Plant and Soil 121, 67–72 (1990).

PLSO 8179

Sorghum root length density and the potential for avoiding Striga parasitism

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Received 16 March 1989. Revised July 1989

Key words: root length density, *Sorghum bicolor*, *Striga hermonthica*

Abstract

Striga hermonthica is a serious root parasite of sorghum in the semiarid tropics. Successful parasitism is dependent on interactions of *Striga* seeds and host roots. Several sorghum cultivars have been found which resist parasitism. The basis of resistance is not well known. One possible method for reducing the chances of parasitism is by restricted host root development. This research was conducted to evaluate this hypothesis in sorghum known to possess resistance to parasitism by *Striga*.

Root length density of 21-day-old pot-grown resistant cultivars, Framida, N-13, IS-9830, Tetron and P-967083, were compared to that of the susceptible check, Dabar, using the line intercept method of measuring root length. There was no significant difference between resistant cultivars and the susceptible cultivar Dabar. The RLD of resistant P-967083 however was significantly less than Framida, another resistant cultivar.

The RLD of Dabar was compared to that of Framida and P-967083 in USA and Niger field trials. Root length density was determined on soil cores taken at flowering with a Giddings Soil Sampler. Each core was divided into 10-cm fractions for estimating RLD by the line intercept method. In the USA Dabar had significantly greater RLD than the two resistant cultivars in the upper 10-cm portion of the soil profile, but only significantly greater than P-967083 in the 10–20-cm portion. Significant differences in RLD between susceptible and resistant cultivars were not found at depths between 20–60 cm. In field trials in Niger, RLD of Dabar was significantly greater than either resistant cultivar in the (0 to 30 cm) portion of the soil core. These results suggest that part of the *Striga* resistance of P-967083 and perhaps Framida may be a result of avoiding interactions between parasitic seeds and host roots.

Introduction

The genus *Striga* (Scrophulariaceae) comprises some thirty species which are obligate root parasites (Musselman and Ayensu, 1984). Of the thirty known species, *Striga asiatica* (L.) Kuntze and *Striga hermonthica* (Del) Benth are of greatest economic importance in sorghum (*Sorghum bicolor* (L.) Moench.) production in Africa. The development of integrated systems, adapted to local small scale farming, has the most potential for controlling the pest (Obilana, 1983; Ogborn, 1972; Parker, 1984; Ramaiah, 1987). Included in the integrated systems for *Striga* control is the use of resistant sorghum cultivars.

Striga resistant sorghum cultivars have been identified (Ramiah, 1984). Exact mechanisms which confer this resistance are as yet unknown, but efforts to define such resistance have been directed towards roots, where host-parasite interactions are initiated. Low production of *Striga* seed germination stimulants by roots might be one mechanism by which sorghum resists parasitism (Parker, 1983; Ramaiah, 1987), although all sorghum cultivars so far tested exude sorgoleone, the only host stimulant identified so far (Netzly *et* *al.*, 1988). Mechanical barriers such as host-root cortical, endodermal, or xylem cell wall silica deposits, or wall suberization, or thickening, might prevent *Striga* haustorium penetration and thereby offer sorghum resistance to parasitism (Ramaiah, 1986). El Hiweris (1987) however, did not find a clear association of sorghum infection by *Striga* and endodermal thickening, pericycle lignification or silica deposition. Roots of resistant sorghum cultivars have been shown to contain greater total phenolic acid content than susceptible cultivars, which may contribute to resistance (El Hiweris, 1987).

A mature *Striga* plant produces up to 500,000 seeds (Dixon and Parker, 1984). Interaction of these seeds and a host root are necessary for parasitism. However not all of the seeds in the soil are equally effective in developing successful interactions. Those seeds which are most effective on sorghum are found in the upper 5 to 30 cm of the soil profile (Babiker *et al.*, 1987; Robinson and Kust, 1962), while parasitism of corn occurred mostly in the top 10-cm of the soil profile (Bebawi *et al.*, 1984). Parasitism appears then to be a phenomena restricted to the upper layers of the soil profile. If *Striga* seeds are more responsive at this depth, and if the host plant possesses less root mass at this depth, then interactions should be reduced. In this circumstance the host would be avoiding interaction with the parasite and may thus appear resistant. Since genetic variation exists in sorghum root morphology (Blum *et al.*, 1977a; Blum *et al.*, 1977b; Jordan *et al.*, 1979; Nour and Weibel, 1978), it seems possible that root distribution in the soil might be associated with *Striga* resistance. Dixon and Parker (1984), using polyethylene bags, found significantly less root branching and length in N-13, a resistant sorghum line, than in Feterita, a susceptible sorghum variety. They suggest that differences in the morphology of roots might contribute in a significant way to reduce *Striga* attack. It appears logical to hypothesize that the interaction of host roots and parasitic seeds could be reduce or avoided by growing genotypes with low root density in the upper portion of the soil. The research reported here compares the root distribution in sorghum genotypes that differ in their response to *Striga* parasitism.

Materials and methods

Experiment 1: pot trials

Pot trials were conducted in a greenhouse at Purdue University with five sorghum cultivars previously reported to have *Striga* resistance [IS-9830, N-13, Framida (Ramaiah, 1987); Tetron, P-967083 (Ejeta, 1983)], and the susceptible cultivar Dabar (Ramaiah, 1986). The method for growing plants and obtaining root length estimates was after Mackay and Barber (Mackay and Barber; 1985a, 1985b). Briefly, seeds were germinated between wet paper towels. After 14 days, seedlings were selected, roots were trimmed to provide uniform length and the plants transferred to two-liter pots containing soil. The soil, [a Raub silt loam (Aquic Agriudoll)] had the following characterization: pH 6.3 (soil/water ratio 1:2.5), Bray P_1 66 mg kg^{-1} (soil:solution ratio 1:10), exchangeable cations K = 0.53, Na = 0.03, Mg = 3.40 and Ca = 10.80, cmol(+) kg^{-1}, and retention at field capacity was 28% by volume at −33 kPa. Soil was packed to a bulk density of 1.2 mg m^{-3} and water added when the gravimetric moisture content reached 0.16 (field capacity 0.22). Plants were grown for 21 days in the greenhouse with natural light supplemented with incandescent and fluorescent lighting to maintain a 17 hour photoperiod. At the end of this 21 day growth period the plants were removed from the pots and root length measured. Most roots were removed from the soil by hand, then the remaining roots were collected by washing the soil through a 0.3-mm opening sieve. Root length was measured by the line intersect method (Tennant, 1975). Root fresh weight was used to calculate the quadratic mean root radius $\tilde{r}_0$ from the relationship $(FW_r/L_r\pi)^{1/2}$ where FW_r is the fresh weight of roots, and L_r the length of roots in cm as in Mackay and Barber (1985a) which is similar to $\tilde{R}_0$ in van Noordwyk (1989). Analysis of variance was run on the root length density (RLD, cm of root length per cubic cm of soil) (cm cm^{-3}) values and where the F-test was significant a Duncan's New Multiple Range Test was done (Steele and Torrie, 1960). Leaf blade area was determined using a leaf area meter (LI-COR Model LI-3000).

Experiment 2: USA field trials

Three cultivars, resistant Framida and P-967083 and the susceptible cultivar Dabar were planted at the Purdue University Agronomy Farm in West Lafayette, IN, USA in the summer of 1985. The experiments were laid out in a randomized complete block design. Three seeds were planted every 15 cm in five 10-cm rows, 76 cm apart in three replicated plots. Three weeks after emergence seedlings were thinned within rows to one plant per 15 cm. Root samples were taken from plants in the three middle rows at heading (approximately one week before anthesis). Soil cores (7.5 cm × 60 cm) were taken with the aid of a Giddings Soil Sampler. Ten cores per replicate were taken at approximately 10 cm from the main stem of plants chosen for uniformity. Cores were divided into 4 fractions, 0–10, 10–20, 20–30 and 30–60 cm. The collected samples were put in plastic bags and stored at 4°C until measured. Root sampling and length measurements were similar to that of Mackay *et al.*, 1987.

Root length measurements were subjected to analysis of variance. Where the F-test was significant a Bayes Least Significant Difference (BLSD) was calculated using a K-ratio of 100 or 50, comparable to 5% and 10% confidence (Smith, 1978).

Experiment 3: Niger field trial

The cultivars Framida, P-967083 and Dabar were planted in three replicated plots on the Tarna Research Station, Maradi, Niger in summer of 1986. Cultural practices were similar to Experiment 2, above. Cores were taken from 5 plants of each cultivar per plot with a Giddings Soil Sampler mounted on a trailer. The trailer mount was more elevated than was desired so cores could only be obtained consistently to 30 cm instead of 60 cm as in the USA. Subsamples of the 7.5 cm by 30 cm cores were 0–10, 10–20 and 20–30 cm. Fewer cores were taken because storage at 4°C was not possible and cores had to be processed soon after sampling. The analysis of root length measurements were the same as above.

Results

In the pot trials RLD (cm of root length per cm^3 of soil), root surface area and leaf area were compared (Table 1). There was quite a variation in leaf area between these cultivars with IS-9830 having the greater leaf area and P-967083 the least. Interestingly IS-9830 is considered to achieve *Striga* resistant by maturing early thus avoiding parasitism. The greater leaf area of IS-9830 may be an indication of this rapid growth and early maturation. The correspondence of leaf area (Table 1) with root surface area ($r = 0.470$) was much less than found by Blum *et al.*, 1977b. They reported a high degree of correlation (0.936) between hybrid leaf area and root length as well as hybrid leaf area and root volume ($r = 0.991$). Perhaps a higher degree of correlation would have been found in this study

Table 1. A comparison of the quadratic mean RLD, root surface and leaf area of sorghum cultivars grown for 21 days in a Raub silt loam

Cultivar	Reaction to Striga	Root length density ($cm\,cm^{-3}$)	R:L area	Root surface area (cm^2)	Leaf area (cm^2)
Dabar	Susceptible	0.55^{ab}	3.6	139^{ab}	39.0^{ab}
Framida	Resistant	0.86^{a}	5.6	245^{b}	43.7^{b}
N-13	Resistant	0.79^{a}	5.7	186^{ab}	32.5^{a}
IS-9830	Resistant	0.64^{ab}	3.1	204^{ab}	65.7^{c}
Tetron	Resistant	0.57^{ab}	3.6	168^{ab}	46.6^{b}
P-967083	Resistant	0.29^{b}	2.2	72^{a}	32.2^{a}

Numbers within columns followed by the same letter are not significantly different at the 5% level determined by the Duncan's new multiple range test.

if fewer cultivars were compared or plants were grown longer or were cultured in solution as were those of Blum *et al.*, 1977b.

The RLD and root surface area results were very similar in the pot trials as might be expected since root length is a component of both (Table 1). The RLD varied from a high of 0.86 cm cm^{-3} for Framida to a low of 0.29 cm cm^{-3} for P-967083. The resistant cultivars, except for P-967083, did not differ significantly from the susceptible cultivar Dabar in RLD and root surface area (Table 1). At the 5% significance level Framida and N-13 had significantly greater RLD and root surface area than P-967083, although all three cultivars are resistant to *Striga*. Root surface area of Framida was also significantly greater than that of P-967083. P-967083 had the least root development in these pot trials while Framida had the greatest.

While the RLD of resistant and susceptible cultivars were not significantly different in pot trials, the results were encouraging in that perhaps the potential for differing mechanisms of resistance to *Striga* could be demonstrated. With this in mind, Framida, P-967083, and Dabar were planted in field trials to obtain root measurements. Our estimates of RLD (Table 2) were similar to that found for field-grown sorghum estimated either using soil cores (0.3 to 2.5 cm cm^{-3}, Burch *et al.*, 1978), or by a video recording system (0.7 to 1.2 cm cm^{-3}, Upchurch and Ritchie, 1983). The RLD found in this study was within range of but generally less than for field grown corn (0.1 to 4 cm cm^{-3}, Mengel and Barber, 1973), or that of sorghum grown in 155 liter lysimeters (0–25 cm cm^{-3}, Merrill and Rawlings, 1979) which had a depth of 108 cm. Root length density here was much greater than that reported for commercial sorghum hybrids grown in the field (0.001–0.03 cm cm^{-3}, Zartman and Woyewodzic, 1979).

In the USA field trials the RLD of the resistant lines, Framida and P-967083 were significantly less than that of the susceptible Dabar in the first 10 cm of the soil core (Table 2). P-967083 continued to have significantly less RLD than Dabar in the next portion of the core (10–20 cm), but the difference was not significant in the 20–30 cm portion of the core. Both resistant cultivars had significantly less RLD than Dabar in the upper 10-cm (Table 2), but only P-967083 differed significantly in the 0 to 20 cm and 0 to 30 cm portions of the soil profile (Table 3). This significance was lost when considering the upper 60 cm of the soil profile.

The field trial results in the USA were encouraging enough to measure RLD of the three cultivars in the field in Niger. Our objective in doing so was to find out if RLD of the susceptible and resistance cultivars was significantly different in an area where *Striga* is a serious weed pest. At the start of the rainy season seedling emergence was poor, but nitrogen application (45 kg ha^{-1}) did alleviate the problem. Nevertheless, precautionary measures were taken to eliminate sample variability. Uniform plants were tagged prior to sampling in all nine plots.

In Maradi, Niger both resistant cultivars produced significantly less RLD than Dabar in the portions of the profile examined (Table 4). Framida which had greater RLD in both the pot trial and the USA field trials showed a notable decrease. Dabar and P-967083 grew more roots than in the USA field trials. However, P-967083 had the same RLD (0.43 cm cm^{-3}) in the upper 10-cm of the soil profile in both locations. Possibly the greater RLD found in Niger resulted from lower fertility. Roots in less fertile soils must explore a greater volume of

Table 2. Quadratic mean RLD (cm cm^{-3}) of sorghum cultivars at four depths of the soil profile taken from field trials in the USA

Cultivar	Soil profile depth (cm)			
	0–10	10–20	20–30	30–60
Dabar	0.70	0.40	0.28	0.35
Framida	0.47	0.47	0.23	0.55
P-967083	0.35	0.25	0.29	0.40
BLSD	0.16*	0.09**	NS	0.05*

* K-ratio of 100 = 5%.
** K-ratio of 50 = 10%.
NS = not significant.

Table 3. Quadratic mean RLD (cm cm^{-3}) of sorghum cultivars at three depths of the soil profile taken from field trials in the USA

Cultivar	Soil profile depth (cm)		
	0–20	0–30	0–60
Dabar	0.55	0.46	0.41
Framida	0.47	0.39	0.47
P-967083	0.30	0.30	0.35
BLSD	0.16*	0.16**	0.09**

* K-ratio of 100 = 5%.
** K-ratio of 50 = 10%.

Table 4. Quadratic mean RLD ($cm\,cm^{-3}$) of sorghum at three depths of soil core taken from field trials in Maradi, Niger

Cultivar	Soil profile depth (cm)			
	0–10	10–20	20–30	0–30
Dabar	0.95	0.87	0.71	0.84
Framida	0.50	0.47	0.52	0.50
P-967083	0.43	0.46	0.47	0.45
BLSD	0.13*	0.22*	0.11*	0.28*

* K-ratio of 100 = 5%.

soil to obtain nutrients. The significantly smaller RLD of the resistant cultivars grown in Niger does suggest that there would have been fewer host root/parasitic seed interactions in these cultivars as compared to Dabar.

Discussion

The results of the pot trial suggest that the resistance of Framida, which had the greatest root development, and P-967083, which had little root growth, achieve resistance by separate mechanisms. In P-967083 part of the resistance should be attributable to avoidance of *Striga* seed and host root interactions. Framida, with higher RLD, might resist parasitism by mechanisms other than avoidance. Similar conclusions can be drawn from the field trials where both varieties showed a reduced root mass in the upper portions of the soil core relative to the susceptible Dabar. The reduced root mass was more pronounced in P-967083 than in Framida reaffirming that avoidance may be the primary mechanism of resistance for P-967083.

Presumably a similar reduction of interaction would exist for the presence of germination stimulants. Sorgoleone the only germination stimulant isolated from sorghum roots is exuded by root hairs (Netzly *et al*., 1988). Less RLD would suggest less potential for root hair development and hence less stimulant available to initiate *Striga* seed germination. The fewer interactions would likely result in fewer emerged *Striga* plants and hence these plants would be classified as resistant.

Behavior of both the host roots and the parasite seeds in the soil is influenced by several factors. Soil type, fertility, moisture, and temperature have marked effect on *Striga* parasitism and on root growth. It is possible that the variability in field resistance often observed in sorghum cultivars between locations, and within *Striga* test plots may result from differences in root growth patterns of host plants as well as variability in the inoculum population.

Our results imply root development might be one mechanism adopted by certain sorghum varieties to avoid *Striga* parasitism. By exposing less root mass in that region of the soil where the parasite seeds are most abundant and more sensitive to germination, the host plant may reduce parasitism.

Acknowledgements

Partial support for this research was provided by Purdue Agricultural Experiment Station and by INTSORMIL (International Sorghum/Millet Collaborative Research Support Program), Purdue Program Support Grant and Niger Cereals Research Project and National Agronomic Research Institute of Agriculture of Niger (INRAN). AES Journal Paper No. 11,628.

References

Babiker A G T, Hamdoun A M and Mansi M G 1987 Influence of some soil and environmental factors on response of *Striga hermonthica* (Del) Benth. seeds to selected germination stimulants. *In* Proceedings of the 4th International Symposium on Parasitic Flowering Plants. Eds. H Chr Weber and W Forstreuter. pp 53–66. Marburg, FRG.

Bebawi F F, Eplee R E and Norris R S 1984 Effect of age, size, and weight of witchweed seeds on host parasite relations. Phytopath 74, 1074–1078.

Blum A, Arkin G R and Jordan W R 1977a Sorghum root morphogenesis and growth. I. Effect of maturity genes. Crop Sci. 17, 149–153.

Blum A, Arkin G R and Jordan W R 1977b Sorghum root morphogenesis and growth. II. Manifestation of heterosis. Crop Sci. 17, 153–157.

Burch G J, Smith R C G and Mason W K 1978 Agronomic and physiological responses of soybean and sorghum crops to water deficits. II. Crop evaporation soil water depletion and root distribution. Aust. J. Plant Physiol. 5, 169–177.

Dixon N H and Parker C 1984 Aspects of the resistance of sorghum varieties to *Striga* species. *In* Proceedings of the Third International Symposium on Parasitic Weeds. Eds. C Parker, L J Musselman, R M Pohill and A K Wilson. pp 123–132. ICARDA/International Parasitic Seed Plant Research Group, Aleppo, Syria.

Ejeta G 1983 ICRISAT Annual Report 1982. Patancheru, A. P., India, 277 p.

El Hiweris S O 1987 Nature of resistance to *Striga hermonthica* (Del.) Benth. parasitism in some *Sorghum vulgare* (Pers.) cultivars. Weed Res. 27, 305–311.

Jordan W R, Miller F R and Morris D E 1979 Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci. 19, 468–472.

Mackay A D and Barber S A 1985a Soil moisture effects on root growth and phosphorus uptake by corn. Agron J. 77, 519–523.

Mackay A D and Barber S A 1985b Effect of soil moisture and phosphate level on root hair growth. Plant and Soil 86, 321–331.

Mackay A D, Kladivko E J, Barber S A and Griffith D R 1987 Phosphorus and potassium uptake by corn in conservation tillage systems. Soil Sci. Soc. Am. J. 51, 970–974.

Mengel D B and Barber S A 1973 Development and distribution of the corn root system under field conditions. Agron. J. 66, 341–344.

Merrill S D and Rawlings S L 1979 Distribution and growth of sorghum roots in response to irrigation frequency. Agron. J. 71, 738–745.

Musselman L J and Ayensu E S 1984 Taxonomy and biosystematics of *Striga*. *In* Striga: Biology and Control. Eds. E S Ayensu, H Dogget, R D Keynes, J Marton-Lefevre, L J Musselman, C Parker and A Pickering. pp 37–45. ICSU Press/IRDC Paris.

Netzly D H, Riopel J L, Ejeta G and Butler L G 1988 Germination stimulants of witchweed (*Striga asiatica*) from hydrophobic root exudate of sorghum (*Sorghum bicolor*). Weed Sci. 36, 441–446.

Noordwijk M van 1989 Methods for quantifications of root distribution pattern and root dynamics in the field. *In* Methodology in Soil-K Research, Proc. 20th Colloq. ipi, Gadenber Wien, 1987. Worblanjen ibern, ipi [1989] pp 263–281.

Nour A M and Weibel D E 1978 Evaluation of root characteristics in grain sorghum. Agron. J. 70, 217–218.

Obilana A T 1983 Socio-economic impact of *Striga* in cereal crops in West Africa. *In* Proceedings of the International Training Course on the Control of Striga in Cereal Crops, North Carolina State University, Raleigh, NC, 8–26 August.

Ogborn J E A 1972 Control of *Striga hermonthica* in peasant farming. *In* Proceedings of the 11th British Weed Control Conference, pp 1068–1077.

Parker C 1984 The Physiology of *Striga* species: Present state of knowledge and priorities for future research. *In* Striga: Biology and Control. Eds. E S Ayensu, H. Dogget, R D Keynes, J Marton-Lefevre, L J Musselman, C Parker and A Pickering. pp 179–193. ICSU Press/IRDC Paris.

Parker C 1983 Factors influencing *Striga* seed germination and host-parasite specificity. *In* Proceedings of the 2nd International Striga Workshop. pp 31–36. IRDC/ICRISAT.

Ramaiah K V 1987 Control of *Striga* and *Orobanche* species — a review. *In* Proceedings of the 4th International Symposium on Parasitic Flowering Plants. Eds. H Chr Weber and W Forstreuter. pp 637–644. Marburg, FRG.

Ramaiah K V 1986 Breeding cereal grains for resistance to witchweed. *In* Parasitic Weeds in Agriculture. I. *Striga*. Ed. L J Musselman. pp 227–242. CRC Press Inc, Boca Raton, FL.

Ramaiah K V 1984 Patterns of *Striga* resistance in sorghum and millets with special emphasis on Africa. *In* Striga: Biology and Control. Eds. E S Ayensu, H Dogget, R D Keynes, J Marton-Lefevre, L J Musselman, C Parker and A Pickering. pp 71–92. ICSU Press/IRDC Paris.

Robinson E L and Kust C A 1962 Distribution of witchweed seeds in the soil. Weeds 10, 335.

Smith C W 1978 Bayes least significant difference: A review and comparison. Agron. J. 70, 123–127.

Steele R G D and Torrie J H 1960 Principles and Procedures of Statistics with Special Reference to the Biological Sciences. McGraw-Hill, New York.

Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995–1001.

Upchurch D R and Ritchie J T 1983 Root observation using a video recording system in mini-rhizotrons. Agron. J. 75, 1009–1015.

Zartman R E and Woyewodzic R T 1979 Root distribution patterns of two hybrid grain sorghums under field conditions. Agron. J. 71, 325–328.