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Striga hermonthica parasitism in maize in response to N and P fertilisers

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ABSTRACT

Parasitism by the parasitic weed, *Striga hermonthica* (*Striga*), constitutes a major biological constraint to maize production in sub-Sahara Africa. Nutrient deficiency is known to aggravate *Striga* infestation and in a number of plant species it was recently shown that this may be due to increased secretion of *Striga* germination stimulants into the soil. The present study was designed to observe the connection between soil fertility, secretion of germination stimulants and *Striga* infection in maize under greenhouse and field conditions. The experiments were conducted during two successive cropping seasons (2008 and 2009). The greenhouse study showed that maize secretes a number of so far unidentified strigolactones that induce *Striga* seed germination and the amount of these strigolactones increases upon N and P deficiency. The increased secretion of germination stimulants under N and P deficiency resulted in increased *Striga* infection in pot experiments. The on-station and on-farm field trials in Western Kenya also showed reduction in *Striga* infestation with the application of mineral nutrients but the results were less consistent than in the greenhouse. Increasing levels of N showed a fair reduction of *Striga* in the field especially during the first year, whereas P application did not have much effect in contrast to the greenhouse study where both N and P clearly reduced *Striga* infection. The likely explanation for this discrepancy is that availability of mineral nutrients under field conditions is less predictable than under greenhouse conditions, due to a number of factors such as soil texture and structure, pH, salinity, drought, leaching and runoff. Hence, further studies are needed on the importance of these factors before a fertiliser application strategy can be formulated to improve control of *Striga* in maize in the field.

1. Introduction

Maize (*Zea mays* L.) is an important cash crop and staple food for many countries in sub-Sahara Africa. Due to its diverse use as food (thick porridge, snack food, pastes, grits, roasted or boiled cobs, and beer), animal feed and industrial raw material, maize use is increasing day by day in African countries and at present the average per capita consumption is over 100 kg/year (Pingali, 2001). Factors like high productivity and low input or labour requirements make maize an attractive crop for farmers in Africa and it is the most widely grown cereal crop in the region. At present maize has the largest acreage of all field crops in Africa, and during 2008 about 29 million ha was under maize cultivation which accounted for 18% of the 161 million hectares of maize grown globally in that year (FAO, 2009). However, the total maize production during 2008 in African countries was about 55 million t, which is only 7% of the 826 million t of maize that was produced globally. The average yield of maize in most African countries is about 1.6 t ha^{-1} (FAO, 2009), which is much lower than the world average yield of 5 t ha^{-1}.

The relatively low maize production in Africa is due to a number of abiotic and biotic constraints. The major abiotic constraints include drought and declining soil fertility (Vanlauwe et al., 2006) whilst the biotic constraints comprise maize diseases, stem borers and *Striga* infestation (Kanampiu et al., 2003; Khan et al., 2006). *Striga* is considered to be one of the most serious constraints to maize productivity in African agriculture (Gethi et al., 2005). It is a root parasitic weed that damages cereal crops by draining off water and nutrients, impairing photosynthesis and causing a phytotoxic effect within days of attachment to its hosts (Gurney et al., 2006). *Striga* is responsible for an annual loss in cereals worth US$ 7 billion in sub-Saharan Africa (Gethi et al., 2005).

The Lake Victoria Basin in Kenya, a representative site for the present study, is considered to be severely infected by *Striga* especially in maize fields. *Striga* has infested about 0.24 million ha or about 15% of the arable land in the Lake Victoria Basin alone, causing yield losses between 10% to total crop failure (Smaling et al., 1991)

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or monetary losses of US$ 41 million (Kanampiu et al., 2003). Grain yields under farmer's field conditions in the Lake Victoria Basin (0.5–1.0 t ha^{-1}) were observed to be less than 70% of the potential yield of 4–5 t ha^{-1} (Tittonell et al., 2005). Nitrogen (N) and phosphorus (P) have been identified as the main deficient nutrients (Vanlauwe et al., 2006) and *Striga* infestation has been found to be closely linked with this deficiency (Vanlauwe et al., 2008). Many studies have reported a decrease of *Striga* infestation with the application of N and P nutrients (Gacheru and Rao, 2001; Adagba et al., 2002).

Striga is very prolific, with an individual *Striga* plant producing thousands of tiny dust-like seeds that can remain viable in the soil for 20 years (Winch, 2007). *Striga* seed germination is dependent on signalling molecules known as strigolactones. Under mineral nutrient deficiency host plants secret these strigolactones into the rhizosphere to stimulate the symbiotic relationship with arbuscular mycorrhizal (AM) fungi that can help the plant to overcome nutrient deficiency (Bouwmeester et al., 2003, 2007). However, parasitic plants also use these signalling molecules to detect the presence of a suitable host. The strigolactones will induce seed germination in *Striga* after which the parasite will attach to the roots of the host and starts to parasitise it. Although the relationship between soil fertility and the *Striga* problem is since long known, a more detailed knowledge on the causal mechanism and the possible relationship with changes in strigolactone production in response to fertility status would be valuable for the optimisation of *Striga* control in cereals. The relationship between strigolactones and *Striga* infection and the effect of nitrogen and phosphorus on this has already been demonstrated in rice (Jamil et al., 2011). Rice releases more strigolactones upon lower availability of N and P hence inducing more *Striga* germination which results in higher *Striga* infection. The dramatic effect of N and P starvation on strigolactone production has also been shown in other plant species such as red clover and tomato (Yoneyama et al., 2007a,b; Lopez-Raez et al., 2008). All this suggests that fertiliser application could play a vital role in reducing germination stimulant production and hence, possibly, *Striga* emergence in the field.

The present study was therefore designed with the aim to investigate the effect of fertility and P levels on strigolactone production and consequently on *Striga* infestation in maize both under greenhouse and field conditions. The aim of the study was to provide the scientific basis required to develop *Striga* control strategies in maize using fertiliser application.

2. Materials and methods

2.1. Experimental sites

The greenhouse study was conducted in Wageningen, the Netherlands, whilst the field trials were carried out at two different sites in two seasons (2008 and 2009) in Western Kenya. One field study was conducted on-station under artificial *Striga* infestation at the Kenya Agricultural Research Institute (KARI) – International Maize and Wheat Improvement Centre (CIMMYT) *Striga* research facility at Kibos (latitude 0°4′0S and 34°49′0E, altitude 329 m a.s.l.). The second field study was performed under natural *Striga* infestation in a farmer's field at Baridi, Kenya (about 20 km from the KARI-CIMMYT Kibos facility), a hot spot for *Striga* infestation. The experimental field plots were laid on soils with sandy loam texture. The soil pH levels and fertility status before sowing and after harvesting of the experiments are given in Table 1. The initial status of N and P nutrients of the washed river sand used in the greenhouse experiments in the Netherlands was maintained at a similar level as found in the soil analysis of Kenya.

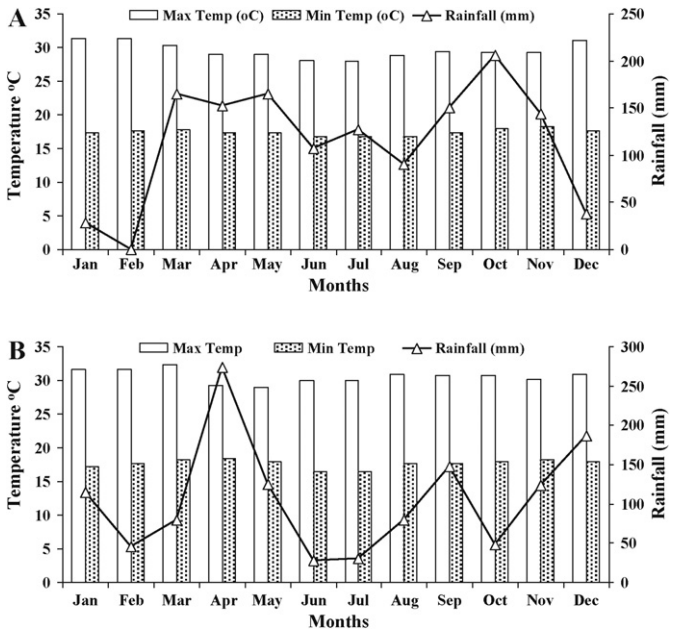

Fig. 1. Meteorological data of field experimental site (Kisumu) during 2008 (A) and 2009 (B) obtained from Kenya Meteorological Department. The bars represent average maximum and minimum temperature (in °C) whilst the line diagram represents monthly average rainfall (in mm).

2.2. Seeds, sowing seasons and growth conditions

The variety used in this study was a commercially available high-yielding maize (*Zea mays* L.) hybrid PHB-3253, purchased locally in Kenya. The same cultivar was also used in Netherlands. *Striga* seeds used in the field trial were collected from a maize field (Baridi farm, Kenya) and *Striga* seeds used in the pot trial were collected from a sorghum field (Wad Medani, Sudan). The viability of *Striga* seeds was in the range of 60–70%. The field experiments were conducted during two cropping seasons, 2008 and 2009. The greenhouse study was completed under controlled conditions (28 °C day for 10 h/25 °C night for 14 h; 65% relative humidity throughout) in Wageningen (2008 and 2009). The climatic conditions for the field studies in Kenya are given in Fig. 1. The average mean temperature of the study sites in Kenya was 30 °C during the cropping season. The experimental details for the studies at Wageningen, the Netherlands and Kenya (KARI-CIMMYT, Kibos and farmer field Baridi) are shown in Table 2.

2.3. Greenhouse experiments at Wageningen University, the Netherlands

2.3.1. Exudate collection and germination bioassays

To assess whether the maize germination stimulants are strigolactones, maize plants were exposed to phosphate starvation and/or treated with the strigolactone biosynthesis inhibitor fluridone after which root exudates were collected for germination bioassays. Maize seeds were germinated on moist rockwool at 28 °C for 48 h. The germinated seeds (6 seeds/pot in 4 replicates) were planted in 1.5 L pots filled with 1 L sand which were placed in the greenhouse. The plants were allowed to grow for four weeks, during which half-strength modified Hoagland's nutrient solution with normal P was applied (250 mL/pot at 48 h intervals). In the 5th week after planting, P was removed from all pots by rinsing the pots with 3 L of nutrient solution without P. Hereto, P deficient nutrient solution was applied on top of each pot and allowed to drain from the bottom of the pot. After washing and draining, nutrient solution was applied with 100% P, 10% P and 10% P + fluridone (0.01 μM).