Recent research progress in combatting root parasitic weeds

Samejima, Hiroaki
Sugimoto, Yukihiro

(Citation)
Biotechnology & Biotechnological Equipment,32(2):221-240

(Issue Date)
2018-01-04

(Resource Type)
journal article

(Version)
Version of Record

(URL)
https://hdl.handle.net/20.500.14094/90004845

Biotechnology & Biotechnological Equipment

ISSN: 1310-2818 (Print) 1314-3530 (Online) Journal homepage: http://www.tandfonline.com/loi/tbeq20

Recent research progress in combatting root parasitic weeds

Hiroaki Samejima & Yukihiro Sugimoto

To cite this article: Hiroaki Samejima & Yukihiro Sugimoto (2018) Recent research progress in combatting root parasitic weeds, Biotechnology & Biotechnological Equipment, 32:2, 221-240, DOI: 10.1080/13102818.2017.1420427

To link to this article: https://doi.org/10.1080/13102818.2017.1420427

BIOTECHNOLOGY & BIOTECHNOLOGICAL EQUIPMENT, 2018
VOL. 32, NO. 2, 221–240
https://doi.org/10.1080/13102818.2017.1420427

Taylor & Francis
Taylor & Francis Group

REVIEW; AGRICULTURE AND ENVIRONMENTAL BIOTECHNOLOGY

Recent research progress in combatting root parasitic weeds

Hiroaki Samejima and Yukihiro Sugimoto

Division of Applied Chemistry in Bioscience, Graduate School of Agricultural Science, Kobe University, Kobe, Japan

ABSTRACT
The obligate root parasitic Orobanchaceae plants *Striga*, *Orobanche* and *Phelipanche* spp. parasitize economically important crops, vegetables and oil plants. They are the most devastating agricultural weed pests worldwide. Based on an analysis of the climatic requirements of these parasites, very large areas of new territory are at risk of invasion if care is not taken. Recent research in combatting root parasitic weeds was reviewed based on scientific papers reported from 2010 and onwards. The countermeasures fell into eight kinds: resistant varieties, tolerant varieties, microbiological approach, cultural practices, chemical controls, host-induced gene silencing, integrated management and dissemination of technologies including the current situation survey. The development of practical, feasible and economical control technologies against root parasitic weeds would be expected by advancing and combining the countermeasures.

ARTICLE HISTORY
Received 23 November 2017
Accepted 19 December 2017

KEYWORDS
Broomrape; *Orobanche*; pest management; *Phelipanche*; *Striga*; witchweed

Introduction

About 4000 flowering plant species have adapted to parasitize other plants [1]. Parasitic plants form specialized organs called haustoria that attach to hosts' organs enabling them to benefit from the hosts' water and nutrition, which severely damages the hosts' growth and yield. Parasitic plants fall into two categories, root or stem parasitic weeds, according to the host organs to which they attach. Among root parasitic plants, the obligate root parasitic Orobanchaceae plants witchweed (*Striga* spp.) and broomrape (*Orobanche* and *Phelipanche* spp.) parasitize economically important crops, vegetables and oil plants. They are the most devastating agricultural weed pests worldwide [2].

The most important parasitic *Striga* spp. are the purple witchweed (*S. hermonthica*) and the Asiatic witchweed (*S. asiatica*). They are distributed throughout sub-Saharan Africa, India and Southeast Asia where they primarily affect cereal grass crops such as maize (*Zea mays*), sorghum (*Sorghum bicolor*), rice (*Oryza sativa*) and millet (*Pennisetum* spp.). Another important species, cowpea witchweed (*S. gesnerioides*), primarily attacks leguminous crops such as the cowpea (*Vigna unguiculata*) in West Africa. Crop losses by these *Striga* spp. can be up to 100% [3] and they have become the greatest biological constraint to food production in endemic areas [4,5].

The problematic weeds *Orobanche* and *Phelipanche* spp. are centred in the Mediterranean and Western Asia, but they are widely distributed throughout many countries all over the world [3]. Seven species, crenate broomrape (*O. crenata*), sunflower broomrape (*O. cumana*), nodding broomrape (*O. cernua*), fetid broomrape (*O. foetida*), small broomrape (*O. minor*), branched broomrape (*P. ramosa*) and Egyptian broomrape (*P. aegyptiaca*) are economically important [2]. Parker [3] determined that the main hosts are the Leguminosae, Apiaceae and Asteraceae for *O. crenata*, the sunflower (*Helianthus annuus*) for *O. cumana*, Solanaceae for *O. cernua*, Leguminosae for *O. foetida*, clover (*Trifolium* spp.) and alfalfa (*Medicago sativa*) for *O. minor*, and many families, including the Solanaceae and Brassicaceae, for *P. ramosa* and *P. aegyptiaca*.

The life cycle of *Striga*, *Orobanche* and *Phelipanche* spp. is strongly cued to that of its host. In nature, the seeds need a conditioning period of 2–14 days in a warm moist environment and subsequent exposure to a germination stimulant, such as strigolactone (SL), that is exuded by the host and some non-host plant roots. Subsequent to germination, which occurs in close proximity to the host roots, a haustorium is formed based on the perception of a second host-derived chemical signal. The haustorium attaches, penetrates the host root and establishes a connection with the host's vascular bundles. Following the establishment of a connection with the host, the parasite remains subterranean and is fully dependent on its host for a certain period of time. After emergence, the absence or presence of functional

CONTACT Yukihiro Sugimoto yukihiro@kobe-u.ac.jp

chloroplasts further defines the parasites as being either hemi-parasitic (*Striga* spp.) or holo-parasitic (*Orobanche* and *Phelipanche* spp.), respectively. Each parasitic plant produces tens of thousands of seeds, which remain viable in the soil for 10 years or more.

It is estimated that 50 million ha in Africa are affected by *Striga* spp. [6] and 16 million ha in the Mediterranean region and Western Asia are affected by *Orobanche* and *Phelipanche* spp. [2]. Based on an analysis of the climatic requirements of *Striga*, *Orobanche* and *Phelipanche* spp., very large areas of new territory are at risk of invasion if special measures are not undertaken to limit the introduction of seeds and to educate farmers and others to be alert for signs of a new infestation [2,7,8]. In this review, we focus on recent research progress in combatting root parasitic weeds, based on scientific papers that were reported during and after 2010.

Resistant varieties

Sorghum

At least four mechanisms were indicated in sorghum as potential resistance mechanisms against *S. hermonthica* using an extended agar gel assay, which allowed researchers to observe the parasites' development in the rhizosphere of its host: (1) low production of germination stimulant, (2) secretion of germination inhibitor, (3) low production of the signals required for haustoria initiation and (4) hypersensitive response (HR) [9]. Two sorghum lines, CK32 and KP33, that exhibit a strong HR to *S. hermonthica* were used to elucidate the inheritance of the resistance mechanism. The results of the segregation suggest that HR in sorghum is conditioned by two nuclear genes with a dominant gene action [10]. As for the mechanisms ascribed to low production of the germination stimulant, there were varietal differences in SL exudation from roots, both quantitatively and qualitatively [11]. Sorghum varieties with a high 5-deoxystrigol (5-DS) level in root exudates had a higher *S. hermonthica* infection in the field, while those with a high orobanchol level had lower infection levels [12]. The functional loss of a gene at the *LOW GERMINATION STIMULANT 1* (*LGS1*) locus resulted in a change of the dominant SL from 5-DS, a highly active *S. hermonthica* germination stimulant, to orobanchol, an SL that is less active to *S. hermonthica* [13]. Microsatellite markers linked to the low germination stimulant gene (*lgs*) for *S. hermonthica* were identified in sorghum and were supposed to be useful in breeding *S. hermonthica*-resistant sorghum varieties [14]. In breeding projects in Sudan and Eritrea, *S. hermonthica* resistance of sorghum was successfully improved by marker-assisted selection [15,16]. Resistance to *S. hermonthica* in wild sorghum accessions was reported as novel sources for sorghum breeding, in which the resistance was ascribed to incompatibility [17].

Rice

An incompatibility between some interspecific upland NEw RICe for Africa (NERICA) cultivars and *S. hermonthica* and between some NERICA cultivars and *S. asiatica* was found under laboratory conditions [18]. Activity to induce germination of *S. hermonthica* seeds and the level of SL production were studied in NERICA cultivars in laboratory and pot experiments and there were significant differences among the cultivars in these parameters [19]. The resistance level of NERICA cultivars screened under controlled environment [18,19] was in good accordance with that under field conditions [20], although they were not always exact. Furthermore, Rodenburg et al. [21] evaluated NERICA and other rice cultivars under field conditions in three regions of Africa and found that 11 and 8 out of 19 rice cultivars were resistant to *S. hermonthica* and *S. asiatica*, respectively. Under field conditions in Western Kenya, two cultivars, NERICA1 and NERICA10, were resistant and a cultivar NERICA4 was susceptible to *S. hermonthica* [22]. An upland rice variety, Umgar, which was released for commercial production in Sudan, showed several resistance mechanisms controlled by a low induction of germination and incompatibility in a series of laboratory, pot and field experiments [23]. The gene, *WRKY45*, modulates a cross talk in the resistance of rice against *S. hermonthica* by positively regulating both salicylic acid (SA) and jasmonic acid (JA) pathways [24].

Pearl millet (Pennisetum glaucum)

Kountche et al. [25] evaluated the response of a diversified pearl millet gene pool to five cycles of recurrent selection targeting *S. hermonthica* resistance and verified that the recurrent selection is effective for enhancing *S. hermonthica* resistance in the crop. A genetic map consisting of single nucleotide polymorphism (SNP) markers was constructed using a genotyping-by-sequencing approach and an F_2 population was derived from a cross between *S. hermonthica*-resistant wild millet and *S. hermonthica* susceptible cultivated millet. The employment of such a map will be useful for the identification of genomic regions associated with *S. hermonthica* resistance and other important agronomic traits [26].

Maize

Although breeding maize varieties for *S. hermonthica* resistance was less successful until recent years [27], massive development has been achieved mainly by the International Institute of Tropical Agriculture, Nigeria. A broad range of genetic diversity among maize varieties with *S. hermonthica* resistance was detected, indicating that a genetic reservoir of resistance can be exploited in breeding [28]. In fact, several *S. hermonthica*-resistant varieties with traits of extra-early maturing [29], early maturing [30] or high quality grains [31,32] were developed for practical uses in Africa. In particular, maize varieties concurrently containing *S. hermonthica* resistance, drought tolerance, low soil N tolerance and a high yield ability [33–36] are expected to give acceptable performances at several growth conditions. In Nigeria, the largest seed company in the country participated in the selection of *S. hermonthica*-resistant varieties [37]. Maize varieties possessing incompatibility to *S. hermonthica* were recently identified [38]. In addition, new *S. hermonthica*-resistant maize varieties based on a low induction of germination were selected from 420 maize landraces, populations and elite inbred lines, although several maize landraces that are popular among smallholder farmers in Western Kenya had higher *S. hermonthica* resistance than the improved varieties [39]. Hybrid maize varieties with *S. hermonthica* resistance have also been recently developed [40,41]. Heterotic grouping among 378 hybrids derived from diallel crosses of 28 early inbreds were evaluated in *S. hermonthica*-infested and *S. hermonthica*-free environments using SSR markers, to utilize the information in a maize hybrid breeding programme [42]. Very recently, the genetic diversity of tropical maize inbred lines combining resistance to *S. hermonthica* with drought tolerance was exhibited using SNP markers [43]. The effectiveness of marker-assisted recurrent selection to improve *S. hermonthica* resistance together with drought tolerance in maize breeding was demonstrated [44]. Hairy roots of transgenic 'composite' maize resulting from *Agrobacterium rhizogenes* transformation were shown to be infected by *S. hermonthica*, and this rapid, high throughput transformation technique will advance our understanding of gene function in parasitic plant–maize interactions [45].

Cowpea

S. gesnerioides exhibits a clear race structure; at least seven races of this parasite have been identified based on genetic diversity analysis and on their differential reaction to a panel of cowpea cultivars, suggesting a gene-for-gene interaction in the host-parasite association [46,47]. The cowpea cultivar B301 is considered resistant to all *S. gesnerioides* races identified in West Africa, except race SG4z from Zakpota, Benin [48]. In the roots of B301, a distinct difference in global gene expression was found between compatible (susceptible) and incompatible (resistant) interactions with *S. gesnerioides* races SG4z and SG3, respectively [49]. Three well-characterized molecular markers (SSR1, C42-2B and 61RM2) for race-specific resistance to *S. gesnerioides* in B301 were used to analyse the genetic diversity of 81 cowpea accessions in Ethiopia, and only two accessions carried the SSR1 resistance allele. This wide diversity within cowpea accessions could contribute to the genetic improvement of cowpea germplasm for *S. gesnerioides* resistance [48]. Rapid DNA collection using FTA® cards (Whatman®) could provide a potential to put the marker-assisted selection of *S. gesnerioides*-resistant cowpea accessions on a fast track and increase the efficiency of breeding activities [50]. Two new cowpea genotypes, IT97K-499-35 and IT98K-205-8, had *S. gesnerioides* (race SG3) resistance comparable to B301, and their resistance was stable even under tremendously severe conditions of high *S. gesnerioides* infestation, low soil fertility and drought [51]. Eleven cowpea genotypes including IT98K-205-8 conferred resistance to several *S. gesnerioides* races [52]. The *S. gesnerioides* resistance is controlled by a single dominant gene (*Rsg5*) in IT98K-205-8 and two duplicate dominant genes (*Rsg5a* and *Rsg5b*) in another resistant accession, IT99K-573-1-1 [53]. An optimized protocol for the rapid generation of transformed hairy roots of 'composite' cowpeas using *A. rhizogenes* was described to study gene expression in resistance or susceptibility responses to *S. gesnerioides* [54].

Sunflower

Vrănceanu et al. [55] used a set of sunflower genotypes and identified that each of them carries one single major gene of resistance (*Or1* to *Or5*) and that these genes control races A to E of *O. cumana*, respectively, conferring resistance to previously described races (termed cumulative resistance). Sunflower varieties with resistance against race A to E of *O. cumana* have been reported. For example, one commercial sunflower in Argentina (cultivar M15) showed complete resistance to *O. cumana* race E [56]. However, it has been pointed out that the majority of the existing resistant genes have become insufficient due to the emergence of race F and higher [57]. Race E avirulence and race F virulence on a sunflower line are allelic and controlled by a single locus [58]. To attain sunflower varieties resistant to *O. cumana* races higher than F, the introduction of resistance genes from wild sunflower species to cultivated sunflowers has been studied [57,59–63]. An inbred line, AB-VL-8, which originated from a population developed from interspecific hybridization with the rough sunflower (*Helianthus* *divaricatus*) was a successful example and had full resistance to races higher than F [57,59]. Successful identification of quantitative trait loci (QTLs) for *O. cumana* resistance in the sunflower has been reported [63–66] and utilization of QTLs in the breeding process is expected. In *O. cumana*-resistant sunflower genotypes, up-regulation of *Phenylalanine Ammonia Lyase* (*PAL*) and *defensin* genes or the *PR5* gene was found, suggesting the implication of these genes in defence responses during infection and limitation of *O. cumana* growth and development [67].

Faba bean (Vicia faba)

Damage caused by *O. crenata*, *O. foetida* and *P. aegyptiaca* is important in faba bean cultivation throughout the Mediterranean and Near East [68]. A number of faba bean cultivars with resistance to *O. crenata* have been released, all of which use an Egyptian line Giza402 as the major donor of resistance [68,69]. Until recently, resistance mechanisms identified in the faba bean against *O. crenata* were ascribed to inhibition of radicle penetration and tubercle development [68]. However, a resistance mechanism in terms of low induction of germination has been found in faba bean cultivars, including Giza402 against *O. crenata*, *O. foetida* and *P. aegyptiaca* [68–73]. Resistance of several faba bean varieties against more than two *Orobanche*/*Phelipanche* spp. was confirmed even under field conditions [68,72,74–77]. Seven QTLs for *O. crenata* resistance and three QTLs for *O. foetida* resistance were identified using the faba bean. Co-localization of QTLs for *O. crenata* and *O. foetida* resistance in chromosome V confirms a common resistance against both parasites [75].

Tomato (Solanum lycopersicum)

Efforts to find natural *Orobanche*/*Phelipanche*-resistant tomato genotypes were unsuccessful, and no *Orobanche*/*Phelipanche* resistance was found in any wild tomato species [78]. However, *Orobanche*/*Phelipanche* resistance based on the low induction of germination has attracted attention in the tomato. Recently, the fast-neutron-mutagenized homozygotic recessive tomato mutant *Sl-ORT1* was found to be highly resistant to various *Orobanche* and *Phelipanche* spp. (*P. aegyptiaca*, *P. ramosa*, *O. cernua* and *O. crenata*), and the resistance was ascribed to the low-induction germination of the parasitic weeds seeds [78–80]. In *Sl-ORT1*, yield loss by the mutation under non-infested field conditions was small [79]. A new improved tomato cultivar 'Red setter tilling', which was developed in the genetic background of a cultivar 'Red setter' using a targeting-induced local lesions in genomes (TILLING) platform, was resistant to *P. ramosa* because of a reduction in the synthesis of the germination stimulant [81]. The germination percentage of *P. ramosa* seeds was reduced by up to 90% with the application of extracts from tomato plants expressing the *SlCCD7* antisense construct due to significantly decreased levels of SL compared with the wild type [82]. In addition, several tomato cultivars with resistance to *P. aegyptiaca* were found in Turkey [83] and Iran [84] under outdoor conditions. Torres-Vera et al. [85] found that three principal defence-regulating hormonal pathways (SA, JA and abscisic acid) and SL biosynthesis genes *SlD27* and *SlCCD8* were induced after *P. ramosa* infection to tomato. These findings imply a complex regulation of plant defences that involves classical defence hormones, and suggest an additional role of SL at the post-attachment stage in the tomato–*P. ramosa* system.

Pea (Pisum sativum)

Recently, a highly *O. crenata*-resistant pea line, named ROR12, was identified [86,87]. The resistance mechanism might involve the low induction of germination due to reduced secretion of SLs. The reduction of SL did not affect the yield of ROR12 [86,87]. The resistance of ROR12 is controlled by one or a few major genes localized on the pea linkage group 3 [86]. QTLs associated with *O. crenata* resistance were identified using recombinant inbred lines derived from a cross between a wild pea, *P. sativum* spp. *syriacum* accession P665, and a susceptible pea variety, *P. sativum* spp. *sativum* cv. Messire [88].

Chickpea (Cicer arietinum)

The resistance of several chickpea genotypes to *O. foetida* has been investigated and three genotypes, FLIP 98-22C, Nayer and Beja 1, show partial resistance. Their resistance was ascribed to incompatibility [89]. Among 30 radiation-mutagenized chickpea mutants, five shared a strong *O. foetida* resistance based on a low induction of germination and incompatibility. When infested by *O. foetida*, most of the resistant mutants shared an enhanced level of soluble phenolic content, PAL activity and guaiacol peroxidase and polyphenol oxidase activities, in addition to glutathione and ascorbate peroxidase genes expression in the roots [90].

Tobacco (Nicotiana tabacum)

Among 89 tobacco genotypes, two ones, TB 22 and Kramograd NHH 659, did not show any susceptibility to *P. aegyptiaca* in pot experiments. Five SSR loci from linkage groups 2, 10, 11 and 18 of a tobacco reference map were identified as DNA markers linked to gene(s) controlling *P. aegyptiaca* resistance in tobacco [91].

Oilseed rape (Brassica napus)

Gauthier et al. [92] characterized resistance to *P. ramosa* in oilseed rape. Three cultivars, ‘Darmor’, ‘Campo’ and ‘Shakira’, had resistance based on a low induction of germination, and the resistance of five cultivars, ‘Darmor’, ‘Campo’, ‘Adrianna’, ‘Expert’ and ‘Shakira’, was ascribed to incompatibility. In particular, infection of *P. ramosa* on the cultivar ‘Darmor’ remained significantly low compared to the other genotypes [92].

Sesame (Sesamum indicum)

Five sesame genotypes with an interesting trait were identified. *P. aegyptiaca* formed tubercles on their roots but no parasite shoots emerged [93]. Such sesame genotypes could be used as both trap crops and as breeding sources for the development of resistant genotypes [93].

Grass pea (Lathyrus sativus)

Promising sources of *O. crenata* resistance have been identified in wild peas (*Lathyrus cicera*) whose resistance was ascribed to a low induction of germination, incompatibility and escape from the parasite due to precocity or small root biomass [94]. Studies on the responses to *O. crenata* of 52 grass pea accessions under field conditions suggested that early maturing accessions and very late maturing accessions were less infected [95]. In addition, nine accessions, which were selected through a calculation of the deviations from the polynomic nonlinear regression between days to flowering of the host and the number of emerged parasites, would have true genetic resistance that was not dependent on the short and long growth length [95].

Tolerant varieties

Tolerance is used to describe the ability of the host plant to withstand the adverse effects caused by the attached parasitic weeds, regardless of their number [96]. Researches on tolerant varieties have not progressed compared to those of resistant varieties. However, tolerance will act as a safety net to prevent a sudden and unforeseen collapse in basic food supply in situations where resistance is overcome by root parasitic weeds [97]. Different tolerance criteria have been suggested, ranging from host plant damage scores to high yield, yield loss or relative yield loss under a *Striga* infestation. However, these criteria fail to distinguish the effects of tolerance and resistance on yield [98]. The relationship between the biomass of *Striga*-infected rice plants compared to uninfected rice plants and the dry weight (DW) of *Striga* attached to the rice roots identified several tolerant varieties [20]. A measurement of the photosynthesis rate at 30 days after sowing was a good indicator of *S. asiatica* tolerance for rice genotypes [21]. Three local landraces of sorghum in Sudan attained a satisfactory grain yield and crop biomass in spite of an *S. hermonthica* infection in field experiments at two locations. They may have tolerance to infection by the parasite [12]. Results from field experiments indicate that the grass pea is a less tolerant species to *O. crenata* parasitism compared to the faba bean and pea [99]. Identification of QTLs for tolerance would facilitate the systematic screening of a large group of crop genotypes and enable researchers to include this trait in cultivars with high levels of resistance [97].

Microbiological approach

Fusarium spp.

The fungal isolates reported to be pathogenic to parasitic weeds are, for the most part, *Fusarium* spp. [1]. Incorporation of *Fusarium oxysporum* (isolate 34-FO) inoculum into sorghum planting hills decreased *S. hermonthica* emergence and increased sorghum biomass in a field in Burkina Faso [100]. Nzioki et al. [101] developed a simple method using toothpicks for fungal delivery and trained smallholder farmers in Kenya to produce the biocontrol agent. In more than 500 farmers’ fields in Kenya, incorporation of *F. oxysporum* f.sp. *strigae* inoculum into the soil resulted in an average of 40%–50% increased maize yield [101]. By contrast, no difference was observed in the plant growth parameters and yield between maize plants grown from seeds inoculated with *F. oxysporum* f.sp. *strigae* and ones without any inoculation in *S. hermonthica*-infested fields in Kenya [102]. Unveiling the conditions under which *Fusarium* spp. can successfully control *Striga* is awaited. Inoculation of *F. oxysporum* f.sp. *strigae* did not have a harmful effect on rhizosphere prokaryotes, indigenous total fungal community and specific arbuscular mycorrhizal fungal taxa [103–105]. Coating sorghum seeds with a biocontrol strain of *F. oxysporum* had no adverse effects on sorghum seed germination, emergence or growth [106,107]. Twelve promising sorghum lines were identified with farmer-preferred agronomic traits and *F. oxysporum* compatibility. Using these sorghum lines, the development of an *S. hermonthica* control method in sorghum through the integration of host resistance and

F. oxysporum inoculation is expected [107]. The identified mechanisms by which *F. oxysporum* f.sp. *strigae* control *S. hermonthica* are (i) complete digestion of *S. hermonthica* seedlings inside the host and (ii) wilting and killing the emerged *S. hermonthica* plants by clogging their vessels with hyphae [108]. The incorporation of three variant strains of *F. oxysporum* f.sp. *strigae*, each of which excrete tyrosine, leucine and/or methionine, decreased *S. hermonthica* emergence and increased maize yield in *S. hermonthica*-infested fields [101]. In addition, the absence of *Fusarium* toxin production by these variants and wild-type *F. oxysporum* f.sp. *strigae* was verified [101]. Plants of *O. cernua* infected by *F. oxysporum* Schltdl. collected from other plants of the parasite, quickly darkened and died. Genetic studies on infected and uninfected *O. cernua* suggested that *F. oxysporum* (i) caused heavy reactive oxygen species damage, (ii) induced significant irrevocable genotoxic effects on the DNA, (iii) disturbed protein metabolism and synthesis and (iv) triggered apoptosis in the parasite [109]. Two *F. compactum* isolates highly pathogenic to *O. crenata* and *O. ramosa* were identified [110].

Arbuscular mycorrhizal (AM) fungi and rhizobium

Mycorrhizal fungi offer two advantages as biocontrol agents: they are not pathogenic to any crop plant, and they provide important additional benefits such as improved water and mineral nutrition. Their use as biocontrol agents offers an attractive complementary approach to breeding strategies and other biocontrol methods [111]. Inoculation of maize cultivars with AM fungi reduced the incidence and biomass of *S. hermonthica*. The inoculation increased N and P contents in maize cultivars, irrespective of the parasite infection [112]. Production and exudation of SL were significantly reduced by AM fungi symbiosis in tomato and the germination-inducing activities of *P. ramosa* were significantly ($p < 0.01$) lower in tomato plants colonized by AM fungi than in non-colonized tomato plants [113]. When sunflower was inoculated simultaneously with *O. cumana* and AM fungi, a moderate level of protection against the parasite was observed. This protection did not only rely on a reduced production of germination stimulants. Mycorrhizal root exudates had a negative impact on the germination of *O. cumana* [111]. Root exudates from pea plants colonized by AM fungi had lower germination-inducing activities to *O. crenata*, *O. foetida*, *O. minor* and *P. aegyptiaca* than those from non-mycorrhizal plants [114].

Several *Rhizobium* strains have been known to decrease the damage caused by parasitic weeds. The mechanisms of induced resistance in the pea by *Rhizobium leguminosarum* against *O. crenata* involve an elevated induction of the phenylpropanoid pathway, conferring mechanical and chemical barriers against the invading parasite [115]. Two *R. leguminosarum* strains (Mateur and Bouselem.96) were selected as potential inoculants to protect faba beans against *O. foetida* and to promote the host's growth in pot and hydroponic co-culture (rhizotron) experiments [116]. Even in a faba bean field, the antagonistic effects of the strain Mateur on *O. foetida* were confirmed [117]. Inoculation of chickpeas with *Rhizobium* strains significantly decreased *O. crenata* and *O. foetida* seed germination and number of tubercles [118,119]. The effects of *Rhizobium* sp. strain PchAZm on *O. foetida* attacking chickpea roots were accompanied by enhanced levels of defence-related enzymes, PAL and peroxidase, in the host [120]. In addition, increased phenolic levels were recorded in the roots of *Rhizobium*-inoculated chickpea in the presence of *O. foetida* [120].

Fernández-Aparicio et al. [121] compared infection by *O. crenata* among a wild type, two non-nodulating and non-mycorrhizal mutants, and a super-nodulated mutant of the pea and barrel medic (*Medicago truncatula*). In both hosts, the establishment of *O. crenata* parasitism increase on the non-nodulating and non-mycorrhizal mutants suggested that *Orobanche* infection was partly controlled by pathways for AM fungi and *Rhizobium* symbiosis in the hosts [121].

Other fungi and bacteria

Aspergillus alliaceus isolated from *O. cernua* in sunflower fields very quickly caused necrosis and then greatly diminished the number of attachments, tubercles and emergent shoots as well as the total shoot number of *O. crenata* in laboratory, pot and field experiments [122]. Among the plant growth-promoting rhizobacteria tested by Mounde et al. [123], *Bacillus subtilis* GBO3 and *Burkholderia phytofirmans* PsJN had considerable potential in both *S. hermonthica* suppression through preventing germination and growth promotion of sorghum. A culture filtrate of an actinomycete strain, *Streptomyces enissocaesilis*, significantly reduced the germination of *O. cumana* seeds in germination tests in Petri dish and rhizotron assays [124]. In addition, reduction of *O. cumana* tubercle formation, increase in activity of a defence enzyme, polyphenol oxidase, in sunflower roots and improvement of beneficial microflora in the rhizosphere soil of host plants were observed in *S. enissocaesilis*-infested pots [124]. An endophytic bacterium, *Pseudomonas* strain *PhelS10*, originating from tomato roots, suppressed *P. aegyptiaca* seed germination and reduced the number of *P. aegyptiaca* on tomato roots [125].

These examples illustrate the potential of some fungal and bacterial isolates as promising biocontrol agents.

Cultural practices

Trap crop and catch crop

Germination activities of rhizosphere soil, rhizosphere soil extracts and plant extracts of soybean (*Glycine max*) and maize collected in pot and field experiments were evaluated, from the view point of using soybean and maize as trap crops for *O. cumana* in sunflower-producing areas. The results suggested that soybean and maize could induce *O. cumana* germination and that they could be used as trap crops to control the parasite [126,127]. Soybean cultivars with many root nodules may have a higher potential as trap crops to control *O. cumana* because the germination percentage of the parasite positively correlates with soybean nodule diameter and DW [127]. A compound from rye (*Secale cereale*) root exudates, ryecarbonitriline A, induced germination of *O. cumana*, suggesting that rye has potential as a trap crop in sunflower production because it is not a host of the parasite [128]. Among other compounds exuded by rye roots, ryecyanatine A promoted a rapid cessation of *O. cumana*, *O. crenata* and *O. minor* radicle growth and ryecarbonitriline B had the same activity against *O. cumana* radicles [128]. Rhizosphere soil of foxtail millet (*Setaria italica*) cultivars had a germination-inducing activity to *O. cumana* seeds and rotation of foxtail millet and sunflower reduced *O. cumana* infection on sunflower. These results suggest that using foxtail millet as a trap crop is an effective way to reduce the incidence of *O. cumana*. The high adaptability of foxtail millet to dry conditions in China where farmers are suffering large-scale *O. cumana* infestation is an advantage of this crop in controlling the parasite [129]. A reduction in the emergence and shoot DW of *O. crenata* in lentil (*Lens culinaris*) fields were observed by growing flax (*Linum usitatissimum*) as a trap crop and lentil as a catch crop two months before the main lentil sowing [130].

The effect of trap crops on the management of *P. aegyptiaca* in tomato cultivation was studied in pot experiments by using eight crops: Egyptian clover (*Trifolium alexandrinum*), sesame, mungbean (*Vigna radiata*), flax, brown Indian hemp (*Hibiscus cannabinus*), cotton (*Gossypium hirsutum*), pepper (*Capsicum annuum*) and black-eyed pea (*Vigna unguiculata*). In particular, sesame and brown Indian hemp decreased the biomass of *P. aegyptiaca* and increased tomato yield and were found to be the best trap crops [131]. The pea is also a potential trap crop to control *P. aegyptiaca* and *O. foetida* because the crop was not parasitized by the parasites but induced their germination [132]. Lilies (*Lilium* spp.), which are popular ornamental and medicinal plants in China, were proposed as a candidate trap crop for *P. aegyptiaca* for the same reasons as those for pea and *O. foetida* [133].

Differences in the germination-inducing activity to *O. minor* among wheat (*Triticum aestivum*) varieties including those with differing ploidy levels were studied as wheat was reported to have potential as a trap crop for the parasite [134,135]. Varietal differences were found in the germination-inducing activity [134], and germination of *O. minor* increased gradually with increasing ploidy levels of wheat [135]. Root exudates collected from cotton grown hydroponically, rhizosphere soil of field-grown cotton and plant extracts from the cotton had a germination-inducing activity to *O. minor* [136]. Selection and breeding of varieties with a high germination-inducing activity to *O. minor* would be possible in wheat and cotton. The screening of more than 600 Chinese medicinal herb species for an investigation of their germination-inducing activities to *O. cumana*, *O. minor* and *P. aegyptiaca* indicated that the methanolic extracts of many Chinese herbal species effectively stimulate seed germination of the parasites [137].

An economic analysis of different *S. hermonthica* control options including soybean-maize rotation, in which soybean was expected to act as a trap crop, was conducted in Western Kenya. The rotation was highly profitable due to increases in maize yield and additional production of soybean, compared to maize mono-cropping [138].

Intercropping and mixed cropping

The development of push-pull technology has been reported. In this technology, *Desmodium* spp. are used as an intercrop due to their allelopathic effects on *S. hermonthica*. Isoschaftoside extracted from silverleaf desmodium (*D. uncinatum*) roots was identified as the main growth inhibitor of germinated *S. hermonthica* radicles [139]. The number of farmers who adopted the technology was reported as 50,000 in 2013 [140], 80,000 in 2015 [141] and 125,000 in 2016 [142] in East Africa. An economic analysis by De Groote et al. [138] showed that push-pull technology was most profitable but required a higher initial investment cost, compared with soybean-maize rotation, green manure crop (*Crotalaria ochroleuca*)-maize rotation and adoption of herbicide-resistant maize (IR-maize) varieties. They pointed out that the limitation of the technology was that *Desmodium* spp. and Napier grass (*Pennisetum purpureum*), which were planted as border crops to attract stem borers, were sensitive to drought and that this technology was only recommended in areas with sufficient livestock and a demand for fodder to make money out of the *Desmodium* spp. and Napier grass pastures [138]. To expand the push-pull technology to areas where livestock is not a major component of the farming system, effects and economic benefits of intercropping maize with food legumes were compared with that with *Desmodium* spp. Although intercropping maize with food legumes was more profitable than a maize mono-crop, greenleaf desmodium (*D. intortum*) provided a more consistent and significant suppression of *S. hermonthica* and higher economic benefits than food legumes [143]. Furthermore, to expand the push-pull technology to drought-prone areas, climate-adapted push-pull technology using drought tolerant *Desmodium* spp. and Napier grass (or other grasses) as the intercrop and border crop, respectively, has been developed [141,142,144–147]. This improved technology is currently practised by more than 54,000 farmers in East Africa [142] and a higher percentage of women perceived the improved technology as very effective compared to men [146]. *D. uncinatum* and *D. intortum* were compared in their own biomass production and in their growth-promoting effects on maize. *D. intortum* consistently gave a higher fodder yield compared with *D. uncinatum*, but resulted in a somewhat lower maize grain yield [148]. Push-pull technology succeeded in controlling *S. hermonthica* in rice [149], finger millet (*Eleusine coracana*) [150] and sorghum [151] cultivation, as well as maize.

Intercropping food legumes (faba bean and pea) with Egyptian clover reduced *O. crenata* infection, irrespective of host food legumes [152]. From the viewpoint of controlling *Orobanche* and *Phelipanche* by intercropping or mixed cropping, attention has been paid to black oat (*Avena strigosa*) because it exudes avenaol, which has a high germination-inducing activity to *P. ramosa* seeds [153]. Mixed cropping of cowpea and sorghum may provide an easy and accessible means for controlling *S. gesnerioides*, as sorghum roots exude sorgolactone, sorgomol and 5-DS [11], which induce germination of *S. hermonthica* seeds but inhibit the germination of *S. gesnerioides* seeds [154]. The inhibiting activities of some SLs to *S. gesnerioides* germination are attributable to their stereostructures [154].

Other cultural practices

Many studies report a decrease in parasitic weeds infection with the application of N and P nutrients. Dramatic increases in SL production by N and P deficiency have been reported in red clover (*Trifolium pratense*), sorghum and tomato, inducing more germination of the parasitic weeds' seeds[155]. This relationship was confirmed in associations of maize–*S. hermonthica* [155], rice–*S. hermonthica* [156], sorghum–*S. hermonthica* [157], tobacco–*O. cumana*/*O. crenata* [158] and faba bean–*O. foetida* [73]. Only P deficiency promoted SL exudation in alfalfa and tomato, and N as well as P deficiencies promoted it in Chinese milk vetch (*Astragalus sinicus*), marigold (*Tagetes patula*), lettuce (*Lactuca sativa*) and wheat [159]. These findings suggest that a fertilizer application could play a vital role in reducing germination stimulant production in host plants and hence, possibly, the infection of parasitic weeds. Micro-dosing of diammonium hydrogen phosphate fertilizer, which is commercially available and popular among farmers in Africa, was proposed as an efficient and cost-effective *S. hermonthica* control option because it reduced *S. hermonthica* damage in sorghum fields in Mali [157]. *Striga* infestation became heavy as soil K content increased in farmers' fields in Tanzania and Nigeria [160,161]. The excess K treatment resulted in an increased germination-inducing activity of tobacco root exudates to *O. cumana* and *P. aegyptiaca* [158].

The effects of organic matter amendment on *S. hermonthica* control have been controversial [162]. High quality organic matter (low C:N ratio) incorporated in the soil significantly depressed *S. hermonthica* seed survival, emergence and biomass [162,163]. Ethylene induced *S. hermonthica* germination but the soil ethylene concentration was not affected by the quality of the applied organic matter, indicating that the effect of high quality organic matter on *S. hermonthica* control was irrelevant to ethylene in the soil [162]. Nutrient release, in particular N, through the decomposition of organic matter was proposed as the probable cause of the depressive effects on *S. hermonthica* [162,163].

Early planting of tomato in Turkey resulted in the lowest *P. aegyptiaca* emergence and the highest tomato yield [83]. Early sowing of sorghum in Nigeria increased *S. hermonthica* emergence and the optimal sowing date differed among sorghum varieties [164]. Investigation of the appropriate planting/sowing date under each target condition would be necessary to control parasitic weeds.

For high-value cash crop production, soil solarization and a biochar application would be options to control parasitic weeds. Soil solarization by covering soil with transparent plastic film was effective to control *P. ramosa* in tomato production under greenhouse conditions in Italy and Turkey [165–167]. The efficacy of this technique was improved when combined with supplementation of organic matter [166,167]. The efficacy also increased when repeated or long-term solarization was conducted [165,167]. In Israel, adding biochar to soil decreased *P. aegyptiaca* germination, leading to improved tomato growth. The major cause of the decrease in the germination percentage was physical adsorption of the stimulant molecule by biochar [168]. Another approach, that of covering soil with maize straw (i.e. mulching), suppressed *S. hermonthica* in maize fields in Kenya, but the effect was much weaker than that of the intercropping of maize with *D. uncinatum* [140].

Chemical control

Suicidal germination

The suicidal germination approach was proposed as far back as 1976. This methodology involves the application of a germination stimulant to the soil in the absence of a host. The seeds of the parasite will germinate but soon die due to the lack of nutrients. However, field trials on the efficacy of artificial germination stimulants to induce suicidal germination of the parasitic weeds have not been conducted, probably because of the instability of the stimulants, particularly in alkaline soils, and lack of a proper formulation [1,169]. Kgosi et al. [170] evaluated the activities of five SL analogues in soil using *S. hermonthica* or *S. asiatica* seeds in packets which were put in pots with pH neutral soil, and then treated with aqueous solutions of the analogues. All of the compounds induced germination under these conditions and the best performing stimulant, which was derived from 1-tetralone, induced 98.0% germination for *S. hermonthica* seeds [170]. Furthermore, a formulated SL mimic, T-010, and a formulated SL analogue, Nijmegen-1, reduced the emergence of *S. hermonthica* in sorghum fields and *P. ramosa* in tobacco fields, respectively; thus, the technical feasibility of suicidal germination was proved [169,171]. It should be pointed out that both T-010 and Nijmegen-1 are hydrolysed faster than an SL analogue, GR24, which had been reported as an unstable compound in soil [169,172]. The feasibility of suicidal germination cannot be disesteemed because of an instability of artificial germination stimulants. The germination-inducing activity of T-010 in Petri dishes was lower than GR24, but T-010 induced significantly more seed germination than GR24 in soil, suggesting that mobility in soils is more important than intrinsic activity for a suicidal germination inducer [169]. Structure modification of artificial germination stimulants resulted in an improvement in the germination-inducing activity [173–176]. Although conditioning prior to applying artificial germination stimulants was a prerequisite for the success of a suicidal germination approach [169,171], Yao et al. [177] reported that conditioning was probably not the indispensable stage of *P. aegyptiaca* based on the finding that the transcript level of genes relating to SL signalling was not up-regulated by the conditioning treatment.

The identification of SL receptors in parasitic weeds unlocks the door for high-throughput chemical screens, similar to the success with *Arabidopsis* KAI2 receptor to identify additional parasite germination agonists [178,179]. Yoshimulactone Green, which activates SL signalling and illuminates signal perception by SL receptors, enabled access to SL receptors and observation of the regulatory dynamics of SL signal transduction in *S. hermonthica* [180]. *Arabidopsis* expressing *ShHTL7*, the most functionally sensitive SL receptor in *S. hermonthica*, could function to screen chemicals to induce germination of the parasite [181].

Studies on natural germination stimulants have progressed. Sesquiterpene lactones, dehydrocostus lactone, costunolide, tomentosin, 8-epidanthatin and a non-sesquiterpene lactone, heliolactone, were isolated from sunflower root exudates as germination stimulants for *O. cumana* [182–184]. Three new polyphenols, named peapolyphenols A–C, isolated from pea root exudates were found to strongly stimulate seed germination of several *Orobanche* and *Phelipanche* spp. [185]. Soyasapogenol B, which specifically induced *O. minor* germination, and trans-22-dehydrocampesterol, which induced *O. crenata*, *O. foetida*, *O. minor* and *P. aegyptiaca* germination, were isolated from common vetch (*Vicia sativa*) root exudates [186]. From oilseed rape root exudates, 2-phenylethyl isothiocyanate was identified as a germination stimulant for *P. ramosa* [187]. Root exudates from black oat contained avenaol, which is a potent germination stimulant of *P. ramosa* seeds, but it exhibited only a weak activity to seeds of *S. hermonthica* and *O. minor* [153]. The structure of a major SL produced by *M. truncatula* was determined and named medicaol [188]. Medicaol has a seven-membered cycloheptadiene in the A ring instead of a typical six-membered cyclohexene [188]. Novel SLs, zealactones, were isolated from maize root exudates as a germination stimulant of *S. hermonthica* seeds [189]. The mechanism of host recognition by *Orobanche* and *Phelipanche* might have been specialized to different combinations of SLs and their concentrations present in each host root exudate [190]. The absolute configurations of enantiomerically pure SL analogue series were elucidated by X-ray analyses and CD spectra. It was confirmed that analogues bearing the *R*-configured butenolide moiety showed enhanced biological activity [191].

Herbicides

One potential option that may offer a practical means for small-scale farmers to control parasitic weeds is the use of a seed treatment with low doses of acetolactate synthase (ALS)-inhibiting herbicides (imidazolinone herbicides) such as imazamox, imazapic and imazapyr.

Imidazolinone resistance (IR) genes were incorporated into tropical maize lines that adapted to the growth conditions in Africa and the imazapyr-coated seeds of these IR maize lines planted under *S. hermonthica* infestation in Nigeria supported very few emerged parasites and sustained a limited yield loss [192,193]. In four countries of Eastern Africa, imazapyr-coated seeds of other IR maize varieties supported significantly fewer *Striga* emergence and showed more grain yield than commercial varieties without the herbicide coating [194]. In Israel, application of imazapic and imazapyr during tomato cultivation using an IR tomato mutant demonstrated high *P. aegyptiaca* control efficacy [195].

Glyphosate disrupts the biosynthesis of aromatic amino acids by inhibiting 5-enolpyrubylshikimate-3-phosphate synthase (EPSPS). This glyphosate activity was confirmed in *P. aegyptiaca* using glyphosate-resistant tomatoes [196].

Dor et al. [197] showed that the main mechanism by which ALS-inhibiting herbicides and glyphosate control *P. aegyptiaca* is direct inhibition of the enzymes ALS and EPSPS, which are present and active in the parasite tissues. Around the same time, a secondary effect of glyphosate action, inhibition of the translocation of phloem-mobile solutes from the tomato to *P. aegyptiaca*, was indicated [198].

Adjustment of doses and timing of the herbicide application is another important topic. In a decision support system developed in Israel for the control of *P. aegyptiaca* in tomato fields, the timing of the herbicide application was based on a thermal time model that was developed to predict parasitism of *P. aegyptiaca* on tomatoes [199]. The model was also effective for predicting the entire parasitism dynamics, not only for predicting the first attachment, and could be used for precise temporal chemical management of *P. aegyptiaca* in carrot (*Daucus carota*) fields [200]. Three sequential foliar applications of glyphosate at 108 g/ha completely controlled *P. aegyptiaca* in carrot fields [201,202]. Moreover, applying glyphosate to carrot plants at high temperature injured them and reduced the *P. aegyptiaca* control efficacy [202]. The effects of temperature and water conditions on *O. crenata* seed germination and radicle growth were determined from the view point of developing a predictive infection model [203].

SA- and JA-mediated plant defence responses

Induction of systemic acquired resistance in host plants to root parasitic weeds by a foliar application of SA and an SA analogue (benzothiadiazole [BTH]) was proposed. The induction was further evidenced using faba bean–*O. crenata* and faba bean–*O. foetida* systems [64,204]. A foliar application of BTH or JA on rice induced an increased resistance against *S. hermonthica*, indicating that BTH and JA induce systemic resistance against the parasite in rice [24]. Interestingly, transgenic SA-deficient (*Nah*G) rice plants exhibited an enhanced resistance to *S. hermonthica*. However, a foliar application of BTH did not complement the loss of SA in *Nah*G rice plants, suggesting that BTH and endogenous SA may have different effects on *S. hermonthica* resistance in rice [24]. Sunflower seeds pretreated with SA and then grown in pots containing *O. cumana* seeds showed an increased biomass via reducing the number and biomass of established *O. cumana*, suggesting that the treatment invokes a defence mechanism of the host against the parasite [205].

SL biosynthesis inhibitors

SLs are biosynthesized through carotenoid cleavage, and possibilities to reduce SL production in rice roots by using carotenoid biosynthesis inhibitors have been studied. A low concentration of carotenoid inhibitors, fluridone, norflurazon, clomazone and amitrole significantly decreased SL production by rice roots with no effect on rice growth, suggesting an effective technology to control parasitic weeds [206]. Ito et al. [207] discovered that a triazole-type chemical, TIS13, is a lead chemical for SL biosynthesis inhibitors in rice, and a TIS13 treatment to rice seedlings reduced SL levels in both roots and root exudates with growth retardation of rice. The structure of TIS13 was modified to develop more potent and specific inhibitors. As a result, TIS108 was found to decrease SL levels in roots and root exudates without growth retardation of rice [207,208]. A gibberellin (GA) treatment in a nutrient solution for a rhizotron experiment reduced the infection of rice plants by *S. hermonthica* due to the novel plant hormone crosstalk in which the application of GA to rice plants reduced the level of SLs [209].

SLs act as endogenous hormones to inhibit shoot branching. The combination of SL-deficient host plants which tend to have many branches with an SL mimic, 4-Br debranone, was proposed because the mimic had a low germination-inducing activity to *S. hermonthica* and a high shoot branching inhibiting activity [210].

Decomposition of SL in soil

Hydrolysis of SLs by either borax or thiourea was verified in a laboratory and a novel concept for parasitic weed control by decomposing SLs in soil was proposed [172]. This concept was proved in experiments where borax and thiourea were applied to root zones of tomatoes growing in *O. crenata*-infested soil. Effective quenching of SLs could be achieved using borax and thiourea at an effective concentration of 1–5 mmol/L, which was well below the damaging range exerting phytotoxicity on tomatoes [211]. These results demonstrate that the concept of timely SL decomposition in soil will be a feasible method for parasitic weed control.

Other chemical control agents

A galactosyl-sucrose trisaccharide, planteose, was found to be a required storage carbohydrate for the early stage of germination of *O. minor* through a metabolomics analysis of germinating seeds of the parasite. Nojirimycin bisulfite inhibited the germination of *O. minor* seeds by blocking the supply of glucose from planteose and sucrose, suggesting that a galactosidase inhibitor such as nojirimycin bisulfite is a lead chemical to develop an *O. minor*-specific herbicide [212]. A proteome analysis of the pea parasitized by *O. crenata* [213], a metabolome analysis of *P. aegyptiaca* at several growth stages [214] and a transcriptome analysis of several parasitic weeds [215] might lead to the identification of new targets for the specific control of parasitic weeds. Holbrook-Smith et al. [216] developed a high-throughput screen for compounds that antagonize SL signalling in the model plant *Arabidopsis thaliana*. One compound selected, soporidine, specifically inhibited the function of an SL receptor in *S. hermonthica* and then the parasite's germination, suggesting that the small molecules that perturb SL signalling are useful for disrupting the lifecycle of *S. hermonthica* [216]. A foliar application of maleic hydrazide to tomato reduced *P. aegyptiaca* attachment on the host roots without any influence on tomato foliage or root DW. Maleic hydrazide was registered for use in Israel in 2013 with the specified protocol, and today it is widely used by most Israeli tomato growers for *P. aegyptiaca* control [217]. Amino acids, lysine, methionine and tryptophan applied to red clover fields by irrigation interfered with *O. minor* early development and may have the potential to be integrated into biorationale programmes of the parasite [218]. Efficacy of a soil fumigant, dazomet, which releases the toxic gas methyl isothiocyanate to control *P. mutelii* was confirmed under field conditions in Australia [219]. Although soil fumigation indiscriminately targets both beneficial and harmful biota [166], this method is an option to eradicate the seed bank of parasitic weeds.

Host-induced gene silencing

The concept of host-induced gene silencing is that the silencing constructs for essential parasite genes are transformed to host plants and suppress the parasite's growth because of movement of the small interfering RNA from the host to the parasite, where the actual silencing takes place [220]. Recently, host-induced gene silencing has been used to silence genes encoding the acetyl-CoA carboxylase in yellowbeak owl's-clover (*Triphysaria versicolor*), a facultative root parasitic plant, and the KNOTTED-like homeobox transcription factor, SHOOT MERISTEMLESS-like in dodder (*Cuscuta pentagona*), a shoot parasitic plant. This successfully reduced parasite viability, confirming the usefulness of this technique [220–222]. To identify putative candidate genes for host-induced gene silencing, high throughput screening protocols using a virus-induced gene silencing system in *S. hermonthica* are useful [223]. Host-induced gene silencing is one of the fields that utilizes results from The Parasitic Plant Genome Project [215].

Integrated management

The package involving the *S. hermonthica*-resistant sorghum variety, water harvesting through tied-ridge tillage and N fertilizer suppressed the parasite development and increased the host's grain yield more efficiently than each component of the package in sorghum fields in Ethiopia. In particular, the resistant variety served as a central component in the package [224]. Reinhardt and Tesfamichael [151] studied how to integrate *S. asiatica* tolerant sorghum cultivars by intercropping *D. intortum* and using N fertilizer, and considered parasite control and host yield. They achieved 100% *S. asiatica* control and a dramatic increase in sorghum yield with 100 kg N/ha in a 1:1 sorghum–*D. intortum* intercropping [151]. The use of an *S. hermonthica*-resistant sorghum variety, biocontrol based on *Fusarium* inoculum and intercropping with cowpea had a synergistic effect in controlling the parasite [100]. In an association of tomato–*P. ramosa*, 12 agronomic, chemical, biological and biotechnological strategies for the control of the parasitic weed were evaluated as basic information for further integrated management. Based on the information, the integrated strategy composed of a biostimulant that contains humic substances, N or S fertilizers, compost activated with *F. oxysporum*, a soil fumigant and resistant tomato cultivars was designed. The strategy successfully mitigated the virulence of the attacks of *P. ramosa* [81]. Since it is generally believed that integrated management is the only way to cope with the parasitic weeds [1], further verification examples are needed to develop effective, economical and applicable management under each target condition.

Current situation survey and dissemination of technologies

Surveys of *S. hermonthica* infestation in Northern Cameroon over the period 1987–2005 assessed *S. hermonthica* dynamics and its control strategies [225]. The percentage of *S. hermonthica*-infested fields increased in the country and *S. hermonthica* incidence increased more in maize fields than in the already heavily infested sorghum fields, where it remains almost constant [225]. Rodenburg et al. [226] conducted the first multi-species (including *S. asiatica* and *S. hermonthica*), multi-country and single crop (rice) impact assessment of parasitic weeds in Africa, using a combination of data mining, spatial analysis and stochastic impact assessment. An estimated 1.34 million ha of rain-fed rice is infected with at least one species of parasitic weed in Africa with estimated economic losses inflicted by all parasitic weeds of roughly US$200 million, which increases by US$30 million annually [226]. In tobacco fields, the relationship between environmental variables, such as soil and bioclimatic factors, and the level of infestation with *P. aegyptiaca* and *P. ramosa* was identified on a massive scale in Greece to provide information for modelling the parasites' infestation based on abiotic factors and to create a baseline for future monitoring of their distribution. Soil pH, total humidity index and organic matter content were the most decisive variables for the severity of *P. aegyptiaca* and *P. ramosa* infestation [227].

Farmers' perceptions and the potential adoption of *S. hermonthica* control measures were evaluated in Western Kenya. Although the level of *S. hermonthica* infestation and damage was increasing in the farmers' fields, the adoption of control options was limited because the farmers thought that the control options were too risky as there was no guarantee of a direct pay-off in increased crop yield [228]. Although parasitic weed infestation was associated with poor soil fertility, farmers did not use fertilizers due to various factors, ranging from fears of undesirable agronomic side effects to a lack of quality control of fertilizers [229]. A lack of coherent policies on parasitic weeds and lack of policy implementation were observed at higher organizational levels. Accordingly, extension systems could not provide farmers with advice [229]. In Kenya, a structure questionnaire evaluated gender-specific perceptions and the extent of adoption of a new technology, in this case, a climate-adapted push-pull technology. The results indicated that a slightly higher percentage of women perceived the technology as effective compared to men [146]. Farmers' appreciation of *S. hermonthica* control technologies changed from year to year and from village to village [230]. In Ethiopia, farmers preferred sorghum landraces to improved released varieties [231]. Adoption of improved *S. hermonthica* control technologies by farmers was also limited due to a lack of information, fear of risks associated with the novel technologies, financial limitations, their preference for traditional control methods and lack of access to new variety seeds [231].

Conclusions

Several promising approaches for combatting root parasitic weeds have been developed recently such as maize varieties possessing concurrent *Striga* resistance with other stress tolerances in West Africa, a simple method using toothpicks for fungal delivery in soil for farmers in Kenya, push-pull technology widely adopted by farmers in East Africa and a decision support system for controlling *P. aegyptiaca* in Israel. In addition, progress in other approaches would increase possible elements in integrated management, which is believed as the only way to cope with parasitic weeds due to the lack of a consistently effective, economical and applicable approach irrespective of conditions. Further researches are imperative because the number of resistant and/or tolerant varieties are not enough in many crops, the validation of many microbiological approaches and chemical controls is expected under practical conditions and adjustment of cultural control to the target conditions is inevitable. Moreover, it takes some time before new biotechnology-based approaches become utilized in the control of root parasitic weeds, and dissemination of technologies including the current situation survey is another important task. A deeper understanding of parasitic weeds, host plants, their growth environment and the social circumstances of people involved should lead to the development of appropriate approaches.

Acknowledgment

This work was supported by the Japan Science and Technology Agency (JST) and Japan International Cooperation Agency (JICA) under a joint programme of Science and Technolgoy Research Partnership for Sustainbable Development (SATREPS).

Disclosure statement

No potential conflict of interest was reported by the authors.

References

[1] Rubiales D, Fernández-Aparicio M. Innovations in parasitic weeds management in legume crops. A review. Agron Sustain Dev. 2012;32:433–449.
[2] Parker C. Observations on the current status of *Orobanche* and *Striga* problems worldwide. Pest Manage Sci. 2009;65:453–459.
[3] Parker C. Parasitic weeds: a world challenge. Weed Sci. 2012;60:269–276.
[4] Ejeta G. Breeding for *Striga* resistance in sorghum: exploitation of an intricate host-parasite biology. Crop Sci. 2007;47:S216–S227.
[5] Ejeta G, Butler G. Host-parasite interactions throughout the *Striga* life cycle, and their contributions to *Striga* resistance. Afr Crop Sci J. 1993;1:75–80.

[6] Ejeta G. The *Striga* scourge in Africa: a growing pandemic. In: Ejeta G, Gressel J, editors. Integrating new technologies for *Striga* control. Singapore: World Scientific Publishing; 2007. p. 3–16.

[7] Mohamed KI, Papes M. Global invasive potential of 10 parasitic witchweeds and related Orobanchaceae. Ambio. 2006;35:281–288.

[8] Grenz JH, Sauerborn J. Mechanisms limiting the geographical range of the parasitic weed *Orobanche crenata*. Agric Ecosyst Environ. 2007;122:275–281.

[9] Mohamed AH, Housley TL, Ejeta G. An in vitro technique for studying specific *Striga* resistance mechanisms in sorghum. Afr J Agric Res. 2010;5:1868–1875.

[10] Mohamed AH, Housley TL, Ejeta G. Inheritance of hyper sensitive response to *Striga* parasitism in sorghum [Sorghum bicolor (L.) Moench]. Afr J Agric Res. 2010;5:2720–2729.

[11] Yoneyama K, Awad AA, Xie X, et al. Strigolactones as germination stimulants for root parasitic plants. Plant Cell Physiol. 2010;51:1095–1103.

[12] Mohemed N, Charnikhova T, Bakker EJ, et al. Evaluation of field resistance to *Striga hermonthica* (Del.) Benth. in *Sorghum bicolor* (L.) Moench. The relationship with strigolactones. Pest Manage Sci. 2016;72:2082–2090.

[13] Gobena D, Shimels M, Rich PJ, et al. Mutation in sorghum *LOW GERMINATION STIMULANT 1* alters strigolactones and causes *Striga* resistance. PNAS. 2017;114:4471–4476.

[14] Satish K, Gutema Z, Grenier C, et al. 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. 2012;124:989–1003.

[15] Mohamed A, Ali R, Elhassan O, et al. First products of DNA marker-assisted selection in sorghum released for cultivation by farmers in sub-Saharan Africa. J Plant Sci Mol Breeding. 2014 [cited 2017 Dec 14]; [10 p.]. DOI:10.7243/2050-2389-3-3

[16] Yohannes T, Abraha T, Kiambi D, et al. Marker-assisted introgression improves *Striga* resistance in an Eritrean farmer-preferred sorghum variety. Field Crop Res. 2015;173:22–29.

[17] Mbuvi DA, Masiga CW, Kuria E, et al. Novel sources of witchweed (*Striga*) resistance from wild sorghum accessions. Front Plant Sci. 2017 [cited 2017 Dec 14]; [15 p.]. DOI:10.3389/fpls.2017.00116

[18] Cissoko M, Boisnard A, Rodenburg J, et al. New Rice for Africa (NERICA) cultivars exhibit different levels of post-attachment resistance against the parasitic weeds *Striga hermonthica* and *Striga asiatica*. New Phytol. 2011;192:952–963.

[19] Jamil M, Rodenburg J, Charnikhova T, et al. Pre-attachment *Striga hermonthica* resistance of New Rice for Africa (NERICA) cultivars based on low strigolactone production. New Phytol. 2011;192:964–975.

[20] Rodenburg J, Cissoko M, Kayeke J, et al. Do NERICA rice cultivars express resistance to *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze under field conditions ? Field Crop Res. 2015;170:83–94.

[21] Rodenburg J, Cissoko M, Kayongo N, et al. Genetic variation and host-parasite specificity of *Striga* resistance and tolerance in rice: the need for predictive breeding. New Phytol. 2017;214:1267–1280.

[22] Atera E, Itoh K, Azuma T, et al. Response of NERICA rice *Striga hermonthica* infections in Western Kenya. Int J Agric Biol. 2012;14:271–275.

[23] Samejima H, Babiker AG, Mustafa A, et al. Identification of *Striga hermonthica*-resistant upland rice varieties in Sudan and their resistance phenotypes. Front Plant Sci. 2016 [cited 2017 Dec 14]; [12 p.]. DOI:10.3389/fpls.2016.00634

[24] Mutuku JM, Yoshida S, Shimizu T, et al. The *WRKY45*-dependent signalling pathway is required for resistance against *Striga hermonthica* parasitism. Plant Physiol. 2015;168:1152–1163.

[25] Kountche B, Hash CT, Dodo H, et al. Development of a pearl millet *Striga*-resistant genepool: response to five cycles of recurrent selection under *Striga*-infested field conditions in West Africa. Field Crop Res. 2013;154:82–90.

[26] Moumouni KH, Kountche BA, Jean M, et al. Construction of a genetic map for pearl millet, *Pennisetum glaucum* (L.) R. Br., using a genotyping-by-sequencing (GBS) approach. Mol Breeding. 2015 [cited 2017 Dec 14]; [10 p.]. DOI:10.1007/s11032-015-0212-x

[27] Gressel J. Needs for and environmental risks from transgenic crops in the developing world. New Biotechnol. 2010;27:522–527.

[28] Menkir A, Adetimirin VO, Yallou CG, et al. Relationship of genetic diversity of inbred lines with different reactions to *Striga hermonthica* (Del.) Benth and the performance of their crosses. Crop Sci. 2010;50:602–611.

[29] Badu-Apraku B, Yallou CG, Alidu H, et al. Genetic improvement of extra-early maize cultivars for grain yield and *Striga* resistance during three breeding eras. Crop Sci. 2016;56:2564–2578.

[30] Badu-Apraku B, Yallou B, Oyekunle M. Genetic gains from selection for high grain yield and *Striga* resistance in early maturing maize cultivars of three breeding periods under *Striga*-infested and *Striga*-free environments. Field Crop Res. 2013;147:54–67.

[31] Badu-Apraku B, Annor B, Oyekunle M, et al. Grouping of early maturing quality protein maize inbreds based on SNP markers and combining ability under multiple environments. Field Crop Sci. 2015;183:169–183.

[32] Badu-Apraku B, Fakorede MAB, Talabi AO, et al. Gene action and heterotic groups of early white quality protein maize inbreds under multiple stress environments. Crop Sci. 2016;56:183–199.

[33] Badu-Apraku B, Fakorede MAB, Oyekunle M. Agronomic traits associated with genetic gains in maize yield during three breeding eras in West Africa. Maydica. 2014;59:49–57.

[34] Badu-Apraku B, Fakorede MAB, Oyekunle M, et al. Gains in grain yield of Early maize cultivars developed during three breeding eras under multiple environments. Crop Sci. 2015;55:527–539.

[35] Ifie BE, Badu-Apraku B, Gracen V, et al. Genetic analysis of grain yield of IITA and CIMMYT early-maturing maize inbreds under *Striga*-infested and low–soil-nitrogen environments. Crop Sci. 2015;55:610–623.

[36] Badu-Apraku B, Fakorede MAB, Oyekunle M, et al. Genetic gains in grain yield under nitrogen stress following three decades of breeding for drought tolerance and *Striga* resistance in early maturing maize. J Agric Sci. 2016;154:647–661.

[37] Badu-Apraku B, Oyekunle M, Menkir A, et al. Comparative performance of early-maturing maize cultivars developed in three eras under drought stress and well-watered environments in West Africa. Crop Sci. 2013;53:1298–1311.

[38] Amusan IO, Rich PJ, Housley T, et al. An in vitro method for identifying postattachment *Striga* resistance in maize and sorghum. Agron J. 2011;103:1472–1478.

[39] Karaya H, Njoroge K, Mugo S, et al. Determination of levels of *Striga* germination stimulants for maize gene bank accessions and elite inbred lines. Int J Plant Prod. 2012;6:209–223.

[40] Menkir A. Effect of genetic divergence of *Striga hermonthica* (Delile) Benth.-resistant maize inbred lines on heterosis and hybrid performance under parasite pressure. Crop Sci. 2011;51:1591–1602.

[41] Menkir A, Makumbi D, Franco J. Assessment of reaction patterns of hybrids to *Striga hermonthica* (Del.) Benth. under artificial infestation in Kenya and Nigeria. Crop Sci. 2012;52:2528–2537.

[42] Akinwale RO, Badu-Apraku B, Fakorede MAB, et al. Heterotic grouping of tropical early-maturing maize inbred lines based on combining ability in *Striga*-infested and *Striga*-free environments and the use of SSR markers for genotyping. Field Crop Res. 2014;156:48–62.

[43] Mengesha WA, Menkir A, Unakchukwu N, et al. Genetic diversity of tropical maize inbred lines combining resistance to *Striga hermonthica* with drought tolerance using SNP markers. Plant Breed. 2017;136:338–343.

[44] Abdulmalik RO, Menkir A, Meseka SK, et al. Genetic gains in grain yield of a maize population improved through marker assisted recurrent selection under stress and non-stress conditions in West Africa. Front Plant Sci. 2017 [cited 2017 Dec 14]; [11 p.]. DOI:10.3389/fpls.2017.00841

[45] Runo S, Macharia S, Alakonya A, et al. *Striga* parasitizes transgenic hairy roots of *Zea mays* and provides a tool for studying plant-plant interactions. Plant Methods. 2012 [cited 2017 Dec 14]; [11 p.]. DOI:10.1186/1746-4811-8-20

[46] Li J, Lis KE, Timko MP. Molecular genetics of race-specific resistance of cowpea to *Striga gesnerioides* (Willd.). Pest Manage Sci. 2009;65:520–527.

[47] Yoder JI, Scholes JD. Host plant resistance to parasitic weeds; recent progress and bottlenecks. Curr Opin Plant Biol. 2010;13:478–484.

[48] Desalegne BA, Mohammed S, Dagne K, et al. Assessment of genetic diversity in Ethiopian cowpea [*Vigna unguiculata* (L.) Walp.] germplasm using simple sequence repeat markers. Plant Mol Biol Rep. 2016;34:978–992.

[49] Huang K, Mellor KE, Paul SN, et al. Global changes in gene expression during compatible and incompatible interactions of cowpea (*Vigna unguiculata* L.) with the root parasitic angiosperm *Striga gesnerioides*. Genomics. 2012 [cited 2017 Dec 14] [15 p.]. DOI:10.1186/1471-2164-13-402

[50] Omoigui LO, Ishiyaku MF, Ousmane B, et al. Application of fast technology for analysis (FTA) for sampling and recovery of deoxyribonucleic acid (DNA) for molecular characterization of cowpea breeding lines for *Striga* resistance. Afr J Biotechnol. 2011;10:19681–19986.

[51] Muranaka S, Fatokun C, Boukar O. Stability of *Striga gesnerioides* resistance mechanism in cowpea under high-infestation level, low soil fertility and drought stresses. J Food Agric Environ. 2011;9:313–318.

[52] Tignegre JBS, Ouedraogo JT, Melis R, et al. Identification of new sources of resistance to *Striga gesnerioides* in cowpea germplasm. Plant Breed. 2013;132:330–336.

[53] Noubissie Tchiagam J-B, Bell JM, Guissai Birwe S, et al. Varietal response of cowpea (*Vigna unguiculata* (L.) Walp.) to *Striga gesnerioides* (Willd.) Vatke race SG5 infestation. Not Bot Hort Agrobot. 2010;38:33–41.

[54] Mellor KE, Hoffman AM, Timko MP. Use of ex vitro composite plants to study the interaction of cowpea (*Vigna unguiculata* L.) with the root parasitic angiosperm *Striga gesnerioides*. Plant Methods. 2012 [cited 2017 Dec 14]; [12 p.]. DOI:10.1186/1746-4811-8-22

[55] Vrănceanu AV, Tudor VA, Stoenescu FM, et al. Virulence groups of *Orobanche cumana* Wallr., differential hosts and resistance sources and genes in sunflower. Proceedings of the 9th International Sunflower Conference. Vol. 1; 1980 June 8–13; Malaga, Spain, Paris: International Sunflower Association; 1980. p. 74–82.

[56] Miladinovic D, Dedic B, Quiróz F. *Orobanche cumana* Wallr. resistance of commercial sunflower cultivars grown in Argentina. J Basic Appl Genet. 2012;23:37–41.

[57] Imerovski I, Dimitrijević A, Miladinović D, et al. Mapping of a new gene for resistance to broomrape races higher than F. Euphytica. 2016;209:281–289.

[58] Rodríguez-Ojeda MI, Pineda-Martos R, Alonso LC, et al. A dominant avirulence gene in *Orobanche cumana* triggers *Or5* resistance in sunflower. Weed Res. 2013;53:322–327.

[59] Cvejic S, Dedic B, Jocic S, et al. Broomrape resistance in newly developed sunflower inbred lines. Proceedings of the 18th International Sunflower Conference; 2012 Feb 27–Mar 1; Mar del Plata, Argentina, Paris: International Sunflower Association; 2012. p. 1037–1042.

[60] Velasco L, Pérez-Vich B, Yassein AAM, et al. Inheritance of resistance to sunflower broomrape (*Orobanche cumana* Wallr.) in an interspecific cross between *Helianthus annuus* and *Helianthus debilis* subsp. *tardiflorus*. Plant Breed. 2012;131:220–221.

[61] Christov M. Contribution of interspecific and intergeneric hybridization to sunflower breeding. Helia. 2013;36:1–18.

[62] Cvejić S, Jocić S, Dedić B, *et al.* Determination of resistance to broomrape in newly developed sunflower inbred lines. Proceedings of the 3rd International Symposium on Broomrape (*Orobanche* spp.) in Sunflower; 2014 June 3–14; Córdoba, Spain, Paris: International Sunflower Association; 2014. p. 184–188.

[63] Louarn J, Boniface M-C, Pouilly N, et al. Sunflower resistance to broomrape (*Orobanche cumana*) is controlled by specific QTLs for different parasitism stages. Front Plant Sci. 2016 [cited 2017 Dec 14]; [14 p.]. DOI:10.3389/fpls.2016.00590

[64] Sillero JC, Rojas-Molina MM, Avila CM, et al. Induction of systemic acquired resistance against rust, ascochyta blight and broomrape in faba bean by exogenous application of salicylic acid and benzothiadiazole. Crop Prot. 2012;34:65–69.

[65] Imerovski I, Dimitrijevic A, Miladinovic D, et al. Identification of PCR markers linked to different *Or* genes in sunflower. Plant Breed. 2013;132:115–120.

[66] Akhtouch B, del Moral L, Leon A, et al. Genetic study of recessive broomrape resistance in sunflower. Euphytica. 2016;209:419–428.

[67] Şestacova T, Giscă I, Cucereavîi A, et al. Expression of defence-related genes in sunflower infected with broomrape. Biotechnol Biothchnol Equip. 2016;30:685–691.

[68] Fernández-Aparicio M, Moral A, Kharrat M, et al. Resistance against broomrapes (*Orobanche* and *Phelipanche* spp.) in faba bean (*Vicia faba*) based in low induction of broomrape seed germination. Euphytica. 2012;186:897–905.

[69] Rubiales D, Rojas-Molina MM, Sillero JC. Characterization of resistance mechanisms in faba bean (*Vicia faba*) against broomrape species (*Orobanche* and *Phelipanche* spp.). Front Plant Sci. 2016 [cited 2017 Dec 14]; [8 p.]. DOI:10.3389/fpls.2016.01747

[70] Abbes Z, Kharrat M, Pouvreau JB, et al. The dynamics of faba bean (*Vicia faba* L.) parasitism by *Orobanche foetida*. Phytopathol Mediterr. 2010;49:239–248.

[71] Fernández-Aparicio M, Kisugi T, Xie X, et al. Low strigolactone root exudation: a novel mechanism of broomrape (*Orobanche* and *Phelipanche* spp.) resistance available for faba bean breeding. J Agric Food Chem. 2014;62:7063–7071.

[72] Trabelsi I, Abbes Z, Amri M, et al. Study of some resistance mechanisms to *Orobanche* spp. infestation in faba bean (*Vicia faba* L.) breeding lines in Tunisia. Plant Prod Sci. 2016;19:562–573.

[73] Trabelsi I, Yoneyama K, Abbes Z, et al. Characterization of strigolactones produced by *Orobanche foetida* and *Orobanche crenata* resistant faba bean (*Vicia faba* L.) genotypes and effects of phosphorous, nitrogen, and potassium deficiencies on strigolactone production. S Afr J Bot. 2017;108:15–22.

[74] Kharrat M, Abbes Z, Amri M. A new faba bean small seeded variety Najeh tolerant to *Orobanche* registered in the Tunisian catalogue. Tunis J Plant Prot. 2010;5:125–130.

[75] Gutiérrez N, Palomino C, Satovic Z, et al. QTLs for *Orobanche* spp. resistance in faba bean: identification and validation across different environments. Mol Breeding. 2013;32:909–922.

[76] Rubiales D, Flores F, Emeran AA, et al. Identification and multi-environment validation of resistance against broomrapes (*Orobanche crenata* and *Orobanche foetida*) in faba bean (*Vicia faba*). Field Crop Res. 2014;166:58–65.

[77] Trabelsi I, Abbes Z, Amri M, et al. Performance of faba bean genotypes with *Orobanche foetida* Poir. and *Orobanche crenata* Forsk. infestation in Tunisia. Chil J Agric Res. 2015;75:27–34.

[78] Dor E, Yoneyama K, Wininger S, et al. Strigolactone deficiency confers resistance in tomato line *SL-ORT1* to the parasitic weeds *Phelipanche* and *Orobanche* spp. Phytopathology. 2011;101:213–222.

[79] Dor E, Alperin B, Wininger S, et al. Characterization of a novel tomato mutant resistant to the weedy parasites *Orobanche* and *Phelipanche* spp. Euphytica. 2010;171:371–380.

[80] Koltai H, LekKala SP, Bhattacharya C, et al. A tomato strigolactone-impaired mutant displays aberrant shoot morphology and plant interactions. J Exp Bot. 2010;61:1739–1749.

[81] Disciglio G, Lops F, Carlucci A, et al. Effects of different methods to control the parasitic weed *Phelipanche ramosa* (L.) Pomel in processing tomato crops. Ital J Agron. 2016;11:39–46.

[82] Vogel JT, Walter MH, Giavalisco P, et al. SlCCD7 controls strigolactone biosynthesis, shoot branching and mycorrhiza-induced apocarotenoid formation in tomato. Plant J. 2010;61:300–311.

[83] Kacan K, Tursun N. Effect of planting time and tomato varieties on broomrape (*Phelipanche aegyptiaca*) emergence and tomato yield in Western Turkey. Res Crops. 2012;13:1070–1077.

[84] Tokasi S, Bannayan Aval M, Mashhadi HR, et al. Screening of resistance to Egyptian broomrape infection in tomato varieties. Planta Daninha. 2014;32:109–116.

[85] Torres-Vera R, García JM, Pozo MJ, et al. Expression of molecular markers associated to defense signalling pathways and strigolactone biosynthesis during the early interaction tomato-*Phelipanche ramosa*. Physiol Mol Plant Pathol. 2016;94:100–107.

[86] Bardaro N, Marcotrigiano AR, Bracuto V, et al. Genetic analysis of resistance to *Orobanche crenata* (Forsk.) in a pea (*Pisum sativum* L.) low-strigolactone line. J Plant Pathol. 2016;98:671–675.

[87] Pavan S, Schiavulli A, Marcotrigiano AR, et al. Characterization of low-strigolactone germplasm in pea (*Pisum sativum* L.) resistant to crenate broomrape (*Orobanche crenata* Forsk.). Mol Plant Microbe Interact. 2016;29:743–749.

[88] Fondevilla S, Fernández-Aparicio M, Satovic Z, et al. Identification of quantitative trait loci for specific mechanisms of resistance to *Orobanche crenata* Forsk. in pea (*Pisum sativum* L.). Mol Breeding. 2010;25:259–272.

[89] Nefzi F, Trabelsi I, Amri M, et al. Response of some chickpea (*Cicer arietinum* L.) genotypes to *Orobanche foetida* Poir. parasitism. Chil J Agric Res. 2016;76:170–178.

[90] Brahmi I, Mabrouk Y, Brun G, et al. Phenotypical and biochemical characterisation of resistance for parasitic weed (*Orobanche foetida* Poir.) in radiation-mutagenised mutants of chickpea. Pest Manage Sci. 2016;72:2330–2338.

[91] Darvishzadeh R. Genetic variability, structure analysis, and association mapping of resistance of resistance to broomrape (*Orobanche aegyptiaca* Pers.) in tobacco. J Agric Sci Technol. 2016;18:1407–1418.

[92] Gauthier M, Véronéci C, El-Halmouch Y, et al. Characterisation of resistance to branched broomrape, *Phelipanche ramosa*, in winter oilseed rape. Crop Prot. 2012;42:56–63.

[93] Teimouri Jervekani M, Karimmojeni H, Brainard DC, et al. Sesame genotype influences growth and phenology of *Phelipanche aegyptiaca*. Ann Appl Biol. 2016;169:46–52.

[94] Fernández-Aparicio M, Rubiales D. Characterisation of resistance to crenate broomrape (*Orobanche crenata* Forsk.) in *Lathyrus cicera* L. Euphytica. 2010;173:77–84.

[95] Fernández-Aparicio M, Flores F, Rubiales D. Escape and true resistance to crenate broomrape (*Orobanche crenata* Forsk.) in grass pea (*Lathyrus sativus* L.) germplasm. Field Crop Res. 2012;125:92–97.

[96] Badu-Apraku B, Akinwale RO, Fakorede MAB, et al. Relative changes in genetic variability and correlations in an

early-maturing maize population during recurrent selection. Theor Appl Genet. 2012;125:1289–1301.

[97] Rodenburg J, Bastiaans L. Host-plant defence against *Striga* spp.: reconsidering the role of tolerance. Weed Res. 2011;51:438–441.

[98] Badu-Apraku B, Akinwale RO. Cultivar evaluation and trait analysis of tropical early maturing maize under *Striga*-infested and *Striga*-free environments. Field Crop Res. 2011;121:186–194.

[99] Fernández-Aparicio M, Flores F, Rubiales D. The effect of *Orobanche crenata* infection severity in faba bean, field pea, and grass pea productivity. Front Plant Sci. 2016 [cited 2017 Dec 14]; [8 p.]. DOI:10.3389/fpls.2016.01409

[100] Yonli D, Traoré H, Sérémé P, et al. Integrated management of *Striga hermonthica* (Del.) Benth. in sorghum using *Fusarium inoculum*, host plant resistance and intercropping. J Appl Biosci. 2012;53:3734–3741.

[101] Nzioki HS, Oyosi F, Morris CE, et al. *Striga* biocontrol on a toothpick: a readily deployable and inexpensive method for smallholder farmers. Front Plant Sci. 2016 [cited 2017 Dec 14]; [8 p.]. DOI:10.3389/fpls.2016.01121

[102] Avedi EK, Ochieno DMW, Ajanga S, et al. *Fusarium oxysporum* f. sp. *strigae* strain Foxy 2 did not achieve biological control of *Striga hermonthica* parasitizing maize in Western Kenya. Biol Control. 2014;77:7–14.

[103] Musyoki MK, Cadisch G, Enowashu E, et al. Promoting effect of *Fusarium oxysporum* [f.sp. *strigae*] on abundance of nitrifying prokaryotes in a maize rhizosphere across soil types. Biol Control. 2015;83:37–45.

[104] Musyoki MK, Cadisch G, Zimmermann J, et al. Soil properties, seasonality and crop growth stage exert a stronger effect on rhizosphere prokaryotes than the fungal biocontrol agent *Fusarium oxysporum* f.sp. *strigae*. Appl Soil Ecol. 2016;105:126–136.

[105] Zimmermann J, Musyoki MK, Cadisch G, et al. Biocontrol agent *Fusarium oxysporum* f.sp. *strigae* has no adverse effect on indigenous total fungal communities and specific AMF taxa in contrasting maize rhizospheres. Fungal Ecol. 2016;23:1–10.

[106] Elzein A, Heller A, Ndambi B, et al. Cytological investigations on colonization of sorghum roots by the mycoherbicide *Fusarium oxysporum* f. sp. *strigae* and its implications for Striga control using a seed treatment delivery system. Biol Control. 2010;53:249–257.

[107] Rebeka G, Shimelis H, Laing MD, et al. Evaluation of sorghum genotypes compatibility with *Fusarium oxysporum* under *Striga* infestation. Crop Sci. 2013;53:385–393.

[108] Ndambi B, Cadisch G, Elzein A, et al. Colonization and control of *Striga hermonthica* by *Fusarium oxysporum* f. sp. *strigae*, a mycoherbicide component: An anatomical study. Biol Control. 2011;58:149–159.

[109] Aybeke M. *Fusarium* infection causes genotoxic disorders and antioxidant-based damages in *Orobanche* spp. Microbiol Res. 2017;201:46–51.

[110] Abouzeid MA, El-Tarabily KA. *Fusarium* spp. suppress germination and parasitic establishment of bean and hemp broomrapes. Phytopathol Mediterr. 2010;49:51–64.

[111] Louarn J, Carbonne F, Delavault P, et al. Reduced germination of *Orobanche cumana* seeds in the presence of arbuscular mycorrhizal fungi or their exudates. PLoS One. 2012 [cited 2017 Dec 14]; [10 p.]. DOI:10.1371/journal.pone.0049273

[112] Othira JO, Omolo JO, Wachira FN, et al. Effectiveness of arbuscular mycorrhizal fungi in protection of maize (*Zea mays* L.) against witchweed (*Striga hermonthica* Del Benth) infestation. J Agric Biotech Sustain Dev. 2012;4:37–44.

[113] López-Ráez JA, Charnikhova T, Fernández I, et al. Arbuscular mycorrhizal symbiosis decreases strigolactone production in tomato. J Plant Physiol. 2011;168: 294–297.

[114] Fernández-Aparicio M, García-Garrido JM, Ocampo JA, et al. Colonisation of field pea roots by arbuscular mycorrhizal fungi reduces *Orobanche* and *Phelipanche* species seed germination. Weed Res. 2010;50:262–268.

[115] Mabrouk Y, Mejri S, Hemissi I, et al. Bioprotection mechanisms of pea plant by *Rhizobium leguminosarum* against *Orobanche crenata*. Afr J Microbiol Res. 2010;4:2570–2575.

[116] Bouraoui M, Abbes Z, Abdi N, et al. Evaluation of efficient *Rhizobium* isolates as biological control agents of *Orobanche foetida* Poir. parasitizing *Vicia faba* L. minor in Tunisia. Bulg J Agric Sci. 2012;18:557–564.

[117] Bouraoui M. Abbes Z, Rouissi M, et al. Effect of rhizobia inoculation, N and P supply on *Orobanche foetida* parasitising faba bean (*Vicia faba* minor) under field conditions. Biocontrol Sci Technol. 2016;26:776–791.

[118] Hemissi I, Mabrouk Y, Abdi N, et al. Growth promotion and protection against *Orobanche foetida* of chickpea (*Cicer aerietinum*) by two *Rhizobium* strains under greenhouse conditions. Afr J Biotechnol. 2013;12:1371–1377.

[119] Mabrouk Y, Belhadj O. Effect of the inoculation of chickpea by rhizobia on growth promotion and protection against *Orobanche Crenata*. G J B A H S. 2014;3:55–59.

[120] Mabrouk Y, Mejri S, Hemissi I, et al. Biochemical analysis of induced resistance in chickpea against broomrape (*Orobanche foetida*) by rhizobia inoculation. Phytopathol Mediterr. 2016;55:54–61.

[121] Fernández-Aparicio M, Rispail N, Prats E, et al. Parasitic plant infection is partially controlled through symbiotic pathways. Weed Res. 2010;50:76–82.

[122] Aybeke M, Şen B, Ökten S. *Aspergillus alliaceus*, a new potential biological control of the root parasitic weed *Orobanche*. J Basic Microbiol. 2014;54:S93–S101.

[123] Mounde LG, Boh MY, Cotter M, et al. Potential of rhizobacteria for promoting sorghum growth and suppressing *Striga hermonthica* development. J Plant Dis Prot. 2015;122:100–106.

[124] Chen J, Xue QH, McErlean CSP, et al. Biocontrol potential of the antagonistic microorganism *Streptomyces enissocaesilis* against *Orobanche cumana*. BioControl. 2016;61:781–791.

[125] Iasur Kruh L, Lahav T, Abu-Nassar J, et al. Host-parasite-bacteria triangle: the microbiome of the parasitic weed *Phelipanche aegyptiaca* and tomato-*Solanum lycopersicum* (Mill.) as a host. Front Plant Sci. 2017 [cited 2017 Dec 14]; [9 p.]. DOI:10.3389/fpls.2017.00269

[126] Ma Y, Jia J, An Y, et al. Potential of some hybrid maize lines to induce germination of sunflower broomrape. Crop Sci. 2013;53:260–270.

[127] Zhang W, Ma Y, Wang Z, et al. Some soybean cultivars have ability to induce germination of sunflower broomrape. PLoS One. 2013 [cited 2017 Dec 14]; [11 p.]. DOI:10.1371/journal.pone.0059715

[128] Cimmino A, Fernández-Aparicio M, Avolio F, et al. Ryecyanatines A and B and ryecarbonitrilines A and B, substituted cyanatophenol, cyanatobenzo[1,3]dioxole, and benzo[1,3]dioxolecarbonitriles from rye (*Secale cereale* L.) root exudates: novel metabolites with allelopathic activity on *Orobanche* seed germination and radicle growth. Phytochemistry. 2015;109:57–65.

[129] Ye X, Chen J, McErlean CSP, et al. The potential of foxtail millet as a trap crop for sunflower broomrape. Acta Physiol Plant. 2017 [cited 2017 Dec 14]; [11 p.]. DOI:10.1007/s11738-016-2300-x

[130] Aksoy E, Arslan ZF, Tetik Ö, et al. Using the possibilities of some trap, catch and Brassicaceaen crops for controlling crenate broomrape a problem in lentil fields. Int J Plant Prod. 2016;10:53–62.

[131] Babaei S, Alizadeh H, Jahansouz MR, et al. Management of *Phelipanche aegyptiaca* Pomel. using trap crops in rotation with tomato (*Solanum lycopersicom* L.). Aust J Crop Sci. 2010;4:437–442.

[132] Fernández-Aparicio M, Rubiales D. Differential response of pea (*Pisum sativum*) to *Orobanche crenata*, *Orobanche foetida* and *Phelipanche aegyptiaca*. Crop Prot. 2012;31:27–30.

[133] Chai M, Zhu X, Cui H, et al. Lily cultivars have allelopathic potential in controlling *Orobanche aegyptiaca* Persoon. PLoS One. 2015 [cited 2017 Dec 14]; [16 p.]. DOI: 10.1371/journal.pone.0142811

[134] Dong SQ, Ma YQ, Wu H, et al. Stimulatory effects of wheat (*Triticum aestivum* L.) on seed germination of *Orobanche minor* Sm. Allelopathy J. 2012;30:247–258.

[135] Dong SQ, Ma YQ, Wu HW, et al. Allelopathic stimulatory effects of wheat differing in ploidy levels on *Orobanche minor* germination. Allelopathy J. 2013;31:355–366.

[136] Ma Y, Lang M, Dong S, et al. Screening of some cotton varieties for allelopathic potential on clover broomrape germination. Agron J. 2012;104:569–574.

[137] Ma YQ, Zhang W, Dong SQ, et al. Induction of seed germination in *Orobanche* spp. by extracts of traditional Chinese medicinal herbs. Sci China Life Sci. 2012;55:250–260.

[138] De Groote H, Vanlauwe B, Rutto E, et al. Economic analysis of different options in integrated pest and soil fertility management in maize systems of Western Kenya. Agric Econ. 2010;41:471–482.

[139] Hooper AM, Tsanuo MK, Chamberlain K, et al. Isoschaftoside, a C-glycosylflavonoid from *Desmodium uncinatum* root exudate, is an allelochemical against the development of *Striga*. Phytochemistry. 2010;71:904–908.

[140] Midega CAO, Pittchar J, Salifu D, et al. Effects of mulching, N-fertilization and intercropping with *Desmodium uncinatum* on *Striga hermonthica* infestation in maize. Crop Prot. 2013;44:44–49.

[141] Murage AW, Midega CAO, Pittchar JO, et al. Determinants of adoption of climate-smart push-pull technology for enhanced food security through integrated pest management in Eastern Africa. Food Secur. 2015;7:709–724.

[142] Khan Z, Midega CAO, Hooper A, et al. Push-pull: chemical ecology-based integrated pest management technology. J Chem Ecol. 2016;42:689–697.

[143] Midega CAO, Salifu D, Bruce TJ, et al. Cumulative effects and economic benefits of intercropping maize with food legumes on *Striga hermonthica* infestation. Field Crop Res. 2014;155:144–152.

[144] Hooper AM, Caulfield JC, Hao, B, et al. Isolation and identification of *Desmodium* root exudates from drought tolerant species used as intercrops against *Striga hermonthica*. Phytochemistry. 2015;117:380–387.

[145] Midega CAO, Bruce TJA, Pickett JA, et al. Climate-adapted companion cropping increases agricultural productivity in East Africa. Field Crop Res. 2015;180:118–125.

[146] Murage AM, Pittchar JO, Midega CAO, et al. Gender specific perceptions and adoption of the climate-smart push-pull technology in Eastern Africa. Crop Prot. 2015;76:83–91.

[147] Midega CAO, Wasonga CJ, Hooper AM, et al. Drought-tolerant *Desmodium* species effectively suppress parasitic *Striga* weed and improve cereal grain yields in Western Kenya. Crop Prot. 2017;98:94–101.

[148] Kifuko-Koech M, Pypers P, Okalebo JR, et al. The impact of *Desmodium* spp. and cutting regimes on the agronomic and economic performance of *Desmodium*–maize intercropping system in Western Kenya. Field Crop Res. 2012;137:97–107.

[149] Pickett JA, Hamilton ML, Hooper AM, et al. Companion cropping to manage parasitic plants. Ann Rev Phytopathol. 2010;48:161–177.

[150] Midega CAO, Khan ZR. Integrated management of *Striga hermonthica* and cereal stemborers in finger millet (*Eleusine coracana* (L.) Gaertn.) through intercropping with *Desmodium intortum*. Int J Pest Manage. 2010;56:145–151.

[151] Reinhardt CF, Tesfamichael N. Nitrogen in combination with *Desmodium intortum* effectively suppress *Striga asiatica* in a sorghum-*Desmodium* intercropping system. J Agr Rural Develop Trop Subtrop. 2011;112:19–28.

[152] Fernández-Aparicio M, Emeran AA, Rubiales D, et al. Inter-cropping with berseem clover (Trifolium alexandrinum) reduces infection by Orobanche crenata in legumes. Crop Prot. 2010;29:867–871.

[153] Kim HI, Kisugi T, Khetkam P, et al. Avenaol, a germination stimulant for root parasitic plants from *Avena strigosa*. Phytochemistry. 2014;103:85–88.

[154] Nomura S, Nakashima H, Mizutani M, et al. Structural requirements of strigolactones for germination induction and inhibition of *Striga gesnerioides* seeds. Plant Cell Rep. 2013;32:829–838.

[155] Jamil M, Kanampiu FK, Karaya H, et al. *Striga hermonthica* parasitism in maize in response to N and P fertilisers. Field Crop Sci. 2012;134:1–10.

[156] Jamil M, Charnikhova R, Cardoso C, et al. Quantification of the relationship between strigolactones and *Striga hermonthica* infection in rice under varying levels of nitrogen and phosphorus. Weed Res. 2011;51:373–385.

[157] Jamil M, Van Mourik TA, Charnikhova T, et al. Effect of diammonium phosphate application on strigolactone production and *Striga hermonthica* infection in three sorghum cultivars. Weed Res. 2012;53:121–130.

[158] Zhang M, Ma Y, Zhong W, et al. N–P–K ratio affects exudation of germination stimulants and resistance of tobacco seedlings to broomrapes. Plant Growth Regul. 2015;76:281–288.

[159] Yoneyama K, Xie X, Kim HI, et al. How do nitrogen and phosphorus deficiencies affect strigolactone production and exudation ? Planta. 2012;235:1197–1207.

[160] Abdul K, Chemining'wa GN, Onwonga RN. Relationships between agronomic practices, soil chemical characteristics and *Striga* reproduction in dryland areas of Tanzania. J Agric Sci Technol. 2012;2:1134–1141.

[161] Kamara AY, Ekeleme F, Jibrin JM, et al. Assessment of level, extent and factors influencing *Striga* infestation of cereals and cowpea in a Sudan Savanna ecology of Northern Nigeria. Agric Ecosyst Environ. 2014;188:111–121.

[162] Ayongwa GC, Stomph TJ, Belder P, et al. Organic matter and seed survival of *Striga hermonthica*—Mechanisms for seed depletion in the soil. Crop Prot. 2011;30:1594–1600.

[163] Ayongwa GC, Stomph TJ, Kuyper TW. Host-parasite dynamics of *Sorghum bicolor* and *Striga hermonthica*—The influence of soil organic matter amendments of different C:N ratio. Crop Prot. 2011;30:1613–1622.

[164] Ekeleme F, Kamara AY, Omoigui LO, et al. Effect of sowing date on *Striga* infestation and yield of sorghum (*Sorghum bicolor* [L.] Moench) cultivars in the Sudan Savanna of northeast Nigeria. Afr J Agric Res. 2011;6:3240–3246.

[165] Boz Ö, Doğan MN, Öğüt D. The effect of duration of solarization on controlling branched broomrape (*Phelipanche ramosa* L.) and some weed species. Julius-Kűhn-Arch. 2012;434:687–693.

[166] Lombardo S, Longo AMG, Lo Monaco A, et al. The effect of soil solarization and fumigation on pests and yields in greenhouse tomatoes. Crop Prot. 2012;37:59–64.

[167] Mauro RP, Lo Monaco A, Lombardo S, et al. Eradication of *Orobanche*/*Phelipanche* spp. seedbank by soil solarization and organic supplementation. Sci Hort. 2015;193:62–68.

[168] Eizenberg H, Plakhine D, Ziadne H, et al. Non-chemical control of root parasitic weeds with biochar. Front Plant Sci. 2017 [cited 2017 Dec 14]; [9 p.]. DOI:10.3389/fpls.2017.00939

[169] Samejima H, Babiker AG, Takikawa H, et al. Practicality of the suicidal germination approach for controlling *Striga hermonthica*. Pest Manage Sci. 2016;72:2035–2042.

[170] Kgosi RL, Zwanenburg B, Mwakaboko AS, et al. Strigolactone analogues induce suicidal seed germination of *Striga* spp. in soil. Weed Res. 2012;52:197–203.

[171] Zwanenburg B, Mwakaboko AS, Kannan C. Suicidal germination for parasitic weed control. Pest Manage Sci. 2016;72:2016–2025.

[172] Kannan C, Zwanenburg B. A novel concept for the control of parasitic weeds by decomposing germination stimulants prior to action. Crop Prot. 2014;61:11–15.

[173] Malik H, Kohlen W, Jamil M, et al. Aromatic A-ring analogues of orobanchol, new germination stimulants for seeds of parasitic weeds. Org Biomol Chem. 2011;9:2286–2293.

[174] Lachia M, Wolf HC, De Mesmaeker A. Synthesis of strigolactones analogues by intramolecular [2 + 2] cycloaddition of ketene-iminium salts to olefins and their activity on *Orobanche cumana* seeds. Bioorg Med Chem Lett. 2014;24:2123–2128.

[175] Takahashi I, Fukui K, Asami T. Chemical modification of a phenoxyfuranone-type strigolactone mimic for selective effects on rice tillering or *Striga hermonthica* seed germination. Pest Manage Sci. 2016;72:2048–2053.

[176] Fukui K, Yamagami D, Ito S, et al. A taylor-made design of phenoxyfuranone-type strigolactone mimic. Front Plant Sci. 2017 [cited 2017 Dec 14]; [11 p.]. DOI:10.3389/fpls.2017.00936

[177] Yao, Z, Tian F, Cao X, et al. Global transcriptomic analysis reveals the mechanism of *Phelipanche aegyptiaca* seed germination. Int J Mol Sci. 2016 [cited 2017 Dec 14]; [19 p.]. DOI:10.3390/ijms17071139

[178] Toh S, Holbrook-Smith D, Stokes ME, et al. Detection of parasitic plant suicide germination compounds using a high-throughput *Arabidopsis* HTL/KAI2 strigolactone perception system. Chem Biol. 2014;21:988–998.

[179] Khosla A, Nelson DC. Strigolactones, super hormones in the fight against *Striga*. Curr Opin Plant Biol. 2016;33:57–63.

[180] Tsuchiya Y, Yoshimura M, Sato Y, et al. Probing strigolactone receptors in *Striga hermonthica* with fluorescence. Science. 2015;349:864–868.

[181] Toh S, Holbrook-Smith D, Stogios PJ, et al. Structure-function analysis identifies highly sensitive strigolactone receptors in *Striga*. Science. 2015;350:203–207.

[182] Joel DM, Chaudhuri SK, Plakhine D, et al. Dehydrocostus lactone is exuded from sunflower roots and stimulates germination of the root parasite *Orobanche cumana*. Phytochemistry. 2011;72:624–634.

[183] Raupp FM, Spring O. New sesquiterpene lactones from sunflower root exudate as germination stimulants for *Orobanche cumana*. J Agric Food Chem. 2013;61:10481–10487.

[184] Ueno K, Furumoto T, Umeda S, et al. Heliolactone, a non-sesquiterpene lactone germination stimulant for root parasitic weeds from sunflower. Phytochemistry. 2014;108:122–128.

[185] Evidente A, Cimmino A, Fernández-Aparicio M, et al. Polyphenols, including the new peapolyphenols A-C, from pea root exudates stimulate *Orobanche foetida* seed germination. J Agric Food Chem. 2010;58:2902–2907.

[186] Evidente A, Cimmino A, Fernández-Aparicio M, et al. Soyasapogenol B and trans-22-dehydrocampesterol from common vetch (*Vicia sativa* L.) root exudates stimulate broomrape seed germination. Pest Manage Sci. 2011;67:1015–1022.

[187] Auger B, Pouvreau JB, Pouponneau K, et al. Germination stimulants of *Phelipanche ramosa* in the rhizosphere of *Brassica napus* are derived from the glucosinolate pathway. Mol Plant Microbe Interact. 2012;25:993–1004.

[188] Tokunaga T, Hayashi H, Akiyama K. Medicaol, a strigolactone identified as a putative didehydro-orobanchol isomer, from *Medicago truncatula*. Phytochemistry. 2015;111:91–97.

[189] Charnikhova TV, Gaus K, Lumbroso A, et al. Zealactones. Novel natural strigolactones from maize. Phytochemistry. 2012;137:123–131.

[190] Fernández-Aparicio M, Yoneyama K, Rubiales D. The role of strigolactones in host specificity of *Orobanche* and *Phelipanche* seed germination. Seed Sci Res. 2011;21:55–61.

[191] Artuso E, Ghibaudi E, Lace B, et al. Stereochemical assignment of strigolactone analogues confirms their selective biological activity. J Nat Prod. 2015;78:2624–2633.

[192] Menkir A, Chikoye D, Lum F. Incorporating an herbicide resistance gene into tropical maize with inherent

polygenic resistance to control *Striga hermonthica* (Del.) Benth. Plant Breed. 2010;129:385–392.

[193] Chikoye D, Fontem LA, Menkir A. Seed coating herbicide tolerant maize hybrids with imazapyr for *Striga hermonthica* (Del.) Benth control in the West African savanna. J Food Agric Environ. 2011;9:416–421.

[194] Makumbi D, Diallo A, Kanampiu F, et al. Agronomic performance and genotype × environment interaction of herbicide-resistant maize varieties in Eastern Africa. Crop Sci. 2015;55:540–555.

[195] Dor E, Smirnov E, Galili S, et al. Characterization of the novel tomato mutant HRT, resistant to acetolactate synthase–inhibiting herbicides. Weed Sci. 2016;64:348–360.

[196] Shilo T, Zygier L, Rubin B, et al. Mechanism of glyphosate control of *Phelipanche aegyptiaca*. Planta. 2016;244:1095–1107.

[197] Dor E, Galili S, Smirnov E, et al. The effects of herbicides targeting aromatic and branched chain amino acid biosynthesis support the presence of functional pathways in broomrape. Front Plant Sci. 2017 [cited 2017 Dec 14]; [15 p.]. DOI:10.3389/fpls.2017.00707

[198] Shilo T, Rubin B, Plakhine D, et al. Secondary effects of glyphosate action in *Phelipanche aegyptiaca*: Inhibition of solute transport from the host plant to the parasite. Front Plant Sci. 2017 [cited 2017 Dec 14]; [16 p.]. DOI:10.3389/fpls.2017.00255

[199] Eizenberg H, Aly R, Cohen Y. Technologies for smart chemical control of broomrape (*Orobanche* spp. and *Phelipanche* spp.). Weed Sci. 2012;60:316–323.

[200] Cochavi A, Rubin B, Achdari G, et al. Thermal time model for Egyptian broomrape (*Phelipanche aegyptiaca*) parasitism dynamics in Carrot (*Daucus carota* L.): field validation. Front Plant Sci. 2016 [cited 2017 Dec 14]; [11 p.]. DOI:10.3389/fpls.2016.01807

[201] Cochavi A, Achdari G, Smirnov E, et al. Egyptian broomrape (*Phelipanche aegyptiaca*) management in carrot under field conditions. Weed Technol. 2015;29:519–528.

[202] Cochavi A, Rubin B, Smirnov E, et al. Factors affecting Egyptian broomrape (*Orobanche aegyptiaca*) control in carrot. Weed Sci. 2016;64:321–330.

[203] Moral J, Lozano-Baena MD, Rubiales D. Temperature and water stress during conditioning and incubation phase affecting *Orobanche crenata* seed germination and radicle growth. Front Plant Sci. 2015 [cited 2017 Dec 14]; [10 p.]. DOI:10.3389/fpls.2015.00408

[204] Abbes Z, Mkadmi M, Trabelsi I, et al. *Orobanche foetida* control in faba bean by foliar application of benzothiadiazole (BTH) and salicylic acid. Bulg J Agric Sci. 2014;20:1439–1443.

[205] Yang C, Hu LY, Ali B, et al. Seed treatment with salicylic acid invokes defence mechanism of *Helianthus annuus* against *Orobanche cumana*. Ann Appl Biol. 2016;169: 408–422.

[206] Jamil M, Charnikhova T, Verstappen F, et al. Carotenoid inhibitors reduce strigolactone production and *Striga hermonthica* infection in rice. Arch Biochem Biophys. 2010;504:123–131.

[207] Ito S, Umehara M, Hanada A, et al. Effects of triazole derivatives on strigolactone levels and growth retardation in rice. PLoS One. 2011 [cited 2017 Dec 14]; [5 p.]. DOI:10.1371/journal.pone.0021723

[208] Seto Y, Kameoka H, Yamaguchi S, et al. Recent advances in strigolactone research: chemical and biological aspects. Plant Cell Physiol. 2012;53:1843–1853.

[209] Ito S, Yamagami D, Umehara M, et al. Regulation of strigolactone biosynthesis by gibberellin signalling. Plant Physiol. 2017;174:1250–1259.

[210] Fukui K, Ito S, Asami T. Selective mimics of strigolactone actions and their potential use for controlling damage caused by root parasitic weeds. Mol Plant. 2013;6:88–99.

[211] Kannan C, Aditi P, Zwanenburg, B. Quenching the action of germination stimulants using borax and thiourea, a new method for controlling parasitic weeds: a proof of concept. Crop Prot. 2015;70:92–98.

[212] Wakabayashi, T, Joseph B, Yasumoto S, et al. Planteose as a storage carbohydrate required for early stage of germination of *Orobanche minor* and its metabolism as a possible target for selective control. J Exp Bot. 2015;66:3085–3097.

[213] Castillejo MA, Fernández-Aparicio M, Rubiales D. Proteomic analysis by two-dimensional differential in gel electrophoresis (2D DIGE) of the early response of *Pisum sativum* to *Orobanche crenata*. J Exp Bot. 2012;63:107–119.

[214] Nativ N, Hacham Y, Hershenhorn J, et al. Metabolic investigation of *Phelipanche aegyptiaca* reveals significant changes during developmental stages and in its different organs. Front Plant Sci. 2017 [cited 2017 Dec 14]; [13 p.]. DOI:10.3389/fpls.2017.00491

[215] Westwood JH, dePamphilis CW, Das M, et al. The parasitic plant genome project: new tools for understanding the biology of *Orobanche* and *Striga*. Weed Sci. 2012;60:295–306.

[216] Holbrook-Smith D, Toh S, Tsuchiya Y, et al. Small-molecule antagonists of germination of the parasitic plant *Striga hermonthica*. Nat Chem Biol. 2016;12:724–729.

[217] Venezian A, Dor E, Achdari G, et al. The influence of the plant growth regulator maleic hydrazide on Egyptian broomrape early developmental stages and its control efficacy in tomato under greenhouse and field conditions. Front Plant Sci. 2017 [cited 2017 Dec 14]; [12 p.]. DOI:10.3389/fpls.2017.00691

[218] Fernández-Aparicio M, Bernard A, Falchetto L, et al. Investigation of amino acids as herbicides for control of *Orobanche minor* parasitism in red clover. Front Plant Sci. 2017 [cited 2017 Dec 14]; [12 p.]. DOI:10.3389/fpls.2017.00842

[219] Prider J, Williams A. Using dazomet to reduce broomrape seed banks in soils with low moisture content. Crop Prot. 2014;59:43–50.

[220] Yoshida S, Cui S, Ichihashi Y, et al. The haustorium, a specialized invasive organ in parasitic plants. Ann Rev Plant Biol. 2016;67:643–667.

[221] Alakonya A, Kumar R, Koenig D, et al. Interspecific RNA interference of *SHOOT MERISTEMLESS*-like disrupts *Cuscuta pentagona* plant parasitism. Plant Cell. 2012;24:3153–3166.

[222] Bandaranayake PCG, Yoder JI. Trans-specific gene silencing of acetyl-CoA carboxylase in a root-parasitic plant. Mol Plant Microbe Interact. 2013;26:575–584.

[223] Kirigia D, Runo S, Alakonya A. A virus-induced gene silencing (VIGS) system for functional genomics in the

parasitic plant *Striga hermonthica*. Plant Methods. 2014 [cited 2017 Dec 14]; [8 p.]. DOI:10.1186/1746-4811-10-16

[224] Tesso TT, Ejeta G. Integrating multiple control options enhances *Striga* management and sorghum yield on heavily infested soils. Agron J. 2011;103:1464–1471.

[225] Ayongwa GC, Stomph TJ, Hoevers R, et al. *Striga* infestation in Northern Cameroon: magnitude, dynamics and implications for management. NJAS Wageningen J Life Sci. 2010;57:159–165.

[226] Rodenburg J, Demont M, Zwart SJ, et al. Parasitic weed incidence and related economic losses in rice in Africa. Agric Ecosyst Environ. 2016;235:306–317.

[227] Lyra D, Kalivas D, Economou G. A large-scale analysis of soil and bioclimatic factors affecting the infestation level of tobacco (*Nicotiana tabacum* L.) by *Phelipanche* species. Crop Prot. 2016;83:27–36.

[228] Atera EA, Itoh K, Azuma T, et al. Farmers' perspectives on the biotic constraint of *Striga hermonthica* and its control in Western Kenya. Weed Biol Manage. 2012;12:53–62.

[229] Rodenburg J, Schut M, Demont M, et al. Systems approaches to innovation in pest management: reflections and lessons learned from an integrated research program on parasitic weeds in rice. Int J Pest Manage. 2015;61:329–339.

[230] De Groote H, Rutto E, Odhiambo G, et al. Participatory evaluation of integrated pest and soil fertility management options using ordered categorical data analysis. Agric Syst. 2010;103:233–244.

[231] Gebretsadik, R, Shimelis H, Laing MD, et al. A diagnostic appraisal of the sorghum farming system and breeding priorities in *Striga* infested agro-ecologies of Ethiopia. Agric Syst. 2014;123:54–61.