Chapter 3
Strigolactones and Parasitic Plants

Maurizio Vurro, Angela Boari, Benjamin Thiombiano, and Harro Bouwmeester

Abstract A parasitic plant is a flowering plant that attaches itself morphologically and physiologically to a host (another plant) by a modified root (the haustorium). Only about 25 out of the 270 genera of parasitic plants have a negative impact in agriculture and forestry and thus can be considered weeds. Among them, the most damaging root parasitic weeds belong to the genera *Orobanche* and *Phelipanche* (commonly named broomrapes) and *Striga* (witchweeds) (all belonging to the Orobanchaceae family). Considering the aims of the book, this chapter will focus only on this group of parasitic weeds, as in these plants strigolactones have a key role both in their life cycle, and in management strategies to control them. Distribution, agricultural importance and life cycle of these parasitic weeds are briefly introduced, after which we focus on the role of strigolactones in seed germination, parasite development, host specificity, plant nutrition and microbiome composition. Furthermore, some weed control approaches involving strigolactones are discussed.

Keywords Parasitic weeds · Orobanche · Phelipanche · Striga · Germination stimulants

3.1 Parasitic Plants

A parasitic plant is an angiosperm (flowering plant) that attaches itself morphologically and physiologically to its host (another plant) by a modified root (the haustorium). Depending on the host organ it is attached to, two main types of parasitic plants can be distinguished: stem parasites and root parasites. Stem parasites occur in several families and include mistletoes (*Viscum* spp.) and dodders (*Cuscuta* spp.),

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H. Koltai, C. Prandi (eds.), *Strigolactones - Biology and Applications*,
https://doi.org/10.1007/978-3-030-12153-2_3

whereas root parasites are more common and belong to diverse taxonomic groups. Considering the aims of the book, attention will be given only to root parasites, and in particular to the root parasitic weeds of the Orobanchaceae, as strigolactones play a key role in their life cycle and in control strategies.

Parasitic plants can also be differentiated into obligate and facultative parasites. The former depend completely on their host, while the latter are capable of completing their life cycle without host contact and only attach to a suitable host if it is available. A further distinction can be made between holoparasites, which lack chlorophyll (and thus are non-photosynthetic), derive all their nutrition from their host and, therefore, are completely dependent upon the host to complete their life cycle; and hemiparasites, which contain chlorophyll (and hence are photosynthetic) and thus absolutely need the connection with the host only during part of their life cycle. All holoparasites are also obligate parasites. Although these definitions imply absolute categories, some parasitic plants display an intermediate behaviour between hemi- and holoparasitism, e.g. *Cuscuta* (dodder).

Many of the photosynthetic root hemiparasites are green with fully formed leaves, such as *Striga* spp. As the degree of parasitic dependence increases (i.e. the evolution from hemiparasitism to holoparasitism), profound changes occur in the morphology of the parasitic plant. In general, holoparasites tend to have leaves reduced to scales, succulent stems and primary (derived from the seedling radicle) and lateral (from developed roots) haustoria, whereas facultative parasites tend to have normal leaves and stems, and only lateral haustoria.

Only about 25 out of the 270 genera of parasitic plants have a negative impact on agriculture and forestry and thus can be considered weeds. Among them, the most damaging root parasitic weeds belong to the genera *Orobanche* and *Phelipanche* (commonly named broomrapes), *Striga* (witchweeds) and, to a lesser extent, *Alectra* and *Rhamphicarpa* (all of them belonging to the Orobanchaceae family). Among the weedy stem parasites, the most important genera are *Cuscuta* (dodder) of the Convolvulaceae family and *Arceuthobium* (dwarf mistletoe), *Viscum* and *Phoradendron* spp. (leafy mistletoes) of the Santalaceae family.

3.1.1 Importance

Witchweeds and broomrapes are responsible for enormous losses in major crops. Seven broomrape species are considered serious weeds, mainly in Europe, North Africa and Asia: *Phelipanche ramosa* (L.) Pomel, *Phelipanche aegyptiaca* (Pers.) Pomel, *Orobanche crenata* Forsk., *Orobanche cumana* Wallr., *Orobanche foetida* Poir., *Orobanche cernua* Loefl. and *Orobanche minor* Sm. With regard to the witchweeds, four species are considered very important weeds, present almost exclusively in Africa: *Striga hermonthica* (Del.) Benth., *Striga asiatica* (L.) Kuntze, *Striga aspera* Willd. and *Striga gesnerioides* (Willd.) Vatke (Parker 2013). Despite the large number of studies on their distribution and impact, in some countries losses and presence of parasitic weeds are probably underestimated because of the lack of data on minor crops or because farmers simply prefer to abandon risky crops in contaminated areas. Below follow brief descriptions of host range, distribution and severity of the main Orobanchaceae root parasitic weed species (see also Box 3.1).

Box 3.1 Some Key Features of the Most Troublesome Parasitic Weeds

	Flower colour	Stem height (cm)	Host range	Distribution
Orobanche crenata Forsk.	Generally whitish with purple veins	Up to 100	Wide. Many species mainly in Fabaceae and Apiaceae. Some Cucurbitaceae, Solanaceae, Lamiaceae, Ranunculaceae and Asteraceae	Predominantly around the Mediterranean including North Africa and into the Near East and Western Asia, with quite recent introductions into Sudan and Ethiopia
Orobanche cumana Wallr.	From white to pale blue	40–65	Specific to sunflower	SE Europe, Middle East and SW Asia. It is also present in China
Orobanche foetida Poir.	Dark red, yellowish or white at the base, shining dark red inside	20–70	Restricted to Fabaceae, wide within that family, mostly wild species but also faba bean, chickpea and vetch	Western Mediterranean: Morocco, Tunisia, Algeria and Libya in North Africa; Spain, Portugal and the Balearic Islands to the north. The weedy populations occur in Tunisia and Morocco
Orobanche cernua Loefl.	Whitish/pale yellow at the base, with deep blue/purple lips	Up to 35	Solanaceous crops, especially tomato, eggplant and tobacco, and, less commonly, potato	Southern Europe, Middle East, South Asia and Northern Africa, with possibly introduced infestations further south in Africa, in Niger, Sudan, Ethiopia, Kenya and Tanzania. On sandy beaches of South Australia

(continued)

Box 3.1 (continued)

	Flower colour	Stem height (cm)	Host range	Distribution
Orobanche minor Sm.	Mainly pale, whitish, with varying amounts of purple in the veins	Up to 50. In Ethiopia may exceed 100	Very wide. Many Fabaceae species (e.g. *Trifolium*, *Medicago*, *Arachis* spp.), Asteraceae (*Lactuca*, *Carthamus* spp.) and Apiaceae (*Daucus*, *Apium* spp.), Solanaceae and other families. Usually herbaceous but even woody hosts	Widely distributed. Native throughout most of Europe, other than the far north, Western Asia and Northern Africa, as far south as Ethiopia and Somalia. Sporadically introduced to Japan, New Zealand, Australia and several countries in North and South America
Phelipanche ramosa (L.) Pomel	From white at the base to pale blue or mauve to blue/purple on the lobes	Usually 10–30, occasionally 50	Many Solanaceae crops, especially tomato, eggplant and tobacco but also pepper and potato, and also Brassicaceae (rapeseed), Cannabaceae (hemp), Fabaceae (e.g. chickpea, clovers, groundnut, faba bean), Apiaceae (carrot, celery) and Asteraceae (lettuce, sunflower and ornamental species). Wild hosts in many families. Reported on onion but not on other monocots	Native distribution: Europe, Middle East, West Asia and North Africa south to Ethiopia and Somalia. New infestations recorded, e.g. Australia

(continued)

Box 3.1 (continued)

	Flower colour	Stem height (cm)	Host range	Distribution
Phelipanche aegyptiaca (Pers.) Pomel	See *P. ramosa*		The same host range as *P. ramosa*, in particular Solanaceae, Fabaceae, Apiaceae and Asteraceae. Wider range of Brassicaceae species and more important on Cucurbitaceae than *P. ramosa*. Occasionally on woody species	Distribution overlapping *P. ramosa* in South Europe, the Mediterranean and North Africa. Much further extended eastwards into South Asia and China
Striga hermonthica (Del.) Benth.	Pink (very occasionally white)	Up to 100, especially in Eastern Africa; about 50 in Western Africa	Most of the major tropical and subtropical cereals, especially sorghum, *Pennisetum*, millet and maize, but also upland rice, sugar cane and finger millet (*Eleusine coracana*)	Mainly northern sub-Saharan Africa from Senegal and Gambia in the west and to Sudan, Ethiopia and Kenya in the east. Except the Arabian Peninsula restricted to Africa
Striga asiatica (L.) Kuntze	Scarlet, occasionally yellow (or brick red in Ethiopia). White-flowered forms attack crops in South Asia	Usually 15–30	Host range as *S. hermonthica*, most notably maize and sorghum	Markedly differing from *S. hermonthica*, being predominantly in Eastern and Southern Africa. The two species overlap in Kenya and Tanzania but rarely occur together

(continued)

Box 3.1 (continued)

	Flower colour	Stem height (cm)	Host range	Distribution
Striga aspera Willd.	Resembling *S. hermonthica* in general appearance and flower colour, usually somewhat smaller		Most of the warm-climate cereals. Less common on sorghum and pearl millet and more common on rice and sugar cane than *S. hermonthica*	Mainly in West Africa but also eastwards to Sudan and south to Malawi
Striga gesnerioides (Willd.) Vatke	From white to mauve to purple	12–30	Only dicotyledons; cowpea is the main host	Mainly in Africa (West in particular) but also South and SE Asia
Alectra vogelii Benth	Yellow, sometimes with purple streaks	30–45	Various Fabaceous crops: cowpea is the main, groundnut, soybean and other legumes	A number of West African countries (especially Nigeria and Burkina Faso) and in other countries of Southern and Eastern Africa

3.1.2 Main Orobanchaceae Root Parasitic Weeds

Phelipanche ramosa **(L.) Pomel.** The host range of *P. ramosa* is extremely wide. It preferably parasitizes Solanaceae species (tomato, potato and tobacco in particular), Asteraceae (e.g. lettuce and sunflower), Brassicaceae (cabbage, rapeseed), Cannabaceae (hemp), Fabaceae (e.g. chickpea and faba bean) and Apiaceae (carrot, celery). Rapeseed, cabbage and hemp are now increasingly affected (Parker 2013). *P. ramosa* is native around the Mediterranean basin and originally infested crops only in Europe, the Middle East, West Asia and North Africa, but new infestations have been reported, e.g. in Australia (Warren 2006). The most severe yield losses in tomato vary between 30 and 50% in Slovakia (Cagáň and Tóth 2003) to over 80% in Chile (Díaz et al. 2006). In Sudan, heavy infestations caused the closure of tomato juicing factories (Babiker et al. 2007). Other countries in which tomato and/or eggplant have been seriously affected include, among others, Italy, Greece, Iran, Hungary and Cuba (Parker 2013). *P. ramosa* also attacks tobacco in Moldova (Timus and Croitoru 2007), Cuba and Italy (Zonno et al. 2000), and rapeseed in France (Gibot-Leclerc 2003).

***Phelipanche aegyptiaca* (Pers.) Pomel.** *Phelipanche aegyptiaca* has a host range similar to that of *P. ramosa*, attacking in particular the Solanaceae tomato, potato, eggplant and tobacco, and crops in the Fabaceae, Apiaceae and Asteraceae, too. It seems to have a wider range of Brassicaceae and to be more important on Cucurbitaceae than *P. ramosa*, being also occasionally occurring on woody species (Eizenberg et al. 2002). Compared to *P. ramosa*, it has almost the same geographical distribution in the Mediterranean countries, South Europe and Northern Africa, but it extends much further eastwards into South Asia and China. The effects of *P. aegyptiaca* on the host are the same of those caused by *P. ramosa*. Damage can be very severe, as advised on lentil in Turkey (Bülbül et al. 2009) or on *Eruca sativa* in India (Bedi et al. 1997), amounting to around 40%. In Iran over 70% yield loss was reported in potato (Motazedi et al. 2010) and severe losses in water melon (Parker and Riches 1993).

***Orobanche crenata* Forsk.** *Orobanche crenata* has a moderately wide host range including species in the Fabaceae and Apiaceae but also some in the Cucurbitaceae, Solanaceae, Lamiaceae, Ranunculaceae and Asteraceae (Musselman and Parker 1982). Its native distribution is predominantly around the Mediterranean Sea including North Africa and into the Near East and Western Asia. *O. crenata* is especially important all around the Mediterranean Sea where it infests the most important legume crops, particularly faba bean (Fig. 3.1), lentil and chickpea but also carrot. Around 180,000 ha were estimated to be infested in Morocco, Portugal, Spain and Syria, representing 50–70% of the areas of these crops grown in those countries. Yield losses amounting to 33% in Egypt, from 50 to 100% in Malta, and up to 70% in Turkey were estimated to occur (Sauerborn 1991).

***Orobanche cumana* Wallr.** *Orobanche cumana* is one of the most important biological constraints of sunflower production and is particularly important in Russia, Ukraine, Moldavia, Romania, Turkey, Bulgaria, Spain, Israel and Hungary but occurs also in Syria and Egypt and along the North African coast (Parker 1994). Areas of sunflower affected have been estimated at 40,000 ha in Greece and 20,000 ha in China, with around 60% and 20–50% losses, respectively. In Turkey, over 50% of the crop area was moderately infested in spite of the use of resistant varieties. Earlier studies estimated a reduction by 37% of the area where sunflower was grown because of heavy infestation in the former Yugoslavia before the introduction of resistant varieties (Sauerborn 1991). *O. cumana* in sunflower has been the subject of extensive research for the breeding of resistant varieties, which has provided only a temporary alleviation of the problem, as this resulted in the development of more virulent races shortly after the introduction of the resistant varieties.

***Orobanche foetida* Poir.** The native range of *O. foetida* is limited to the Western Mediterranean countries, e.g. Morocco and Tunisia in North Africa and Spain and Portugal in Europe. Although *O. foetida* occurs on a number of wild leguminous hosts, it is only a significant problem in faba bean, chickpea and vetch, for example, in Tunisia, since the last couple of decades (Román et al. 2007). This should be

Fig. 3.1 *Orobanche crenata* plant attacking faba ben

particularly worrying in the other countries around the Western Mediterranean, where it still occurs only on wild hosts. Damage to faba bean can be severe, resulting in losses of over 90% of seed yield (Abbes et al. 2007).

***Orobanche cernua* Loefl.** *Orobanche cernua* is almost exclusively a parasite of Solanaceae, especially tomato, tobacco and eggplant. Its distribution extends from Southern and Eastern Europe to North Africa but also from Asia to Australia. *O. cernua* is a very serious problem on tobacco in Asian countries, e.g. Pakistan, Iran and India. In the latter country, on thousands of hectares, severe infestation in tobacco has been reported causing large qualitative and quantitative yield losses. In tomato, severe infestations have been reported in countries such as Ethiopia, Israel and Kenya (Parker 1994).

***Orobanche minor* Sm.** *Orobanche minor* is a smaller problem compared to the other broomrapes. It is broadly distributed throughout most of Europe (except the Northern countries) and the Middle East and also along the western coast of North Africa. It has also been sporadically introduced to other countries, e.g. Japan or North- and South-American countries. Clover and alfalfa are the main crops affected, although not severely. Hosts are usually herbaceous but can also be

Fig. 3.2 *Striga hermonthica*

woody, e.g. pecan. Reductions in total host weight up to 50% were reported (Lins et al. 2006), with problems for the quality of the crop, that cannot be sold due to the contamination with seeds of the parasite (Mallory-Smith and Colquhoun 2012).

Striga hermonthica **(Del.) Benth.** This is the most damaging of the *Striga* species (Fig. 3.2), occurring mainly in northern sub-Saharan African countries such as Senegal, Sudan, Ethiopia, Mali, Benin, Nigeria and Kenya. It occurs in the Arabian Peninsula but is otherwise restricted to Africa. *S. hermonthica* is considered the most serious worldwide parasitic weed, with an estimated affected area amounting to many millions of hectares (Sauerborn 1991; Parker 2009, 2013). Most of the major tropical and subtropical cereals are affected, in particular sorghum, millet and maize but also upland rice and sugar cane. *S. hermonthica* is a photosynthetic species, although not very efficient (Press et al. 1987). The effects of an infection are visible well before emergence and consist in stunting of the host shoot (Parker 1994) and chlorotic blotching of its foliage. The overall effect on the host can be devastating and lead to total crop failure. Losses of maize in Kenya may reach 80% in case of heavy infestation (Manyong et al. 2007). Estimates for all cereals in 1991 varied from 40 to 50% in Ghana, Cameroon and Nigeria to over 70% in Benin and Gambia (Sauerborn 1991; Gressel et al. 2004; Labrada 2007; Ejeta 2007; Scholes and Press

2008). In countries such as Togo, Mali and Nigeria, the infested area is estimated to be around 40%, reaching over 60% in Benin (De Groote et al. 2008), and even over 80% in north-east Nigeria (Dugje et al. 2006). Across the whole of Africa between 50 and 300 million ha are estimated to be infested by the parasite.

***Striga asiatica* (L.) Kuntze.** *Striga asiatica* attacks the same crops as *S. hermonthica* and in particular maize and sorghum. It is distributed predominantly in Eastern and Southern Africa, with an overlap of the two species in Kenya and Tanzania. However, they rarely occur together. Although the damage caused by *S. asiatica* is similar to *S. hermonthica*, it represents a lower economic problem worldwide compared to the latter. The physiological effects on the host are stunting, a change in host root-to-shoot ratio, reduction of host photosynthesis and wilting even under moist conditions. Crop losses between 10 and 40% are common. Up to 80% losses were estimated to occur in maize in several Southern African countries (De Groote et al. 2008).

***Striga aspera* Willd.** *Striga aspera* resembles *S. hermonthica* in the general appearance and the effects on the parasitized crops. It can attack most of the warm-climate cereals, but it is less common on sorghum and pearl millet and somewhat more common on rice and sugar cane than *S. hermonthica* (Parker and Riches 1993). *S. aspera* occurs mainly in West Africa but also more to the east in Sudan and to the south in Malawi. A reduction of around 50% in rice yield as a consequence of *S. aspera* infection has been recorded (Johnson et al. 1997).

***Striga gesnerioides* (Willd.) Vatke.** This autogamous species has different races, differing from each other in host species and/or genotype range and to some extent in morphology (e.g. number of branches, colour of stem and corolla). Among the *Striga* species, it is the most widely distributed (Mohamed et al. 2001), being particularly important on cowpea in West Africa, where crop losses can exceed 50%. Sweet potato, tobacco and a number of other wild species can also be attacked by *S. gesnerioides* races.

***Alectra vogelii* Benth.** As the related *Striga* spp., *A. vogelii* is an obligate hemiparasite having green foliage. Cowpea represents its main host, but a number of other legume crops, such as groundnut and soybean, can be attacked, too. This species occurs across much of Africa, with cowpea seriously affected in several West African countries, especially Nigeria and Burkina Faso. Damage can be very severe, and even complete yield losses have been reported (Emechebe et al. 1991).

Consideration. Parasitic weeds may represent an increasing problem in agriculture, due to changes in crop production and rotations, in response to global warming, and due to socioeconomic and political changes. For example, changes in the dietary wishes of consumers and more attention for the environment and the preservation of soil fertility are favouring the increase in legume production area in Western Europe, which in combination with a warmer climate could increase the risk of *O. crenata* establishment.

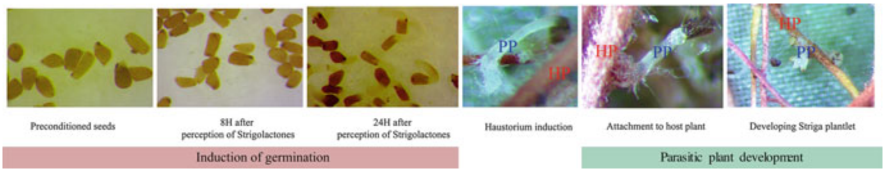

Fig. 3.3 *Striga* developmental cycle (*PP* parasitic plant, *HP* host plant)

The production of biofuels all over the world is dramatically increasing in this last decade. Some of the crops used for biofuel production, i.e. oilseed rape and sunflower, are broomrape hosts and have started to be grown in new areas, thus increasing the potential area of broomrape hosts and therefore the risk of an increase in the infested area.

Other problems could be represented both by the introduction of new crops, where traditional non-host crops potentially are replaced by host crops, and by the introduction of parasitic weeds in noninfested areas, due to global warming changes and international (sometimes not checked or tracked) trading and traffic.

3.1.3 Life Cycle

Although *Orobanche* and *Phelipanche* spp. are obligate holoparasites, whereas *Striga* spp. are obligate hemiparasites, the species of these three genera share many similarities. Their flower shoots have a spike, bearing from 10 to 20 flowers in most species, to even 100 or more. Fruits are capsules, each producing between around 500 extremely small (200–400 µm) seeds (Joel et al. 2007). Each plant can produce several tens of capsules and thus up to 1 million seeds. The life cycle of these parasites starts with seed germination, followed by the attachment to the host, which represents the beginning of the parasitic life phase (Fig. 3.3).

Some preparatory metabolic processes take place before the seed can react to stimuli and germinate. This preparatory phase, known as “conditioning”, is a complex metabolic and developmental process that consists of a series of events, each crucial for achieving germination. When a ripe seed comes in contact with water, it imbibes in less than 1 day; however, a moist environment is required for several days together with a suitable temperature in order to make the imbibed seed ready to perceive a chemical stimulus to germinate (see next sections). If conditioned seeds are not exposed to a germination stimulant and germination does not occur, their sensitivity gradually decreases again, and the seeds enter into secondary dormancy (Matusova et al. 2004). Upon germination, the radicle emerges from the seed reaching a length of a few mm up to 1 cm long (Fig. 3.4). Upon contact with a host root, the radicle develops intrusive cells that penetrate the root (Losner-Goshen et al. 1998) forming the haustorium, a physiological bridge between the vascular system of the host and that of the parasite. In *Striga* spp., the haustorium establishes a

Fig. 3.4 Germinated seeds of *Phelipanche ramosa*

xylem–xylem connection with the host from where it can withdraw water and nutrients. *Phelipanche* and *Orobanche* spp. form connections with both phloem and xylem (Westwood 2013). If the germinating seed fails to reach a host, it will die. The haustorium first serves as an attachment organ and structure to penetrate the host tissues and then becomes an organ that absorbs water and nutrients from the host, the real beginning of the parasitic phase. Therefore, this phase is essential and crucial to any further development of the parasite. After the establishment of the haustorium, the parasite develops a tubercle, which is the juvenile parasite that accumulates water and nutrients. Subsequently, the parasite develops a shoot that emerges from the soil, produces flowers and set seeds that can remain vital over decades in the soil, thus completing its life cycle.

The production of many tiny seeds increases the dispersion of the parasite into the soil profile, and therefore the chance to meet the roots of a suitable host that will induce germination and allow attachment. Host plant density and root shape can result in improved reproduction conditions for the parasites, increasing the probability of infecting the crop. This supports the build-up of enormous seed banks, which represent one of the main problems in parasitic weed management, as the seeds may remain dormant in the soil for many years, also if a host is not grown.

In *Orobanche* and *Phelipanche* spp. the reduction in biomass of infected hosts can be largely explained by the biomass accumulation of the parasite. However, the strong depression of the host growth caused by *Striga* spp. is only partially correlated with the increase in parasite biomass. The negative impact on host growth in *Striga*-infected plants can already be observed even before the parasite has emerged from the soil, suggesting that *Striga* spp. have a pathological or phytotoxic effect on the host plant.

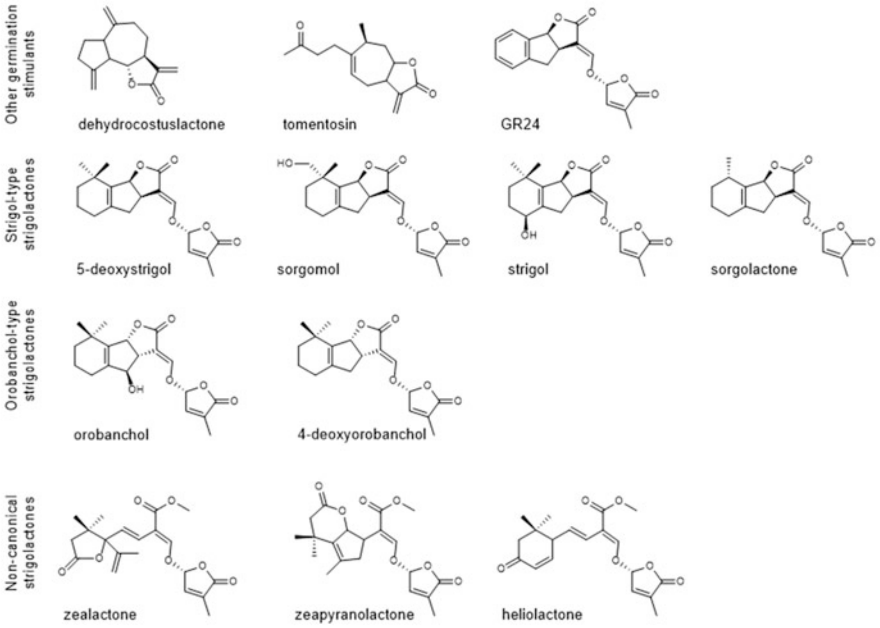

Fig. 3.5 Chemical structures of some of the SLs mentioned in the chapter

3.2 Role of SLs in Seed Germination and Parasite Development

3.2.1 SLs and Seed Germination

Several different compound classes have been described acting as germination stimulants in many different roots parasitic plant species. Examples are isothiocyanate, which stimulates the germination of *P. ramosa* that infects rapeseed, and dehydrocostus lactone and tomentosin (Fig. 3.5) which stimulate the germination of *O. cumana* that infects sunflower (Pérez-de-Luque et al. 2000; Auger et al. 2012). Strigolactones (SLs)—which are biosynthetically derived from the carotenoids (Matusova et al. 2005)—are, however, the major class of germination stimulants and have been shown to induce the germination of many of the Orobanchaceae root parasitic plants (Bouwmeester et al. 2003; Yoneyama et al. 2010). SLs are actively transported into the rhizosphere by a range of plant species and were—decades after their discovery as germination stimulants—shown to play an important role also in the interaction of plants with arbuscular mycorrhizal (AM) fungi. On top of that, they also have an endogenous signalling role in plants and are a new class of plant hormones controlling shoot branching and root development (Domagalska and Leyser 2011; Koltai 2011; Ruyter-Spira et al. 2013). Root exudate analysis of parasitic plants hosts shows that they may contain different classes of SLs (Wang and Bouwmeester 2018). Whereas in exudates of sorghum, the main SLs are 5-deoxystrigol, strigol, sorgomol and sorgolactone (all strigol-type strigolactones) (Fig. 3.5), those in tomato are orobanchol-type strigolactones such as orobanchol, solanacol and didehydro-orobanchol isomers (Fig. 3.5) (Wang and Bouwmeester 2018). In addition to these canonical SLs, species such as maize and sunflower also produce so-called noncanonical SLs, such as zealactone, zeapyranolactone and heliolactone (Fig. 3.5) (Ueno et al. 2014; Charnikhova et al. 2017, 2018) (Also see Chap. 1). In some species and/or genotypes, these different categories also occur together, such as in certain sorghum genotypes that produce orobanchol as well as 5-deoxystrigol (Gobena et al. 2017).

These exuded SLs are essential signalling molecules in the parasitic plant life cycle as their detection by responsive (conditioned; see above) parasitic plant seeds results in the induction of germination (Fig. 3.4). In general, the configuration of SLs is determining their germination stimulatory activity towards the different species of parasitic plants. For example, seeds of *S. gesnerioides* are more sensitive to orobanchol-type SLs, while *S. hermonthica* generally is more responsive to strigol-type SLs (Ueno et al. 2011a, b; Gobena et al. 2017).

3.2.2 SLs and Parasitic Plant Development

As described above, after germination of the parasite the infection process of the host plant continues with the formation of the haustorium, induced by haustorium inducing factors released by the host root (Riopel and Timko 1995), which results in a connection between the parasitic plant and the host plant. At this stage the host plant becomes a source of nutrients for the parasitic plant, as well as the exchange of signalling molecules between the two (Press et al. 1987; Těšitel et al. 2010; Liu et al. 2014; Lei 2017; Spallek et al. 2017).

Plant hormones such as auxin have been suggested to play a role in the successful establishment of the connection between parasite and host (Bar-Nun et al. 2008) and defence hormones such as salicylic acid and jasmonic acid have been implicated as possible defence inducers (Letousey et al. 2007; Dita et al. 2009; Torres-Vera et al. 2014). As SLs are also a plant hormone, a possible role of SLs from the host on parasitic plant development would not be unlikely. Indeed, a number of studies have shown the importance of host plant SLs, also after germination, in the infection process. Silencing of CCD8, one of the core SL biosynthesis pathway genes, in tomato resulted in a stronger infection by *P. ramosa* upon infection with pre-germinated seeds (Cheng et al. 2017). The authors proposed that this may be caused by a modification in the auxin levels as a result of the lower SL production in the mutant, which would facilitate the formation of a vascular connection with the host or by a reduction in the levels of defence-related hormones such as salicylic acid and jasmonic acid. Also in rice, it seems that lower SL production results in decreased induction of germination but in increased impact of the infection (lower tolerance) after attachment (Cardoso et al. 2014).

Although SLs—with the exception of host SLs (Liu et al. 2014)—have not been detected in any of the root parasitic plant species so far, there are strong indications that they can produce them as they have and express all the SL biosynthetic genes (Liu et al. 2014; Das et al. 2015). Clear evidence of the involvement of endogenous SLs of parasitic plants in the infection comes from the work of Aly et al. They showed that trans-silencing CCD7 and CCD8 genes using VIGS in *P. ramosa* resulted in a strong reduction in the formation of tubercles (by more than 90%) during the infection process (Aly et al. 2014). In addition to their own SLs, there is evidence that host SLs are transported from the host to *Striga* (Liu et al. 2014). It is unknown whether these also have an effect on the development of the parasite.

3.3 SLs and Host Specificity

Among parasitic plants, a certain degree of host specificity can be observed (see Sect. 3.1.2). For some parasitic plant species, the host range is very narrow, such as *O. cumana* on sunflower. For others the host range is very wide. For example, *P. ramosa* can infect Solanaceae including tomato and potato and Brassicaceae including cabbage and oilseed rape (Gibot-Leclerc et al. 2016; Perronne et al. 2017). This broad host range does, however, seem to coincide with host specificity in ecotypes of one species. For example, even if they are able to colonize different hosts, the exposure of *P. ramosa* seeds to exudates from different host species led to different germination rates (Perronne et al. 2017). The same holds for *S. hermonthica*. This species can infect a large variety of cereals (maize, sorghum, millet, rice), but there are ecotypes of the species which are more successful on millet than on sorghum and maize and vice versa (Kim et al. 1994; Mohemed et al. 2018). The question whether this host specificity (including in ecotypes) is due to germination stimulants is intriguing. In sunflower this seems to be the case, as *O. cumana* preferentially germinates with dehydrocostus lactone (Fig. 3.5), a molecule present in the exudate of sunflower and not in response to SLs (Auger et al. 2012). For *S. hermonthica*, SLs seem to be the major germination stimulant, and there are indications that SL composition plays a role in host specificity. The *S. hermonthica* sorghum ecotype germinates much less well with a millet exudate and vice versa (Mohemed et al. 2018). Work on sorghum, maize and rice aiming at the identification of varieties resistant to *S. hermonthica* points to a higher susceptibility for cultivars producing more 5-deoxystrigol (Jamil et al. 2011a; Yoneyama et al. 2015; Mohemed et al. 2018). Conversely, sorghum genotypes that produce more orobanchol than 5-deoxystrigol are much less sensitive to *S. hermonthica* (Gobena et al. 2017; Mohemed et al. 2018).

The individual evaluation of SLs for their ability to induce parasitic plant seed germination has confirmed that seeds of different species differentially respond to different SLs (Wang and Bouwmeester 2018). For example, *O. minor* germination can be achieved with about 200 times less *ent*-2′-*epi*-orobanchol when compared to *S. hermonthica* (Ueno et al. 2011b). In a similar way, exposure of *S. gesnerioides* and *S. hermonthica* to the same concentration of 5-deoxystrigol induced only germination of the latter (Ueno et al. 2011a).

3.4 Role of SLs in Belowground Interactions of the Host

3.4.1 Plant Nutrition (Phosphate, Nitrogen)

When plants are subjected to stress such as phosphate or nitrogen deficiency, they use several adaptation strategies, of which the most important are the modification of the root and shoot architecture, the establishment of favourable interactions with microorganisms and the modification of the rhizosphere pH (Bouwmeester et al. 2007; Péret et al. 2011; Yoneyama et al. 2012; Kumar et al. 2015). All these mechanisms aim to increase the proportion of nutrients available for the plants. Interestingly, when plants are grown on nitrate, but especially phosphate, deficient media, an increase in the production of SLs is induced (López-Ráez et al. 2008; Yoneyama et al. 2012, 2015; Marzec et al. 2013; Ito et al. 2016). There are several indications that this upregulation of SL production plays a role in the adaptation of plants to the low nutrient conditions. In the absence of phosphate, for example, plants favour the production of lateral roots (Péret et al. 2011) in order to increase the surface in contact with the soil. Auxin has been shown to play an important role in this adaptation as it is implicated in the initiation of lateral root primordia and the emergence of lateral roots (Chiou and Lin 2011; Sun et al. 2014). In addition to auxin, more and more work is also pointing to a role for SLs in the adaptation of root architecture to phosphate deficiency (Ruyter-Spira et al. 2011; Sun et al. 2014; Kumar et al. 2015). Under phosphate deficiency, a cross talk between SLs and auxin is taking place which results in an increase in lateral root density (Ruyter-Spira et al. 2011). This change in root architecture may also have an effect on parasitic plant infection, as it seems to increase the chance of a host root to come into the vicinity of seeds of the parasite. The increased production and exudation of SLs under these conditions also trigger the improved colonization of the roots by symbiotic microorganisms (see Sect. 3.4.2) but also results in increased germination of parasitic plant seeds and therefore in higher infection (Jamil et al. 2012, 2013, 2014a, b).

3.4.2 Microorganisms

SLs are also actors in the structuring of the biotic environment around the roots of plants. They promote the effectiveness of colonization by arbuscular mycorrhizal fungi (AM fungi), as hyphal branching factors (Akiyama et al. 2005; Besserer et al. 2006). In addition to the symbiotic interaction with AM fungi, SLs have also been shown to play a role in nodulation. A pea *rms1* mutant showing undetectable SL levels in roots tissue and in root exudates displayed a strongly reduced nodule number that was 40% lower than in the *wt* (Foo et al. 2013). In soybean a decrease in nodulation was observed in *GmMAX3b* knockdown lines, while overexpression of the same gene in transgenic hairy roots displayed an increased nodule number (Haq et al. 2017). It is yet unclear whether this is due to a signalling function of the SLs or their hormonal effect. SLs are not the only chemicals that are exuded by plants. The rhizosphere is a zone surrounding the plant roots, which has a very large chemical diversity. The exuded molecules serve not only as a carbon source for microorganisms but also play a role as signalling molecules. This chemical diversity is likely the engine of recruitment and selection of specific microorganisms. One of the most studied cases today remains that of phenylpropanoids that are involved in both symbiotic (Abdel-Lateif et al. 2012; Liu and Murray 2016) and allelopathic mechanisms (Bais et al. 2006).

Do SLs also play a role in microbiome recruitment? Recent work on sorghum demonstrates the ability of different genotypes to recruit different bacterial communities from the soil in which they are grown. The *Striga*-resistant genotype SRN39 has a different SL profile as other sorghum genotypes (Gobena et al. 2017) and recruited a microbiome that was different from that of the others (Schlemper et al. 2017). An intriguing question is if these changes at the microbiome level have an effect on the infection of the host by parasitic plants. Indeed, from a Kenyan *Striga*, suppressive soil bacteria could be isolated that induced up to 45% of decay in *Striga* seeds (Neondo et al. 2017). Other mechanisms by which soil microorganisms could suppress parasitic plants include the production of germination inhibiting factors, inhibitors of radicle growth and haustorium formation, strengthening the vigour of the host plant by activating plant defence mechanisms or competitive utilization of signalling molecules inducing parasitic plant seed germination.

3.5 SLs and Parasitic Weed Management

The main difficulties in controlling parasitic Orobanchaceae weeds are on the one hand related to the intrinsic characteristics of the parasitism (i.e. the physic and physiological connection between host and parasite) and on the other hand to the properties of their seeds (i.e. the enormous number produced by each plant, the minute size, their longevity and the easy dispersal). The first characteristics hamper all the classical interventions attempting to control the weed without damaging the host (e.g. mechanical, physical and chemical). This causes a rapid increase in the soil seed bank, even when the original infested area is very limited, or even when only a few plants are left after effective management practices. Containment of infested areas and prevention of seed distribution should therefore be a major objective of parasitic weed management strategies, in addition to direct control interventions against the parasites (Rubiales et al. 2009). In this chapter, we will not review all possible control and management strategies of parasitic weeds but focus on methods—which are already used or can potentially be developed—that are based on the importance of SLs in the life cycle of these parasites. Indeed, there are several strategies of weed management focussing on the SLs, trying to avoid the stimulation of germination, or conversely to favour it, in the absence of a host. These practices are briefly considered in the next sections.

3.5.1 Trap and Catch Crops

The aim of the use of trap and catch crops is not to directly control the parasitic weeds, but rather to reduce the infestation over time, by reducing the seed bank in the soil. Trap crops are non(false)-host crops of which the roots release strigolactones, thus stimulating parasitic plant seed germination, but—since they are not a host—without allowing further development of the parasite, by impeding a viable connection of the haustorium to the host root (Parker and Riches 1993). This effect is also defined as "suicidal" germination. Trap crops can be used both for intercropping, i.e. by growing it in between the main crop, and as a main crop on itself. Besides its main effect, the induction of seed germination, a non-host crop can potentially also contribute to parasitic weed control by providing shade and reducing soil temperature (as a cover crop).

One of the best examples of an effective intercrop species with proven success in *S. hermonthica* suppression is *Desmodium uncinatum* Jacq. (Pickett et al. 2010; Hooper et al. 2010). This forage legume not only improves the soil fertility but also causes suicidal seed germination and inhibition of the parasite attachments to the host roots, by producing simultaneously both stimulatory and inhibitory flavonoid compounds in their root exudates (Khan et al. 2010). *Striga* may also be controlled by rotating or intercropping the cereal crop with other plant species, e.g. groundnut (*Arachis hypogea*) (Carson 1989), pigeon pea (*Cajanus cajan*) (Oswald and Ransom 2001) or cotton (*Gossypium* spp.) (Swanton and Booth 2004).

Several trap crops have been reported to reduce broomrape seed banks (even if some of them were effective only under controlled conditions), such as, sorghum (*Sorghum bicolor*), flax (*Linum usitatissimum*) and soybean (*Glycine max*) (Al-Menoufi 1989; Saxena et al. 1994; Kleifeld et al. 1994; Abebe et al. 2005). Other examples of effective broomrape trap crops include flax against *O. crenata*; different wheat cultivars against *O. minor*, radish, linseed, fennel and cumin against *P. aegyptiaca*; and hybrid maize against *O. cumana* (Gbèhounou and Adango 2003; Acharya 2014; Aksoy et al. 2015).

Conversely, catch crops are host plants that also produce strigolactones but do allow attachment by the parasite. In this case, the crop is simply removed from the field after the parasite seeds have germinated (and possibly attached), but before flowering and seed dispersal of the parasite are initiated. Important crops reported as potential catch crops for broomrape control are faba bean (*Vicia faba*), field mustard (*Brassica campestris*), white mustard (*Sinapis alba*), lentil (*Lens culinaris*), berseem clover (*Trifolium alexandrinum*) and fenugreek (*Trigonella foenum-graecum*) (Sauerborn and Saxena 1986; Parker and Riches 1993; Kleifeld et al. 1994; Dhanapal et al. 1996; Acharya et al. 2002; Fernández-Aparicio et al. 2008, 2010).

3.5.2 Suicidal Germination by SLs, Analogues and Mimics

As an alternative to trap and catch crops, which require that they are grown for a certain period of time on the contaminated field, suicidal germination can potentially also be provoked by applying compounds with stimulatory activity directly to the field. The parasitic seeds would germinate in the absence of a host and would hence not survive. Generally, the most active molecules inducing seed germination are the naturally occurring SLs, including 5-deoxystrigol and orobanchol. Unfortunately, the structures of these natural SLs are rather complex. As a result, synthesis of these SLs for effective field applications is not feasible. Therefore, alternative approaches to produce germination stimulants have been explored. Examples are the synthesis of simpler and cheaper SL analogues, the use of more easily available, natural compounds from other sources and the use of other compounds from whatever origin with stimulatory activity.

The first encouraging attempts to achieve suicidal germination with synthetic SLs in the field were obtained by using GR7 (Babiker and Hamdoun 1982) (this is GR24 (Fig. 3.5) lacking the aromatic A-ring, see Chap. 6). Interesting results in field experiments were also reported using Nijmegen-1 as SL analogue in tobacco infested by *O. cumana* (Zwanenburg et al. 2009). Although they proved to work effectively in reducing the parasitic seed load and protecting the host plants subsequently grown in the affected field, problems regarding their production cost, potential off-target effects in the soil and low stability remain to be solved (Zwanenburg and Pospíšil 2013; Zwanenburg et al. 2016). Some SL analogues have been used with promising results in pot experiments (Kgosi et al. 2012) formulated in an emulsion, which prevented hydrolysis and leaching down to lower soil layers.

Natural products that have similar activity as SLs have been isolated from a variety of sources. For example, dihydrosorgoleone was identified in the root exudate of sorghum and was shown to have germination stimulating activity for *S. asiatica* (Chang et al. 1986); dehydrocostus lactone (Fig. 3.5) was identified in the root exudates of sunflower as the natural germination stimulant for *O. cumana*, a root parasite specific of sunflower (Joel et al. 2011). Peagol and peagoldione, which bear some structural similarities to the SLs, were isolated from pea (*Pisum sativum*) root exudates and exhibited germination stimulatory activity in particular on *O. foetida* (only peagol) and *P. aegyptiaca* (Evidente et al. 2009), whereas soyasapogenol B and trans-22-dehydrocampesterol were isolated from common vetch (*Vicia sativa*) exudates and stimulated germination of different broomrape species (Evidente et al. 2011). However, most of these compounds proved to have only a modest stimulatory activity only under lab conditions. Thus, their use for controlling parasitic weeds is very far from being put into practice.

In recent years, a group of compounds not having the SL bioactiphore has been described. These compounds are based on the D-ring with an appropriate substituent at C-5. These compounds are referred to as SL mimics. Currently, two types of SL mimics are available. The first has a substituted phenyloxy group at C-5. Para-bromo-phenyloxy butenolide is weakly active on *S. hermonthica*. This group of phenoxy-substituted butenolides are also called debranones (debranching furanones). Synthetically, these SL mimics are very easy to prepare from either bromo butenolide or hydroxy butenolide, opening up new possibilities for a practical use of these compounds for clearing of parasitic weed infested fields (Zwanenburg et al. 2016). The second group of compounds, which was reported almost at the same time, contains an aroyloxy group at C-5. These SL mimics are modestly active as germination agents for *S. hermonthica* seeds but are remarkably active for *O. cernua* seeds (Zwanenburg et al. 2016). A carbamate with moderate germination-inducing activity and facile preparation, named T-010, formulated as a 10% wettable powder, was evaluated for germination-inducing activity towards the purple witchweed (*S. hermonthica*) in greenhouse and field experiments showing very promising preliminary effects (Samejima et al. 2016).

A compound not related to SLs, used for control of *Striga* spp., is ethylene (Rodenburg et al. 2005). It is injected into the soil and provokes seed germination of *Striga* spp. and successive death due to the absence of a suitable host. Although ethylene application has been successfully employed as part of the *Striga* eradication programme in the USA (Tasker and Westwood 2012), the practice is very expensive—so not suitable for use in the developing world—and its use not a guarantee for total eradication.

3.5.3 SL Degradation

A different approach for controlling root parasitic weeds would be the degradation of the SLs soon after they are released into the soil by the host roots, and before the stimulatory signal reaches the seeds of the parasite. The ultimate goal of this approach would not be a reduction of the seed bank over time, but rather to enable growing susceptible crops on infested fields. To achieve this, both chemical and biological approaches were explored. For the chemical approach, borax was used, an inexpensive and eco-friendly salt. It was successfully demonstrated under laboratory conditions that borax can be used to decompose germination stimulants prior to their interaction with seeds of parasitic weeds (Kannan and Zwanenburg 2014). For practical field applications, formulation of borax would be necessary, and the method would require optimization because in the long run, its continued use could give rise to too high boron concentrations in the soil, resulting in undesirable soil intoxication. The possibility to prepare a film of borax emulsion, formulated with a salt, around the seeds of the parasites has been suggested (Kannan and Zwanenburg 2014). This would ensure that no active stimulant would reach the seeds even if some of the stimulants would escape decomposition after being exuded. This would be an example of double gatekeeping: decomposition of the stimulant when exuded from the roots and when approaching the seeds of the parasite. Another agent for rapid decomposition of SLs could be a renowned nucleophilic agent, namely thiourea, acting in a similar way as borax. It can be easily formulated, is an inexpensive eco-friendly compound, a bio-regulatory molecule for plant growth stimulation, and also acts as an antioxidant in plant protection (Kannan and Zwanenburg 2014).

SLs have been reported to be present in the root exudates of a wide range of different plant species (see above), and thus it would not be surprising if these compounds also act as signals for microorganisms other than AM fungi that could be beneficial to the host (e.g. ectomycorrhizal fungi, biocontrol agents, biofertilizers, resistance inducers) and phytopathogenic to the parasites (also see above). These aspects could be highly interesting from a practical point of view, allowing novel approaches for parasitic plant management. For example, the potential of some beneficial microorganisms to metabolize SLs and to be rhizosphere competent (i.e. able to grow along the root system of the crop plants) has been hypothesized. They could be applied to the soil as biofertilizers together with the crop, persist seasonally and avoid signal recognition by the seeds of the parasitic plants, thus preventing parasite seed germination and successive attachments to the host root (Boari et al. 2016). So far, these control methods have only been investigated in lab experiments and are thus, still far from practical field application.

3.5.4 Host Tolerance Through Low-SL Exudation

As discussed above SLs are the main germination stimulants for root parasitic plants. In studies that evaluated the induction of parasitic plant seed germination by exudates from different genotypes and cultivars of several crop species, a positive correlation was demonstrated between the SL concentration in the root exudate and the germination rate (Jamil et al. 2011a; Fernández-Aparicio et al. 2014; Yoneyama et al. 2015; Mohemed et al. 2018).

An approach for the management of parasitic plants in agricultural crops could thus be to reduce germination of the parasitic plant seeds by reducing the exudation of the germination stimulants. Several studies explored natural variation in germination stimulant production, for example, in the New Rice for Africa (NERICA) rice cultivars. This work showed that several NERICA cultivars (1, 2, 5, 10 and 17) displayed post-germination resistance to *S. hermonthica* and *S. asiatica* unlike

NERICA 7, 8 and 11, which were susceptible (Rodenburg et al. 2015). In parallel, variation in SL production in the NERICA genotypes was demonstrated, resulting in differences in *Striga* germination induction (Jamil et al. 2011b). The combination, by breeding, of germination-related resistance with post-germination resistance could result in better durable *Striga* resistance (Cissoko et al. 2011; Jamil et al. 2011b).

Also in pea there is evidence for a relationship between the total amount of SLs exuded and sensitivity to *O. crenata* infection (Pavan et al. 2016). A genotype with reduced SL exudation displayed partial field resistance. Evidence about this positive correlation does exist in sorghum as well. For example, sorghum-resistant genotype SRN39 produced much less 5-deoxystrigol than the susceptible Tabat (Yoneyama et al. 2010). Later, SRN39 proved to produce more orobanchol, instead of 5-deoxystrigol—due to a tentative modification in the SL biosynthetic pathway (Gobena et al. 2017). This mechanism occurs broader than just in SRN39 and was also observed in a number of other *Striga*-resistant sorghum genotypes (Mohemed et al. 2018). The same can be observed in maize where a modification in the SL composition seems to cause resistance. The *Striga*-susceptible cultivar (Pioneer 3253) produced mostly 5-deoxystrigol, whereas the *Striga*-resistant (KST 94) produced mostly sorgomol. Interestingly, the differences in SL composition in maize and sorghum did not affect the level of AM colonization (Yoneyama et al. 2015; Gobena et al. 2017).

Aside of exploiting natural variation, biotechnological approaches aiming to generate low SL exuding plants could be a strategy to reduce infestation by parasitic plants (López-Ráez et al. 2008). Indeed, it was demonstrated that tomato in which SL biosynthesis was knocked down through genetic modification was more resistant to *O. ramosa* infection (Kohlen et al. 2012). A reduction in SL production to obtain parasitic weed resistance was also achieved unintentionally. Dor and co-workers by using fast-neutron mutagenesis developed a tomato mutant (Sl-ORT1) resistant to various broomrape species (Dor et al. 2010). The Sl-ORT1 tomato was then discovered to be a SL-deficient mutant, and the resistance was thus associated to the low amount of strigolactones exuded (Dor et al. 2010). Breeding—through conventional or biotechnological approaches—for a reduction in the SL amount in exudates potentially also has negative consequences given their importance for the control of shoot and root architecture and the acquisition of nutrients through AM fungi (López-Ráez et al. 2008). This could possibly be prevented by approaches that reduce transport of SLs into the rhizosphere, which is facilitated by an ABC transporter, PDR1 (Borghi et al. 2015). However, under certain abiotic stress conditions, this could still negatively affect the adaptive capacity of plants by hampering AM fungi colonization. Particularly the example of sorghum and of maize shows that solutions in which the composition rather than the level of the SLs is changed may be the best solution (Yoneyama et al. 2015; Gobena et al. 2017). Nevertheless, several examples show that a reduction in SL production results in an acceptable level of resistance without large consequences for the plant phenotype (Jamil et al. 2011a; Pavan et al. 2016). In order to prevent that this partial germination-based resistance is overcome, a combination of pre- and post-attachment resistance mechanisms is necessary.

3.5.5 *Parasitic Plant Seed Germination Bioassay*

Plant seeds germinate when they are exposed to appropriate temperature, humidity, oxygen and, often, light. In case of seeds of parasitic plants, these conditions except light are also required, but SLs have a pivotal role in the regulation of germination. As said above, seeds of these root parasites will only germinate if they perceive the presence of the stimulants, which in the field means they are within the host rhizosphere and thus after germination they have a better chance to rapidly attach to the host root.

Considering the extreme biotic and abiotic complexity of the rhizosphere, a simple bioassay for studying SLs has been used extensively since the discovery of the stimulating compounds. This assay (Mangnus et al. 1992), with a number of adaptations and variants, is based on the reproduction, in vitro, of the steps necessary for parasitic seeds to germinate. Thus, seeds are first kept in a moist environment (i.e. on wet paper discs in Petri dishes), at a constant temperature (around 22–25 °C), for some days depending on the species. This mimics the so-called conditioning phase (see above). After that, seeds are placed in contacts with the stimulant in a proper concentration (usually at ppm or ppb levels) in order to induce germination. This happens a few days after stimulant application. Several observations can be then performed, e.g. percentage of germination, shape and length of the germination tubes, seed viability. More recently, high-throughput germination bioassays have been developed based on a standardized 96-well plate test coupled with spectrophotometric reading of tetrazolium salt (MTT) reduction (Pouvreau et al. 2013). These bioassays can be useful for different purposes, e.g. to guide the purification steps for the identification of novel stimulants; to test dose-response effectiveness of SLs, derivatives and analogues; to evaluate SL selectivity/specificity in parasitic species/strains; to bioassay germination inhibitors; and to study the physiology of the first stages of the parasitism.

3.6 Prospects

The research on SLs and parasitic plants has received an enormous attention in the last one to two decades, both because of the discovery of other important roles of the SLs (see above), and because of the extraordinary technological progresses, which made available equipment and tools unimaginable just a few years ago. High-throughput bioassays allow a faster and more accurate evaluation of the compound bioactivity, purification and analytical procedures, and structure determination has been simplified by more sophisticated, sensitive and automated equipment; “omics” approaches allow an easier understanding of the mechanisms of action of stimulants and inhibitors. Considering the key role of SLs in plant parasitism, parasitic weed management strategies should be developed in this perspective. Indeed, the level of success in controlling these parasites is very often still inadequate. The factors influencing the parasitic weed cycle have not yet been completely deciphered and thus the capability of predicting their infectiveness and infestation is still limited. The only option for success in such a difficult field of research is to bring together scientists representing a wide spectrum of disciplines, advanced research approaches and geographical representation of parasitic plant research. Assembling specialists with different perspectives, all focused around the common theme of plant parasitism, could provide a stimulating opportunity for finding widely usable, novel strategies for parasitic weed management.

Glossary

ABC transporter (ATP-binding cassette transporter) Transport protein, consisting of a transmembrane domain and membrane-associated ATPase, that utilizes the energy of ATP to transport substrates across cellular membranes.

Allelopathy The phenomenon that plants release molecules (called allelochemicals) that affect seed germination, plant physiology, growth and survival of other plants.

Arbuscular mycorrhizal (AM) fungi A group of obligate fungal root biotrophs that engage in symbiosis with 80% of all land plants. They penetrate the cortical cells of the roots of a vascular plant, forming unique structures, arbuscules, that help plants to capture nutrients such as phosphorus, sulphur, nitrogen and micronutrients from the soil and get photoassimilates of the plant in return.

Aromatic ring A cyclic (ring-shaped), planar (flat) molecule with a ring of resonance bonds that confers high stability to the molecule. The simplest aromatic compound is benzene, and the most common aromatic compounds are derived from it.

Bioactiphore The active part of a molecule responsible for the biological activity of the compound.

Biofuel Fuel derived directly from plants or indirectly from agricultural, commercial, domestic and/or industrial waste.

Carotenoids Organic pigments produced by plants and algae, in which they play an important role as accessory pigments in photosynthesis, as well as by several bacteria and fungi. Carotenoids are also precursors for cell signalling molecules, e.g. abscisic acid, which regulates plant growth, seed dormancy, embryo maturation and germination, cell division and elongation, floral growth and stress responses.

Seed dormancy A process that prevents germination of an intact viable seed in a specified period of time under any combination of normal physical environmental factors that are otherwise favourable for its germination.

Gene silencing Interruption or suppression of the expression of a gene at the transcriptional or translational level.

Intercrop A crop grown between the rows of another crop.

Isomer A molecule with the same molecular formula as another molecule but with a different chemical structure.

Nodulation The process of forming root nodules containing symbiotic, nitrogen fixing and bacteria.

Noncanonical SLs SLs lacking the A, B or C ring but still retaining the enol ether-D ring moiety, which is essential for biological activity.

Nucleophilic agent A reagent that forms a bond to its reaction partner (the electrophile) by donating both bonding electrons.

Phloem The living tissue that transports the soluble organic compounds made in the leaves during photosynthesis to all other parts of the plant.

Rhizosphere The zone of soil surrounding a plant root where the biology and chemistry of the soil are directly affected by a plant's root system, associated root secretions and microorganisms.

Xylem *Plant* vascular tissue that conveys water and dissolved minerals from the roots to the rest of the plant and also provides physical support.

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