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STABLE ISOTOPES ESTIMATE THE DEPENDENCE OF THE PARASITIC ANGIOSPERM *STRIGA HERMONTICA* ON ITS MAIZE HOST

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Abstract

The dependence of the root hemi-parasitic angiosperm *Striga hermonthica* on its host for carbon (C) and nitrogen (N) was estimated by labelling the leaves of maize (grown in sand culture at three rates of nitrogen) with ^{13}C and ^{15}N. The *Striga* × N interaction on the responses measured was not significant. The dependence of the parasite on host nitrogen varied from 75 to 83 per cent in the leaf, and from 70 to 80 per cent in the stem compared with a total dependence of between 74 and 82 per cent. The dependence of the parasite on its host for nitrogen was not significantly affected by the rate of nitrogen fertilizer applied. The heterotrophic carbon derived by *S. hermonthica* from its maize host varied from 20 to 32 per cent in the leaf, 23 to 41 per cent in the stem, with a total dependence of 22 to 36 per cent. The heterotrophic carbon in the leaf increased as the rate of nitrogen fertilizer applied increased ($P < 0.05$). The total dependence of the parasite on the host for carbon also increased as the rate of nitrogen fertilizer applied increased ($P < 0.01$). The presence of *S. hermonthica* reduced the shoot biomass of its maize host by about 40 per cent ($P < 0.001$), whilst the root biomass was unaffected. Infected plants also partitioned about 41 per cent of their total biomass to the root compared with 27 per cent for the uninfected ($P < 0.001$). The application of nitrogen increased the shoot and root biomass ($P < 0.001$) but did not affect the proportion of the total biomass partitioned to the root. The results show that (i) the dependence of *Striga* on its maize host of C and N can be estimated with stable isotopes of C and N and (ii) *Striga* derives more nitrogen than carbon from the host.

Résumé

AFLAKPUI, G. K. S.:*Isotopes stables donnent l'état estimatif de la dépendance d'angiosperme parasitaire* Striga hermonthica *sur son hôte-maïs.* La dépendance de l'angiosperme hémi-parasitaire de racine *Striga hermonthica* sur son hôte-maïs pour le carbon (C) et l'azote (A) était estimée par létiquetage de feuilles de maïs (cultivé dans le sable à trois proportions d'azote) avec ^{13}C et ^{15}A. Le *Striga* × A interaction sur les réactions évaluées n'était pas considérable. La dépendance du parasite sur le hôte-azote variait de 75% à 83% dans le feuille et 70% à 8% dans la tige comparée avec une dépendance totale d'entre 74% et 82%. La dépendance du parasite sur son hôte pour azote n'était pas considérablement influencé par la proportion d'engrais azoté appliqué. Le carbone hétérophique dérivé par *S. hermonthica* de son hôte-maïs variait de 20% à 32% dans la feuille, 23% à 41% dans la tige avec une dépendance totale de 22% à 36%. Le carbone hétérotrophique dans la feuille augmentait comme la proportion d'engrais azoté appliquée augmentait ($P < 0.05$). La dépendance totale du parasite sur le hôte pour le carbone augmentait également comme la proportion d'engrais azoté appliqué augmentait ($P < 0.01$). La présence de *S. hermonthica* réduisait la biomasse de la pousse de son hôte-maïs par environ 40% ($P < 0.001$) alors que la biomasse de racine n'était pas influencée. Les plantes infectées répartisaient environ 41% de leur biomasse totale à la racine par comparaison avec 27% pour les non-infectées ($P < 0.001$). L'application d'azote augmentait la biomasse de la pousse et la racine ($P < 0.001$) mais n'influençait pas la proportion de la biomasse totale répartie à la racine. Les résultats montrent que (i) La dépendance de *Striga* sur son hôte-maïs pour C et A pourrait être estimé avec les isotopes stables de C et A et (ii) *Striga* dérives plus d'azote que de carbone de la hôte.

Introduction

Striga species (witchweeds) in the family Scrophulariaceae are obligate chlorophyllous root hemi-parasites of host crops such as sorghum (*Sorghum bicolor* (L.) Moench.), millet (*Pennisetum* spp.), maize (*Zea mays* L.) (Okonkwo, 1966a; Parker, 1984), rice (*Oryza* spp.) (Harahap, Ampong-Nyarko & Olela, 1993; Johnson *et al.*, 1997) and cowpea (*Vigna unguiculata* (L.) Walp) (Okonkwo & Nwoke, 1978) in tropical and subtropical regions. The importance of *Striga* spp. as weeds is often greatest in low-input extensive farming systems. As a result of the types of farming systems affected by *Striga*, it is very problematic to determine the extent of their effect on host crop yield. It is estimated that *Striga* is present in 40 per cent of arable land in Africa, south of the Sahara, and 67 per cent of the 73 Mha under cereal production in the savanna zones (Mboob, 1989; Lagoke, Parkinson & Agunbiade, 1991). Yield losses due to *Striga* is very variable, ranging from virtually nothing to total crop failure. Sauerborn (1991), for example, quotes losses of between 6 and 21 per cent of sorghum grain yield in West Africa.

A common response of *Striga*-infected plants compared to uninfected controls is a reduction in leaf and shoot dry weight but no significant effect on root dry weight (Aflakpui, Gregory & Froud-Williams, 1998), whilst other studies have shown preferential allocation of dry matter to below-ground rather than above-ground parts (Graves, 1995). The differences in dry weight of infected and uninfected host crops is, however, not accounted for by the dry weight of the parasite. As a result, it has been hypothesised that *Striga* does not only rely on its host for carbon and compete with it for water and inorganic ions (Stewart & Press, 1990) but also impairs the photosynthetic efficiency through the effect of a toxin (Musselman, 1980). Attempts have been made to estimate the amount of heterotrophic carbon that the parasite obtains from its host with ^{14}C-labelling studies (Rogers & Nelson, 1962; Okonkwo, 1966b) and measurements of stable carbon isotopes (Press *et al.*, 1987; Cechin & Press, 1993). Another approach has been to construct a carbon balance model from measurements of photosynthesis, respiration, and dry mass of all plant parts of the sorghum- and millet- *S. hermonthica* associations (Graves, Press & Stewart 1989; Graves *et al.*, 1990). Press *et al.* (1987) showed that 28-35 per cent of the carbon in the parasite leaves was derived from sorghum photosynthate whilst in the *Pennisetum typhoides-S. hermonthica* association the carbon derived by the parasite from the host was 87 per cent in the root, 70 per cent in the stem and 49 per cent in the leaf (Graves *et al.*, 1990). The result from the carbon balance model showed that about 38 per cent and 85 per cent of the parasite carbon was obtained from sorghum and millet, respectively (Graves, Press & Steward, 1989; Graves *et al.*, 1990).

From the above studies, estimating the proportion of carbon derived by the parasite from the host by labelling the host crop with stable isotopes has not been documented. In addition, data on the proportion of nitrogen derived by the parasite from the host is virtually non existent.

The objective of this study was to investigate the feasibility of using stable isotopes, ^{13}C and ^{15}N to estimate the proportion of carbon and nitrogen derived by *S. hermonthica* from its maize host. The main advantage of using stable isotopes is that it is safer and devoid of stringent regulatory measures or controls compared to the use of the radio-isotope, ^{14}C.

Experimental

Experimental site

The experiment was conducted in a glasshouse at the University of Reading (51°27' N, 00°56' W), UK, between May and Sep 1997. Day and night temperatures in the glasshouse were maintained at 30/20 °C.

Conditioning Striga seed

Seeds of *S. hermonthica* collected on a maize host in 1993 at Nyankpala, Ghana was used. A 5 g

portion of *Striga* seed was added to 1 kg of sand in a polythene bag and mixed thoroughly by shaking for 10 min. Acid-washed sand (100 g) was weighed into pots (7.5 cm diameter), and 5 g of the sand : seed mixture added (about 3500 *Striga* seeds per pot). Another 95 g sand was added to cover the *Striga* seed and 50 ml water added. The pots were covered with a black polyethylene sheet and placed in a seed propagator box at 30 °C for 2 weeks to condition the *Striga* seed. After 2 weeks, during which the pots were monitored daily to ensure that the sand was moist, the content of each pot was air-dried, thoroughly mixed, and used to infect maize plants.

Growing the host crop

The experimental design was completely randomized three (N rates × 2 (*Striga* infection) factorial, three replicates. A total of 36 pots were used in this experiment, 18 labelled and the other 18 unlabelled. The unlabelled plants were used to determine the natural abundance of the stable isotopes.

The growing medium was a 1 : 1 mix of sterilized loam (8 per cent silt, 18 per cent clay, 74 per cent sand, 3 per cent organic matter) and coarse sand. The mixture had a mean *p*H of 7.2, total carbon of 0.78 per cent, total N of 0.05 per cent, extractable P of 31.8 mg kg^{-1} and exchangeable K of 0.31 $cmol_c$ kg^{-1}. Each pot was filled with 4 kg mixture together with 5 g of conditioned seed : sand mixture in the pots which were infected. Seeds of maize (*Zea mays* L. cv. Okomasa) was surface- sterilized with 1 per cent sodium hypochlorite, washed with water and planted at a depth of about 2.5 cm. Two seeds were sown in each pot and, subsequently, thinned to one after expansion of the first leaf. Plants were watered with 200 ml full strength, nitrogen-free Long Ashton nutrient solution three times a week; on other days the plants were watered with tap water. Nitrogen was applied at 44.4, 133.2 and 266.4 mg per pot (equivalent to 20, 60 120 kg N ha^{-1}) as NH_4NO_3 at 14 days after planting (DAP). The rates of N applied were chosen for their agronomic relevance.

To prevent $^{13}CO_2$ respired from labelled plants being taken up by unlabelled plants, the two groups of plants were isolated on opposite sides of a 4-m wide bench on which several other experimental and non-experimental plants were grown. In practice, the ^{13}C enrichment of unlabelled plants was shown by analysis to lie within the normal range of values of natural abundaance throughout the experiment.

Labelling with ^{13}C and ^{15}N

Plants were first labelled with $^{13}CO_2$ at 19 DAP and 24 h later the plants were labelled with ^{15}N. The entire canopy of all the 18 plants was fed with $^{13}CO_2$ in a perspex chamber (1.5 m × 1 m × 1.3 m) on a bright sunny day. Plants were labelled with 50 ml bicarbonate solution made of 0.28 g analar $NaH^{13}CO_3$ (99.1 atom per cent) and 5.52 g $NaH^{12}CO_3$ dissolved in water. This gave an estimated abundance of 5.83 atom per cent. The chamber was made with a smaller container inside it into which both $NaH^{13}CO_3$ solution and hydrochloric acid were injected with a hypodermic needle. The chamber was sealed with masking tape to ground-sheets of polyethylene placed beneath the pots. Air within the chamber was stirred with a 20-cm diameter fan. The transparent chamber was covered with a black polyethylene sheet for about 5-10 min after injection of hydrochloric acid into the chamber column containing the bicarbonate solution to allow uniform distribution of the $^{13}CO_2$ before photosynthesis was permitted. The plants were allowed to take up $^{13}CO_2$ for 3 h as earlier trials showed that a minimum of 1 h was needed for the plants to take up the label.

Maize plants were labelled with ^{15}N by immersing the cut tips of the four youngest fully expanded leaves in 1 ml of 30 m*M* stock solution of $(^{15}NH_4)_2SO_4$ (99.1 atom per cent) in plastic resealable bags and clipped to the leaves. The leaves were then left to take up ^{15}N for 4 days (Palta *et al.*, 1994).

Harvesting and chemical analyses

Plants were grown for 75 days from planting

and then harvested. At harvest, both labelled and unlabelled maize plants were divided into leaves, stem and root, dried to constant weight, and ground into a fine powder and analyzed for N, C ^{15}N and ^{13}C with a mass spectrometer [Roboprep CN Biological Sample Converter (Europa Scientific, Crewe, UK)]. The leaf and stem of emerged *S. hermonthica* were similarly analyzed.

The proportion of ^{13}C or ^{15}N derived by the parasite from the host was estimated as the ratio of the atom per cent (A per cent) in excess to that of natural abundance in parasite part to the A per cent in excess of natural abundance in maize leaf (Svejcar, Boutton & Trent, 1990).

Statistical Analyses

All data were subjected to analysis of variance, and the nitrogen effect on all measured responses partitioned into linear and quadratic components using orthogonal polynomials with SAS (GLM Procedure).

Results

Only the main effects of *Striga* and nitrogen are presented because the *Striga* × N interaction was not significant.

The presence of the parasite *S. hermonthica* reduced the shoot biomass of its maize host by about 40 per cent ($P < 0.001$), whilst the root biomass was unaffected (Table 1). Infected plants also partitioned about 41 per cent of their total

TABLE 1

Biomass of 75-d-old maize as influenced by Striga hermonthica *infection and N supply SE is from a 2 × 3 factorial experiment with 3 replicates*

	Shoot (g/plant)	*Root (g/plant)*	*Root: Total biomass (per cent)*
Infected	25.36	17.36	40.6
Uninfected	42.14	15.60	27.0
SE	0.89	1.79	2.15
N rate (kg ha^{-1})			
20	25.59	4.89	16.0
60	35.45	14.43	28.9
120	48.89	23.21	32.2
SE	1.12	2.01	3.89
Contrasts			
Striga	***	NS	***
Nitrogen			
Linear	***	***	NS
Quadratic	NS	NS	NS
Striga × N	NS	NS	NS

SEs are for means in each column; *** - contrasts for means in each column differ at $P \leq 0.001$; NS- not significant

TABLE 2
Concentration of carbon and nitrogen of 75-d-old maize leaf and stem as influenced by Striga hermonthica *infection and N supply. SE is from a 2 × 3 factorial experiment with 3 replicates*

	Carbon (per cent)		*Nitrgen (per cent)*	
	Leaf	*Stem*	*Leaf*	*Stem*
Infected	43.4	40.9	1.40	0.70
Uninfected	42.7	42.4	1.21	0.60
SE	0.44	0.48	0.28	0.22
N rate (kg h^{-1})				
20	44.2	42.5	1.23	0.54
60	42.9	41.9	1.48	0.64
120	41.8	42.0	1.54	0.69
SE	0.53	0.34	0.39	0.31
Contrasts				
Striga	NS	NS	NS	NS
Nitrogen				
Linear	NS	NS	NS	NS
Quadratic	NS	NS	NS	NS
Striga × N	NS	NS	NS	NS

SEs are for means in each column; NS- not significant at $P \leq 0.001$; NS- not significant

biomass to the root compared with 27 per cent for the uninfected ($P < 0.001$). The application of nitrogen increased the shoot and root biomass ($P < 0.001$) but did not affect the proportion of the total biomass partitioned to the root.

The concentration of carbon and nitrogen in either maize leaf or stem was neither affected by *Striga* nor by the rate at which nitrogen was applied (Table 2). The dependence of the parasite on its maize host for carbon and nitrogen is shown in Table 3. The percentage of heterotrophic carbon derived by the parasite from its maize host ranged from 20 to 32 per cent in the leaf, 23 to 41 per cent in the stem whilst the total heterotrophic carbon derived from the host ranged between 22 and 36 per cent. The heterotrophic carbon found in the stem of the parasite was not affected by the rate of nitrogen fertilizer applied whilst that in the leaf increased as the rate of nitrogen fertilizer applied increased ($P < 0.05$). Similarly, the total dependence of the parasite on the host for carbon was increased as the rate of nitrogen fertilizer applied increased ($P < 0.01$).

The percentage of nitrogen derived by the parasite from the host ranged from 75 to 83 per cent in the leaf, 70 to 80 per cent in the stem, whilst the total dependence on the host ranged between 74 and 82 per cent (Table 3). The percentage of nitrogen derived by the parasite from the host was, however, not affected by the rate of nitrogen fertilizer applied.

TABLE 3
Estimates of the dependence of the parasitic angiosperm Striga hermonthica *on its maize host for C and N as influenced by N supply. SE is from a 2 × 3 factorial experiment with 3 replicates*

	Carbon (percent)			*Nitrogen (per cent)*		
	Leaf	*Stem*	*Total*	*Leaf*	*Stem*	*Total*
N rate (kg ha)						
20	20	23	22	75	70	74
60	22	34	26	81	71	79
120	32	1	36	83	80	82
SE	1.35	2.28	1.31	3.09	4.21	4.49
Contrasts						
Linear	*	NS	**	NS	NS	NS
Quadratic	NS	NS	NS	NS	NS	NS

SEs are for means in each column; **, *- contrasts for means in each column differ at $P < 0.01$ and 0.05, respectively; NS - not significant

Discussion

The dependence of *Striga hermonthica* on its maize host for carbon and nitrogen was estimated successfully by labelling young maize plants with stable isotopes of carbon (^{13}C) and nitrogen (^{15}N). The dependence of the parasite on host nitrogen varied from 75 to 83 per cent in the leaf and 70 to 80 per cent in the stem compared with a total dependence which ranged between 74 and 82 per cent. The dependence of the parasite on its host for nitrogen was, however, not significantly affected by the rate of nitrogen fertilizer applied. Previous studies on the *Striga*-host plant associations concentrated on heterotrophic carbon derived from the host hence there are no data from studies on similar associations for comparison. This results is, however, similar to that reported for the concentration of nitrogen in *S. hermonthica* leaf and stem in an earlier study (Aflakpui *et al.* 1998). Jescheke *et al.* (1994), in modelling the study of the holoparasite *Cuscuta reflexa* and its host *Lupinus albus*, predicted that the parasite derived 93.6 per cent of its nitrogen from the phloem of its host.

The heterotrophic carbon, derived by *S. hermonthica* from its maize host varied from 20 to 32 per cent in the leaf, 23 to 41 per cent in the stem, with a total dependence that ranged from 22 to 36 per cent. Unlike the results for nitrogen, the total heterotrophic carbon, as well as that in leaf of the parasite, increased with increased rate of nitrogen fertilizer applied, whilst that in the stem was unaffected. This result contrasts with that of Cechin & Press (1993) who reported that the balance between autotrophic and heterotrophic carbon supply differed markedly between nitrogen treatments. They estimated that the heterotrophic carbon derived by *Striga* from its sorghum host was 27 per cent at 0.5 mol N m^{-3}, 22 per cent at 1 and 2 mol N m^{-3}, respectively, and 6 per cent at 3 mol N m^{-3}. This contrasting results might be attributed to the higher levels of nitrogen fertilizer applied by Cechin & Press (1993). The highest rates of nitrogen fertilizer applied in this study (60,120 kg N ha^{-1}) are only equivalent to the two lower levels used by Cechin & Press (1993).

Despite the presence of chlorophyll, it has been reported that root and shoot hemi-parasites obtain a significant propportion of their carbon from the host. Marshall & Ehleringer (1990) estimated

that the photosynthetic stems of the leafless *Phoradendrum juniperinum* contain 60-64 per cent host-derived carbon, whilst Schulze *et al.* (1991) estimated that the green leafy mistletoes *Septulina glauca* and *Tapinanthus oleifolius* received 64 and 47 per cent, respectively, of their carbon from their CAM hosts *Aloe dichotoma* and *Euphorbia virosa*. Other studies have also reported lower proportions of host-derived carbon for mistletoe associations. For example, Pate, True & Rasins (1991) estimated that 24 per cent of the carbon requirements for dry matter accumulation in *Amyema linophyllum* were met by intake of xylem sap solutes from its host, *Casuarina obesa*, whilst Richter & Popp (1992) estimated that *Viscum album* receives between 22 and 43 per cent of its carbon from host xylem sap. Jeschke *et al.* (1994) also modelled the association of the holoparasite *Cuscuta reflexa* and its host, *Lupinus albus,* and predicted that the parasite derived 99.5 per cent of its carbon from the phloem of its host.

The concentration of carbon in the host tissue was unaffected by the rate of nitrogen fertilizer applied in this study. In contrast, Cechin & Press (1993) reported that the concentration of carbon in sorghum tissue was highest at the lowest concentration of nitrogen. The values reported were 50.64 per cent at 0.5 mol N m^{-3}, 42.26 per cent at 1 mol N m^{-3}, 43.31 per cent at 2 mol N m^{-3}, and 43.99 per cent at 3 mol N m^{-3}. However, a critical look at their results shows that only the concentration at the lowest rate of nitrogen was very different; a trend similar to the heterotrophic carbon discussed above.

The shoot biomass of infected maize was reduced significantly, whilst *Striga* infection did not affect root biomass. Infected plants also partitioned about 41 per cent of their total biomass to the roots compared with 27 per cent for the uninfected plants. These results are consonant with that of Aflakpui *et al.* (1998) and Graves, Press & Stewart (1989) but inconsistent with the findings of Taylor, Martin & Seel (1996), who reported greater root biomass for infected maize than for uninfected maize, and Frost *et al.* (1997), who observed a similar phenomenon for sorghum.

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