

Full Length Research Paper

Effectiveness of arbuscular mycorrhizal fungi in protection of maize (*Zea mays* L.) against witchweed (*Striga hermonthica* Del Benth) infestation

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Accepted 04 April, 2012

Striga hermonthica is one of the most important obligate root hemiparasitic weeds of cereals such as maize and sorghum. This study investigated the impact of arbuscular mycorrhizal fungi (AMF) on the *Striga*-maize host interaction and its potential application in management of *Striga* infestation. Two maize varieties: *Striga*-susceptible Nyamilambo and *Striga*-tolerant KSTP94; three species of AMF; *Glomus etunicatum*, *Scutellospora fulgida*, *Gigaspora margarita* and *Striga hermonthica* seeds were used in a greenhouse experiment. Colonization of maize roots was fastest with *Glomus* spp. (51.98%) than other AMF species; however, *Striga* infestation reduced root colonization but conversely increased relative mycorrhizal dependency (*Glomus* spp. = 6.12%) in both maize cultivars. Inoculation of Nyamilambo maize cultivars with AMF reduced *Striga* plant incidence (9.50) and biomass (5.40 g) to significantly lower (4.90 and 3.82 g) levels. Mycorrhizal Nyamilambo and KSTP94 had higher nitrogen (154.01 and 116.88 mg) and phosphorus (25.33 and 31.07 mg) content compared to non-mycorrhizal cultivars (63.37 mg N and 16.81 mg P) in absence and presence of *Striga* infestation. While mycorrhizal maize had increased height (100.50 to 135.20 cm) and biomass (75.70 to 87.54 cm), their *Striga* damage score (4.07) was significantly lower than with non-mycorrhizal maize (8.10). *Glomus* spp. had most significant positive effect compared to both *Gigaspora* and *Scutellospora* spp. In conclusion, AMF inhibits germination and reduces growth of *Striga hermonthica* while enhancing maize host growth and development.

Key words: Arbuscular mycorrhiza, *Striga*, maize growth.

INTRODUCTION

World food security depends on ample supply of three major cereals, namely, maize (*Zea mays*), wheat (*Triticum aestivum*) and rice (*Oriza sativa*) (Ferrari, 1995). In Sub-Saharan Africa, maize is of greatest importance in terms of tonnage, consumption and financial value, while sorghum (*Sorghum bicolor*) follows as a very popular food crop. Production of maize and sorghum in Sub-Saharan Africa and Asia are threatened by *Striga* spp.

weed infestation. The crop loss was estimated to cost US\$ 7 billion per year, directly affecting the welfare and livelihoods of over 10 million people in sub-Saharan Africa (Esilaba and Ransom, 1997). Being a parasitic angiosperm, it attaches to roots of a wide range of tropical cereals and leguminous crops and deprive them of water, soluble mineral salts and metabolites. The host often shows draught symptoms, resulting in total yield loss (Press et al., 1990; Kanampiu and Friesen, 2004). Existing *Striga* control measures include crop rotation, roguing, use of resistant crop varieties, breeding for resistant varieties, biological control, soil fumigation, herbicides, high nitrogen nutrition, synthetic germination

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stimulants and trap cropping (Lagoke et al., 1991; Eplee, 1992; Ejeta et al., 2000; Kabambe et al., 2005). However, these *Striga* control methods have given no conclusive and consistent feasible results for the peasant farmer. They are expensive, labour intensive, may require skilled personnel and, the returns are not immediate on investment, as well as mismatch between technologies and the farmer's socio-economic conditions.

The arbuscular mycorrhizal fungi (Phylum Glomeromycota) are characterized by the production of intracellular absorptive structures (vesicles, arbuscules) and are the most widespread of soil fungi followed by ectomycorrhizal fungi (Koide and Mosse, 2004; Walker and Schüßler, 2004; Schüßler et al., 2001). The external mycelium of arbuscular mycorrhizal fungi (AMF) acts as an extension of host plant roots and serves as a direct link between roots and soil nutrient reserves. Mycorrhizal fungi play a key role in terrestrial ecosystem functioning along with environmental factors such as climate, disturbances, food web interactions, mutualism and ecological history (Wardle and Van der Putten, 2002). In many ecosystems, the major benefits of AMF to symbionts includes enhanced nutrient uptake, increased tolerance to root pathogens, drought resistance, tolerance to aluminium and manganese toxicity and improved soil aggregation and structure (Cardoso and Kuyper, 2006; Xavier and Germida, 1998). Endomycorrhizae formation can also affect water relations, hormonal balance and root colonization by other microorganisms, hence, are important for optimum plant health and development (Gianinazzi and Gianinazzi-Pearson, 1986). In agricultural ecosystems, the composition and vitality of the AMF mycoflora is altered by the introduction of exotic weeds and crops, cultivation and chemicals (Douds et al., 1993). Mutual relations between plant roots and vesicular mycorrhizal fungi have been found to increase plant vigour and consequently crop productivity especially under unfavourable conditions. The mutualistic symbiosis between AMF and crop plants results in increased uptake of phosphorus, potassium, nitrogen, and other nutrients, increased growth at high soil temperatures, better growth in low moisture soils, more efficient water utilization, increased levels of cytokinins, and also increased photosynthetic rates and stomatal conductance (Lendzemo, 2004).

Several species of mycorrhizal fungi have also been shown to increase plant biomass and compensate for damage by *Striga hermonthica*, and their metabolites either stimulate or inhibit weed germination in sorghum, *Sorghum bicolor* (Lendzemo and Kuyper, 2001). This could become a useful biotic interaction for effective and sustainable integrated management of *S. hermonthica* infestation for the resource-poor farming situations. This study investigated the effectiveness of AMF inoculation on growth and development of maize under *S. hermonthica* infestation.

MATERIALS AND METHODS

Sources of biological materials

Pure isolates of AMF, *Glomus etunicatum* Becker and Gerdemann, *Scutellospora fulgida* Walker and Sanders and, *Gigaspora margarita* Beck and Hall were obtained from National Museums of Kenya, Nairobi. Field isolates were trapped from farmers' sorghum field soils at Alupe, Kibos, Lambwe, and Oyugis in Western Kenya, as well as Njoro wheat fields in Rift Valley. Mycorrhizal soils obtained from the farmers' fields were analyzed for their physico-chemical characteristics at Egerton University (data not shown). Two maize cultivars used in this study, *Striga*-tolerant KSTP94 and *Striga*-susceptible Nyamilambo, provided by KARI's Kakamega Research Station.

Preparation of mycorrhizal inoculum

To obtain single spore culture, healthy spores of each isolate were placed on root tips of sorghum seedlings freshly germinated in the greenhouse on autoclaved sand. Before spore placement, the seedling was placed in a 2 cm depression made in sterilized growth medium contained in a 7 cm diameter plastic pot. After spore placement, the depression was gently covered with the growth medium taking care not to dislodge the spore from the root tip. Sorghum plants were watered appropriately and supplied with Hoagland's solution minus phosphorus (Murakoshi et al., 1998). General greenhouse sanitation was maintained to ensure purity of the cultures. Potting medium was dried by stopping watering to the pot. After the host plant had wilted, the dried soil was stored and used as mycorrhizal inoculum for greenhouse pot experiments.

Soil preparation and infestation

In the greenhouse, pots (20 cm diameter, perforated, bottom lined with filter paper) was sterilized and filled with steam sterilized (121°C, 2 h) soil-sand mixture. The physicochemical characteristics of the mixture was determined to be: clay-loamy with 0.6% organic matter, 0.3% total carbon, 0.05% total N, 7 C/N ratio, 12 ppm P-Bray 1 and pH (1:2 H₂O) of 5.4. To disinfect fungal propagules, they were incubated in 2% chloramines T, 200 ppm of streptomycin sulphate, and a trace of Tween-20 for 20 min followed by at least five changes of sterile water. A layer of AMF inoculum, which consisted of a soil mixture (10 g/pouch) containing heavily colonized roots of sorghum, spores and mycelium, was put below maize seed and grown under conducive environment for 3 months. Soil inoculation was simultaneously achieved at transplantation using 10 g of inocula for each AMF isolate (Wacheke et al., 2001). Taking desired infestation as 3000 germinable seeds per pot, weight of *S. hermonthica* seeds required per pot = 3000/% germinability × 5 × 10⁻⁶. This weight was mixed with 10 ml of water to infest one pot. The total amount of *S. hermonthica* seeds and amount of water needed to prepare the inoculum for all pots was measured and mixed in a container, from which a 60 ml syringe was used to draw inoculum to infest 6 cm hole at the centre of each pot, then allowed 7 days conditioning period before planting (Berner et al., 1997).

Striga-mycorrhizal maize interaction experiments

Sixty four 20 cm diameter pots were arranged in randomized complete block design with four replicates. The treatments were two contrasting maize cultivars; uninoculated; inoculated with selected AMF species (*Glomus*, *Scutellospora* and *Gigaspora* spp.); and

Table 1. Effects of arbuscular mycorrhizal fungi (AMF) inoculation on frequency of colonization and relative mycorrhizal dependency (RMD) of two maize cultivars.

Maize cultivars	Treatment	Colonization (%)	RMD (%)
Nyamilambo	<i>Glomus</i> spp.	69.03 ±2.19 ^a	13.53 ±1.26 ^c
	<i>Striga</i> spp. + <i>Glomus</i> spp.	51.98 ±1.98 ^c	16.12 ±0.78 ^a
	<i>Scutellospora</i> spp.	41.66 ±1.10 ^e	13.89 ±0.24 ^{bc}
	<i>Striga</i> spp. + <i>Scutellospora</i> spp.	39.04 ±1.54 ^f	9.55 ±0.61 ^e
	<i>Gigaspora</i> spp.	43.11 ±1.28 ^e	14.20 ±0.51 ^{bc}
	<i>Striga</i> spp. + <i>Gigaspora</i> spp.	38.01 ±1.03 ^f	12.11 ±0.63 ^d
KSTP94	<i>Glomus</i> spp.	54.63 ±3.14 ^b	11.65 ±1.09 ^d
	<i>Striga</i> spp. + <i>Glomus</i> spp.	46.11 ±2.69 ^d	14.50 ±1.16 ^b
	<i>Scutellospora</i> spp.	38.97 ±1.26 ^f	12.03 ±1.29 ^d
	<i>Striga</i> spp. + <i>Scutellospora</i> spp.	34.46 ±1.28 ^g	7.87 ±0.32 ^f
	<i>Gigaspora</i> spp.	31.67 ±1.14 ^h	9.98 ±0.61 ^e
	<i>Striga</i> spp. + <i>Gigaspora</i> spp.	23.06 ±1.04 ⁱ	11.28 ±0.78 ^d

Values are mean ± SE; letter show vertical comparisons among treatments at P = 0.05 probability level; means with the same letter are not significantly different from each other.

and inoculated with *S. hermonthica*. Seeds of *Z. mays* were surface sterilized in hydrogen peroxide (15% v/v) for 3 min, then washed in sterile distilled water. The seeds were then incubated in water agar at 28°C in the dark for 2 days. One pre-germinated seed of each variety was planted in pot filled with 1 kg sterilized sand-soil (1:1) mixture. The plants were watered with tap water for the first 2 weeks, then, 100 ml per pot of Steiner universal nutrient solution. Plants were grown in a glasshouse under a day/night cycle of 12 h each, 30/25°C and 60% relative humidity. The pots were weighed daily and water loss compensated for by top watering. Final harvest was done after 4 months and the roots washed clean with tap water (Berner et al., 1997).

Data collection and analysis

Percentage root mycorrhizal colonization was assessed by gridline intersect method of Giovannetti and Mosse (1980). The mycorrhizal root system was collected, washed, oven-dried, cleared with 10% KOH at 121°C for 10 min, then rinsed, acidified with 5% HCl for 1 min, stained with 0.01% acid Fuschin for 30 min, dissolved in destaining solution (14:1:1, lactic acid:glycerol:water), drained and destained in water overnight. The stained roots were examined microscopically at between 10 and 100X to observe AM fungal structures. Relative mycorrhizal dependency (RMD) of maize was calculated by expressing the difference between shoot dry weight of mycorrhizal plant and the shoot dry weight of non-mycorrhizal plant as a percentage of the shoot dry weight of the mycorrhizal plant (Waceke et al., 2001). Data on mycorrhizal colonization was subjected to GLM procedures for Windows statistical packages. *Striga* count and emergence were recorded in the course of experiment just as height of maize. Biomass of dry shoot and root of maize and *Striga* were measured 80 days after emergence (DAE) by destructive sampling, and recorded after oven-drying at 65°C for 3 days. Maize damage scores (MDS) were done using *Striga* syndrome rating with a scale of 1 to 9, where 1 = healthy plant and, 9 = dead/dying plant. The MDS are based on leaf, stem and ear symptoms (Berner et al., 1997). Shoot phosphorus and nitrogen mineral content of mycorrhizal maize plants were determined using standard analytical methods: colorimetry for nitrogen after Kjeldahl digestion (Soon and Kalra, 1995) and

phosphorus by the molybdenum blue procedure (Boltz and Mellon, 1947).

Data on biomass, maize height, mineral content and emerged *Striga* count were subjected to analysis of variance (ANOVA) with the help of SAS statistical package (SAS System for Windows, 1990) and SPSS v6.1 where applicable (Norusis, 1994). The means of parameters that showed significant differences were separated by Fisher's LSD test at p = 0.05 confidence level. Relationship between *Striga* parameters and AMF types as wells as maize plant development were assessed by regression analysis. All data were checked and transformed appropriately to normalize skewed distributions before statistical analysis.

RESULTS AND DISCUSSION

Mycorrhizal colonization of maize roots

Typical AMF structures, arbuscules, vesicles and hyphae were regularly found in stained roots. Thus, establishment of AMF was effective within roots of both maize cultivars. In absence of *S. hermonthica* infestation, Nyamilambo and KSTP94 had 69.0 and 54.63% mycorrhizal colonization, respectively (Table 1). In the presence of *S. hermonthica* infestation, percent mycorrhizal colonization reduced to 51.98 and 46.11% for Nyamilambo and KSTP cultivars, respectively. In the absence of AMF inoculation, all maize plants remained free of mycorrhizal colonization. Generally, all treatments involving Nyamilambo cultivar had higher percent mycorrhizal colonization than those with KSTP94 cultivar. In both maize cultivars, there was higher root colonization after inoculation with *Glomus* spp., than inoculation with either *Scutellospora* or *Gigaspora* spp. Mycorrhizal fungi differ in their ability to infect and colonize roots. *Glomus* spp. has ability to infect and colonize plant roots faster than *Scutellospora* and *Gigaspora* spp., making it highly

Table 2. Effects of arbuscular mycorrhizal fungi (AMF) inoculation on emergence and total biomass of *Striga* under two maize varieties.

Maize cultivars	Treatment	<i>Striga</i> count	<i>Striga</i> biomass (g)
Nyamilambo	<i>Striga hermonthica</i>	9.50 ±1.36 ^a	5.40 ±0.26 ^a
	<i>Striga</i> spp. + <i>Glomus</i> spp.	4.90 ±0.29 ^c	4.20 ±0.93 ^c
	<i>Striga</i> spp. + <i>Scutellospora</i> spp.	6.13 ±0.55 ^b	3.82 ±0.51 ^{cd}
	<i>Striga</i> spp. + <i>Gigaspora</i> spp.	5.22 ±0.10 ^c	4.81 ±0.24 ^b
KSTP94	<i>Striga</i> spp.	3.50 ±0.34 ^d	2.93 ±0.41 ^e
	<i>Striga</i> spp. + <i>Glomus</i> spp.	1.81 ±0.06 ^e	3.53 ±0.20 ^d
	<i>Striga</i> spp. + <i>Scutellospora</i> spp.	2.93 ±0.32 ^d	3.84 ±0.39 ^{cd}
	<i>Striga</i> spp. + <i>Gigaspora</i> spp.	2.12 ±0.09 ^e	2.71 ±0.23 ^e

Values are mean ± SE; I letter show vertical comparisons among treatments at P = 0.05 probability level; means with the same letter are not significantly different from each other.

competitive (Kurle and Pflieger, 1994). The higher mycorrhizal colonization in *Striga*-susceptible maize could be due to strigolactones exuded by host plant roots and taken up by AMF since strigolactones stimulate fungal metabolism and branching (Parniske, 2008).

The relative mycorrhizal dependency (RMD) varied from 7.87% in KSTP94-*Striga*-*Scutellospora* spp. treatment to 16.12% in Nyamilambo-*Striga*-*Glomus* spp. treatment, among the various treatments (Table 1). Both maize cultivars showed greatest dependency with *Glomus* spp. and least dependency with *Scutellospora* spp. However, the calculated RMD was lower than 50% in all the experiments. In both cultivars, RMD was higher in presence of *Striga* (16.12% with *Glomus* spp.) than in absence of *Striga* (13.53% with *Glomus* spp.). Relative mycorrhizal dependency (RMD) refers to the degree of plant responsiveness to mycorrhizal colonization by producing maximum growth or yield at a given level of soil fertility. RMD is related to morphological and physiological properties of root systems (Diop et al., 2003). The significant differences in mycorrhizal colonization as well as RMD also support the fact that response of plants to AMF inoculation depends on fungus-plant combination (Abbot and Robson, 1985). Successful colonization and functional interaction between host plant and mycobiont are based upon exchange of signaling molecules at different stages of symbiosis development. The role of strigolactones as key signaling compounds in the interaction between plants and soil-borne symbiotic AMF has been recently suggested (Soto et al., 2010). Strigolactones, a novel class of phytohormones involved in the regulation of shoot branching in plants are secreted by plant roots and stimulates presymbiotic growth of AMF.

With the identification of strigolactones as the branching factor, not only its production, exudation into the rhizosphere and perception by the AMF but also its specific action in arbuscular mycorrhizal symbiosis (AMS) can now be explored in more details (Bucher et al., 2009)

Influence of AMF inoculation on *Striga* performance

The *Striga*-susceptible Nyamilambo maize cultivar had 9.50 and 4.90 *Striga* plants per pot in absence and presence of *Glomus* spp., respectively (Table 2). Non-mycorrhizal KSTP94 maize cultivar had 3.50 *Striga* plants per pot compared to 1.81 with *Glomus* spp. The average number of *Striga* plants emerging per pot significantly differed between the maize cultivars. Fewer shoots of *Striga* plants were observed in pots with KSTP94 compared to those with Nyamilambo (Table 2). The emergence of *Striga* shoots was reduced in all mycorrhizal treatments with *Glomus* spp. being the most significant. Inoculation with AMF reduced *Striga* biomass, especially in treatments with Nyamilambo cultivar than those with KSTP94 cultivars. Nyamilambo cultivar colonized with *Glomus* spp. significantly reduced *Striga* biomass from 5.40 to 4.20 g. The *Striga* biomass significantly differed between the maize cultivars and less biomass was observed in treatments with KSTP94 compared to those with Nyamilambo maize cultivars. The non-significant effects of *Gigaspora* spp. in *Striga*-infested maize cultivars could be due to its low percent colonization.

The ability of AMF to reduce *Striga* count can be explained in three ways: (i) The formation of metabolites, especially strigolactones that are responsible for the induction of *Striga* germination is down regulated upon mycorrhizal colonization; (ii) Plant metabolites, such as cyclohexenones which arise through carotenoid degradation, that are up-regulated upon mycorrhizal colonization inhibit *Striga* germination and; (iii) Mycorrhizal colonization induces mycorrhizosphere effects that negatively impact on *Striga* germination (Lendzemo et al., 2007). There are further roles of AMF that affect the performance of *Striga*. The observation that *Striga* incidence and biomass is reduced in mycorrhizal maize, lends support to rhizosphere changes as a mechanism by which *Striga* damage could be

Table 3. Effects of arbuscular mycorrhizal fungi (AMF) inoculation on nitrogen and phosphorus shoot content under *Striga hermonthica* infestation.

Maize cultivar	Treatment	Nitrogen (mg)	Phosphorus (mg)
Nyamilambo	Without any additive	63.37 ±1.69 ^e	16.81 ±0.61 ^d
	<i>Striga</i> spp.	58.41 ±2.85 ^e	10.37 ±0.28 ^e
	<i>Glomus</i> spp.	154.01 ±6.09 ^a	25.33 ±0.94 ^a
	<i>Striga</i> + <i>Glomus</i> spp.	115.22 ±4.88 ^b	22.08 ±0.71 ^b
	<i>Scutellospora</i> spp.	110.80 ±3.32 ^{bc}	22.16 ±0.28 ^b
	<i>Striga</i> + <i>Scutellospora</i> spp.	104.28 ±3.45 ^c	19.31 ±0.69 ^c
	<i>Gigaspora</i> spp.	96.47 ±2.83 ^d	21.45 ±0.23 ^b
	<i>Striga</i> + <i>Gigaspora</i> spp.	93.75 ±3.09 ^d	19.60 ±0.76 ^c
KSTP94	Without any additive	64.19 ±1.95 ^e	16.81 ±0.28 ^f
	<i>Striga</i> spp.	61.46 ±1.50 ^e	11.42 ±0.41 ^g
	<i>Glomus</i> spp.	116.88 ±4.11 ^a	31.07 ±0.33 ^a
	<i>Striga</i> + <i>Glomus</i> spp.	110.64 ±3.28 ^b	23.35 ±0.50 ^b
	<i>Scutellospora</i> spp.	101.05 ±2.75 ^c	21.11 ±0.19 ^c
	<i>Striga</i> + <i>Scutellospora</i> spp.	98.26 ±2.13 ^c	20.32 ±0.69 ^c
	<i>Gigaspora</i> spp.	84.31 ±1.99 ^d	18.94 ±0.31 ^{de}
	<i>Striga</i> + <i>Gigaspora</i> spp.	83.72 ±2.87 ^d	18.52 ±0.22 ^e

Values are mean ± SE; letter show vertical comparisons among treatments at P < 0.05 probability level; means with the same letter are not significantly different from each other.

reduced. Upon colonization by AMF, the quality and quantity of root exudates substantially change. Marschner et al. (1997) observed that mycorrhizal colonization simplified the composition of the rhizosphere soil solution. In this study, both a direct simplification of the root exudate composition and a simplification due to changes in the rhizosphere community composition with its specific metabolites could have occurred. Such community-wide changes may also affect the germination of *Striga* seeds. The observed decline in *Striga* in mycorrhizal maize could be attributed to increased nitrogen availability (Mumera and Below, 1993). According to Swift (2001), mycorrhizal fungi exercise a greater benefit when soil phosphorus levels are at or below 50 ppm (50 mg/kg). Other studies have also reported that fertilisers that are high in phosphorus or nitrogen reduce AMF colonisation (Azcón et al., 2003; Xu et al., 2000).

Sood (2003) also showed that plant growth-promoting rhizobacteria prefer mycorrhizal over non-mycorrhizal roots, which feed back to germination of *Striga* seeds. It has also been observed that *Fusarium solani* inhibited *S. hermonthica* seed germination in *Striga*-infested farmlands by 100% due to presence of extracellular metabolites in the fungal filtrate which most likely inhibits

ethylene action rather than its synthesis (Bethlenfalvai, 1993).

Influence of AMF inoculation on mineral status of maize

In absence of *Striga* infestation, colonization with *Glomus* spp. increased nitrogen content in *Striga*-susceptible Nyamilambo from 63.37/100 to 154.01 mg/100 g and from 64.19/100 to 116.88 mg/100 g in *Striga*-tolerant KSTP94 maize cultivars (Table 3). In presence of *Striga* infestation, mycorrhizal maize of both cultivars had higher nitrogen content above controls. Similarly, mycorrhization with *Glomus* spp. increased phosphorus content in both Nyamilambo and KSTP94 maize cultivars from 16.81/100 and 16.81 mg/100 g to 25.33/100 and 31.07 mg/100 g, respectively. In general, all AMF species studied increased nitrogen and phosphorus content in both maize cultivars in absence and presence of *Striga* infestation. Earlier studies by Bethlenfalvai (1993) have similarly shown that species and strains of AMF differ in their effectiveness in increasing nutrient uptake and plant growth. The function of extra- and intra-radical forms of AMF hyphae could also explain differences in phosphorus

Table 4. Effects of arbuscular mycorrhizal fungi (AMF) inoculation on growth parameters of Nyamilambo and KSTP94 maize cultivars under *Striga hermonthica* infestation.

Maize cultivar	Treatment	Maize height (cm)	DSW (g)	DRW (g)	Syndrome rating
Nyamilambo	Without any additive	100.50 ±2.09 ^d	75.70 ±3.76 ^d	17.84 ±0.61 ^f	1.73 ±0.71 ^{9h}
	+ <i>Striga</i> spp.	81.30 ±1.83 ^f	53.24 ±4.10 ⁱ	15.41 ±0.78 ⁱ	8.10 ±0.42 ^a
	+ <i>Glomus</i> spp.	135.20 ±3.01 ^a	87.54 ±5.35 ^a	22.51 ±1.28 ^a	1.30 ±0.09 ^h
	+ <i>Striga</i> + <i>Glomus</i> spp.	114.50 ±2.62 ^b	77.78 ±3.14 ^c	18.66 ±1.26 ^{de}	4.07 ±0.11 ^f
	+ <i>Scutellospora</i> spp.	107.89 ±2.16 ^c	78.33 ±3.27 ^c	18.61 ±1.35 ^{de}	1.78 ±0.13 ^g
	+ <i>Striga</i> + <i>Scutellospora</i> spp.	96.01 ±1.29 ^e	72.13 ±3.45 ^e	16.96 ±1.03 ^g	5.98 ±0.29 ^c
	+ <i>Gigaspora</i> spp.	111.23 ±2.19 ^{bc}	80.76 ±4.13 ^b	19.94 ±1.77 ^c	1.95 ±0.41 ^g
	+ <i>Striga</i> + <i>Gigaspora</i> spp.	102.50 ±1.98 ^d	74.23 ±4.57 ^d	16.33 ±1.62 ^h	6.67 ±0.22 ^b
KSTP94	Without any additive	74.75 ±1.12 ^g	66.13 ±3.32 ^g	15.73 ±1.53 ⁱ	1.65 ±0.20 ^{9h}
	+ <i>Striga</i> spp.	61.00 ±1.09 ^j	61.03 ±2.85 ^h	13.57 ±0.21 ^k	5.89 ±0.71 ^{cd}
	+ <i>Glomus</i> spp.	83.00 ±2.19 ^f	74.85 ±4.03 ^d	20.42 ±1.99 ^b	1.23 ±0.12 ^h
	+ <i>Striga</i> + <i>Glomus</i> spp.	71.00 ±1.16 ^h	71.38 ±3.55 ^e	18.21 ±0.24 ^{ef}	5.07 ±0.87 ^e
	+ <i>Scutellospora</i> spp.	80.00 ±2.08 ^f	72.24 ±3.95 ^l	18.70 ±1.37 ^d	3.67 ±0.28 ^f
	+ <i>Striga</i> + <i>Scutellospora</i> spp.	76.50 ±1.18 ^g	66.24 ±3.17 ^g	14.33 ±1.15 ^j	5.53 ±0.51 ^d
	+ <i>Gigaspora</i> spp.	75.66 ±1.14 ^g	69.88 ±3.79 ^f	17.03 ±0.75 ^g	4.11 ±0.64 ^f
	+ <i>Striga</i> + <i>Gigaspora</i> spp.	64.50 ±0.88 ⁱ	68.79 ±3.45 ^f	15.48 ±0.24 ⁱ	5.70 ±0.95 ^{cd}

Values are mean ± SE; letter show vertical comparisons among treatments at P = 0.05 probability level; means with the same are not significantly different from each other. Key: DSW = dry shoot weight and DRW = dry root weight.

phosphorus acquisition among the AMF isolates. Hence, the status of the extra-radical mycelium development in the soil appears to be a major determinant of the efficiency of AMF to phosphorus uptake (Rakshit and Bhadoria, 2009). Similar results have been found on soybean cultivars indicating that phosphorus uptake by mycorrhizal plants fluctuate with fungal isolates and genetic variability within cultivars (Diop et al., 2003).

The nitrogen and phosphorus transfer to the maize plants may also be as a consequence of the fungal demand for the nutrients, with both host plant and fungus evolving transporters to take advantage of localized increases in nutrients.

Influence of AMF inoculation on maize growth

The AMF inoculation had significant positive effect on height of both Nyamilambo and KSTP94 maize cultivars in presence and absence of *Striga* infestation (Table 4). *Glomus* spp. increased height of Nyamilambo maize cultivar from 100.50 to 135.20 and 114.50 cm in absence and presence of *Striga*, respectively. Similarly, in absence of *Striga* infestation, KSTP94 maize cultivar increased in height from 74.75 to 83.00 cm with *Glomus* spp. Analysis of variance showed that both maize shoot and root biomass were positively affected by maize cultivar, *Striga*, and mycorrhiza and the interaction among these

factors. In absence of *Striga*, *Glomus* spp. increased shoot biomass of Nyamilambo (75.70 g) and KSTP94 (66.13 g) maize cultivars to 87.54 and 74.85 g, respectively. The dry shoot biomass of both mycorrhizal Nyamilambo and KSTP94 maize cultivars were higher with all the AMF species used. The AMF effectively cancelled out damage by *S. hermonthica* in both cultivars but the tolerant cultivar had significant gain in shoot biomass compared to its control. The dry root biomass of Nyamilambo maize cultivar (17.84 g) was significantly reduced (15.41 g) by *Striga* infestation in absence of mycorrhizal fungi (Table 4). But *Glomus*-colonized Nyamilambo cultivar had increased dry root biomass of 22.51 and

18.66 g in absence and presence of *Striga* infestation. The other mycorrhizal fungal isolates, *Scutellospora* and *Gigaspora* spp. did not improve dry root biomass as much. Based on *Striga* syndrome rating scale, AMF colonization significantly reduced *Striga* damage score on Nyamilambo cultivar from 8.10 to 4.07 with *Glomus* spp, 5.98 with *Scutellospora* spp. and 6.67 with *Gigaspora* spp. With KSTP94 cultivar, reduction in *Striga* damage score was not significantly different from control. In absence of *Striga* infestation, *Glomus* spp. reduced *Striga* damage score from 1.73 and 1.65 to 1.30 and 1.23, with Nyamilambo and KSTP94 maize cultivars, respectively.

The observed differences among treatments with *Striga*-susceptible Nyamilambo and *Striga*-tolerant KSTP94 maize cultivars (Table 4) is an indication that the overall significant effect of treatment obtained for growth parameters were largely attributed to

the presence or absence of AMF or *S. hermonthica*. The ability of *Glomus* spp. to significantly improve maize shoot dry biomasses (Table 4) confirms previous reports on the ability of AMF to enhance plant growth. AMF might have enhanced growth of untreated and *Striga* infected plants through enhanced nutrient uptake and synthesis of plant growth promoting hormones, in particular, auxins, cytokinins and gibberellins (Allen et al., 1982). Improved nutrient uptake results from increased absorptive surface of the root system by AMF external mycelia. The fungi might have in addition, improved water uptake from the growth medium, which results indirectly from improved plant nutritional status (Harley and Smith, 1983), increased cytokinin levels and/or increased number of vascular bundles (Allen et al., 1982). The differences in efficacy of AMF isolates to alter maize growth parameters might be further explained by differences in their effectiveness to colonize maize and their ability to grow in the soil and enhance nutrient uptake. *Glomus* spp. was the most effective in promoting maize growth, since high root colonization reflects high degree of AMF effectiveness. The ability of AMF to increase nutrient uptake is related to their ability to form extensive and well distributed hyphae in soil and throughout the developing root system. Additionally, the maize-AMF compatibility, mycorrhizal dependency of maize, as well as fungal inoculum density might have played a significant role in influencing improved maize growth parameters (Abbott and Robson, 1985).

Increased nitrogen and phosphorus uptake could also subsequently lead to increased plant height and biomass and reduced *Striga* syndrome rating, leading to increased productivity. It is evident that AMF could play a role within the *S. hermonthica* cereal pathosystem. This is in line with the observations by Lenzemo and Kuyper (2001) who found out that AMF could increase sorghum output and cancel out damage by *S. hermonthica*. Gworgwor and Weber (2003) observed that AMF do not colonize *S. hermonthica* roots and have the potential to reduce or

compensate for damage caused by *S. hermonthica* infestation especially in sorghum varieties that are mycorrhiza-responsive. The highly significant difference in heights of the maize cultivars could be due to the inherent differences in the maize genotypes and not due to AMF inoculants since KSTP94 is a relatively shorter variety than Nyamilambo. Increased dry root biomass of mycorrhizal plants is often due to an increase in the proportion of lignified and suberized higher order roots due to secondary thickening than an increase in root biomass (Rajapakse and Miller, 1992).

The non-significant effects of *Scutellospora* and *Gigaspora* spp. on maize could be due to their low percent colonization and relative mycorrhizal dependency of maize.

Conclusion

Result of this study indicated that the colonization of maize roots was fastest with *Glomus* spp. than other AMF species. *Striga* infestation reduced root colonization but conversely increased relative mycorrhizal dependency in both maize cultivars. Inoculation of Nyamilambo maize cultivars with AMF reduced *Striga* plant incidence and biomass to significantly lower levels. Mycorrhizal Nyamilambo and KSTP94 had higher nitrogen and phosphorus content compared to non-mycorrhizal cultivars in absence and presence of *Striga* infestation. While mycorrhizal maize had increased height and biomass, their *Striga* damage score was significantly lower than with non-mycorrhizal maize. The extent of influence of AMF depends on maize variety as well as on fungal species and strains used. *Glomus* spp. had most significant positive effect compared to both *Gigaspora* and *Scutellospora* spp. In conclusion, AMF reduces *Striga* growth while enhancing maize host growth and development. All these results are indicative of the effectiveness of AMF in protecting *Striga*-susceptible maize against damage by *Striga* infestation. Hence, mycorrhizal association can be used as a promising strategy to develop tools for *Striga* control.

ACKNOWLEDGEMENTS

The authors highly appreciate Egerton University and German Academic Exchange Service (DAAD) for financial support to carry out this study and Kenya Agricultural Research Institute (KARI), Kibos Field Station where pot experiments were carried out.

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