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Agronomic assessment of phosphorus efficacy for potato (*Solanum tuberosum* L) under legume intercrops

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ABSTRACT

Phosphorus (P) is an essential element and its efficient use is of global importance. This study evaluated the effect of growing potato under legume intercrops on P uptake and use efficiency indices: P harvest index (PHI), P uptake efficiency (PuPE), P partial factor productivity (PPFP) and P partial balance (PPB). The experiment was carried out for four consecutive seasons with treatments comprising potato cultivated under legume intercrops: none (T1), dolichos (*Lablab purpureus* L) (T2), peas (*Pisum sativum* L) (T3) and beans (*Phaseolus vulgaris* L) (T4). Across the seasons, the mean haulm P uptake for T2 (6.7 kg P ha⁻¹), T4 (5.5) and T3 (4.5) were 6%, 23% and 36% lower than that observed in T1 (7.1 kg P ha⁻¹), respectively. On the other hand, tuber P uptake was highest in T1 (21.8 kg P ha⁻¹) and T2 (21.3 kg P ha⁻¹) and were significantly higher than 13.2 kg P ha⁻¹ in T3 and 15.1 kg P ha⁻¹ in T4. This had a profound effect on PuPE, which was equally highest in T1 (0.26 kg total P uptake kg⁻¹ P supply) and T2 (0.25) and lowest in T3 (0.16) and T4 (0.18). Similarly, PPFP, PHI and PPB followed a similar trend, with highest values in T1 (57 kg tuber dry matter yield kg⁻¹ P supply, 76.4 kg tuber P uptake kg⁻¹ total plant's P uptake and 0.20 kg tuber P uptake kg⁻¹ P supply, respectively). Among the tested legume intercrops, dolichos competed least for P with the main crop (potato) hence it can be integrated into potato-based cropping systems without compromising potato tuber yield.

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intercropping; phosphorus harvest index; phosphorus partial factor productivity; phosphorus partial balance; phosphorus uptake; phosphorus uptake efficiency

Introduction

Phosphorus (P) is a critical element in agricultural systems globally without a pertinent gaseous atmospheric constituent in its biogeochemical cycle as it is the case for nitrogen and sulfur (Manghabati et al. 2018; Mikkelsen 2019; Withers 2019). This means in a natural environment, P can only be supplied either through weathering of parent material or recycling of organic P compounds (Gitari, Gachene, et al. 2019a; Lemming et al. 2019). Under such circumstances it is impossible to sustain continuous cultivation of heavy P demanding crops such as potato (*Solanum tuberosum* L). P is an essential nutrient in potato production and a key component of crop's processes such as metabolism, synthesis of nucleic acid, photosynthesis, energy transformation, structural development and movement of nutrients within the plant therefore, its deficiency

results in considerable yield losses (Fernandes and Soratto 2012; Hopkins, Horneck, and MacGuidwin 2014; Manschadi et al. 2014); Naumann et al. 2019). The element is low in most tropical soils such as Nitisols, the most dominant soils in Kenyan highlands, which are the main potato-growing areas (Jaetzold et al. 2006; Gitari, Gachene, et al. 2018b; Gachene, Nyawade, and Karanja 2019; Nyawade et al. 2019c). The low availability of P is due to its high fixation and slow mobility as it undergoes chemical precipitation reactions with oxides of aluminum (Al) and iron (Fe), get adsorbed on soil constituents and/or bound in organic forms (Hinsinger et al. 2011; Hopkins, Horneck, and MacGuidwin 2014; Hill et al. 2015). Ideally, this implies that it is not readily available in the inorganic forms (primarily as H_2PO_4^- and HPO_4^{2-}) for plant uptake. Soil acidity exacerbated the situation and thus, crops exhibit P deficiency despite the fact that the total P content typically exceeds the plants' requirement in such soils (Richardson et al. 2009; White et al. 2013; Gitari, Mochoge, and Danga 2015; Li et al. 2019).

Potato production in developing countries relies on continuous input of large amounts of P in form of mineral fertilizers that are manufactured largely in China, Russia, Morocco and United States from phosphate rock, a nonrenewable resource that is declining at an unsustainable rate (EcoSanRes, 2008; Schröder et al. 2011; Mikkelsen 2019; Tonini, Saveyn, and Huygens 2019). Such disparity in spatial distribution of P reserves compounded with high energy equipment required during its exploitation results in price volatility and supply disruptions especially in P importing nations such as Kenya (Schröder et al. 2011). This increases potato production costs significantly, with about 20% of operating costs in potato production being incurred from fertilizer purchases (Stark, Westermann, and Hopkins 2004; Rens et al. 2018; Gitari, Gachene, et al. 2019b). Research has shown that crops such as potato utilize less than 30% of the applied fertilizer P due to its fixation especially under soils with low pH, resulting in considerable yield losses (Westermann 2005; Hill et al. 2015). In such soils, P is innately found in Fe-P and Al-P forms, which have to be exploited by roots or otherwise it ends up being immobilized (Hill et al. 2015; Flaten et al. 2019), lost in sediments through run-off (Nyawade et al. 2019a) or leached (Roberts et al. 2019);). Therefore, there is a need to develop innovative strategies that would reduce P losses hence, increasing its use efficiency especially under smallholder farming systems that dominate most of the agriculture in Africa.

Improving P use efficiency is desirable but difficult especially under acidic soil conditions due to its poor solubility and mobility (Wortmann et al. 2019). Therefore, to achieve increased P use efficiency in crop production without further increasing fertilizer inputs, there is need to ensure better exploitation of the available soil resources (Rosen et al. 2014; Zhang et al. 2017). Incorporation of legume intercrops into potato cropping systems has been practised previously as a way of soil moisture conservation and/or increasing productivity and profitability of such cropping systems (Sharaiha and Hadidi 2008; Gitari, Gachene, et al. 2018a; Nyawade et al. 2019b). Such practices as intercropping can result in improved nutrients uptake and use efficiency without necessarily incurring extra cost on fertilizers (Gitari, Gachene, et al. 2019b). Efficiency in nutrient use is feasible due to the complementarity and niche facilitation occurring in intercropping systems (Richardson et al. 2009; Faucon et al. 2015; Zhang et al. 2017; Schneider et al. 2019). For instance, legumes can fix atmospheric N, which can subsequently be transferred and made available for uptake by the companion crops (Hauggaard-Nielsen et al. 2009). With regard to P, integration of P-mobilizing crops such as dolichos creates a spatio-temporal niche, which enhances the ability to colonize the soil profile and exploit soil P from a larger surface area accessible by the roots under intercropping system compared to a monoculture (Li et al. 2019). Additionally, some legumes can produce carbon-based exudates that have the ability of solubilizing fixed P and bringing it into solution hence making it accessible to non-legume intercrops (Hinsinger et al. 2011; Zhang et al. 2017). Nonetheless, there is a paucity of documented information on the contribution of legumes to P efficacy especially under tropical conditions. This study builds on previous work (Gitari, Gachene, et al. (2018a, 2018b; Nyawade et al. 2019a) and aimed

at quantifying the impact of cultivating potato under legume intercrops on potato productivity with focus on four P use efficiency indices: P harvest index (PHI), P uptake efficiency (PuPE), P partial factor productivity (PPFP) and P partial balance (PPB).

In agronomic terms, PHI indicates the proportion of P accumulated in the harvested tubers to the total plant's P uptake (tubers plus haulms) (Dobermann 2007; Manschadi et al. 2014; Sandana 2016). It indicates the plant's capacity to transform nutrients into economic yield. The PuPE reflects the proportion of applied nutrients that ends up being taken up by the plant (Dobermann 2007). The harvested product (tuber) (kg) divided by kg of the applied nutrient denotes the phosphorus partial factor productivity (PPFP) (Cassman et al. 2002; Norton 2014). This index is generally used to indicate the productivity and sustainability of a cropping system by showing the mass-based balance between the available nutrient and the harvested yield (Ladha et al. 2005; Dua et al. 2007; Weih, Westerbergh, and Lundquist 2017). One merit of this index is that it measures the total economic returns from any specific factor/nutrient, in relation to its utilization from all the system resources, including the native soil nutrients plus those from applied inputs like fertilizers. The PPB is used to indicate the proportion of nutrients that is removed from the system through the harvested part of the plant in relation to the applied nutrients (Norton 2014). Therefore, information regarding P uptake by potato under legume intercrops may assist in the selecting the best legumes to be incorporated in the potato-legume intercrops with the aim of maximizing the positive interactions that can be drawn from such intercropping systems.

Materials and methods

Description of the site

The experiment was conducted at a research farm based at the University of Nairobi (1.15° S, 36.44° E) at an altitude of 1860 m. This area receives a mean annual rainfall of about 1000 mm distributed in a bimodal pattern, from October to December (short rains) and March to June (long rains). The soil type is Nitisol, which is among the best agricultural soils of the Kenyan Highlands where potato cultivation takes place (Sombroek, Braun, and van der Pouw 1982; IIUSS Working Group WRB, 2015; Gitari, Gachene, et al. 2018a; Nyawade et al. 2018). At the beginning of this experiment, the soil (0–30 cm depth) was moderately acidic with a pH of 5.6, bulk density of 1.03 g cm⁻³, total nitrogen of 2.7 g kg⁻¹ and available phosphorus of 17.1 mg kg⁻¹. This P was measured using a UV-vis spectrophotometer (Murphy and Riley 1962) from the soil extract obtained after leaching the soil with NH₄-acetate (Rhoades and Polemio 1977).

Experimental layout and crop establishment

This study was carried out from 2014 to 2016 covering four successive seasons as described by Gitari, Gachene, et al. (2018a, 2018b). Treatments comprised potato planted under legume intercrops: T1 (none), T2 (dolichos - *Lablab purpureus* L.), T3 (garden peas - *Pisum sativum* L.) and T4 (climbing beans - *Phaseolus vulgaris* L.). These treatments were laid in quadruplicate in 4 by 6 m plots. Seed potato (pre-sprouted with a diameter of 35–55 mm) were planted at a depth of 0.1 m with an inter-row and intra-row spacing of 0.9 and 0.3 m, respectively such that the final plant density was 3.6 plants m⁻². Legume rows were located between potato rows, with two legume seeds were planted per hill at a spacing of 0.25 m within a row to achieve a plant density of 8.8 plants m⁻². All potato received 88 kg N ha⁻¹ and 15 kg P ha⁻¹ supplied in form of 200 kg ha⁻¹ of NPK (17:17:17) fertilizer at planting and an equivalent quantity of calcium ammonium nitrate (27:0:0) fertilizer, 28 days after planting (DAP). Potato was sprayed to control blight on fortnight bases with Ridomil Gold MZ 68WG containing 640 g kg⁻¹ of Mancozeb and 40 g kg⁻¹ of Mefenoxam. All plots were kept weeds free with potato being hilled up 28 DAP.

Table 1. Abbreviations, calculations and units of potato yield components, phosphorus uptake and use efficiency indices measured under legume intercrops.

Parameter	Abbreviation	Calculation	Unit
Haulm dry matter yield	HDY	–	Mg ha ⁻¹
Tuber dry matter yield	TDY	–	Mg ha ⁻¹
Haulm phosphorus uptake	HPU	HPC * HDY	kg ha ⁻¹
Tuber phosphorus uptake	TPU	TPC * TDY	kg ha ⁻¹
Total potato P uptake	ToPU	HPU + TPU	kg ha ⁻¹
Phosphorus harvest index	PHI	TPU/ToPU	kg tuber P uptake kg ⁻¹ total P uptake
Phosphorus uptake efficiency		ToPU/P supply	kg total P uptake kg ⁻¹ P supply
Phosphorus partial factor productivity	PPFP	TDY/P supply	kg tuber dry matter yield kg ⁻¹ P supply
Phosphorus partial balance	PPB	TPU/P supply	kg tuber P uptake kg ⁻¹ P supply

Phosphorus concentration in tubers (TPC) and haulms (HPC) were determined as explained in Section 2.3.

Plant tissue sampling and analyses

Plant samples (tuber and haulms) were taken when about 50% of natural crop senescence was observed. The sampling area consisted of the central four potato rows with 0.5 m borders excluded from each end. Ten potato plants were randomly selected, then their haulm (shoot, stems and leaves) biomass cut using a knife at 10 cm above the ground level and chopped. The tubers from the same plants were harvested manually, with the number of tubers per plant, and their weight being recorded. Ten tubers were randomly selected from the harvested batch and chopped into small pieces (5 cm long). About 500 g subsamples for tubers and haulms were taken separately, oven dried at 70 °C to a constant weight and were then ground using a tissue grinder and passed through a 1.0 mm sieve in preparation for analysis. The subsamples were digested using a block digester with sulfuric acid at 230 °C for six hours. Phosphorus concentration was then quantified colorimetrically following procedures outlined by Murphy and Riley (1962) using a UV–vis spectrophotometer. Table 1 summarizes the various phosphorus uptake and efficiency indices and how they were estimated (Ladha et al. 2005; Valle, Pinochet, and Calderini 2011; Norton 2014; Sandana 2016).

Estimation of root length density

Root samples were extracted 60 days after planting from each plot at 0–30, 30–60 and 60–90 cm depths using metal cores with an inside diameter of 0.03 m and length of 0.1 m (Bohm 1979). This was done by driving cores directly between the two potato rows in control plots, and between the potato and legume plants in plots with intercrops. In addition, samples were taken at the stem base of potato and legume plants. The samples were composited per plot and sampling depth, by placing the soil cores in a bucket half filled with water and swirling gently to remove debris and soil particles attached to the roots. The roots were sieved out using a 2 mm mesh placed in a shallow water tub, arranged on a glass tray and scanned using Epson Expression 1680 Scanner. Root length density (RLD) was then estimated using WinRHIZO Root Analyzer System (Regent Instruments Inc., Quebec, Canada) (Eq. 1).

$$\text{Root length density (cm cm}^{-3}\text{)} = \frac{\text{Root length (cm)}}{\text{Soil volume of corresponding depth (cm}^3\text{)}} \quad (1)$$

Statistical data analysis

The effects of legume intercrops on potato dry matter yield (haulm dry matter yield and tuber dry matter yield), and P uptake and use efficiencies were tested using generalized linear models in R Software (R Core Team, 2015) using *lme4* package (Bates et al. 2015). Whenever the factors

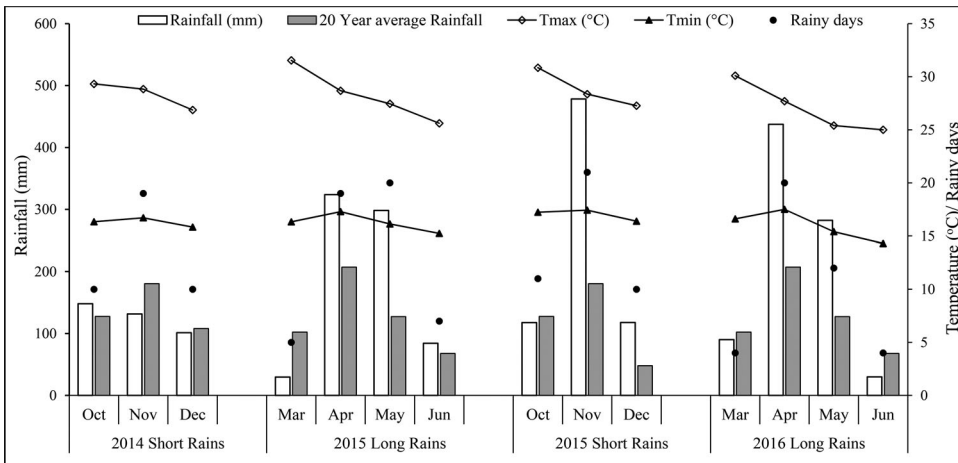


Figure 1. Monthly rainfall in comparison with the 20-year (1994–2013) average, and monthly rainy days and average temperature (maximum: Tmax and minimum: Tmin) as recorded at Kabete Meteorological Station during the four growing seasons from October 2014 to June 2016. Modified from Gitari, Gachene, et al. (2018a).

were significantly contributing to the differences, the means were separated at $p \leq 0.05$ using the Tukey's Honest Significant Difference (HSD) test. In addition, principal component analysis (PCA) was performed using ordispider and ordiellipse functions in *vegan* package. Further, regression analysis was conducted to establish the relationships between P uptake and selected P use efficiency indices.

Results

Precipitation and temperature characteristics during the study period

Rainfall recorded in all seasons was above the long-term average (460 mm) except in 2014 short rains (Figure 1) as described by Gitari, Gachene, et al. (2018a). On average, 788 mm were recorded for long rains and 547 mm for short rains in which the rainfall was received in 46 and 35 days, respectively. The wettest month for the short rains was November whereas, for long rains, it was April. Temperature remained nearly constant during the study period ranging between 20 and 25 °C with 2015 short rains and 2016 long rains being the warmest (23.3 °C) and the coolest (21.4 °C) seasons, respectively.

Root length density as affected by different legume intercrops

Generally, root length density (RLD) decreased with increasing soil depth and it varied significantly ($p \leq 0.05$) within the treatments (Figure 2). For instance, at 0–30 cm depth, intercropping resulted in 10, 24 and 30% higher RLD in peas-intercropped (T3), beans-intercropped (T4) and dolichos-intercropped (T2) plots, respectively than in control (T1). At 30–60 cm depth RLD was highest (8.8 cm cm⁻³) in T2, intermediate (5.4 cm cm⁻³) in T3 and T4 and lowest (4.4 cm cm⁻³) in T1. Similar differences were observed in 60–90 cm depth, but with relatively lower RLD values ranging from 0.7 to 3.6 cm cm⁻³.

Effect of legume intercrop on potato dry matter yield and phosphorus uptake

Haulm dry matter yield (HDY), tuber dry matter yield (TDY), haulm phosphorus uptake (HPU) and tuber phosphorus uptake (TPU) were significantly ($p \leq 0.05$) affected by the type of legume

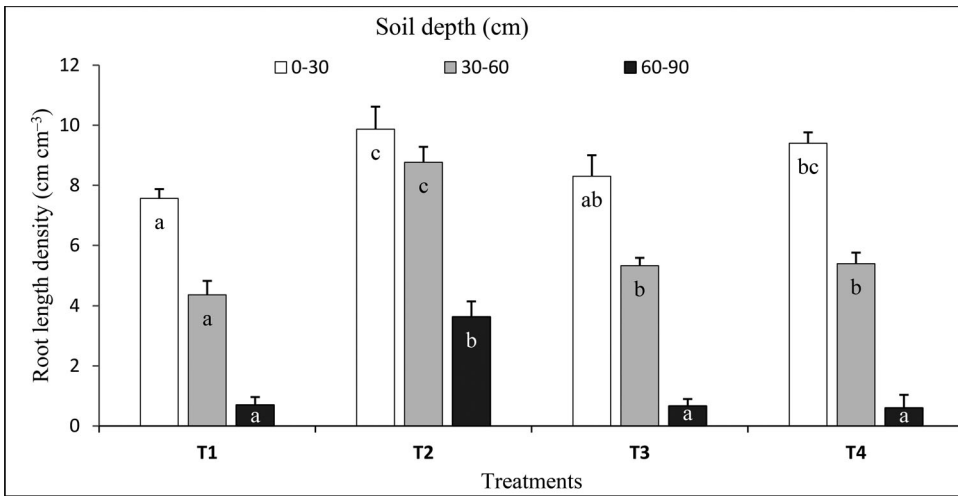


Figure 2. Root length density at 0–30 cm depth (clear bars), 30–60 cm (light gray bars) and 60–90 cm (dark gray bars) as influenced by legume intercrops: T1 (none), T2 (dolichos), T3 (peas), and T4 (beans). Bars bearing the same letter across the treatments and within the same soil depth present means that are not significantly different at $p < 0.05$. Error bars signify standard error of the means.

Table 2. Analyses of variance values associated with the studied variables (yield components, phosphorus uptake and efficiency indices) as influenced by legume intercrops and seasons.

Variable	Source of variation	Degrees of freedom	F value	p value
<i>Potato yield components</i>				
Haulm dry matter	Intercrop	3	46.51	<0.001
	Season	3	48.30	<0.001
	Intercrop × Season	9	1.65	0.129
Tuber dry matter	Intercrop	3	269.80	<0.001
	Season	3	301.83	<0.001
	Intercrop × Season	9	3.09	0.006
<i>Phosphorus uptake</i>				
Haulm P uptake	Intercrop	3	66.32	<0.001
	Season	3	99.73	<0.001
	Intercrop × Season	9	2.65	0.015
Tuber P uptake	Intercrop	3	291.11	<0.001
	Season	3	51.41	<0.001
	Intercrop × Season	9	1.92	0.043
<i>Phosphorus use efficiency indices</i>				
Phosphorus harvest index	Intercrop	3	5.21	0.004
	Season	3	38.66	<0.001
	Intercrop × Season	9	1.42	0.206
Phosphorus uptake efficiency	Intercrop	3	361.49	<0.001
	Season	3	115.65	<0.001
	Intercrop × Season	9	3.20	0.004
Phosphorus partial factor productivity	Intercrop	3	271.23	0.005
	Season	3	303.59	<0.001
	Intercrop × Season	9	3.10	0.006
Partial phosphorus balance	Intercrop	3	230.93	<0.001
	Season	3	37.71	<0.001
	Intercrop × Season	9	1.44	0.200

intercrops and seasons (Table 2). Higher values were recorded in 2015 long and short rains than in 2014 short rains and 2016 long rains. Across the seasons, HDY was highest (2.3 Mg ha^{-1}) in control (T1) treatment, intermediate (2.0 Mg ha^{-1}) in dolichos-intercropped (T2) and lowest (1.7 Mg ha^{-1}) in pea-intercropped (T3) and bean-intercropped (T4) plots (Figure 3). Similarly, TDY and TPU were higher in T2 (6.1 Mg ha^{-1} and 21 kg ha^{-1} , respectively) and T1 (6.3 Mg ha^{-1} ; 22 kg ha^{-1}) and low in T3 (5.2 Mg ha^{-1} ; 13 kg ha^{-1}) and T4 (5.4 Mg ha^{-1} ; 15 kg ha^{-1}).

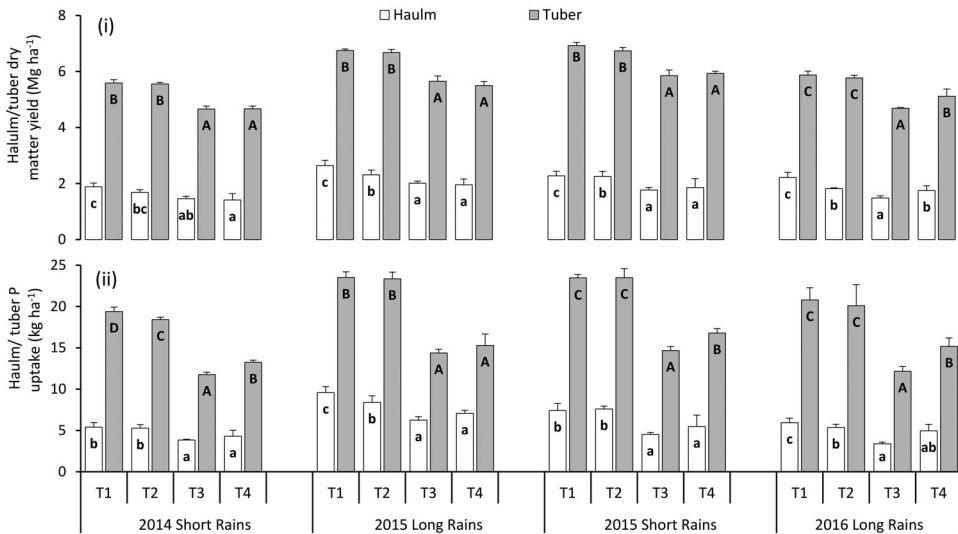


Figure 3. Dry matter yield (i) and phosphorus uptake (ii) for haulms (clear bars) and tubers (gray bars) as influenced by legume intercrops: T1 (none), T2 (dolichos), T3 (peas), and T4 (beans). Bars bearing the same letter (lower case for haulms and upper case for tubers) across the treatments and within the same season denote means that are not significantly different at $p < 0.05$. Error bars signify standard error of the means.

HPU differed between treatments with values ranging from 4.5 to 7.1 kg P ha⁻¹ in the order of T3 > T4 > T2 > T1.

Effect of legume intercrops on phosphorus efficiency indices

Legume intercrops had significant influences on P harvest index (PHI), P uptake efficiency (PuPE), P partial factor productivity (PPFP) and P partial balance (PPB), and the differences varied with seasons (Table 2). In the second (2015 long rains) season, the PHI in T2 differed significantly from T3 and T4 but not from T1 whereas, in the fourth (2016 long rains) season, PHI in T4 differed from T3 and T2 but not T1 (Table 3). However, in the first (2014 short rains) and third (2015 short rains) seasons, the PHI did not differ between treatments. Across the seasons, PHI was such that T1 (76.4 kg tuber P uptake kg⁻¹ total plant's P uptake) > T2 (75.7) > T4 (74.9) > T3 (73.8).

In all the four seasons, a comparable observation was made with regard to phosphorus uptake efficiency (PuPE) with the higher values recorded in T1 (0.26 kg total P uptake kg⁻¹ P supply) and T2 (0.25) than T3 (0.16) and T4 (0.18) (Table 3). Phosphorus partial factor productivity (PPFP) was correspondingly higher in T1 (57 kg tuber dry matter yield kg⁻¹ P supply) and T2 (56) while T3 and T4 recorded 17 and 16% lower PPFP values than T1. Phosphorus partial balance (PPB) exhibited 38 and 31% decrease in T3 and T4 compared with the highest value (0.20 kg tuber P uptake kg⁻¹ P supply) recorded in T1 and T2. Generally, PPFP and PPB decreased in the order of T1 > T2 > T4 > T3.

Generally, there was significant separation ($p < 0.01$) of treatments T1 and T2 (which recorded higher P efficacy variables) from T3 and T4 treatments along the first PC axis (Figure 4a). There was also separation of the four seasons, with season 2 (long rains 2015) separated from the other three seasons along axis 2 (Figure 4b), which could have been brought about by the high rainfall and therefore higher tuber yield which could have affected the yield/efficiency components.

Table 3. Phosphorus efficiency indices (means ± standard error) as influenced by legume intercrops and seasons.

Variable	Legume intercrop	2014 Short Rains	2015 Long Rains	2015 Short Rains	2016 Long Rains
Phosphorus harvest index (kg tuber P uptake kg ⁻¹ total plant's P uptake)	None	78.26 ± 1.8 ^a	71.08 ± 2.0 ^{ab}	76.01 ± 2.3 ^a	77.71 ± 2.6 ^{ab}
	Dolichos	77.72 ± 1.3 ^a	73.57 ± 1.8 ^a	75.53 ± 1.2 ^a	78.78 ± 3.0 ^a
	Peas	75.33 ± 0.3 ^a	69.70 ± 1.9 ^b	76.46 ± 0.8 ^a	78.18 ± 1.8 ^a
	Beans	75.55 ± 3.3 ^a	68.32 ± 1.9 ^b	75.70 ± 4.2 ^a	75.49 ± 1.8 ^b
Phosphorus uptake efficiency (kg total P uptake kg ⁻¹ P supply)	None	0.23 ± 0.1 ^a	0.30 ± 0.3 ^a	0.28 ± 0.1 ^a	0.24 ± 0.2 ^a
	Dolichos	0.22 ± 0.1 ^b	0.29 ± 0.0 ^a	0.28 ± 0.2 ^a	0.23 ± 0.2 ^a
	Peas	0.14 ± 0.1 ^d	0.19 ± 0.2 ^b	0.18 ± 0.1 ^c	0.14 ± 0.1 ^c
	Beans	0.16 ± 0.2 ^c	0.20 ± 0.1 ^b	0.20 ± 0.1 ^b	0.18 ± 0.1 ^b
Phosphorus partial factor productivity (kg tuber dry matter yield kg ⁻¹ P supply)	None	50.55 ± 1.1 ^a	61.04 ± 0.5 ^a	62.64 ± 1.1 ^a	53.11 ± 1.3 ^a
	Dolichos	46.24 ± 0.5 ^b	60.41 ± 1.0 ^a	60.93 ± 1.1 ^a	52.19 ± 0.8 ^a
	Peas	42.14 ± 1.0 ^c	51.11 ± 1.7 ^b	52.90 ± 1.9 ^b	42.39 ± 0.2 ^c
	Beans	42.23 ± 1.9 ^c	49.73 ± 1.3 ^b	53.65 ± 0.7 ^b	46.27 ± 2.3 ^b
Partial phosphorus balance (kg tuber P uptake kg ⁻¹ P supply)	None	0.18 ± 0.9 ^a	0.21 ± 0.6 ^a	0.21 ± 0.5 ^a	0.19 ± 1.1 ^a
	Dolichos	0.17 ± 0.6 ^a	0.21 ± 1.3 ^a	0.21 ± 1.2 ^a	0.18 ± 2.4 ^a
	Peas	0.13 ± 0.3 ^b	0.13 ± 0.4 ^b	0.13 ± 0.6 ^c	0.11 ± 0.4 ^c
	Beans	0.12 ± 0.6 ^c	0.14 ± 1.5 ^b	0.15 ± 1.8 ^b	0.14 ± 1.8 ^b

Means followed by different letters down the column within a variable differ significantly at $p < 0.05$.

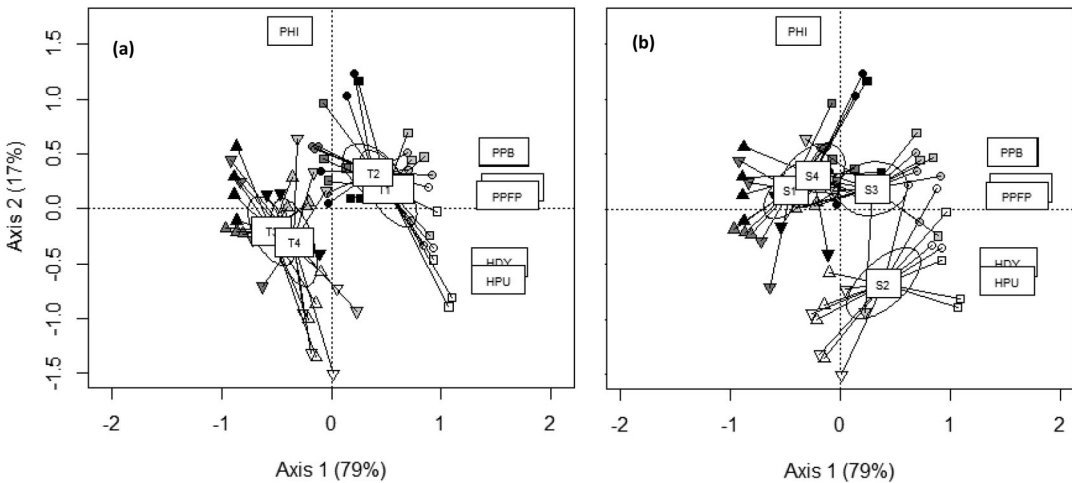


Figure 4. Projection of potato haulms (HDY) and tuber (TDY) dry matter yield, phosphorus uptake for haulms (HPU) and tuber (TPU), and P use efficiency indices: P harvest index (PHI), P uptake efficiency (PuPE), P partial factor productivity (PPFP) and P partial balance (PPB) along the first and second principal component axes. The symbols represent intercrops treatments (a): none (□), dolichos (○), peas (△) and beans (▽) with their centroids located at point T1, T2, T3 and T4, respectively. Point S1, S2, S3 and S4 marks location of the centroids for each season (b) indicated by the color of the symbols: 2014 short rains (dark gray), 2015 long rains (white), 2015 short rains (light gray) and 2016 long rains (black), respectively. The ellipses signify the standard errors.

Relationship between phosphorus uptake and selected P use efficiency indices

Regression analyses indicated a higher coefficient between total dry matter yield (ToDY) and tuber P uptake ($R^2 = 0.55$) than haulm P uptake ($R^2 = 0.41$) (Figure 5a and b), an indication that with the other factors being kept constant, a unit increase in haulm and tuber P uptake could result in 410 kg and 210 kg increase in potato total dry biomass, respectively. Phosphorus uptake efficiency (PuPE) had a lower association with haulm P uptake ($R^2 = 0.78$) than tuber P uptake ($R^2 = 0.96$) (Figure 5c and d), a suggestion that there would be an increase of 30 g for every additional kg in

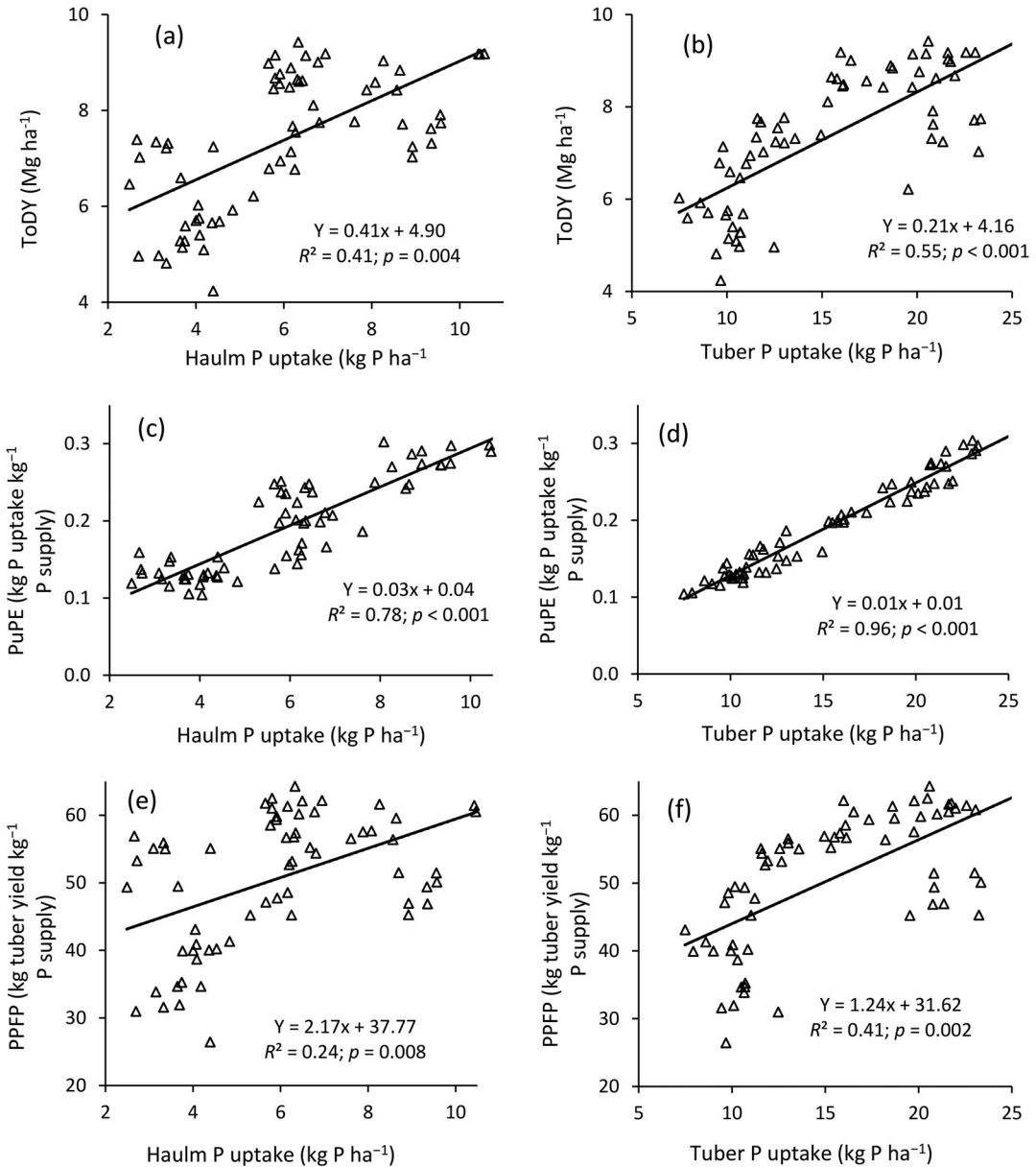


Figure 5. Relationship between total dry matter yield (ToDY) and haulm P uptake (a) and tuber P uptake (b), between P uptake efficiency (PuPE) and haulm P uptake (c) and tuber P uptake (d), and P partial factor productivity (PFP) and haulm P uptake (e) and tuber P uptake (f).

haulm P uptake and 10 g in tuber P uptake. PFP did not show strong relations with haulm ($R^2=0.24$) and tuber P uptake ($R^2=0.41$) (Figure 5e and f). Thus, PFP would increase by 2.47 kg and 1.24 kg for a unit increase in shoot P uptake and tuber P uptake, respectively.

Discussion

Potato is a high P demanding crop and therefore, nutrient uptake is directly related to its availability (Hopkins, Horneck, and MacGuidwin 2014; Thornton, Novy, and Stark 2014). The present

study has indicated that potato can take up a high amount of P under dolichos intercrops, which was comparable to the uptake under sole potato crop but significantly higher than under pea and bean intercrops. This could be attributed to mechanisms related to root's morphology. It is expected that when crops are intercropped, there would be root interaction, some of which could be negative such as decreased concentration of available P in the rhizosphere of the companion crops due to competition (Craine, Fargione, and Sugita 2005; Gitari, Gachene, et al. 2018b; Schneider et al. 2019). Peas and beans, which are known to have a shallow rooting system similar to that of potato, probably extracted P from the same soil stratum as potato, thus affecting potato yield negatively. In contrast, dolichos was observed to have a rooting system with a large surface area that grew up to a depth of about 100 cm as indicated by the higher root density (Figure 2). The deep rooting systems perhaps enabled dolichos to access the P in the sub soil (Crusciol et al. 2019) thus minimizing competition for P between potato and dolichos at the surface stratum which could have resulted in high potato tuber P uptake. This dimorphism within rooting systems and architectural differentiation is an essential factor in co-optimising early nutrient acquisition; a vital attribute for adequate growth especially for drought sensitive and heavy nutrient requiring crops such as potato (Hopkins, Horneck, and MacGuidwin 2014; Thornton, Novy, and Stark 2014; White et al. 2018 Nyawade et al. 2019,b). These findings are in agreement with earlier research that reported that rooting depth plays a key role in controlling nutrients uptake under intercropping systems (Mushagalusa, Ledent, and Draye 2008; Zhang et al. 2016). Besides the ability to access the sub soil P, dolichos have also been shown to secrete organic substances such as phosphatases, which promote release of P from organic materials (Hinsinger et al. 2011; Schneider et al. 2019). This could have not only resulted in adequate P for consumption by dolichos but also in surplus that could also be available for uptake by the companion potato crop. These findings agree with Mushagalusa, Ledent, and Draye (2008) who observed that potato and maize when intercropped they extract nutrients from the upper soil horizon. This is also in accordance with results from a field experiment by Nuruzzaman et al. (2005) which indicates that pea is poor at accessing soil residual P, hence competes for the inorganic sources of the element.

The high phosphorus harvest index values reported in this study indicate that potato is a more efficient crop in translocation of nutrients to the tubers. This index did not exhibit much variation between treatments indicating that translocation of P taken up to the tubers is not dependent on its uptake patterns. This is in agreement with Sandana (2016) who observed that potato tend to utilize P well even when it is in inadequate supply despite the low uptake of the nutrient. Such findings concur with those obtained by Wang et al. (2015) who reported that P uptake efficiency is paramount when the nutrient supply is limited. The higher P partial factor productivity observed in dolichos-integrated treatments over those with pea or bean can largely be attributed to the higher tuber dry matter yield. This can be supported by the positive relationships between dry tuber yield and P use efficiency indices, which is in line with findings by Sandana (2016) and White et al. (2018). Such relationships may imply any factor that improves P uptake would equally increase potato yield (Sandana 2016; Nyiraneza et al. 2017). It is also an indication that potato can be grown under legume intercrops such as dolichos without compromising its P uptake. This can contribute to optimal potato production because of increased soil-P uptake due to minimized loss through fixation and leaching especially in soils with low available P (Hopkins, Horneck, and MacGuidwin 2014; Flaten et al. 2019). The approach of using P uptake efficiency is key especially to smallholder resource poor farmers in developing countries where use of external soil inputs is minimal. This may be an important strategy since most of these soils have large reserves of P either in organic forms or fixed by Al or Fe hydroxyoxides (Richardson et al. 2009).

The observed seasonal effects on P use efficiency indices indicate that crop performance was influenced not only by types of legume intercrops but also by seasonal variability. Similar findings were reported by Nyiraneza et al. (2017) who observed a significant variation of P partial factor productivity with seasons. The authors attributed this to differences in rainfall amount.

Westermann (2005) and Tein et al. (2014) observed that nutrient uptake increases with rainfall, and this could explain the observed low P use efficiency in our study in 2014 short rains, which received only 380 mm of rainfall compared to a minimum of 500 mm required by potato for optimal performance as reported by Sood and Singh (2003) and Ierna and Mauromicale (2012). Generally, in this season, P uptake was very low leading to P partial factor productivity values that were below 50%. Losses of up to 50% of the applied nutrients have been reported by Shrestha, Cooperband, and MacGuidwin (2010). Conversely, the other seasons (2015 long rains, 2015 short rains and 2016 long rains), which recorded optimal rainfall, had higher P uptake with a resultant higher potato yield. High soil moisture is expected to increase P solubilization in the effective root zone hence making it available for plant uptake (Zhang et al. 2017; Flaten et al. 2019; Hopkins 2019).

Generally, the low partial P balance levels recorded in all treatments (<22 kg tuber P uptake kg^{-1} P supply) suggest there was less nutrient removal in relation to what was added through fertilizers. This could be attributed to P fixation as the soil had low pH (Fernandes and Soratto 2012; Hopkins, Horneck, and MacGuidwin 2014). This suggests the need for improving P use efficiency while upholding crop's productivity. Nevertheless, partial balance levels recorded in dolichos-integrated and sole potato treatments were significantly higher than in other treatments. This implies that potato removed more P from the soil through the tubers. Though this can be viewed as a limitation, the benefit outweighs the demerit because it was accompanied by higher yields. With the high P uptake efficiency observed in dolichos-integrated similar to sole potato treatments is a clear suggestion that potato cultivation is feasible under dolichos intercropping. This has extensive paybacks such as reducing ex-situ catastrophes such as environmental pollution related to P losses to surface water bodies where it causes detrimental eutrophication and nuisance algal blooms (Ruark, Kelling, and Good 2014; Faucon et al. 2015; Flaten et al. 2019). In addition, such strategies can help in achieving P-sustainable intercropping systems, hence reducing reliance on imported P, which is mined from phosphate rock (Withers 2019).

Conclusion

This study has established that dolichos is the best legume that can be adopted for incorporation into potato-based production systems with a minimal penalty on potato yield due to the relatively higher P use efficiency. This can be an important crop, particularly in tropics where soils have low pH, hence prone to P fixation. Further, dolichos-potato intercrop had higher P uptake than the other legume intercrops (peas and beans), which resulted in higher P use efficiency by potato. This could be a crop an indication of low competition for P, which is a desirable characteristic especially rain-fed agriculture where unfavorable local conditions such as low soil fertility and unpredictable rainfall are common phenomena. Nonetheless, future research can focus on the long-term effects of these intercrops with the aim of increasing sustainability.

Disclosure statement

The authors declare that they have no potential conflict related to the manuscript and the study as a whole.

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