Biology and Physiology of Witchweed (Striga spp.): A Review

¹ Awadallah B. Dafaallah

¹ Department of Crop Protection, Faculty of Agricultural Sciences, University of Gezira, Sudan *E-mail address: awadna@hotmail.com; awadna@uofg.edu.sd (Corresponding author)

Abstract: Striga species (Striga spp.), obligate parasitic weeds belong to the family Orobanchaceae, are the major and most persistent biotic constrain to production of the cereal and legume crops mostly grown in the sub-Saharan Africa, Middle East and Asia. The objective of this article was to review and evaluate the past and current status of knowledge of the biology and physiology of the witchweed (Striga spp.) and to identifying gaps in this knowledge. Available literature on Striga life cycle was carefully reviewed in details. The result of this reviewing showed that the basis and background studies on Striga spp life cycle made some significant advances in the understanding of the biology and physiology of Striga spp. such as after- ripening, germination, haustorial initiation, attachment, penetration and establishment of parasite. However, continued effort is needed in the laboratory and in the field researches to gain a better understanding of factors influencing the different stages of the parasite life cycle so as to develop integrated Striga management strategies that will lead to effective, economically feasible and environmentally sound management of the parasite.

Keywords: Biology; Haustorium; Physiology; Striga; Witchweed

1. INTRODUCTION

Striga species (Striga spp.), belong to the family Orobanchaceae, are obligate parasitic weeds. The name Striga has been derived from the Latin words "strait or witch" which, presumably because plants infested by the parasite display stunted growth and an overall drought-like phenotype long before Striga plants appear [1]. The main Striga species parasitizing cereals include Striga hermonthica (Del.) Benth. and S. asiatica (L.) Kuntze. [2]. They attack sorghum (Sorghum bicolor [L.] Moench), millet (Pennisetum glaucum [L.] R. Br.), maize (Zea mays L.), rice (Oryza sativa L.) and sugarcane (Saccharum officinarum L.) [3]. While, the main Striga species parasitizing other crops include Striga gesnerioides (Willd) Vatke that attacks primarily dicotyledonous species cowpea [Vigna unguiculata (L.) Walp], tobacco [Nicotiana tabacum L.] and sweet potato (Ipomoea batatas L.) [3].

Striga is completely dependent on its host for survival, and its life cycle is closely linked with that of the host plant [4]. *Striga* produces numerous minute seeds which remain viable in the soil for many years and do not germinate unless host plant root grows very near to them. Once connected, the parasite withdraws water, mineral nutrients, carbohydrates, aminoacides and possibly hormones from its host. As a consequence, the parasite causes stunted shoot growth, leaf chlorosis and reduced photosynthetic capacity of the host. Once established, it is therefore very difficult to eradicate and in some areas where infestation is heavy there may be a total crop failure in some years [5].

The occurrence of economically important *Striga* species is reported in more than 40 countries, especially in Africa as well as Asia [6]. In Africa, the occurrence of the *Striga* spp. has been reported in 25 countries and the most severely

affected being located in sub-Saharan Africa [7]. The impact of Striga is complicated further by its predilection for attacking crops already under moisture and nutrient stress, the conditions that prevail throughout the semi-arid tropics. Severity of Striga attack is modulated by the size of the seed bank, existence of strain, variants and races with different virulence, the reaction of the host cultivar, and the environment [2]. It is estimated that over 50 million hectares of arable farmland under cultivation with cereals and legumes in sub Saharan Africa are infested with Striga spp. [8, 9]. In many of these regions the parasite has reached epidemic proportions presenting a desperate situation in subsistence agriculture. The weed causes annual losses of yield estimated to be in excess of US\$10 billion. The Striga spp. affect the welfare and livelihoods of over 100 million people in Africa1 and hence impacted on the sub region's economy [8, 10].

Several Striga control measures, including cultural, physical, biological control, chemical, host plant resistance and genetically modified crops have been developed. However, the huge seed production, prolonged viability of the seeds, breeding behavior that maintains enormous genetic variability, ability to parasitize a broad host range and the subterranean nature of the early stages of parasitism make control of the parasite by a single method difficult if not impossible [11, 12]. Today there is no single control method that can effectively solve the problem. The integrated Striga management based on destroying incipient populations, confining core infestations, minimizing reproduction of the parasite, devitalizing the parasite seed bank and reducing crop damage is recommended as the best method in controlling Striga [2, 13]. The integrated Striga management depends mainly on studying the biology and physiology, which influenced by many factors such as climatic changes.

Many climatic changes were occurred in the last 20 years of the past century and also in the first 20 years in 21Th century. These changes were more obvious in climatic factors such as temperature, rainfall and wind. Agricultural systems are expected to face an increasing risk of erosion, runoff, soil degradation and alternating high temperatures and rainfall. Alternating high temperatures and rainfall may assist breaking of dormancy in the parasite whilst severe winds greatly aid dispersal and dissemination of the Striga seeds. In general, production of the germination stimulants, haustorial initiation factors, attachments, seed production and dispersal were expected to increase as temperature rises like other biological processes. So that the Striga epidemic is going to increase under the new climate. The parasitic weed is likely going to become a more serious biological threat and constrain to the crop production [14].

Therefore, the objective of this article was to review and evaluate the past and current status of knowledge of the biology and physiology of the witchweed (*Striga* spp.) and to identifying gaps in this knowledge so as to propose research strategies that will lead to effective, economically feasible and environmentally sound management of the parasite.

2. STRIGA GENERAL

Parasitic flowering plants have been recognized since the first century A.D where Pliny the elder wrote in his remarkable book "Natural History" that some plants cannot grow in the earth, but take root in other plants, because they have no abode of their own and consequently they live in that of others [15]. Almost all crop species are potential hosts of parasitic plants, but outbreaks of severe incidence are usually limited to certain parasite species. The evolutionary strategy of exchanging self-atrophy to rely on host plants (parasitism) may seem strange, however it has evolved evolutionary success of several plant species. Plant parasitism has risen at least 12 times independently, generating more than 4000 parasitic dicotyledonous plant species. Although some parasitic plants are still photosynthetically active (hemiparasitic), others are not, and depend entirely on ahost (holoparasitic) [16].

2.1. Origin of the name Striga

There are a number of possible origins of the name *Striga*. It could have been derived from Latin words meaning variously "strait, horshy", lean or witch'. *Striga* often refer to the word "witch", presumably because plants infested by the parasite display stunted growth and an overall drought-like phenotype long before *Striga* plants appear [1].

2.2. Taxonomy and identification

Parasitic plants are found in about 17 families. However, only five of them include agricultural pests [17]. In among these families, Orobanchaceae received considerable attention, because of its relevance in world agriculture. This family is of interest in evolutionary studies, and because it encompasses closely related parasites with vast differences in their host requirements [18].

Among all flowering plant families only Orobanchaceae in comprised of various genera ranging from completely eutrophic to specialized obligate parasites. The genus *Striga* (witchweed) belongs to the Orobanchaceae family (ex Scrophulariaceae) and are obligate root hemiparasitic plants [19]. This genus currently comprises of 42 species worldwide, which are parasitic by nature, of which at least 11 are known to attack crops. In compensation for its rudimentary root system, *Striga* penetrates the roots of other plants and diverts essential nutrients for its growth and development [1].

Identification of the main *Striga* species is not difficult. However, there can be a problem in separating *S. hermonthica.* and *S. aspera* (Wild) Benth. in Africa. On the other hand, identification of the white-flowered species; *S. asiatica* (L.) Kuntze, *S. densiflora* (Benth.). and *S. angustifolia* (Don.) Saldanha, that commonly attack cereals in India, is confusing because they look similar at first [20]. The main *Striga* species parasitizing cereals include: *S. hermonthica, S. aspera, S. densiflora, S. passargei* Engle, *S. asiatica, S. angustifolia, S. forbesii* Benth, *S. laterica* Vatke, *S. multiflora* Benth, *S. parviflora* Benth and *S. curviflora* Benth. [2].

2.3. Description of the plant

Striga plants are herbaceous. The genus is characterized by opposite leaves, irregular bright colored flowers with corolla divided into a tube spreading lobes, herbaceous habitat, small seeds, and parasitism. *S. hermonthica* has bright to dark green leaves, erect and usually branched stems grow up to 77 cm or more. Stems are stout and quadrangular. Leaves are linear, lanceolate or lanceolate with actuate or acuminate tips, 1-3 in. long, very scabrous. The inflorescence possesses 6-10 open flowers that are 1-2 cm across. The flowers are pink, red, white, purple or yellow. The spike has occasionally more than 10 open flowers and the corolla normally drops a few days after fertilization [21, 22].

The number of capsules per plant may be on the average 42-110. The number of seeds per capsule varies from about 700 in *S. hermonthica* to 800 in S. asiatica and 1800 in S. *Striga*. In a single growing season, each *Striga* plant is capable of producing up to 76628-minute dust like seeds which are easily dispersible by wind, crop seeds, water, people and may stay in the soil for up to 20 years [21, 22]. Seeds of *S. hermonthica* are extremely small, about 0.15 x 0.31 mm, 0.38 mm diameter. and weighing about 3-15 μ g. Seeds have a characteristic surface pattern of ridges [21]. The embryo is highly reduced, lacking cotyledons and root cap. It is enclosed in an endosperm, which function as storage tissue [23].

2.4. Distribution

The economically important root-parasitic weeds have their center of origin in the old world. Africa was described as the place of origin of the agriculturally important genera of the family Orobanchaceae [8]. The species are found in most regions south of the Sahara except in areas, where precipitation is too high or temperatures are too low for development [24]. The parasite prevails from sea-level up to 2,000 meters above sea level and in almost all soil types [13]. *Striga* was thought to have originated in the vast tropical areas of the savannah between the Simien Mountains of Ethiopia and the Nuba hills in Sudan [25]. This region has also been reported to be the center of origin of domesticated sorghum (*Sorghum bicolor* L.).

Striga spp. are sensitive to waterlogging and are more prevalent in poor soils than on fertile soils. Surveys conducted in 2007 indicated that the parasite is spreading rapidly [2]. Economically important *Striga* species have broad distribution setting conditions for genetically structured populations based on geographic locations [26]. *Striga hermonthica* is mainly distributed throughout the semi-arid area of northern tropical Africa, but extends into south west Arabia and South tropical Africa; including Angola, Namibia and Malagasy. It is less widespread than *S. asiatica* in southern tropical Africa [21]. Reference [27] believed that the species originated from Sudan, northeast Africa on the basis of its common occurrence there on wild grass hosts.

2.5. Host range

Striga hermonthica is the most widespread and most damaging among Striga species. The range of crops attacked by S. hermonthica includes all major tropical cereals. Occurrence is also reported on some temperate crops, including teff (*Eragrotis tef* (Zuccagni) Trotter) and barley (*Hordeum vulgare* L.) [21]. The main cereal crops parasitized by S. hermonthica are sorghum, millet, maize, rice and sugarcane (Saccharum officinarum L.) [3].

Striga aspera has been recorded on most of the major cereal crops, i.e. maize, sorghum and sugarcane. Host crops attacked by S. asiatica are virtually the same as those for S. hermonthica, sorghum and maize being the most widely damaged especially in India and southern Africa [21]. S. gesnerioides has an extensive host range that includes species of the family Fabaceae. Acanthaceae. Redaliaceae Convolvulaceace, Euphorbiaceae, and Solanaceae. However, this parasitic weed is only of economic significance in cowpea (Vigna unguiculata (L.) Walpe.) in west Africa and revealed the sporadic occurrence on tobacco (Nicotiana tabacum L.) in south Africa and rarely on sweet potato (Ipomoea batatas (L.) Lam.) in south Africa [7].

2.6. Damage and economic importance

Striga spp. are the major and most persistent biotic constrain to production of the cereal crops, mostly grown in the hottest and driest marginal regions of sub-Saharan Africa, Middle East, and large parts of Asia [7]. Considerable losses in growth and yield of many food crops are caused by *Striga* species. Most of the damage on hosts is affected during the subterranean stage of development of the parasite [28]. The damage by the subterranean phase of the parasites makes its control less rewarding and less captivating to farmers [2]. The *Striga spp*. are one of the problems of low-input drought affected rain-fed farming systems where sorghum, millet and cowpea are the main crops [29].

The occurrence of economically important Striga species is reported in more than 40 countries, especially in east and West Africa as well as Asia [6]. In Africa, the occurrence of the Striga spp. has been reported in 25 countries and the most severely affected being located in sub-Saharan Africa [7]. The area infested by Striga in sub-Saharan Africa has been estimated to be over 50 million ha of the arable farmland under cereals [16]. The area infested by the parasite in West Africa is estimated to be about 17.2 million ha, covering about 64% of the total area of the sorghum and millet [30]. Losses in grain yield due to Striga infestation vary from 5 to 75%, according to the host species, the variety grown, climatic conditions, infestation level and nature of the soil [31]. The overall loss in grain production amounts to 4.1 million tons. The reduction in grain yield varies from 70 to 90 % for improved cultivars and 40 to 50 % for the local ones [32]. The annual yield loss has been estimated to exceed US\$10 billion [33]. Farmers have reported losses between 20% and 80%, and are eventually forced to abandon highly infested fields [25]. There are indications that these figures are much higher today, as the rate of spread to previously un-infested areas has been rapid and extensive [34]. Moreover, the Striga epidemic is going to increase and the parasite is likely going to become a more serious threat to crop production [14]. The parasite also causes indirect losses comprising changes in production strategies, land abandonment and in extreme cases human migrations in response to heavy infestations [35].

3. CO- ORDINATION OF HOST AND PARASITE LIFE CYCLE

Striga's complete dependence upon a host for survival requires close coordination of its life cycle with that of the host. *Striga* seeds are minute with limited stored food reserves and *Striga* germilings survive only for about three days unless attachment to a host root is achieved [36]. It is not surprising, therefore, that germination of *Striga* seeds is under control of the host through chemical signals exuded from its roots, so that germination usually occurs only when a plant root is available. Subsequent to germination, haustorium initiation occurs in response to a second host-derived signal. The haustorium penetrates the cortex, guided

possibly by the internal chemistry of the host root and establishes connection with the vascular system. Following connection with the host xylem, the plumular end comes out of the seed coat and further development occurs.

The life cycle of the parasite is divided into a non-parasitic or vegetative phase and a parasitic mode (Figure. 1). The non-parasitic mode includes the processes of after-ripening, conditioning and germination. The parasitic mode starts with the initiation of a haustorium from the vegetative to the parasitic mode of life [37].

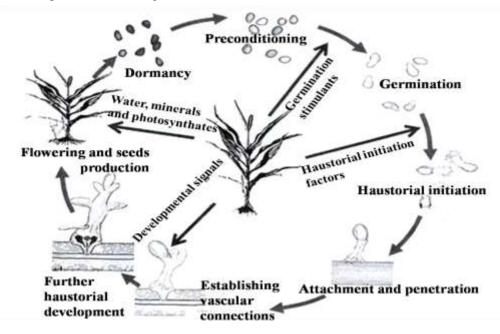


Figure. 1. The Striga life cycle showing intricate association between the parasite, its hosts, and the environment, after [8].

3.1. Non parasitic mode (Vegetative phase)

3.1.1. After- ripening

The seeds of parasitic weeds are tiny relative to those of free-living angiosperms. Energy reserves in small seeds are limited and sufficient for a short period of autonomous growth. *Striga* seeds have an after-ripening requirement and cannot germinate in the season in which they were produced [38]. This requirement is an evolutionary adaptation to prevent newly matured *Striga* seeds from germinating too late in a growing season, when host plants are normally senescing and are not capable of supporting a parasitic plant to maturity [39].

A difference in the length of after-ripening periods exists between *Striga* species. Reference [40] found a minimum period of six months for *S. asiatica* while [41] reported low germination of *S. hermonthica* in the first six months after harvest. The after-ripening process is described as a means of adaptation of *Striga* to the semi-arid climate [29]. Warm and dry conditions are pre-requisites for after ripening [42].

3.1.2. Conditioning

After-ripened, seeds will not germinate until they have passed through a preconditioning period. A complication in the germination of *S. hermonthica* and other *Striga* species is their inability to germinate, even in the presence of a suitable stimulant, until they receive a pre-treatment period in warm and moist conditions (conditioning or preconditioning) for at least a few days, ideally 1-2 weeks. The optimum temperature for conditioning is between 25 and 35° C for *S. hermonthica* [43].

The duration and temperature optimum for the conditioning period of *Striga* seeds vary with species. In *S. asiatica* the optimum conditioning period is 21 days at 22°C and is two weeks at 33°C for *S. hermonthica*. Higher temperatures will, however, result in rapid conditioning of this species, but percentage germination will not be as high even after several weeks [44].

Striga, a native of the semi-arid tropics, seeds are conditioned in wet soils in the rainy period when suitable host plants, including sown crops, are beginning to germinate [38]. The biochemical changes that occur during conditioning are not well known. However, conditioning is presumed to reduce germination inhibitors within the seed [45], or they may increase endogenous stimulatory substances [46]. During preconditioning, metabolic pathways in the seed are activated. Hence, respiration and the synthesis of DNA, protein and hormones increase after stimulation [47].

There is evidence that prolonged conditioning of *S. hermonthica* beyond a few weeks, especially at higher temperatures, results in secondary or wet dormancy, which

may or may not be recovered by drying and reconditioning [48]. A further complexity in the behavior of both *S. hermonthica* and *S. asiatica* is that application of germination stimulants, natural or synthetic, including ethylene, before or during conditioning result in reduced germination reception of a terminal stimulant treatment [49].

3.1.3. Seed germination

Striga seeds germinate only when they receive an exogenous stimulant subsequent to conditioning [50]. The natural stimulant is exuded by the host's roots and some non-host plants. Following germination, the radicles grow towards the host roots, indicating a chemotrophic effect [51].

Several germination stimulants have been isolated and include strigolactones, dihydrosorogoleone, sesquiterpene, kinetin, coumarin, jasmonate, ethylene and fungal metabolites [43]. A large number of investigators have attempted to isolate, characterize and/ or identify the stimulant from many hosts and non-host plants [52]. The natural stimulants are highly active, but are present in root

exudates in such extremely low levels that their isolation. purification and identification have been difficult [53]. The first natural germination stimulant is "Strigol". Strigol was isolated from cotton [Gossypium hirsutum (L.)], non-host plant [54]. Strigol is active on the S. asiatica at 10^{-16} M. Several years after the discovery of strigol several natural germination stimulants were identified from the roots of sorghum [55]. Five different stimulants, strigol, strigyl acetate, sorgolactone, alectrol and orobanchol were isolated from host and non- host plants. These compounds, because of similarity in chemical structure, are collectively referred as to strigolactones (Figure.2). Strigolactones are associated with the negative regulation of root and shoot branching (tillering). They also induce hyphal branching of arbuscular mycorrhizal (AM) fungi, presumably to attract them in lownutrient environments. It is at least known that most of the important Striga species will respond to strigol and to the "Strigol analogues" that have been synthesized and tested as possible means of control [37].

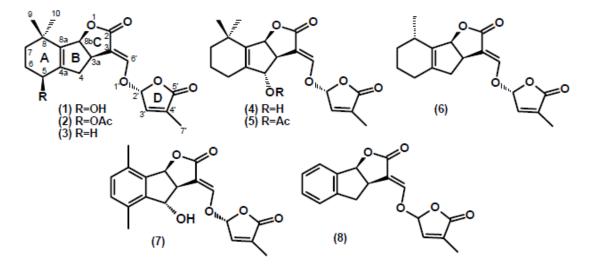


Figure. 2. Perception structures of strigolactones: strigol (1), strigyl acetate (2), 5-deoxystrigol (3), orobanchol (4), orobanchyl acetate (5), sorgolactone (6), solanacol (7), the synthetic germination stimulant GR24 (8), after [56].

Ethylene was reported to stimulate *S. asiatica* germination [57]. Ethylene gas was the main strategy of the US program of eradication of the parasite [58]. Genes encoding the key enzymes in ethylene biosynthesis, ACC synthase and ACC oxidase are regulated by germination stimulants and conditioning [42, 59]. Reference [60] summarized available information on substances stimulating germination of *S. asiatica* including a number of cytokinins, coumarin derivatives, scopletin, thiourea and allythiourea, sulphuric acid, sodium hypochlorite and L. methionine. Reference [61] reported that conditioned *Striga* seeds will germinate in the absence of a stimulant if they are punctured through the

aleurone layer but not at the side. Scarification by sulphuric acid could have the same effect [21].

The optimum temperature for germination of *S. hermonthica* is about 35° C, but, it is capable of germination over a wide range of temperatures (20-40°C) above which damage occurs [21]. Light reduces germination of *S. asiatica* when the seeds are exposed within one or two days before or up to 4 h after exposure to a germination stimulant [60, 61]. Once conditioned and then exposed to a stimulant under suitable temperature and moisture the seeds of most *Striga* species will germinate within 24 h.

3.2. The parasitic mode

3.2.1. Contact and attachment (Haustorial initiation)

Once the seeds of Striga have germinated up to several mms (2-4 mm) from a host root, radicle has to come in contact with the host root in order to parasitize it. Given the purely random directional growth after germination, it has been estimated that the chance of contact with a single root with small diameter may be less than 10% [62]. It is to be expected that in the course of evolution these chances might have been improved by the development of some chemotropic or other direction-seeking assistance. Indeed, reference [63] presented evidence for chemotropism in S. hermonthica, while [40] observed the phenomenon in S. asiatica. Effective chemotropism could result from a gradient in pH around the root [63] or an inhibitory effect of the root exudates on the side of the radicle nearest to host root. Witchweed germilings survive only for about three to seven days unless attachment to a host root is achieved [36].

In contact with host root the elongation of the radicle stops and a specialized organ of attachment, a haustorium (organ of attachment and a physiological bridge between the host and the parasite), is initiated in response to a second derived signal. Haustorium initiation, which represents the switch from the vegetative to the parasitic mode of life, occurs on or near the host root. This process has been shown to depend on a haustorium-imitating substance. The substance responsible for initiating haustorial development has been identified as 2, 6-dimethoxy-p-benzoquinone (2,6-DMBQ). The 2, 6-DMBQ cannot normally be detected in the exudates from sorghum roots, although it is present in its extract [64, 65]. Many phenolic and flavonoid substances can also initiate haustoria development in both S. asiatica and S. hermonthica [66], presumably acting as the substrate for the production of 2, 6-DMBQ via on enzyme systems. Cytokinins are also known to be initiators of haustorial development. Thidiazuron, which has some cytokinin activity, can also initiate haustorial development [67]. Haustoria-like structures and the early stages of nodule development [68] are induced by cytokinins, whereas indole acetic acid appears to be important for the initiation, morphogensis and continued development of lateral roots [69]. Compounds that inhibit auxin transport also induce nodule-like structures [70]. In S. asiatica, the radicles are most responsive and more able to form haustoria within 4 days of germination. However, at 30°C it may begin to lose this ability even 2 days after germination [21].

The haustorium penetrates the host root, establishes connection with host xylem, guided possibly by host-derived secondary metabolites [71]. Unlike its response to germination stimulants and haustorium initiators, *Striga* is non-specific with response to the attachment. Attachment frequencies were reported to be similar for host and non-host plant species [72]. The process of haustorial development and penetration of the host is similar in *S. hermonthica* [73] and *S. asiatica* [74]. Sticky hairs on the

young haustorium help the parasite germiling to adhere to any surface. After attachment by these hairs, intrusive cells develop at the root tip and penetrate the cortex of the host.

3.2.2. Penetration and establishment of the parasite

Penetration is aided by enzymatic secretion leading to separation of the host cortex cells. The haustorium sometimes fails to complete its penetration of the cortex and may also fail to cross the endodermis which sometimes provides a barrier. In S. asiatica, the time from the first penetration of the epidermis to an established connection with the host stele is 60 hours [74]. Following a successful connection to the host xylem, the plumular end of the seedling emerges from the seed coat and Striga becomes fully dependent on the host. The successful parasite establishment creates a strong nutrients sink leading, to drastic reductions in host growth and yield [75]. On emerging from the soil, the aerial parts of the parasite turn green Striga plants begin to photosynthesize. However, the low CO₂ fixation and high dark respiration rates of Striga result in a negative carbon gain over the 24-h period, thus making the parasite still unable to survive in the absence of host attachment. Striga is described by the high transpiration rates. These rates suggest that most host photoassimilates are obtained by transpirational pull, explaining why high humidity is inhibitory to Striga growth. Indeed, Striga stomata show high conductance and respiration rates and little response to dark-induced closure [76].

Flowering time is species and environment dependent. *S. gesnerioides* begins to flower as it emerges. *S. hermonthica*, *S. asiatica* and *S. aspera* begin to flower 4 weeks after emergence. Flowering begins basally on the raceme, and seeds are mature 4 weeks after flowering [21, 50] [21]. When conditions are favorable for parasite growth, the parasite will normally germinate and attach to the root system within 2-3 weeks after host germination, emerge after 4-7 weeks and flower within 7-8 weeks. Viable seeds are probably produced within 2 weeks of flower opening and are fully matured and shed about 2 weeks later [29]. The minimal length of the life cycle of the parasite, from germination to seed production comprises an average of 4 months [2].

Striga species exhibit variation in their mode of reproduction. *S. hermonthica* and *S. gesneriodes* are allogamous that is they observe cross pollination and usually rely on vectors such as bees and other agents of pollination for pollen transfer [77]. *S. asiatica* on the other hand is autogamous that is it observes self-pollination and so, no vectors are needed for pollination instead pollens are picked by the elongation of style and fertilization takes place [1]. The development of the Striga spp. is influenced by the Soil type, soil temperature, tillage systems and the parasite thrives best under conditions of mono-cropping of susceptible host [44].

As much as half of the *Striga* life cycle is subterranean, growing completely at the expense of its host and the parasite inflicts most of its damage to the host during this phase of its life cycle. Symptoms displayed by infected hosts, include stunting, toxic' effects, reduction of internode expansion, wilting, chlorosis, increased root: shoot ratio, reduced photosynthetic rate and decreased growth and yield. Parasitism by *S. hermonthica* leads to perturbation of hormonal balance and a marked change in the amino acid content of the grains [78].

CONCLUSION

It concluded that the basis and background studies on *Striga* spp life cycle made some significant advances in the understanding of the biology and physiology of *Striga* spp. such as after- ripening, germination, haustorial initiation, attachment, penetration and establishment of parasite. However, continued effort is needed in the laboratory and in the field researches to gain a better understanding of factors influencing the different stages of the parasite life cycle so as to develop integrated *Striga* management strategies that will lead to effective, economically feasible and environmentally sound management of the parasite.

REFERENCES

- [1] Spallek, T., Mutuku, J.M. & Shirasu, K. (2013). The genus *Striga*: a witch profile. *Molecular Plant Pathology*, 14, 861-869.
- [2] Babiker, A. G. T. (2007). Striga: The Spreading Scourge in Africa. Regulation of Plant Growth and development, 42, 74-87.
- [3] Runo, S. & Kuria, E.K. (2018). Habits of a highly successful cereal killer, *Striga*. <u>PLoS Pathog</u>., 14(1). e1006731. https://doi.org/10.1371/journal.ppat.1006731.
- [4] Haussmann, B. I. G., Hess, D. E., Welz, H. G. & Geiger, H. (2000). Improved methodologies for breeding
- Striga-resistant sorghum. Field Crop Research, 66, 195-211.
 [5] Ejeta, G. H. & Butler, L. G. (2000). Parasitic plants. In: Frederiksen, R.A. and Odvody, G. N. (eds).
- Frederiksen, R.A. and Odvody, G. N. (eds). *Compendium of Sorghum Diseases*, 2nd edition. APS Press, The American Phytopathological Society, pp. 53-56.
- [6] Teka, H.B. (2014). Advance research on *Striga* control: a review. *Afr. J. Plant Sci.* 8 (11), 492-506.
- [7] Parker. C. (2012). Parasitic weeds: A world challenge. Weed Sci, 60. 269–276. https://doi.org/10.1614/WS-D-11-00068.1.
- [8] Ejeta, G. H. (2007). Breeding for *Striga* Resistance in Sorghum: Exploitation of an Intricate Host–Parasite Biology. *Crop science* 47(S3), S216–S227.
- [9] Scholes, J.D. & M.C. Press (2008). *Striga* infestation of cereal crops - an unsolved problem in resource limited agriculture. *Curr. Opin. Plant Biol.*, 11, 180-186.

- [10] Ronald, M., Charles, M., Stanford, M. & Eddie, M. (2016). Existence of different physiological 'strains' of *Striga asiatica* (L.) Kuntze on sorghum species [*Sorghum bicolor* (L.) Moench and *Sorghum arundinaceum* (Desv.) Stapf] in Zimbabwe. *Res. Crops*, 17, 468-478.
- [11] Dawud, M. A. (2017). Striga Resistance in Cereal Crops: Recent Progress and Future Prospects. A Review. Global Journal of Science Frontier Research, 17(3), 1.
- [12] Garba, Y., Musa, A. & Alhassan, J. (2017). Management of giant witch weed (*Striga hermonthica*) infestation in integrated maize field at Southern Guinea Savannah, Nigeria. *Scholarly Journal of Agricultural Science*, 7(4), 89-94.
- [13] Oswald, A. (2005) Striga control technologies and their dissemination. Crop Protection, 24. 333-342.
- [14] Ronald, M., Charles, M., Stanford, M. & Eddie, M. (2017). Predictions of the *Striga* Scourge under New Climate in Southern Africa: A Perspective. Journal of Biological Sciences, 17 (5): 194-201.
- [15] Knuston, D.M. (1979). How parasitic seed plants induce disease in other plants In: Horsefall, J. G and Cowling, E. B. (eds.) *Plant Disease: An Advanced treatise. How Pathogens Induce Disease* Academic Press New York 4, 293-312.
- [16] Westwood, J.H., Yoder, J.I., Timko, M.P. & Pamphilis, C.W. (2010). The evolution of parasitism in plants. *Trend. Plant Sci.* 15 (4), 227-235.
- [17] Parker, C. (1991). Protection of crops against parasitic weeds. *Crop Protection*, 10: 6-22.
- [18] Babiker, A. G. T, Ejeta, G., Butler, L. G. & Woodson, W. R. (1993). Ethylene biosynthesis and strigol-induced germination of *Striga asiatica*. *Physiologia Plantarium*, 88,359-365.
- [19] Yoshida, S. (2019). Genetic basis for host and parasitic plant communication. *In the Proceeding of the*15th World Congress on Parasitic Plants. June 30 July 5 2019, Amsterdam, The Netherlands.
- [20] Mohamed, K.I. & Musselman, L.J. (2008) Taxonomy of agronomically important *Striga* and Orobanche species. In: Progress on Farmer Training in Parasitic Weed Management (Labrada, R., ed.), pp. 7–14. Rome: FAO.
- [21] Parker, C. & Riches, C. (1993). *Parasitic Weeds of the World: Biology and Control.* Wallingford CAB international. 1993 pp. 4-332.
- [22] Dafaallah, A. B., Babiker, A.G.T & Zain El abdeen, M. H. (2015). Variability in *Striga hermonthica* (Del.) Benth, Populations in Gadarif Area, Eastern Sudan. *Sudan University of Science and Technology Journal of Agricultural and Veterinary Sciences*, 16 (2),119-132.
- [23] Kuijt, J. (1969). The Biology of Parasitic Flowering Plants. University of California Press, Berkeley, pp 346.

- [24] Ejeta, G. & Gressel, J. (2007) Integrating New Technologies for Striga Control: Towards Ending the Witch-Hunt. Singapore; Hackensack, NJ: World Scientific.
- [25] Atera, E. & Itoh, K. (2011) Evaluation of ecologies and severity of *Striga* weed on rice in sub-Saharan Africa. *Agric. Biol. J. N. Am.* 2, 752–760.
- [26] Mohamed, K., Bolin, J., Musselman, L. & Peterson, A. (2007). Genetic diversity of *Striga* and implications for control and modeling future distributions. In: Ejeta, G. and Gressel, J. (eds.) *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*. 71-84.
- [27] Musselman, L. J. & Hepper, F. (1986). The witchweed (*Striga*, Schrophulariaceae) of the Sudan Republic. *Kew Bullettin*, 41, 205-221.
- [28] Dafaallah, A. B., Babiker, A.G.T & Zain El abdeen, M. H. (2016 a). Variability and Host Specificity of Witchweed [*Striga hermonthica* (Del.) Benth.] Populations on Performance of (*Sorghum bicolor*) 'Abu sabeen' in Sudan. University of Khartoum Agriculture. Journal of Agricultural Sciences, 24(1), 99-121.
- [29] Doggett, H. (1988). *Sorghum*. (second edition) John-Wiley and Sons, New York, London, pp. 512.
- [30] Gressel, J., Hanafi, A., Head, G., Marasas, W., Obilana, B. & Ochanda, J., (2004). Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Prot.* 23, 661-689.
- [31] Gwary, D. M, Rabo, T. D. & Gwary, S. D. (2001). Effects of *Striga hermonthica* and anthracnose on the growth and yield of sorghum in Sudan, savanna of Nigeria. *Nigerian, Journal of Weed Science*. 14, 47-51.
- [32] Showemimo, F. A., (2006). Effect of *Striga hermonthica* on yield and yield components of sorghum in Northern Guinea Savanna of Nigeria. *Journal of Plant Science*, 1: 67-71.
- [33] Pennisi, E. (2015). How crop-killing witchweed senses its victims. *Science*, 350, 146-147.
- [34] Christopher, J. B. Jennifer, G. K., Berner, D.K. & Michael, P. T. (2002). Genetic variability of *Striga asiatica* (L.) Kuntz based on AFLP analysis and host parasitic interaction. *Euphytica*, 128: 375-388.
- [35] Obilana, A.T. & Ramaiah, K.V. (1992). Striga (Witchweeds) in sorghum and millet: Knowledge and future research needs. In: de Milliano, W.A.J., Frederiksen, R.A. and Bengston, G.D. (eds.). Sorghum and Millet Disease: A second World Review (Patancheru, India: International Crop Research Institute for the Semi-Arid Tropics). pp. 187-201.
- [36] Riopel, J. L. & Baird, W. V. (1987). Striga morphologensis. In: Musselman, L. J. (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton. 1, 107-126.
- [37] Yoneyama, K., Awad, A.A., Xie, X., Yoneyama, K. & Takeuchi, Y. (2010). Strigolactones as germination

stimulants for root parasitic plants. *Plant Cell Physiol*. 51, 1095-1103.

- [38] Riches, C. R. & Ejeta, G. (2007). Biology of host parasite interaction in *Striga* species. In: Ejeta, G. and Gressel, J. (eds.) *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*. pp. 19-32.
- [39] Berner, D. K., Winslow, M. D., Awad, A. E., Cardwell, K. F., Mohn Raj. D. R., & Kim. S. K. (1997). *Striga* Research Methods - A manual, 2nd edition. International Institute of Tropical Agriculture, PMB 5320, Ibadan, Nigeria. Pp 1-80
- [40] Saunders, A. (1933). Studies in phenorogamic parasitism with particular reference to *Striga lutea* (Lour). *South Africa Department of Agriculture, Science Bulletin*, 128, 1-57.
- [41] Parker, C. (1984). The influence of *Striga* species on sorghum under varying nitrogen fertilization. *In:* Parker, C. Musselman, L. J., Polhill, R. M. and Wilson, A. K. (eds.) *Proceedings*, 3rd *Internationa Symposium on Parasitic Weeds*. Aleppo, Syria, 1984. ICARDA, Aleppo. pp. 90-98.
- [42] Babiker, A. G. T, Ma Y, Sugimoto, Y. & Inanaga, S. (2000) Conditioning period, Co₂ and GR24 influence ethylene biosynthesis and germination of *Striga hermonthica. Plant Physiology*,109, 75–80
- [43] Cardoso, C., Ruyter-Spira, C. & Bouwmeester, H.J. (2011) Strigolactones and root infestation by plantparasitic *Striga*, *Orobanche* and *Phelipanche* spp. *Plant Sci.* 180, 414–420.
- [44] Parker, C. & Reid, D. C. (1979) Host specificity in *Striga* species: Some preliminary observations. In: Musselman L. J., Worsham, A. D. and Eplee, R. E. (eds.) *Proceeding of the Second International Symposium on Parasitic Weeds*. North Carolina State University, Raleigh, pp 79-90.
- [45] Kust, C.A. (1966). A germination inhibitor in *Striga* seeds. *Weeds*, 11,327-329.
- [46] Brown, R. (1946). Biological stimulation of germination. *Nature* 157, 64-68
- [47] Ejeta, G. (2005). Integrating biotechnology, breeding and agronomy in the control of the parasitic weed *Striga* spp. in sorghum. In: Tuberosa R., Phillips R. L. and Gale, M. (eds.) *In the Wake of the Double Helix: From the Green Revolution to the Gene Revolution*. Avenue media, Bologna, pp 239-251.
- [48] Pieterse, A. H., Ebbers, A. E. H. & Pesch, C. J. (1984).
 A study on wet dormnacy in seeds of *Striga hermonthica* (Del.) Benth. *In vitro*. In: Parker, C., Musselman, L. J., Polhill, R. M. and Wilson, A. K. (eds.) *Proceedings of the 3rd International Symposium on Parasitic Weeds*. Aleppo, Syria, 1984. ICARDA, Aleppo, pp. 99-107.
- [49] Babiker, A. G. T. & Hamdoun, A. M. (1983). Factors affecting the activity of ethephon in stimulating

germination of *Striga hermonthica* (Del.) Benth. *Weed Research*, 23[50], 125-131.

- [50] Sugimoto, Y. Wigchert, S., Thuring., J. and Zwaneburg, B. (1998). Synthesis of all eight stereo isomers of the germination stimulant sorgolactone. *Organic Chemistry*, 63,1259-1267.
- [51] Dube, M. M. P & Olivier, A. A. (2001). Le *Striga gesnerioides* et son hote, le niebe: interaction et methodes de lutte. Canadian *Botany* 79, 1225-1240.
- [52] Awad, A. A., Sato, D., Kusumoto, D., Kamioka, H., Yasutomo, T. & Yoneyama, K. (2006). Characterization of strigolactones, germination stimulants for the root parasitic plants *Striga* and *Orobanche*, produced by maize, millet and sorghum. *Plant Growth Regulation*, 48, 221-227.
- [53] Musselman, L. J. (ed.) (1987). Taxonomy of witchweeds. *Parasitic Weeds in Agriculture*, 1, 317.
- [54] Cook, C. E., Whichard, L. P., Wall, M. E., Egley, G. H., Coggan, P., Luhan, P. A. & McPhail, A. T. (1972). Germination stimulants 2. The structure of Strigol-a potent seed germination stimulant for witchwed (*Striga lutea* lour.). *Journal of the American Chemical Society*, 94, 6198-6199.
- [55] Hauck, C., Muller, S. & Schilknecht, H. (1992). A germination stimulant for parasitic plants from *Sorghum bicolor*, a genuine host plant. *Plant Physiology*, 139: 474-478.
- [56] Sun, Z. (2008). Biosynthesis of germination stimulants of parasitic weeds Striga and Orobanche. Ph.D. Thesis. Wageningen University, The Netherlands with summaries in English and Dutch ISBN 978-90-8504-826-8. pp. 5.
- [57] Chanceller, R. J., Parker, C. & Teferedegn, T. (1971). Stimulation of dormant weed seed germination by 2chloroethyl-phosphonic acid. *Pesticide Science*, 2: 35-37.
- [58] Logan, D. C. & Stewart, G. R. (1991). Role of the ethylene in the germination of the parasite *Striga hermonthica*. *Plant Physiology*, 97, 1435-1438
- [59] Sugimoto, Y, Ali, A. M., Yabuta, S, Kinoshita, H, Inanaga, S & Itai, A. (2003). Germination strategy of *Striga hermonthica* involves regulation of ethylene biosynthesis, *Physiologia Plantarum*, 119, 137-145.
- [60] Worsham, A. D. and Egley, G. H. (1990). Phyisology of witchweed seed dormancy and germination. In: Sand, P. F., Eplee, R. E. and Westbrooks, R. G. (eds.) Witchweed Research and Control in the United States. Weed Science Society of America. Champaign. pp. 11-26.,
- [61] Egley, G. H. (1972). Influence of seed envelope and growth regulators upon seed dormancy in witchweed (*Striga lutea* [Lour]). *Annals of Botany*, 36: 755-770.
- [62] Dixon, N. H. & Parker, C. (1984). Aspects of the resistance of sorghum varieties to *Striga* species. In: Parker, C., Musselman, L.J., Polhill, R. M. and Wilson, A. K. (eds.) *Proceedings 3rd International symposium*

on Parasitic Weeds., Aleppo., ICARDA, Syria, Aleppo. pp. 81-85.

- [63] Williams, C. N. (1961). Tropism and morphogensis of *Striga* seedlings in the host rhizosphere. *Annals of Botany*, 25, 407-415.
- [64] Dafaallah, A. B., Babiker, A.G.T & Hamdoun, A. M. (2014). Effects of 2,4-D, DMBQ and sorghum root extract on haustorium induction and attachment of witchweed [Striga hermonthica (Del.) Benth.] to roots of Sorghum bicolor (L.) Moench. Gezira Journal of Agricultural Sciences, 12 (2), 1-13.
- [65] Dafaallah, A. B., Babiker, A.G.T, Hamdoun, A. M. & Mohamed, E. Y. (2017). Influence of DMBQ, sorghum root extracts and temperature on haustorium initiation of *Striga hermonthica* (Del.) Benth.. *Neelain Journal of Science and Technology*, 1 (1), 8-14.
- [66] Chang, M. & Lynn, D. G. (1986). The haustorium and the chemistry of host recognition in parasitic angiosperms. *Chemical Ecology*, 12, 561-579.
- [67] Babiker, A. G. T., Parker, C. & Suttle, J. C. (1992). Induction of *Striga* seeds germination by thiadiazuron. *Weed Research*, 32, 243-248.
- [68] Crespi, M. & Galvez, S. (2000). Molecular mechanism in root nodule development. Journal of Plant Growth Regulation, 19, 155-166.
- [69] Deklerk, G. J., Van der Krieken, W. & De Jong, J. C. (1999). The formation of adventitious roots: new concepts, new possibilities. Cell development. *Biology* of *Plant*, 35, 189-199.
- [70] Hirsch, A. M., Bhuvaeswari, T. V. Torrey, J. G. & T. Bisseling. (1989). Early nodulation genes are induced in alfalfa root outgrowths elicited by auxin transport. *Proceedings of National Academy of Science*, 86,1244-1248.
- [71] Bouwmeetster, H., Matusova, R., Zhongkui, S. & Beale, M. (2003). Secondary metabolic signaling in host- parasitic plant interactions. *Current Opinion in Plant Biology*, 6, 358-364.
- [72] Hood, M. E, Condon, J. M., Timko, M. P. & Riopel, J. L. (1998). Primary haustorial development of *Striga asiatica* on host and non-host species. *Phytopathology*, 88, 70-75.
- [73] Olivier, A., Benhamou, N. & Leroux, G.D. (1991). Cell surface interactions between sorghum roots and the parasitic weed *Striga hermonthica*. Cytochemical aspects of cellulose distribution in resistant and susceptible host tissues. *Canadian Journal of Botany*, 69, 1679-1690.
- [74] Ramaiah, K. V., Chidley, V. I. & House, L. R. (1991). A time-course study of early establishment stages of parasitic angiosperm *Striga asiatica* on susceptible sorghum roots. *Annals of Applied Biology*, 118 (2), 403-411.
- [75] Joel, D. M., Hershenhorn, Y., Eizenberg, H., Aly, R., Ejeta, G., Rich, P.J., Ransom, J.K., Sauerborn, J. & Rubiales, D. (2006). Biology and management of weed

root parasites. *Horticultural Reviews*, 38. John Wiley and Sons, Inc.

- [76] Satish, K., Gutema, Z., Grenier, C., Rich, P.J. & Ejeta, G. (2012). Molecular tagging and validation of microsatellite markers linked to the low germination stimulant gene (lgs) for *Striga* resistance in sorghum [*Sorghum bicolor* (L.) Moench]. *Theor. Appl.Genet.* 124, 989–1003.
- [77] Dugje, I.Y., Kamara, A.Y. & Omoigui, L.O. (2008). Influence of farmers' crop managementpractices on *Striga hermonthica* infestation and grain yield of maize (*Zea mays* L.) in the savanna zones of northeast Nigeria. *Journal of Agronomy*, 7(1), 33-40.
- [78] Dafaallah, A. B., Babiker, A.G.T & Zain El abdeen, M. H. (2016 b). Assessment of the Damage Caused by *Striga hermonthica* (Del.) Benth. on the Performance of Cereals Hosts in Gadarif State, Eastern Sudan. University of Khartoum Agriculture. *Journal of Agricultural Sciences*, 24(2), 99-121.