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Soil Microbes as Bioherbicides: An Eco-friendly Approach to Control Striga

Urgesa Tsega Tulu

Ethiopian Institute of Agricultural Research, National Agricultural Biotechnology Research Center, P.O.Box 249, Holeta, Ethiopia
***Corresponding author:** urgesatsega@gmail.com

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ABSTRACT

Striga, also called witch weed, is a notorious obligate root hemiparasitic weed of global food security crops such as sorghum, maize, millet and upland rice causing considerable yield loss in Sub Saharan Africa. Several Striga control measures have been developed which include cultural, chemical and resistance breeding. However, many of these methods are either not practically successful or are not economically feasible for low-income farmers. Furthermore, the negative effects of agrichemicals on the environment have attracted scientist to look for an alternative weed management strategy. The use of microorganisms naturally occurring in the soil as biological control agents offer an alternative approach to control the parasitic weeds. Soil is the natural home of numerous forms of beneficial microorganism playing vital role in maintaining the dynamic equilibrium. In recent time, soil born microbes, primarily bacteria and fungi, become the most effective Striga management strategy that targets Striga seed bank in the soil. Hence, this review presents a comprehensive and new approach on the roles of soil microbes in fight against Striga.

Key words: Biological control, Hemiparasite, Seed bank, Soil born microbes.

INTRODUCTION

Striga, also commonly called 'Witch weed', are important root parasites of many cereal and legume crops. It is one of the greatest biological constraints to food production in arid and semi-arid regions of Sub-Saharan Africa (SSA) where sorghum is widely grown (Spallek *et al*., 2013). The genus Striga is under the family Orobanchaceae that contains the highest number of parasitic species (Atera *et al*., 2011). Approximately, more than 30 Striga species have been described and most parasitize cereals including sorghum, pearl millet, finger millet, upland rice and maize grown in most semi-arid and tropical regions of the world (Adagba *et al*., 2002; Atera *et al*., 2011; Spallek *et al*., 2013). Complex host-parasite interactions, production of large number of seeds with prolonged viability (about 800,000 seeds per plant which can remain viable in the soil for up to 20 years) and special germination requirements make Striga the most problematic weed (Mourik, 2007: Atera *et al*., 2011; Teka, 2014).

Available Striga control methods include cultural and mechanical, chemical, resistance breeding and biological control (Teka, 2014; Sibhatu, 2016) and genetic engineering and/or mutation breeding (Pixley *et al*., 2019). These strategies help to improve soil fertility or directly target the parasite by chemical or mechanical means and include the use of resistant varieties as well as cultural measures (Teka, 2014). Though these approaches have helped in reducing the impact of this parasitic weed, they could not effectively address the problem as intended (Kountche *et al*., 2019). Hence, these limitations triggered weed scientist to look for an alternative and eco-friendly approach to control Striga and such methods rely on the use of soil microorganisms.

Origin and Distribution of Striga

Striga originated along a region between Ethiopia and Sudan (Atera *et al*., 2011). This parasite weed is generally native to SSA but has been observed in more than 40 countries (Ejeta, 2007). Out of more than 30 species of Striga described, nine species are found outside Africa and three species: S. curvilflora, S. multiflora and S. parviflora are present in the Australian continent (Berner *et al*., 1995; Spallek *et al*., 2013).

S. hermonthica is widely spread in semi-arid areas and is found in northern tropical Africa, from West Africa (Senegal) to Eastern Africa (Ethiopia, Uganda and Kenya), and the Democratic Republic of Congo, and extends from the western Arabian region and southwards into Angola, Namibia, Madagascar and Tanzania (Parker and Riches 1993; Atera *et al*., 2011). Nigeria, Sudan, Ethiopia, Mali and Burkina Faso are heavily affected counties in Africa (Sibhatu, 2016).

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Striga asiatica is the most widely distributed and is found throughout African tropical parts from portions of southern (including Madagascar), central, and western Africa and Australia (Cochrane and Press, 1997). It is also native to Asia including the Philippines, Cambodia, Indonesia, China, Malaysia, Thailand, Vietnam, Mauritius, India and the Arabian Peninsula. S. asiatica has been introduced to the United States. S. gesnerioides is endemic to Africa, Arabia and Asia and it has been introduced to the United States (Mohamed *et al*., 2007).

Economic Importance of Striga

Among Striga species described, five Striga species, S. hermonthica, Striga asiatica, S. gesnerioides Striga aspera Striga forbesi, are currently of economic importance, with Striga hermonthica causing the most serious damage to Sub-Saharan cereal production (Parker, 2009). The most devastating Striga species to staple crops in Sub SSA are S. hermonthica, S. asiatica, and S. gesnerioides. (Spallek *et al*., 2013; Teka, 2014). Most Striga species parasitize grass species, but S. gesnerioides has evolved the capacity to parasitize dicotyledonous plants (Spallek *et al*, 2013).

S. hermonthica is particularly harmful to sorghum, maize and millet, but it is also increasingly being found in sugarcane and rice fields (Atera *et al*., 2011). Depending on Striga seed density, soil fertility, rainfall distribution, variety grown and degree of Striga infestation, the parasitic weeds damage ranges from 20-80% of staple food crops in the semi-arid tropics of Africa and Asia. The situation in Sudan is even worse, where yield losses in cereal crops heavily infested by S. hermonthica may reach up to 100% yield loss (Ejeta, 2007; Atera *et al*., 2011).

The annual crop losses due to Striga are estimated at US$ 7 billion in SSA and particularly in Ethiopia, Mali and Nigeria, it is estimated at US$75 million, US$87million and US$1.2 billion, respectively (AATF, 2011). Yield losses due to Striga can reach up to 100 percent in susceptible cultivars under a high infestation level and when compounded by drought conditions (Haussmann *et al*., 2000).

The parasitic life cycle of Striga

Striga species are annual plants completing most of their life cycle underground. The life cycle of Striga can be divided into three critical stages: germination, haustorium development and establishment of parasitism and its maintenance until seeds are set (Spallek *et al*., 2013).

Striga seed germination is elicited when ripened seeds are preconditioned by exposure to warm moist conditions for several days, in a process known as conditioning or preconditioning, followed by exogenous chemical signals produced by host roots (strigolactones) and some non-hosts (germination stimulant) (Ejeta and Butler, 1993; Babiker 2007). After germination the radicle elongates towards the root of the host, develops an organ of attachment, the haustorium, that helps to penetrates into the host vascular tissue and establish parasitism. This follows the deprivation of water, mineral nutrients and carbohydrates of host plant, causing drought stress and wilting (Berner *et al*., 1997; Musselman, 1980).

Conditioning, germination, parasitic contact (attachment) and penetration are mediated by elegant systems of chemical communication between host and parasite (Sato *et al*., 2003). After several weeks of growth, the parasite emerges above the soil surface and starts to flower and produce seeds (Kroschel, 2002; Rich and Ejeta, 2007).

Role of Soil Microbes in Striga Management

Soil microbes constitute a dynamic component of soil that carry out many beneficial functions in the soil system (Toor and Adnan, 2020). Plants and microbes are interacting in the soil in various ways. For example, fungi and bacteria have beneficial effects in agriculture including nitrogen fixation, mineralization, pesticide decomposition, and production of growth promoters, antibiotic production and biological weed control (Manoharachary *et al*., 2002; Kremer, 2005; Rodriguez *et al*., 2019).

Furthermore, the limitations of chemical herbicides encouraged researchers to look for alternative systems of weed control (Boyette *et al*., 1991). Biological control is considered as a potential cost effective, safe and environmentally beneficial alternative as a means of reducing weed populations in crops (Charudattan, 2001). Beneficial microorganisms used as bio-control agents and with potential of enhancing plant growth and health include bacteria belonging to the genera Pseudomonas, Burkholderia, Bacillus; fungi belonging to the genera Trichoderma, Gliocladium and nonpathogenic Fussarium oxysporum (Raaijmakers *et al*., 2009). Majority of microbes used as bioherbicides are fungal pathogens, though there are increasing number of bacterial strains being explored and developed as bio-control of weed as well (Bailey and Falk 2011).

Among bacteria species used as potential biological control of weed, Pseudomonas fluorescens and Xanthomonas campestris have been widely investigated for their use as bioherbicides (Babalola *et al*., 2007; Harding and Raizada, 2015). For example, a virulent strain of Xanthomonas campestris was shown to control common cocklebur (Xanthium strumarium L.) which is an important weed in soybean, cotton and peanut production (Boyette and Hoagland, 2013). In contrast to Xanthomonas ssp. not all Pseudomonas ssp. are phytopathogens. Pseudomonas chlororaphis and P. fluorescens strains have been also used as biocontrol agents, while several strains of Pseudomonas aeruginosa and Pseudomonas. stutzeri show strong plant growth-promoting activities (Shen *et al*. 2013). Several P. putida strains were also used to control velvetleaf and S. hermonthica, P. fluorescens strains to control S. hermonthica, broomrape and wild radish (Stubbs and Kennedy, 2012). Furthermore, strains belonging to the genera Burkholderia, Aeromonas, Chryseomonas, Agrobacterium and Vibrio spp., were tested for potential use as bioherbicides (Li and Kremer, 2006; Babalola *et al*., 2007).

The Mycorrhizal Fungi

Mycorrhizal is mutually beneficial symbiotic association between particular soil inhabiting fungi (called mycorrhizal fungi) and roots of higher plants (Sieverding, 1991) for their role in supplying important nutrients and increasing health (Bonfante and Anca, 2009; Parihar *et al*., 2020). Arbuscular mycorrhizal (AM) fungi have gained significance as a result of their role in soil fertility, nutrient uptake, biocontrol of plant diseases and weed management (Jordan *et al*., 2000; Manoharachary *et al*., 2002).

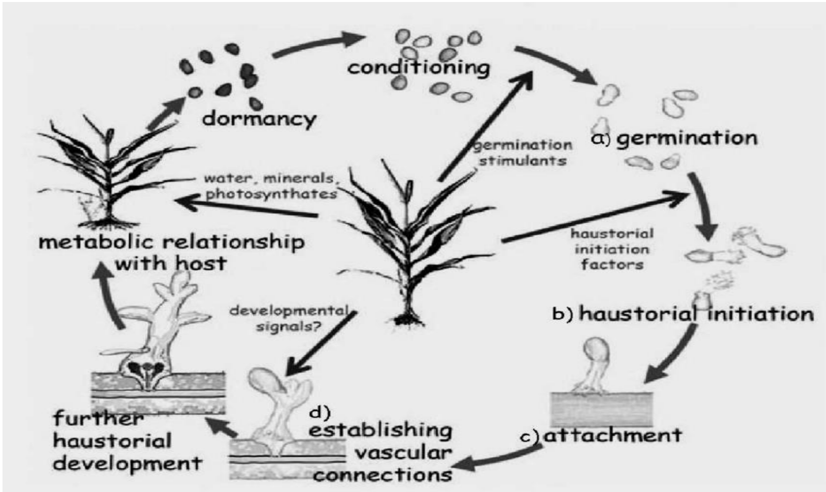

Fig. 1: Generalized *Striga* life cycle (Rich and Ejeta, 2007)

Fungal have received great attention as biocontrol agents against pest (Benitez *et al*., 2004). The fungal pathogen, Fusarium oxysporum f.sp are reported to play significant role in Striga bio-control in sorghum, particularly when the method is integrated with other Striga control strategies. Most importantly, this fungus has capability to destroy Striga prior to its penetration to the root of the sorghum and compete with host (Rebeka *et al*. 2013). Pot and field experiment showed that AM fungi inhibited Striga seed germination, reduced the number of Striga seedlings attaching and emerging, preventing attachment to host, delayed the emergence time of Striga and enhanced the performance of the host plant (Lendzemo *et al*, 2006).

Moreover, the genus Trichoderma comprises a great number of free-living fungi inhabiting in soil and plant root ecosystems, capable to decompose various substrates, promote plant grwoth and with antimicrobial properties (Harman *et al*., 2004; Celar and Valic 2005) and that act as biological control agents. Out of the fungi utilized as biocontrol, majority of them were Trichoderma strains (Benítez *et al*., 2004). Tichoderma strains reported to have potential of promoting plant growth and enhance defense mechanisms in plant (Monte, 2001). Aqueous extracts of Trichoderma viride and Trichoderma. harzianum inoculated with seed resulted in significant reduction in Striga germination with T. harzianum 97% germination inhibition (Hassan *et al*., 2013; Hassan *et al*., 2019).

The Rhizobacteria

Rhizosphere is the narrow region of soil that is directly influenced by living roots, and the primary site of interaction between plants and microorganism (Raaijmakers *et al*., 2009). The microbe-plant interaction in the rhizosphere can be beneficial, neutral or deleterious on the basis of their effects on plant growth (Glick, 1995). The potential of using bioherbicides to control weeds such as S. hermonthica has received increasing attention (Charudattan, 2001; Gafar *et al*., 2016) for the purposes briefly discussed below.

Germination Induction

Bacterial effect on Striga seed could be either germination induction, in the absence of host plant or inhibition (Berner *et al*., 1999; Ahonsi *et al*., 2002). For example, bacterial strains of P. syringae pv. glycinea induced early germination of Striga seeds, pseudal germination, and reduced subsequent establishment of Striga. The main growth regulators hormones acting as germination promoters produced by P. syringae are indoleacetic acid (IAA) and ethylene (Babalola *et al*., 2007). P. syringae strains stimulated more germination of S. hermonthica seeds as compared to the synthetic ethylene gas (Berner *et al*., 2003).

This bacterium can be highly applicable in inducing pseudal germination of Striga seeds but its use in agriculture is limited because of its pathogenesis. A procedure of testing bacterial stimulation of Striga germination through the action of ethylene in the absence of host plant has been also developed (Babiker *et al*., 1993; Berner *et al*., 1999)

Furthermore, some other bacteria produce growth-regulators like auxins, cytokinins and gibberellins which are necessary in priming Striga seeds prior to germination thus reducing the preconditioning period and promotes germination (Hoagland and Williams 2003; Joel *et al*., 2007). Although little is known about the mechanism of action of IAA prior to Striga seed germination, the hormone is critical in establishing the orientation of xylem differentiation between host and parasite (Hoagland and Williams 2003; Delavault *et al*., 2017).

Germination Inhibition

Some microorganisms colonizing the root surface have growth inhibition effect on parasitic weeds like Striga. Soil bacteria including Pseudomonas sp., Enterobacter sakazakii and Klebsiella oxytoca have been evaluated for their potential to inhibit S. hermonthica seed germination (Babaloala and Odhiambo, 2008). Other studies have also shown that P. fluorescens and Pseudomonas putida isolates significantly inhibit germination of S. hermonthica seeds (Babalola and Glick, 2012; Babalola *et al*., 2007). Furthermore, an in vitro evaluation of the effect of Azospirillum cells on Striga seed in the presence of GR24 demonstrated unsuppressed germination but shortened radicles. It has also been suggested that phytohormones such as IAA or lipophilic compounds released by the bacteria caused suppressed germination, radical growth and cell differentiation (Miché *et al*., 2000).

Modes of Action of Bioherbicides

Microorganisms act as bioherbicides through promoting plant growth, enhancing defense mechanisms and antibiosis, mycoparasitism, competition, phosphate solubilization, nitrogen fixation and production of phytohormones such as indole acetic acid and (IAA) and cytokinins (Tripura *et al*., 2005; Idris *et al*., 2007; Vinale *et al*., 2008). Many Pseudomonas strains are characterized as deleterious rhizobacteria. These are group non-parasitic pathogens which excrete exopolysaccharides and allelochemicals in the form of phytotoxins, phytohormones, cyanide, siderophores and that can negatively affect the metabolism of plants (Li and Kremer, 2006). Soil bacteria or endophytes may produce host-specific phytotoxic secondary metabolites. For example, bacterial pathogens like Agrobacterium spp. and Pseudomonas savastanoi pv. savastanoi produce auxins, which cause tumor and gall formation, and Enterobacter sp. strain produces IAA and seedlings of lettuce and radish inoculated with this strain showed reduced biomass production (Carvalho *et al*., 2007).

Phosphate Solubilization

Soil fertility and Striga infestation is reported to correlate negatively (Larsson, 2012). Nitrogen and phosphorous deficiency when compounded with drought or water stress found to exacerbate severity of Striga damage to hosts plants (Adagba *et al*., 2002). Microbial community increases soil fertility by mineralization and solublization of insoluble phosphates in soil (Kang *et al*., 2002; Chen *et al*., 2006). Certain bacteria and fungi are known to have capacity to mobilize insoluble phosphates in the soil and play significant role in availing phosphorous (P) to plants (Zhang *et al*., 2020). Group of fungi under the genera Aspergillus and Penicillium and bacterial general including Pseudomonas, Bacillus, Rhizobium, Enterobacter are known to be among the potential phosphate solubilizers (Whitelaw, 2000; Patil *et al*., 2012; Saxena *et al*., 2016).

Nitrogen Fixation

Nitrogen (N2) is the most abundant and essential element for all forms of life (Frank *et al*., 2003; Egamberdieva and Kucharova, 2008). Plant growth promoting free living microorganisms play a vital role in fixing nitrogen from the unavailable gaseous form in the atmosphere to forms those plants can use (Vitousek *et al*., 2002; Shridhar, 2012). Rhizobium, Azospirillum, Azotobacter, Enterobacter species are group of N- fixing bacteria used for improving plant growth and development by synthesizing gibberellins (GA), auxin, cytokinins, indole-3 acetic acid (IAA) hormones (Affourtit *et al*., 2001; Gonzalez *et al*., 2005; Lee *et al*., 2006; Emtiazi *et al*., 2007).

Due to the negative correlation between severity of infestation and soil fertility, Nitrogen is reported to be an essential element for suppressing Striga infection on host plants (Parker and Riches, 1993; Lendzemo, 2004). Evaluation of the effects of nitrogen on Striga infestation resulted in delayed germination, reduced radicle elongation, decreased stimulant production and decreased seeds response to the germination stimulant by host plants (Rajn *et al*., 1990; Singh *et al*., 1991).

Production of Phytotoxin and other Secondary Metabolites

Secondary metabolites produced by microbes have comparably shorter life spans and are biodegradable than conventional halogenated chemical structures. Rhizobacteria for biological control of weeds likely metabolize phytotoxins at root surfaces where they're readily absorbed by the plant. It's not known how widespread phytotoxin production is among weed biocontrol rhizobacteria, but evidence is accumulating showing that phytotoxins play a causal role in deleterious activity (Kao-Kniffin *et al*., 2013; Shirdashtzadeh, 2014). Metabolites such as phaseolotoxin, tabtoxin, and coronatine were produced by Pseudomonas sp. and found to exhibit good herbicidal activity (Saxena, 2014). Within the rhizosphere of plants, the metabolites produced are often can be phytotoxic at beyond physiologic concentrations and these include the indole acetic acid (IAA), auxins and hydrogen cyanide. Other herbicidal compounds prevent the germination of seeds through inhibition or arrestment (Kao-Kniffin *et al*., 2013).

Many rhizobacterial genera are known to produce IAA and auxin-related compounds. The best examples are the genera of Acetobacter, Agrobacterium, Arthobacter, Azospirillum, Azotobacter, Bacillus, Klebsiella, Pseudomonas and Xanthomonas (Idris *et al*., 2007; Spaepen *et al*., 2008; Ali *et al*., 2010; Spaepen and Vanderleyden, 2011; Saha *et al*., 2012).

In addition, Cyanide was identified as secondary metabolite produced by many rhizosphere bacteria and having growth inhibition effects to suppress weeds (Kremer and Souissi, 2001). It is produced by a wide range of plants, bacteria and algae and it is proved to be accontable for growth reduction of weeds (Lakshmi *et al*., 2015). The production of this toxic chemical could be a common trait of many Rhizosphere Pseudomonas spp. Cyanide is a potential inhibitor of enzymes involved in various plant metabolic processes (Reetha *et al.*, 2014). Other herbicidal compounds prevent the germination of seeds through inhibition or arrestment (Kao-Kniffin *et al*., 2013).

Some rhizobacteria are also capable to intracellularly produce many antibiotics and secrete through cell membranes into the surrounding vicinity. Some of these are toxic compounds that inhibit seed germination and growth in various weed plants. Example of these group of bacteria include Streptomyces saganonensis, Streptomyces hygroscopicus; Streptomyces viridochromogenes; Streptomyces hygroscopicus; Streptomyces acidiscabies; Pseudomonas syringae pv. Tagetis (Hoerlein, 1994; Heisey, 1990; Mallik, 2001; Lee *et al*., 2003; Singh *et al*., 2003; Lydon *et al*., 2011; Kao-Kniffin *et al.*, 2013).

Conclusion

In conclusion, Striga is a major biotic constraint causing a serious threat to production of cereal crops including sorghum, maize, finger millet, pearl millet and up land rice in sub-Saharan Africa. Though many control options available, none of them could effectively manage Striga parasitism. However, biological control using soil microbes, particularly fungi and bacteria, is getting momentum and offering an alternative approach to control Striga infestation. Since Striga causes considerable damage before it emerges above the ground, its control measures has to target its seed bank in the soil. This can be achieved with naturally occurring soil microbes capable of depleting its seed bank. Microbes play a great role in Striga management by inhibiting Striga seed germination, improving soil fertility, secreting phytotoxic and secondary metabolites and promoting host plant growth and development.

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