic performance

A similar pattern of genotypic response was observed with the application of phosphorus at Ambo and Ginchi but relatively higher values of plant tissue phosphorus contents, phosphorus uptake and use efficiency and agronomic responses were recorded at the latter than the former (Table 4). This, despite better relative contents of phosphorus and other minerals in the soil of Ambo, may be related to the confounded effects of many other factors like better moisture holding capacity of the soil at Ginchi because of the gentler slope.

The comparison of the average genotypic performances with and without phosphorus showed different levels of reductions among a number of characters in absence of phosphorus. The average relative reductions due to phosphorus unavailability ranged from 25-38% in characters related to plant tissue phosphorus contents and phosphorus yields.

The relative changes in magnitudes of yield and yield components under no phosphorus application as compared to their magnitude in the presence of phosphorus fertilizer showed that shoot phosphorus content, shoot and biomass phosphorus yields, biomass and grain phosphorus contents and grain phosphorus yield were more sensitive to phosphorus unavailability in that order. Phosphorus harvest index showed rather a tendency to decrease with the application of phosphorus.

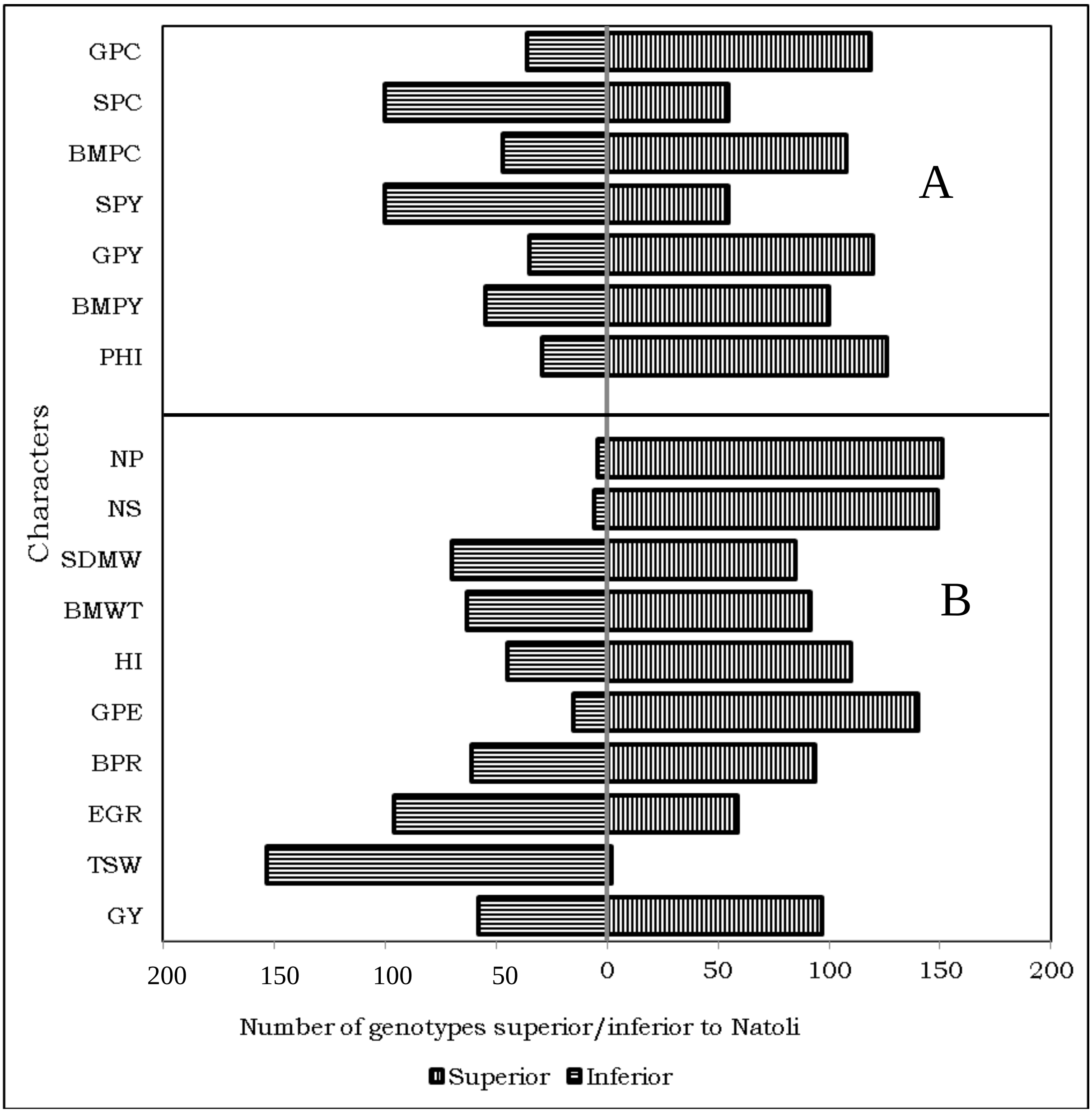

Figure 2a. Proportion by number of the 155 chickpea genotypes superior and inferior to the recently released check, Natoli, for (A) plant tissue phosphorus contents and phosphorus yield, and (B) agronomic characters showing superiority of a number of landraces without phosphorus application at two locations in Ethiopia (see Table 3 above for abbreviations of the characters)

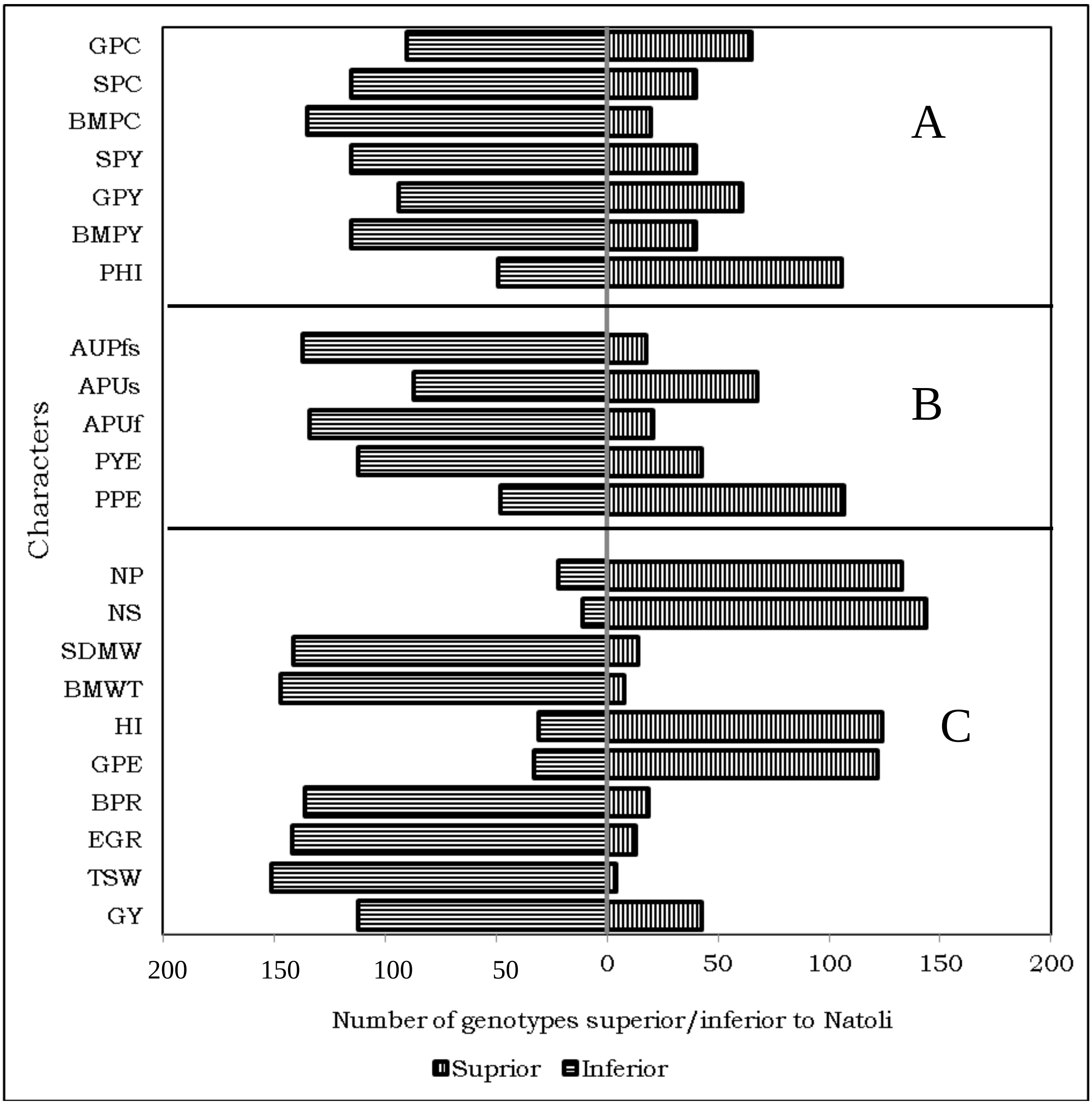

Figure 2b. Proportion by number of the 155 chickpea genotypes superior and inferior to the recently released check, Natoli, for (A) plant tissue phosphorus contents and phosphorus yield, (B) phosphorus uptake and use efficiency and (C) agronomic characters showing superiority of a number of landraces with phosphorus application at two locations in Ethiopia (see Table 3 above for abbreviations of the characters)

Table 4. Mean performances of 155 chickpea genotypes for attributes of phosphorus use and agronomic performance at two P levels and relative reductions due to lack of phosphorus at two locations in Ethiopia

Character*	Ambo			Ginchi			Combined		
	With P	Without P	Relative reduction	With P	Without P	Relative reduction	With P	Without P	Relative reduction
Phosphorus related characters									
GPC (g/5 plants)	0.196a	0.150b	0.235	0.251a	0.186b	0.259	0.224a	0.168b	0.250
SPC (g/5 plants)	0.131a	0.081b	0.382	0.116a	0.071b	0.388	0.123a	0.076b	0.382
BMPC (g/5 plants)	0.774a	0.571b	0.262	0.882a	0.653b	0.260	0.828a	0.612b	0.261
GPY (mg/5 plants)	196.01a	150.13b	0.234	250.77a	186.05b	0.258	223.33a	168.09b	0.247
SPY (mg/5 plants)	131.23a	81.98b	0.375	115.51a	71.42b	0.382	123.37a	76.30b	0.382
BMPY (mg/5 plants)	327.24a	231.32b	0.293	366.28a	257.47b	0.297	346.76a	244.39b	0.295
PHI	0.600b	0.650a	-0.083	0.688b	0.723a	-0.051	0.644b	0.686a	-0.065
Agronomic characters									
DTF	54.99a	55.01a	0.000	58.17a	58.28b	-0.002	56.58a	56.64a	-0.001
DTM	113.70a	113.73a	0.000	114.42a	114.40a	0.000	114.06a	114.07a	0.000
GFP	58.71a	58.72a	0.000	56.25a	56.12a	0.002	57.48a	57.42a	0.001
NP	424.19a	352.32b	0.169	392.56a	333.84b	0.150	408.37a	343.08b	0.160
NS	456.63a	390.80b	0.144	454.03a	384.18b	0.154	455.33a	387.49b	0.149
SDMW(g /5 plants^{-1})	121.43a	96.91b	0.202	113.53a	91.60b	0.193	117.48a	94.25b	0.198
BMWT (g/5 plants^{-1})	172.21a	145.67b	0.154	163.49a	139.38b	0.147	167.85a	142.53b	0.151
HI	33.75b	35.51a	-0.052	35.52a	35.84a	-0.009	34.63a	35.67a	-0.030
GPE (g/5 plants^{-1})	61.82a	52.59b	0.149	56.26a	46.59b	0.172	59.04a	49.59b	0.160
BPR (%)	151.21a	121.92b	0.194	143.16a	116.98b	0.183	147.19a	119.45b	0.188
EGR (%)	97.81a	83.62b	0.145	102.22a	85.12b	0.167	100.02a	84.37b	0.156
TSW (g)	110.43a	115.99a	-0.050	113.46a	115.31a	-0.016	111.94a	115.65a	-0.033
YLD (g/5 plants^{-1})	57.19a	48.76b	0.147	57.30a	47.66b	0.168	57.25a	48.21b	0.158

*see Table 3 above for abbreviations of the characters; **Figures within a row and location sharing the same letter indicate statistically non-significant response of the respective character to P application

This was attributed to the fact that the application of phosphorus fertilizer resulted in higher relative increase in the gross amount of phosphorus (but not concentration) in the shoot relative to the seed. By the same token, the average relative reductions in a number of quantitative agronomic characters ranged from 0-20% (Table 4). The comparison of the whole set of genotypes grown without phosphorus showed a relative yield reductions of 15-17% or, on average, 16% as compared to the same genotypes grown with phosphorus fertilizer. Ali *et al*. (2002) also reviewed that, depending on the agroclimatic environment and the genotype, phosphorus deficiency may cause yield losses of 0–45% in chickpea.

Other agronomic characters which showed more sensitive response to phosphorus unavailability include shoot dry matter weight, biomass production rate, number of pods, grain production efficiency, economic growth rate, biomass weight and number of seeds, their relative reductions being in the range of 15-20%. This may indicate that a significant portion of yield reduction was attributed not only to the direct sensitivity of grain yield itself but also to the indirect effects through a number of other component traits associated with grain yield. Differences in plant tissue phosphorus level and yield increments due to the application of phosphorus fertilizer were also previously reported in genetic resources of many legume crops (Beebe *et al*., 2006; Krasilnikoff *et al*., 2003; Daoui *et al*., 2012) including chickpea (Walley *et al*., 2005; Srinivasarao *et al*., 2006).

Phenological characters (i.e. days to flowering and maturity and grain filling period), harvest index and seed size were least influenced with phosphorus application. Like phosphorus harvest index, grain harvest index rather showed a tendency to reduce with the application of phosphorus fertilizer because phosphorus resulted in higher relative increase in shoot dry matter weight than it resulted in grain yield.

In many food legume crops, root size, microbial symbioses and surface chemical characteristics like root exudates are normally known mechanisms to solubilize and mobilize the limiting nutrients including phosphorus (Ascher *et al*., 2001; Ali *et al*., 2002; Ojo *et al*., 2006; Vesterager *et al*., 2006; Fageria *et al*., 2008). Chickpea was also reported to produce extensive roots and substantial quantities of organic acids to solubilize phosphorus from the soil (Alloush *et al*., 2000; Veneklaas *et al*., 2003; Gahoonia *et al*., 2007) and mobilize it for the formation of assimilates (Srinivasarao *et al*., 2006). The association with various fungi, particularly vesicular arbuscular micorrhizal fungi (VAM), may also facilitate uptake of nutrients (Goicoechea *et al*., 1997; Nogueira *et al*., 2007; Chen *et al*., 2010).

Grouping of the genotypes into phosphorus efficiency classes

Based on the criteria of nutrient efficiency classification suggested by Gerloff (1977), an efficient cultivar has higher mean performance than the other cultivars under low nutrient supply, while a responder cultivar has higher mean performance under high nutrient supply. Accordingly, 34% of the genotypes were grouped as inefficient, non-responder; 24% as inefficient, responder; 23% as efficient, responder; and 19% as efficient, non-responder for biomass yield (Figure 3A). The corresponding classification for grain yield grouped 34% of the genotypes as inefficient, non-responder; 19% as inefficient, responder; 32% as efficient, responder; and 15% as efficient, non-responder (Figures 3B and 4A). From this result, it can be concluded that different possible breeding strategies may be sought in order to address different needs under different phosphorus levels as production domains. First, where soil phosphorus level is sufficient or where farmers can apply adequate amount of phosphorus, varieties that are responsive to soil fertility level may be developed from the responsive sources in order to exploit the yield potential. Secondly, breeding phosphorus efficient chickpea cultivars that are able to mobilize the limited amount of phosphorus in the soil and yield better under phosphorus deficient conditions where farmers cannot afford the application of phosphorus fertilizer or when farm income of small-holder framers cannot allow use of phosphorus could be considered as an alternative strategy. And, thirdly, developing genotypes which consistently better perform at both high and low soil phosphorus levels could also be a possibility as such categories also existed among the genotypes tested in this study (Figure 3B).

Plant breeders cannot change the genetic make of crops unless they have full control over the number and type of genotypes to be advanced from one stage of variety trial to another. From the breeding point of view, therefore, we feel that this classification could be reluctant and may not enable plant breeders to impose the proper amount of selection intensity. Particularly in characterization of genetic materials by genebanks and preliminary evaluation of breeding lines, where hundreds or even thousands of genotypes may be concomitantly tested, a more tense selection pressure may be needed. In a normally distributed population, using the mean performance of the same population at the respective nutrient level as the cutting point would be expected to more or less divide the population into two equal places and then bi-directionally into quarters as efficient, inefficient in one direction and responder, non-responder in another direction. Selection of any one of these quarters depending on the objective of plant breeding under a given circumstance would definitely escalate the number of genotypes to be handled in consecutive tests and, hence, may result in unmanageable number of selected genotypes.

In addition to low expected genetic gains from selection (Falconer, 1989), low selection intensity also places upward pressure on costs of germplasm evaluation. Plant breeders, if possible, are interested in genotypes that combine desirable levels of nutrient responsiveness and efficiency. When the number of population is large, from the breeders perspective, a new modification to this method may be sought by flexibly lifting up the cutting points from $\overline{X}$ to $\overline{X}$ + (α * LSD), where $\overline{X}$ is mean performance of the same population at the respective phosphorus level, α is a constant that down adjusts the number of responder, efficient genotypes to be selected in order to advance only the best 5-10% of the total genotypes and LSD is the least significance difference level (at $P \leq 0.05$) of the same genotypes at the respective phosphorus level.

When we lifted up the cutting points from $\overline{X}$ to $\overline{X}$ + (1/3 * LSD) for grain yield in the present population, for example, the percentage of the genotypes grouped as inefficient, non-responder (i.e. undesirable genotypes) increased from 34 to 62% and that of efficient, non-responder from 15 to 18%. On the contrary, the percentage of the genotypes grouped as inefficient, responder decreased from 19 to 15% and that of efficient, responder from 32 to 5% (Figures 3B and 4A and B). Therefore, separate optimization of the cutting points for each population depending on the number of population and the desired level of selection intensity may be advisable. Different combinations of cutting points can also be applied depending on the pattern (skewness) and extent (dispersion) of distribution of the population at the respective nutrient level.

In the present case, we identified the best 5% of the efficient, responder genotypes for grain yield as: Acc. No. 41274, Acc. No. 41111, Acc. No. 207742, Acc. No. 207563, Acc. No. 207763, Acc. No. 231328, ICC 19180 and Acc. No. 41114. Three of the accessions, namely Acc. No. 41274, Acc. No. 207563 and Acc. No. 41111, also repeated best performances as efficient, responder genotypes for biomass weight. Other efficient, responder genotypes for biomass weight include: Acc. No. 207743, Acc. No. 41015, Acc. No. 41066, Acc. No. 41185 and Ejere (Figure 3A). This indicated that chickpea genotypes that were found to be efficient and responder based on grain yield may not necessarily repeat the same performance for biomass weight as reported by Srinivasarao *et al.* (2006).

This modification, beyond per se classification, would be expected at least to provide a two-prong comparative advantage in terms of improving genetic gains from selection. First, selection of genotypes superior to the mean performance merely due to "chance" would be minimized while selection of "true" statistical superiority would be maximized. Secondly, our modification obviously increases the level of selection intensity for efficient, respondent genotypes with least emphasis on the inefficient, non-respondent ones which are not as such required be it under low or high soil nutrient levels. This "directional" selection, in turn, should increase the frequency of desirable genotypes and result in positive genetic progress from breeding. However, it should be noted that the modification we suggested may not be applicable when only a few genotypes are evaluated from the agronomic perspectives.

A disaggregated comparison of the best responder, efficient genotypes for grain yield and their response to phosphorus application was made with the released varieties. The best genotypes gave yields of 63-80g/5 plants with phosphorus and 53-73g/5 plants without phosphorus. Similarly, the varieties released so far gave yield ranges of 32-72g/5 plants and 32-55 g/5 plants with and without phosphorus fertilizer, respectively. The selected genotypes revealed yield responses ranging from 0-33%, the best being Acc. Nos. 207763 (33%), 207742 (26%) and 207563 (19%) (Figures 5A and B). Similarly, the released varieties showed ranges of no yield response in Shasho to 32% yield increment in Habru, the average being 16% as compared to the same varieties grown without phosphorus fertilizer.

From among the released varieties, the three top varieties with best yield response to application of phosphorus include Habru (32%), Arerti (28%) and Natoli (18%) in that order (Figure 5B). Whether the yield increase associated with phosphorus application is related to the direct effect of phosphorus on yield and yield components or if it is also related to an indirect effect of phosphorus through enhanced symbiotic nitrogen fixation may need an in depth analysis. However, it was observed that two of the non-nodulating genotypes were not only grouped as inefficient, non-responder but also found to be among the most inferior for grain yield with and without phosphorus (Figure 4B). Whatever the case may be, this study clearly showed that the application of phosphorus alone can lead to certain levels of yield increment and that it is possible to improve yield performances of the Ethiopian chickpea landraces through selection under both phosphorus fertilized and unfertilized conditions. It is established that landraces have considerable breeding values under marginal conditions as they contain valuable adaptive genes to different circumstances (Ceccarelli, 1994).

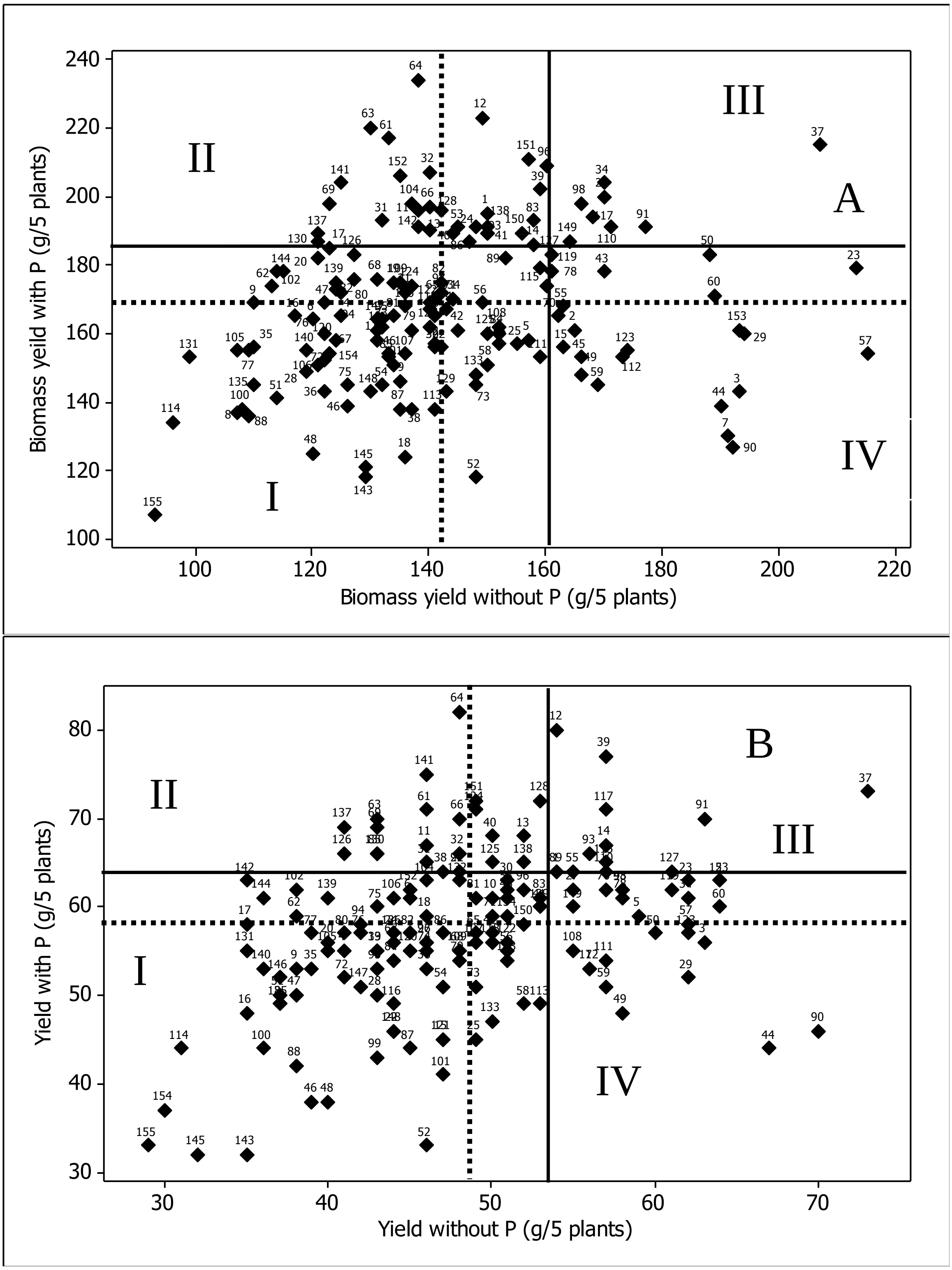

Figure 3. The relationship between (A) biomass and (B) grain yield in 155 chickpea genotypes grown with and without phosphorus at two locations in Ethiopia showing different phosphorus response and use efficiency groups: (I) inefficient, non-responder; (II) inefficient, responder; (III) efficient, responder; and (IV) efficient, non-responder. The broken and the solid lines represent $\overline{X}$ and $\overline{X}$ + 1/3LSD values, respectively, as the cutting points. The names of genotypes is given in Table 1

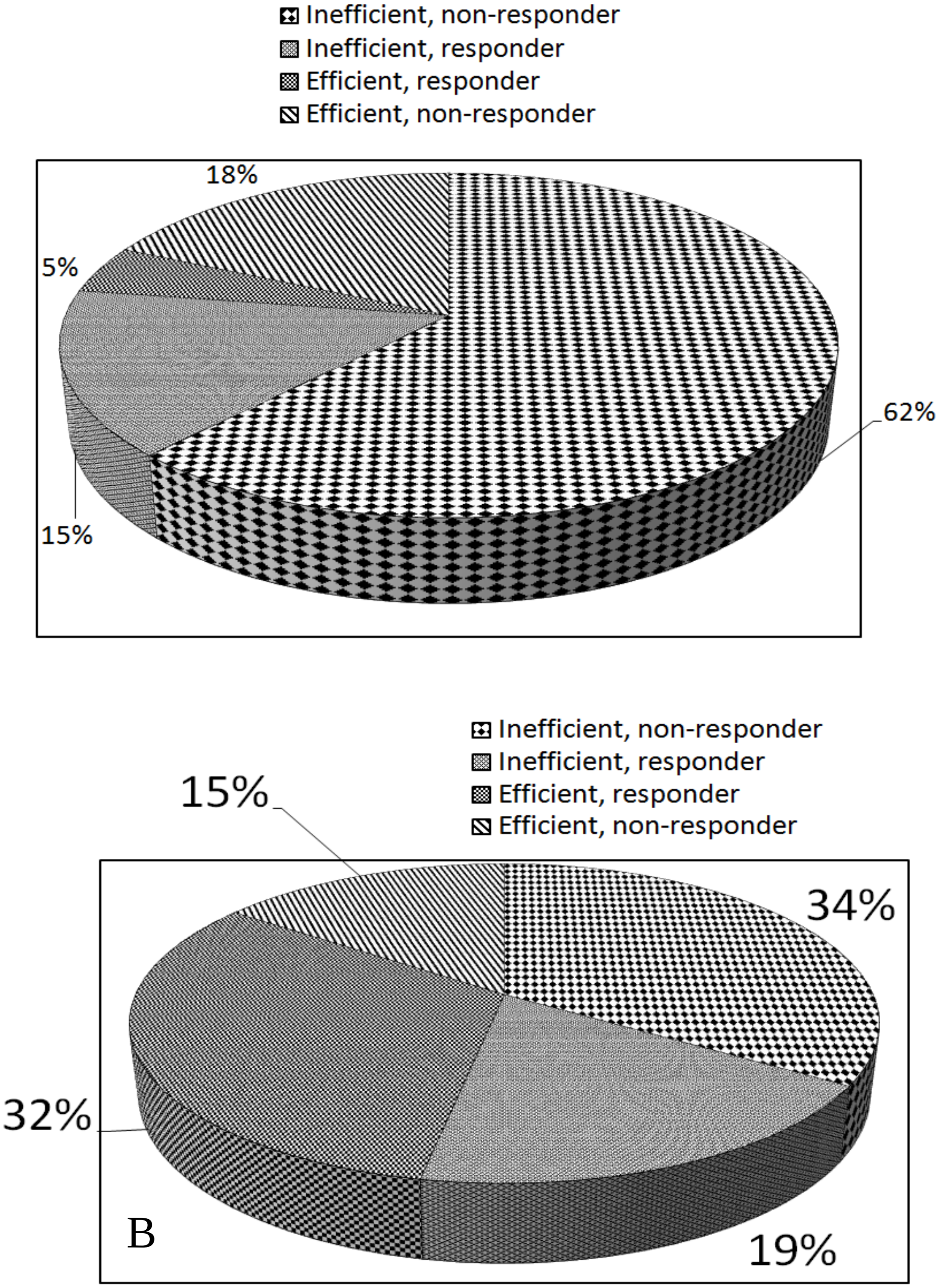

Figure 4. Proportion of inefficient, non-responder; inefficient, responder; efficient, responder; and efficient, non-responder chickpea genotypes grown with and without phosphorus at two locations in Ethiopia using two cutting points (A) $\overline{X}$ and (B) $\overline{X}$ + 1/3LSD value ($P \leq 0.05$).

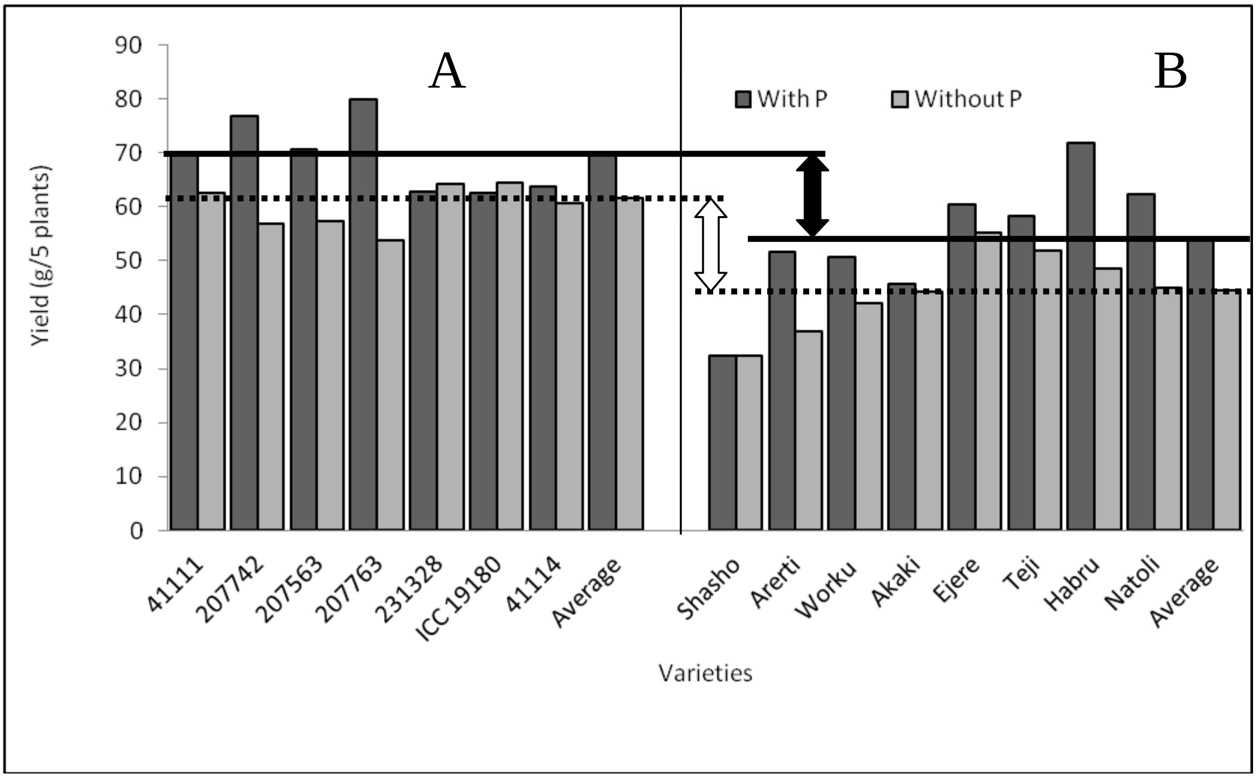

Figure 5. Grain yield performances and response to P application of the (A) 5% best efficient, responder genotypes as compared to (B) the released chickpea varieties grown with and without P at Ambo and Ginchi. The double arrows show the yield advantages expected from the selected genotypes as compared to the released varieties under no phosphorus application (gray) and with phosphorus (dark)

CONCLUSIONS

The genotypic variation revealed in this gene pool for attributes of phosphorus uptake and use efficiency justifies the need for the initiation of a planned breeding program for improving plant-phosphorus relations in chickpea. However, the mechanisms of efficient uptake and use of phosphorus by the genotypes was not clear from this study. Generally, even though a number of specific mechanisms of nutrient uptake and use efficiency have been claimed to be investigated in different legumes as discussed earlier, it yet appears that much remains the subject of future investigation in understanding the dynamics and detailed mechanisms underlying the efficient uptake and use of soil nutrients in crops including chickpea (Ali *et al.*, 2002). Therefore, the mechanisms involved must be studied and the genes regulating phosphorus uptake and use efficiency in these chickpea genotypes need to be genetically characterized and manipulated in order to effectively improve them. The results from this study also suggest the generalization that "chickpea does not significantly respond to phosphorus" is speculated based on evaluations of only a few varieties from agronomic perspectives.

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Appendix 1. Average performances of the 155 chickpea genotypes for some important characters of phosphorus uptake and use efficiencies

Genotypes	P uptake and use efficiency*				
	APUfs (%)	APUs (%)	APUf (%)	PYE	PPE
Acc. No. 231327	71.84a-r	49.46a-l	22.38b-s	73.50a-t	51.24a-m
Acc. No. 231328	63.59a-s	35.91c-o	27.69a-r	78.93a-k	50.32a-n
Acc. No. 209093	66.94a-s	62.72ab	4.218s	54.14t-z	45.00a-r
Acc. No. 208829	75.86a-p	47.92a-o	27.94a-r	58.51l-z	44.08b-r
Acc. No. 209094	66.32a-s	43.37a-0	22.94a-s	70.38a-w	46.92a-p
Acc. No. 209092	71.64a-r	42.41a-o	29.22a-p	67.83a-z	48.74a-n
Acc. No. 209096	58.75f-s	52.60a-j	6.148p-s	62.39e-z	42.34c-r
Acc. No. 209097	59.30e-s	36.52c-o	22.78a-s	65.90b-z	38.86d-r
Acc. No. 209098	70.38a-r	35.43c-o	34.95a-j	61.40g-z	42.36c-r
Acc. No. 41002	70.00a-r	36.94c-o	33.06a-l	70.15a-x	49.15a-n
Acc. No. 207761	81.05a-g	48.09a-o	32.96a-l	67.35a-z	53.56a-l
Acc. No. 207763	84.49a-c	46.03a-o	38.46a-d	76.46a-p	63.97ab
Acc. No. 207764	77.71a-l	46.16a-o	31.55a-n	71.11a-w	54.77a-j
Acc. No. 41268	64.25a-s	45.65a-o	18.60b-s	77.04a-n	53.28a-l
Acc. No. 41026	69.81a-r	48.18a-o	21.63b-s	51.92v-z	36.09g-r
Acc. No. 41074	67.65a-r	42.82a-o	24.83a-s	56.50o-z	38.04e-r
Acc. No. 41075	72.74a-q	37.69c-o	35.06a-i	64.71c-z	46.47a-r
Acc. No. 41073	56.43i-s	37.14c-o	19.29b-s	76.66a-o	46.94a-p
Acc. No. 41076	62.37b-s	23.83no	38.54a-d	62.41e-z	44.02b-r
Acc. No. 41021	71.90a-r	40.14a-o	31.76a-m	61.74e-z	44.47b-r
Acc. No. 41027	72.77a-q	49.51a-l	23.25a-s	71.97a-v	50.82a-m
Acc. No. 41222	68.63a-r	57.01a-g	11.62k-s	54.74r-z	36.55f-r
Acc. No. 207734	75.95a-p	39.22b-o	36.73a-f	66.59a-z	50.10a-n
Acc. No. 41103	87.36a	58.70a-d	28.66a-p	52.25u-z	45.25a-r
Acc. No. 41320	72.87a-q	59.05a-c	13.82f-s	51.47w-z	36.22g-r
Acc. No. 41029	65.52a-s	32.23g-o	33.29a-l	69.45a-x	45.01a-r
Acc. No. 41015	85.70ab	64.29a	21.41b-s	57.31n-z	49.31a-n
Acc. No. 41271	61.35c-s	38.79b-o	22.56b-s	66.33a-z	40.11d-r
Acc. No. 41272	61.97b-s	49.97a-l	12.00i-s	65.50b-z	41.22c-r
Acc. No. 41276	58.74f-s	38.33b-o	20.41b-s	78.20a-l	50.75a-m
Acc. No. 207745	73.40a-q	45.56a-o	27.84a-r	71.15a-w	52.02a-l
Acc. No. 41275	80.78a-h	42.37a-o	36.56a-f	61.62f-z	52.64a-l
Acc. No. 41277	55.07k-s	37.22c-o	17.86c-s	79.75a-i	43.66b-r
Acc. No. 207743	65.82a-s	48.00a-o	17.82d-s	73.04a-t	49.09a-n
Acc. No. 207744	57.32g-s	35.74c-o	21.58b-s	73.27a-t	42.21c-r
Acc. No. 41273	53.90l-s	25.91k-o	27.99a-r	59.85h-z	42.31c-r
Acc. No. 41274	82.78a-f	58.79a-d	23.99a-s	71.47a-w	58.63a-e
Acc. No. 207741	50.31q-s	44.00a-o	6.309p-s	74.32a-s	51.02a-m
Acc. No. 207742	77.90a-l	58.26a-e	19.64b-s	79.29a-j	61.40a-c
Acc. No. 41316	64.41a-s	36.15c-o	28.27a-q	63.79c-z	54.27a-k
Acc. No. 41298	68.54a-r	32.36g-o	36.18a-g	69.49a-x	47.85a-n
Acc. No. 41311	61.93b-s	46.05a-o	15.89d-s	74.35a-s	45.47a-r
Acc. No. 41313	65.52a-s	44.23a-o	21.29b-s	75.53a-q	49.53a-n
Acc. No. 41280	53.41m-s	43.01a-o	10.40l-s	65.96b-z	35.22i-r
Acc. No. 41312	54.41k-s	34.44c-o	19.96b-s	81.82a-e	48.75a-n
Acc. No. 41315	59.05e-s	48.15a-o	10.91l-s	52.04v-z	30.34m-r
Acc. No. 41308	61.61c-s	31.83h-o	29.78a-o	67.53a-z	40.31d-r
Acc. No. 41299	42.95s	23.99m-o	18.97b-s	72.57a-t	30.32m-r
Acc. No. 41046	56.71i-s	34.33c-o	22.38b-s	59.08k-z	38.62d-r
Acc. No. 41047	70.73a-r	50.65a-k	20.08b-s	64.41c-z	45.83a-r
Acc. No. 41304	57.29g-s	39.46a-o	17.84d-s	67.94a-z	39.98d-r
Acc. No. 41303	50.21q-s	44.93a-o	5.280q-s	55.96q-z	26.17p-r
Acc. No. 41295	73.42a-q	37.94b-o	35.48a-h	66.85a-z	49.33a-n

Appendix 1. Continued…..

Genotypes	P uptake and use efficiency*				
	APUfs (%)	APUs (%)	APUf (%)	PYE	PPE
Acc. No. 41296	56.91h-s	37.80b-o	19.11b-s	72.23a-u	40.46c-r
Acc. No. 41289	63.93a-s	41.63a-o	22.30b-s	80.72a-g	51.30a-m
Acc. No. 41290	53.26n-s	40.00a-o	13.26g-s	81.70a-f	43.91b-r
Acc. No. 41284	55.09k-s	37.21c-o	17.88c-s	78.49a-l	46.67a-q
Acc. No. 41291	58.74f-s	44.12a-o	14.62e-s	67.23a-z	39.34d-r
Acc. No. 41297	52.87o-s	43.32a-o	9.554m-s	71.12a-w	40.84c-r
Acc. No. 41293	59.65d-s	46.37a-o	13.28g-s	80.43a-g	47.69a-n
Acc. No. 41019	73.20a-q	41.59a-o	31.62a-m	69.15a-x	57.01a-g
Acc. No. 41048	64.81a-s	38.24b-o	26.56a-s	73.67a-t	46.86a-p
Acc. No. 41049	78.01a-k	42.80a-o	35.22a-h	72.60a-t	55.71a-i
Acc. No. 41053	83.10a-e	45.48a-o	37.63a-e	78.76a-k	65.65a
Acc. No. 41054	61.61c-s	42.56a-o	19.05b-s	76.26a-p	45.53a-r
Acc. No. 41052	69.87a-r	42.33a-o	27.55a-r	78.75a-k	55.79a-i
Acc. No. 209082	54.74k-s	38.60b-o	16.15d-s	79.35a-j	44.57b-r
Acc. No. 209083	66.90a-s	39.53a-o	27.36a-r	66.69a-z	44.01b-r
Acc. No. 209084	67.22a-r	40.56a-o	26.65a-s	83.10a-c	55.53a-i
Acc. No. 209091	61.95b-s	44.60a-o	17.35d-s	80.78a-g	49.26a-n
Acc. No. 209087	68.14a-r	49.15a-l	18.98b-s	70.15a-x	47.22a-o
Acc. No. 209088	63.69a-s	44.36a-o	19.33b-s	65.14b-z	41.74c-r
Acc. No. 209089	53.34n-s	47.08a-o	6.262p-s	75.65a-q	40.73c-r
Acc. No. 209090	62.33b-s	31.23i-o	31.10a-n	70.14a-x	43.68b-r
Acc. No. 209081	56.92h-s	47.50a-o	9.418m-s	77.52a-m	48.33a-n
Acc. No. 41159	63.97a-s	43.74a-o	20.23b-s	72.05a-v	45.58a-r
Acc. No. 41160	59.17e-s	34.69c-o	24.47a-s	71.75a-v	45.79a-r
Acc. No. 41161	69.70a-r	51.03a-j	18.67b-s	72.04a-v	49.02a-n
Acc. No. 207661	67.01a-r	39.60a-o	27.41a-r	67.19a-z	43.21b-r
Acc. No. 207667	71.57a-r	45.05a-o	26.52a-s	63.95c-z	45.22a-r
Acc. No. 207666	76.11a-p	41.87a-o	31.43a-n	63.69c-z	48.60a-n
Acc. No. 41141	75.72a-p	47.88a-o	27.84a-r	60.97g-z	45.38a-r
Acc. No. 207665	77.24a-n	52.66a-j	24.58a-s	63.03c-z	48.63a-n
Acc. No. 41134	67.37a-r	41.27a-o	26.09a-s	63.62c-z	43.18b-r
Acc. No. 41128	56.90h-s	30.31i-o	26.59a-s	79.97a-h	52.82a-l
Acc. No. 41168	75.63a-p	54.03a-i	21.60b-s	60.81g-z	45.63a-r
Acc. No. 41129	58.19g-s	42.70a-o	15.49d-s	62.01e-z	34.95i-r
Acc. No. 41130	57.76g-s	39.42a-o	18.34b-s	57.50m-z	33.53k-r
Acc. No. 41110	68.75a-r	50.39a-l	18.36b-s	74.94a-q	50.88a-m
Acc. No. 207657	52.11p-s	45.27a-o	6.845o-s	70.73a-w	36.47f-r
Acc. No. 41111	71.02a-r	54.43a-i	16.60d-s	69.55a-x	55.86a-i
Acc. No. 41106	73.28a-q	50.62a-k	22.66a-s	66.52a-z	51.51a-l
Acc. No. 207658	64.20a-s	39.88a-o	20.57b-s	75.10a-q	52.80a-l
Acc. No. 41142	62.12b-s	30.96i-o	34.46a-k	67.73a-z	46.66a-q
Acc. No. 41207	57.51g-s	39.63a-o	18.60b-s	64.62c-z	42.64c-r
Acc. No. 41215	83.42a-d	45.29a-o	29.51a-o	54.70r-s	49.36a-n
Acc. No. 41216	65.55a-s	41.52a-o	33.27a-l	63.80c-z	44.91a-r
Acc. No. 41066	77.47a-m	53.60a-i	23.93a-s	57.47m-z	49.40a-n
Acc. No. 41011	58.79f-s	37.53c-o	21.26b-s	59.57j-z	34.36j-r
Acc. No. 41007	60.51c-s	33.34e-o	27.17a-s	59.72i-z	35.56h-r
Acc. No. 41008	61.38c-s	38.98b-o	22.39b-s	54.25s-z	32.97l-r
Acc. No. 41186	63.05b-s	35.75c-o	27.30a-s	78.69a-k	49.26a-n
Acc. No. 209035	69.14a-r	41.50a-o	27.65a-r	62.88d-z	43.13b-r
Acc. No. 41176	74.64a-p	42.69a-o	31.95a-m	68.38a-x	50.01a-n
Acc. No. 41175	63.38a-s	37.86b-o	25.52a-s	70.43a-w	44.28b-r
Acc. No. 41174	56.01i-s	43.29a-o	12.72h-s	77.42a-n	49.00a-n
Acc. No. 209027	53.49m-s	33.85d-o	19.64b-s	82.67a-d	44.62b-r
Acc. No. 41170	62.51b-s	35.34c-o	27.17a-s	68.83a-x	43.69b-r

Appendix 1. Continued…..

Genotypes	P uptake and use efficiency*				
	APUfs (%)	APUs (%)	APUf (%)	PYE	PPE
Acc. No. 41171	64.66a-s	32.99f-o	31.67a-m	73.21a-t	44.33b-r
Acc. No. 41185	73.69a-q	56.66a-h	17.03d-s	69.30a-x	50.85a-m
Acc. No. 209036	52.52p-s	47.45a-o	5.063rs	77.31a-n	43.15b-r
Acc. No. 41190	62.16b-s	48.16a-o	13.99f-s	67.51a-z	42.18c-r
Acc. No. 41195	59.47d-s	33.19f-o	26.28a-s	67.32a-z	39.01d-r
Acc. No. 41197	54.00k-s	30.52i-o	23.48a-s	66.99a-z	34.86i-r
Acc. No. 207150	60.08d-s	41.26a-o	18.82b-s	86.43a	51.79a-l
Acc. No. 207151	58.92f-s	30.35i-o	28.56a-p	67.04a-z	39.53d-r
Acc. No. 207563	66.70a-s	48.95a-m	17.75d-s	84.97ab	56.45a-h
Acc. No. 207564	69.51a-r	47.13a-o	22.38b-s	64.42c-z	44.58b-r
Acc. No. 207894	62.78b-s	49.69a-l	13.09g-s	79.20a-k	49.41a-n
Acc. No. 207895	58.55g-s	28.17j-o	30.38a-n	75.99a-q	43.78b-r
Acc. No. 213224	75.82a-p	46.12a-o	29.70a-o	48.27yz	35.82h-r
Acc. No. 219797	66.16a-s	47.27a-o	18.89b-s	68.04a-y	44.92a-r
Acc. No. 219799	56.26i-s	47.33a-o	8.928m-s	80.85a-g	45.37a-r
Acc. No. 219800	74.14a-q	47.70a-o	26.44a-s	76.56a-o	56.99a-g
Acc. No. 219803	68.06a-r	48.51a-n	19.55b-s	76.52a-o	52.24a-l
Acc. No. 221696	77.96a-l	47.98a-o	29.97a-o	67.53a-z	52.53a-l
Acc. No. 41114	66.09a-s	44.19a-o	21.90b-s	68.31a-y	51.05a-m
Acc. No. 212589	73.17a-q	45.33a-o	27.84a-r	71.43a-w	57.28a-f
Acc. No. 41113	55.71i-s	47.30a-o	8.416n-s	74.75a-r	47.65a-n
Acc. No. 207659	72.65a-q	42.18a-o	30.46a-n	74.85a-r	52.72a-l
Acc. No. 207660	65.98a-s	36.69c-o	29.29a-p	67.10a-z	44.31b-r
Acc. No. 41115	61.18c-s	29.83i-o	31.35a-n	82.70a-d	50.06a-n
Acc. No. 225878	64.16a-s	23.17o	40.99a-c	57.94m-z	37.26f-r
Acc. No. 225873	65.22a-s	52.41a-j	12.81h-s	72.80a-t	47.16a-o
Acc. No. 225874	55.43j-s	25.46l-o	29.98a-o	72.83a-t	39.50d-r
Acc. No. 225877	63.81a-s	47.84a-o	15.97d-s	72.35a-u	45.98a-r
Acc. No. 207645	76.00a-p	40.84a-o	35.16a-i	71.99a-u	55.02a-j
Acc. No. 207646	79.36a-j	54.69a-i	24.67a-s	65.52b-z	52.27a-l
Acc. No. 225876	69.82a-r	43.71a-o	26.11a-s	69.42a-x	48.74a-n
ICC 5003	62.91b-s	41.68a-o	21.24b-s	67.40a-z	42.71c-r
ICC 4918	78.01a-k	39.46a-o	38.54a-d	76.42a-p	59.64a-d
ICC 4948	74.76a-p	33.40e-o	41.35ab	67.36a-z	50.55a-m
ICC 4973	50.53q-s	38.69b-o	11.84j-s	50.21x-z	25.60r
ICC 15996	70.82a-r	38.82b-o	32.00a-m	68.16a-y	48.94a-n
Shasho	55.03k-s	45.59a-o	9.447m-s	47.41z	25.84qr
Arerti	60.89c-s	25.77k-o	35.12a-i	68.68a-x	41.40c-r
Worku	63.99a-s	34.25c-o	29.74a-o	66.77a-z	40.56c-r
Akaki	48.58rs	37.59c-o	10.99l-s	75.23a-q	36.58f-r
Ejere	70.54a-r	56.79a-h	13.75f-s	66.76a-z	48.40a-n
Teji	79.30a-j	53.89a-i	25.41a-s	56.33p-z	46.61a-q
Habru	79.62a-i	33.92d-o	45.70a	71.89a-v	57.43a-f
Natoli	76.83a-o	43.90a-o	32.93a-l	65.54b-z	49.80a-n
ICC 19180	63.62a-s	45.86a-o	17.76d-s	66.54a-z	50.07a-n
ICC 19181	75.92a-p	57.91a-f	18.01c-s	38.16z	29.30n-r
PM 233	57.38g-s	46.92a-o	10.46l-s	47.93z	26.58o-r
Mean	65.75	42.57	23.15	68.52	45.80

*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 (GY/P applied, g/g) and PPE = phosphorus physiological efficiency (GY/P in plant, g/g).