Wheat (*Triticum aestivum*) Is Susceptible to the Parasitic Angiosperm *Striga hermonthica*, a Major Cereal Pathogen in Africa

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ABSTRACT

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Striga hermonthica is a parasitic weed endemic to sub-Saharan Africa. It most commonly parasitizes sorghum, maize, pearl millet, and upland rice, lowering yields and affecting the welfare of over 100 million people, principally subsistence farmers. Cereal crops with complete resistance to this pathogen have not been reported. In southern and eastern Africa, where *Striga* spp. are endemic, 5.6 million ha of wheat are cultivated annually. Despite this, there are only isolated field reports of wheat infected with *Striga* spp. It is not clear whether this is due to resistance in this cereal or to environmental factors. In this article, we examined the ability of root exudates from five cultivars of wheat (Chablis, Cadenza, Hereward, Riband, and Brigadier) to trigger germination of *S. hermon-*

thica seed. A study of the development of *S. hermonthica* on two cultivars of wheat (Hereward and Chablis) and on a range of ancestral relatives of wheat (*Triticum* and *Aegilops* spp.) then was conducted. Last, the effect of *Striga* spp. on host growth and yield was examined using wheat cv. Chablis and compared with that of a highly susceptible sorghum cultivar (CSH-1). Wheat was able to support the germination, attachment, and subsequent development of *Striga* spp. All wheat cultivars and ancestral species of modern wheat (*Triticum* and *Aegilops* spp.) were susceptible to *S. hermonthica*. In addition, in wheat, infection severely lowered plant height (–24%) and biomass accumulation (–33%); a small parasite biomass elicited a large host response. In conclusion, wheat is highly susceptible to *S. hermonthica* and, in light of global climate change, this may have implications for wheat-producing areas of Africa.

Additional keywords: wild relatives, yield loss.

Striga spp. are obligate root parasites that infect many of the world's principal grain and legume crops. Although endemic to Africa, *Striga* spp. occur in over 40 countries worldwide, ranging from Asia to North America. In sub-Saharan Africa, more than two-thirds of the 73 million ha of land used for cereal cultivation is severely infested (38). Of the 11 *Striga* spp. known to infect crops, the most important economically is *Striga hermonthica*. It attacks all the major African cereals, including maize (*Zea mays*), sorghum (*Sorghum bicolor*), and millet (*Pennisetum glaucum*), and can cause total crop failure (10,37). Over time, the impact of *Striga* spp. has increased and it has been described as one of the most serious biological constraints to food production in Africa (38).

The population of Africa is expected to double from 600 million in 1995 to 1.2 billion by 2020 (23). The areas where *Striga* spp. are most prevalent are some of the world's poorest, affecting the welfare of more than 100 million Africans (25). Therefore, the identification of material with genetic resistance to this parasite is vital. Control using resistant crops could be immediately effective, rapidly implemented, inexpensive, and environmentally benign. Various cultivars have been produced with some level of resistance to *Striga* spp., especially in sorghum (4,26,27,30). However, despite decades of effort, breeders have been unable to produce crops with complete resistance.

Wheat (*Triticum aestivum*) is an important crop in Africa. In southern and eastern Africa, for example, where *Striga* spp. are

prevalent, 5.6 million ha of wheat are farmed annually, yielding 9.3 million tons of grain (34). Curiously, despite the wide host range of most *Striga* spp. within the family Gramineae, there are only isolated field reports of *Striga* spp. infecting wheat (39,41). This might reflect the presence of some level of resistance to *Striga* spp. in this cereal. Alternatively, wheat might produce lower levels of the different host-derived signals required for parasite development. If resistance is present, wheat or its wild relatives could provide a novel source of genetic material for controlling this parasite. If completely susceptible, there are clear implications for wheat-growing areas, both in Africa and other parts of the world.

The ancestry of modern-day wheat is linked to a number of wild grass species, including various *Aegilops* and *Triticum* spp. Three of the key species involved in the domestication of wheat include *Triticum monococcum* (einkorn wheat), *T. turgidum* subsp. *dicoccoides* (emmer wheat), and species in the closely related grass genus *Aegilops*. Some of these relatives have been found to have enhanced resistance to disease. For example, species in the genus *Aegilops* contain resistance to fungal, insect, and nematode pathogens (5,28). By crossing *Aegilops tauschii* with durum wheat (*T. aestivum* subsp. *durum*), new synthetic wheat cultivars with enhanced resistance to karnal bunt, Septoria tritici blotch, and Fusarium head blight have been produced (34). Such species may also possess resistance to *Striga* spp.

Given the lack of understanding of the nature of the interaction between *Striga* spp. and wheat, the aim of this study was, first, to determine whether wheat possessed the signals necessary for *Striga* germination, attachment, and haustorium formation and the subsequent development of the parasite. The second aim was to examine the effect of infection on the growth and biomass of wheat and to examine whether resistance or tolerance to *S. hermonthica* was present in ancestral relatives of modern-day wheat.

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MATERIALS AND METHODS

Plant material. *S. hermonthica* (Del.) Benth. seed was collected from infected maize plants in Kibos, Kenya, in 1997. Sorghum (*Sorghum bicolor* (L.) Moench) cv. CSH-1 was obtained from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India. This cultivar is highly susceptible to *Striga* spp. and its response to infection has been characterized (13,35). The wheat cultivars used were Chablis, Cadenza (CPB-Twyford, Cambridge, UK), Hereward, Riband (PBIC Seeds, Cambridge, UK), and Brigadier (Advanta Seeds, Sleaford, UK). All *Triticum* spp. were obtained from the Wheat Genetic Resources Center, Kansas State University, Manhattan. *A. tauschii* accessions were obtained from the International Maize and Wheat Improvement Centre (CIMMYT), Mexico.

Assay of root exudates for germination stimulant production. *S. hermonthica* seed was preconditioned as described previously (16). Cereal seed were germinated in pots of vermiculite for 4 days at 25°C. Seedlings were transferred to 20-cm³ glass tubes filled with 40% Long Ashton solution containing 1 mol m⁻³ ammonium nitrate (18). Tubes were wrapped with aluminum foil to exclude light from the roots. Plants were maintained in a controlled environment room with a 12-h photoperiod and photon flux density of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The day and night temperature was 25 and 24°C, respectively. Nutrient solution was changed completely every 3 to 4 days. At 14 days after planting (dap), the roots of seedlings had contacted the bottom of the tube. Nutrient solution then was removed from each tube and replaced with distilled water. After 24 h, the volume of water in the tube was made up to 20 cm³ and the exudates collected. Exudate (200 μl) was aliquoted into a microtiter plate, each well containing 20 to 40 preconditioned *Striga* seed. To determine seed viability, *Striga* seed also were immersed in 200 μl of the synthetic germination stimulant GR-24 (0.1 mg liter⁻¹). The plates were maintained in darkness for 2 days at 30°C. The percent germination of *Striga* seed then was recorded.

Rhizotron study of *Striga* attachment and development on wheat and its ancestral relatives. Four-day-old cereal seedlings germinated in vermiculite as described above were transferred into 15-cm-diameter petri dishes on a 15-cm-diameter disk of glass-fiber filter paper (Whatman GF/A; Whatman International, Maidstone, UK), overlaying a sheet of rockwool, which filled the base of the dish. This root observation chamber, or rhizotron, contained a hole in the top through which the shoot grew, together with a hole in the base to permit drainage. A layer of black plastic surrounding the dish excluded light from the roots. This system was modified from that described previously (13). Plants were watered from above every 7 days, using the nutrient solution described for the germination assay.

Plants were infected with 20 mg of preconditioned *Striga* seed at 21 dap. The same quantity of *Striga* seed was used to infect both wheat and sorghum. At the time of infection, the density of the root system was comparable between species. In infection studies, either nongerminated or pregerminated *Striga* seed was used. Where pregerminated seed was used, germination was induced by the application of GR-24 (0.1 mg liter⁻¹) 24 h prior to inoculation. Parasite seed was placed adjacent to host roots using a brush, then further manipulated to be oriented toward the host root, facilitating attachment. In infection studies examining *Striga* spp. development on wheat and sorghum, parasite development was recorded at 14 and 28 days postinoculation (dpi). Attachments were classified according to their stage of development from stage 1 (least advanced) to stage 5 (most advanced): stage 1 = parasite attached but inside seed coat; stage 2 = parasite emerged from seed coat, cotyledons visible; stage 3 = shoot formed with one to three pairs of leaves; stage 4 = shoot with four to six pairs of leaves; stage 5 = shoot with seven to nine pairs of leaves.

Examination of infected tissue by light microscopy. Plants were grown and infected as described above, then harvested at 21 dpi. *Striga* plants and 1-cm of host root surrounding the site of attachment were excised and fixed for 24 h in 3% paraformaldehyde in 100 mM sodium phosphate buffer, pH 7.2. Roots were washed twice in sodium phosphate buffer and dehydrated in each of 30, 50, 75, 95, and 95% ethanol for 1 h. Material then was infiltrated with 50% LR White embedding resin: 50% ethanol for 3 h, followed by three changes of 100% resin (for 2 h, 2 h, and overnight). Samples were transferred to resin-filled gelatin capsules and polymerized for 48 h at 60°C. Sections (3 μm) were cut on a Reichert Ultracut E microtome (Reichert, Vienna, Austria), collected on glass slides, and immersed for 1 min in stain solution (0.5% methylene blue, 0.5% Azure II+, 0.5% sodium borate). Carboxylated polysaccharides stained purple, whereas polyphenolics stained blue. Sections were allowed to dry overnight at 37°C and mounted in Eukitt mounting medium. Sections were examined using a transmission microscope (Olympus BX51; Olympus Optical Ltd., London) and photographed using a digital camera (Olympus DP11). All microscopy consumables were from Agar Scientific Ltd., Stansted, UK.

Pot study of the effect of *Striga* spp. on host growth and development. Pot studies were conducted in a heated glasshouse during the summer of 2001, with ambient light, a day temperature of 25 to 30°C, and a night temperature close to 20°C. Pots (2 cm³) were filled with sand to a depth of 6 cm from the top and 20 mg of unconditioned *Striga* seed was applied evenly to the surface. The remainder of the pot was filled with sand. Pregerminated cereal seed was inserted into pots at a depth of 3 cm. Pots were arranged in a completely randomized design. Plants were drip irrigated with 40% Long Ashton nutrient solution containing 1 mM ammonium nitrate four times per photoperiod, providing a total volume of 250 cm³ day⁻¹.

Starting at 21 dap, plant height, including that of wheat secondary tillers, was recorded every 7 days until the final harvest 50 dap, because plant height is a sensitive indicator of *Striga* infection (36). At final harvest, plants were separated into stem, leaves, and roots. Attached *Striga* plants also were collected. Material was dried at 70°C for 7 days and then weighed.

Statistical analyses. The data were subjected to Student's *t* test or analysis of variance (ANOVA) as appropriate using Minitab (version 13.1; Minitab Inc., State College, PA). Differences between individual means determined by ANOVA were tested for significance using Tukey's multiple comparison test (42). Proportional data were analyzed after arcsine square root transformation of raw data.

RESULTS

***S. hermonthica* germination, attachment, and development on wheat and sorghum.** The ability of root exudates to induce *Striga* germination was assayed in five wheat cultivars and compared with that of the susceptible sorghum cv. CSH-1. Exudates of all wheat cultivars tested induced *Striga* germination (Table 1). Germination was significantly higher in sorghum than in all wheat cultivars tested ($P < 0.002$). There also were significant differences in percentage of *Striga* germination among wheat cultivars. Specifically, percent germination using exudates from cv. Cadenza was significantly higher than that in either Chablis ($P = 0.042$) or Riband ($P = 0.048$) (Table 1).

To investigate whether *Striga* spp. would germinate and attach to wheat roots in vivo, an infection study was conducted in rhizotrons using wheat cvs. Hereward and Chablis. Plants were infected with either nongerminated or pregerminated *Striga* seed and the number of haustorial attachments recorded at 14 dpi (Fig. 1). In wheat cvs. Hereward and Chablis, the average number of attachments per plant using nongerminated seed was low, averaging only 42 and 38, respectively, compared with 180 on sorghum.

However, using pregerminated seed, the average number of attachments on Hereward and Chablis increased to 116 and 145, respectively, much closer to the number on sorghum (Fig. 1).

Having demonstrated that *Striga* spp. would germinate and attach to wheat, the subsequent development of the parasite was examined and compared with that on sorghum. Plants were grown in rhizotrons and infected with pregerminated *Striga* seed. Parasite development was recorded at 14 and 28 dpi (Fig. 2). Attachments were scored according to their stage of development from stage 1 (least advanced) to stage 5 (most advanced). At 14 dpi, stages 3 (parasite with one to three pairs of leaves) and 4 (parasite with four to six pairs of leaves) were the most advanced stage reached (Fig. 2). In all, 80% of parasites attached to sorghum were at stage 3 and 4, compared with 51 and 60% in wheat cvs. Hereward and Chablis, respectively. Compared with sorghum, the percentage of attachments at the most advanced stage was significantly lower on both Chablis ($P = 0.001$) and Hereward ($P < 0.001$), but did not differ between wheat cultivars ($P = 0.025$).

TABLE 1. Effect of root exudates from wheat cultivars on germination of *Striga hermonthica* seed^z

Crop	Cultivar	<i>Striga</i> seed germination (%)
Wheat	Brigadier	31.5 ab ± 5.06 (38.4)
Wheat	Cadenza	50.3 a ± 6.72 (61.3)
Wheat	Chablis	29.5 b ± 5.03 (35.9)
Wheat	Hereward	31.2 ab ± 3.22 (38.0)
Wheat	Riband	30.3 b ± 4.95 (36.9)
Sorghum	CSH-1	72.8 c ± 2.17 (88.8)
GR-24	...	82.0 ± 2.01 (100)

^z Data expressed as percentage of germination (mean ± standard error, $n = 8$). Data was arcsine square root transformed, then analyzed by analysis of variance (ANOVA). Differences between individual means determined by ANOVA analysis were tested for significance using Tukey's multiple comparison test (42). Means not sharing the same letter differ significantly ($P \leq 0.05$). Germination as a percentage of viable seed (as determined by GR-24) is presented in parentheses.

Fig. 1. Number of *Striga* attachments on roots of wheat cvs. Chablis and Hereward and on sorghum cv. CSH-1 at 14 days postinoculation. Plants were infected with either pregerminated (black bar) or nongerminated (open bar) *Striga* seed. Data are means ± standard error, $n = 6$. Differences between individual means determined by analysis of variance were tested for significance using Tukey's multiple comparison test. Means not sharing the same letter are significantly different ($P \leq 0.05$).

At 28 dpi, the most advanced parasites were at stages 4 (four to six pairs of leaves) and 5 (seven to nine pairs of leaves). A total of 67% of parasites attached to sorghum were at these stages, compared with 47 and 57% in Hereward and Chablis, respectively. At this later time point, the percentage of attachments at the most advanced stage on sorghum was greater than that on Hereward ($P = 0.006$) but not significantly different from that on Chablis ($P = 0.059$).

Development of *Striga* spp. inside wheat and sorghum. The overall structure of the haustorium inside and outside the host root was comparable in wheat and sorghum at 21 dpi. A large and highly developed haustorium was visible in both wheat (Fig. 3A) and sorghum (Fig. 3B), which contained three main structures. First was an outer layer of cortex cells that were only lightly stained. These surrounded a layer of very densely stained cells, representing the hyaline body. This large structure accounted for a high proportion of the haustorium. This further surrounded a central core of tissue rich in vascular elements, which extended into the vascular system of the host (Fig. 3C and D). Parasite xylem elements were visible as hollow tubes with heavily reinforced cell walls.

Fig. 2. Development of *Striga hermonthica* on wheat cvs. Hereward and Chablis and on sorghum cv. CSH-1 at 14 and 28 days postinoculation. Plants were infected with pregerminated *Striga* seed. Attachments were classified according to their stage of development from stage 1 (S1, least advanced) to stage 5 (S5, most advanced): stage 1 = parasite attached but inside seed coat; stage 2 = parasite emerged from seed coat, cotyledons visible; stage 3 = shoot formed with one to three pairs of leaves; stage 4 = shoot with four to six pairs of leaves; and stage 5 = shoot with seven to nine pairs of leaves. White bars indicate the numbers of attachments at each development stage; black bars indicate the total number of attachments. Data are means ± standard error, $n = 7$ to 8.

In both plant species, the response at the site of infection was minimal. A layer of polyphenolic material was visible at the flanks of the penetrating endophyte. The extent of this deposition in wheat was comparable with that in sorghum. In both cases, this had not prevented the formation of vascular connections between parasite and host.

Growth and biomass partitioning. To examine the effect of infection on host growth and development, an infection study was conducted in pots using wheat cv. Chablis and sorghum cv. CSH-1. From 28 dap, the height to the youngest ligule of infected plants was significantly lower than in uninfected plants in both wheat and sorghum (Fig. 4). Differences in height became more marked with time, such that, by the end of the experiment at 50 dap, the height of infected plants was 24% (Chablis) and 43% (CSH-1) lower than in uninfected controls. In addition, the average total number of tillers in infected wheat ($4.8 \pm 0.24 \text{ plant}^{-1}$) was 26% lower than in control plants ($6.5 \pm 0.29 \text{ plant}^{-1}$) ($P = 0.009$).

S. hermonthica had a negative impact on total dry weight in both wheat and sorghum (Fig. 5). Total dry weight in infected wheat and sorghum was 33 and 53% lower, respectively, than in uninfected control plants. In sorghum, *S. hermonthica* also influenced the partitioning of dry matter between different plant organs in favor of roots, with the result that the ratio of root to shoot (stem and leaves) tissue was significantly higher in infected plants

(0.89 ± 0.07) than in uninfected controls (0.50 ± 0.03) ($P = 0.007$). However, at the time of harvest, a significant increase in root/shoot ratio was not observed in infected wheat plants (0.40 ± 0.04) compared with uninfected controls (0.40 ± 0.02) ($P = 0.945$).

Despite the large effect on host biomass, the dry weight of *Striga* spp. collected from wheat roots ($0.023 \pm 0.007 \text{ g}$) was an order of magnitude lower than that collected from sorghum ($0.157 \pm 0.035 \text{ g}$) ($P = 0.005$). However, this relatively small *Striga* biomass had a significant impact on wheat, lowering total dry weight by 1.8 g. Therefore, the reduction in host biomass was an order of magnitude greater than that acquired by the parasite.

Development of *Striga* spp. on ancestral relatives of wheat. The development of *S. hermonthica* on a selection of grass species linked to the ancestry of modern-day wheat also was examined. Plants were grown and infected in rhizotrons and development compared with that on the susceptible wheat cv. Chablis. The study included species from a range of geographic areas, in order to maximize the genetic diversity of the material tested (Table 2). Included were subspecies of *T. monococcum* (einkorn wheat), *T. turgidum* subsp. *dicoccoides* (emmer wheat), and two subspecies of *T. timopheevii*. In addition, *Striga* spp. development was examined on nine lines of *A. tauschii*, a grass species closely related to wheat. All material examined was highly susceptible to *Striga* spp., with the parasite attaching and developing fully (Table 2).

Fig. 3. Development of *Striga hermonthica* inside **A** and **C**, wheat cv. Chablis and **B** and **D**, sorghum at 21 days postinoculation. In both **A**, wheat and **B**, sorghum, the parasite has crossed the cortex of the host root (HC) and penetrated into the vascular system. A large external haustorium has formed. The outer haustorium comprises three main structures. First is an outer layer of lightly stained cortex cells (SC). This surrounds a large region of densely stained cells, representing the hyaline body (H). The hyaline body, in turn, surrounds a central core of cells rich in vascular tissue (X). Vascular elements from the parasite (X) penetrate into the host vascular cylinder of wheat (**C**) and sorghum (**D**). Polyphenolics stain blue and carboxylated polysaccharides stain purple. Bar = 200 μm .

Fig. 4. Height from the base of the stem to the ligule of the youngest fully expanded leaf of wheat (Chablis) and the susceptible sorghum cv. CSH-1. Plants were grown in pots in the presence (open symbol) or absence (closed symbol) of *Striga hermonthica*. Height was recorded every 7 days from 21 days after planting (dap) until harvesting at 50 dap. Data are means $\pm$ standard error; $n = 10$ to 13.

DISCUSSION

This study has demonstrated that wheat is highly susceptible to *S. hermonthica*. *Striga* spp. require the presence of multiple cues derived from the host to trigger germination, haustorium formation, and subsequent development, and all these signals clearly are present in wheat. Furthermore, *Striga* infection caused severe reductions in growth and biomass. To our knowledge, this is the first detailed study of the interaction between *Striga* spp. and wheat, and the implications of this research are discussed below.

***Striga* spp. development on wheat.** Exudates of wheat roots induced *Striga* germination, though their ability to do so was lower than in sorghum, suggesting that the quantity or activity of stimulants produced was lower. In both rhizotron and pot studies, following attachment, the parasite developed more slowly on wheat than on sorghum. This may have been because the biomass of wheat plants was lower than that of sorghum, so that fewer resources were available to the parasite. However, in the rhizotron study, differences in parasite development between wheat and sorghum became less marked with time and, in the pot study, parasite emergence and flowering did occur.

The haustorium is essential for parasite survival, acting to attach to the host root, penetrate the vascular system, and extract

Fig. 5. Dry weight partitioning of wheat and sorghum when harvested 50 days after planting. Material was grown in pots in the presence or absence of *Striga hermonthica*. Plants were separated into root (R), stem (S), and leaves (L), dried, and then weighed. Percentage values in each graph represent biomass not gained in infected plants when compared with biomass of uninfected controls. Note that scales on y axis differ between plots; $n = 10$ to 14.

water and solutes. The internal structure of haustoria attached to wheat and sorghum was comparable, with a highly developed hyaline body and extensive vascular connections into the host. Overall, the germination assay, rhizotron study, and sections of infected tissue confirm that wheat possesses the signals required for successful infection by *Striga* spp.

The infection study in pots confirmed that wheat is highly susceptible to *Striga* spp., with large decreases in biomass and plant height. Most striking is that a small *Striga* biomass had such a severe impact on the host. Overall, the biomass lost by the host was 78-fold greater than that acquired by the parasite. This is a common effect of *Striga* infection on other cereals, such as maize and sorghum (15). For example, one study estimated that the reduction in aboveground maize biomass was up to 14.4 times greater than could be explained by competition with the parasite for resources (36). It has been suggested that this effect may be due to a toxin produced by *Striga* spp. (29).

Another common effect of infection is an increase in allocation of tissue to roots, which increases carbon loss through respiration (15). In this study, an alteration in host growth in favor of root tissue occurred in sorghum but not in wheat. However, the experiment ended 50 dap and it may be that, given more time, such an effect would become apparent.

Relatives of wheat as novel sources of resistance to *Striga* spp. Various studies have identified novel sources of resistance to

TABLE 2. Development of *Striga hermonthica* seed on different ancestral grass species of modern-day wheat^z

Grass species	Subspecies or line number	Location collected	S or R
<i>Triticum monococcum</i>	<i>monococcum</i>	Bosnia	S
<i>Triticum monococcum</i>	<i>aegilopoides</i>	Iraq	S
<i>Triticum turgidum</i>	<i>dicoccoides</i>	Turkey	S
<i>Triticum timopheevii</i>	<i>timopheevii</i>	Yugoslavia	S
<i>Triticum timopheevii</i>	<i>armeniicum</i>	Iraq	S
<i>Aegilops tauschii</i>	Line numbers: SQ180, SQ208, SQ257, SQ309, SQ314, SQ452, SQ1024, SQ1027, SQ1030	...	S

^z Plants were grown in rhizotrons and infected with pregerminated *S. hermonthica*, and parasite development recorded at 14 and 28 days postinoculation. *Triticum aestivum* cv. Chablis was used as a susceptible control; $n = 8$ to 10; S or R = susceptible or resistant.

fungal and bacterial pathogens in wild relatives of wheat (5,28). Therefore, a selection of these ancestral grass species were screened for resistance to *Striga* spp. However, all the *Triticum* spp. and *A. tauschii* lines screened were susceptible to *Striga* spp. and resistance was not observed. Although there are a number of *Aegilops* spp. and lines that were not examined in this study, these results still highlight the fact that the genus *Striga* has a very broad host range within the family Poaceae.

***Striga* spp. on wheat in Africa and future implications for agriculture.** Given the susceptibility of wheat to *Striga* spp., it is surprising that this parasite has not been reported on wheat in sub-Saharan Africa. One explanation is that wheat is grown in cooler, highland regions of Africa, whereas maize and sorghum are grown in warmer, semi-arid lowland areas (11). For example, in Kenya and Tanzania, wheat is grown at elevations above 1,500 m, with an average daily temperature below 20°C (12). The optimum temperature for *Striga* germination and attachment is $\approx 30^\circ\text{C}$ (1,9). This may be one factor that has limited the spread of *Striga* spp. to areas where wheat is cultivated. Temperature is, however, unlikely to be the sole determinant of the geographic distribution of *Striga* spp. In a study of 2,227 *S. asiatica* specimens in European herbaria, although the majority of specimens were from lower altitudes, 4.4% were collected from areas 2,000 m or more above sea level. Therefore, *Striga* spp. can persist at higher altitudes in wheat-growing areas where temperatures are lower (8).

In addition to temperature, *Striga* spp. also are affected by soil moisture and fertility (33). The incidence of *Striga* spp. is negatively correlated with soil fertility, especially nitrogen availability (32). Various studies have demonstrated the beneficial effect of nitrogen in controlling *Striga* spp. (2,6,7,17,31). The highland areas where wheat is grown are more fertile than the lowland areas where *Striga* spp. are prevalent. Therefore, higher soil fertility could have helped to limit the spread of *Striga* spp. to areas where wheat is cultivated.

Global climate change is expected to affect agroecosystems in various ways, impacting on crop productivity. It has been estimated that temperatures in Africa will increase by between 2 and 5°C by 2100 (19). In addition, certain climate change scenarios predict that rainfall in Africa could become more erratic or decrease in some areas (20). Such changes may negatively affect maize yields. For example, one study predicted that climate change could reduce maize yields in African smallholder rain-fed farming systems by 10% by 2055, causing crop losses of \$2 billion a year (22). In the future, therefore, production of maize and other cereals may expand into cooler, higher elevations where wheat is grown (21). Such changes also could favor the growth of *Striga* spp. and other pathogens at higher altitudes. Therefore, the geographic overlap between wheat and *Striga* spp. may increase in the future.

In addition to temperature, carbon dioxide (CO₂) concentrations are also expected to increase and may exceed 700 $\mu\text{mol mol}^{-1}$ by 2100 (21). Current CO₂ concentrations limit carbon assimilation in C₃ plants such as wheat. Therefore, increasing CO₂ concentrations are expected to stimulate photosynthesis and water use efficiency, benefiting wheat production (14). For example, in one study, elevated CO₂ stimulated grain yield in wheat and rice by up

to 15% (24). It can also to some extent counteract the negative effect of higher temperatures and water shortage on wheat yield (3,40). Therefore, wheat and other C₃ cereals may become more prominent in African agriculture in the future. The susceptibility of wheat to *Striga* spp., one of the major constraints to food production in Africa, thus may have important implications for future African food security.

In summary, wheat is highly susceptible to *Striga* spp. This pathogen is prevalent in over 40 countries throughout the world and infects a large number of hosts. Climate change may broaden the geographic range of this pathogen into highland areas of Africa where wheat is grown. The relatives from which modern wheat is derived may possess many useful agronomic traits, such as enhanced resistance to disease. Although no source of resistance in such material has been identified to date, further screening may identify novel sources of resistance to *Striga* spp.

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