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Nutritional management and maize variety combination effectively control *Striga asiatica* in southern Africa

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Abstract

Maize (*Zea mays* L.) is an important staple food crop in sub-Saharan Africa (SSA) and contributes significantly to food security. Due to *Striga*, maize yield loss is estimated between 20 and 80% forcing some farmers to abandon their land therefore threatening food security. Many strategies have been applied to combat *Striga* infested fields to improve maize yields but alternative feasible approaches are still required. This study aimed at determining effects of phosphorus (P) and maize variety on *Striga asiatica* germination and attachment. A factorial experiment of eight P levels (0, 10, 20, 30, 40, 50, 60 and 70 kg ha⁻¹), six maize varieties and *Striga* (inoculated and non-inoculated) in a 4 × 24 α-lattice design with three replications was set in a glasshouse at the University of Zimbabwe. A similar experiment was set under laboratory conditions using agar gel plates to determine *S. asiatica* germination using a complete randomized design with three replications. Adding P (at 40 kg ha⁻¹) to soil infected with *Striga*, significantly ($p < 0.05$) reduced *Striga* counts and haustorial root attachments in all varieties with CV4 and R201 supporting lowest numbers. P also significantly ($p < 0.05$) improved plant height, chlorophyll content, leaf, cob, total biomasses and grain yield across all maize genotypes. Cultivar CV4 produced the highest grain yield under *Striga* attack. Furthermore, cultivars CV4 and CV1 had significantly ($p < 0.05$) lowest *Striga* seed maximum germination distance and percentages at zero P. Application of P reduced *Striga* germination, attachments and emergence in all varieties and increased tolerance of maize varieties.

Keywords: *Striga asiatica*, *Striga* counts, *Striga* germination distance, *Striga* germination percentage, Phosphorus nutrition, *Zea mays* L.

Background

Maize (*Zea mays* L.), is a major, staple food crop in Eastern and Southern African grown mostly by resource poor farmers (Jamil et al. 2012). Maize production in sub-Saharan Africa (SSA) is affected by biotic and abiotic stresses which have led to low grain yields among poor resource farmers. These biotic and abiotic stress include pests and diseases, parasitic weeds, poor soil fertility,

and drought. Among the major biotic stresses that affect maize is *Striga asiatica* L. Kuntze, which has forced some farmers to abandon their arable land. The yield loss due to *Striga* can vary from 30 to 100% equating to more than 7 billion USD annual in SSA (Badu-Apraku et al. 2014). *Striga* has known to be more prevalent under infertile soils, which are predominant among resource poor farmers in SSA as they do not have enough resources to purchase agricultural inputs such as lime and inorganic fertilizers.

Striga control strategies relies heavily on hand pulling, trap cropping (suicidal germination), use of fertilizers, fallowing, tolerance of the host and the use of resistant

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crop cultivars as the major control strategy that should be exploited by subsistence farmers (Kannan and Zwanenburg 2014). For instance, the use of resistant varieties has been reported to be the most feasible option for *Striga* control (Yallou et al. 2009; Badu-Apraku and Akinwale 2011). Resistant genotypes have been identified which include the ZD05 *Striga hermonthica* resistant genotype developed by the International Institute of Tropical Agriculture (IITA) (Yallou et al. 2007; Menkir et al. 2010). However, efficiency of *Striga* control methods relies solely on integrating them with sound agronomic practices (Rich and Ejeta 2008).

Nutrient management as a control strategy of *Striga* has demonstrated to be effective. Phosphorus (P) is one of the essential plant nutrients naturally obtained from weathering of soil minerals, and is greatly involved in adenosine triphosphate (ATP), an energy-rich compound as well as in nucleic acids and nucleotides (Czarnecki et al. 2013) and is also involved in phosphorylation reactions (Umehara 2011). Availability of P in the soil is limited because of its low mobility and also where it is fixed by ions (López-Ráez et al. 2011). P is important to plants as it is required during the early stages of plant development for early root formation and development and as part of the energy carrier molecule ATP. Apart from being one of the most essential plant nutrients, P seems to play a significant role in strigolactone (SL) production when P shoot levels decline (Yoneyama et al. 2012). Strigolactone are products of carotenoid-synthesis pathway produced by a number of plants, through the action of known enzymes, to serve various physiological and biochemical processes in different plant species (Koltai 2014). Carotenoids are compounds that give the red, yellow and orange colour in tomatoes, bananas and oranges, respectively. They play a pivotal role in plants by absorbing light during photosynthesis and are localized in plastids. For SLs to be produced, beta-carotene is first acted upon by enzymes [one isomerase and two carotenoid cleavage dioxygenases (CCD7 and CCD8)], and then isomerized and converted to lactone (carlactone) which is later oxidized by cytochrome P₄₅₀ enzyme to form SLs in the cell cytosol (Smith 2014).

Studies by Yoneyama et al. (2012) using red clover and rice revealed that a deficiency in P resulted in higher exudation of witchweeds germination stimulants; orobanchol and 5-deoxystrigol, respectively. Similar findings were also obtained by Boyer et al. (2012) when red clover was grown under low-phosphate conditions where orobanchol was produced in abundance suggesting that SL production is negatively correlated to P supply and uptake. Movement of SLs from roots to shoots (as shoot branching inhibitors) is an energy requiring process which is catalyzed by ATP-binding molecules hence

shortage of P entails a decrease in this transport process and also automatically in the decrease of stomatal conductance and photosynthesis (Czarnecki et al. 2013). A lower plane of nutrition in terms of nitrogen (N) and P (P) in rice promoted more SL production and hence higher *Striga* infection (Jamil et al. 2011, 2012). In most cases, where P was deficient, parasitic plants were shown to flourish making this nutrient to have a role in *Striga* control. In fact, P plays an important role especially on stimulant production since parasitic weeds germinate in response to SLs. This entails that direct application of P to crops could offer a relief to farmers whose fields are infected by parasitic weeds (Cardoso et al. 2011) as P regulates SL production (Foo et al. 2013). Jamil et al. (2014) noted that seed priming with P could provide an affordable and effective way of reducing the *Striga* germination. Hence, the application of P will help to suppress *Striga* germination as well as boosting crop nutrition (Pandey et al. 2015) and thereby contributing to increased yields and food security. Moreover, most researches on the effect of P on *Striga* have been conducted on rice and crops other than maize. Therefore, it is upon this basis of nutrient management being able to control and/or reduce *Striga* burden that this research is built on by valuating P and varietal effects on *S. asiatica* germination and attachment in maize. The objective of this study was to determine the effects of P and maize variety on *Striga asiatica* germination and attachment.

Results

Glasshouse experiment

Striga, P and variety main effects

Striga main effects were significant ($p < 0.05$) for leaf and root biomass. Significant variations were also recorded among the varieties for all the recorded traits with the only exception of chlorophyll content and root biomass (Table 1). P main effects were significant for all the recorded traits (Table 1).

Maize plant height

Striga effects were significant ($P < 0.05$; Additional file 1: Table S2) on the height of the maize hybrids, during weeks 3, 4, 10 and 11 the effects were not significant ($P > 0.05$; Additional file 1: Table S2). No significant ($P > 0.05$; Additional file 1: Table S2) influence on maize height has been observed from the varieties under study as well as from the interaction of *Striga* and variety and also that of *Striga* and P in week 7 and 8. Highly significant ($P < 0.001$; Additional file 1: Table S2) differences were noted in P levels across the whole experiment. The interaction of *Striga* and P was significant ($P < 0.05$; Additional file 1: Table S2). P addition improved the height of maize hybrids and reduced

Table 1 Mean squares of biomass parameters of maize hybrids

Source of variation	DF ^z	Chlorophyll	Leaf	Cob	Stem	Shoot	Root	Grain	Total	Root:shoot
Replication	2	166.56**	48.47*	718.1 ^{ns}	1528.3**	1899.30***	79.48 ^{ns}	539 ^{ns}	7457*	0.02009 ^{ns}
Replication/block	69	42.48*	27.26***	730.4**	627.1***	781.0***	45.67 ^{ns}	374.7*	3326**	0.18790***
Treatment	95	68.04***	83.22***	1362.6***	758.7***	1247.0***	71.27***	800.7***	9674***	0.28857***
<i>Striga</i>	1	1.21 ^{ns}	57.87*	904.3 ^{ns}	2.5 ^{ns}	84.5 ^{ns}	1590.40***	10.4 ^{ns}	15 ^{ns}	2.20695 ^{ns}
Variety	5	16.95 ^{ns}	160.69***	3535.4***	645.60*	1304.80***	39.74 ^{ns}	1978.8***	18,180.0***	0.07357***
P-level	7	446.35***	767.05***	9143.0***	6860.70***	12,058.9***	554.2***	5397.7***	88,543***	1.35946 ^{ns}
<i>Striga</i> × variety	5	9.51 ^{ns}	27.34 ^{ns}	1408.0**	189.1 ^{ns}	304.6 ^{ns}	18.46 ^{ns}	965.9**	6762**	0.08118 ^{ns}
<i>Striga</i> × phosphorus	7	72.56*	44.74**	1207.9**	388.2 ^{ns}	508.8 ^{ns}	10.86 ^{ns}	841.3**	6443**	1.39376***
Variety × phosphorus	35	54.08**	16.75 ^{ns}	405.6 ^{ns}	236.3 ^{ns}	318.7 ^{ns}	12.66 ^{ns}	264.7 ^{ns}	1885 ^{ns}	0.07233 ^{ns}
<i>Striga</i> × variety × phosphorus	35	22.98 ^{ns}	18.28 ^{ns}	490.6 ^{ns}	254.00 ^{ns}	320.1 ^{ns}	14.01 ^{ns}	239.9 ^{ns}	1812 ^{ns}	0.07514 ^{ns}
Residual	121	28.8	14.06	453	236.6	264.4	34.85	258.7	1944	0.08507
Total	287	46.04	40.37	822.6	512.3	725.3	49.82	468	4873	0.08507
Coefficient of variation (%)		14.86	22.52	47.19	37.11	27.99	43.43	52.49	29.9	90.81

*, **, *** specifies significance at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively; ns shows insignificance at $P > 0.05$

^z DF denotes degrees of freedom

the gap between *Striga* infected and non-infected plants (Fig. 1). In addition, the three factor interaction was significant ($P < 0.05$; Additional file 1: Table S2) in weeks 3, 4, 5, 6 and 7 and not significant ($P > 0.05$; Additional file 1: Table S2) in weeks 1, 2, 8 to 11.

Striga plant counts

Striga counts were observed from week 5 after maize emergence to week 11. P effects on *Striga* counts were highly significant ($P < 0.001$; Additional file 1: Table S3) from week 5 to week 11. *Striga* counts were

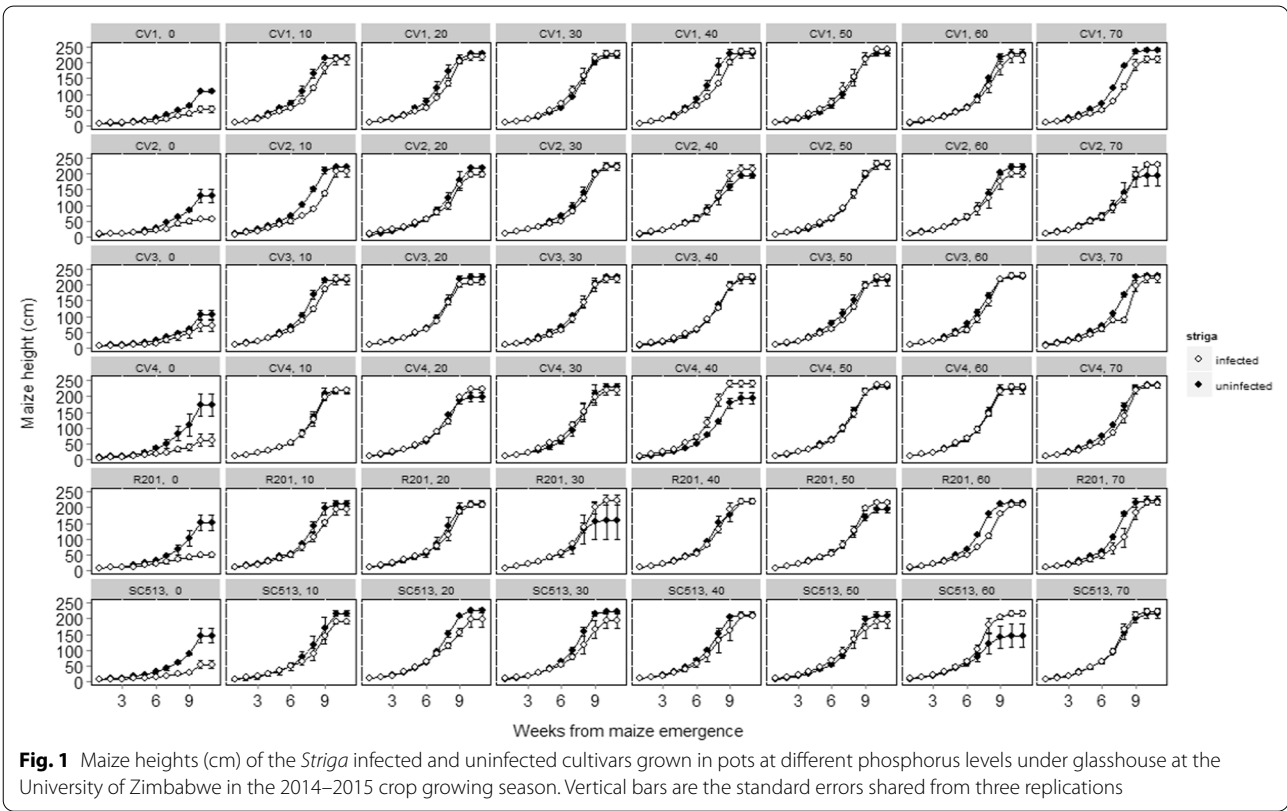


Fig. 1 Maize heights (cm) of the *Striga* infected and uninfected cultivars grown in pots at different phosphorus levels under glasshouse at the University of Zimbabwe in the 2014–2015 crop growing season. Vertical bars are the standard errors shared from three replications

variable across all the six maize varieties and P additions greatly reduced *Striga* counts (Fig. 2). By adding at least 10 kg ha⁻¹ of P, *Striga* counts were tremendously reduced (Fig. 2). During the fifth and sixth week, varietal effects on *Striga* counts were not significant ($P > 0.05$; Additional file 1: Table S3), but thereafter, significant ($P < 0.001$; Additional file 1: Table S3) effects of the varieties on *Striga* counts were observed. Highest *Striga* counts were observed in CV6 while CV4 and CV5 had the lowest counts (Additional file 1: Fig. S1). However, variety-P interaction did not have any significant ($P > 0.05$; Additional file 1: Table S3) influence on *Striga* counts.

Chlorophyll content

Highly significant ($P < 0.001$; Table 1) differences in P levels were recorded from the chlorophyll content of plants. Also significant ($P < 0.05$; Table 1) differences were observed from the *Striga*-variety and *Striga*-P interactions. However, *Striga* and variety effects did not manage to have any significance ($P > 0.05$; Table 1) influence on the chlorophyll content together with the interaction of the three factors. Chlorophyll content varied across all P levels within the varieties (Table 1) and addition of P managed to increase the chlorophyll

content and reduced the deleterious effects of *Striga* on chlorophyll.

Biomass production

Results obtained showed that maize varieties, *Striga*, and P levels significantly ($P < 0.05$; Table 1) influenced leaf biomass. There was a significant ($P < 0.01$; Table 1) interaction between *Striga* and P on leaf biomass produced. However, the interaction of *Striga* and variety as well as *Striga* and variety and P was not significant ($P > 0.005$; Table 1). Additional file 1: Figure S2 shows that addition of at least 30 kg ha⁻¹ P improved the leaf biomass of maize by reducing the injurious effects of *Striga*.

Maize varieties and P levels significantly ($P < 0.001$; Table 1) influenced the cob biomass. In addition, *Striga* variety and *Striga* P interaction was significant ($P < 0.01$; Table 1). Cultivar effects on cob biomass were variable, with CV4 producing the highest biomass (Additional file 1: Fig. S3). Also observed was that the addition of at least 20 kg ha⁻¹ P improved the cob biomass by reducing the effects of *Striga*. However, *Striga* effects alone did not significantly ($P > 0.05$; Table 1) reduce cob biomass and the interaction of the three factors was not significant ($P > 0.05$; Table 1).

From the results obtained P levels and maize varieties significantly ($P < 0.01$; Table 1) influenced stem biomass.

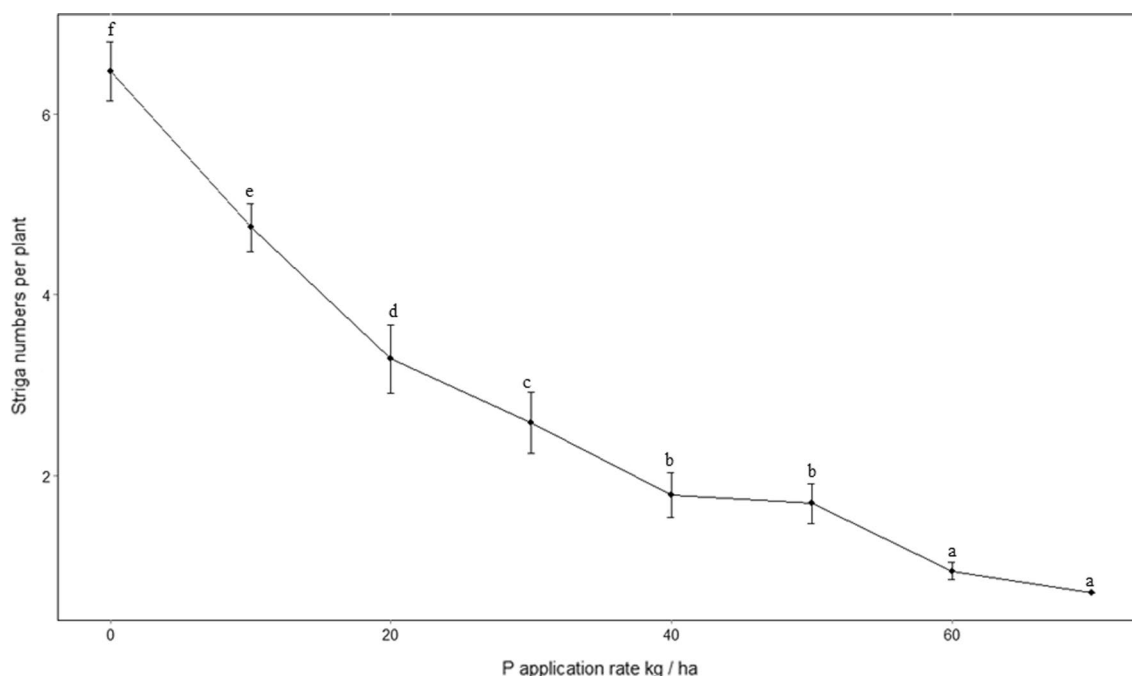


Fig. 2 *S. asiatica* counts in response to phosphorus addition in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines are the standard errors shared from three replications

Striga effects, its interaction with maize varieties and P levels did not significantly ($P > 0.05$; Table 1) influence the stem biomass. Stem biomass increased with increase in P and the effects of varieties on stem biomass were variable.

Effects of maize varieties and P levels were highly significant ($P < 0.001$; Table 1) on stem biomass. *Striga* effects on stem biomass were not significant ($P > 0.05$; Table 1). The interaction of *Striga* with variety and/or P and the interaction of the three factors did not significantly ($P > 0.05$; Table 1) influence the stem biomass produced. Additions of P brought about an increase in shoot biomass. Also, varieties performed differently in terms of shoot biomass (Table 1).

There was a significant ($P < 0.001$; Table 1) influence of the *Striga* effects and P levels on the root biomass of maize. However, the varieties and all the interactions from the three factors were not significant ($P > 0.05$; Table 1). The results on root biomass showed that infected plants produce more root biomass than uninfected plants.

Different maize varieties and P levels significantly ($P < 0.001$; Table 1) influenced the maize total plant biomass. The interactions of *Striga* and variety as well as that of *Striga* and P had significant ($P < 0.01$; Table 1) effects on the total maize plant biomass. P addition has been observed to have a resultant increase in total plant

biomass by reducing the effects of *Striga* on total plant biomass. However, variety-P interaction and the three-factor interaction was not significant ($P > 0.05$; Table 1). Also to have no significant ($P > 0.05$; Table 1) influence were the *Striga* effects which failed to reduce the total biomass.

Haustorial root attachments

Significant ($P < 0.05$; Additional file 1: Table S3) differences on haustorial root attachments were recorded from the effects of varieties and P levels. However, the P-variety interaction was not significant ($P > 0.05$; Additional file 1: Table S3). Varieties had variable effects on attachments and P addition resulted in a reduction in the number of attachments. By adding at least 10 kg ha^{-1} of P, the attachments were greatly reduced (Fig. 3). In addition, CV5 supported the least attachments while CV6 had the most attachments (Additional file 1: Fig. S4).

Root: shoot ratio

Striga, variety together with their interaction and the three-factor interaction did not have a significant ($P > 0.05$; Table 1) influence on the root: shoot. However, the interaction of *Striga* and P on root to shoot ratio was significant ($P < 0.001$; Table 1). Infected plants resulted in high root volume compared to non-infected plants and

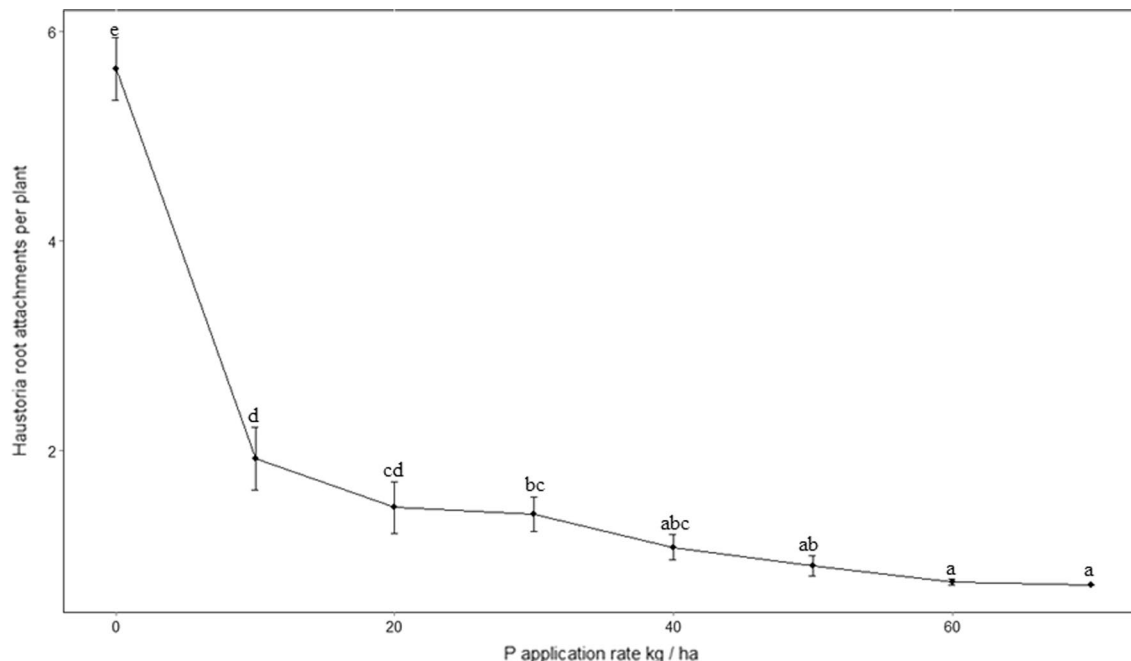


Fig. 3 *Striga* haustorial attachments on roots of six maize hybrids as influenced by phosphorus application in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines represent standard errors pooled from three replications

the effect of P on the root: shoot is shown in Additional file 1: Fig. S7.

Grain yield

From the results, the effects of different varieties and P levels were observed to influence significantly ($P < 0.001$; Table 1) the grain yield of maize. Also to have high significant effects ($P < 0.01$; Table 1) were the interactions of *Striga* and variety as well as *Striga* and P. Different varieties influenced independently the grain yield, with CV4 producing the highest yield under infestation (Additional file 1: Fig. S5). It was observed that *Striga* deleterious effects on grain yield could be reduced by adding at least 20 kg ha⁻¹ P as shown in (Additional file 1: Fig. S6). Nonetheless, the interaction from the three factors together with variety and P were not significant ($P > 0.05$; Table 1). Also, *Striga* effects were not significantly ($P > 0.05$; Table 1) strong enough too to reduce the grain yield.

Agar gel laboratory experiment

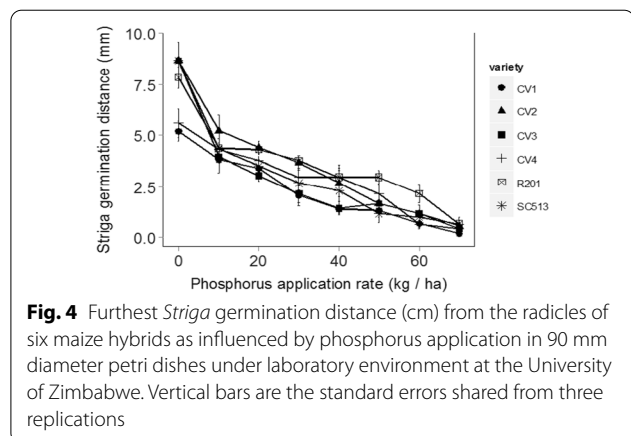
The main effects of variety and P were significant ($P < 0.01$; Table 2) on the *Striga* maximum germination distance. There was a highly significant ($P < 0.01$; Table 2) interaction between variety and P. Varieties had variable effects on *S. asiatica* seed germination distance and P addition resulted in a reduction in the germination distance (Fig. 4). From the results, the effects of different varieties and P levels were observed to influence significantly ($P < 0.001$; Table 2) the germination percentage of *Striga*. Also to have high significant ($P < 0.001$; Table 2) influence were the interactions of variety and P. Different varieties influenced independently the germination percentage of *Striga* and P additions managed to reduce the percentage germination regardless of infection as shown in Fig. 5. Where P was not added, the least germination percentage was obtained from CV4 followed by CV1 and CV5.

Table 2 Mean squares of *S. asiatica* germination distance and percentage

Source of variation	DF ²	Germination percentage	Germination distance
P-level	7	3010.74***	90.5249***
Variety	5	125.11***	5.4664***
P-level x variety	35	47.36***	1.3184**
Residual	96	14.09	0.6098
Total	143	172.80	5.36
Coefficient of variation (%)	22		26.4

, * indicates significant at $P \leq 0.01$ and $P \leq 0.001$ respectively

² DF: degrees of freedom

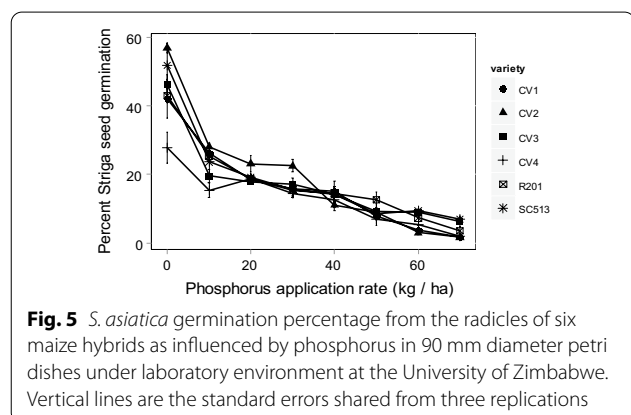


Discussion

Glasshouse experiment

The sole purpose of this experiment was to determine the effects of maize genotypes as well as P addition on the growth of maize, *Striga asiatica* counts and attachment, plant biomass and grain yield of maize. The experiment also had some interests in developing a *S. asiatica* management program based on P that could be made available to farmers in *S. asiatica* prone areas and particularly the smallholder sector.

P addition had beneficial effects on the growth of maize cultivars as compared to treatments where P was not applied on both *S. asiatica* infected and non-infected plants. A dose of between 10 and 20 kg ha⁻¹ was enough to improve the height of maize plants across all varieties. In the absence of P, CV6, CV5 and CV4 proved to succumb to *S. asiatica* attack than cultivars CV1, CV2 and CV3, which seemed to possess some desirable level of tolerance to *S. asiatica*. Results by Watling and Press (1997) indicated that maize and sorghum under *Striga* attack were of smaller stature compared to non-infected plants. Heights of maize obtained from treatments where P was not applied were lower compared to maize treated with



P and these results are similar to those obtained by Taylor et al. (1996) where *Striga* infected plants were shorter than non-infected plants, indicating the usefulness of P in alleviating *Striga* effects. Height reduction in response to *Striga* parasitism is a clear indication of susceptibility and those varieties which managed to maintain their height where control measure was not put in place are deemed to possess some tolerance to the parasite (Makoko and Sibuga 2003). However, *Striga* effects on maize heights were shown to have been reduced through P application indicating the role that this nutrient could serve as a *Striga* control strategy.

Additions of P proved to be of significance in reducing the number of *S. asiatica* counts as compared to treatments which were not supplied with P. However, the dose of P which justifies this reduction in *S. asiatica* numbers seemed to be variety dependent as well. All the cultivars responded well to 10 kg ha⁻¹ of P application except for CV6 which needed about 40 kg ha⁻¹ to justify *S. asiatica* count reduction. Where P was not applied, it was the cultivar CV5 (*S. asiatica*-resistant check variety, R201) and CV4 which proved to have some degree of tolerance to *S. asiatica* attachment. CV5 has been reported by Chitagu et al. (2014) to possess some level of tolerance to *S. asiatica* which the authors related to avoidance of the host to attachment by the parasite. Where no control method has been used, *Striga* plant counts can be used as a measure of cultivar resistance to attack (Mbogo et al. 2015; Rodenburg et al. 2015). *Striga* numbers in maize cultivars were reported to be correlated to the amounts of germination stimulants produced by roots of host plants, with susceptible cultivars (CV6) having more counts than resistant ones (Rimawu 2012). The results from the present study are in line with those obtained by Mbogo and Osoro (1992) in their P study in sugarcane and Pandey et al. (2015) in maize. These authors reported high *Striga* counts where no P was applied, but the counts decreased with increase in P. In addition, the authors also reported cultivar differences to have effects on *Striga* counts, with variety Co617 having less counts than variety Co421, which the authors related to tolerance and susceptibility, respectively, but they strongly complimented the role of P in *Striga* counts reduction in variety Co42. In a micro dosing study by Jamil et al. (2014) using Diammonium Phosphate (DAP) the authors observed that *S. hermonthica* plant counts reduced greatly as the fertilizer concentration increased in pearl millets. This made the authors to conclude that N and P fertilizer management can alter stimulant production and thus helping alleviating the *Striga* scourge.

Varieties and *Striga* did not differ in their effects on chlorophyll content. However, P levels significantly affected the chlorophyll content and as such, where P was

not applied, the chlorophyll was reduced greatly in *Striga* infected plants than non-infected plants. *Striga* effects however, were counteracted with P additions. Similar findings were also reported by Mauromicale et al. (2008) when they were studying effects of branched broomrape (*O. ramosa*) on tomato photosynthesis and growth. These authors observed that this parasite reduced greatly the chlorophyll content of tomatoes and this brought about significant decrease in photosynthesis which they reported to be a result of parasite damage to the PSII electron transport. Similar findings were also reported by Gurney et al. (2002) who alluded that *Striga* infection in plants reduce the host's chlorophyll content and thus reducing its ability to carry out normal photosynthesis. Xu et al. (2007) observed low chlorophyll content a condition they equated to P-starvation in their study with rice plants, and thus such plants will be limited in their capacity to harvest light and to fix carbon dioxide. This tally with treatments where P was not added. However, additions of P managed to reduce *Striga* effects on chlorophyll content.

Striga asiatica exerted detrimental effects on the leaf biomass of all maize cultivars in treatments where P was not applied. Adding just 10 kg ha⁻¹ of P saw a reduction of *S. asiatica* impacts on leaf biomass. Taylor et al. (1996) also observed similar findings and reported that *Striga* infected plants had lower leaf biomass because of fewer number of fully expanded leaves than the uninfected plants. Under *S. asiatica* infestation, plants produce a small leaf area (Watling and Press 2001) and in conditions of P deficiencies, root-derived SLs are found in the shoots where they inhibit shoot growth and branching (Cardoso et al. 2011; Ćavar et al. 2014; Czarnecki et al. 2013). Smith (2014) later concluded that when plants are infected with *Striga*, they will then favour the development of below-ground parts at the expense of above-ground parts, and this is in line with the results from this study where leaf biomass was reduced in *S. asiatica* infected plants than uninfected plants at zero P.

CV1 seemed to be very sensitive to *S. asiatica* in terms of cob biomass as compared to other cultivars. In the absence of P, *S. asiatica* managed to cause reductions on cultivars' cob biomasses and by adding 20 kg ha⁻¹ P, these effects were quashed. This therefore supports the fact that P addition to *Striga*-infected soils can neutralize *Striga* effects on maize and helps the crop to produce better cobs.

Striga asiatica effects were not felt among all the varieties as well as its interaction with varieties and P levels. Stem biomass is one of the parameters which is known to be reduced significantly under the burden of *Striga*. Failure to cause significant reduction in stem biomass is a sign of tolerance in these cultivars opposing the

mechanisms of stem biomass reduction employed by *S. asiatica* where the parasite act as a stronger sink of photosynthates in susceptible hosts (Gurney et al. 2003). This tolerance is achieved by the ability of cultivars to avert attachment of germinated *Striga*, or by making no provision of the nearby germinated *Striga* to attach to host roots and through incompatibility (incompatible response) (Ejeta 2005), by not supporting the growth of the attached *Striga*, causing abnormal growth (Chitagu et al. 2014). The maize cultivar CV5 has been reported to be tolerant to *S. asiatica* attack by Chitagu et al. (2014). Results from this study are not in line with what has been obtained by Pierce et al. (2003) and Taylor et al. (1996) where *Striga* infected plants suffered much loss of stem biomass than their uninfected controls. Osman et al. (2013) also reported a decrease in maize stem biomass in treatments inoculated with *Striga* as compared to non-inoculated treatments.

Shoot biomass was not affected by *S. asiatica* although cultivar differences as well as P levels had significant effects on shoot biomass. The fact that *S. asiatica* did not have reduction effects on shoot biomass is in contrast with the findings by Umehara (2011) who reported that under P deficiency, SLs are produced and transported to shoots where they will inhibit shoot branching and thus limiting shoot growth at the expense of root growth. In addition, Taylor et al. (1996) reported lower shoot biomass in infected plants than uninfected plants indicating the severity of *Striga* when no control strategy was employed. Jamil et al. (2012) also produced similar findings in sorghum when DAP was used. These authors reported that shoot biomass was not reduced by *S. hermonthica* in treatments where this fertilizer was applied. The fact that *S. asiatica* did not manage to have influence on shoot biomass has been reported by Makoko and Sibuga (2003) who related this to the ability of the varieties to withstand parasitism and that they maybe possessing some genes for resistance to *Striga* attack.

Striga asiatica effects on root biomass have been felt more on infected plants. This is in line with findings by Umehara (2011) who postulated that plants under *Striga* infection produced more root densities than non-infected ones, in order to withstand the parasite pressure and increase its nutrient acquisition (Makoko and Sibuga 2003). Similar findings were reported by Taylor et al. (1996). Results from this study are also in correspondence with those obtained by Osman et al. (2013), where root biomasses of *Striga* infected plants were much more than those from *Striga* free plants in order to maintain a balance between nutrient acquisition and demand by the shoot. Chitagu et al. (2014) documented that *Striga* attack in plants will act as an additional sink of assimilates and also causes hormonal imbalances and as such,

there is a tendency of plants favouring below ground growth at the expense of above ground biomass.

Addition of P managed to reduce the number of *S. asiatica* root attachments as compared to treatments where it was not added across all the varieties. Cultivars responded differently to *S. asiatica* attachment. At zero P, some cultivars proved to support more attachments than others. In addition, response to P addition was cultivar dependent. Some cultivars responded well to 30 kg ha⁻¹ P whilst others needed up to 50 kg ha⁻¹ P to illicit response to *S. asiatica* attachment. *Striga* germination and attachment to host roots is initiated in response to SLs whose production is related to P availability or deficiency (Jamil et al. 2012). Under P deficiency, SLs are synthesized by the host plant to illicit a symbiosis relationship with arbuscular mycorrhizal fungi (AMF) so that the fungi will scavenge for P which will benefit the host plant (Koltai 2014; Yoneyama et al. 2012). Unbeknown to the host is that those same SLs will be exploited by the parasitic weeds which utilizes them to germinate and also establishes an association with the host roots though the association will be a parasitic one (Akiyama and Hayashi 2006). In terms of cultivar differences, Ejeta (2005) reported that susceptible genotypes produce more SLs than resistant ones and as such they suffer more attachments than their resistant counterparts. This is in line with observations from this study where susceptible CV6 supported more attachments than other varieties. Similar findings has been reported by Yoneyama et al. (2010) who observed fewer germinated *S. hermonthica* seeds near sorghum roots a scenario which they related to low SL production in cultivars which they assumed to be resistant to *Striga*.

Striga asiatica did not manage to have detrimental effects on grain yield when compared to their *S. asiatica* uninfected treatments. Cultivars responded differently to reduce *S. asiatica* impacts on grain yield with CV4 producing highest yield than others. Grain yield response increased with P additions compared to treatments with no P. Where no control measure has been put in place, *Striga* managed to reduce grain yield and this has also been reported by Osman et al. (2013) who observed that grain yield of infected controls suffered much damage than uninfected controls. Grain yield is one of the crop growth parameters which is very sensitive to *Striga* attack, but the ability of some maize genotypes to produce more grain yield than others is related to tolerance and resistance to attack by the parasite (Gurney et al. 2003; Rodenburg et al. 2015). These maize genotypes possess the ability to maintain optimum rates of photosynthesis regardless of *S. asiatica* attack and by so doing, they will be able to avert destructive effects of photo-inhibition (Gurney et al. 2002). If this ability of a crop

to produce higher grain yield than others under *Striga* infestation is introgressed into local cultivars with superior grain and yield qualities, it can provide food security measure to farmers in *Striga* endemic areas (Rodenburg et al. 2015). Under the burden of *Striga*, leaves of infected plants have reduced leaf area and also exhibit low carbon gain resulting in reduced photosynthesis due to photo-inhibition (Watling and Press 2001). Discrepancies in yield among the varieties has been reported to be a result of genetic variation among the cultivars making them to respond differently to *Striga* infection (Osman et al. 2013). However, *Striga* effects on grain yield were reduced by P according to this study, since an increase in P came with an increase in yield as compared to no P treatments. This is in congruent with what Opondo et al. (2015) reported in their baseline survey where they indicated that the loss of yield by farmers to *Striga* is a result of low use and application of major nutrients nitrogen and P. Mbogo and Osoro (1992) also reported yield increased in sugarcane susceptible variety Co421, which the authors attributed to P usage. Similar findings were also reported by Magani et al. (2008) who observed increase in cowpea pod weight and yield in response to 20 kg ha⁻¹ P unlike the no P treatments which recorded about 7.9% decrease in cowpea yield when cowpea was infected with *Alectra vogelii*.

P addition had beneficial effects on total plant biomass as compared to treatments where P was not applied on both *S. asiatica* infected and non-infected plants. Total plant biomass increased with increase in P. Cultivar CV4 proved to produce more total plant biomass than other cultivars and CV5 and CV6 were affected most. Watling and Press (1998) indicated that low biomass in sorghum and maize was a result of low photosynthetic capacity of infected plants. The decrease in whole plant biomass was also reported by Pierce et al. (2003) in *Striga* infected treatments which were not treated with nitrogen but an increase in nitrogen supply caused an increase in whole plant biomass. Obilana and Ramaiah (1992) concluded that *Striga* effects in reducing photosynthetic capacity of the host plants contribute significantly to the loss of biomass production and yield by the host. This is in agreement with what was observed in *Striga* infected treatments where P was not applied which produced very small plant biomass.

The root to shoot ratio was higher in *S. asiatica* infected plants than in uninfected plants where P was not applied. Plants under *S. asiatica* burden exhibit unbalanced biomass partitioning and as a result, they will have higher root to shoot ratio than uninfected plants (Hibberd et al. 1996). Similar findings were also reported by Taylor et al. (1996) who observed high root: to shoot ratio in *Striga* infected plants than

uninfected plants. This has been supported by Makoko and Sibuga (2003) who reported that high root to shoot ratio in infected plants than non-infected plants is so because the plants will be trying to maintain the balance in nutrient acquisition and avert possible detrimental effects brought about by the parasite. However, *Striga* effects on root to shoot ratio seems to have been reduced by addition of P in this current study. It was observed that adding P to the crops reduced the gap between infected and uninfected plants and this justifies what impacts P has in reducing *Striga* effects in plants.

Laboratory experiment

The laboratory experiment was meant to determine the effects of different concentrations of P on the germination of *S. asiatica* seed and as such, *Striga* germination percentage was calculated as well as the distance of the furthest germinated *Striga* seed from the host root was recorded. Varietal effects were also observed to have an impact on the germination distance and percentage of *S. asiatica*. The addition of at least 10 kg ha⁻¹ P reduced greatly both the germination distance and percentage. In terms of germination distance, CV4 and CV3 proved to have lower distances of about 1 cm compared to other varieties at 40 kg ha⁻¹ P. Where P was not added, the least germination percentage was obtained from CV4 followed by CV1, CV5 and lastly CV3. The highest percentage was obtained from CV2 and CV6. Highest germination percentages were recorded around the oldest parts of the root radicle and this according to Reda et al. (1994) is an indication of more SLs being produced in this area than towards the root apex. Low *Striga* germination percentage in cultivars is linked to low stimulant production by the host and this gives an indication of cultivar resistance to the parasite Makoko and Sibuga (2003) and in sorghum, varieties that exude stimulants within a distance of 10 mm are deemed to be resistant (Omany et al. 2000). Mbwaga and Massawe (2001) reported similar findings in sorghum where in some varieties, few germinated *Striga* was observed as a result of low germination stimulant production a case the authors linked to resistance. Varieties that are low SL producers reduces the chances of processes that lead to infection to occur and this is seen by reduced number of emerged *Striga* (Rodenburg and Bastiaans 2011). Such characteristics have been observed in varieties CV4, CV1 and CV5. Previously, CV5 has been reported by Chitagu et al. (2014) to tolerate *Striga* attack. CV6 was one of the varieties which supported the highest number of germinated *Striga* seeds and also the furthest germination distance. Rimawu (2012) reported that CV6 supported many *Striga* counts and was deemed

to be a susceptible variety. However, through P additions, the number of germinated *Striga* and the distance from which they germinated were reduced making P addition a concrete solution to *Striga* problems. Studies by Mbogo and Osoro (1992) in sugarcane proved that by adding P to the soil, the number of emerged *Striga* was reduced drastically. This showed that the addition of P reduced *Striga* infection.

Conclusion

It was concluded that the addition of P fertilizer reduced *S. asiatica* attachment and emergence. The addition of P maintained the maize heights, maize biomass, and grain yield of all the maize genotypes under *Striga* infestation. P application reduced the maximum *Striga* seed germination distance and *Striga* seed germination percentage across all maize cultivars. The low *S. asiatica* counts and haustorial root attachments coupled with the resultant high yields could be an attribute of P (at least 40 kg ha⁻¹ application) to a large extent as well as an attribute of cultivar tolerance in controlling *S. asiatica*.

Materials and methods

Experimental site

The research project was carried out at the University of Zimbabwe, Department Crop Science in Harare, under glasshouse and laboratory conditions. The university is located at 17.78 °S, 31.05 °E and 1523 m above sea level with an average annual rainfall of 750–950 mm. Temperature and humidity ranges of 25–30 °C and 50–70% respectively, were maintained throughout the greenhouse experiment.

Glasshouse experiment

Germplasm

In the greenhouse experiment, six maize hybrids were used. Among these hybrids, four of them were developed by IITA for *S. hermonthica* resistance and were also evaluated for *S. asiatica* resistance whilst two were local checks. *S. asiatica* seeds used in the study had been collected from different fields of farmers in Rushinga communal area in Northern Zimbabwe during the 2013/14

cropping season. Table 3 gives a more detailed description of the genotypes used and their codes that were given to them during the course of the project.

Experimental design

The experiment was an 8 × 6 × 2 factorial treatment. Factor one was the P levels (0, 10, 20, 30, 40, 50, 60, 70 kg ha⁻¹), factor two was variety (CV1, CV2, CV3, CV4, CV5, CV6) and factor three was *Striga* (with or without infestation). The P levels were selected to cover the range of optimum, sub-optimal and the maximum doses that are normally used by farmers in Zimbabwe based on soil chemical analysis recommendations. This was laid out in a 4 × 24 α-lattice design with three replications.

Experimental procedure

Sandy soils collected from Henderson Research Station (17° 35" S and 30° 38" E; 1292 m above sea level) and 25 km from Harare, was used in the experiment. These soils pattern majority of *Striga* affected small-holder farmers' field conditions. The P composition of the soil was 2 parts per million (ppm) based on soil samples chemical analysis. A total of 288 black polythene plastic pots measuring 20 cm in diameter and 20 cm in height were filled to three quarters with dry sand soil. The soil in each pot was thoroughly mixed with 1.18 g of ammonium nitrate (34.5% N) across the whole treatment. After fertilizer application, the pots were physically separated into two groups (each with 144 pots), with group one representing the pots that were going to be inoculated with *S. asiatica* while group two being *Striga*-free pots. Within each row, three replications for each level of P were made. Single Super Phosphate (SSP 19% P₂O₅) was used as a source of P and was thoroughly mixed with the soil (Additional file 1: Table S1).

After P treatment, the inoculation process with *Striga* for pots in group one was carried out as follows: eight polythene bags representing eight P levels were set aside for use in mixing the soil with *Striga*. Top 10 cm of the soil from each P level in each pot was removed and mixed with 0.05 g of *S. asiatica* seeds and vigorously

Table 3 Details of plant materials used

Cultivar abbreviation	Name	Genotype name	Source
CV1	12C19024B	(1393/ZDiploBC4-19-4-1-#-3-1-B-1-B*4)-12-BB/IWD-SYN-STR-C3-52-1-BBB/TZLCompIC4S1-37-1-B*6	IITA
CV2	12C19026B	(1393/ZDiploBC4-19-4-1-#-3-1-B-1-B*4)-40-BB/IWD-SYN-STR-C3-50-2-BBB/TZLCompIC4S1-37-1-B*6	IITA
CV3	12C19028B	(1393/ZDiploBC4-19-4-1-#-3-1-B-1-B*4)-43-BB/IWD-SYN-STR-C3-52-1-BBB/TZLCompIC4S1-37-5-B*5	IITA
CV4	12C19030B	(1393/ZDiploBC4-19-4-1-#-3-1-B-1-B*4)-32-1-1/IWD-SYN-STR-C3-50-2-BBB/TZLCompIC4S1-37-1-B*6	IITA
CV5	R201	–	ARDA seeds
CV6	SC 513	–	Seed Co Pvt Ltd

shaken in separate polythene bags of respective levels and thereafter returned to the respective pots. All the pots were then put in greenhouse on the 13th of January 2015 at a spacing of 0.76 m × 0.20 m and labelled for the presence or absence of *Striga*, variety and P level were put on each and every pot to which it belongs. The pots were watered to field capacity and maintained for a week. During this process, temperatures fluctuated between 25 and 39.9 °C and a clean sheet pertaining the arrangement of pots was maintained.

Three kernels of each of the six hybrids were planted 4 cm deep spaced at 3 cm apart and later thinned to one plant per pot. On the 4th week after emergence, another 1.18 g of 34.5% ammonium nitrate (AN) was applied as top dressing to make a total nitrogen supply of 30 kg ha⁻¹ across the whole experiment.

Data collection

Data was collected on maize plant height, leaf, stem, cob, root and total biomass and grain yield. Grain yield was estimated using the measured field weight as cob weight per plot adjusted to 12.5% grain moisture content and 80% shelling percentage using the following formula: $GY = \text{Field weight (kg)} \times 10,000 \text{ m}^2 \times (100 - \text{MOI}) \times \text{shelling \%} / 1000 \text{ (kg)} \times \text{plot area (m}^2) \times (100 - 12.5)\%$, where: GY = Calculated grain yield per ha, MOI = measured grain moisture content at harvest, shelling % = assumed to be 80% for all genotypes. For maize plant biomass respective plant parts were cut and oven dried at 80 °C for 72 h and later weighed to get the dry mass. Chlorophyll content was measured during week 6 using a portable chlorophyll meter (SPAD 502). *Striga* plant counts were recorded from week five up to week nine. Haustorium root attachments were also recorded at the end of the experiment.

Data analysis

Maize and *Striga* data from the glasshouse was subjected to the analysis of variance (ANOVA) at $P < 0.05$ using GenStat Statistical package version 14 (Genstat 2011). The means were separated using Fisher's least significant difference (LSD) test. Graphical analysis and illustrations was done using R-statistics. The following model was used for ANOVA:

$$Y_{ijl(k)} = r_i + r_i(b_k) + s_j + p_l + g_m + s_j g_m + g_m p_l + s_j p_l + s_j g_m p_l + e_{ijl(k)},$$

where $Y_{ijl(k)}$ is the response of the m th genotype and j th *Striga* level and l th P level in the k th block within the i th replication, r_i is the effect the i th replication, $r_i(b_k)$ is the

effect of the k th block nested within the i th replication, s_j , p_l and g_m are the main effects of the *Striga*, P and genotype, respectively, $s_j g_m$, $g_m p_l$ and $s_j p_l$ are the first order interactions and $s_j g_m p_l$ is the second order interaction, and finally $e_{ijl(k)}$ is the pooled error term. The terms $i = 1, 2, 3$; $j = 1, 2$; $k = 1, 2, 3, \dots, 24$; $l = 1, 2, 3, \dots, 8$ and $m = 1, 2, 3, \dots, 6$.

Laboratory experiment

Experimental design and procedure

The experiment was laid as a Complete Randomized Design (CRD) with eight P levels (0, 10, 20, 30, 40, 50, 60, 70 kg ha⁻¹) and six hybrids (CV1, CV2, CV3, CV4, CV5, CV6), two of which were local checks and the experiment had three replicates. The P levels were selected to cover the range of optimum, sub-optimal and the maximum doses that are normally used by farmers in Zimbabwe based on soil chemical analysis recommendations.

Incubation of maize seedlings for germination

Surface sterilization of maize kernels was achieved by immersing them in 1% sodium hypochlorite solution for 30 min (Badar-uz-Zaman et al. 2012). Thereafter seeds were rinsed three times using double distilled water and placed on filter paper in 9 cm diameter Petri dishes wetted with 10 ml of water. From each hybrid, 32 kernels were used and the Petri-dishes were put in glasshouse where temperatures were maintained between 25 and 30 °C. This process was done four days before the completion of conditioning of the *Striga* seed to achieve a better synchrony in terms of the emergence of maize radicle and maximum germination point of the *S. asiatica* seeds.

Agar gel preparation

Bacto agar, and potassium dihydrogen phosphate (KH₂PO₄) were used as a sources of P. In order to correct for potassium, potassium chloride (KCl) was used as an adjustment of potassium (K) so that it was uniform across the experiment. Bacto agar gel, was prepared by mixing 2 g of bacto-agar with 1000 ml of double distilled water and to these, corresponding P and K levels were added. After this, 150 ml of the solution was drawn from the corresponding P and K level and these were centrifuged to ensure that all the components completely dissolved in water. This process was repeated across all the varieties with solutions being prepared according to the P and K levels assuming a plant population of 37,000 plants ha⁻¹. The mixture was placed in an autoclave that achieved 150 °C in 30 min and thereafter, the solution was left to cool enough for use before solidifying.

Assay set up

The process of setting up the assay required swiftness and carefulness in terms of pipetting *Striga* seeds and pouring the agar as well as placement of the maize seeds before the agar solidifies. Conditioned *Striga* seeds were placed in a sterile 40 ml container and thoroughly mixed with 35 ml double distilled water to form an evenly distributed solution. 50 µl of the pre-conditioned *Striga* seeds in solution were pipetted into sterile 90 mm diameter Petri dishes.

When the autoclaved agar gel was warm enough not to kill the *Striga* seeds, it was poured on top of the seeds and in the process, the *Striga* seeds were distributed evenly in the agar as described by Berner et al. (1997) and Reda et al. (1994). Where the seeds failed to distribute evenly, the Petri dishes were gently swirled for even distribution of *Striga*. Just before agar solidified, one germinated maize seed was submerged with the portion containing the radicle facing downwards and pointing right across the Petri dish so that it grew from one end to the other across the Petri dish. When the agar had completely solidified, the Petri dishes were closed and incubated at 27 °C in dark for 5 days before induced *Striga* germination was assessed.

Data collection in agar gel technique

Striga germination assessment was done on day 5 after incubation by focusing a graduated dissecting microscope from the bottom of the Petri dishes. The maximum distance (mm) of germinating *Striga* from the root of maize seedling was used as an index for stimulant production by the host plant and all germinated *Striga* were recorded as described by Berner et al. (1997) and Reda et al. (1994). Germination percentage was expressed as the mean number of germinated *Striga* seeds over total visible *Striga* seeds from the four positions where the dissecting microscope was focused.

Data analysis

Analysis of variance (ANOVA) for the maize hybrids was accomplished through the use of GenStat 14th Edition (Genstat 2011). The means were separated using Fisher's least significant difference (LSD) test. All graphical plotting was achieved through the use of R-statistical package.

Abbreviations

ATP: Adenosine triphosphate; N: Nitrogen; P: Phosphorus; SL: Strigolactone; SSA: Sub-Saharan Africa.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43170-022-00108-4>.

Additional file 1: Table S1. Amounts of single super phosphate and phosphorus used. **Table S2.** Mean squares for maize heights from week 1 to week 11 after crop emergence. **Table S3.** Mean squares for *S. asiatica* attachments and counts. **Figure S1.** *S. asiatica* counts across the six maize genotypes in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines represent standard errors pooled from three replications. **Figure S2.** Leaf biomass (g) of the *Striga* infected and uninfected maize hybrids grown in pots in response to different phosphorus levels under glasshouse environment at the University of Zimbabwe in the 2014–2015 crop growing season. Vertical bars are the standard errors shared from three replications. **Figure S3.** *Striga* infected and uninfected cultivar effects on cob biomass (g) of the maize hybrids grown in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines denotes standard errors shared from three replications. **Figure S4.** Effects of variety on *Striga* haustorial attachments on roots of six maize hybrids grown in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines shows standard errors shared from three replications. **Figure S5.** *Striga* infected and uninfected cultivar effects on grain yield (g) of the maize hybrids grown in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines shows standard errors shared from the three replications. **Figure S6.** Maize grain yield (g) of the *Striga* infected and uninfected maize hybrids grown in pots at different phosphorus levels under glasshouse environment at the University of Zimbabwe in the 2014–2015 crop growing season. Vertical bars are the standard errors shared from three replications. **Figure S7.** Phosphorus effects on root:shoot of the *Striga* infected and uninfected maize hybrids grown in pots under glasshouse conditions at the University of Zimbabwe in the 2014/15 rainfall season. Vertical lines depicts standard errors shared from three replications.

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Author contributions

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Declarations

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Competing interests

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