Dynamics of Moisture, Nitrogen, and *Striga* Infestation on Pearl Millet Transpiration and Growth

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ABSTRACT

The parasitic weed *Striga hermonthica* (Del.) Benth. (witchweed) is a major biotic constraint to pearl millet [*Pennisetum glaucum* (L.) R. Br.] production in Sahelian Africa. To address this constraint, more information is needed on host-parasite relations under varying conditions of soil water and nutrient availability typically found in the Sahel. The dynamics of moisture, N, and *Striga* infestation on pearl millet transpiration and growth were investigated. The effects of *Striga* infestation, water deficit stress, and N availability on root length and dry weight, shoot dry weight, and transpiration ratio (TR; g dry matter kg^{-1} transpiration) were evaluated. Millet was grown in 36-L pots for 45 d in a glasshouse, using two levels of water and N availability and three levels of *Striga* infestation. With no N, shoot dry weight of uninfested millet plants was low. Shoot weight was further reduced by 42% at the high level (71 000 seeds pot^{-1}) of *Striga* infestation. With the addition of 60 kg ha^{-1} of N, shoot weight of uninfested millet plants increased five- to sixfold. A reduction of 36% in shoot weight was observed in plants with N and highest infestation of *Striga*. Root dry weight was also low without N, but unaffected by *Striga* infestation. With the addition of N, root dry weight of millet plants increased under adequate and water-stressed conditions. Root length in the upper 0.10 m followed a similar trend. Transpiration ratio decreased due to *Striga* infestation, increased with reduced water availability, and increased with greater N supply. The number of *Striga* haustoria attached to millet roots increased with water deficit stress, N addition, and increased level of infestation. The number of haustoria per unit root length increased with water stress and *Striga* infestation, but was substantially decreased by N addition. The number of haustoria per unit root length increased linearly with the total number of haustoria present. This slope was independent of water supply, but was four times greater for unfertilized plants compared with those receiving N. This study confirms that *Striga* attack is more severe in the presence of nutrient and water stress, and reduces whole-plant water-use efficiency. It also suggests a physiological mechanism by which N addition permits the host to better resist *Striga* attack.

THE ANGIOSPERM ROOT PARASITE *Striga hermonthica* (witchweed) constitutes a major biotic constraint to pearl millet production in the African Sahel (Doggett, 1988; Ejeta and Butler, 1993a). Pearl millet in the Sahel is typically cultivated on soils of low fertility (Jones and Wild, 1975; Manu et al., 1991) and low water-holding capacity (Payne et al., 1991). These conditions are exacerbated by rainfall that is erratic both in time and in space (Cochemé and Franquin, 1967; Sivakumar, 1989).

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An association between *Striga* infestation, low soil moisture availability, and poor soil fertility has long been hypothesized (Basinski, 1955; Parker, 1984a) but seldom quantified.

Priorities identified by Parker (1984a) for *Striga* research included (i) the establishment of a relation between host resistance and root anatomy; (ii) an analysis of the importance or the abundance of haustoria to host development under different growing conditions; (iii) an elucidation of the mechanism by which fertilizer application (especially N) afforded a measure of *Striga* control; and (iv) the establishment of the importance of soil moisture to the host–parasite relationship.

Root growth analyses of pot-grown sorghum genotypes yielded no clear relation between early root proliferation (17–26 days after sowing [DAS]) and *Striga* reaction in the field (Cherif-Ari et al., 1990; Olivier and Leroux, 1992). However, field measurements of root length density suggested that the *Striga*-resistant reaction of some sorghum cultivars may result from avoiding interactions between *Striga* seeds and host roots in the 0- to 30-cm portion of the soil profile (Cherif-Ari et al., 1990). Similar information for pearl millet is lacking.

In contrast to the massive primary haustorium of *Striga gesnerioides* (Willd.) Vatke, the primary haustorium of *S. hermonthica* remains small: 1 to 2 mm in diameter (Parker, 1984a). However, the seedling of *S. hermonthica* produces adventitious roots that form secondary haustoria wherever there is contact with host roots, greatly increasing capacity to absorb water and nutrients from the host (Doggett, 1988). The influence of varying growing conditions on haustorial frequency has not been reported in the species.

In vitro germination, attachment and early growth of the parasite on the sorghum host were lower with 3 m*M* than with 1 m*M* ammonium nitrate in the nutrient solution (Cechin and Press, 1993). Although suppression by urea of *Striga* seed germination and radicle elongation in vitro was described by Pesch and Pieterse (1982), contradictory results are reported from the field (Bebawi, 1987; Pieterse, 1991). On infertile and highly infested soils, application of nitrogenous fertilizers frequently increases *Striga* emergence (Doggett, 1988; Ogborn, 1987). Although the role of N in reducing *Striga* infestation is incompletely understood, one of its effects is to decrease exudation by host roots of *Striga* seed germination stimulants (Bebawi, 1987).

With regard to the last research priority, Press et al. (1987) found that *Striga* infestation reduced the ratio of

Abbreviations: DAS, days after sowing.

leaf CO_2 flux density to H_2O flux density, which is a measure of water-use efficiency. Working with pearl millet plants of differing P status, Payne et al. (1992) found that this ratio was well correlated with whole-plant transpiration ratios (TR: g plant dry matter kg^{-1} transpiration). To our knowledge, the effect of *Striga* infestation on pearl millet TR has not been reported.

In this study, we investigated the effect of *Striga* infestation on host root development, studied the dynamics of moisture, N, and *Striga* infestation on haustorial number, and tested the hypothesis that *Striga* infestation reduces pearl millet TR.

MATERIALS AND METHODS

The experiment was carried out in a glasshouse at ICRISAT Sahelian Center at Sadoré, Niger. Treatments consisted of two N levels, two water regimes, and three levels of *Striga* infestation. A randomized complete block design with ten replications was used. The pearl millet landrace Haïni Kiré Bengou was sown in pots (36 L soil volume) containing a loamy sand (West et al., 1984) with a clay content of 3% and a silt content of 2%. The soil had a pH in water of 5.3, available P (Bray 1) of 3.2 mg kg^{-1}, organic C content of 1.7 g kg^{-1}, and total N content of 98 mg kg^{-1}.

Pot Preparation

Approximately 60 m^3 of soil were excavated from below a depth of 0.2 m in a farmer's field free of *Striga* infestation near Sadoré. The field had been continuously cropped in millet for the past 26 yr by the present farmer. The soil was air-dried and thoroughly mixed prior to use. Sixty kg of soil were placed into each of 120 pots (0.21 m radius, approximately 0.23 m depth) fitted with plastic liners. Prior to sowing, 0, 18 000, or 71 000 viable *Striga* seeds collected in 1989 from an infested millet field near Bengou, Niger, were mixed into the upper 0.05 m of soil. Seven days prior to sowing, pots were watered to an average water content of 0.10 m^3 m^{-3} to precondition *Striga* seed.

Ten millet seeds were sown into each pot on 11 Mar. 1994. Plants were thinned to 2 per pot at 10 DAS. At 12 DAS, plastic liners were sealed around the base of plants so that water loss was by transpiration only.

Fertilizer

All pots received 0.5 g P in the form of single super phosphate (equivalent to a field rate of 9 kg P ha^{-1}). Half of the pots received a total of 3.26 g of urea (equivalent to a field rate of 60 kg N ha^{-1}) in two equal applications, one at sowing and the other at 21 DAS. Fertilizer was thoroughly mixed into the upper 0.15 m of soil before sowing and was surface broadcast just prior to irrigation at the second application (N).

Water

For each level of N there were two water treatments to simulate water-deficit-stressed and non-water-stressed conditions. Pots designated for non-water-stressed conditions were watered before sowing, to an average water content of 0.16 m^3 m^{-3} (assuming a bulk density of 1.65 Mg m^{-3}, after Payne et al., 1991), which approximates field capacity. Pots containing water-stressed plants were maintained at an average water content of 0.07 m^3 m^{-3}. Pots were weighed to determine average soil water content every two d with a load-cell balance that was accurate to 0.01 kg. At each weighing, pot liners were opened and sufficient water was added to bring average soil water content back to 0.07 m^3 m^{-3} for water-stressed plants, and to 0.16 m^3 m^{-3} for non-water-stressed plants. Cumulative pearl millet transpiration (T) was calculated from the equation

$$T = I - \Delta S$$

where I is the total amount of water added to pots and ΔS is the change in pot weight.

Harvest

At 45 DAS (well before maturity), the number of emerged *Striga* shoots below the plastic liner was counted and pearl millet shoots were harvested. Plant material was oven-dried at 70°C for 24 h and weighed. Pearl millet roots in the upper 0.10 m of soil were harvested separately from the rest, divided into eight equal subsamples and carefully washed. *Striga* haustoria associated with millet roots were counted in one subsample. Remaining roots were washed, all samples were combined, and total root length was determined using the line intersect method as described by Payne et al. (1996). Roots were then dried and weighed. The number of haustoria was divided by the total root length to obtain a measure of how host resistance was related to root anatomy under different growing conditions.

RESULTS AND DISCUSSION

Root and Shoot Weight

Dry weight of pearl millet shoots and roots increased with addition of N (Fig. 1a,b,c,d). Increased water supply enhanced pearl millet growth only with added N (Fig. 1b,d). Increasing *Striga* infestation decreased shoot weight at both fertility levels (Fig. 1a,b), but damage was greater with added N (Fig. 1b). Reduction in shoot weight was 21 and 36% at low and high infestation levels, respectively. The response of pearl millet roots to *Striga* attack contrasted sharply to that of shoots (Fig. 1c,d). With addition of N, root weight of plants was increased by about 26% at both *Striga* infestation levels (Fig. 1d), whereas root weight was unaffected by *Striga* in the absence of N (Fig. 1c).

The stimulation of root growth by *Striga* attack has been reported previously by Parker (1984b), and was attributed to a "downward flow of photosynthate" (Parker, 1984a). Host shoot stunting and root stimulation by *Striga* attack caused a marked increase in pearl millet root: shoot ratio (Fig. 1e,f). What remains unclear is whether this constitutes a host response to *Striga* attack, due perhaps to a drastic change in growth regulators (Drennan and El Hiweris, 1979), or a pathological effect (Parker, 1984a) driven by increased *Striga* demand for nutrients, C, and water.

Transpiration

Plants receiving no N transpired least, possibly due to their stunted growth (Table 1). There was an apparent trend of reduced T in plants receiving no supplemental N and that were subjected to water deficit stress and *Striga* infestation. With added N, T was reduced by almost 5 L under water stress. *Striga* infestation slightly decreased T in water-stressed plants, but decreased T by nearly 7 L in non-water-stressed plants. The reduction of *T* due to *Striga* infestation is consistent with reduced stomatal conductance reported by Press and Stewart (1987) and Press et al. (1987).

Transpiration Ratio

The addition of N increased TR at all infestation levels (Fig. 2b). *Striga* infestation had the opposite effect, decreasing TR at both fertility levels (Fig. 2a,b). Water stress significantly increased TR but only in the absence of *Striga* (Fig. 2a,b).

Increased TR in pearl millet associated with increased N is comparable to similar increases in TR due to added P in an outdoor pot study (Payne et al., 1992) and due to added fertilizer and manure application in a field study (Payne et al., 1995). These two studies reported a greater increase in TR due to water stress than was observed in this study, but drought stress had been more severe, and was reflected in greater reductions in *T*.

Decrease in TR due to *Striga* infestation has not been previously reported, but it is consistent with gas exchange measurements of Press et al. (1987). It remains unclear, however, how much of the reduction in TR is due to export of C from the host, and how much is part of a general stress response. In a C balance model, Graves et al. (1990) estimated that about 80% of the predicted C loss for *Striga*-infested sorghum [*Sorghum bicolor* (L.) Moench] was due to reduction of host photosynthesis, the rest being due to host C export, which accounted for approximately one-third of the total *Striga* C requirement. However, reduction in photosynthesis per se does not reduce the CO_2/H_2O flux density ratio if there is a compensatory decrease in stomatal conductance (Payne et al., 1992). In the earlier study by Press et al. (1987),

Table 1. Pearl millet cumulative transpiration as influenced by N fertilization, water regime, and *Striga* infestation.

Nitrogen†	Water‡	*Striga*§	Cumulative transpiration¶
			L
low	low	0	4.55
low	low	low	4.74
low	low	high	3.97
low	high	0	5.08
low	high	low	4.89
low	high	high	4.22
high	low	0	16.29
high	low	low	16.38
high	low	high	14.53
high	high	0	23.65
high	high	low	20.41
high	high	high	17.62
			SE = 0.69

† Nitrogen: low = 0 kg N ha^{-1}; high = 60 kg N ha^{-1}.
‡ Water regime: low = 0.07 m^3 m^{-3}; high = 0.16 m^3 m^{-3}.
§ *Striga* infestation: 0 = none; low = 18 000 seeds; high = 71 000 seeds.
¶ Means of 10 replications.

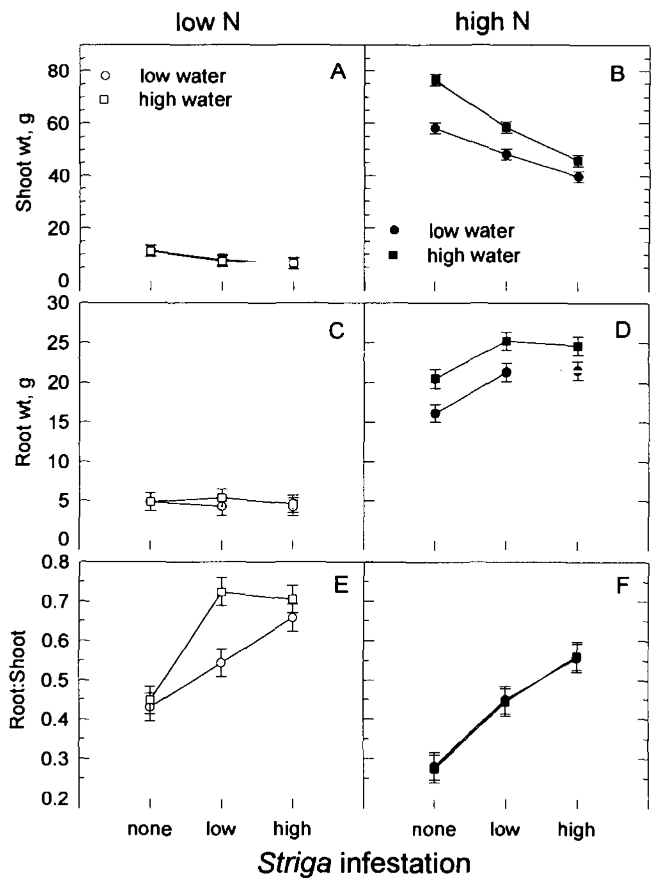

Fig. 1. Effect of *Striga hermonthica* infestation, water deficit stress, and N on shoot and root growth of pearl millet. Bars represent ±1 SE.

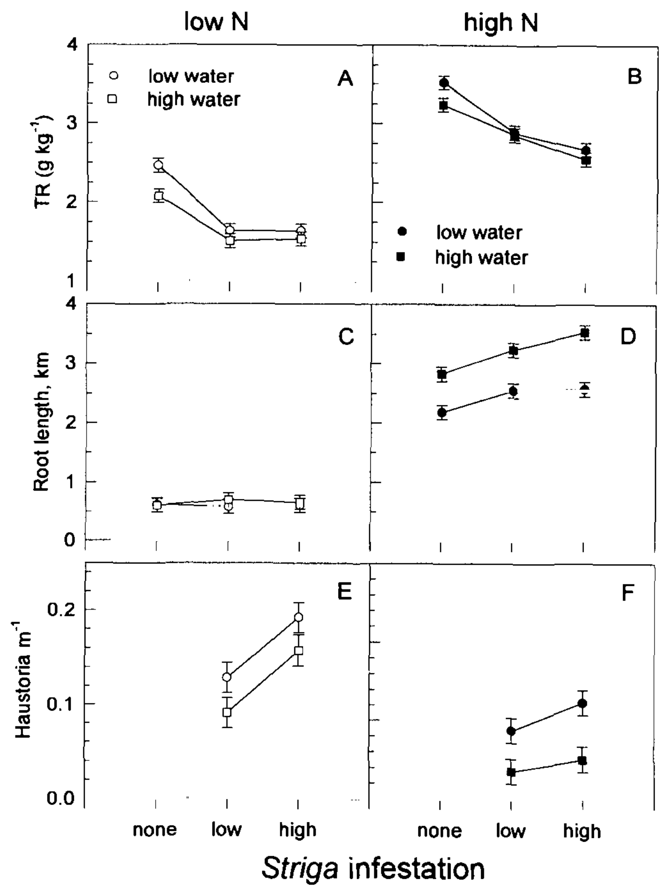

Fig. 2. Effect of *Striga hermonthica* infestation, water deficit stress, and N on water use efficiency and root growth of pearl millet and intensity of *Striga* attack. Bars represent ±1 SE.

Striga infestation was associated with a decrease in stomatal conductance, but this was more than offset by photosynthesis reduction.

Root Length and *Striga* Growth Parameters

Root length response to water supply, added N, and *Striga* infestation (Fig. 2c,d) was essentially similar to that of root dry weight (Fig. 1c,d). More *Striga* haustoria were found on roots of plants sown in pots infested with 71 000 *Striga* seeds than in those infested with 18 000 seeds (Table 2). More haustoria were found on roots of plants with added N than those without added N in both water treatments. This may be due to larger host root systems resulting from the addition of N. However, water-stressed plants with added N had more haustoria than did non water-stressed plants, despite their smaller root system. The same trend of increased haustoria number in water-stressed plants is shown for plants without added N, although differences were not statistically significant.

Striga plants first appeared above the soil (but remained under the plastic liner) at 29 DAS and continued to emerge through 45 DAS. For plants without added N, there was no significant difference between water regimes in the number of emerged *Striga* (Table 2). For plants with added N, however, water stress increased the number of emerged *Striga* plants.

The increased number of haustoria and emerged *Striga* plants in water-stressed plants support the assertion that *Striga* thrives under modest drought stress (Parker, 1984a; Ejeta and Butler, 1993b). The stimulating affect of N on number of emerged *Striga* plants observed here has also been reported under certain field conditions (e.g., Bebawi, 1981, 1987; Ogborn, 1987; Osman et al., 1991). Reduction in *Striga* populations through N fertilization is dependent on factors including host cultivar (Bebawi, 1981) and adequate N being applied (Gworgwor and Weber, 1991; Hess and Ejeta, 1987). The higher the *Striga* infestation, the higher the N dosage required to inhibit *Striga* emergence (Ogborn, 1987).

Because added N in this experiment stimulated pearl millet root development more than it did the number of *Striga* haustoria, the resulting number of haustoria per unit length of pearl millet root was greatly reduced by added N (Fig. 2f). Decreased water supply further increased the number of haustoria per unit length in both N treatments (Fig. 2e,f), again supporting the assertion that mild water stress encourages severity of *Striga* attack.

Positive linear relationships were found between the number of haustoria per unit root length and the total number of haustoria attached to the root system (Fig. 3). Under these experimental conditions, the slope of this relation was unaffected by water stress, but was greatly decreased by improved plant N status. As severity of the attack (measured by number of attached haustoria) increased, plants with added N increased investment into roots such that the fraction of the root system exposed to *Striga* attack was small compared with plants without added N. These data illustrate that pearl millet under N stress is more susceptible to *Striga* attack, and lend evidence to the statement by Ejeta and Butler (1993b) that *Striga* has a predilection for attacking crops already under nutrient stress. These last authors suggest that the problem of *Striga* infestation is worsening in West Africa due to declining soil nutrient availability (van Keulen and Breman, 1990).

Sorghum cultivar P967083 may avoid *Striga* seed and host root interactions through reduced root development in the upper 0.2 m soil layer (Cherif-Ari et al., 1990). Within this context, it is noteworthy that local pearl millet landraces, which have evolved under *Striga* pressure, tend to have greater root growth than most modern varieties in the upper 0.2 m soil layer (Payne et al., 1996), where both soil nutrients and *Striga* attack are concentrated. The ability to maintain a low ratio of number of haustoria to root length might constitute a physiological resistance mechanism to *Striga* attack. We are currently evaluating whether the type of data presented in Fig. 3 can provide useful information for the

Table 2. Effect of N fertilization, water regime, and *Striga* infestation on attachment and emergence of *S. hermonthica*.

Nitrogen†	Water‡	*Striga*§	Haustoria¶	Emerged *Striga*¶
low	low	low	8.5	5.9
low	low	high	13.6	12.0
low	high	low	7.1	12.2
low	high	high	13.0	13.6
high	low	low	26.9	43.2
high	low	high	37.1	69.8
high	high	low	13.7	10.7
high	high	high	21.5	32.6
			SE = 3.13	SE = 6.19

† Nitrogen: low = 0 kg N ha^{-1}; high = 60 kg N ha^{-1}.
‡ Water regime: low = 0.07 m^3 m^{-3}; high = 0.16 m^3 m^{-3}.
§ *Striga* infestation: low = 18 000 seeds pot^{-1}; high = 71 000 seeds pot^{-1}.
¶ Means of 10 replications. Haustoria counted were on a subsample (1/8) of roots harvested from the infested soil horizon. Emerged *Striga* were counted in the entire pot.

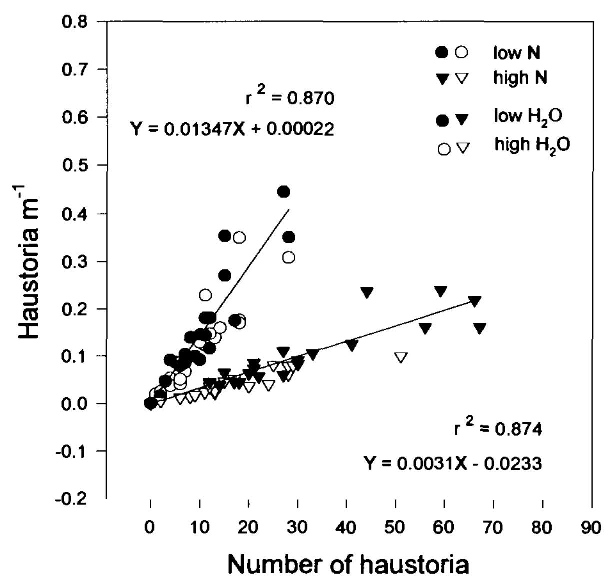

Fig. 3. Relationship between the number of *Striga* haustoria per unit root length and the total number of haustoria on the pearl millet root system.

evaluation of varietal differences in resistance to *Striga* attack.

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REFERENCES

Basinski, J.J. 1955. Witchweed and soil fertility. Nature (London) 175:431.

Bebawi, F.F. 1981. Response of sorghum cultivars and *Striga* population to nitrogen fertilization. Plant Soil 59:261–267.

Bebawi, F.F. 1987. Cultural practices in witchweed management. p. 159–171. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1. *Striga*. CRC Press, Boca Raton, FL.

Cechin, I., and M.C. Press. 1993. Nitrogen relations of the sorghum–*Striga hermonthica* host-parasite association: Germination, attachment and early growth. New Phytol. 124:681–687.

Cherif-Ari, O., T.L. Housley, and G. Ejeta. 1990. Sorghum root length density and the potential for avoiding *Striga* parasitism. Plant Soil 121:67–72.

Cochemé, J., and P. Franquin. 1967. Une étude d'agroclimatologie de l'Afrique sèche au sud du Sahara en Afrique. Tech. Rep. 86. World Meteorol. Org., Geneva.

Doggett, H. 1988. Witchweed (*Striga*). p. 368–404. *In* Sorghum. 2nd ed. Longman Scientific & Technical, Harlow, Essex, UK.

Drennan, D.H., and S.O. El Hiweris. 1979. Changes in growth regulator substances in *Sorghum vulgare* infected with *Striga hermonthica*. p. 144–155. *In* L.J. Musselman et al. (ed.) Proc. Int. Symp. Parasitic Weeds, 2nd. North Carolina State University, Raleigh, North Carolina. 16–19 July 1979. NCSU, Raleigh, North Carolina.

Ejeta, G., and L.G. Butler. 1993a. Host-parasite interactions throughout the *Striga* life cycle, and their contributions to *Striga* resistance. African Crop Sci. J. 1:75–80.

Ejeta, G., and L.G. Butler. 1993b. Host plant resistance to *Striga*. p. 561–569. *In* D.R. Burton et al. (ed.) International Crop Science I. Crop Science Society of America, Madison, WI.

Graves, J.D., A. Wylde, M.C. Press, and G.R. Stewart. 1990. Growth and carbon allocation in *Pennisetum typhoides* infected with the parasitic angiosperm *Striga hermonthica*. Plant, Cell and Environment 13:367–373.

Gworgwor, N.A., and H.-C. Weber. 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.

Hess, D.E., and G. Ejeta. 1987. Effect of cultural treatments on infestation of *Striga hermonthica* (Del.) Benth. (Scrophulariaceae) on sorghum in Niger. p. 367–375. *In* H.-C. Weber and W. Forstreuter (ed.) Parasitic flowering plants. Marburg, Germany.

Jones, M.J., and A. Wild. 1975. Soils of the West African Savanna. Tech. Commun. 55. Commonw. Bur. of Soils, Commonw. Agric. Bureaux, Farnham Royal, UK.

Manu, A., A. Bationo, and S.C. Geiger. 1991. Fertility status of selected millet producing soils of West Africa with emphasis on phosphorus. Soil Sci. 152:315–320.

Ogborn, J.E.A. 1987. *Striga* control under peasant farming conditions. p. 145–158. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1. *Striga*. CRC Press, Boca Raton, FL.

Olivier, A., and G.D. Leroux. 1992. Root development and production of a witchweed (*Striga* spp.) germination stimulant in sorghum (*Sorghum bicolor*) cultivars. Weed Sci. 40:542–545.

Osman, M.A., P.S. Raju, and J.M. Peacock. 1991. The effect of soil temperature, moisture and nitrogen on *Striga asiatica* (L.) Kuntze seed germination, viability and emergence under field conditions. Plant and Soil 131:265–273.

Parker, C. 1984a. The physiology of *Striga* spp.: Present state of knowledge and priorities for future research. p. 179–193. *In* Ayensu, E.S., H. Doggett, R.D. Keynes, J. Marton-Lefevre, L.J. Musselman, C. Parker, and A. Pickering (ed.) *Striga*: Biology and Control. ICSU Press, Paris.

Parker, C. 1984b. The influence of *Striga* species on sorghum under varying nitrogen fertilization. p. 90–98. *In* C. Parker et al. (ed.) Proc. Int. Symp. Parasitic Weeds, 3rd. Int. Parasitic Seed Plant Res. Group. 7–9 May 1984. ICARDA, Aleppo, Syria.

Payne, W.A., H. Brück, B. Sattelmacher, S.V.R. Shetty, and C. Renard. 1996. Root growth and soil water extraction of three pearl millet varieties as affected by phosphate application. *In* Dynamics of roots and nitrogen in cropping systems of the semi-arid tropics. Proc. Int. Workshop, Patancheru, India. 21–25 Nov. 1994. ICRISAT Asia Ctr., Patancheru, AP, India (in press).

Payne, W.A., M.C. Drew, L.R. Hossner, R.J. Lascano, A.B. Onken, and C.W. Wendt. 1992. Soil phosphorus availability and pearl millet water-use efficiency. Crop Sci. 32:1010–1015.

Payne, W.A., B. Gérard, and M.C. Klaij. 1995. Subsurface drip irrigation to evaluate transpiration ratios of pearl millet. p. 923–931. *In* F.R. Lamm (ed.) Microirrigation for a changing world: Conserving resources/preserving the environment. Proc. Int. Microirrigation Congr., 5th, Orlando, FL. 2–6 Apr. 1995. ASAE, St. Joseph, MI.

Payne, W.A., R.J. Lascano, and C.W. Wendt. 1991. Physical and hydrologic characterization of three sandy millet fields of Niger. p. 199–207. *In* M.V.K. Sivakumar et al. (ed.) Proc. Int. Workshop Soil Water Balance in the Sudano-Sahelian Zone. 18–22 Feb. 1991. ICRISAT Sahelian Center, Niamey, Niger. ICRISAT, Patancheru, India.

Pesch, C., and A.H. Pieterse. 1982. Inhibition of germination in *Striga* by means of urea. Experientia 38:559–560.

Pieterse, A.H. 1991. The effect of nitrogen fertilizers on the germination of seeds of *Striga hermonthica* and *Orobanche crenata*. p. 115–124. *In* K. Wegmann and L.J. Musselman (ed.) Progress in *Orobanche* Research. Proc. Int. Workshop *Orobanche* Research, Obermarchtal, Germany. 19–22 Aug. 1989. Eberhard-Karls-Universität, Tübingen, Germany.

Press, M.C., and G.R. Stewart. 1987. Growth and photosynthesis in *Sorghum bicolor* infected with *Striga hermonthica*. Ann. Bot. (London) 604:657–662.

Press, M.C., J.M. Tuohy, and G.R. Stewart. 1987. Gas exchange characteristics of the sorghum–*Striga* host-parasite association. Plant Physiol. 84:814–819.

Sivakumar, M.V.K. 1989. Agroclimatic aspects of rainfed agriculture in the Sudano-Sahelian zone. p. 17–38. *In* Soil, crop and water management systems for rainfed agriculture in the Sudano-Sahelian zone: Proceedings of an International Workshop. ICRISAT Sahelian Center, Niamey, Niger. 11–16 Jan. 1987. ICRISAT, Patancheru, India.

van Keulen, H., and H. Breman. 1990. Agricultural development in the West African Sahelian region: A cure against land hunger? Agric. Ecosyst. Environ. 32:177–197.

West, L.T., L.P. Wilding, J.K. Landeck, and F.G. Calhoun. 1984. Soil survey of the ICRISAT Sahelian Center, Niger, West Africa. Soil and Crop Sciences Dep./Tropsoils, Texas A&M Univ. System, College Station, TX.