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Effects of N, P and K on *Striga asiatica* (L.) Kuntze seed germination and infestation of sorghum

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Summary: Résumé: Zusammenfassung

Sorghum (*Sorghum bicolor* (L.) Moench) plants were grown in pots with 12·5 and 50 mg applied N kg^{-1} soil. With an increase of soil N, the *Striga asiatica* (L.) Kuntze infestation, as well as the sorghum shoot dry matter losses due to infestation, decreased. The relative differences in stimulant capacity to induce *Striga* seed germination among the four sorghum genotypes were not consistent over the 0 to 150 mg N l^{-1} range. The sorghum root exudate was considerably more active at 0 mg N l^{-1}, than at 30 mg N l^{-1}, and the stimulant produced at 150 mg N l^{-1} failed to induce *Striga* seed germination. Presence of N in the growth medium considerably reduced the effectiveness of the stimulating substance produced by sorghum roots, whereas K promoted stimulant activity only in the absence of N. The presence or absence of P in the growth medium did not affect *Striga* seed germinability, probably due to the inability of this element to interfere with the production or activity of the stimulating substance from the host plants. It can be concluded, therefore, that sorghum plants seem to produce active root exudate only in conditions of N deficiency.

Effets de N, P et K sur la germination des graines de Striga asiatica *(L.) Kuntze et l'infestation du sorgho*

Des plantes de sorgho (*Sorghum bicolor* (L.) Moench) ont été cultivées en pots avec des sols ayant reçu 12,5 et 50 mg de N kg^{-1} de sol. Avec une augmentation de l'azote du sol, l'infestation en *Striga asiatica* (L.) Kuntze aussi bien que les pertes en matière sèche des pieds de sorgho dues à l'infestation one baissé. Les différences relatives dans la capacité d'induction de la germination des graines de *Striga* entre les 4 génotypes de sorgho n'étaient pas importantes dans un éventail de 0 à 150 mg N l^{-1}. L'exsudat de racine de sorgho était beaucoup plus actif à 0 mg N l^{-1} qu'à 30 mg N l^{-1}, et le stimulant produit à 150 N l^{-1} n'aboutit pas à une induction de la germination des graines de *Striga*. La présence d'azote dans le milieu de croissance a réduit considérablement l'efficacité des substances stimulantes produites par les racines de sorgho, tandis que K a favorisé l'activité stimulante seulement en absence de N. La présence ou l'absence de P dans le milieu de culture n'a pas affecté l'aptitude à germer des semences de Striga, probablement ceci est du à la non possibilité pour cet élement d'interférer avec la production ou l'activité des substances stimulantes venant de la plante-hôte. On peut donc conclure que les plantes de sorgho pourraient produire des exsudats racinaires actifs seulement en situation de carence en azote.

Wirkung von N, P und K auf die Samenkeimung von Striga asiatica *(L.) Kuntze und den Befall von Sorghumhirse*

In einem Topfversuch mit 12,5 und 50 mg N kg^{-1} Boden nahmen mit dem Anstieg des Stickstoffgehalts sowohl der Befall mit *Striga asiatica*

als auch der sonst durch den Befall eintretende Verlust an Trockenmasse der Sorghumhirse (*Sorghum bicolor* (L.) Moench) ab. Die Samenkeimung von *Striga asiatica* wurde bei 4 Sorghum-Genotypen im Bereich von 0 bis 150 mg N l^{-1} nicht gleichmäßig gefördert. Sorghum-Wurzelexudat wirkte bei 0 mg N l^{-1} deutlich stärker als bei 30 mg N l^{-1}, und das bei 150 mg N l^{-1} gewonnene Stimulans versagte zur Samenkeimung von *Striga asiatica*. Die Gegenwart von N im Substrat setzte die Wirksamkeit der von Sorghum-Wurzeln entwickelten Stimulationssubstanz erheblich herab, während K die Wirksamkeit nur bei Abwesenheit von N erhöhte. Vorhandensein oder Fehlen von P im Substrat wirkte sich auf die Keimfähigkeit von *Striga*-Samen nicht aus, weil dieses Element wahrscheinlich nicht an der Bildung der Stimulationssubstanz durch die Wirtspflanze beteiligt ist. Sorghum-Pflanzen scheinen also nur bei N-Mangel ein aktives Wurzelexudat bilden zu können.

Introduction

Many *Striga* (witchweed) species are root parasitic weeds. *S. hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze parasitize crop plants and reduce yields in Africa and India (Doggett, 1965; Parker, 1984). Use of crop rotations, trap crops, herbicides, soil fumigation with ethylene, and resistant crop cultivars have been suggested for *Striga* control (Bebawi, 1987; Ogborn, 1987). However, economically feasible control methods are not available for the resource-poor subsistence farmer.

The factors affecting *Striga* seed germination and infestation are not properly understood. The reasons for non-uniformity of *Striga* infestation in experimental plots and large seasonal variation in *Striga* populations need to be known for establishing reliable screening procedures for use in *Striga*-resistance breeding programmes.

Studies of the effects of soil N on *Striga* infestation have often led to varying conclusions. Addition of N fertilizers reduced *Striga* emergence on fertile soils but increased *Striga* emergence on infertile soils (Doggett, 1984, 1988). In other studies, high N levels in the soil enhanced the growth of both the host and parasite (Egley, 1971; Parker, 1984). Thus, the effects of N fertilization on *Striga*-host relationships still remain unresolved. Increased crop vigour following N fertilization may enhance host tolerance to *Striga*. There is little published information on the effects of K and P on *Striga* infestation. This study was conducted to determine the effects of N, P and K on the stimulating capacity of sorghum root exudate and associated *Striga* incidence.

Materials and methods

Nitrogen effects on infestation

The experiment was conducted in a growth chamber with 14 h light (32°C) and 10 h dark (24°C) periods. Fluorescent and incandescent bulbs provided a light intensity of 350 μmol $m^{-2}s^{-1}$. The relative humidity was maintained at 60%.

Seeds of sorghum (*Sorghum bicolor* (L.) Moench) genotype Swarna (*Striga* susceptible) were sown in polyvinyl chloride (PVC) tubes (75 cm tall and 16 cm in diameter) filled with steam-sterilized Alfisol (fine, mixed, hypothermic udic Rodustalf). The PVC tubes were slit along two sides and resealed with silicone sealant to facilitate root removal later. A polyethylene sheet tied to the base of each tube held the soil. The soil with a pH 6·8, contained 7·2 μg NH_4–N and 6·5 μg NO_3–N kg^{-1}. Phosphorus and potassium were not measured, but most soils in ICRISAT are known to contain little P but sufficient K (El-Swaify *et al.*, 1985). Supplements of KH_2PO_4 provided 25·0 mg P and 31·5 mg K kg^{-1} soil.

A 2×3 factorial in a completely randomized design, with five replications, was used for the study. The *Striga* treatment consisted of 0 (control) and 100 mg (approximately 16,000 seeds) of one-year old *Striga asiatica* seeds having 70–85% germinability. These seeds were mixed into the top 4 cm soil. The N treatment consisted of 0, 12·5, and 50·0 mg N kg^{-1} soil (equivalent to 0, 25, and 100 kg N ha^{-1}) applied as NH_4NO_3. Seven days after sowing, the sorghum plants were thinned to three per tube. Four hundred milliliters of distilled water was added after sowing and 100 ml was added daily, thereafter. Sixty-five days after sowing, the *Striga* seedlings that emerged, as well as those that remained below the soil surface, were

counted. Sorghum shoots and roots were dried at 70°C and weighed.

Nutrient effects on stimulant capacity to induce Striga *seed germination*

The double pot technique developed by Parker, Hitchcock & Ramaiah (1977) was used to obtain sorghum root exudates containing *S. asiatica* seed germination stimulants. A 4×3 factorial in a completely randomized design, with five replicates, was used to study the effects of sorghum genotypes and N levels on stimulant activity, as measured by the ability of host root exudate to induce *Striga* seed germination. Seeds of two *Striga*-susceptible (Swarna and CSH 1) and two *Striga*-resistant (N 13 and SRN 4841) sorghum genotypes (ICRISAT, 1984) were surface sterilized with a 1% NaOCl solution for 20 min, washed with distilled water, and incubated for 24 h at 25°C for germination. Fifteen germinated sorghum seeds were placed on 150 g washed and heat-sterilized quartz sand held in a styrofoam container, 7 cm in diameter, and with a perforated base. Another 100 g sand was added, and the container was placed in an identical container without basal perforations. Twenty-five millilitres of half-strength Long Ashton nutrient solution (Hewitt & Smith, 1975) containing 0, 30 and 150 mg N l^{-1} as NH_4NO_3 were added. The containers were transferred to an incubator at 30°c, with 14 h light and 10 h dark periods. Fifteen milliliters of nutrient solution was added daily to each container. After seven days, root exudates were collected by applying suction to the base of the inner container.

Striga seeds were surface sterilized with a 1% NaOCl solution for 5 min and preconditioned at 30°C for 10 days on wet glass fibre filter paper discs of 7 mm in diameter. To air-dried discs, each containing approximately 30 preconditioned *Striga* seeds, 25 µl freshly collected root exudate was applied. Each exudate sample was applied to eight discs. After incubation at 30°C for 24 h, the discs were observed under a light microscope and the percentage of *Striga* seed germination determined.

A 2×2×2 factorial in a completely randomized design, with eight replicates, was used to study the effects of N, P and K on stimulant efficiency to induce *Striga* seed germination. Seedlings of the susceptible sorghum genotype Swarna were grown with half-strength Long Ashton nutrient solution, modified to provide 0 and 50 mg N l^{-1} as NH_4NO_3, 0 and 25 mg P l^{-1} as $NaH_3PO_4 \cdot 2H_2O$, and 0 and 50 mg K l^{-1} as KCl. Root exudates were obtained and percentage *Striga* seed germination determined as described earlier.

Whenever required angular transformations were made of the *Striga* emergence data before using analysis of variance. However, data in Table 1 are reported as number of seedlings emerged to allow for quick comparison.

Results and discussion

Nitrogen effects on infestation

Striga infestation of sorghum decreased with increase of soil N (Table 1). Sixty-five days after planting, the numbers of *Striga* seedlings that emerged, as well as those that remained below the soil surface, were highest at 0, intermediate at 12·5, and least at 50 mg N kg^{-1} soil. The mechanism by which N reduces *Striga* infestation is not clearly established. Teferedegn (1973) suggested that N fertilization reduced root exudate activity from the host plant, thereby reducing *Striga* germination. Solomon (1952) and Egley (1971) reported that high N supply increased the osmotic concentration of the host cell sap, thus significantly reducing mass flow of materials from the host plants to the parasite, and thereby inhibited *Striga* parasitism. Williams (1961) found that

Table 1 Mean *Striga* seedling numbers above and below the soil surface, and sorghum shoot and root dry mass in different N treatments

Applied N mg kg^{-1} soil	*Striga* seedling number			Dry mass (g $plant^{-1}$)	
	Above	Below	Total	Shoot	Root
	Striga treatment				
0	11·6	18·0	29·6	3·12	1·33
12·5	5·2	10·2	15·4	4·91	1·85
50·0	4·6	2·4	7·0	6·08	1·83
S.e.d. (12 df)	2·2	3·7	5·6	0·52	0·17
	Control treatment				
0	0	0	0	4·49	1·47
12·5	0	0	0	5·87	1·82
50·0	0	0	0	7·16	1·75
S.e.d. (12 df)	—	—	—	0·51	0·19

N-deficient hosts supported higher relative weights of the parasite, and that N applications reduced *Striga* incidence.

In the present study, stimulant from sorghum roots seems to be more effective in inducing *Striga* germination only in conditions of N deficiency. High soil N may have directly or indirectly weakened stimulant strength, reduced its quantity, or delayed stimulant exudation by the sorghum roots, thereby inhibiting *Striga* seed germination.

Regardless of the presence or absence of *Striga* infestation, increased N level in the growth medium increased sorghum shoot growth but did not affect root growth (Table 1). However, within the same rate of N application, infested sorghum plants had lower shoot dry matter than the control. The data presented in Table 1 show that *Striga* infested plants had 31, 16 and 15% lower shoot dry-matter yields than the control plants at 0, 12·5 and 50 mg N kg^{-1} soil, respectively. These results suggest that the effect of N, at least on sorghum shoot growth, was far more pronounced than that of parasite attack. The reduced *Striga* infestation and enhanced sorghum shoot growth with N application may have caused lower percentage reductions in sorghum shoot dry matter yields at 12·5 and 50 mg N kg^{-1} soil. Parker (1984) reported that higher N application increased shoot growth rate whereas low soil N favoured root growth. Younis & Agabawi (1965) observed that N addition resulted in reductions only in shoots, whereas Andrews (1945) reported reductions in both shoots and roots of sorghum. Agabawi & Younis (1965) stated that parasitized sorghum plants were less efficient in N utilization than nonparasitized plants. As suggested by Parker (1984) and Bebawi (1987), N fertilization appears to have a large influence on the partitioning of host food resources between shoots and roots, and most of the available food material goes to the shoots when N is applied. In the present study, increased N availability and reduced *Striga* infestation with N application appeared to have reduced the shoot dry-matter losses due to the poor N-use efficiency of parasitized plants. The *Striga*-infested and control plants, however, had similar root dry-matter yields at each applied N level.

As Parker (1984) and Bebawi (1987) suggested, the increased sorghum shoot vigour at higher soil N levels (Table 1) might have enhanced the competitiveness of the sorghum plant with the weed and thereby reduced the *Striga* infestation. Also, the increased N uptake by the host plant at higher soil N levels may have acted systemically by increasing the host root tissue N to a level at which *Striga* parasitism was directly inhibited (Stewart *et al.*, 1984).

Nutrient effects on stimulant capacity to induce Striga *seed germination*

The relative differences in stimulant capacity to induce *Striga* seed germination among the four genotypes were not consistent over the 0 to 150 mg N l^{-1} range (Table 2). Based on the capacity of host root exudate to induce *Striga* seed germination, the four sorghum genotypes produced considerably more active amounts of stimulant at 0 than at 30 mg N l^{-1}. Root exudates collected from sorghum plants receiving 150 mg N l^{-1} failed to induce *Striga* seed germination. Therefore, the stimulant activity of sorghum roots decreased with increased N in the growth medium. This is in agreement with the findings of Teferedegn (1973), who indicated that sorghum root exudate activity was inversely proportional to soil N content. Similarly, Pesch, Pieterse & Stoop (1983) observed that urea concentrations of 200 mg l^{-1} and above markedly inhibited *Striga* seed germination as well as radicle growth. Therefore, sorghum genotypes should be screened for stimulant production/activity only at low (0 N where possible) soil N in *Striga* resistance/tolerance breeding programmes.

Table 2 Mean percentage *Striga* seed germination in different sorghum genotype and N treatments (an angular transformation was used)

		Nitrogen, mg l^{-1}; germination (%)		
Genotype	Reaction to *Striga*	0	30	150
Swarna	susceptible	50·0	25·5	0
CSH 1	susceptible	32·2	19·5	0
N 13	resistant	24·5	9·8	0
SRN 4841	resistant	16·4	5·7	0
S.e.d. (3 df)		3·9	3·9	—

Chang (1986) recently described the biochemical mechanisms underlying *Striga* parasitism of sorghum. He observed the stimulation of *Striga* seed germination, the growth of *Striga*

root meristem toward the host root, and the recommitment of the meristem for the formation of haustorium on contact with the host root as three distinct events, each controlled by a low molecular weight compound released by the host. An auto-oxidatively labile hydroquinone in sorghum root exudates was found to stimulate *Striga* seed germination. In the present study, it is possible that the N increase in the growth medium adversely affected the first and most critical of the recognition events, namely, stimulation of *Striga* seed germination.

The genotypes N13 and SRN 4841 produced less active or smaller amounts of stimulant than the genotypes Swarna and CSH 1 at both 0 and 30 mg N l^{-1}. The low stimulant activity/production by N 13 and SRN 4841 may be a factor contributing to their low *Striga* infestation in the field (Ramaiah, 1984). Use of sorghum genotypes that produce less active or low amounts of stimulant, combined with high N applications to soil, are likely to reduce and control *Striga* infestation.

The relative differences in activity of stimulant produced by sorghum plants grown at 0 and 50 mg N l^{-1} were not similar at 0 and 50 mg K l^{-1} (Table 3). However, the N effect was overriding and the presence of 50 mg N l^{-1} in the growth medium considerably reduced stimulant ability to induce *Striga* germination, regardless of the presence or absence of K. The presence of 50 mg K l^{-1} in the growth medium promoted stimulant effectiveness to induce *Striga* germination only in the absence of N. Teferedegn (1973) found similar effects of K on *Striga hermonthica* seed germination. The presence or absence of 25 mg P l^{-1} did not affect *Striga* germination, irrespective of N and K.

Table 3 Mean percentage *Striga* seed germination in different N, P and K treatments (an angular transformation was used)

Treatment combination (mg l^{-1})			
N	P	K	Germination %
0	0	0	39·9
0	0	50	50·9
0	25	0	41·6
0	25	50	48·3
50	0	0	16·8
50	0	50	18·8
50	25	0	17·9
50	25	50	19·4
S.e.d. of transformation (1 df)			2·4

In a field trial, Farina, Thomas & Channon (1985) observed that application of 180 kg N ha^{-1} reduced *S. asiatica* infestation of maize (*Zea mays* L.) by 93%. The beneficial effects of N were similar in both high and low fertilizer applications. Potassium applications of 150 kg ha^{-1} considerably increased *Striga* germination in the absence of applied N. It appears from the present study that such observed N, P and K effects on *Striga* infestation may be due to the effects of soil nutrients on the production or activity of *Striga* seed germination stimulants from the sorghum plants.

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