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Interactive effects of phosphorus and water stress on plant development and yield resilience in common beans (*Phaseolus vulgaris* L.)

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An experiment was conducted to determine the effects of increasing soil phosphorus under water stress conditions on yield and plant development in bean (*Phaseolus vulgaris* L.) genotypes with contrasting drought susceptibility tolerances. A split-split plot design with genotypes (main plot), two water regimes (split plot) and three phosphorus rates (split-split plot) was used. Water regimes were imposed by irrigating at 50% ET (water stress) and 100% ET (no stress). Phosphorus (P_2O_5) was applied at planting at the following rates- 0, 40 and 70 kg P ha^{-1}. The two bean lines used were Gadra (high drought susceptibility) and KE- 3 (low drought susceptibility). Water stress significantly reduced plant height, shoot biomass, pod length, seeds per pod, pods per plant, days to maturity and grain yield in both genotypes. Phosphorus significantly increased grain yields mainly through increased number of pods per plant and 100-seed weight. Higher increases were observed in Gadra where moderate P application increased yield from about 250 to 1,000 kg ha^{-1} and high P increased yield to 1,600 kg ha^{-1}. The results suggested that high P foraging and utilisation efficiency were inversely related.

Key words: Biomass, soil nutrients, phytotoxicity, yield, yield components.

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is the grain legume with the highest volume of direct human consumption in the world and is the most important legume in Eastern and Southern Africa cultivated over an area of about 4 million ha (Beebe et al., 2014). Worldwide per capita consumption is high but varies according to region, being as high as 60 kg in East Africa and about 4 - 17 kg in Latin America (Beebe et al., 2013; Broughton et al*.,* 2003). Generally, productivity is low, with a global average yield of 715 kg ha^{-1} against a potential yield of 1,500 to 3,000 kg ha^{-1}. In Africa, the average yield is about 500 kg ha^{-1} which is well below the global potential yield (Namugwanya et al., 2014). The reasons for this low productivity are due to both biotic and abiotic factors. Beans are particularly sensitive to abiotic factors rendering them unable to reach their productive potential

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(Assefa et al., 2015; Velho et al., 2018). Drought and soil infertility, especially phosphorus deficiency, are primary constraints to crop production in many developing countries, affecting over 80% of bean production regions in the world, and they frequently co-occur throughout the tropics (Suriyagoda et al*.,* 2014). In Sub Saharan Africa drought is the most important risk, potentially affecting as much as one- third of the production area (Beebe et al*.,* 2014).

Water is essential for many plant processes, primarily acting as a solvent for different metabolites, providing means for nutrient and solute transport and also involved in plant temperature regulation (Baker, 1984). Soil water deficits severely retard plant development, reducing yield (Mataa et al., 1998). It is reported that 60% of common bean production is located in drought prone areas and the increasing competition with major crops continues to push common beans into marginal lands with increased risk of drought stress (Mukeshimana et al*.,* 2014). The amount of fresh water is finite and water has multiple and competing uses including direct human, industrial and agriculture uses. Efficient utilization of fresh water in agriculture can greatly contribute to water conservation.

Besides nitrogen, phosphorus is the most limiting nutrient for plant growth in arable soils (Suriyagoda et al., 2010). Phosphorus in plants is important for variety of processes particularly in maintenance of energy-metabolic systems, enhanced root development and root hydraulic conductance (Jin et al*.,* 2014). Plants have evolved different strategies for P acquisition and use in limiting environments (Ho et al*.,* 2005; Vance et al*.,* 2003). These include increased mycorrhizal symbioses, decreased growth rate, remobilization of internal inorganic phosphate, modification of carbon metabolism bypassing P-requiring steps, increased synthesis and secretion of phosphatase, exudation of organic acids, and enhanced expression of P transporters (Raghothama, 1999; Plaxton, 2004; Vance et al., 2003). In response to low P, bean genotypes can either exhibit high P acquisition efficiency (PAE) and/or P utilization efficiency (PUE) (Atemkeng et al*.,* 2011; Cichy et al*.,* 2009; Vandamme et al*.,* 2016). PUE is the efficiency at which P taken up is converted to biomass whereas PAE is the ability of a plant to mobilize and absorb more P from the fertile soil layers (Atemkeng et al*.,* 2011). Typically, PAE includes modifications in root architecture to increase capacity of the plant roots to explore more soil in the upper soil layers which have higher P content. Since P is relatively immobile in the soil, it is important that the ability of plants to explore greater soil volume is enhanced if they are to access more of the nutrient. To achieve this, plants develop traits that include increased root development, higher root: shoot ratios, finer roots and longer root hairs (Suriyagoda et al*.,* 2010). However these adaptations are usually inadequate to meet the minimum phosphorus requirements for normal plant development and the application of external phosphorus is still a primary requirement for crop cultivation (Vance et al*.,* 2003). Soil water deficits further restrict phosphorus movement in the soil and this situation is projected to worsen with climate change. Although low soil P and soil water deficits are recognized as primary factors limiting bean productivity, most research has tended to focus on each of these factors separately despite them tending to occur as together (Namugwanya et al*.,* 2014; Suriyagoda et al*.,* 2014). It is known that soil related constraints can seriously limit the potential expression of drought resistance and it is therefore important to address multiple stresses (Beebe et al*.,* 2014; Suriyagoda et al*.,* 2014).

The objective of the study was to evaluate the effect of varying soil phosphorus content and water stress on yield and plant development in common bean genotypes with differing drought susceptibility tolerances.

MATERIALS AND METHODS

Experimental site

The study was carried out at National Irrigation Research Station (S 15° 046’ 43” and E 27° 055’ 14”, in Mazabuka, Southern Zambia from September to December 2012. The soils belong to the Nakambala series and according to USDA soil taxonomy are classified as *typic kanhaplustalf*.

Chemical analysis

Total nitrogen (N) was determined by the Kjeldahl digestion-distillation method (Bremner and Mulvancy, 1982). The determination of available phosphorus (Bray 1 Method) was conducted according to Bray and Kurtz (1945). Soil pH ($CaCl_2$) was determined using a digital electronic pH meter. Soil organic matter was determined according to the Walkley and Black (1934). Soil analyses showed that total nitrogen was 0.09% and available phosphorus was 8.5 mg kg $^{-1}$.

Plant materials

Two bean genotypes (Gadra and KE-3) genotypes were obtained from the Seed Control Certification Institute, Zambia. Selection of the genotypes was based on differences in drought susceptibility index with Gadra having high drought susceptibility and KE-3 low drought susceptibility (Kalima, 2013).

Field layout and crop management

There was 1.0 m space separating each treatment of phosphorus and variety within sub plots. There were 5 m buffer rows surrounding the field and a 2-m buffer zone separating the different irrigation regime portions of the field. The entire field received 40 kg N ha^{-1} as urea and 40 kg K ha^{-1}. For the three P treatments; low P- no P was added (0 kg P ha^{-1}), medium P- 40 kg P ha^{-1} was applied, and the high phosphorus rate field received 70 kg P ha^{-1}. The phosphorus fertilizer was applied as basal dressing of mono ammonium phosphate at planting.

Planting was done on the 6th of September, 2012. Standard bean management practices were used as recommended in Zambia. The field was kept weed free by regular weeding and monocrotophos was applied to control the bean fly, *(Ophiomyia phaseoli)* (Tryon) (Diptera: Agromyzidae). Commercial termiticide and nematicides were applied at planting to prevent termite and nematode attack, respectively.

Water stress application

For irrigation, the field was divided into blocks of 4.0 m × 7.4 m per replicate, with each block receiving either, 100% irrigation (no stress) or irrigation at 50% evapotranspiration (stress). Water stress was imposed at pre-flowering stage (V8), and discontinued when the plants were in their late reproductive stage (R8) (Kandel, 2010). Plants were harvested after physiological maturity in second week of December before seed shattering.

Measured parameters

The following parameters: (1) number of pods per plant; (2) number of grains per pod, were measured after harvest of the crop. (3) number of pods per plant; (4) number of days from emergence to physiological maturity of the crop [this was done by visual observation on the number of days to the time when the leaves start losing the green colour (Kandel, 2010)]. Plants were considered physiologically mature when at least 80% of the pods turned yellow (Kandel, 2010). (5) length of the vegetative phase (days to flowering); (6) plant height. Plant height was measured at physiological maturity by determining the distance from the ground level to the tip of the shoot apex; (7) pod length (cm) at physiological maturity of the crop. Pod length was expressed as the average of about 10 pods per plant. 8) 100-seed weight. The harvested seeds were air-dried in the shade for about 2 weeks and 100-seed samples from each plot were measured. 9) aboveground biomass accumulation was obtained by cutting the plants at ground level and drying the biomass in a forced drought oven at 60°C for 72 h.

Experimental design and data analysis

A split-split plot design, with genotypes (main plot), water regimes (split plot), phosphorus levels (split-split plot) replicated three times was used (Sokal and Rolfe, 1981). Data was analysed using GenStat 16 Software. Data was subjected to analysis of variance and where significant treatments effects ($p \leq 0.05$) were discerned, means were separated using least significant difference (LSD).

RESULTS

Table 1 summarizes the single, multiple and interactive effects of the treatment factors. All the three factors exerted significant effects on most of the measured parameters. There were similarities and differences in the way the two genotypes responded to water supply and phosphorus supply. Vegetative parameters such as plant height, days to maturity, and canopy biomass were affected by the water stress and phosphorus treatments. The water and phosphorus parameters affected yield and all yield components. Except for days to maturity and number of seeds per pod, very highly significant interactions between water stress and phosphorus levels were observed.

Vegetative parameters

Plant height

Effects of genotype, water stress and phosphorus on vegetative parameters are presented in Table 2. The genotype KE-3 had taller plants compared to Gadra. Overall, water stress significantly reduced plant height. In terms of effects of P on plant height, additional P increased plant height ($p \leq 0.001$). There were highly significant interactions between genotype and water regime (Table 1). The reduction in plant height due to water stress was higher in Gadra than KE-3. There were significant differences in response of the two genotypes to P; in both genotypes, P increased plant height but for Gadra, the lower P (40 kg ha^{-1}) rate caused about 25% height increase whereas the higher rate (70 kg ha^{-1}) reduced plant height, possibly indicating phyto toxicity. KE-3 had a consistent increase in plant height as more P was added; the 40 kg ha^{-1} treatment caused a 35% increase and the 70 kg P had an 80% plant height increase. There was a significant interaction between water regime and soil P; adding P increased plant height for both normally irrigated and water stressed treatments but the response was higher under the normally irrigated plots. Compared to the no- P addition, increases in plant height for the 40 and 70 kg ha^{-1} P treatments were 18 and 15% respectively under water stress and 19 and 68% respectively for the normally irrigated treatments.

Figure 1A showed the interaction of all the 3 factors-genotype, water regime and P levels on plant height. There was a highly significant interaction between genotype, water regime and phosphate application ($p \leq 0.001$) (Table 1). Applying P under normal irrigation increased plant height consistently in KE 3, but under water stress, additional P (70 kg ha^{-1} P) caused reduction in plant height in Gadra. For Gadra, addition of 70 kg ha^{-1} of P caused about 10% height reduction compared to the plant height of the 40 kg ha^{-1} P treatment.

Days to full maturity

The effects of treatments on days to full maturity (DFM) are given in Table 2. Gadra had a significantly shorter DFM phase compared to KE-3. Water stress had a highly significant ($p \leq 0.001$) effect on the days to full maturity. Overall, when the plants were subjected to water stress the DFM decreased by almost 15%. On average, addition of P had a highly significant effect ($p \leq 0.001$) on DFM; it increased the DFM from about 63 to 69 days under the 40 kg ha^{-1} P and to 74 for the 70 kg ha^{-1} treatment respectively. The increase was significantly larger under the 70 kg ha^{-1} P treatment compared to the 40 kg ha^{-1} P rate. Significant genotype and water stress interactions were observed (Table 2). Generally, water stress reduced the DFM, and the decrease was higher in Gadra (21%) compared to KE (10%). Highly significant ($p \leq 0.001$)

Table 1. Summary ANOVA table showing significance of different sources of variability.

Source	Plant height	Days to maturity	Canopy biomass	Seeds per pod	Pods per plant	Pod length	100- seed weight	Yield
Water (W)	***	**	**	*	***	**	ns	**
Phosphorus (P)	***	***	**	***	**	**	***	***
Genotype (G)	**	***	***	ns	***	ns	***	***
W × P	***	***	***	*	***	***	ns	***
W × G	***	***	***	ns	***	***	***	***
P × G	***	***	***	ns	***	***	***	***
G × W × P	***	ns	***	ns	***	***	**	***

Factor significance; *** highly significant ($p \leq 0.001$); **very significant ($p \leq 0.01$); * significant ($p \leq 0.05$) and ns- non significant.

genotype and phosphorus interactions were observed (Table 1). Addition of P increased the DFM with KE-3 having a larger increase compared to Gadra. Water stress and phosphorus interacted in responses to DFM ($p \leq 0.003$). The increase in DFM due to P under water stress conditions was less compared to normally irrigated treatments.

Significant genotype, water stress and phosphorus interactions in DFM were observed (Figure 1B, Table 1). DFM increased with increase in P addition, but these increases occurred where irrigation was normal. Water stress reduced DFM when accompanied with P addition and reduced DFM in Gadra at the 70 kg ha^{-1} P level. However, KE-3 showed consistent increase in DFM with more P. Overall, the highest DFM occurred in KE-3 under normal irrigation and 70 kg ha^{-1} P application.

Effect of water supply and phosphorus application on biomass accumulation

The effects of water and phosphorus application on biomass for the two genotypes are presented in Table 2 and Figure 1C). The effects of water stress and P on biomass were similar to those observed for plant height and DFM. However, canopy biomass was more sensitive to water stress and changes in soil P. Water stress had a significant effect ($p \leq 0.005$) on biomass accumulation. On average water stress reduced canopy biomass by about 25%. In terms of effects of P application, plant biomass increased with P addition, with higher responses being detected for the 40 kg ha^{-1} P application compared to the 70 kg ha^{-1} treatment.

Highly significant ($p \leq 0.001$) genotype and water stress interactions were observed. Biomass accumulation in Gadra was more sensitive to water stress as it experienced a 41% biomass reduction under water stress compared to KE-3 which had a 14% decrease. Highly significant genotype and P interactions were observed. Both genotypes responded to P addition by increasing biomass but the response patterns were different. KE-3 had a consistent increase in biomass with P addition. On the other hand, Gadra was less tolerant of high soil phosphorus. The application of 70 kg ha^{-1} P resulted in a significant reduction in canopy biomass compared to both the 40 kg ha^{-1} P and the treatment where no P was added. Significant water and P interactions were evident (Table 2). Under water stress conditions, although both P additions caused significant increases in canopy biomass, the lower P (40 kg ha^{-1}) treatment showed a larger increase in biomass (51%) compared to 12% increase for the 70 kg ha^{-1} P treatment. Under normally irrigated treatments the increases for the 40 and 70 kg ha^{-1} treatments were 21 and 114%, respectively. This showed larger increases for the normally irrigated treatments and possibly indicating that water deficit reduced the plant's ability to use additional P to increase its biomass. P addition only caused higher canopy biomass production if there was no water stress.

Reproductive parameters

Yield

Table 3 shows the effects of genotype, soil water stress and phosphorus content on seed yield. As noted earlier with the vegetative parameters, water stress caused highly significant reductions

Table 2. Single and 2 way interactive effects of genotype, water regime and phosphorus levels on vegetative development of common beans (*P. vulgaris* L.).

Factor			Parameter		
			Plant height (cm)	**Days to maturity (days)**	**Canopy biomass(g/plant)**
Genotype (G)					
Gadra		G1	25.7	59.9	27.2
KE 3		G2	54.4	76.1	45.4
	Lsd Genotype (G)		0.73	0.70	0.002
Water regime (W)					
Stressed		W1	37.1	62.6	30.9
Normal		W_2	43.1	73.4	41.7
	Lsd Water regime (W)		1.81	2.52	0.005
Phosphorus (P)					
		P_0	30.8	61.7	28.8
		P_1	40.5	68.5	41.2
		P_2	49.1	73.9	42.9
	Lsd Phosphorus (P)		1.21	0.59	1.04
G × W		$G_1 W_1$	23.7	52.9	20.2
		$G_2 W_1$	50.6	72.3	41.6
		$G_1 W_2$	27.8	67.0	34.2
		$G_2 W_2$	58.3	79.9	49.2
	Lsd G x W		1.45	2.01	1.66
G × P		$G_1 P_0$	22.3	52.8	17.2
		G_1P_1	28.0	62.2	36.7
		$G_1 P_2$	27.0	64.8	27.8
		G_2P_0	39.2	70.5	30.5
		G_2P_1	53.0	74.8	45.8
		$G_2 P_2$	71.2	83.0	60.0
	Lsd G × P		1.40	0.98	1.32
W × P		$W_1 P_0$	30.2	60.2	22.5
		$W_1 P_1$	35.7	62.8	36.3
		$W_1 P_2$	45.5	64.8	34.0
		$W_2 P_0$	31.3	63.2	25.2
		$W_2 P_1$	25.3	74.2	46.2
		$W_2 P_2$	52 7	83.0	53.8
	Lsd W × P		1.69	2.05	1.66
Factor significance		**Genotype (G)**	0.005	≤ 0.001	0.002
		Water regime (W)	≤ 0.001	0.003	0.005
		Phosphorus (P)	≤ 0.001	≤ 0.001	≤ 0.001
		G × W	≤ 0.001	≤ 0.001	≤ 0.001
		W × P	≤ 0.001	≤ 0.001	≤ 0.001
		G × P	≤ 0.001	≤ 0.001	≤ 0.001

on reproductive parameters ($p \leq 0.003$). In terms of genotype, KE-3 had a higher yield compared to Gadra. Addition of phosphorus to the soil increased yield significantly by about 160 and 230% under the 40 and 70 kg ha^{-1} P treatments, respectively. With respect to yield, water stress and genotype showed significant

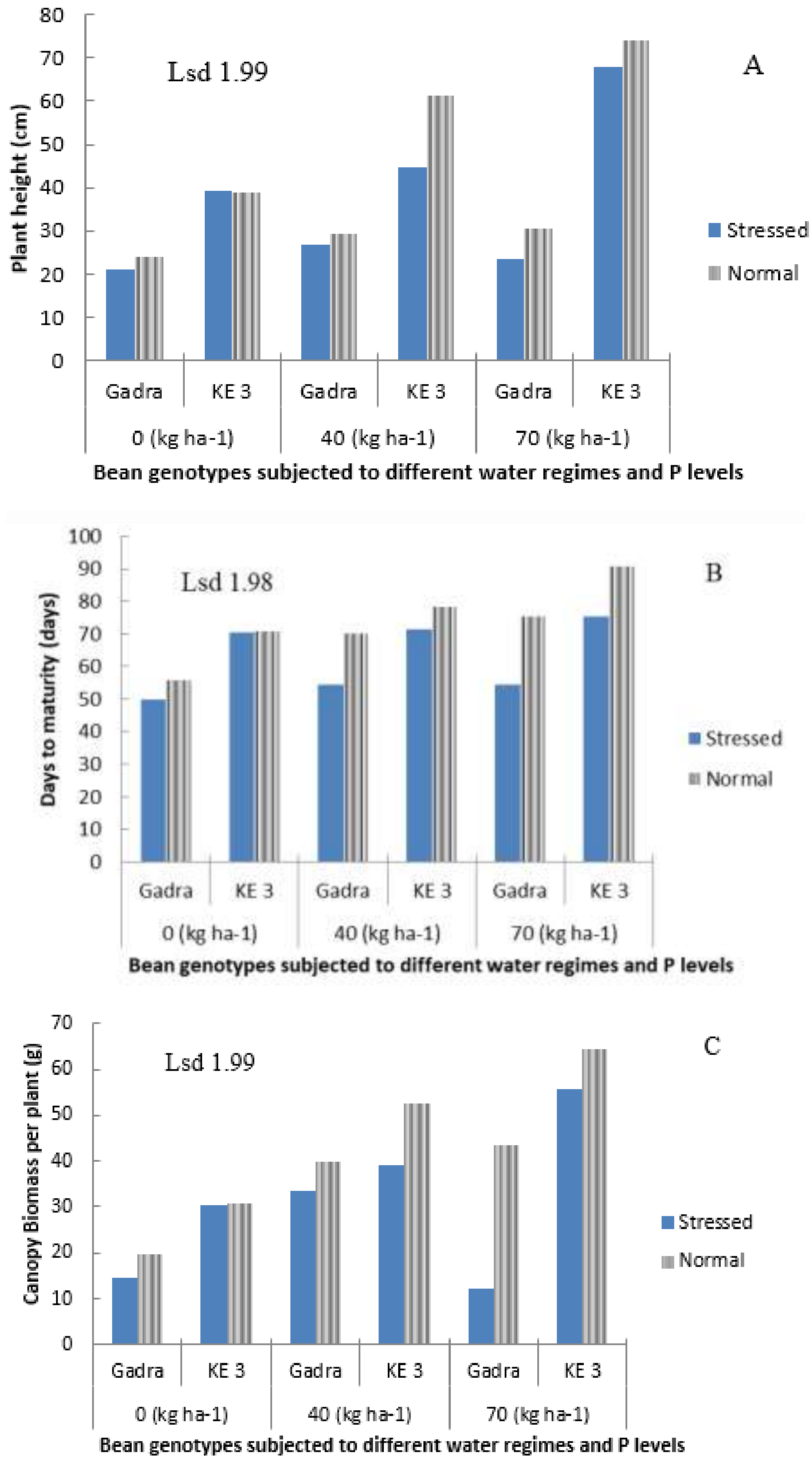


Figure 1. Three way interactive effects of genotype, water regime and phosphorus levels on vegetative development of common beans (*P. vulgaris* L.).

Table 3. Single and 2 way interactive effects of genotype, water regime and phosphorus levels on reproductive parameters in common beans (*P. vulgaris* L.).

Factor			Parameter		
			Yield	Pods/Plant	Pod length
Genotype (G)					
Gadra		G1	894.2	20.8	7.9
KE 3		G2	1410.6	16.9	7.6
	Lsd Genotype (G)		24.97	0.82	0.40
Water regime (W)					
Stressed		W1	683.1	15.2	6.9
Normal		W_2	1621.7	22.5	8.6
	Lsd Water regime (W)		49.96	1.96	0.48
Phosphorus (P)					
		P_0	499.6	5.7	5.1
		P_1	1295.8	23.2	9.4
		P_2	1661.7	27.8	8.8
	Lsd Phosphorus (P)		32.17	0.92	0.48
G × W		$G_1 W_1$	349.4	15.3	6.4
		$G_2 W_1$	1016.7	15.1	7.4
		$G_1 W_2$	1438.9	26.2	9.3
		$G_2 W_2$	1804.4	18.8	7.8
	Lsd G x W		38.82	1.50	0.57
G × P		$G_1 P_0$	649.2	6.5	5.5
		G_1P_1	1046.7	28.3	10.0
		$G_1 P_2$	986.7	27.5	8.2
		G_2P_0	350.0	4.8	4.7
		G_2P_1	1545.0	18.0	8.8
		$G_2 P_2$	2336.7	28.0	9.3
	Lsd G × P		41.18	1.5	0.54
W × P		$W_1 P_0$	255.8	5.00	4.8
		$W_1 P_1$	538.3	18.2	9.0
		$W_1 P_2$	1255.0	22.5	7.0
		$W_2 P_0$	743.3	6.33	5.3
		$W_2 P_1$	2053.3	28.2	9.8
		$W_2 P_2$	2068.3	33.0	10.5
	Lsd W × P		45.01	1.55	0.42
Factor significance		**Genotype (G)**	≤ 0.001	≤ 0.001	0.15
		Water regime (W)	0.003	0.004	0.005
		Phosphorus (P)	≤ 0.001	≤ 0.001	≤ 0.001
		G × W	≤ 0.001	≤ 0.001	≤ 0.001
		W × P	≤ 0.001	≤ 0.001	≤ 0.001
		G × P	≤ 0.001	≤ 0.001	≤ 0.001

interactions ($p \leq 0.001$). Yield in Gadra was more susceptible to soil water deficit. The reductions in yield under water stress were 76% for Gadra and 44% for KE-3. Compared to treatments where no P was added, the addition of P either at 40 kg ha^{-1} or 70 kg ha^{-1} caused highly significant yield increases.

Significant genotype and P interactions in yield were observed. The increases under the 40 kg ha^{-1} and 70 kg ha^{-1} P treatments were 61 and 52% respectively for Gadra and 340 and 560% respectively for KE-3. For Gadra, the lower P application rate increased yield more than the high P application, whereas at the 70 kg ha^{-1} P level the yield declined. This reduction in yield was higher under water stress regime for the 70 kg ha^{-1} P treatment. Gadra increased yield with P addition under both water regimes only at the 40 kg ha^{-1} P treatment. It was unable to utilize the increased availability of P at the high P treatment. Significant water stress and P interactions were observed with P application reducing the negative effects associated water stress. The effect was higher in the 40 kg ha^{-1} P and less in the 70 kg ha^{-1} P treatment. Across genotypes, under water stress condition, the increases in yield were 60 and 50% respectively for the 40 and 70 kg ha^{-1} P additions. Under normal irrigation, the respective increases were close to 340 and 570%.

Also, highly significant genotype, water stress and P interactions were noted ($p \leq 0.001$) in Table 1. Figure 2A shows yield interactions between the 3 factors. Without normal water supply, yield declined in both genotypes; however, yield increased under water stress when it was coupled with P additions. Increasing soil P to 40 kg ha^{-1} increased yield in both genotypes but the yields were lower in the water stressed treatments. Further increase in P reduced yield in Gadra under water stress. The highest yields were obtained in KE-3 under normal irrigation. Application of high P (70 kg ha^{-1}) to the soil in KE-3 was able to sustain high yields even under water stress.

Effects on yield components

Yield responses to changes in phosphorus and water stress were transduced mainly through changes in yield components such as pods per plant, pod length, and 100-seed weight (Table 1). There were significant interactions between water and phosphorus, genotype and water regime, genotype and phosphorus and water, as well as genotype and phosphorus for these yield components.

Number of pods per plant

Effects of treatments on pod number are shown in Table 3. The number of pods per plant in Gadra was significantly higher than for KE-3. Water stress as previously noted with yield and vegetative components reduced the number of pods per plant, with the average reduction being 32%. Addition of P increased the number of pods highly significantly ($p \leq 0.001$) with about 300% for the 40 kg ha^{-1} P application and close to 390% in the high P treatment. The number of pods per plant showed a significant interaction between genotype and water stress treatments. Overall, water stress reduced number of pods per plant to an average of 42% in Gadra and 20% in KE-3.

There was a significant interaction between genotype and P level in pod number per plant (Table 3). P increased the number of pods per plant for Gadra by 335 and 320% for 40 and 70 kg ha^{-1} P level, respectively. Regarding KE-3, the increases were 270 and 480% for the 2 respective P treatments. Highly significant interactions between water stress and P levels were seen ($p \leq 0.001$). Increases in pod number as a result of increased soil P were observed in both water stress and normal irrigated treatments. The increases under water stress treatments were 263 and 350% for the 40 and 70 kg ha^{-1} P, respectively compared to 345 and 421% respectively under normal irrigation.

Figure 2B shows the interactive effects of genotype, water regime and P levels on pod number. There were significant genotype, water stress and soil P interaction in terms of pods per plant. Water stress reduced pod number, with the lowest pod numbers occurring in the no P addition treatment. Addition of P increased the number of pods but there were differences in response among the genotypes. For Gadra, the largest increase occurred with the 40 kg ha^{-1} P but the high P treatment (70 kg ha^{-1} P) coupled with water stress reduced pod number per plant. For KE-3, the 70 kg ha^{-1} P treatment still caused further increases of almost the same magnitude with the 40 kg ha^{-1} P treatment.

Pod length

The effects of treatments on pod length are presented in Table 3. There were no differences in pod length among the genotypes. Whereas water stress reduced pod length by an average of 19%, there were no differences among the genotypes. Phosphorus increased the length of pods significantly, with the 40 and 70 kg ha^{-1} treatments causing 85 and 72% increases respectively.

There was a significant genotype by water stress interaction for pod length. Gadra showed a 13% pod reduction from water stress whereas KE-3 had a slight increase (20%) in pod length. Significant genotype and P interactions were discerned with the 40 kg ha^{-1} P addition causing an 85% increase in pod length for Gadra, and the high P increasing the pod length by a lesser magnitude of 72%. KE-3 showed consistent increases of 90 and 100%, respectively. Water stress interacted with P significantly in pod length. Under water stress, the low P (40 kg ha^{-1}) increased pod length by a greater magnitude (86%) compared to 45% for the 70 kg ha^{-1} treatment. Under normal irrigation, the pod length increased consistently- 84% (40 kg ha^{-1} P) and 97% (70 kg ha^{-1} P), thus showing a comparatively larger response

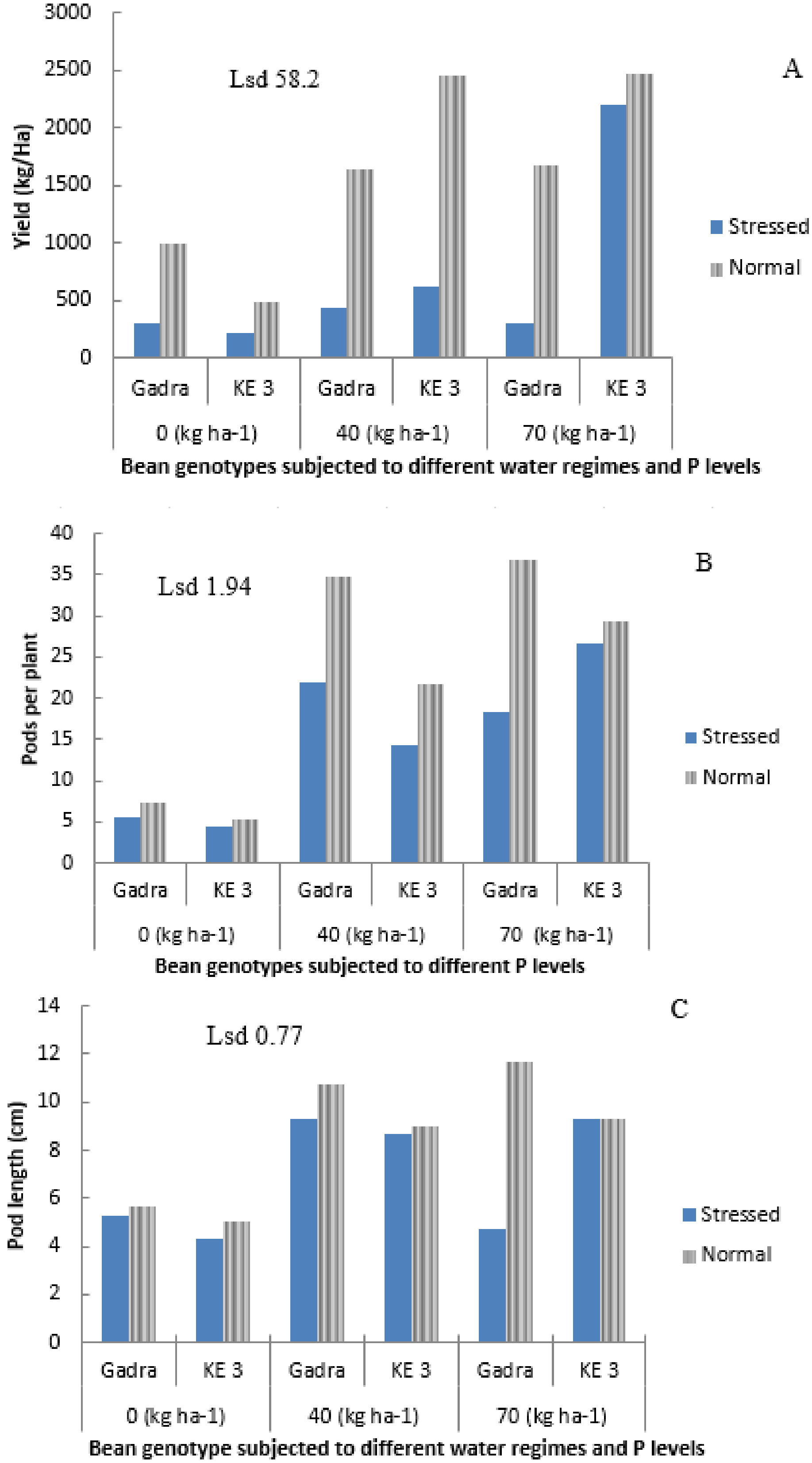
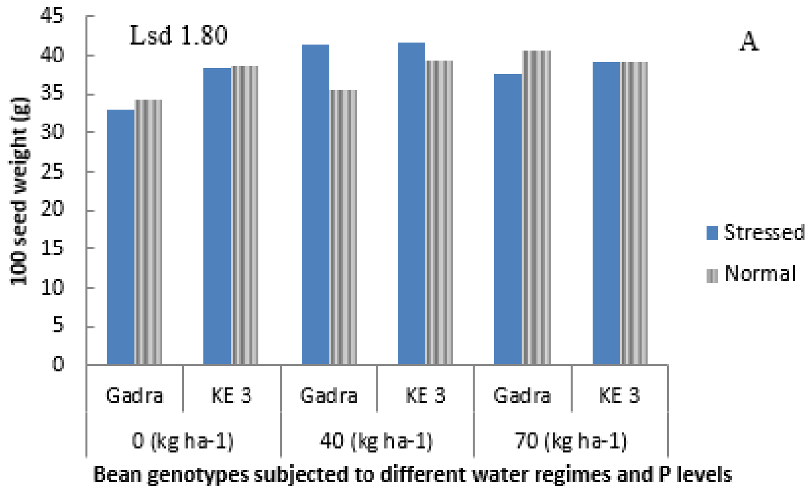


Figure 2. Three way interactive effects of genotype, water regime and phosphorus levels on yield pods per plant and pod length in common beans (*P. vulgaris* L.).



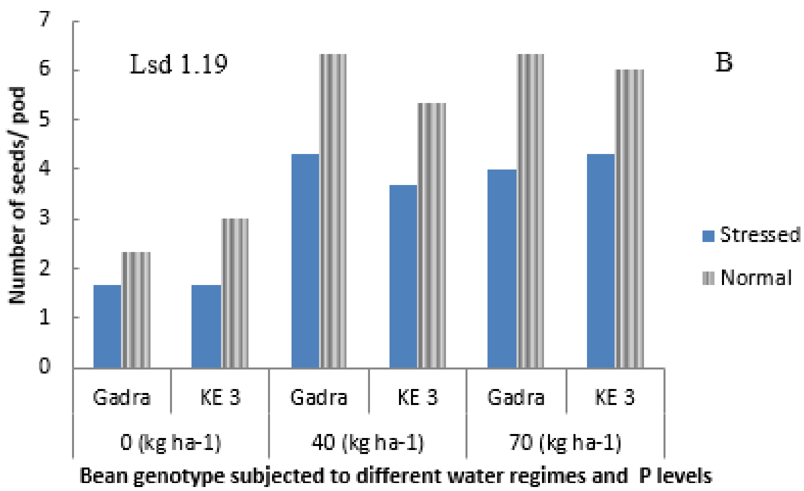


Figure 3. Three way interactive effects of genotype, water regime and phosphorus levels on seed weight, seeds per pod of common beans (*P. vulgaris* L.).

in the higher P level.

Figure 2C shows the highly significant genotype, water stress and P interaction in pod length ($p \leq 0.001$). Water stress reduced pod length; however for KE-3 at the high P level, pod length increased under the water stress treatment. Generally, P increased pod length but this was dependent on genotype and soil water status. For Gadra, increase in P occurred only in the normally irrigated plots; at the high P the pod length reduced under the water stress. KE-3 consistently increased with P, and at the high P was able to overcome the negative effect water stress so that the pods under water stress were longer compared to the no stress treatment.

Seed weight

The effect of treatments on 100-seed weight is presented in Table 1 and Figure 3A. Genotype had a highly significant effect on seed weight, with KE-3 having higher seed weight compared to Gadra. Overall, soil water stress did not have an effect on seed weight ($p = 0.24$) whereas P increased seed weight. Similar to the yield response, the lower P addition increased yield more than the high P rate. No interaction between water stress and P were observed ($p = 0.75$). There was a highly significant genotype and P interaction ($p \leq 0.001$), with Gadra having a higher response to P addition and both P addition causing about 15% increase in seed weight. KE-3 increased seed weight only under the 40 kg/ha treatment (5%). Water stress and P interacted significantly for seed weight with larger increases in seed weight under the water stressed than normal irrigated treatments. Under water stress, the 40 and 70 kg ha^{-1} P increased seed weight by 16.2 and 7.2% compared to 2.7 and 9.0%, respectively under normal irrigation. Significant genotype, water stress and P interaction were observed ($p = 0.009$) in Figure 3A. P increased seed weight higher in Gadra than in KE-3, and at high P level the negative effects of water stress were counteracted by P. For KE-3 at high P, there was no difference between water stressed and normal irrigated plots.

Number of seeds per pod

The number of seeds per pod was least sensitive to treatment effects (Table 2 and Figure 3C). Genotype did not exert a significant treatment effect on seed number per pod. Water stress significantly reduced the number of seeds per pod, whereas P caused highly significant increase in seeds per pod. The increase for both the 40 and 70 kg ha^{-1} P was the same- about 130%. These increases were reduced by water stress in both genotypes. No significant interaction was observed for either water stress by genotype, P by genotype or genotype by water stress by P level.

DISCUSSION

This study demonstrates the interrelationship between water stress tolerance and phosphorus in common beans. In particular, it highlighted impact of the simultaneous occurrence of low soil P and soil water deficit on plant development and yield. This is a common situation in many bean growing regions where drought occurs in areas that also have low soil phosphorus (Namugwanya et al., 2014). Plant responses to stress are highly complex and involve changes at the transcriptome, cellular and physiological levels (Suriyagoda et al*.,* 2014); and evidence shows that plant response to multiple stresses differs from that of the individual stresses (Atkinson and Urwin, 2012). Muller et al*.* (2014) identified genes induced in response to drought stress and demonstrated the differential gene expression during flowering and grain filling in common bean grown under drought stress conditions.

Characteristically, soils become deficient in P after prolonged degradation by erosion and repeated removal in crop harvest without replacement by fertilization of removed P (Henao and Baanante, 2006). The advent of climate change has increased the frequency and extent of extreme weather patterns including drought (Godfray et al*.,* 2010; Jin et al*.,* 2014). Our study demonstrated that in cases where P deficiency and water stress occur simultaneously, addition of P to the soil can increase the robustness of plants thereby increasing biomass and ultimately seed yield. This ameliorates the negative effects of soil water deficits. Previous studies have shown that these responses are mediated through either increased phosphorus acquisition efficiency (PAE) and/or phosphorus use efficiency (PUE) (Atemkeng et al*.,* 2011; Cichy et al*.,* 2009; Vandamme et al*.,* 2016). The former invariably involves modification in root architecture and the latter able to produce biomass even under limited soil P. The two genotypes used in the current study exhibited differences in responses to low P and soil moisture stress. KE-3 appeared to be more efficient at using P under water stress especially at the high P level but Gadra was more efficient only under normal irrigation supply and low (40 kg ha^{-1}) P addition. Another difference was in responses on the number of pods per plant and pod length. P increased the number of pods per plant, as for Gadra, the increase was more at the low P addition (40 kg ha^{-1} P) and under non-water limiting conditions. For KE-3, the increases in pod numbers were moderate at low P (270%) and particularly high at the high P addition (480%), and were still reasonably high even under low soil moisture conditions. The results were similar for pod length. Mndolwa et al*.* (2018) who evaluated P responses to common beans and used almost similar P application rates (50 kg and 100 kg ha^{-1} P) reported similar findings. These authors observed increased biomass and seed yield associated with increases in soil P and suggested improved PUE as the main reason for the improvement.

In their work on evaluation of P- efficient germplasm in tropical regions, Beebe et al. (2006) suggested that genotypes selected for adaptation to low- P soils may be more sensitive to drought. This may be due to their predominantly shallow branching characteristic that allows for more efficient soil foraging but prevents them from accessing water in lower soil horizons (Nielsen et al., 2001). We noted that Gadra that was reported to be drought susceptible (Kalima, 2013) had a better PUE. Studies on cowpea (*Vigna unguiculata*), a close relative of common beans have shown that yield in legumes is strongly dependent on water supply during reproductive phase with less influence of vegetative phase water deprivation (Ziska and Hall, 1983; Hall, 1999). Better performance of plants under soil water deficits when P is adequate is thought to be due to increased water use efficiency (Suriyagoda et al*.,* 2010). Additionally, it has been reported that among other traits seed yield is positively correlated with ability to maintain high leaf chlorophyll content (Ambachew et al*.,* 2015). Nielsen et al*.* (2001) showed that under low P, inefficient genotypes utilise more of their net carbon assimilation on root respiration thus further reducing carbon availability for maintenance, construction of plant tissues and ion uptake.

Lynch et al. (1991) postulated that P availability affects bean growth primarily through effects on leaf appearance and biomass partitioning between photosynthetic and respiring organs, rather than through effects on leaf photosynthesis. The days to full maturity can be used as a proxy for green leaf duration because after this period the leaves begin to lose their chlorophyll. The green leaf duration is an important phase in annual crops as it is the period in which the crop actively synthesizes photo assimilates and uses them for general development or accumulates them in reserve for later remobilization in peak demand (Sadras and Tripani, 1999). Our results showed that water stress generally reduced the days to full maturity (DFM), and the decrease was higher in Gadra (21%) compared to KE (10%). Highly significant genotype and phosphorus interactions were observed. Although P addition increased the DFM, KE-3 had a significantly larger increase compared to Gadra. DFM increased with increase in P addition but these increases occurred only where irrigation was normal. For Gadra, water stress reduced DFM when accompanied with P addition at the 70 kg ha^{-1} P level. On the other hand, KE-3 showed consistent increase in DFM with more P addition. The effect of low soil P shortening DFM related to early onset of senescence. Common beans are annual plant with typical monocarpic type of senescence, where the plant dies entirely after formation of seeds and fruits. The key processes involved in senescence are changes in chlorophyll, proteins and consequently changes in photosynthesis and respiration rates (Mataa et al*.,* 2018). Drought escape mechanisms involve rapid phenological development, early flowering and maturity (Namugwanya et al., 2014). Both genotypes exhibited longer DFM under high soil P. It is possible that low P in the plant initiated early senescence or it may just be a stress response where reproductive phase is initiated early to ensure seed production before the plant dies. In either case, the grain filling period was reduced and the overall yield lowered compared to optimal soil P treatments.

This study did not analyse root development, therefore, we can only postulate that Gadra which had more yield robustness under low soil phosphorus may have a shallow and adventitious root system and was therefore able to forage for phosphorus more efficiently under low P soils. Although root architectural traits that increase topsoil foraging are advantageous for phosphorus acquisition they may incur trade-offs for the acquisition of deep soil resources such as water (Ho et al*.,* 2005). These same authors suggested that under low soil phosphorus, shallow rooted genotypes grow best, whereas under drought stress, deep rooted genotypes grew best. It has been further reported that adventitious roots have lower metabolic cost than basal roots and P efficient genotypes have lower root respiration rates (Nielsen et al*.,* 2001). It has also been reported that in some species, P efficient genotypes under low soil P exhibit increased root aeronchyma which may decrease root respiration (Galindo-Casteñeda et al., 2018). Boutraa (2009) and Liao et al*.* (2004) suggested that improved PUE is related to the capacity of the plant to accumulate dry matter despite inadequacy of soil P. Such genotypes are able to produce more pods and seeds than non-low P tolerant genotypes (Atemkeng et al*.,* 2011; Boutraa, 2009). In our study, high production of pods was clearly demonstrated in the genotype Gadra at the high soil P rate (at 40 kg ha^{-1}) where the number of pods increased under the normal irrigation treatments.

Phosphorus improved crop performance under low soil moisture conditions or drought conditions. According to Frahm et al*.* (2004) and Beebe et al. (2013), drought tolerance mechanisms include capacity to avoid dehydration, while preserving comparatively high tissue water potential, which is partly due to improved root length, density and depth that maximises the available soil moisture for uptake by the crop. Another mechanism is through escape mechanism which is the ability of the plant to complete its life cycle before onset of harsh soil moisture deficits (Beebe et al*.,* 2013). Liu et al*.* (2017), working on dwarf bamboo showed that P application enhanced leaf photochemical activity, increased chlorophyll content, reduced thermal dissipation, increased scavenging of reactive oxygen species and reduced lipid peroxidation in water-stressed plants.

It is interesting to note that this apparently more P efficient genotype developed P toxicity symptoms at high soil P as evidenced by reduction in biomass. Shane et al. (2004) reported that P toxicity symptoms include growth reduction, early leaf senescence and leaf chlorosis. It has been suggested that P toxicity develops when P uptake exceeds utilization (Shane et al., 2004) and is more evident in slow growing or smaller genotypes (Shane et al., 2003). Gadra had less shoot biomass and shorter plant height. KE-3 responded more positively to both P application treatments, increasing plant height by 35% (low P) and 82% (high P).

Conclusion

The ability of P to increase yield was demonstrated even under soil water deficits. Phosphorus significantly increased grain yields mainly through increasing the number of pods per plant and seed weight. However, there was a tradeoff between ability to forage for P under low soil conditions and ability to tolerate and efficiently utilise high P applications. Thus, the genotype that exhibited higher yield at low soil P possibly due to higher P foraging was not able to utilise high applications of P to increase grain yields and actually showed P phytotoxicity. Our results showed the benefits of P application but suggest that attempts to improve yield by high application of P fertiliser particularly under soil water deficits should consider genotype morphology, the ability and efficiency to utilise the phosphorus.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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