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Parasitic Weeds: A World Challenge

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While witchweed is nearing eradication in the United States, it continues to thrive in other parts of the world, especially in Africa, together with other witchweed species. The continuing problems from witchweeds and other parasitic weeds, the broomrapes, dodders and mistletoes, are outlined, including their extent, the degrees of damage caused, and the difficulties in their control. While a small minority are being successfully controlled by the use of immune varieties, most are currently controlled by existing techniques only partially, or on a local basis, and they may even be spreading or intensifying. The challenges they present are emphasised.

Nomenclature: witchweed, *Striga asiatica* (L.) Kuntze; dodders, *Cuscuta* spp.; broomrapes, *Orobanche* spp.; mistletoes, Viscaceae, Loranthaceae.
Key words: Parasitic weeds.

After 50 yr of research and control programs, the problem from witchweed [*Striga asiatica* (L.) Kuntze] in the United States is all but extinguished. However, this is not true in other parts of the world and this article reviews the continuing challenge from this species and the many other parasitic weeds, affecting crops and forests here and elsewhere.

The major groups considered are the witchweeds themselves: *S. asiatica* and other species including *S. hermonthica* (Del.) Benth. and *S. gesnerioides* (Willd.) Vatke and the closely related *Alectra vogelii* Benth, all previously placed in Scrophulariaceae but now included in a broadened Orobanchaceae, which includes the broomrapes, *Orobanche* and *Phelipanche* species; the dodders, *Cuscuta* species (previously placed in Cuscutaceae but now in Convolvulaceae); and the mistletoes, especially *Viscum* species and dwarf mistletoes, *Arceuthobium* species in Viscaceae, and a range of other mistletoe genera in the related Loranthaceae.

The Witchweeds

Striga asiatica (*sensu lato*) is distributed widely across Africa and Asia (Figure 1). It is a normal looking plant, up to 30 cm high, scabrid to the touch, with simple green leaves. It is self pollinated and occurs in a wide range of distinct morphotypes with varying flower color and host specificity. Some of these in Africa are given specific status, e.g., as *S. hirsuta* Benth. and *S. lutea* Lour. (Mohamed et al. 2001) and are less likely to attack crops, while *S. asiatica* (*sensu stricto*) is the form responsible for the major infestations in eastern and southern countries of Africa (and in the United States). This is mainly scarlet-flowered though yellow-flowered individuals may also occur in these populations, and a brown-flowered form occurs in Ethiopia. Elsewhere in Africa it is a parasite of wild grasses and causes little damage to crops. In India, it is less widespread, but a white-flowered form of *S. asiatica* (or closely related taxon) affects sorghum and sugar cane locally (Patil and Angadi 2008).

Where crops are affected these can include virtually all the main tropical cereals: corn (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench] and millets (*Pennisetum, Panicum, Eleusine, Digitaria*, etc.) as well as rice (*Oryza sativa* L.) and sugar cane (*Saccharum officinarum* L.).

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Although the *Striga* species are green, their photosynthesis is very inefficient and they depend on the host for most of their nutrition. Furthermore their effect on the hosts is vastly greater than mere removal of nutrients. Photosynthesis in sorghum may be reduced by 62% by infestation with *S. asiatica* (Press et al. 1987) and there are other physiological effects of drought stress (wilting even under moist conditions) and an increase in root development at the expense of the shoots. The losses are not well documented but the proportion of, e.g., corn crops affected in southern Africa include estimates of 63 to 80% in Malawi and substantial proportions in Angola, Swaziland, and other southern African countries (de Groote et al. 2008), also in Madagascar (Geiger et al. 1996). Rice is seriously affected in Tanzania (Kayeke et al. 2007). Infestation can involve total crop failure, and average losses of 10 to 40% are almost certainly common. Furthermore, the problem is tending to increase rather than decrease as intensive land use and the expense, or lack, of fertilizers leads to continuing decline in soil fertility, which greatly favors *Striga* growth.

Meanwhile the control measures are neither fully effective nor easy to apply. Those used to bring the problem under control in the United States have involved sophisticated use of ethylene gas, methyl bromide, and herbicides, and intensive quarantine and monitoring procedures. None of these are readily available or practical in Africa. Plant breeders have developed sorghum, corn, and rice varieties with partial resistance, but these are not yet widely used or available. The use of herbicide treated seed involving an imidazolinone-resistant corn variety can be effective for control of *S. asiatica* as well as for *S. hermonthica* (Kabambe et al. 2008), but good results depend on suitable soil moisture conditions. The use of *Desmodium* intercrops (e.g., Khan et al. 2008) has not yet been proven effective for *S. asiatica*. In rice in Tanzania, legume green manure crops have provided valuable suppression (Kayeke et al. 2007). Partial control is achieved in many places by other cultural practices, especially extra manuring, but without a long-term build up in soil fertility, complete control will be extremely difficult to achieve.

Hence *S. asiatica* continues to present a challenge for the foreseeable future, not only in the areas already affected but also in terms of possible introduction to new areas. As shown by Mohamed et al. (2006), *S. asiatica* (*s.s.*) has the potential to infest large new areas of North and South America and of Asia, as well as parts of Africa where only the less aggressive forms exist so far.

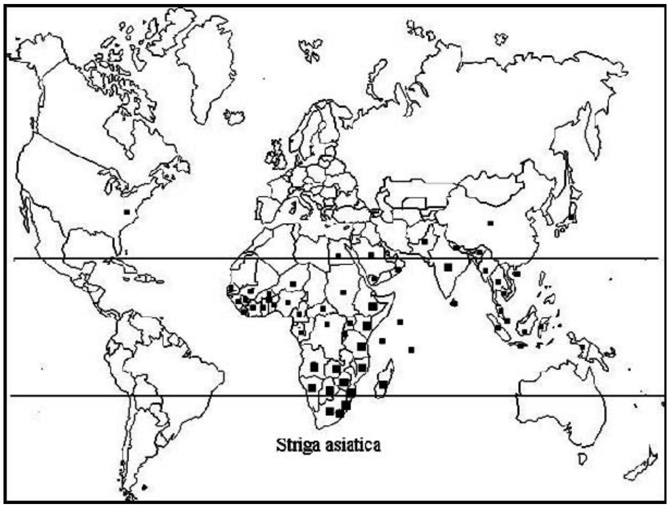

Figure 1. World distribution of *Striga asiatica*. Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage.

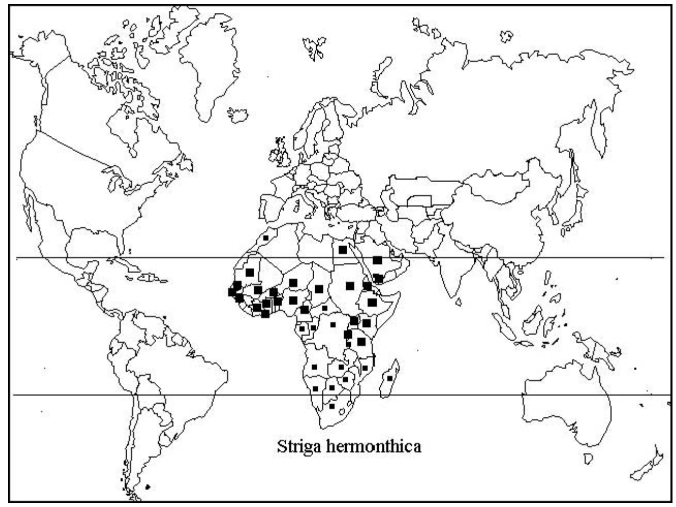

Figure 2. World distribution of *Striga hermonthica.* Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage.

Striga hermonthica is a greater problem than *S. asiatica* in every sense. It is a larger plant, growing up to 1 m high in eastern Africa, though usually not more than 50 cm in West Africa; it causes even greater damage over much larger areas of crop in many more countries. The range of crops affected is much the same, but the regions where it is most damaging are curiously different, mainly in northern Africa (East and West) and with little incidence south of the equator (Figure 2). It occurs in the Arabian Peninsular but is otherwise restricted to Africa. The foliage is comparable in shape to that of *S. asiatica*, but more robust, while the inflorescence is a much larger raceme with many more flowers, these being larger and almost invariably pink, with occasional white individuals.

The damaging effects on host crops are at least as severe as those from *S. asiatica* but slightly different in character. Photosynthesis of the host is similarly reduced, e.g., by 58% in sorghum (Press et al. 1987) and root:shoot ratio is again much increased, but whereas *S. asiatica* causes drought symptoms, *S. hermonthica* causes distinctive chlorotic blotching in the host foliage. The disproportionate reduction in host biomass, relative to the biomass of the parasite was illustrated in a pot experiment where, at 5 wk after sowing (prior to weed emergence) 14 mg dry weight of parasite caused 997 mg reduction in host dry weight (Parker 1984).

Crop loss can again be up to 100%, and a recent detailed survey in western Kenya suggests average losses of corn are about 50% under "moderate" infestation and 80% under severe infestation (Manyong et al. 2007). Estimates of corn crop area infested vary up to 20 to 30% in Ethiopia, Cameroon, Cote d'Ivoire, and Guinea, 30 to 40% in Togo, Mali, and Nigeria, and 65% in Benin (de Groote et al. 2008). A survey in north-east Nigeria suggested 85% of fields were infested (Dugje et al. 2006). Proportions of sorghum and pearl millet [*Pennisetum americanum* (L.) K. Schumm.] crops infested are likely to be at least as great. 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), and there is little evidence for any diminution of the problem since then (Parker 2009).

Control methods have been no more fully successful than those for *S. asiatica.* Most research effort has gone into plant breeding for resistance, and some success has been achieved using conventional methods for corn in West Africa (Kamara et al. 2007; Menkir et al. 2007) and sorghum in Sudan and Ethiopia (e.g., Tesso et al. 2007), but resistance is never complete. Research efforts continue with ever more advanced genetic modification techniques, which should bear fruit eventually. Meanwhile, in West Africa, integrated control involving tolerant varieties and various cultural approaches have proved valuable (e.g., Kamara et al. 2008), but these have to be tailored to local conditions. In East Africa, there has been local success with *Desmodium* intercrops (Khan et al. 2007, 2008) and with herbicide-coated seed of imidazolinone-resistant corn (de Groote et al. 2007; Kanampiu et al. 2003), but neither technique is yet widely adopted. Trap-cropping, the use of crops that stimulate germination but are not themselves attacked, and a range of other cultural approaches can help to reduce the problem (e.g., de Groote et al. 2010), but as with *S. asiatica*, most approaches are doomed to only partial success in the absence of significant increases in soil fertility.

Overall, many million farmers and many million hectares of crop are affected by *S. hermonthica* and economic losses may exceed $1 billion annually (Parker 2009). The challenge is to develop successful control strategies at a faster rate than the current spread and intensification of the problem and to prevent further introductions to the completely new areas in the Americas and Asia where conditions could favor it (Mohamed et al. 2006).

Other *Striga* species affecting cereal crops, not considered in detail here, include the pink-flowered *S. aspera* Willd., occurring mainly in West Africa but also eastwards to Sudan and south to Malawi, and locally damaging to corn in Nigeria, Cameroon, and Cote d'Ivoire and to rice in Cote d'Ivoire and Senegal (Parker and Riches 1993). In northeast Nigeria, 40 to 59% of rice fields were estimated to be infested with *S. aspera* (Dugje et al. 2006). The pale pink-flowered *S. forbesii* Benth., with a slightly wider distribution into southern Africa and Madagascar, is locally damaging to corn and sorghum in Zimbabwe and Tanzania and to rice in Cote d'Ivoire. Two further white-flowered species attack cereals in India: *S. densiflora* (Benth.) Benth. and *S. angustifolia* (Don) Saldanha,

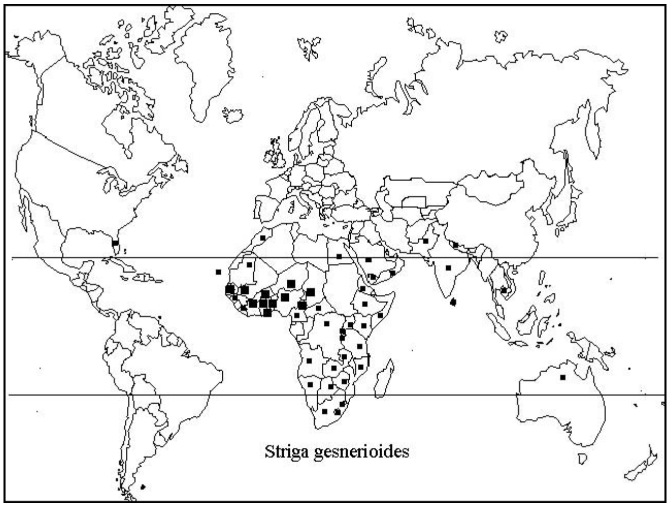

Figure 3. World distribution of *Striga gesnerioides.* Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes little or no crop damage.

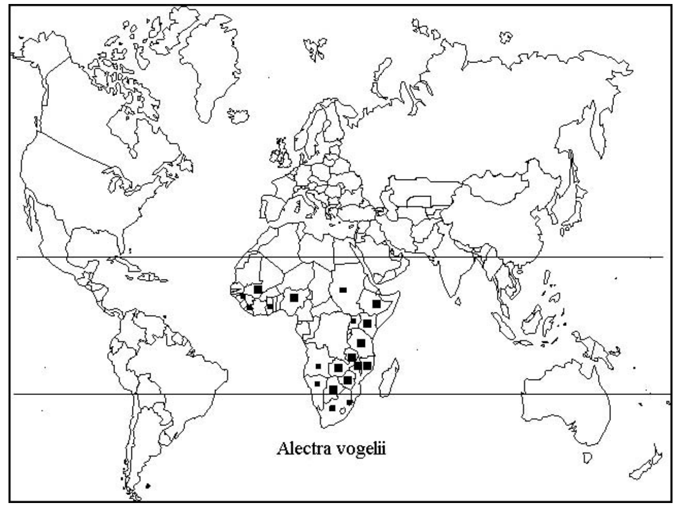

Figure 4. World distribution of *Alectra vogelii.* Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage.

but their current importance there relative to *S. asiatica* is uncertain.

Striga gesnerioides is almost unique among *Striga* species in attacking only broad-leaved hosts and not cereals or other grasses. Like *S. asiatica* it is autogamous and exists in a range of distinct morphotypes (Botanga and Timko 2006; Tonessia et al. 2009) but with even narrower host range, such that there is a range of ''races'' with differential virulence on varieties within the main crop host cowpea [*Vigna unguiculata* (L.) Walp.]. It is a short, much-branched plant up to 30 cm, with scale-like leaves and very little chlorophyll. Flower color varies from white through to deep purple.

It is mainly African in distribution, and the forms attacking cowpea are restricted to western Africa (Figure 3). In northeast Nigeria, 81% of cowpea fields were estimated to be infested (Dugje et al. 2006), but many other species in a range of families are parasitized almost throughout Africa and across southern Asia. Other crops that have been affected very locally include tobacco (*Nicotiana tabacum* L.) in South Africa and Zimbabwe (Koga et al. 2011) and sweet potato [*Ipomoea batatas* (L.) Poir.] in Botswana (Parker and Riches 1993).

The damaging effect of *S. gesnerioides* on cowpea can be severe to the point of complete crop loss. However, thanks to the extreme host specificity of this species, and its autogamy, it has been possible to find crop varieties each differing in a single dominant gene, with complete immunity to one or more of its races (Li et al. 2009; Singh et al. 2006). One of the most valuable sources of resistance to be identified (from cowpea landrace line B301 with coincidental resistance to *A. vogelii* in Botswana) has proved effective against almost all the six or seven recognized races but not to a local race in Benin, which is thought to have evolved relatively recently (Dube and Belzile 2010). This and some other sources identified in West Africa have been used in breeding programs to produce varieties resistant to the local races of the parasite and with other desirable characters (Singh et al. 2006). This has been a rare success story in terms of parasitic weed control, but the challenge now is to ensure that new more virulent races do not develop and spread. This may require continued selection and breeding.

Other Hemi-Parasites in Orobanchaceae

Alectra vogelii has normal-looking green foliage but is broader-leaved than the *Striga* species and has yellow flowers. But like *Striga* it is an obligate parasite, depending totally on its host for its development and survival. Like *S. gesnerioides* it attacks cowpea and both parasite species can occur in the same field, but it may also attack peanut (*Arachis hypogaea* L.), bambara [*V. subterranea* (L.) Verdc.], soybean [*Glycine max* (L.) Merr.] and a number of other legume crops.

Distribution is restricted to Africa (Figure 4) and the extent of infestations is relatively small, but there is plenty of scope for extension of the problem to new areas. The infestation in Ethiopia (Parker 1988) seems likely to be the result of relatively recent chance introduction.

Damage to cowpea can be severe: up to 100% yield loss has been reported in Nigeria (Emechebe et al. 1991). Thanks to the work of Riches in Botswana (Riches et al. 1992), a number of resistant lines of cowpea have been identified and these have been used as the basis for commercially viable varieties, recently released for use in Zambia (C. R. Riches, personal communication), while *S. gesnerioides*-resistant varieties incorporating genes from line B.301 also show at least partial resistance (Singh et al. 2006). As with *S. gesnerioides*, however, there is evidence for variation in *A. vogelii* that will require further selection and breeding for different regions.

Rhamphicarpa fistulosa (Hochst.) Benth. is another relatively minor problem, but it causes serious damage locally to rice crops across both West and East Africa (Johnson et al. 1998; Rodenburg et al. 2010). It is another hemi-parasite with green, highly dissected foliage, and white flowers. There are no established control methods, but its occurrence mainly around the fringes of rice fields suggests that water depth may be critical for germination and that cultural methods might be applicable.

The Broomrapes

Orobanche crenata Forsk. is the largest of the weedy broomrapes and probably the most damaging. Like other

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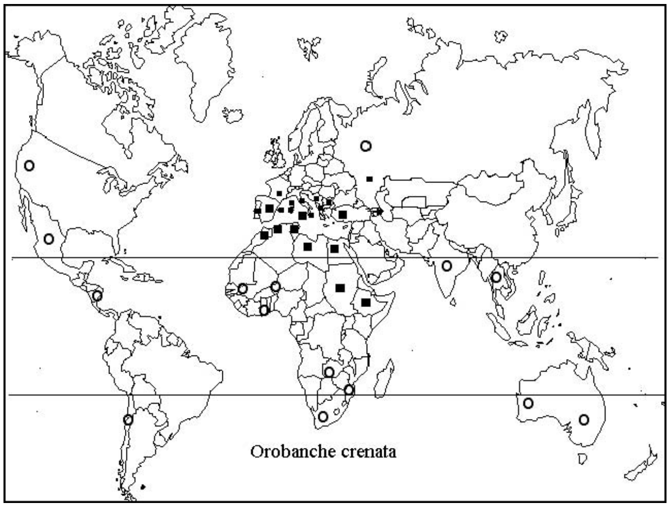

Figure 5. World distribution of *Orobanche crenata.* Larger square symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage. Circles indicate other countries with potentially suitable climates for its growth (Grenz and Sauerborn 2007).

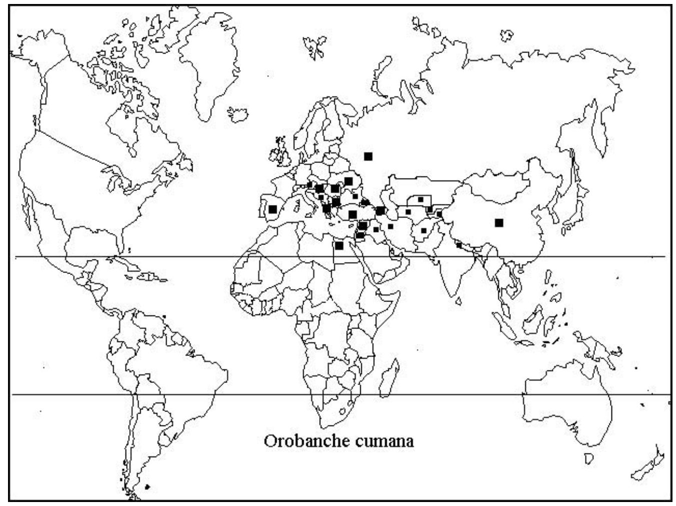

Figure 6. World distribution of *Orobanche cumana*. Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts or causes lesser crop damage.

Orobanche and *Phelipanche* species, it is a holoparasite with no apparent chlorophyll. It develops from a minute seed, stimulated, like *Striga* spp., to germinate by exudation of strigolactones from host roots. It attaches to the root and forms a swollen nodule, from which a shoot develops forming a single sturdy erect spike up to 1 m high with numerous showy, fragrant white flowers up to 2 cm across, streaked with purple.

Native distribution is throughout the Mediterranean basin, but with relatively recent introductions further afield into Ethiopia (Reda 2006) and Sudan (Babiker et al. 2007) (Figure 5). The main host crop is faba bean (*Vicia faba* L.), but many other legumes are attacked, particularly pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medick.), and to a lesser extent, a range of crops in Apiaceae, especially carrot (*Daucus carota* L.), and Asteraceae. Sauerborn (1991) estimated that over 50% of faba bean crops were infested in Spain, Portugal, Syria, and Morocco. Other countries in which *O. crenata* is a significant problem on legumes include Algeria, Cyprus, Iraq, Italy, Jordan, Lebanon, Israel, and Tunisia. *Orobanche* spp. do not have the same subtle physiological effects on their hosts as *Striga* spp. but damage the host via diversion of a substantial proportion of host resources, such that yield losses can be over 50% in Malta and Turkey and over 30% in Egypt. Where there is moisture stress, there can be greater damage to the point of total crop failure.

Orobanche crenata is out-crossing and very genetically diverse. Hence it has proved difficult to select consistently resistant varieties. An Egyptian line Giza-402 has shown partial resistance, and together with others has been used in breeding programs but with limited success. Some herbicides have shown selectivity but none are widely used. Cultural methods, based on time of planting, etc., may succeed but at the cost of yield. The problem has been avoided in some regions by simply giving up growing the susceptible legume crops at a cost to the local diet and economy.

Thus *O. crenata* remains a very serious challenge throughout the Mediterranean, while threatening to expand further in Ethiopia and Sudan, and, as indicted by Grenz and Sauerborn (2007) (see Figure 5), there are risks of introduction to many other countries where the climate is thought to be suitable for its growth.

Orobanche foetida Poir. is a closely related species occurring along the North African coast and in Iberia. It is similar in stature but with much darker flowers. It also attacks faba bean and causes serious damage to the crop in Tunisia. Varietal screening has suggested variation in susceptibility among faba bean lines (e.g., Abbes et al. 2007). Otherwise, there are no established control measures.

Orobanche cumana Wallr. also produces single unbranched fleshy erect stems but is smaller than *O. crenata*, growing to about 50 cm high while the flowers are smaller, narrowly tubular and markedly down-curved, white to pale bluish in color. The native range is the eastern Mediterranean and eastern Europe where it naturally occurs on *Artemisia* spp. However, at some stage it has evolved to attack cultivated sunflower (*Helianthus annuus* L.) and now occurs on that crop somewhat more widely, from Spain in the west to China in the east (Figure 6).

Although under some experimental conditions the loss of biomass of the crop is no more than the biomass of the parasite (Grenz et al. 2008), it is assumed that there may be much greater damaging effects under conditions of moisture stress, which can result in very severe crop losses. Areas affected include 40,000 ha in Spain, 20,000 ha in Greece and China, and 10,000 ha in Turkey (Parker 2009). Yield losses have been estimated at 60% in Greece and 20 to 50% in China (Parker 2009). Other countries in which it is an acute problem include Hungary, Romania, Bulgaria, Russia, Ukraine, Moldova, Syria, and Egypt. The areas affected and degree of crop loss has varied over time, according to the successful introduction of resistant varieties. Resistance in sunflower was discovered in Russia early in the 20th century but was gradually overcome by more virulent races of the parasite. This process has been repeated such that at least seven races are now recognized and the latest races F and G continue to pose a challenge to plant breeders in several countries. Furthermore, while it has been possible to transfer resistance genes from wild *Helianthus* spp. to the oil-crop varieties, it has proved more difficult for confectionary

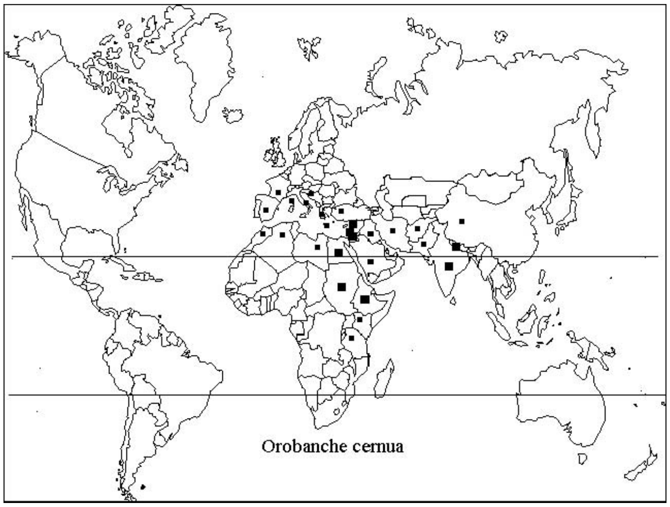

Figure 7. World distribution of *Orobanche cernua.* Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage.

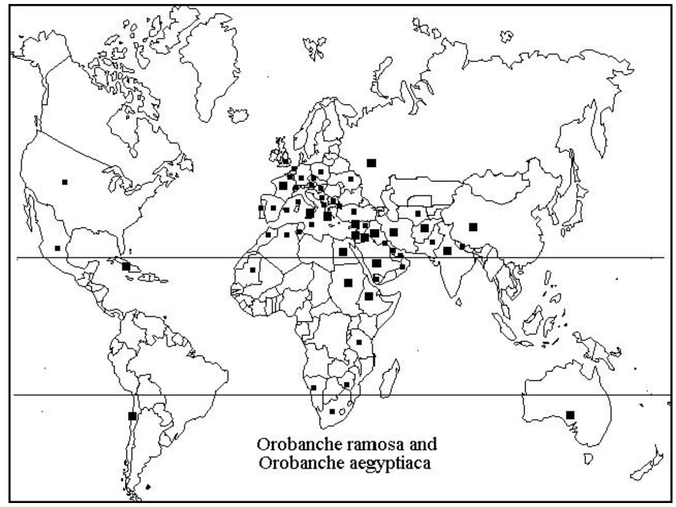

Figure 8. World distribution of *Orobanche ramosa/O. aegyptiaca.* Larger symbols indicate countries in which they cause significant crop losses. Smaller symbols indicate countries in which they occur mainly on wild hosts and cause lesser crop damage.

varieties and these tend to be more widely susceptible. Herbicides have been used in the confectionary crop, imazapic, proving selective in Israel (Aly et al. 2001). It is quite certain that *O. cumana* could thrive in many other parts of the world where sunflower is grown. It thus continues to be a major challenge to the plant breeders, to keep up with the evolution of new virulent races, and for regulatory authorities to minimize the risk of further spread.

Orobanche cernua Loefl. is closely related to *O. cumana*: the latter was previously known as *O. cernua* ssp. *cumana*, but they are now considered quite distinct (Joel et al. 2007; Katzir et al. 1996). *Orobanche cernua* is similar morphologically, but the flowers are less narrowly tubular, less markedly bent, and the flowers more deeply blue/mauve colored. The distribution of true *O. cernua* is not readily disentangled from that of *O. cumana*, but it has a rather more southern distribution, extending further into North Africa and South Asia, while there has been more recent introduction into some East and West African countries (Figure 7). It also has a very different host range, mainly in the Solanaceae, affecting particularly tomato (*Lycopersicon esculentum* Mill.), tobacco, and eggplant (*Solanum melongena* L.).

Often in combination with *O. ramosa*, *O. cernua* can steadily built up massive populations in large-scale tomato plantations, to the point where crop losses are unsustainable and commercial exploitation of tomato for juicing has had to be abandoned, e.g., in Sudan and in Ethiopia. Thanks to the long life of the seed in the soil, it may be 10 to 20 yr before the growing of susceptible crops can be resumed. Where tomato and other Solanaceae are grown less intensively the problem may be less acute, but there are still significant yield losses in Israel, Jordan, Pakistan, Nepal, Iran, and Yemen. In southeast India, it is a major and increasing problem in tobacco, with 40,000 ha affected not only in yield but also in quality.

No fully resistant crop varieties have been developed and while herbicides have been used in Israel, selectivity is limited and they have to be very carefully applied. Hence control options are very poor indeed, providing yet another challenge.

Orobanche minor Sm. is indeed a relatively minor problem. It resembles the above species in having simple unbranched stems, up to 50 cm or more in height. Flowers are white varyingly streaked with purple, rather like *O. crenata* but smaller, about 1 cm across. It is widely distributed in Europe and the Mediterranean and has been introduced to many countries outside, including the United States, South Africa, Japan, New Zealand, and Australia. It has a wide host range, the main crops affected being clovers and alfalfa (*Medicago sativa* L.) with localized occurrence on other Fabaceae, Asteraceae, Apiaceae, and tobacco. It is currently causing concern in Oregon where it causes over 50% loss in seed yield of red clover (*Trifolium pratense* L.) seed crops (Lins et al. 2007). Eizenberg et al. (2006) developed a procedure for selective control by imazamox but it requires careful timing.

***Orobanche ramosa* L. [*Phelipanche ramosa* (L.) Pomel] and *O. aegyptiaca* Pers. (*P. aegypticaca* Pomel).** These two species, together with *O. nana* (Reut.) Beck and *O. mutelii* F.J. Schultz form a complex that are not always well distinguished in the field and are treated here together. Collectively they are centered on the Mediterranean and western Asia but also extend to eastern Asia and have been introduced sporadically to many other parts of the world (Figure 8). They have a wide host range attacking many species in many families, with the Solanaceae (tomato, eggplant, and tobacco) and Brassicaceae (mustards, *Brassica* spp. and rapeseed, *Brassica napus* L.) among the most seriously affected. As noted above for *O. cernua*, massive populations can build up in large-scale tomato plantations leading to abandonment of the crop and even closure of dedicated juicing factories (Babiker et al. 1994). This is believed to have occurred in Ethiopia and in Sudan, while acute problems have been reported in many other countries as indicated on the map (Figure 8). Yields may be reduced by 50% or more, especially where soil moisture is lacking. Methyl bromide has been used to eradicate localized infestations, but this is no longer available and alternatives are so far either less effective or excessively expensive. Attempts to identify resistant varieties of tomato have been generally unsuccessful, and although selective herbicide treatments have been developed in Israel,

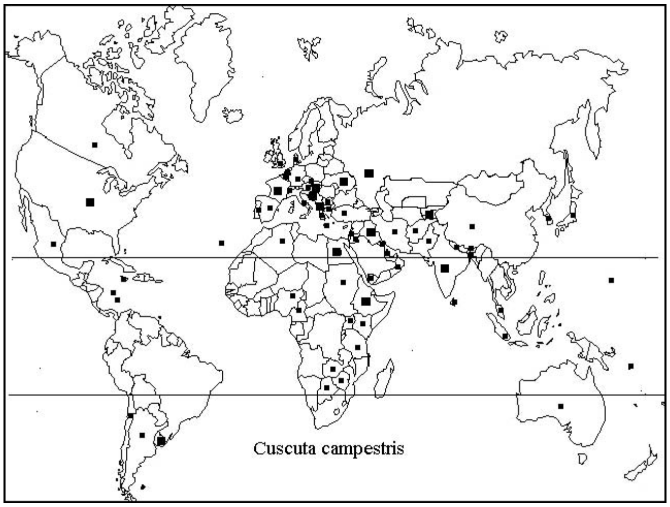

Figure 9. World distribution of *Cuscuta campestris.* Larger symbols indicate countries in which it causes significant crop losses. Smaller symbols indicate countries in which it occurs mainly on wild hosts and causes lesser crop damage.

for control of *O. aegyptiaca* in carrot, they require very careful application and are not being used elsewhere. New infestations are being recorded, as in Australia where 6,000 ha are infested (Warren 2006), costing several million $U.S. per annum in quarantine and control operations.

The Dodders

***Cuscuta campestris* Yuncker.** There are over 100 species of *Cuscuta* among which there are just a few of concern to agriculture. By far the most important of these is *C. campestris* (field dodder in the United States). All the dodders have very similar morphology, consisting of narrow, yellow stems and sometimes tendrils, which twine round the host, the leaves reduced to inconspicuous scales. They are virtually holoparasitic, most species having very low levels of chlorophyll and only a few show noticeable greenness. The species are distinguished almost exclusively by their floral characters, by size of flower, density of clusters, the number of floral segments (four or five), and stigma and capsule characters. *Cuscuta campestris* has five-part flowers in quite dense clusters, petals characteristically deflexed, and a very conspicuous capsule topped by two capitate stigmas.

Cuscuta campestris is native to North America but has been spread all over the world as a result of transfer in contaminated seed of clovers (*Trifolium* spp.) and alfalfa (Figure 9). The seeds are of similar size and are extremely difficult to separate. While these are the crops most often infested, together with niger seed [*Guizotia abyssinica* (L.f.) Cass.], also because of seed contamination, many others in a wide range of families can be attacked, including trees and shrubs. Sugar beet (*Beta vulgaris* L.) is seriously infested in many south European countries. *Cuscuta campestris* can also persist on many weed species, ensuring that it is not readily controlled by crop rotation. Wolswinkel (1974) demonstrated how *C. campestris* creates a nutrient sink resulting in complete inhibition of seed formation in faba bean. Yield losses of over 50% have been recorded in forage alfalfa, while losses of seed yield may be even greater and made more serious by the danger of contamination of crop seed, reducing its value or precluding its sale altogether because of quarantine restrictions. Some herbicides show selectivity in alfalfa and a few other crops but none give fully reliable control, for which growers often have to resort to rigorous removal of the parasite together with host to prevent spread and seeding.

Other economically important species of *Cuscuta* include *C. reflexa* Roxb. and *C. monogyna* Vahl occurring on fruit and shrub crops in the Middle East and South Asia, *C. gronovii* Willd. ex Roem. et Schult., an acute problem in cranberry (*Vaccinium macrocarpon* Ait.) in the United States, *C. epithymum* (L.) L. on clovers and alfalfa in the Middle East, and *C. chinensis* Lam. on soybean and other crops in East Asia.

Collectively the dodders affect many thousands of hectares worldwide, reducing yields, restricting choice of crop, and interfering with international trade. Improved control methods are urgently needed.

Lauraceae

***Cassytha filiformis* L.** *C. filiformis* is a relatively unimportant parasite but is mentioned here as it closely resembles *Cuscuta* species in growth form and the two genera are often confused. It is, however, a perennial, more robust than most *Cuscuta* spp. and always shows some distinct green coloration. It has solitary white flowers and fleshy fruit. It occurs across the tropics of New and Old Worlds, usually near the coast but sometimes inland and is an obligate parasite mainly on perennial hosts, including grasses. The only recent reports of any economic significance refer to damage on neem trees in Kenya (Scmuttere 1998) and on *Eucalyptus* spp. in Australia (Reid and Yan 2000). There were earlier reports of damage to citrus in India and Tanzania, and to pine trees in China (Parker and Riches 1993).

The Mistletoes

Economically important mistletoes fall into two families, the mainly temperate Viscaceae and the mainly tropical Loranthacae.

Viscaceae. The most familiar of all mistletoes, *Viscum album* L., emblem of Christmas and subject of folklore, is widespread across Europe and causes locally serious damage to fruit trees, especially apple and pear, and to forest trees, including silver fir (*Abies alba* Mill.) in Croatia (Idžojtic et al. 2008), in Romania (Barbu and Boriaud 2010), and in other Balkan states, and Crimean pine in Turkey (Catal and Carus 2011). While economically negative in these respects, it also has uses as a source of compounds active against cancer (e.g., Olaku and White 2011; Ziegler and Grossarth-Maticek 2010). Other *Viscum* species cause minor problems across Europe and Africa, while the *Phoradendron* species do likewise across North America. These mistletoes are fully green and have a largely functional photosynthesis so do not depend greatly on their hosts for nutrition, but they may reduce leaf nitrogen content in the host (Galiano et al. 2011), and require water, causing serious damage under conditions of moisture stress.

The most important members of Viscaceae, however, are the dwarf mistletoes, the *Arceuthobium* species, which collectively are regarded as "the single most destructive pathogen of commercially valuable coniferous timber trees" in North America and Mexico, with losses estimated at 11 million m^3 of wood annually (Hawksworth and Wiens 1996).

They have a much reduced shoot system, consisting of short branches bearing very reduced leaf scales, yellow green, low in chlorophyll. Most of the plant consists of an extensive endophyte permeating the host tissues. Apart from drawing heavily on the host for both water and nutrition, they have profound physiological effects on the host, causing witches' brooms and other growth abnormalities, affecting the strength and quality of timber as well as its volume. There are 39 North American taxa, 8 to 10 species of particular importance, each affecting a very narrow range of host trees, all conifers. Other species occur outside North America, notably *Arceuthobium minutissimum* Hook.f., aptly named as the shoots barely exceed 5 mm in height, damaging blue pine (*Pinus wallichiana* A.B. Jackson) in Bhutan and throughout the Himalayas, *A. oxycedri* damaging juniper widely across Asia, especially in Pakistan (Sarangzai et al. 2010) and *A. sichuanense* seriously damaging *Picea* spp. in south China and Tibet (Xia Bo et al. 2010). Control of *Arceuthobium* spp. has been achieved with sprays of ethephon (Coria Ávalos et al. 2010), but application over large areas of forest is generally uneconomic and in practice control depends on management, clear felling, controlled fire, etc. In spite of these efforts, losses inevitably continue.

Loranthaceae. Loranthaceae are generally comparable to *Viscum* species in having fully green foliage and competing with their hosts mainly for water, but they differ in having much larger, showy flowers, often pollinated by birds. The family has about 75 genera and 1,000 species. Of these just a few are of economic importance such as *Dendrophthoe falcata* (L.f.) Ettsingh. damaging a wide range of fruit and forest species in India. It can cause 40% reduction in annual growth of teak (*Tectona grandis* L.f.) (Ghosh et al.1984). *Struthanthus orbicularis* (H.B.K.) Blume has shoots that can make secondary attachments to the host and lead to a total blanket over citrus (*Citrus* spp.) and other host trees in Central America, especially Belize. *Tapinanthus* spp. including *S. bangwensis* (Engl. and Krause) Dans., *S. globiferus* (A. Rich.) van Tiegh., and *S. dodoneifolius* (DC) Danser cause serious damage to cocoa (*Theobroma caco* L.), coffee (*Coffea arabica* L.), citrus, shea butternut [*Butyrospermum paradoxum* (Gaertn.f.) Hepper], and other fruit and ornamental trees in West Africa. For none of these are there currently any simple economic control measures.

Conclusion

Parasitic weeds have been the target of research for at least 100 yr and it would be wrong to suggest that there has been little progress in their control. There are many examples of dedicated work leading to useful control, based on resistant varieties, cultural, chemical, or integrated methods providing near-adequate suppression of problems on at least a local basis. However, in spite of all these efforts, it has been concluded (Parker 2009) that the major problems have not been reduced to any significant degree over really large areas, and in the case of *Striga* there may even continue to be some spread and intensification of the problems. It is improbable that many of these species will be completely overcome in the foreseeable future, but there has to be continued effort on the most important, especially on *Striga* and *Orobanche* species. Most effort currently is perhaps devoted to the possibilities for resistance, achieved through conventional or genetic engineering approaches. Biological control continues to receive attention and could have valuable contributions to make. Perhaps the biggest impact on *Striga* could eventually come from the introduction of nitrogen fixation into cereal crops. Meanwhile, for *Striga* specifically, there is an urgent need to find other ways to maintain and increase soil fertility in Africa.

This short review emphasises the enormous scale of losses from the full range of parasitic weeds worldwide and the need for sustained, and where possible, increased effort to find economic solutions for the sake of the farmers and growers affected and for the sake of maintaining world food and timber supplies.

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