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Research Article

Yield Response of Groundnut (*Arachis hypogaea* L.) to Boron, Calcium, Nitrogen, Phosphorus and Potassium Fertilizer Application

^{1,2}Meki Chirwa, ¹Jerome Peter Mrema, ¹Peter Wilson Mtakwa, ¹Abel Kaaya and ³Obed Isaac Lungu

¹Department of Soil and Geological Sciences, Sokoine University of Agriculture, Morogoro, Tanzania

²Department of Geology, University of Zambia, Lusaka, Zambia

³Department of Soil Sciences, University of Zambia, Lusaka, Zambia

Abstract

Background and Objective: The decline in soil fertility in the smallholder farmers' fields has resulted in low kernel yields in Zambia. Therefore, a field study was conducted to improve kernel yields by assessing the effect of B, Ca, N, P and K fertilizer application on groundnuts. **Materials and Methods:** A field trial was conducted at Golden Valley Agricultural Trust (GART) in Chisamba District of Zambia for two consecutive growing seasons of 2014/15 and 2015/16. The field experiment was laid out in a randomised complete block design with three replications. Randomisation of the following treatments was done per block: (i) No fertilizer, (ii) N₂₀, (iii) N₂₀P₃₀, (iv) N₂₀P₃₀Ca₁₀₀, (v) N₂₀P₃₀Ca₁₀₀K₄₀ and (vi) N₂₀P₃₀Ca₁₀₀K₄₀B₁. The numbers in subscript indicate rates of the nutrients in kg ha⁻¹. Analysis of variance was used to analyse the data. **Results:** Compared to the control (0 kg ha⁻¹), groundnuts responded to the application of N₂₀P₃₀Ca₁₀₀K₄₀B₁ kg ha⁻¹ to result in an increase of Ca uptake by 21%, N uptake by 55.5% and P uptake by 51%. The response of groundnuts to N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ resulted in an increase in kernels by 65.5% and haulm yield by 83.4%. **Conclusion:** The uptake of nutrient-elements by MG5 depended on application of all the nutrients at the rate of Ca₁₀₀N₂₀P₃₀K₄₀B₁ kg ha⁻¹. The appropriate rate of Ca, N and P fertilizers vital in attaining optimum kernel and haulm yields on a low fertility status acid soils in Zambia and areas with similar agro-ecological conditions is Ca₁₀₀N₂₀P₃₀ kg ha⁻¹.

Key words: Low soil fertility, groundnut production, kernel yield, fertilizer application, groundnut response, nutrient uptake, improve groundnuts

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Corresponding Author: Meki Chirwa, Department of Geology, School of Mines, University of Zambia, P.O. Box 32379, Lusaka, Zambia
Tel: +260 973 728 518

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Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Groundnuts (*Arachis hypogaea* L.) are one of the most important legume crops grown in Zambia¹. The crop is widely grown in Zambia both as a cash and food crop^{1,2}. Groundnuts are produced mainly by smallholder farmers in Zambia under rain fed conditions³. In terms of area planted, the crop ranks second to maize⁴ and covers 8.8 % of the cultivated land in the country⁵. The crop is indispensable for household food security because it provides 25-30% proteins and 45-52% edible oil in household diets^{1,6,7}. The by-product of the oil extraction process and the vegetative part of the crop (haulm) are used as stock feed^{1,6}.

However, the decline in soil fertility has resulted in low grain yields in the country averaging⁸ 642 kg ha⁻¹. Low fertility in Zambia has been attributed to inherently low N and P in the soils⁹. This problem is compounded by the widespread occurrence of acid soils especially in the high rainfall areas of Zambia¹⁰. Unbalanced fertilizer application, sole-cropping, removal of crop residues and early burning which leaves the soil bare and susceptible to erosion, have been reported as some of the factors responsible for degraded soils in Zambia¹⁰. In both Asia and Africa, groundnuts are grown under low input agriculture and therefore, yields tend to be low¹¹. The crop is an oilseed and its nutrient requirements are high¹². This means that, low fertile soils, compounded by practising Low External Input Agriculture (LEIA), cannot meet the nutrient needs of the crop. When one of the essential nutrients is missing from the soil solution, crop productivity is reduced^{13,14}. Therefore, to improve groundnut yields, the crop must be optimally fertilized.

Although groundnuts fix N₂, they require a starter dose of 10-20 kg N ha⁻¹ at planting time especially if total N in the soil is less than 0.1%^{15,16}. The crop does not require top dressing because the nodules can fix N₂ after 15-20 days of growth¹⁷. Crop production throughout the world has been limited by soil P deficiency¹⁸. Phosphorus deficiency is the major constraint to nodulation of legumes¹⁹. The supply of P below its critical level of 10 mg P kg⁻¹ soil^{17,20} has been reported to reduce legume grain production by as much as 50%²¹. Groundnuts require 15-40 kg P ha⁻¹ for the development of roots and nodules¹⁶ and optimum yields¹⁵⁻¹⁷. Results from Nigeria showed that groundnuts responded to 20 kg P ha⁻¹ which resulted in an increase of grain yields by 39.04%²². In India, application of 17.46 kg P ha⁻¹ to groundnuts resulted in the increase in kernel yields by 51%²³. Field trials in Zambia have shown that banding 35 kg P ha⁻¹ of either mono-ammonium

phosphate (NH₄H₂PO₄) or Partially Acidulated Rock Phosphate (PAPR) increased the yields of groundnuts by 50%²¹. Compared to broadcasting, side-placement of P had an advantage of additional yield increase of 0.78 kg ha⁻¹ in groundnut production²⁴.

Calcium is another critical nutrient in groundnut production²⁵. It is the most limiting nutrient to groundnut production in Zambia especially on acid soils⁶. On Ca deficient acid soils in Zambia, groundnut yields as low as 560 kg ha⁻¹ are common^{7,26}. The critical level of Ca in soils for groundnuts ranges between 87-125 mg Ca kg⁻¹ soil²⁷. Below this level, groundnuts responded to the application of 100 kg Ca ha⁻¹ which resulted in a 49% increase in kernel yields²⁸. Kirthisinghe *et al.*²⁹ applied gypsum to supply 250 kg Ca ha⁻¹ at flowering which resulted into an increase in kernel yields by 69%. Groundnuts responded to the application of 110 kg Ca ha⁻¹ resulting in an increase of kernels yields by 64%³⁰. To enhance pod yields, application of 120-200 kg Ca ha⁻¹ just before or at flowering stage has been recommended for various soil textures¹⁵. Similarly, MAFF⁶ recommended that Ca should be applied during early bloom of groundnuts. This is because the developing pods and pegs absorb Ca directly from the root zone²⁵. According to FAO¹⁵, the application of high K can potentially cause Ca deficiencies in groundnut production. In K deficient soils, the K requirement of the crop can be met by applying potassium sulphate (K₂SO₄) to supply¹⁵ 16.60-41.55 kg K ha⁻¹. Boron deficiencies in groundnuts result in damaged seeds³⁰. Boron deficiency can be corrected by application of boric acid (H₃BO₃) to supply¹⁵ 1 kg B ha⁻¹.

Therefore, appropriate fertilizer application to groundnuts is critical for improving low kernel yields in Zambia. However, the Ministry of Agriculture's blanket fertilizer recommendations is based on old varieties^{1,6} and lacks empirical evidence especially on the new varieties such as MGV 5. The response of groundnuts to blanket recommendations of NPK (10:20:10) fertilizer rate⁶ of 150 kg ha⁻¹ which was later reviewed¹ to 200 kg ha⁻¹ has produced inconsistent results. The 150 kg ha⁻¹ NPK (10:20:10) translated into supplying of 15 kg N ha⁻¹, 12.45 kg K ha⁻¹ and 13.09 kg P ha⁻¹, while 200 kg ha⁻¹ NPK resulted into supplying of 20 kg N ha⁻¹, 16.6 kg K ha⁻¹ and 17.46 kg P ha⁻¹. These two blanket recommendations for groundnuts did not include B which when deficient results in internally damaged seeds. Additionally, the crop requires more Ca especially at seed filling and pod development which must be readily available in the pegging zone¹⁵, Ca was not included in the blanket recommendation. The studies which have been conducted so far in Zambia did not systematically eradicate NPK challenges in groundnut production and did not

consider Ca and B as limiting to groundnut production. Previous studies focused on spacing, earthing-up, weeding, diseases and breeding programmes¹. There is paucity of information on groundnut production in Zambia. Therefore, this study was commissioned to determine the yield of groundnuts supplied with B, Ca, N, P and K fertilizers.

MATERIALS AND METHODS

Field study: A field trial was conducted at Golden Valley Agricultural Research Trust (GART) for two consecutive growing seasons, 2014/15 and 2015/16. The study site is located in Chisamba District, in the Central Province of Zambia. The District is located between latitude 14°30' and 15°00'S and longitudes 28°00' and 28°30' E. It is 1, 138 m a.s.l. Chisamba District is located in agro-ecological zone (AEZ) II (a) which receives comparatively high and well distributed rainfall ranging from 800-1000 mm and is one of the two most productive AEZs in the country^{1,31}. The mean annual temperatures in AEZ II (a) range from 14.31-27.31 °C during the 120-150 days of the region's growing season^{1,9}. The district is dominated by smallholder farmers whose livelihoods depend on rain fed groundnut and maize production⁵. This means that the low kernel yields averaging⁸ 340 kg ha⁻¹, deprive the rural poor of the much needed cash and food. The region contributes over 60% of the total national groundnut production⁵.

The chemical and physical properties of the soil at the study site are presented in Table 1. The soil belongs to the Kazwanya family, an Alfisol^{32,33} with a sandy clay loam top soil texture class. The soil is of low soil fertility and exhibits low CEC, total N, available P, S and deficient in B. The soil is moderately acidic.

The experiment was laid out in a randomised complete block design with three replications. Each of the three blocks had 6 experimental units of size 4.5×1.0 m to result into 18 experimental units. Randomisation of the following treatments was done per block: (i) No fertilizer (control) (ii) N₂₀, (iii) N₂₀P₃₀, (iv) N₂₀P₃₀Ca₁₀₀, (v) N₂₀P₃₀Ca₁₀₀K₄₀ and (vi) N₂₀P₃₀Ca₁₀₀K₄₀B₁. The numbers in subscript indicate rates of the nutrients in kg ha⁻¹. Groundnuts were planted at a spacing of 75 cm between rows and 10 cm between stations⁶. Msekera Groundnut Variety 5 (MGV 5) an improved variety, which is resistant to rosette disease and matures after 115-120 days, was grown as a sole-crop. Urea (H₂NCONH₂) and single super phosphate (Ca (H₂PO₄)₂) were applied at planting, 5 cm from station, while gypsum (CaSO₄) was applied at 50% flowering stage.

The Kjeldahl method was used to determine the uptake of total N in ground kernels and plant tissue³⁴. For

Table 1: Chemical and physical properties of soil at the GART study site

Parameters	Values
pH (0.01 M CaCl ₂)	5.14
Soil organic matter (%)	4.50
Total nitrogen (%)	0.14
Available P (mg kg ⁻¹)	0.04
Available S (mg kg ⁻¹)	0.40
K (cmol kg ⁻¹)	0.21
Ca (cmol kg ⁻¹)	2.25
Mg (cmol kg ⁻¹)	1.06
Na (cmol kg ⁻¹)	0.02
Al ³⁺ (cmol kg ⁻¹)	0.64
H ⁺ (cmol kg ⁻¹)	0.48
Exchangeable acidity (cmol kg ⁻¹)	1.12
CEC (cmol kg ⁻¹)	8.00
Total exchangeable bases (cmol kg ⁻¹)	3.54
Base saturation (%)	44.22
Exchangeable sodium percentage (%)	0.24
Cu (mg kg ⁻¹)	2.68
Fe (mg kg ⁻¹)	19.04
Mn (mg kg ⁻¹)	21.00
Zn (mg kg ⁻¹)	0.76
B (mg kg ⁻¹)	<0.001
Sand (%)	56.40
Clay (%)	25.60
Silt (%)	18.00
USDA texture class	Sandy clay loam

Table 2: Relative 100 seed weight of groundnuts

Fertilizers (kg ha ⁻¹)	Relative 100 seed weight (%)		
	Growing season (2014/15)	Growing season (2015/16)	Mean
0	102	89	95
N ₂₀	110	94	102
N ₂₀ P ₃₀	107	93	100
N ₂₀ P ₃₀ Ca ₁₀₀	109	95	102
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀	110	102	106
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀ B ₁	100	100	100
p-value	0.454	0.521	

Ca and P, 1 g of ground kernels and haulm were ashed at 500°C. The ash was dissolved in 6 M HNO₃ acid before determining the elements in the digest³⁴. Calcium was determined by Atomic Absorption Spectrophotometry (AAS) while P was determined using the Uv-visible spectrophotometer³⁴. Total nutrient-element uptake was calculated as the sum of the nutrient-element taken up by kernels and that taken up by haulm.

Statistical analysis: The data were evaluated by analysis of variance using the GenStat programme³⁵. The means were separated at $\alpha = 0.05$, by the Duncan's Multiple Range Test (DMRT)³⁶.

RESULTS

The mean relative 100 seed weight are presented in Table 2. The relative mean 100 seed weights observed in the

Table 3: Relative haulm, kernel and pod yields of groundnuts

Fertilizers (kg ha ⁻¹)	Relative yield (%)					
	Growing season (2014/15)			Growing season (2015/16)		
	Haulm	Pod	Kernel	Haulm	Pod	Kernel
0	71 ^a	112 ^a	94 ^a	68 ^a	86 ^a	74 ^a
N ₂₀	97 ^a	178 ^b	138 ^b	65 ^a	79 ^a	96 ^{cd}
N ₂₀ P ₃₀	135 ^b	152 ^{ab}	98 ^a	108 ^{ab}	87 ^a	83 ^{ab}
N ₂₀ P ₃₀ Ca ₁₀₀	97 ^a	172 ^b	161 ^b	158 ^b	108 ^b	117 ^e
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀	102 ^{ab}	135 ^{ab}	97 ^a	139 ^b	84 ^a	87 ^{bc}
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀ B ₁	100 ^{ab}	100 ^{ab}	100 ^a	100 ^{ab}	100 ^b	100 ^d
p-value	0.005	0.048	0.02	0.045	0.006	<0.001

Different letters next to values in the same column indicate level of significance at p<0.05 by the Duncan's Multiple Range Test (DMRT)

Table 4: Effect of B, Ca, N, P and K fertilizer application on the total uptake of Ca, N and P by groundnut variety MG5

Fertilizers (kg ha ⁻¹)	Relative nutrient uptake (%)					
	Growing season (2014/15)			Growing season (2015/16)		
	Calcium	Nitrogen	Phosphorous	Calcium	Nitrogen	Phosphorous
0	78 ^a	41 ^a	63 ^a	80 ^a	48 ^a	35 ^a
N ₂₀	78 ^a	63 ^b	72 ^a	80 ^a	74 ^{bc}	54 ^{ab}
N ₂₀ P ₃₀	102 ^a	73 ^{bc}	122 ^b	94 ^a	69 ^b	90 ^d
N ₂₀ P ₃₀ Ca ₁₀₀	84 ^a	82 ^c	88 ^{ab}	88 ^a	82 ^c	88 ^{cd}
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀	101 ^a	71 ^{bc}	89 ^{ab}	85 ^a	72 ^{bc}	67 ^{bc}
N ₂₀ P ₃₀ Ca ₁₀₀ K ₄₀ B ₁	100 ^a	100 ^d	100 ^{ab}	100 ^a	100 ^d	100 ^d
p-value	0.149	0.012	0.022	0.43	<0.001	<0.001

Different letters next to values in the same column indicate level of significance at p<0.05 by the Duncan's Multiple Range Test (DMRT)

control fields (0 kg ha⁻¹) were numerically lower than the 100 seed weight observed in the fields supplied with fertilizers but statistically not different. There was a highly significant difference amongst the means of the kernel yields of groundnuts for the first (p = 0.02) and the second (p = 0.001) growing seasons (Table 3). The lowest kernel yield of groundnuts for both growing seasons was obtained in the control fields (Table 3), indicating deficiency in nutrients of the study site (Table 1). The addition of nutrients from N₂₀ kg ha⁻¹ resulted in an increase of kernel yields. The steady increase continued on addition of nutrients indicating crop response (Table 3). In both growing seasons, the highest kernel yields were obtained in the field supplied with N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ (Table 3). Compared to the control field (0 kg ha⁻¹), the response of groundnuts to N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ fertilizer application resulted in a 71.3% increase in kernel yields in the 2014/15 growing season, while in the 2015/16, the kernels increased by 58.1%. Table 3 also shows that there was a highly significant difference amongst the means of pod yields for season one (p = 0.048) and season two as well (p = 0.006). The highest mean relative pod yield was observed in the fields supplied with N₂₀P₃₀Ca₁₀₀ kg ha⁻¹. The response of groundnuts to N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ application resulted in a 40.8% increase in pod yield. The haulm yield for season one (p = 0.005) and season two (p = 0.045) were

significantly different. The relative mean haulm yield was observed to be highest in fields supplied with N₂₀P₃₀Ca₁₀₀ kg ha⁻¹. The response of groundnuts to N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ resulted in an increase of the relative mean haulm yield by 83.4%.

The total uptake of nutrients by MG5 is presented in Table 4. In the current study, total nutrient uptake of the groundnut variety MG5 was calculated as the sum of the particular nutrient-element taken up by the kernels and that taken up by haulm. There was a highly significant difference amongst the means of total N uptake by groundnuts in season one (p = 0.012) and season two (p = 0.001). There was a highly significant difference amongst the means of P uptake by the groundnut crop for season one (p = 0.022) and season two (p = 0.001). Compared to the control (0 kg ha⁻¹), groundnuts responded to the application of N₂₀P₃₀Ca₁₀₀K₄₀B₁ kg ha⁻¹ to result in an increase of Ca uptake by 87.5%, N uptake by 130% and P uptake by 167%.

DISCUSSION

Seed weight: The 100 seed weight of kernels were non-significantly different. This means that the crop response to the control and to the fields supplied with

fertilizers were similar; which is contrary to the expectation. Crop response was expected because the soil of the study site is low in nutrient-elements (Table 1). Since the control fields was non-significantly different from the fields supplied with fertilizers, the nutrients (Ca, N, P, K and B) did not influence seed size. Similar results were reported by Kalita *et al.*³⁷ who applied 21.82 kg P ha⁻¹ to groundnuts in India and it increased pod and kernel yields but had no effect on the 100 seed weight of kernels. This means that P did not influence seed size. On the contrary, Gashti *et al.*³⁸ reported that groundnuts responded to Ca when they supplied the crop with 90 kg Ca ha⁻¹ on a clay loam soil in Iran resulting in significantly different 100 seed weights ($p < 0.05$), with 72 g being the highest, which they attributed to Ca fertilizer application. This means that Ca influenced seed size. Therefore, other factors such as moisture stress were likely to play for Ca not to affect the seed size of groundnuts in the current study. According to Singh and Kumar³⁹, the performance of groundnut varieties which are not resistant to drought decreases tremendously under water stress affecting the crop's pod filling and development and consequently resulting in poor seed quality and yield reduction. It follows therefore, that with its high water requirement (800-1000 mm rainfall), MG 5 was affected by the prolonged intra-seasonal dry spells in February and March of 2014/15 growing season. It did not rain for 25 days consecutively in March of 2014/15 growing season. The intra-seasonal dry spell in March of 2015/16 was only for 14 days.

Kernel, pod and haulm yields of groundnuts: Since the highest kernel yields were observed in the fields supplied with N₂₀P₃₀Ca₁₀₀ kg ha⁻¹ for both growing seasons, Ca, N and P were critical in attaining optimum grain yields of groundnuts. Further, this means that Ca, N and P influenced kernel production. Similar results were reported by Kamara *et al.*²⁸, when they applied Ca₁₀₀P₄₀ kg ha⁻¹ which resulted in a 50% increase in kernel yields. The findings of the current study are also in agreement with Ha⁴⁰, who reported an increase in kernel yields by 59.12% when they applied 39.28 kg P ha⁻¹ to groundnuts. It was also observed that the highest mean relative pod yield was obtained in the fields supplied with N₂₀P₃₀Ca₁₀₀ kg ha⁻¹, indicating that Ca, N and P are vital in attaining optimum pod yields. Since this rate application (N₂₀P₃₀Ca₁₀₀ kg ha⁻¹) was non-significantly different from the all treatment application, K and B are also important in attaining optimum pod production. The findings are in line with Nawaz *et al.*⁴¹, who applied basal fertilizer of N₃₀P_{34.91}K_{41.51} kg ha⁻¹ and assessed the response of

groundnuts to B₁ kg ha⁻¹, which resulted in a 34% increase of pods of ICGV 92023, one of the groundnut varieties they had grown.

Results also showed that relative to the fields supplied with all nutrients, Ca, N and P are vital in improving pod and haulm yields of groundnuts. This is in agreement with Tarawali⁴², who applied 90 kg P ha⁻¹ to groundnuts in Sierra Leone to result in the highest haulm yield of 2.57 t ha⁻¹, which was a 24.88% increase in haulm. The results are also consistent with Katsaruware and Mabwe⁴³, who applied Ca at the rate of 60 kg Ca ha⁻¹ to result in an increase in haulm yield by 67.68%. The results of the current findings are also in agreement with those reported by Yadav *et al.*⁴⁴, who applied N₂₅P₅₀K₂₀Ca₈₀ kg ha⁻¹ which resulted in an increase of haulm yields by 277.8%. These findings are important in improving haulm yields. Haulm yields are essential in smallholder farmer's farming systems for feeding livestock and improving nutrient cycling when incorporated⁴⁵.

Uptake of Ca, N and P by groundnuts: There was a non-significant difference amongst the means of uptake of Ca by groundnuts in season one ($p = 0.149$) and season two ($p = 0.43$). This is because the Ca content of the study site (2.25 cmol kg⁻¹) was above the critical limit (0.8 cmol kg⁻¹) for groundnut production⁴⁶. The lower uptake of total N in the control fields shows N deficiency of the study site. Application of N₂₀ kg ha⁻¹ resulted in the crop response with a 52.7% increase in N uptake by groundnuts. This means that N fertilizer application influenced the crop's ability to take up N. Compared to the control fields, the increase in response continued with a corresponding addition of nutrients. This resulted in the highest uptake of N being obtained in the fields supplied with all the nutrients, N₂₀P₃₀Ca₁₀₀K₄₀B₁ kg ha⁻¹. The crop benefited from balanced fertilizer application of the critical nutrients in groundnut production.

The lower values of P uptake in both the control field (0 kg ha⁻¹) and the N₂₀ kg ha⁻¹ plots for both seasons indicate severe P deficiency of the study site. Supplying P in the N₂₀P₃₀ kg ha⁻¹ treatment resulted in the increase in P uptake by 117.5%. This showed that P fertilizer application to groundnuts influenced the uptake of P by the crop. Similar to N, the highest P uptake was obtained in the fields supplied with all nutrient treatment. This means that apart from the three critical nutrients in groundnut production, K and B are important too in attaining optimum performance of groundnuts especially when deficient in soils. Similar results were reported by Gashti *et al.*³⁸, who stated that Ca and K are critical in improving groundnut crop performance. The current results are also consistent with findings reported by

Kabir *et al.*³⁰, who applied $\text{Ca}_{110}\text{P}_{50}\text{B}_{2.5}$ kg ha^{-1} which resulted in the increased number of filled pods and a harvest index of 27%. Kabir *et al.*³⁰ reported that Ca, P and B were critical in obtaining optimum groundnut crop performance, which is in agreement with the current study.

CONCLUSION

Groundnuts responded to the application of $\text{N}_{20}\text{P}_{30}\text{Ca}_{100}\text{K}_{40}\text{B}_1$ kg ha^{-1} which resulted in an increase of Ca uptake by 21%, N uptake by 55.5% and P uptake by 51%. The uptake of Ca, N and P by MG5 depended on the application of all the nutrients at the rate of $\text{Ca}_{100}\text{N}_{20}\text{P}_{30}\text{K}_{40}\text{B}_1$ kg ha^{-1} . It was noted that higher kernel and haulm yields were obtained in fields which were applied with fertilizers, with the highest yields being obtained in the fields supplied with $\text{N}_{20}\text{P}_{30}\text{Ca}_{100}$ kg ha^{-1} . Therefore, to improve kernel and haulm yields of groundnuts on a low fertility status acid soils, application of $\text{N}_{20}\text{P}_{30}\text{Ca}_{100}$ kg ha^{-1} is recommended.

SIGNIFICANCE STATEMENTS

The importance of this study is to improve groundnut kernel yields critical in mitigating widespread hunger amongst the smallholder farmers in Zambia and areas with similar agro-ecological conditions.

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