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Arbuscular mycorrhizal fungi-parasite-host interaction for the control of *Striga hermonthica* (Del.) Benth. in sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract Five *Glomus* species (*G. intraradices*, *G. albidum*, *G. mosseae*, *G. fasciculatum*, and *G. etunicatum*) were compared against a check [without arbuscular mycorrhizal (AM) fungi, plus *Striga*] and control (without AM fungi or *Striga*) treatments for the control of *Striga* in a tolerant sorghum variety (War-wara bashi) in an experiment carried out in 12-cm-diameter clay pots. The experiment was carried out in a controlled growth chamber. *G. mosseae* significantly reduced the number of *Striga* emerging per plant, increased plant growth, shoot and total dry matter yield of sorghum, did not affect the root dry matter compared with the other AM fungi species, but had a comparable effect to the control treatment. All the AM fungi except *G. mosseae*, and also the *Striga*-infested treatment, increased the root:shoot ratio compared to the control treatment. The percent reduction (62%) of *Striga* emergence after *G. mosseae* inoculation resulted in about a 30% increase in total dry matter yield of sorghum over the control, while the total loss in dry matter yield of sorghum due to *Striga* infestation was 36%. Root colonization of sorghum by AM fungi was highest for *G. mosseae* (44%) followed by *G. intraradices* (24%) and *G. albidum* (23%) then *G. fasciculatum* (18%), with the lowest recorded for *G. etunicatum* (14%). No colonization of *Striga* roots was observed. The potential of AM fungi to reduce or to compensate for *Striga* infestation could be important for soil management, especially in the tropics, and for the reduction of *Striga*-resistant varieties of sorghum which are mycorrhiza-responsive.

Keywords Arbuscular mycorrhizal fungi · *Striga hermonthica* · Sorghum · Control

Introduction

Striga is a genus comprising about 30–40 species, reaching its greatest diversity in tropical Africa, where about 35 species occur (Raynal-Roques 1991; Gworgwor et al. 2001). They are terrestrial parasites, penetrating host roots by a primary haustorium and/or secondary haustoria (Weber 1987a, 1993). Several species, for example, *S. hermonthica* (Del.) Benth., *S. asiatica* (L.) Kuntze and *S. gesnerioides* (Willd.) Vatke are serious pathogens of important crop plants. In fact, in rain-fed areas of semi-arid Africa *S. hermonthica* may be the most serious cause of a reduction in yields of sorghum [*Sorghum bicolor* (L.) Moench], and pearl millet [*Pennisetum glaucum* (L.) R. Br.], the main crops of subsistence farmers. *S. asiatica* causes serious damage in maize (*Zea mays* L.) and sorghum, while *S. gesnerioides* can be devastating in cowpea [*Vigna unguiculata* (L.) Walp.]. In Africa these weeds are considered to pose a serious threat in 17 countries and a moderate threat in 25 countries to the lives of >100 million people (Mboob 1989). Two-thirds of the 73 million ha devoted to cereal crop production in Africa are seriously affected. The actual crop losses caused by *Striga* are variable, but can range from 10% to 90%, and sometimes lead to complete crop failure in the field depending on the crop species and the degree of infestation (Mboob 1989; Doggett 1975; Carson 1986; Sauerborn 1991; Gworgwor and Weber 1991; Gworgwor 1993, Gworgwor et al. 2001). The loss of revenue from sorghum, pearl millet, and maize due to parasite infection could total 2.9 billion US dollars (Sauerborn 1991).

The control of *Striga* [as well as *Orobancha* L. (*Orobanchaceae*)] has been more difficult than of any other common weeds. This is because they produce large quantities of minute seeds (0.2×0.3 mm), which remain viable in the soil for up to 20 years (Saunders 1933; Bebawi et al. 1984) until conditions suitable for germi-

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nation occur. Furthermore, because of their pre-ripening requirements (Saunders 1933; Vallance 1951; Reid and Parker 1979) the seeds are not all pre-conditioned for germination at the same time. Thus, there is a need for persistent methods of control. Various control methods, therefore, have been tried over the years, but without conclusive and consistent results for use by peasant farmers (Weber 1993; Parker and Riches 1993; Press and Graves 1995). These methods include cultural and agronomic practices (land preparation, hand pulling, hoe-weeding, nitrogen fertilization, and trap and catch cropping); others are the use of chemical stimulants, herbicides, breeding for resistance and biological control (Musselman 1987; Weber and Forstreuter 1987; Parker and Riches 1993; Gworgwor et al. 1998). The failure of the individual methods to produce a single effective control method calls for an integrated approach, where more than one of these methods can be used (Ogborn 1984; Gworgwor and Weber 1990).

The potential for including mycorrhizal fungi in pest control packages has not been widely explored, although the use of chemicals for fumigation and disease/pest control is progressively being discouraged and the cost of fertilizer application is becoming a proportionally larger component of the cost of production, especially among tropical peasant farmers. Arbuscular mycorrhizal (AM) fungi are reported to improve nutrition of their host plants, and they may enhance resistance against pathogenic organisms (Dehne 1982; Powell and Bagyaraj 1984; Bodker et al. 1998; Branzanti et al. 1999; Abdalla and Abdel-Fattah 2000; Kasiamdari et al. 2002). Weber (1987b) reported that parasitic Scrophulariaceae can easily be infected by AM fungi, and if the infection starts very early on, in the seedlings, in most cases the parasitic plants stop growing and die. Krause (1988) has specifically reported the presence of AM fungi in *S. asiatica* roots and suggested that such a symbiosis might lead to a form of biological control. However, Klein et al. (1991) observed no infection of *S. asiatica* roots by AM fungi, although the host plant maize was colonized by AM fungi. Gworgwor and Weber (1992) reported no emergence of *S. hermonthica* on sorghum when inoculated with *G. fasciculatum*, although plant growth was significantly reduced, while Lenzemo and Kuyper (2001) reported that AM fungi significantly reduced the number of *S. hermonthica* infesting a tolerant sorghum variety and improved its growth relative to the more susceptible variety. In other studies of host-parasite-AM fungi interactions, however, it has been demonstrated that the parasite benefited significantly at the expense of the host in the presence of AM fungi. For example, the hemiparasitic *Rhinanthus serotinus* L. attached to a mycorrhizal host (*Trifolium pratense* L.) had a higher biomass and produced more flowers than plants growing with non-mycorrhizal hosts (Salonen et al. 2001). Similarly, Davies and Graves (1998) found enhanced performance of a root hemiparasite (*Rhinanthus minor* L.) growing with a mycorrhizal host (*Lolium perenne* L.), even though mycorrhizal colonization has no significant effect either

on the phosphorus and nitrogen status or biomass and photosynthetic rate of the host. Growth and reproductive output of *R. minor* rose by 58% and 47%, respectively, when the host was mycorrhizal. Also, Salonen et al. (2000) found that symbiosis with ectomycorrhizal fungi increased host (*Pinus sylvestris* L.) growth and phosphorus content in host tissue in ways that enhanced the growth and flower production of the attached hemiparasitic plant (*Melampyrum pratense* L.). In this study various *Glomus* species were used with a sorghum variety considered to be tolerant to *Striga* in order to investigate whether they could influence the behaviour of *S. hermonthica* infestation and reduce its harmful effects on sorghum.

Materials and methods

A pot trial was carried out using 12-cm-diameter perforated clay pots in the Department of Biology, Philipps Universität, Marburg, Germany. The pots were sterilized and filled with a sterile sandy loam soil, which had been previously steam sterilized at 121°C at 1 bar for 2 h. A local sorghum variety (War-warabashi) tolerant to *S. hermonthica* obtained from Maiduguri, Nigeria was used for the experiment. Seeds of *Striga* were obtained from a sorghum field in Maiduguri. Treatments included five species of *Glomus*, namely, *G. intraradices* Schenck and Smith, isolate T 510 (H. van Alten, Hannover), *G. albidum* Walker and Rhodes (H. C. Weber, Marburg), *G. mosseae* (Nicol. and Gerd.) Gerd. and Trappe, isolate BEG 12, *G. fasciculatum* isolate BEG 53, and *G. etunicatum* Becker and Gerdmann, isolate 139 (H. van Alten). All *Glomus*-inoculated pots were infested with *S. hermonthica* seeds. Treatments without AM fungi plus *Striga* and without AM fungi or *Striga* seed served as controls. These treatments were laid out in a randomised complete block design replicated 6 times.

Approximately 1,000 seeds pot⁻¹ of *S. hermonthica* were mixed thoroughly with the top 6 cm of soil. AM fungi were also mixed with the top 6 cm of the soil at the rate of 20 g inoculum pot⁻¹ (the inoculum was soil and mycorrhizal maize root plus spores from a 6-month-old inoculum). The same amount of inoculum which was devoid of AM fungus due to steam sterilization was added to the control pots. Fertilizer at the rate of 1.0 kg N kg⁻¹ soil in the form of Nitrophoska (12:12:17; N:P:K) was used, and was applied 1 day before sowing sorghum, which was watered immediately, and there was no further application after this initial dressing. Sorghum seeds were sown at 2 seeds pot⁻¹ 1 day after watering the pots. Sorghum seedlings were then thinned to one seedling pot⁻¹ at 1 week after sowing. The treatments were kept in a growth chamber with growing conditions similar to tropical conditions with day/night temperatures of 28–32°C/18–22°C, relative humidity 60%, and a 13-h day with a light intensity of 500 Wm² and plants watered every day to soil field capacity.

Data were collected on the number of *Striga* plants pot⁻¹, sorghum height, root, shoot and total dry matter (DM). Plants were harvested and the root system washed thoroughly but carefully under running tap water at 120 days after sowing (DAS). Shoots and roots were oven-dried at 70°C for 48 h before weighing. The root:shoot ratio was also calculated. A random sample was collected from each washed root system before oven-drying for AM root colonization assessment. Roots were preserved in FPA solution. Fragments were cut into approximately 1-cm pieces, cleared for 10 min in 10% KOH at 121°C in an autoclave, rinsed with water, acidified in 5% HCl for 1 min, stained for 30 min in 0.01% acid Fuschin dissolved in a destaining solution [14:1:1 (v/v/v) lactic acid:glycerol:water]. The root pieces were washed thoroughly with water before destaining overnight then mounted on a microscope slide. Percentage of root length colonized by mycorrhizal fungi was estimated with the aid of a compound

microscope equipped with a cross-line eyepiece gradicule (McGonigle et al. 1990). Data were statistically analysed using ANOVA according to Gomez and Gomez (1984), with a WISTAT Programme (Franzen and Leschner 1988). Percent values were arcsine transformed before analysis. Comparison of means was done where the *F*-value was significant using LSD at the 5% level of probability.

Results

Sorghum roots were colonized by all the AM fungi to varying degrees, *G. mosseae* giving highest values (44%) followed by both *G. intraradices* (24%) and *G. albidum* (23%), then *G. fasciculatum* (18%); the lowest rate of colonization was by *G. etunicatum* (14%). There was no colonization of *Striga* roots by any of the AM fungi, and sorghum not inoculated with the *Glomus* species remained non-mycorrhizal.

Glomus mosseae significantly reduced *Striga* emergence (62%) compared with the treatment without *Glomus* and with *Striga* (Fig. 1). Inoculation by the other AM fungi had no significant effect on *Striga* infestation

except for *G. etunicatum* which increased emergence of the parasite (Fig. 1).

Sorghum height was significantly increased by *G. mosseae* in the presence of *Striga* to the same extent as in non-inoculated controls (minus *Glomus*, minus *Striga*). None of the AM fungi affected plant height as compared to the non-mycorrhizal, *Striga*-infested treatment (Fig. 1).

Significant differences were observed among the treatments in shoot and total dry matter, but not in the root dry matter of sorghum (Table 1). *G. mosseae* significantly increased shoot and total dry matter compared with other AM fungi and this was comparable with the control treatment (Table 1). The total dry matter yield loss of sorghum due to *Striga* infestation in the absence of *Glomus* was 36% that of the control treatment, while the positive effect of *G. mosseae* in reducing *Striga* development resulted in a 30% increase in dry matter yield of sorghum. Furthermore, there was a high root:shoot ratio with all the AM fungi species, except *G. mosseae*, which had a reduced root:shoot ratio comparable to the control treatment (Table 1). Root:shoot ratio was also high for the *Striga*-only treatment (Table 1).

Fig. 1 Effect of arbuscular mycorrhizal fungi (*Glomus* spp.) on the number of *Striga* per pot and plant height of sorghum. Data points marked with the same letter(s) are not significantly different according to Duncan's multiple range test ($P=0.05$)

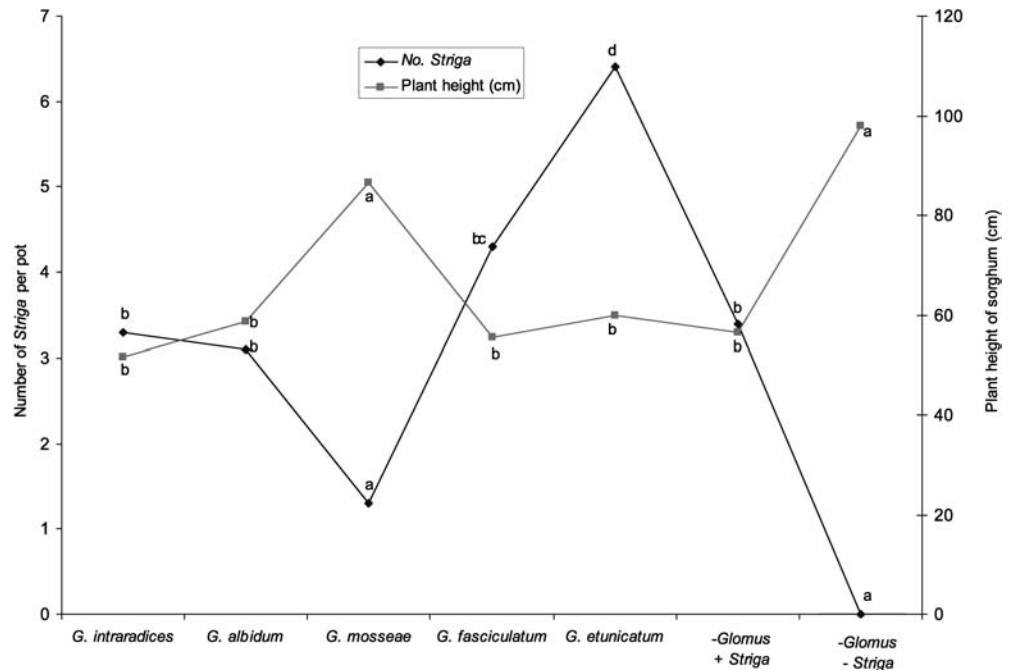


Table 1 Effect of AM fungi on root, shoot, root:shoot ratio and total dry matter of sorghum infested with *Striga hermonthica*. Figures followed by the same letter(s) in the same column are not

significantly different according to Duncan's multiple range test at the 5% level of probability

Treatment	Root dry matter (g)	Shoot dry matter (g)	Root:shoot ratio	Total dry matter (g)
<i>Glomus intraradices</i>	13.9a	7.2bc	1.9	21.1bc
<i>G. albidum</i>	12.7a	6.9bcd	1.8	19.6bc
<i>G. mosseae</i>	13.7a	11.8a	1.2	25.5a
<i>G. fasciculatum</i>	14.0a	6.2cd	2.2	20.2bc
<i>G. etunicatum</i>	10.8a	5.6d	1.9	16.4c
Without <i>Glomus</i> , with <i>Striga</i>	12.5a	6.4cd	1.9	18.9bc
Without <i>Glomus</i> , without <i>Striga</i>	15.9a	13.4a	1.2	29.4a
±SE	2.10	0.98	—	2.79

Discussion

G. mosseae significantly reduced *Striga* infestation in sorghum, which resulted in taller plants, higher shoot weight, total biomass, and lower root:shoot ratio but failed to have any significant effect on the root biomass. This shows the potential of AM fungi for the control of *Striga* on sorghum. Gworgwor and Weber (1992) have reported the successful use of *G. fasciculatum* in controlling *S. hermonthica* in developed resistant varieties of sorghum, although it behaved pathogenically by reducing the growth and total biomass of sorghum. However, in this experiment *G. fasciculatum* showed the contrary. This discrepancy could be attributed to perhaps the differences in crop varietal response to AM fungi infestation. Lenzemo and Kuyper (2001) reported a successful reduction in *S. hermonthica* in a tolerant sorghum variety but not in a susceptible variety. This situation calls for a wider varietal screening of all available varieties of sorghum with available AM fungi species.

G. etunicatum increased *Striga* emergence as in work reported by Salonen et al. (2000, 2001), and Davies and Graves (1998), where the growth and reproduction of the hemiparasites attacking the hosts were significantly stimulated, while the other AM fungi tested had no effect. Several explanations are possible for this discrepancy since AM fungal effects on plants depend on plant AM dependency, AM fungal community size and structure, soil and climatic conditions, and the interaction between these factors (Kahiluoto et al. 2000).

Root dry matter of sorghum was not affected by *Striga* in any treatment, whereas shoot dry matter was significantly reduced, except in the presence of *G. mosseae* where the amount of shoot dry matter was restored to that of the control. Likewise there was a high root:shoot ratio in treatments, except for in the *G. mosseae* treatment where the ratio was as in the control. *G. mosseae* is the only AM fungal species in this study that is effective in improving plant growth and in controlling *Striga*. The high shoot weight produced by sorghum inoculated with *G. mosseae* indicates an efficient compensatory effect of the AM in the presence of *Striga*, as well as the significant control of *Striga*.

It appears that effective control of *Striga* is related with percent root colonization of the host by the AM fungi. This was apparent with *G. mosseae* which showed the highest root colonization of sorghum and effectively controlled *Striga*, while *G. etunicatum* had a very low level of colonization of sorghum roots and showed the poorest control of *Striga*. The mechanism involved in the control of *Striga* in sorghum is, however, not clear and needs further investigation. This study also revealed that there was no colonization of *Striga* roots by the AM fungi, which is in agreement with Klein et al. (1991) for *S. asiatica*, Gworgwor (1993) for *S. hermonthica* and Solanen et al. (2001) for *O. vulgaris* L. and *R. serotinus* L.. In contrast, Weber (1987b) reported an early colonization of roots of the Scrophulariaceae (Rhinanthoideae),

related to the death of the parasite, and Krause (1988) observed the presence of AM fungi in *S. asiatica*, and suggested that this could lead to the possible biological control of *Striga*. This situation also requires further careful investigation in order to elucidate the actual interaction phase and infestation of the parasite and what happens thereafter.

The potential use of AM fungi to control *Striga* or compensate for the negative effects of the parasite will be important for soil management, especially in the tropics, where herbicides and fertilizers are an expensive input for farmers. Breeding for resistance to *S. hermonthica* should consider mycorrhizal responsiveness of sorghum varieties. Lenzemo and Kuyper (2001) have reported that the effects of AM fungi cancelled out the damage caused by *S. hermonthica* in a tolerant variety of sorghum, but not in a sensitive cultivar. Therefore, it is imperative to compare sorghum cultivars that differ in *Striga* tolerance for mycorrhizal responsiveness as well as rate of mycorrhizal colonization.

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References

- Abdalla ME, Abdel-Fattah GM (2000) Influence of the endomycorrhizal fungus *Glomus mosseae* on the development of peanut in Egypt. *Mycorrhiza* 10:29–35
- Bebawi FF, Eplee RE, Harris CE, Norris RS (1984) Longevity of witchweed (*Striga asiatica*) seed. *Weed Sci* 32:494–497
- Bodker L, Kjoller R, Rosendahl S (1998) Effect of phosphate and arbuscular mycorrhizal fungus *Glomus intraradices* on disease severity of root rot of peas (*Pisum sativum*) caused by *Aphanomyces euteiches*. *Mycorrhiza* 8:169–174
- Branzanti MB, Rocca E, Pisi A (1999) Effect of ectomycorrhizal fungi on chestnut ink disease. *Mycorrhiza* 9:103–109
- Carson AG (1986) Research and development strategies for the control of *Striga hermonthica* in the Gambia. In: Robson TO, Broad R (eds) Proceedings of the FAO/AOU All African Government Consultation on *Striga* Control, 20–24 October, Maroua, Cameroun. FAO, Rome, pp 100–117
- Davies DM, Graves JD (1998) Interactions between arbuscular mycorrhizal fungi and the hemiparasitic angiosperm *Rhinanthus minor* during co-infection of a host. *New Phytol* 139:555–563
- Dehne HW (1982) Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. *Phytopathology* 72(8):1115–1119
- Doggett H (1975) *Striga hermonthica* on sorghum in East Africa. *J Agric Sci* 65:183–194
- Franzen U, Leschner T (1988) WISTAT. Wissenschaftliche Inferenzstatistik, Marburg/Lahn, Germany
- Gomez AK, Gomez AA (1984) Statistical procedures for agricultural research, 2nd edn. Wiley, New York
- Gworgwor NA (1993) Studies on the biology and control of *Striga* species (Scrophulariaceae). PhD thesis. Philipps-Universität, Marburg, Germany
- Gworgwor NA, Weber HC (1990) *Striga hermonthica* (Del.) Benth control in sorghum. In: Faivre-Dupaigre (ed) Proceedings of the 14th COLUMA International Conference on Weed Control, 23–

- 24 January, 1990. Versailles, France, ANPP, Paris, vol 1. pp 389–395
- Gworgwor NA, Weber HC (1991) Effect of N-application on sorghum growth, *Striga* infestation and the osmotic pressure of the parasite in relation to the host. *J Plant Physiol* 139:194–198
- Gworgwor NA, Weber HC (1992) A preliminary observation on the control of *Striga hermonthica* (Del.) Benth by vesicular-arbuscular mycorrhiza (VAM) in sorghum (*Sorghum bicolor* L. Moench). In: Gasquez J (ed) Proceedings of the IXth International Conference on the Biology of Weeds, 16–18 September, 1992. Dijon, France, ANPP, Paris, pp 173–182
- Gworgwor NA, Hudu AI, Bdiya BS (1998) Herbivore of *Striga hermonthica* in the semi-arid zone of Nigeria and its potential as biocontrol agent. *ESN Occas Publ* 31:183–186
- Gworgwor NA, Ndahi WB, Weber HC (2001) Parasitic weeds of north-eastern Nigeria: a new potential threat to crop production. In: BCPC (ed) Proceedings of the British Crop Protection Council (BCPC) – Weeds 2001 Conference, Brighton, UK. BCPC, 12–15 November 2001. Brighton, pp 181–186
- Kahiluoto H, Ketoja E, Vestberg M (2000) Creation of a non-mycorrhizal control for bioassay of AM effectiveness. I. Comparison of methods. *Mycorrhiza* 9:241–258
- Kasiamdari RS, Smith SE, Smith FA, Scott ES (2002) Influence of the mycorrhizal fungus, *Glomus coronatum*, and soil phosphorus on infection and disease caused by binucleate *Rhizoctonia* and *Rhizoctonia solani* on mung bean (*Vigna radiata*). *Plant Soil* 238:235–244
- Klein W, Krause D, Weber HC (1991) Anatomical studies on parasitic flowering plants (*Orobanche romosa* and *Striga asiatica*) parasitizing host plant infected with vesicular-arbuscular mycorrhiza (VAM). In: Wegman K, Musselman LJ (eds) Progress in Orobanchae research. Eberhard-Karls-Universität, Tübingen, Germany, pp 49–54
- Krause D (1988) Vesicular-arbuscular mycorrhizae (VAM) in *Striga*: an undesired symbiosis? *Haustorium* 20:2
- Lenzemo VW, Kuyper TW (2001) Effects of arbuscular mycorrhizal fungi on damage by *Striga hermonthica* in two contrasting cultivars of sorghum, *Sorghum bicolor*. *Agric Ecosyst Environ* 87:29–35
- Mboob SS (1989) A regional program for *Striga* control in West and Central Africa. In: Robson TO, Broad R (eds) *Striga* – improved management in Africa. FAO, Rome, pp 190–194
- McGonigle TP, Miller MH, Evans DG, Fairchild DG, Swann JA (1990) A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol* 115:495–501
- Musselman LJ (1987) Parasitic weeds in agriculture, vol I. *Striga*. CRC, Boca Raton, Fla.
- Ogborn JEA (1984) Research priorities with specific reference to agronomy. In: Ayensu ES, Doggett H, Keynes HD, Marton-Lefevre J, Musselman LJ, Parker C, Pickering A (eds) *Striga: biology and control*. ICSU, Paris, pp 195–212
- Parker C, Riches CR (1993) Parasitic weeds of the world: biology and control. CAB International, Wallingford
- Powell CL, Bagyaraj DJ (1984) VA mycorrhiza. CRC, Boca Raton, Fla.
- Press MC, Graves JD (1995) Parasitic plants. Chapman & Hall, London
- Raynal-Roques A (1991) Diversification of the genus *Striga*. In: Ransom JK, Musselman LJ, Worsham AD, Parker C (eds) Proceedings of the 5th International Symposium on Parasitic Weeds, 24–30 June 1991. Nairobi, Kenya. CIMMYT, Nairobi, pp 251–261
- Reid DC, Parker C (1979) Germination requirements in *Striga* species. In: Musselman LJ, Worsham AD, Eplee RE (eds) Proceedings of the 2nd International Symposium on Parasitic Weeds, 15–18 June 1979. Raleigh, N.C. Uni. N.C. Press, Raleigh, N.C. p 201
- Salonen V, Setälä H, Puustinen S (2000) The interplay between *Pinus sylvestris*, its root hemiparasite, *Melampyrum pratense*, and ectomycorrhizal fungi: influences on plant growth and reproduction. *Ecoscience* 7:195–200
- Salonen V, Vestberg M, Vauhkonen M (2001) The effect of host mycorrhizal status on host-plant parasitic plant interactions. *Mycorrhiza* 11:95–100
- Sauerborn J (1991) The economic importance of the phytoparasites *Orobanche* and *Striga*. In: Ransom JK, Musselman LJ, Worsham AD, Parker C (eds) Proceedings of the 5th International Symposium on Parasitic Weeds, 24–30 June, 1991. Nairobi, Kenya. CIMMYT, Nairobi, pp 137–143
- Saunders AR (1933) Studies in phanerogamic parasitism. Department of Agriculture science bulletin no. 128. Department of Agriculture, Republic of South Africa
- Vallance KB (1951) Studies on the germination of the seed of *Striga hermonthica*. III. On the nature of pre-treatment and after ripening. *Ann Bot* 15:109–128
- Weber HC (1987a) Evolution of the secondary haustoria to primary haustorium in the parasitic Scrophulariaceae/Orobanchaceae. *Plant Syst Evol* 156:127–131.
- Weber HC (1987b) Untersuchungen an parasitischen Scrophulariaceen (Rhinanthoideen) in Kultur. II. Interaktionen zwischen Parasit und Wirt. *Flora* 179:35–44
- Weber HC (1993) Parasitismus von Blütenpflanzen. Wissenschaftliche Buchgesellschaft, Darmstadt
- Weber HC, Forstreuter W (1987) Parasitic flowering plants. In: Weber HC, Forstreuter W (eds) Proceedings of the 4th International Symposium on Parasitic Flowering Plants, 4–7 August, 1987. Marburg, Germany, Druckerei Kempkes, Gladenbach, pp 844