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Striga Infestation in Maize and Sorghum Relative to Cultivar, Herbicides, and Nitrate

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ABSTRACT

Seed plants belonging to the genus Striga are parasitic on many of our tropical grain crops such as maize (Zea maize L.), sorghum (Sorghum vulgare L.), millet (Eleusine corocana L.), and sugarcane (Saccharum officinarum L.). Inflicted damage may result in crop losses that range from 70% to total failure. Of the 50 or so species, two are extremely noxious: (Striga asiatica (L.) Kuntze) is found predominantly in South Asia, Africa, and parts of Australia, whereas (Striga hermonthica (Del.) Benth), the more devastating of the two, is most common in Africa.

This report summarizes the results of experiments on Striga control conducted at the National Sugar Research Station, Kibos, Kenya. The station is located in the low altitude areas of the Lake Victoria basin where mean monthly temperatures of 23°C and light impoverished soils favor Striga infestation.

One experiment involved the use of nitrogen as a means of Striga control. Nitrogen, in the form of calcium ammonium nitrate, was applied as a top dressing at the rate of 0, 13, 26, and 52 kg ha^{-1} to sorghum and at 0, 39, 78, and 156 kg ha^{-1} to maize. The Striga infestation was reduced significantly from 21,000 plants ha^{-1} in the check to 26,000, 24,000, and 10,000, respectively, in the treated maize plots. However, N application in sorghum did not result in any appreciable reduction in Striga counts. Count responses to nitrogen are summed over herbicide effects.

In another investigation, four recommended sorghum varieties, which are expected to yield about the same under normal circumstances, were screened for resistance to Striga. Results showed that varieties '2KX'

and 'MY 146' had similar Striga infestations of 49,000 and 58,000 ha^{-1}, respectively. These parasite counts were significantly higher than those sustained by 'Serenex' with 38,000 plants ha^{-1} and 'Serena' with 20,000 plants ha^{-1}. The parasite counts on these latter varieties are not statistically different. It was also observed that the grain yields, 5,000 kg ha^{-1} from 'Serena', 4,000 kg ha^{-1} from 'Serenex', and 5,000 kg ha^{-1} from 'MY 146' were about the same but far greater than the low yield of 2,500 kg ha^{-1} from '2KX'. The important inference from both the parasite counts and the yield data is that 'Serena' is the most resistant as well as the highest yielding variety, 'MY 146' is most susceptible to Striga but at the same time it is the most tolerant, whereas '2KX' exhibits high susceptibility and low tolerance. In this context, resistant varieties may not stimulate Striga germination or may resist attachment and/or development of the parasite if germination is stimulated. A tolerant variety is one which stimulates parasite germination and allows parasite attachment and development, but is not seriously damaged.

The third line of investigation was a screening of three herbicides for efficacy against Striga in maize. Pendimethalin [N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzeneamine] was applied to the soil preemergence to Striga and maize at 2 kg ha^{-1}, Oxyfluorfen [2-chloro-1-(3-Ethoxy-4-nitrophenoxy)-4-(trifluormethyl-benzene] was applied as directed spray to the soil, preemergence to Striga but when maize was about 60 cm tall at 1 kg ha^{-1}. The third treatment was a mixture of atrazine (2-chloro-4-ethylamino-6-isopropylamino-s-triazine) and pendimethalin at 1 kg and 1.7 kg ha^{-1}, respectively, directed to the soil, preemergence to Striga but late postemergence to maize.

The *Striga* counts in oxyfluorfen and pendimethalin treatments were 12,000 and 27,000 parasites ha^{-1}, which was similar to the control 22,000. Surprisingly, the atrazine + pendimethalin mix carried a parasite infestation of 72,000 which was significantly in excess of not only each of the other treatments but also the check. However, the grain yields from each of the treatments and the untreated control were almost the same, averaging about 4,000 kg ha^{-1}. This would seem to suggest that the upsurge in *Striga* germination on the atrazine-pendimethalin mix was too late in the season to adversely affect maize grain filling. Although none of the herbicide treatments resulted in significant yield gains nor *Striga* infestation reductions, the fact that the parasite count for the oxyfluorfen treatment was only 55% of the control may have biological significance in the long-term *Striga* eradication program, costs not withstanding.

In view of the lack of capital and low technical skills in peasant farming systems, the use of *Striga* resistant varieties offers the best chance against this parasite.

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CHAPTER I

INTRODUCTION

Crop production in the lowlands of the Lake Victoria basin in Western Kenya is limited by a number of factors: inadequate rainfall, impoverished soils, and voracious pests, most of which are beyond the peasant farmers' control due largely to limited capital and appropriate technical skills.

Among the most damaging of these pests is *Striga*, whose parasitism can result in severe losses in maize, sorghum, and millet, by far the most important grain crops in the country. An otherwise high yielding crop, if susceptible to *Striga*, may produce no yield under heavy *Striga* infestation. *Striga* is an all the more serious agricultural problem because it attacks these grain crops in environments where few other food crops can be profitably grown.

Because of the specialized and insidious physiological relationship the *Striga* parasite establishes with the host, conventional methods of weed control, such as cultivation and herbicidal use, are as yet not particularly effective.

In the past, the farmer had developed quite an effective strategy against *Striga* that is better described as 'living with *Striga*'. That is, the peasant farming system survived then because of methods that tolerated *Striga*. Unfortunately, 'development' changes have handicapped the tradional farmer's defense. For example, in the past, the farmer in this area grew sorghums and millets from which varieties resistant or tolerant to *Striga* could be selected, but with the coming of British rule, maize was introduced into Kenya and has been prefered over sorghum because it is sweeter and less labor demanding. Yet maize has no resistance to *Striga* and is much less drought-tolerant than sorghum. A lot of research has been done in Kenya on maize breeding and improved production practices but little if any attention has been given to the sorghums. It is only lately that the government has realized the need to support research programs that will select and develop sorghum varieties that are sweet yet *Striga* resistant. Doggett and Last, working in the 1950's and early sixties, had identified some indigenous sorghum varieties such as 'Dobbs' that are highly resistant to *Striga* (17, 45). But these initial breakthroughs have not been adequately pursued towards criteria for selecting new varieties for farmers.

Another old practice the farmers used against *Striga* was the application of farmyard manure. But, because of increasing populations, less land is available for animal grazing, and the manure supply has diminished. There has been little investigation to determine whether it was the added nutrients to the soil or its improved water retention as a result of manurial application that inhibited *Striga* germination. Moreover, the significance of nitrogen application in *Striga* control is still very controversial. For example, Crowther, in 1942, observed that *Striga hermonthica* may be reduced by use of nitrogenous fertilizers (14), yet two years later, Last concluded that the effects of nitrogen application in *Striga* infestation may vary depending on the variety of sorghum (45). Even more glaring, there has been a serious lack of information about the mode of action on the nitrogen-induced *Striga* resistance (61).

There is another dimension of the *Striga* control problem. In recent years, the Kenya Government has stepped up sugarcane production in Western Kenya, with the hope of making the nation self-sufficient in sugar supply. But some cane varieties are highly susceptible to *Striga* although their yields are good in the absence of *Striga* parasitism. The sugarcane growing companies have the capital and technical know-how to be able to use herbicides against *Striga*, but none is available.

With this background, I set my investigations: 1) to determine whether nitrogen mediates maize and sorghum resistance or tolerance to *Striga*, 2) to establish whether there is differential resistance to *Striga* among currently marketed sorghum varieties in Kenya, and 3) to explore the extent of control of *Striga* from atrazine, oxyfluorfen, and pendimethalin in maize.

My conviction is that resistant crops hold the best chance for the peasant farmer against *Striga*. But research efforts into the biology of *Striga* need to be supported so that crop breeding programs can be hastened and effective agronomic practices whose scientific principles have been understood can be integrated. The *Striga* suppression program cannot be left entirely to the farmers' ingenuity nor exclusively to pot experiments overseas. It is too complex for that.

CHAPTER II

LITERATURE REVIEW

A. BIOLOGY AND ECONOMIC IMPORTANCE OF STRIGA

The development of an effective control program against a pest is difficult without an understanding of the basic aspects of its life cycle and growth requirements. It is necessary to know, for example, why Striga is so resilient and difficult to control. Equally important is a realistic assessment of the extent of damage inflicted by the pest so that an accurate cost-benefit analysis can be made before a control strategy is drawn.

1. Classification, Botanical Characteristics, and Distribution

The genus Striga belongs to the family Scrophulariaceae and is one of the four major groups of parasitic angiosperms sometimes collectively referred to as phanerogamic parasites. The other three are broomrapes (Orobanche spp.), dodders (Cuscuta spp.), and mistletoes (Tapinanthus spp.). The genus is principally parasitic to tropical grasses, notably maize, sorghum, millet, and sugarcane (27, 30, 31, 32, 34, 39, 80).

There are over 50 species of Striga but three are the more economically important pests. Striga hermonthica (Del.) Benth is the most noxious and occurs mainly in Africa and parts of Asia. It is an erect, usually branched parasitic herb up to 1.25 m tall, with a coarse, hairy, quadrangular fibrous stem. The flowers generally are purplish pink and are arranged in terminal spikes usually about 15-45 cm long.

Striga asiatica (L.) Kuntze is less damaging and is found mainly in South Asia and a few parts of Africa. It is this species that was introduced into North and South Carolina in the mid-fifties. It is a much smaller plant ranging 10 to 30 cm in height, also with an erect branching and coarse, hairy, quadrangular stem. Its flowers occur in terminal spikes and are yellowish orange in color.

Striga gesnerioides is the only species known to be significantly parasitic on dicots, particularly leguminosae such as cowpeas (*Vigna unguiculata*). The world distribution and appearance of these species are available in Figures 1 to 4; further details on botany and distribution can be found in Holm (30), Ivens (32), Kasasian (34), and Shaw (80).

2. Inoculum Production, Survival, and Dissemination

Each mature *Striga* plant is capable of producing as many as half a million or more seeds in a single growing season. The dark microscopic seed about 0.3 mm long and 0.1 mm wide is the inoculum and principle mode of survival against adverse environmental conditions. Each seed has a potential viability of up to 20 years and earlier investigations have determined that *Striga* seed is often distributed in the soil profile from surface down to 150 cm deep, but most is found within the plow layer (30 cm) (20, 29, 71, 79, 80). Some of these investigators estimate that *Striga* seed population in an infested soil may vary in density up to 865 million ha^{-1} (45). However, regulating factors associated with innate and induced dormancy ensure that only a few seeds will germinate in any one season even if ordinary environmental factors associated with enforced dormancy are favorable for germination. When favored cultivated hosts such as maize are not available, *Striga* will survive on wild grasses such as the Sudan grass (*Sorghum* spp.) and Goose grass (*Eleusine indica*). Dispersal is primarily by water, wind, and animals.

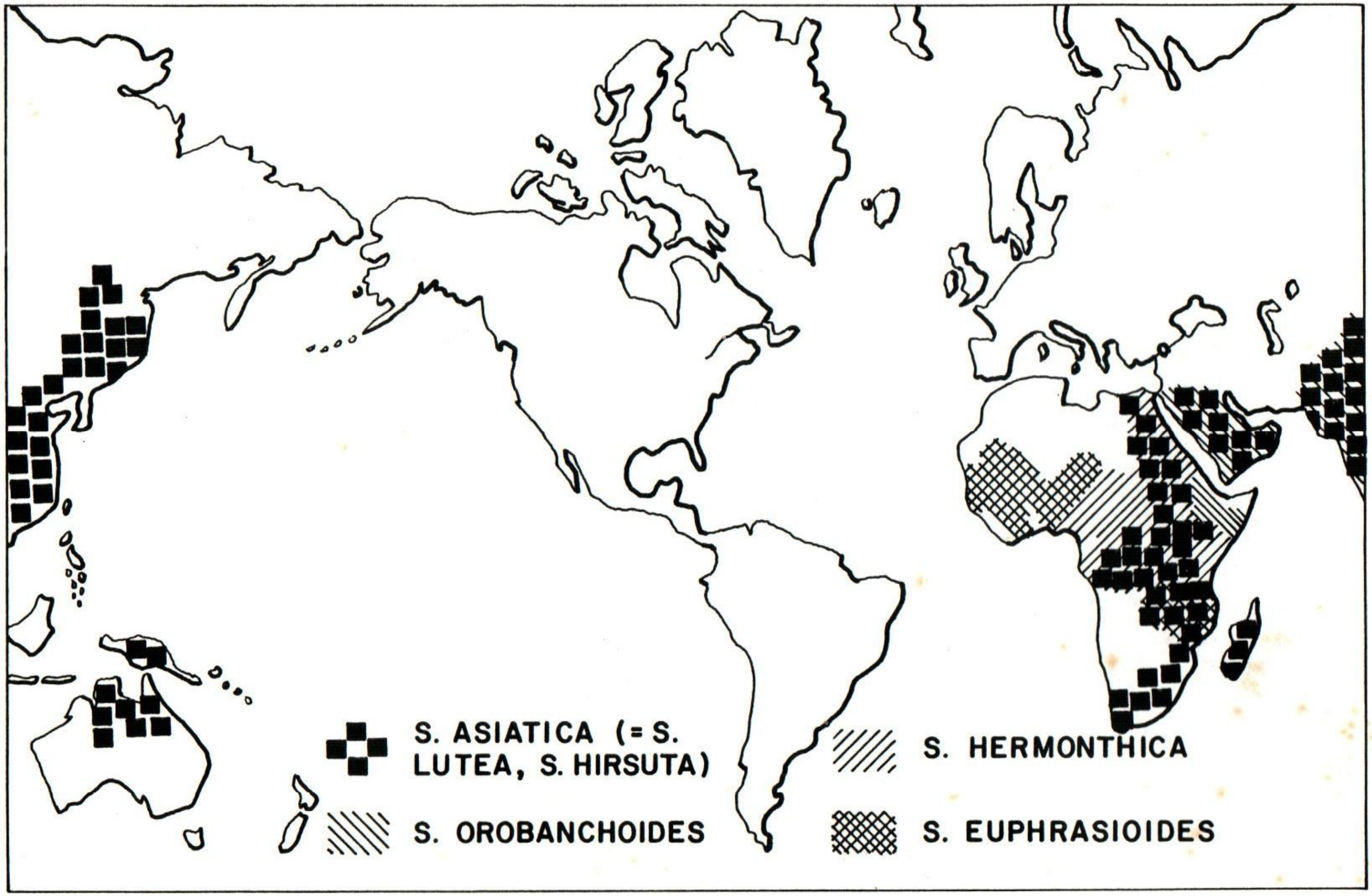

Figure 1. The world distribution of some major *Striga* species (after Shaw *et al.*, 1962).

Figure 2. Striga hermonthica on sorghum

Figure 3. Striga hermonthica on maize

Figure 4. Striga hermonthica on sugarcane

3. Germination, Inoculation, and Host Penetration

a. Germination requirements. Some important aspects of Striga germination have been studied and documented (12, 13, 20, 25, 33, 49, 53, 65, 71, 80, 82). Striga undergoes three important phases before the germination process is completed.

The first phase is commonly called 'after-ripening' or 'post-harvest ripening'. This is the period of time after shedding or physiological maturity during which the seeds will not germinate by any means. Little precise data on Striga after-ripening is available.

The next phase is called the 'pre-conditioning' or 'pre-treatment' phase. At this stage, seeds imbibe water for at least seven days during which time the soil temperatures must be within the range 23°C to 33°C. However, Vallance (82), Reid and Parker (71) have shown that prolonged imbibition beyond 14 days without seed being exposed to the necessary germination stimulant results in a steady decline in Striga seed germination potential. This water-induced reversion to dormancy is sometimes refered to as 'wet dormancy'. This concurs with Nelson's study which showed that ideally Striga germinates best in light well-drained, coarse-textured soils, temperature not limiting (53). The reason behind this wet-dormancy is probably that excessive moisture would over dilute the required germination stimulant as explained by Parker (66) and Vallance (82).

Water imbibition at suitable temperature will only initiate the germination process. In addition, the imbibed seed must absorb a germination stimulant, usually exudated by the host, to effect elongation and emergence of the radicle. This process of exposure of imbibed seed to an appropriate stimulant is called 'conditioning' or 'treatment'.

A natural stimulant, Strigol, has been identified; it is exudated from the roots of the host crop and has been described by Cook as an unsaturated lactone ($C_{19}H_{22}O_6$). Figure 5 shows the basic structure (12, 13, 68). There is growing evidence that there may be a wide range of stimulant compounds exudated by crops of different species and this may explain the host specificity of Striga (49). Johnson and co-workers have been able to produce Strigol analogues in the laboratory but this is not yet at a commercial level (33). Besides, Eplee has demonstrated that ethylene gas (C_2H_4) is an effective germination stimulant and practical applications of this will be reviewed later in this report (20, 23).

Lastly, several researchers point out that Striga germination seems to have a low soil fertility requirement, particularly low nitrogen (2, 7, 19, 45, 53, 59, 61, 80). But as will be pointed out later, nitrogen probably has no direct role on Striga germination, rather, it mediates a reduced level of stimulant exudate.

b. Haustorial development and attachment to host. As pointed out, Striga seed is so tiny that it cannot support seedling development beyond 10 mm in length. Consequently, adaptation is such that it will only germinate when seed is within 2.0 mm of the host root. Under natural conditions, only at this close proximity will the exudate concentration be sufficient to induce radicle elongation and emergence. It is suspected that there is a chemotropic attraction of the haustorium towards the host root or source of the stimulant.

The haustorium is a specialized radicle that is essentially an organic conduit for the transfer of mineral nutrients and water from the host root xylem to the parasite. Once the haustorium reaches the

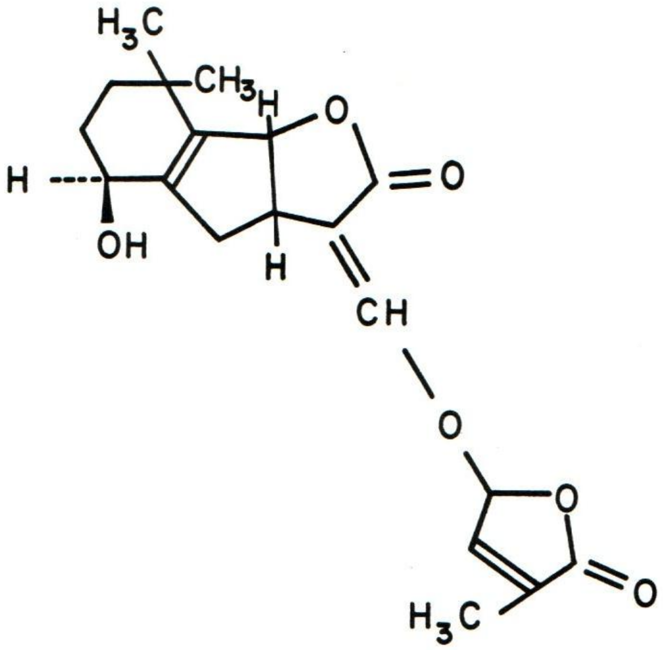

Figure 5. Lactone ($C_{19}H_{22}O_6$) structural formula.

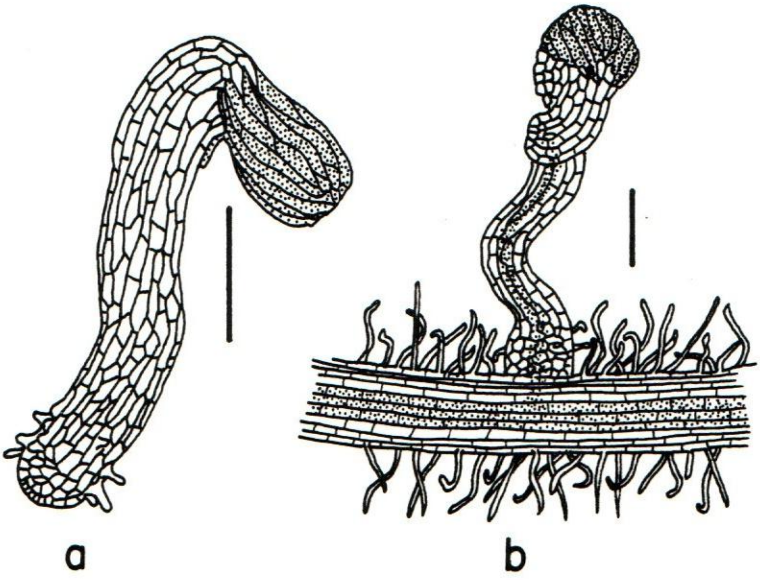

Figure 6. Striga haustoria: a. development to host, and b. attachment (reproduced from Nickrent).

surface of the host root, it penetrates the host tissue by enzymatic action eventually linking the xylem systems of the host and the parasite (36, 38, 39, 55).

A recent study by Ba in West Africa (6) suggests that certain enzymes, namely acid phosphatase, ATPase, peroxidase, succinic dehydrogenase, and cytochrome oxidase, are involved in the functioning of the haustorium. These results may eventually be useful in explaining the mechanism of haustorial penetration of the host tissue as well as the mode of transport of nutrients through the haustoria. In fact, the haustorium must be at the center of our thinking on the development of control programs against Striga because it is the salient organ through which all nutrient transfers between the host and the parasite are made. Figures 6 and 7 are generalized illustrations of haustorial development, structure, and attachment (38, 39).

To sum up, Striga survives as seed in the soil. Under ideal conditions of moisture and temperature and in the presence of a suitable stimulant exudated by the host root, the seed will germinate and attach to the host by a haustorium through which nutrients are transfered. Subterranean development takes about six weeks during which injury to the host is most severe. Flowers form within four weeks of emergence and seeds ripen about a month later, thus a life cycle of 90 to 120 days (39, 80).

4. Inducement of Disease Condition and Host Response (Pathogenesis)

The relationship between Striga and its host is a complex one and not as yet completely understood. It is known

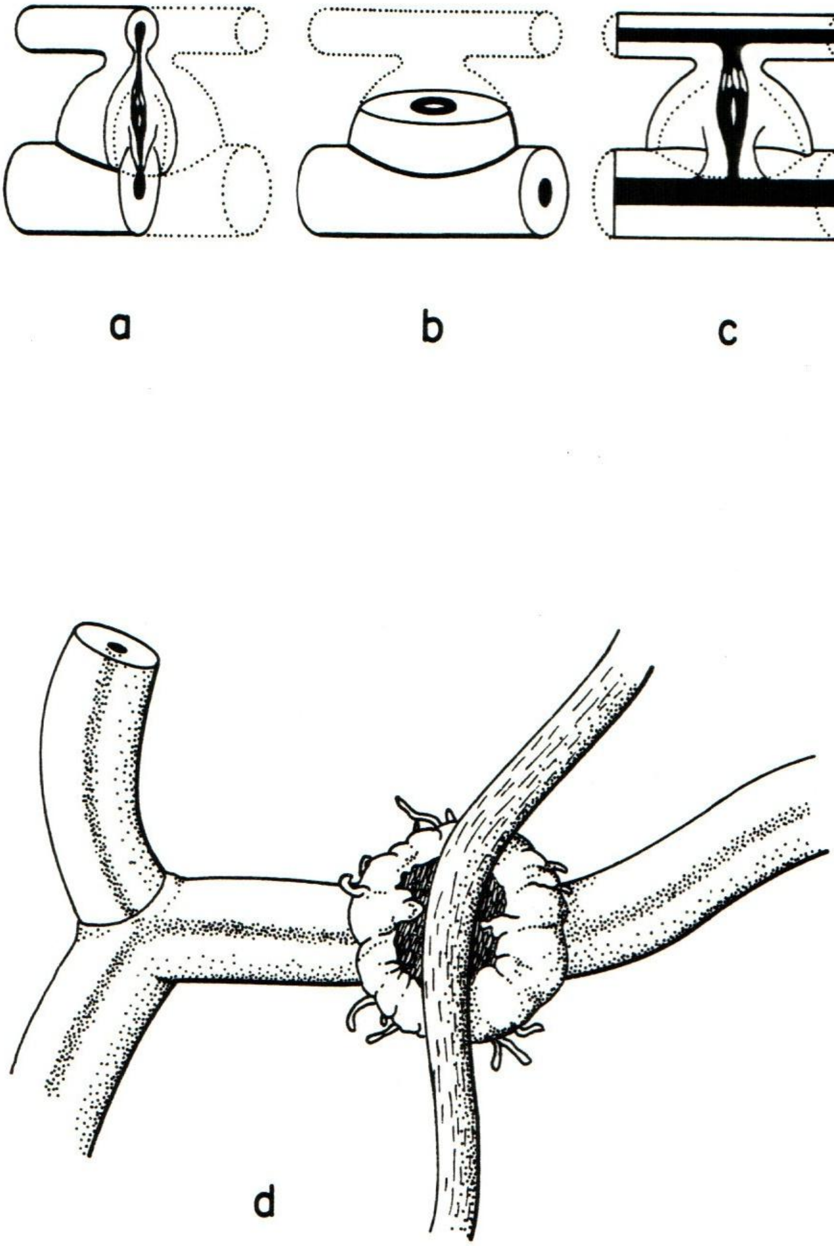

Figure 7. Haustorial planes and overview (after Kuijt): a. longitudinal, b. traverse, c. longitudinal, and d. attachment (reproduced from Kuijt).

for sure, however, that Striga is not allelopathic to its host and the relationship is primarily parasitic (21, 36, 49).

There are several aspects of the disease inducement process. Disturbance at the site of infection leads to increased respiration and cell division together with increased demand for energy resulting in diversion of metabolites to the infection site, which thus acts as a sink for the nutrients. Physiologically, therefore, the parasite has priority of access to nutrients and its demand is satisfied at the expense of the host.

The second disease inducement process is related to water. Under normal circumstances, Striga has a higher transpirational rate than its host. This means that osmotic pressure in the parasite cells is higher than that in the host cells. This imbalance in osmotic pressure helps to maintain a relatively steep water potential gradient that favors the parasite. Since the parasite is located in the host roots close to the water source, the host shoot is short-circuited for water supply. Along with the water come mineral nutrients, so again in both processes the parasite has priority over the host for supplies.

If the available water and nutrients are inadequate for the demand of both the host and the parasite, the former will be first to show stress symptoms. In typical situations, the host leaves curl in and appear spindly as if scalded by hot water. Later, chlorosis, stunting, and wilting will become evident and in severe cases, death may result (17, 23, 45).

El-Hiweris' recent findings while investigating Striga sorghum relationship at Reading University (21) suggest that there may be more than just simple deprivation as a result of Striga parasitism. She found that parasitism resulted in hormonal imbalance in the host as well. The level of growth promoters such as cytokinnins and gibberellins was lower, while that of growth inhibitors such as abscicid acid and farnesol was higher in the parasitized host when contrasted with a non-parasitized check. This may be a better explanation to the observed profound stunting effect by the much smaller Striga on a proportionately much bigger host. Cytokinnins are normally produced in the roots of plants and it does seem reasonable that stress and disturbance conditions from Striga on host roots would inhibit the normal production of these hormones.

El-Hiweris further observed that Striga tolerant plants resemble drought tolerant ones in that both have relatively higher cytokinnins concentrations. She also noted that increased nitrogen supply resulted in higher cytokinnins levels in the host suggesting that nitrogen helps to compensate for otherwise critically reduced levels of cytokinnins and gibberellins in the host.

B. THE METHODS OF CONTROL

1. Mechanical Eradication

Hand pulling is one of the most ancient and most commonly used methods of Striga control by the peasant farmers of East Africa. Striga plants are pulled once or twice in a season after flowering but before seed maturation. Two studies have examined the efficacy of this method. Doggett working in Tanzania concluded that hand pulling resulted in 15% yield benefit in the first year followed by even more enormous benefits in the subsequent years as treatments were repeated (17). These results were corroborated by Ogborn in West Africa (59). Both workers caution, however, that in some cases hand pulling merely increased Striga emergence and consequently the number to be pulled if all seeding were to be prevented. The general opinion is that on short-term basis, hand pulling is of limited value, especially since the more serious damage to the host has already been inflicted. Worse still, if a large area of infestation is involved, it would be onerous if not impossible to hand pull effectively.

2. Crop Rotation

This approach has been investigated by some, particularly Andrews, Doggett, and Last (4, 17, 18, 45, 59, 80). It is recommended that *Striga* infested land should be rested from host crops by rotating to other crops, especially to trap crops that stimulate *Striga* germination but are not themselves parasitized. Examples here are cotton (*Gossypuim hirsutum*), beans (*Phaseolus vulgaris*), groundnuts (*Arachis hypogea*), and sunflower (*Helianthus annuus*). However, such surrogate hosts would have to be grown on infested land for at least four successive seasons for an effective clean-up of *Striga* seed. Unfortunately, most peasant farmers cannot afford not to grow a cereal crop, their staple food, for that length of time. The general practice in the *Striga* infested areas of East Africa, is to grow sorghum or maize interplanted with a legume grain crop, in the long rainy season starting in March and then rotate this to cotton in the short rainy season starting about August/September. In this scheme, the farmer is obviously giving priority to his food crop by sowing it during the long, more stable rains. From a theoretical point-of-view, it would have been better for the farmer to grow cotton first because it is in the long rainy season that *Striga* is more likely to germinate.

The use of catch crops that are parasitized, such as sorghum, then plowed under before the Striga seeds, although practiced in the United States, is not an acceptable alternative to the small scale peasant farmer. Limited land compels him to grow a food crop that he can harvest in that season.

Crop rotations therefore have limited value in East Africa, where a majority of the farmers practice multiple cropping systems. However, some successes in the use of rotations in Senegal and Niger have been cited by Parker but details of the rotations were not given (61).

3. Soil Moisture and Temperature Regulation

It was pointed out earlier that excessively high moisture does induce 'wet-dormancy' in Striga seed, presumably because the moisture over dilutes the stimulant (82). It is true that in extremely wet years, on medium to heavy textured soils, hardly any Striga germinates. This may have practical applications in irrigated farming systems. For example, in Sudan, irrigated sugarcane, when first planted into old rain-fed sorghum land is severely damaged by Striga, but after a few months under irrigation no further Striga was seen (4, 61). In another example, upland rice has been observed to be more affected by Striga than the lowland flooded rice (61).

It is also possible that excessive soil moisture could adversely affect Striga germination by lowering soil temperatures to below the 23°C required minimum. Heavy clouds associated with a prolonged wet season will have the same effect.

4. Soil Fertility: Effects of Nitrogen

It has been noted that soil fertility, especially nitrogen, is a determinant in the incidence of Striga, which is generally associated with light, well-drained low-nitrogen soils. However, studies conducted to determine the influence of nitrogen application have had conflicting results (2, 7, 14, 17, 19, 44, 45, 59, 60, 80).

In general, most of the recent investigations support the conclusion of Crowther, the pioneer in this field, that high nitrogen reduced Striga emergence and even more importantly, it reduced the amount of damage suffered by the crop host (14, 21, 60).

Last and Doggett, working separately on sorghums in the Sudan and Tanzania, respectively, demonstrated that increasing levels of nitrogen supply to the host, decreased Striga (17, 45). But Last had an exception: if nitrogen application was made on very infertile soils that were heavily infested, it increased Striga. No plausible explanation was given.

Parker and his team at the Weed Research Organization (WRO), England, concluded that the form of nitrogen and the time of application are unimportant (61). Yet this contradicts an earlier finding by Last that early application was more effective than late, in Striga suppression (45). Even more recently, Pesch et al. had an opposite conclusion that when compared to sulphate of ammonia and sodium nitrate, urea was more effective in reducing Striga germination (67). Andrews, using pot experiments, concluded that N application increased Striga on sorghum (4). Eplee, in a personal communication, has indicated that his experience in the United States suggest that one would have to apply nitrogen at four times the recommended level to effect significant reduction in Striga infestation. This is in tune with reports by Oblina and others that one would have to apply as much as 100 to 200 kg N ha^{-1} instead of the recommended 33 kg N ha^{-1} to see significant reduction in *Striga* (57, 59). At these high application rates, nitrogen would not only be expensive but probably toxic to the host as well.

Another aspect of inconsistencies in the nitrogen effects is reflected in Last's experiments on sorghum (45). He noted that while N application decreased *Striga* in some varieties such as 'Feterita', 'Dwarf White Milo', and 'Wad Fahl', no such reduction in *Striga* was evident on 'Debekri'.

Lastly, while El-Hiweris results on hormones explains why nitrogen increases host tolerance (21), knowledge about the mode of action involving N in *Striga* resistance is limited (61).

5. The Use of Resistant and Tolerant Varieties

There is no known resistance to *Striga* in maize, but according to Parker, several forms of *Striga* resistance in sorghum have been identified (60, 66, 79). In one form of resistance, stimulant exudation from the host crop is low or nil and consequently, *Striga* is not triggered to germinate. Alternatively, a sorghum variety may exudate normal amounts of stimulant and induce *Striga* to germinate but then resist penetration or attachment of the haustorium. The reasons for this unsuccessful attachment are not fully understood but Saunders has found that in some resistant plants it is as a result of a mechanical obstruction such as thick-walled silicated endodermis (79). It may also be due to as yet unspecified incompatibility.

There are other instances where the host crop is highly susceptible but at the same time tolerant to *Striga*. Such varieties yield well in spite of severe infestation. Such varieties may have high levels of cytokinnins as explained by El-Hiweris (21).

Peasant farmers in East Africa and wherever Striga exists have traditionally selected Striga resistant or tolerant varieties, so this approach is not altogether new to them. However, they have lacked the support of a scientifically based breeding program to develop new cultivars that are not only Striga resistant but also more palatible.

Some of the original studies on sorghum resistance to Striga in Sudan and East Africa were undertaken by Doggett (17) and Last (45). Doggett found that 'Dobbs', a local cultivar from Western Kenya, was more resistant to Striga than another cultivar 'Bukura Mahemba', from Tanzania. Earlier, Last had observed that 'Feterita' was more resistant than 'Debekri'.

Field observations and pot experiments by Parker at WRO have isolated varieties 'Serena', 'Framida', 'SRN 4841', 'IS 7091', 'IS 7471', and 'IS 2643' as substantially resistant to Striga (1, 16). Recent West African studies also include 'SRN 4841' and 'N 13' as varieties showing the most stable field resistance or tolerance to Striga (69, 82). 'N 13' is only 16% susceptible to Striga but does not yield as high as 'SRN 4841' which is 60% susceptible to Striga.

The Kenya Seed Company markets the following sorghum varieties to farmers: 'Serena', 'Seredo', '2KX', 'NES 7360', 'SC 566', 'IS 76', 'IS 8595', 'E 1291', '954063', and MY 146', but as yet there is little information on their Striga resistance or tolerance status.

One of the major constraints on breeding work is the lack of information on the genes responsible for conference of resistance. One needs to know whether it is a single gene vertical resistance or the more stable multiple genes horizontal resistance. Without this information, there can be little progress on this option. Also, a variety that is *Striga* resistant may not also be palatible. And, a variety that is tolerant to one physiological strain of *Striga* may not stand well against another strain.

6. The Use of Herbicides and Germination Stimulants

a. *Germination stimulants*. Reference has already been made to the fact that strigol, a natural *Striga* germination stimulant, has been identified by Cook *et al.* (12). The initial exudates for the research were taken from cotton roots but it is most likely that the exudates from maize and sorghum are also strigol. However, more recent inquiry suggests that strigol may be only one of a family of stimulatory compounds (60, 84, 85).

Following the discovery of strigol, Johnson *et al.* prepared a series of synthetic germination stimulants called 'GR compounds'. They are, in fact, analogues of strigol. *In vitro* studies show that GR-7, GR-45, and GR-60 can cause significant germination of *Striga* seed at concentrations as low as 10^{-9} M. Johnson further claims that initial outdoors box trials of these compounds in India resulted in *Striga* reduction of up to 65% after a single treatment, six weeks before planting sorghum (33). But recently, Stevens and Eplee cautioned that synthetic analogues are not so effective in stimulating *Striga* under field conditions (50). The other constraint is that it takes as many as 20,000 maize seedlings to obtain only 2 mg of chemically pure strigol (80). More efficient extraction methods would have to be developed to make this a commercial proposition.

Chancellor (9a), Egley (20), and Eplee (23), working separately in the United States, have demonstrated that ethylene and the ethylene-releasing compound ethephon (2-chloroethyl phosphonic acid) stimulate the germination of pre-conditioned Striga seed. At the rate of 1 to 2 kg ha^{-1} ethylene has induced Striga germination in a matter of hours resulting in 90% reduction as contrasted to non-treated control. Ethylene diffuses 90 cm deep and 120 cm horizontally from the point of injection and hence easily saturates the plow-layer zone of 30 to 60 cm. Unfortunately, the capital costs of this method cannot be afforded by the ordinary peasant farmer.

b. Herbicides. As opposed to stimulants, herbicides are inherently phytotoxic. The most significant advances in chemical control of Striga have been made in the United States, where the government has heavily subsidized control programs aimed at eventual eradication of Striga asiatica from North and South Carolina (22, 25, 26, 40, 42, 78). The Weed Research Organization, in England, has also done substantial amounts of work screening herbicides for efficacy against Striga (63).

The trend in most of these studies was that quite a number of herbicides killed emerged Striga and consequently reduced further seeding. But, hardly any prevented Striga germination to enable the crop to escape damage; and whichever ones showed efficacy were often non-selective. 2,4-D is an exception to this trend. It has some residual as well as post-emergence activity against Striga and it is reasonably inexpensive (22, 25, 26). But, Last, who has used 2,4-D under East Africa conditions, cautions that if the application is post-emergence to maize and pre-emergence to Striga, it must be done at the 2nd or 3rd week after planting to be effective. If initial spraying is delayed beyond this time, it increases infestation and decreases yield, and also that if moisture conditions are not right, serious injury to the crop may result (45).

More recently, there have been claims that Dinitroanilines, especially trifluralin (α,α,α-trifluoro-2,6-dinitro-M,M-dipropyl-p-loluidine) and oxyfluorfen are promisingly active against Striga (37, 40, 41, 56, 85). However, there is no indication that any significant reduction in Striga has resulted in higher crop yields, perhaps because even though above ground Striga was killed, parasitism underground persisted.

One of the more suprising results came from studies by Bebawi and Farah (7) who found that nitrogen-atrazine combinations were significantly more effective in controlling Striga than sole treatments of either nitrogen or atrazine. This, they claimed, demonstrated the synergistic effect of nitrogen-atrazine.

Generally, herbicides would appear to be the least significant of the alternatives to be considered for peasant farmers. Even if efficacy and selectivity were satisfied, there would still be the prohibitive costs and technical skills required to apply them.

7. Biological Control

a. Insects as natural enemies of Striga. One of the most elaborate surveys by Greathead and Milner noted that there are several species of insects in East Africa that were photophagous to Striga, but that none was host-specific and that most had their own natural enemies, thus seriously limiting the prospects of bio-control (27).

The stem mining fly Ophiomyia strigalis is the most common of these natural enemies of Striga but the damage caused by the larvae is very slight and infestations build up only towards the end of the season by which time mature seed has already formed.

Platyptilia taprobanes is a plume moth that is also widespread in East Africa, but the damage caused in the field is even less noticeable. The moth appears to be oliphagous and Striga may be a less favored host.

The larvae of a butterfly Junonia orithya cause considerable damage to single plants of Striga. One larvae may devour several plants during its development. However, the butterfly is not common enough in East Africa to cause appreciable reduction in Striga infestations. It may be that the butterfly has predators too.

The seed pod galling weevils, Smicronyx spp., cause only a few galls, perhaps because they are polyphagous and are very sparsely distributed in East Africa.

For an annual plant with enormous seed production potential such as Striga, the natural enemy must be capable of preventing reproduction. Hence seed and flower feeders such as Platyptilia and Smicronyx species would be preferable. But until these insects can be protected from their natural enemies, biological control cannot yet be considered a viable option for Striga control.

b. Diseases on Striga. From West Africa, Zummo reports that three diseases on Striga have been positively identified: a leaf spot caused by Cercospora spp., a fungus; a vascular stem wilt caused by Fusarium equisiti; and a stem lesion caused by a fungus Phoma spp. Of these, Fusarium wilt apparently can kill large numbers of Striga and may offer some promise for reducing Striga infestations (86). A similar wilt was observed by the author at Kibos but not positively identified.

CHAPTER III

MATERIALS AND METHODS

A. EXPERIMENTAL SITE

1. Geographic Location and Soils

This research was conducted at the National Sugar Research Station, Kibos, which lies about 10 km northeast of Kisumu in Western Kenya. It lies just below and to the south of the Nandi escarpment, 1350 km above sea level.

The Kenya Soil Survey team, headed by De'Costa and Nyadat, have developed a publication fully characterizing the soils of the station and only important highlights will be mentioned here (52).

Both the maize and sorghum trials were adjacent and located on soil #4, which developed from unconsolidated mineral deposits washed from granitoid gneiss of the Nandi escarpment. The Nandi escarpment itself is part of a pre-Cambrian batholith which outcrops from Maseno to the west to Miwani in the east.

The top soil is generally dark reddish brown to yellowish red sandy loam overlying reddish to greyish brown sandy clay loam. The clay mineral composition indicates the dominance of kaolin (70%) with some amount of illite. The silt and sand fractions are mostly plagioclase feldspars (45%) and quartz (55%). The top soil averages 1.85% carbon. This is low and application of organic manures and nitrogen fertilizers is considered desirable. The pH of the soil is slightly acid to neutral (5.7 to 6.8) and this is very consistent throughout the depth. The phosphate content is marginal.

Application of phosphate fertilizers is thus considered necessary. Details on the soil physical character and chemical composition are available in Appendix A.

2. Climate

Kibos has a tropical climate with an average annual rainfall of 1250 mm that peaks in March, April, and May with December, January, and February being the off-season dry months.

The mean daily temperature is usually around 23°C, however, the day-night variations are considerable so that often night temperature may be down to 15°C. Temperature details are in Appendix B. A careful glance at these weather data suggests that conditions are ideal for *Striga* germination in the March-May quarter of the year.

3. Experimental Designs and Data Analysis

a. *The maize trial*. A two factor split-plot treatment arrangement in a Randomized Complete Block Design, with four replications, was used to assess the effects of four herbicides as the main factor and four nitrogen rates as the sub-factor. Unfortunately, wild pigs damaged part of the fourth replication leaving only three replications with a total of 48 experimental units each 6 x 4 m that could be assessed for treatment effects. *Striga* counts and maize grain yield per sampling unit of 4 x 3 m were the dependent variables observed.

b. *The sorghum trial*. This was also a two factor factorial split-plot treatment arrangement in a Randomized Complete Block Design with four replications. Four sorghum varieties were assigned to the main plot and four rates of nitrogen to the subplots, both factors being investigated for effects on *Striga* infestation and sorghum grain yield.

Plot and sampling unit sizes were the same as for the maize experiment, except in this case all the four replicates were assessed giving a total of 64 experimental units. Again, Striga counts and sorghum grain yields were the dependent variables.

c. Data analysis and statistical procedures used. All the data were subjected to analysis of variance and F tests but before this the Striga counts data in the maize and sorghum trials were transformed to the square root and logarithm of Y + 1, respectively, in order to reduce the coefficient of variation and improve the precision of the experiments. Consequently, all the analyses, the coefficient of variation, and standard error on Striga counts are based on transformed data. However, original parasite counts data is still used for general discussion in this thesis report.

Duncan's Multiple Range Test with a 5% protection level was used for testing herbicide and sorghum variety effects on Striga counts and crop yields because the aim was to pick out the herbicide with greatest efficacy against Striga or the sorghum variety with most resistance against Striga. But orthogonal polynomials were prefered for determining the nitrogen effects because nitrogen treatments were quantitative and equally spaced (11, 46, 81).

Unless otherwise stated, all the dependent variable data as reported in graphs or tables of the main thesis report are based on observation from a 4 x 3 sampling unit within a 6 x 4 m experimental unit.

B. THE MAIZE TRIAL

1. Establishment and Soil Fertility Treatments

The field was disc plowed late, towards the end of the dry season on 17th March, 1982, thus breaking a two-year fallow. Plot demarcations as well as soil sampling for chemical analysis were done on March 29.

On the 30th of March, hybrid maize 'H 625' was hand planted, one seed per hole at 75 x 30 cm spacing (44,444 plants ha^{-1}) with 45 kg P_2O_5 ha^{-1} (as carried in triple phosphate). Rain remained scanty and intermitent until about April 17, nonetheless, the germination was good at about 95%.

Nitrogen was top-dressed on the maize on April 29 at the treatment levels of 0, 39, 78, and 156 kg N ha^{-1} as calcium ammonium nitrate (CAN).

2. Herbicide Treatments

There were three herbicide treatments and a non-treated check. All the chemicals were applied as liquid spray solutions using a 20-liter knapsack sprayer and in accordance with manufacturers' recommendations or previous research experience (10, 15, 22, 37).

Pendimethalin was sprayed on the soil on April 6, preemergence to both maize and *Striga* at 2 kg ha^{-1} (6 lit 'Stomp 330 E'). While spraying this herbicide it was sunny, a little breezy, soil conditions were dry and remained so until April 8 when appreciable amounts of rain fell.

Atrazine and pendimethalin were mixed and applied at 1 kg and 1.7 kg ha^{-1}, respectively (Gesaprim 500 FW + Stomp 500 FW). Dry conditions forced delay in date of application until May 7 when soil was moist and the maize crop had grown sufficiently tall to escape injury, but it was still in time to be preemergence for *Striga*. Environmental conditions at spray were sunny, calm, and moist.

Oxyfluorfen was applied on May 7 at 1 kg ha^{-1} (4 Lit Goal 2E) as directed spray to the soil, late post-emergence to maize but still preemergence to *Striga*. Most of the crop was 60 cm tall but some maize plants less than 60 cm tall sustained injury (chlorotic streaks and necrotic spots on the leaves) but they recovered well within a week.

3. Maintenance

Weeds other than *Striga* were kept under check by hand cultivation and hand pulling until the time of *Striga* emergence when no further weeding was done to minimize damage to *Striga*.

Trichlorphon ('Dipterex' 3.5%) was used at 0.14 kg ha^{-1} on May 4 to control the stalk borer (*Busseola fusca*). Three watchmen were employed to guard the crop round the clock against thieves and wild pigs. A rain storm hit the field on June 6, but the maize recovered from the lodging.

12-14

4. Data Collection

Data was collected from a 4 x 3 m sampling unit within each experimental plot of 6 x 4 m. The quadrant had 4 rows and an average of 40 to 50 crop plants. *Striga* counts were taken on May 18, June 18, and July 17 on site, without pulling them off ground. Maize was harvested on August 23, sun-dried for three days to 12% moisture content, shelled, and weighed.

C. THE SORGHUM VARIETY TRIAL

1. Establishment, Variety, and Soil Fertility Treatments

This and the maize experiment were adjacent to one another and all the basic procedures of land preparation, plot demarcation, and soil tests are similar.

Four sorghum varieties, '2KX', 'MY 146', 'Serena', and 'Serenex', were obtained from the Alupe Agricultural Research Station, Busia. The cultivars are available for farmers in the region and should yield similarly at about 4,000 kg grain ha^{-1} (70, 77, 83). Each variety was planted to a main plot on March 31 at a spacing of 60 x 30 cm, 4 seeds per hole, but later thinned to 2 plants per hole, to give a plant population of 110,000 plants ha^{-1}. Phosphate was applied at planting at 20 kg P_2O_5 ha^{-1} (45 kg TSP). Scanty rains after planting resulted in uneven germination, particularly in replication four and one necessitating gapping on April 27.

Nitrogen treatments to subplots were top-dressed on May 3 at 0, 13, 26, and 52 kg N ha^{-1} (as CAN).

2. Maintenance

As for maize, all weeds in sorghum other than Striga were kept under check until Striga emergence in mid-May. Shootfly larvae (Atherigonia varia) will bore into young sorghum seedlings and cause substantial losses unless controlled by Endosulfan at 1 kg ha^{-1}. This was done on May 8. The same dose of Endosulfan was used to check the midge (Contanaria sorghicola). The larvae of this fly will feed on the ovary preventing seed development. Two sprayings per week started on May 31 and lasted until mid-July.

3. Data Collection

Samples were taken using the same procedure as described for maize. The 12 m^2 quadrant contained about 120 sorghum plants. Counts were taken on May 20, June 18, and July 17. Harvest was done on July 30.

CHAPTER IV

RESULTS AND DISCUSSION

A. THE MAIZE TRIAL

1. Nitrogen Effects on Striga Infestation and Maize Yield

a. Nitrogen effects on Striga counts. Very significant differences were observed amongst nitrogen effects on *Striga* counts, and without significant herbicide x nitrogen interacion, the effects were consistent at all levels of herbicide ($P < 0.005$). Orthogonal polynomial procedures showed that the linear regression model best explains the relationship that is basically inverse. As nitrogen rates were increased from zero to 156 kg N ha^{-1}, the overall *Striga* counts, summed over levels of herbicide, decreased from 85 to 12 plants per 12 m^2 (Table 1; Figure 8). It is interesting to note that if Duncan's Multiple Range Test were used on the nitrogen effects, the rates 39, 78, and 156 kg N ha^{-1} would be carrying statistically similar *Striga* counts of 31 , 29 , and 12 plants per 12 m^2, respectively. However, the non-treated check had a significantly higher infestation of 85 *Striga* plants per 12 m^2. The main conclusion from this must be that nitrogen significantly suppressed *Striga*, even when the application rate was as low as half the recommended level for maize.

These results agree with those of Bebawi (7), Crowther (14), Doggett (17), Last (44), and Parker (64). However, they don't agree with one of Last's experiments that indicated an increase in *Striga* with nitrogen application. But, of course, Last was working with sorghum. Neither do these results concur with the suggestions from Eplee and Oblina that high rates of N would be required before

Table 1. *Striga* counts in maize as influenced by herbicides and nitrogen application at Kibos, Kenya, 1982.[a]

Nitrogen Treatment	Herbicide Treatment				Nitrogen Mean[b]
	Control	Atrazine + Pendimethalin	Oxyfluorfen	Pendimethalin	
(kg/ha)	--------------------counts/12 m^2--------------------				
0	34	202	42	61	85a
39	41	62	1	21	31b
78	21	45	9	42	29b
156	9	36	2	2	12b
Herbicide Mean[b]	26a	86b	14a	32a	

[a] Data transformed to square root y + 1 before analysis; Mean = 4.9; SE = 0.75; C.V. = 53% (original data mean = 39).

[b] Herbicide or nitrogen means followed by a common letter are not significantly different at 5% level on Duncan's Multiple Range Test.

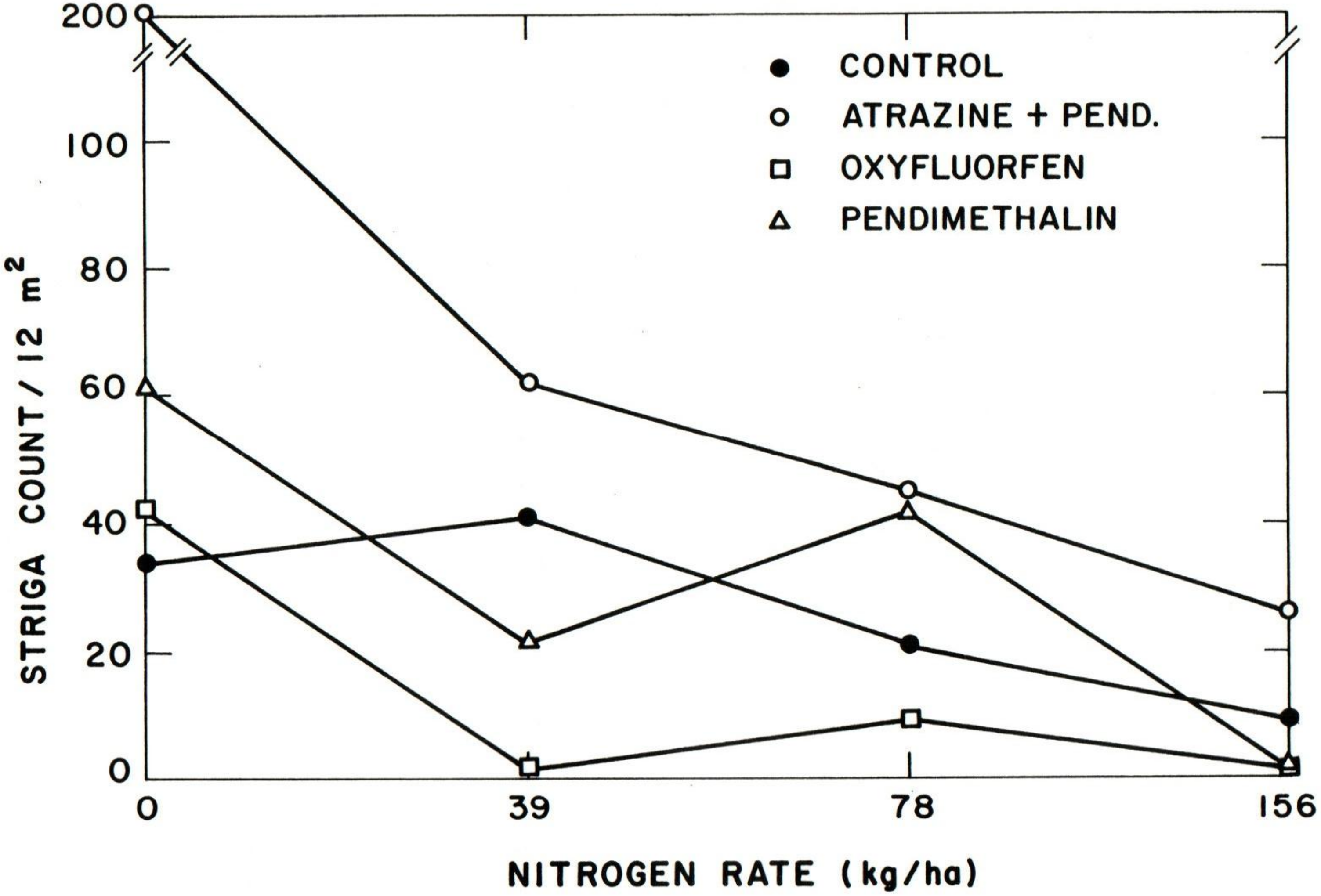

Figure 8. _Striga_ counts in maize as influenced by herbicide and nitrogen.

significant reductions in Striga were realized (57, 59).

b. Nitrogen influence on maize yield. The nitrogen effects on maize yield differed significantly ($P < 0.05$) (Table 2; Figure 9). Orthogonal polynomial analysis indicated a linear regression model as best explanation of the nitrogen-yield relationship. The positive correlation implies that as nitrogen rates were increased, grain yields increased proportionately as well. A covariance inference can be made that since Striga infestation influences maize yield and since nitrogen has a significant effect on Striga counts, some of the variation in maize yield is as a result of indirect effects of nitrogen acting through Striga suppression. These results are corroborated by Doggett (17) and Last (45).

2. Herbicide Effects on Striga Counts and Maize Yield

a. Herbicide influence on Striga counts. The F test on herbicide effects on Striga counts was significant ($P < 0.05$) indicating that there was at least one dissimilarity among the effects. In the absence of significant interaction, this difference was consistent over all levels of nitrogen (Table 1; Figure 8). On the Duncan's Multiple Range Test, the atrazine + pendimethalin combination sustained a Striga population of 86 per 12 m^2 that significantly exceeded the oxyfluorfen, pendimethalin, and non-treated infestations of 14, 32, and 26 plants/12 m^2, respectively. However, the oxyfluorfen and pendimethalin influence on Striga was not large enough to differ significantly from the control. It is important to note, nonetheless, that the oxyfluorfen treatment had the least parasite count and the difference, when compared to the control or pendimethalin was biologically appreciable though not statistically significant.

Table 2. Maize grain yield under *Striga* parasitism as influenced by herbicides and nitrogen at Kibos, Kenya, 1982.[a]

	Herbicide Treatment				
Nitrogen Treatment	Control	Atrazine + Pendimethalin	Oxyfluorfen	Pendimethalin	Nitrogen Mean[b]
(kg/ha)	---------------------kg/12 m^2---------------------				
0	4.0	2.5	2.4	4.6	3.4 a
39	4.4	4.0	5.1	5.3	4.7 b
78	5.1	5.0	4.9	5.1	5.0 b
156	4.7	4.5	5.1	5.3	4.9 b
Herbicide Mean[b]	4.6a	4.0a	4.4a	5.1a	

[a] Original Data: Mean = 4.5 kg; N = 12; SE = 0.38 kg; C.V. = 29%.

[b] Herbicide or nitrogen mean with common letter, not significantly different at the 5% level on Duncan's Multiple Range Test.

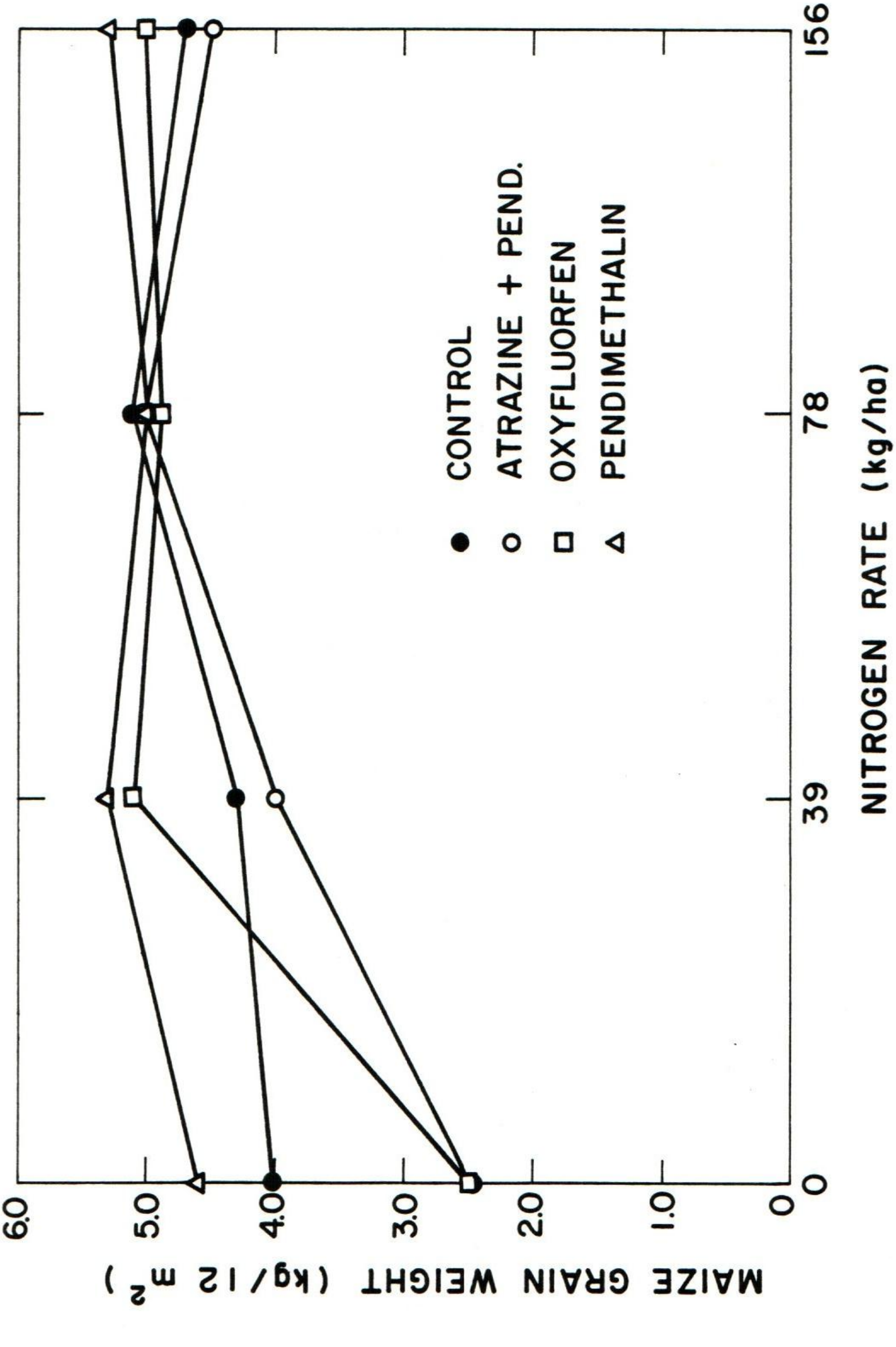

Figure 9. Maize grain yield under _Striga_ as influenced by herbicide and nitrogen.

The fact that parasite counts on the atrazine + pendimethalin treatment were significantly higher than the untreated check is difficult to explain. But, there is one other published experiment that had similar unexpected results: in 1960, Last (45) found that 2,4-D, when applied later than three weeks after planting sorghum stimulated more Striga germination instead of suppressing it. Last had no plausible explanation for the unexpected response and none is available now. However, since Bebawi (7) reported recently that increasing levels of atrazine and nitrogen together progressively reduced Striga population, and seeing that pendimethalin alone in our experiment also carried more Striga than the control, one might suspect that pendimethalin is the major partner associated with increased Striga germination. Further research is required on this.

Also, if the hypothesis that the atrazine + pendimethalin combination substantially stimulates Striga emergence is true, it might be an interesting potential as a suicidal germination of Striga assuming the activity is not mediated by the host.

b. Herbicide effects on yield. Surprisingly, herbicide effects on Striga counts did not translate into differences in grain yield (Table 2; Figure 9). Although the atrazine + pendimethalin treatment with the highest Striga counts also had the lowest grain yield, of 4.0 kg/12 m^2, it wasn't significantly different from the yields of 4.4, 5.1, and 4.6 kg/12 m^2 from oxyfluorfen, pendimethalin, and the check, respectively. This result could be due to several reasons, including statistical imprecision that is associated with the fact that herbicides were the main factor assigned to the main plot in a split-plot arrangement. It could also be that timing of application and weather conditions were not optimal for some herbicides, so that efficacy was reduced. Also, the extra germination on atrazine + pendimethalin mix may have come too late to affect maize grain filling.

c. *A general remark on herbicides*. One might wonder why these particular herbicides were selected in the first place if efficacy is so low. Enthusiasm for atrazine effects developed after Bebawi's report in 1981 that atrazine + nitrogen were synergistic in *Striga* suppression (7). His results were suprising because although atrazine is active against seedlings, especially broad-leaved ones, it inhibits photosynthesis, but *Striga* is capable of being entirely parasitic; that is, it can depend on the host for photosynthates as well. So, one would not expect atrazine alone to do too much harm to *Striga*. Maybe the combination with nitrogen made the stimulatory difference.

Pendimethalin was an attractive choice because as a member of dinitroanilines and like most of the family, as a mitotic poison, it is active against germinating seedlings by inhibiting normal cell division and consequently shoot and root development. Moreover, it has a 6 months residual activity in the soil (3, 5, 35).

Not much is known yet about oxyfluorfen because its use is still experimental. But, some investigators and the manufacturers claim that it has efficacy against *Striga* (41, 50, 74). However, most of the experiments conducted so far have been post-emergence on *Striga* and the activity is by contact. It was earlier noted that post-emergence applications on *Striga* are too late to benefit the current host. Early in the season, oxyfluorfen seemed to have an impressive hold on *Striga*, but later this phytotoxicity seems to break down, perhaps due to rapid degradation, resulting in an upsurge of *Striga* parasites. There is still another drawback with oxyfluorfen. Time of application is even more hazardous with this chemical when used as preemergence to Striga. If sprayed too early before the maize is at least 60 cm tall, the crop will sustain injury, but this late, some Striga may have already germinated (41).

B. THE SORGHUM VARIETY TRIAL

1. Influence of Variety on Host-Parasite Relations

a. Effects of variety on Striga infestation. There were significant differences among variety influences on Striga infestation ($P < 0.05$). Variety '2KX' and 'MY 146' had about the same level of infestation at 58 and 70 Striga plants/12 m^2, respectively, but these parasite numbers were significantly greater than the 24 plants on 'Serena' or '46' plants on 'Serenex'. The latter two varieties were also similar to one another in parasite infestation. These results are summarized in Table 3 and Figure 10.

'Serena' can be described as the most resistant of the varieties tested. This is not surprising since it was developed by hybridizing another resistant local 'Dobbs' to a short cultivar 'P 127' from Swaziland. Earlier, Doggett (17) and Parker (66) had made similar observations that 'Dobbs' and its progeny 'Serena' tend to be more resistant than other varieties to which they were compared.

From this data it appears that variety '2KX' and 'MY 146' have very low resistance to Striga and although the two have statistically similar infestation, 'MY 146' is clearly the most susceptible. We have little background information on these two cultivars except that '2KX' was developed using at least one parent from Texas, USA; sweet taste and short robust growth are some of its desirable qualities. 'MY 146'

Table 3. *Striga* counts in sorghum as influenced by cultivar and nitrogen at Kibos, Kenya, 1982.[a]

Nitrogen Treatment	Cultivar				Nitrogen Mean[b]
	2KX	MY 146	Serena	Serenex	
(kg/ha)	---------------counts/12 m^2---------------				
0	98	85	6	79	67a
13	19	65	22	13	30a
26	44	86	8	45	46a
52	74	45	62	49	58a
Cultivar Mean[b]	59b	70b	24a	46a	

[a] Data transformed to log y + 1 for analysis: Mean = 0.89; S.E. = 0.10; C.V. = 45%. Original data mean = 50, N = 16.

[b] Cultivar or nitrogen mean with common letter not significantly different on Duncan's Multiple Range Test at 5% level.

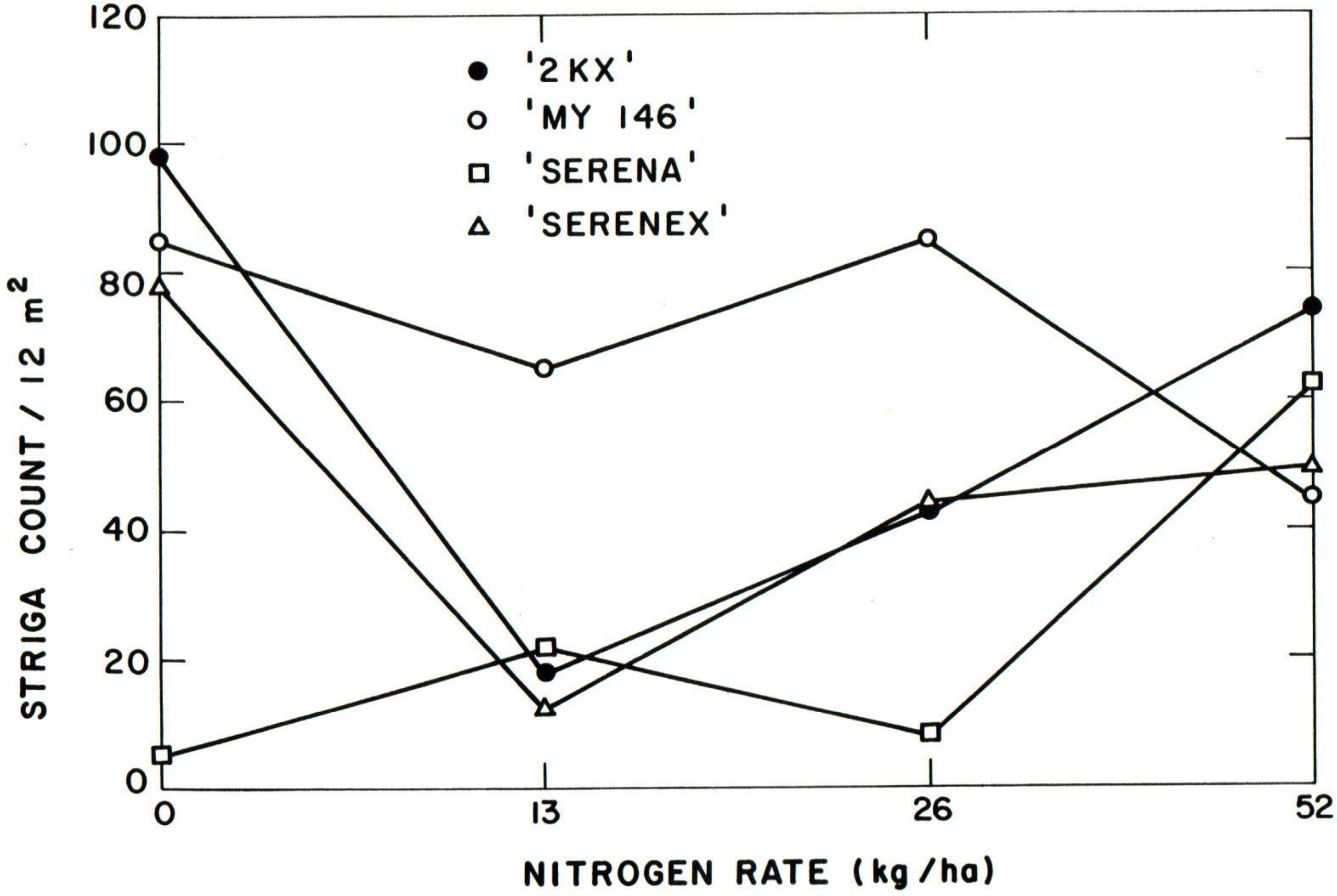

Figure 10. Striga counts in sorghum as influenced by cultivar and nitrogen.

was developed from two Kenya local varieties (Machakos and Yatta), it has considerable drought tolerance.

The physiological basis for high resistance in 'Serena' is low-stimulant exudation (66). However, no histological studies are available that would confirm whether or not it also has a silicated endodermis that would prevent haustorial attachment as well.

b. Varietal effects on yield. Although the varieties used in the experiment are expected to yield similarly at a level of about 4500 kg ha^{-1} under normal, non-parasitized conditions (70, 85), this investigaton suggests that significant differences in yield occur when these same varieties are subjected to Striga parasitism. The F test for differences among varieties on yield was remarkably high ($P < 0.005$). On Duncan's Multiple Range Test the 5.6, 5.8, and 5.0 kg/12 m^2 yields from MY 146, Serena, and Serenex were comparable but each of these was distinctly superior to the lower yield of 3.2 kg/12 m^2 from 2KX (Table 4; Figure 11).

c. General remarks on varieties. Although significance of covariance was not determined, some biologically important inferences can be made when the parasite count and yield data are examined together. First, 'Serena' is not only the most resistant variety but also the highest yielder and is clearly the best choice against Striga.

Second, 'MY 146', although the most susceptible, is also the most tolerant to Striga. Despite the severe infestation, its yield is high, second only to 'Serena'. Since it is also drought tolerant it would be a wise choice for Striga-sick areas that are also marginal in rainfall. However, because it supports a considerable level of parasites it would

Table 4. Sorghum grain yields under *Striga* parasitism relative to cultivar and nitrogen at Kibos, Kenya, 1982.[a]

Nitrogen Treatment	Cultivar				Nitrogen Mean[b]
	2KX	MY 146	Serena	Serenex	
	kg/12 m^2				
0	3.0	4.6	5.5	5.3	4.6a
13	3.4	4.5	6.0	3.7	4.4a
26	3.0	6.6	5.9	4.9	5.1a
52	3.3	6.6	5.9	6.2	5.5a
Cultivar Mean[b]	3.2a	5.6b	5.8b	5.0b	

[a] Original data: Mean = 4.90; N = 16; S.E. = 0.27; C.V. = 22%

[b] Cultivar or nitrogen means with a common letter, not significantly different on Duncan's Multiple Range Test at 5% level.

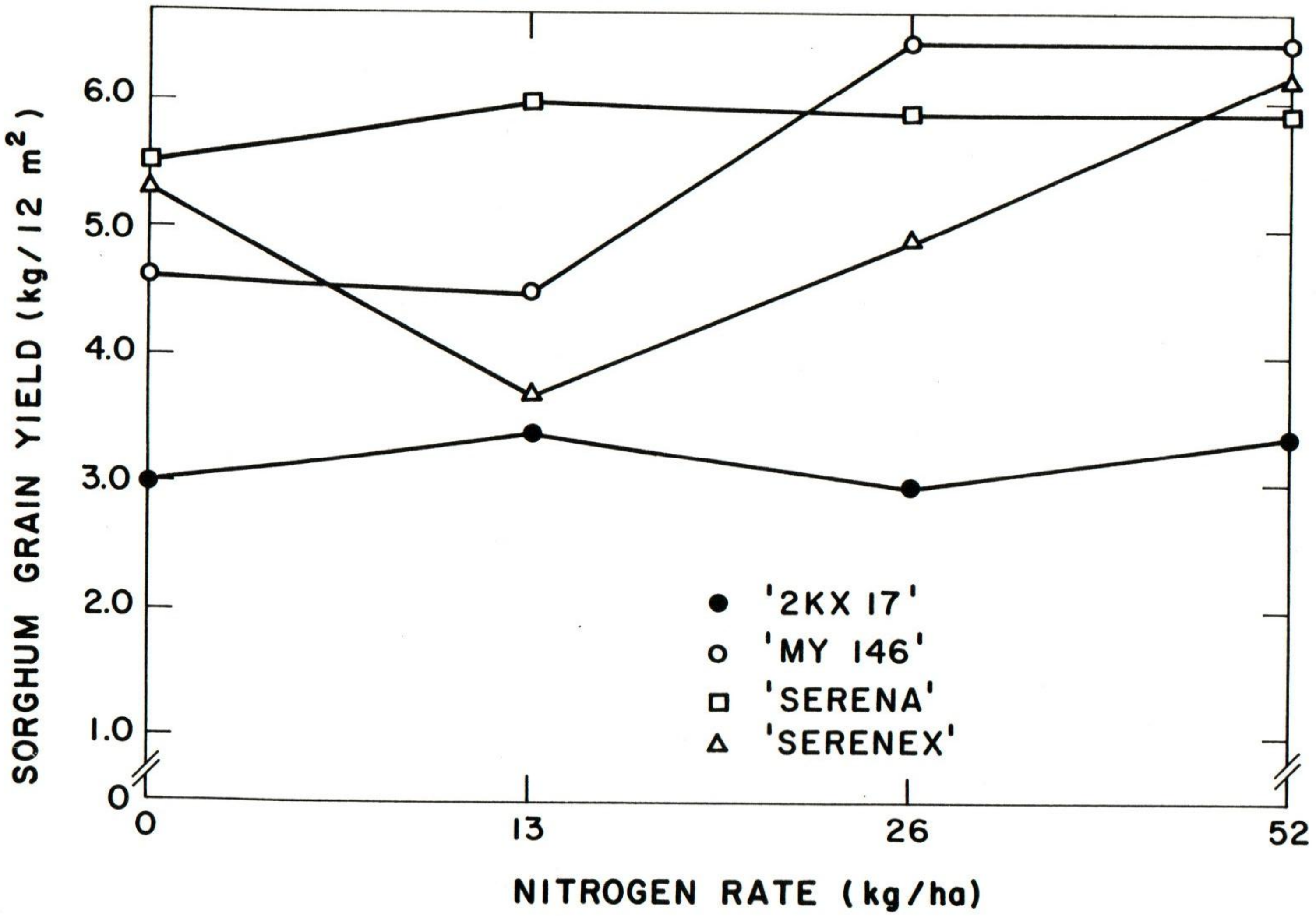

Figure 11. Sorghum grain yield under Striga relative to cultivar and nitrogen.

frustrate long-term Striga eradication programs, as a contribution to the inoculum. Also, in the light of El-Hiweris' finding (21) one can explain the 'MY 146' tolerance to Striga as being derived from higher than normal levels of cytokinnins inherent in the cultivar. In this regard 'MY 146' does seem to resemble 'SRN 4841' developed in Nigeria for Striga tolerance. The latter has a 60% susceptibility to Striga but yields comparably well (69).

Lastly, a comment on '2KX'. Although it is sweet grained, its record against Striga is poor. It has neither the resistance nor the compensatory tolerance to Striga; it would thus seem to be a wrong choice for infertile Striga-sick soils.

2. Nitrogen Effects on Striga-Sorghum Relationships

a. Nitrogen application and Striga counts. Striga emergence in response to nitrogen application in sorghum was statistically similar for all cultivars ($P < 0.05$). Even an orthogonal polynomial analysis picked up no significant differences in nitrogen effects (Table 3; Fig. 10).

The reasons for this lack of response can only be speculated. Other researchers have come across such responses but have been unable to explain them. For example, Last (45) found that the effectiveness of N application on Striga suppression was dependent on the time of application, being more effective if N is applied early, at planting. In our experiment, nitrogen was top-dressed a month after planting. The less dramatic response to nitrogen in sorghum may also be that this crop's demand for nitrogen is much lower than that of maize.

Despite the lack of statistical significance there are trends that could have biological significance. A careful examination of Figure 10 shows that nitrogen influence on Striga in 'MY 146' is minimal. Striga population in this tolerant variety remained invariably high at the lower rates of nitrogen, although at the high nitrogen level the parasite counts declined appreciably. An opposite trend is apparent in the resistant variety 'Serena', where the parasite levels remained very low at low nitrogen rates and then seemed to increase at the high nitrogen level. In a similar experiment, Last (45) observed that nitrogen applied to some varieties like 'Debekri' never significantly decreased the *Striga* infestation but increased it instead (45).

b. *Nitrogen effects on sorghum yield under Striga*. The relationship between nitrogen and sorghum yield could not be explained by simple linear or quadratic models when subjected to orthogonal analysis. But a few general remarks can be made with the aid of Figure 11.

Variety '2KX' is the lowest yielder at 3.2 kg grain/12 m^2 and it shows little response to nitrogen application. 'Serena', although the highest yielder and the most resistant variety, also shows little response to nitrogen. This would imply, at least indirectly, that the *Striga* resistance in 'Serena' is not mediated by applied nitrogen. On the other hand, yield-wise, 'MY 146' reponded readily to applied nitrogen implying that tolerance to *Striga* appears to be improved by applied nitrogen.

C. WHY NITROGEN INDUCES RESISTANCE: A HYPOTHESIS

It has been known for quite some time that a host crop growing on fertile soil, especially nitrogen-rich soil, was able to grow well and yield reasonably even though it might be supporting a lot of *Striga* parasites. In other words, nitrogen induced greater tolerance to *Striga*. But the mode of action by which nitrogen induced this response was not understood until 1979 when El-Hiweris demonstrated that nitrogen actually compensates for growth promoting hormones such as cytokinnins and gibberellins, whose production in the parasitized host had been inhibited. This explanation is plausible partly because nitrogen is known to be involved in the synthesis of cytokinnins. This basically settles the question of nitrogen-induced tolerance.

But how does nitrogen induce resistance to _Striga_? As late as last year, at the 2nd international _Striga_ workshop, Parker, one of the leading scientists on _Striga_ control, confessed that the mode of action by which nitrogen induced resistance was little understood (60, 61). Parker _et al._ (66) have demonstrated that nitrogen added to the crop reduced the amount of strigol exudate from the roots. But why should there be a negative correlation between nitrogen supply and strigol exudation?

As a help to answering this and the broader question about the role of nitrogen in resistance induction one needs to look at the experience of other scientists in the interrelated areas of the physiology of plant nutrition, exudation of organic compounds from roots, and the incidence of disease (8, 9, 28, 29, 47, 72, 75, 76).

For example, Hamlin, Bloom, and Lukezic in 1973 found that clipping alfalfa shoots stimulated hatching of the eggs of the nematode _meloidogyne incognita_. Further research revealed that the clipping resulted in an increase in levels of reduced sugars in the roots and exudates of such sugars from the roots. It was concluded that the nematode egg hatch was associated with carbohydrate exudates from alfalfa roots (28).

An even more pertinent example is reported by Richards (72). He found that increasing applied sodium nitrate produced a progressive reduction in mycorrhiza development in pine trees (Pinus taeda L.). Further experimentation proved that extensive development of mycorrhiza occurs only when carbohydrate synthesis in the pines exceeds carbohydrate utilization and soluble carbohydrates accumulate in the roots. In other words, accumulation of soluble sugars in the roots preceeded the development of mycorrhiza or that mycorrhiza development was associated with carbohydrate exudation from roots.

If this general principle is accepted, then one only needs to explain how nitrogen supply might slow down soluble sugar accumulation in the roots. One of the pioneer scientists that adequately linked this aspect of plant nutrition and plant parasitology was Björkman in 1942 (8). He explained that when photosynthesis is not restricted by adverse environmental conditions, the amount of soluble carbohydrates which accumulates in plant tissue will be determined by the rate at which it is utilized in respiration and growth. Thus, a moderate deficiency of nitrogen severe enough to limit protein synthesis but not so severe as to cause chlorosis, would retard growth and permit accumulation of soluble sugars in roots. Consequently, mycorrhiza or other root exudate induced parasites would be expected to increase. Conversely, an increase in the N/P ratio in the plant results in increased protein synthesis, a process which utilizes soluble sugars thus diminishing their levels. Consequently, mycorrhiza or other root parasite inducement would be expected to decline.

The logic of this model is powerful and the author believes it probably explains the mode of nitrogen in inducing resistance to Striga, although nothing in the literature directly suggests this connection. Björkman's model is used in Figures 12 and 13 to illustrate how nitrogen

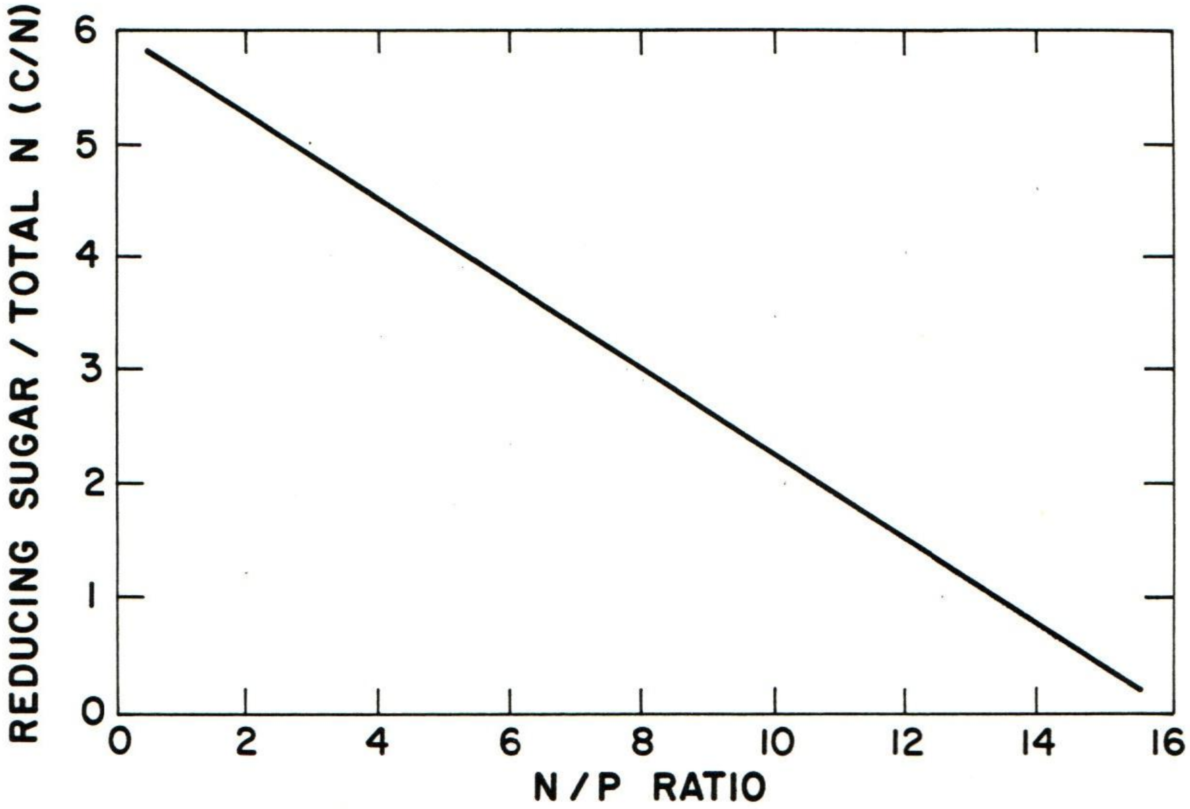

Figure 12. Relationship between N/P intake and C/N (hypothetical model).

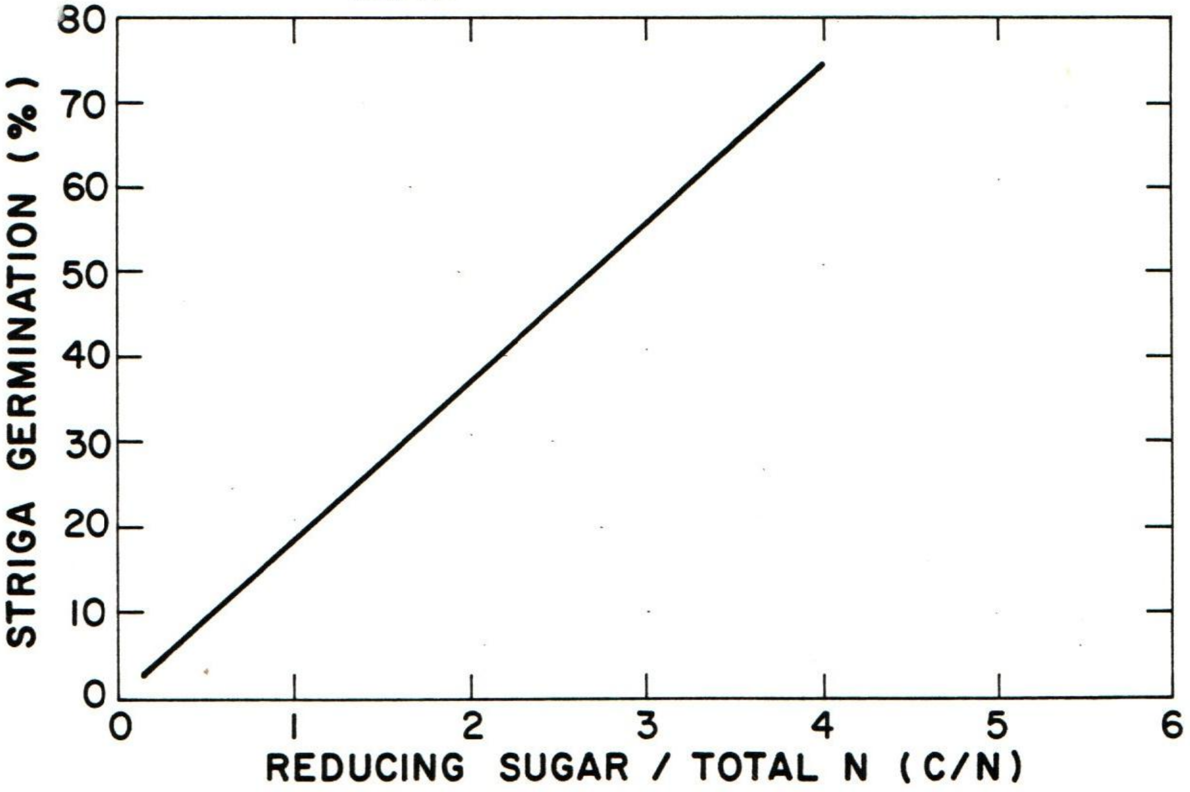

Figure 13. Relationship between C/N ratio and <u>Striga</u> germination (hypothetical model; after Björkman).

might induce *Striga* resistance. It appears to be credible, but further supportive experimentation is required.

CHAPTER V

SUMMARY AND CONCLUSION

Striga is a semi-parasitic plant causing serious losses of tropical cereal crops and cowpeas in Asia and Africa. The need to control it hardly requires emphasis. But because it has a much closer physiological relationship with the host crop the conventional weed control methods have not always been successful against it.

In this study, I investigated three approaches to *Striga* control. First, it was decided to re-examine a relatively classical concept that soil fertility, particularly nitrogen, is instrumental in *Striga* suppression. Literature is full of controversies on this. Some investigations have concluded that nitrogen does indeed suppress *Striga*; others find that on the contrary, nitrogen encourages *Striga*. This report shows that nitrogen effects, at least in part, depend on the host crop. In maize it was a clear but negative correlation. As nitrogen application rate was increased, from zero to 39, 78, and 156 kg N ha^{-1}, *Striga* population decreased from 71,000 to 26,000, 24,000, and 10,000 plants ha^{-1}, respectively. This means that even at half the recommended rate of 39 kg N ha^{-1}, *Striga* population was reduced by 64%. This nitrogen effect was apparently also translated into a yield increase of 25% from 3,000 kg ha^{-1}, at zero nitrogen supply to 4,000 kg ha^{-1} at 39 kg N ha^{-1}. It is concluded that nitrogen supply to *Striga*-sick infertile soils is significantly beneficial to *Striga* control and yield increase in maize.

However, the nitrogen effects on *Striga* in sorghum were much less dramatic. On average, the *Striga* populations on treated plots were as high as on the untreated check. This concurs with Last's finding that late applied, top-dressed, nitrogen is not as effective as that applied early at planting (45). This suggests the current recommendations for top-dressing nitrogen on sorghum should be altered so that at least some nitrogen is applied at planting (70).

Sorghum varietal effects on Striga were among the most interesting in this research. The cultivars screened were differentially resistant and tolerant to Striga. 'Serena' and 'Serenex' had low but similar parasite counts of 20,000 and 38,000 plants ha^{-1}, respectively. Infestations on these two varieties were, however, much less severe when contrasted with the 49,000, and 58,000 parasite counts ha^{-1} sustained by '2KX' and 'MY 146', respectively, although these latter two counts were themselves statistically similar. Thus 'Serena' is the most resistant while 'MY 146' appears to be the most susceptible cultivar.

If yield data are considered too, a somewhat different picture emerges. 'MY 146', 'Serena', and 'Serenex' yield equally well at about 5000 kg ha^{-1} each. But the '2KX' yield is significantly lower at 2,500 kg ha^{-1}.

It can be infered from all this that 'Serena' is not only the most resistant but also the highest yielder. Its form of resistance is probably one of low-stimulant exudation. 'MY 146', though the most susceptible, is also the most tolerant. It must be assumed to have a high level of indigenous cytokinnins as a compensation for inhibitions as a result of parasitism. If one is thinking of Striga eradication per se, 'MY 146' may be a handicap since it adds to the Striga seed pool or the inoculum potential. But, since it is also drought tolerant, it is an attractive choice for the small scale farmer in the marginal areas whose soils may already be overriden with Striga seed. Perhaps the ideal would be to develop a new cultivar that continues the resistance of 'Serena' and the tolerance of 'MY 146'.

The results of the herbicide investigations are of little application to peasant agriculture. First, none of the herbicides used suppressed Striga sufficiently to differ from the control. Oxyfluorfen applied at 1 kg ha^{-1} had a Striga population of 12,000 ha^{-1}. This was 55% of the 22,000 plants ha^{-1} in the check but the difference, though biologically impressive was not statistically significant. Pendimethalin applied at 2 kg ha^{-1} had a population of 27,000 plants ha^{-1}, which is slightly greater than that on the control plot. But, on the whole, Striga numbers on both these treatments were similar to those on the check.

The mixture of atrazine and pendimethalin at 1 kg and 1.7 kg ha^{-1}, respectively, gave unexpected responses. As much as 72,000 Striga plants ha^{-1} were recorded for this treatment, which is significantly greater than any others, including the control. None of the herbicide treatments resulted in significant yield increase; leading us to conclude that herbicides used have little real efficacy against Striga, not to mention the high capital and skill required for their use.

It should be evident from the foregoing that resistant and tolerant cultivars, when available, together with improved soil fertility management, offer the best strategy against Striga in peasant agriculture.

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APPENDIX A

Soil Analysis and Characterization
(Experimental Site)

Table 5. Soil test report, soil #4, Kibos Sugar Research Station.[a]

Physical Analysis

Pit. #	11			15				
Lab #68	3882	3883	3884	3889	3890	3891	3892	3893
Depth (cm)	0-23	23-94	94	0-12	12-38	38-70	70-90	90
Sand %	78	84	60	77	87	81	55	67
Silt %	8	4	10	10	4	4	10	8
Clay %	14	12	30	13	9	15	35	25
Text. Class[b]	SL	LS	SCL	SL	LS	SL	SCL	SCL
Gravel	13	11	16	11	--	12	--	--
Chemical Test Results (Available Nutrients)								
pH	6.0	6.2	5.8	5.8	5.9	5.9	5.7	6.0
Na m.e.%	Trace	0.07	0.17	0.17	Trace	Trace	0.03	0.02
K m.e.%	0.10	0.04	0.07	0.35	0.10	0.07	0.07	0.14
Ca m.e.%	2.4	2.0	3.0	2.0	1.2	1.4	3.6	3.6
Mg m.e.%	1.2	1.2	2.8	0.09	0.5	0.6	2.0	2.0
Mn m.e.%	0.3	0.4	0.78	0.50	0.19	0.20	0.50	0.60
P ppm	6	6	6	19	19	17	8	12
N %	0.04	--	--	0.04	--	--	--	--
C %	1.58	--	--	2.02	--	--	--	--

Notes: a. Obtained from official Soil Characterization Bulletin for Kibos Research Station

b. SL = sandy loam; SCL = sandy clay loam, LS = loamy sand

Table 6. Soil test report, soil #4, Kibos Sugar Research Station.[a]

Chemical Test Results

Site #	IA					
Field #	82-87	82-88	82-89	82-90	82-91	82-92
Lab #	6357	6358	6359	6360	6361	6362
Depth (cm)	0-10	10-20	20-30	30-40	40-50	50-60
pH	6.4	6.5	6.4	6.4	6.6	6.6
Na m.e.%	0.08	0.10	0.10	0.13	0.40	0.20
K m.e.%	0.27	0.27	0.30	0.25	0.16[b]	0.12
Ca m.e.%	3.3	3.1	3.1	3.9	2.7	3.7
Mg m.e.%	2.8	2.9	2.3	2.4	2.4	3.0
Mn m.e.%	1.00	1.06	0.85	0.72	0.80	0.25
P ppm	12	10	12	13	13	14
N %	0.09	0.08	0.07	--	--	--
C %	0.69	0.69	0.66	--	--	--
Hp m.e.%	--	--	--	--	--	--

Site #	IB					
Lab #	6363	6364	6365	6366	6367	6368
Depth (cm)	0-10	10-20	20-30	30-40	40-50	50-60
pH	6.6	6.4	6.6	6.5	6.5	6.4
Na m.e.%	0.10	0.11	0.10	0.15	0.16	0.15
K m.e.%	0.43	0.28	0.34	0.25	0.16	0.16
Ca m.e.%	2.9	2.9	3.3	3.1	3.1	3.3
Mg m.e.%	2.6	2.3	2.6	2.8	2.9	3.4
Mn m.e.%	0.72	0.77	0.98	0.82	0.64	1.24
P ppm	13	13	18	10	12	12
N %	0.08	0.08	0.10	--	--	--
C %	0.61	0.52	0.69	--	--	--
Hp m.e.%	--	--	--	--	--	--

Notes: a. Soil samples taken just before trial

b. Deficiencies underlined

APPENDIX B

Weather Conditions at National Sugar Research Station, Kibos

Table 8. Daily temperature (°C) observations, Kibos Sugar Research Station, 1982.

	Jan.		Feb.		March		April		May		June		July		Aug.	
Day	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	32.7	16.3	30.0	15.3	34.5	15.7	29.4	17.2	23.1	16.6	27.0	17.6	28.7	13.1		
2	32.0	17.1	31.8	14.8	32.0	15.8	27.5	18.5	29.3	16.7	27.0	15.7	29.0	14.5		
3	32.1	14.1	29.6	18.0	32.0	15.0	28.3	18.8	30.6	16.5	28.9	14.6	28.2	14.9		
4	32.7	17.1	30.7	16.3	31.5	14.6	30.6	17.7	29.8	16.4	28.5	17.6	28.5	16.9		
5	30.4	14.3	31.5	16.1	33.1	15.6	31.0	16.7	29.3	17.5	27.4	16.6	28.4	16.2		
6	31.9	15.2	32.2	14.9	33.0	17.4	30.0	15.3	28.5	17.6	28.9	16.5	28.5	17.5		
7	30.7	14.5	32.5	15.8	31.3	17.0	30.5	17.2	26.4	15.0	27.8	14.5	27.0	15.8		
8	32.7	14.7	32.1	16.6	33.5	16.0	31.3	16.5	29.0	16.3	29.1	15.2	28.2	15.7		
9	32.3	13.5	30.5	19.0	33.9	17.5	28.5	16.5	28.5	17.9	28.6	18.2	57.9	14.8		
10	31.6	14.5	30.2	16.5	30.6	15.5	30.5	15.7	28.0	16.9	28.6	16.5	27.2	13.8		
11	31.6	15.1	32.1	15.5	33.0	15.2	31.0	16.5	27.8	17.7	29.0	15.9	28.0	13.6		
12	32.6	15.0	32.0	15.3	34.9	15.6	31.0	17.5	25.8	17.0	29.0	15.0	28.9	13.1		
13	30.5	15.5	31.0	19.5	35.0	15.2	30.0	19.5	27.3	17.0	28.5	16.5	28.5	14.7		
14	31.0	16.0	30.1	19.5	34.1	17.0	28.5	18.9	28.6	16.7	27.5	16.9	28.0	14.0		
15	30.0	15.9	29.8	15.8	33.4	15.2	29.5	18.6	27.2	17.6	29.0	13.5	29.1	16.0		
16	30.0	15.4	29.5	16.3	33.6	16.1	27.5	18.6	28.0	15.2	29.5	14.5	27.5	15.5		
17	30.3	18.0	30.5	17.5	32.8	15.2	25.0	17.5	27.6	18.2	29.2	16.0	27.5	16.6		
18	30.0	16.0	32.2	16.1	35.0	15.4	29.0	17.5	27.1	17.6	29.5	16.0	28.2	14.8		
19	31.5	15.1	30.9	15.3	34.1	18.1	26.5	17.2	25.3	15.6	28.3	17.5	28.6	14.6		

Table 8 (Continued).

	Jan.		Feb.		March		April		May		June		July		Aug.	
Day	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
20	32.1	15.5	30.7	14.5	33.7	17.5	28.0	14.9	29.0	16.0	29.5	16.4	29.0	11.5		
21	32.0	15.4	33.3	12.0	31.7	17.8	28.6	16.0	29.0	15.4	27.1	16.0	29.0	12.6		
22	31.0	14.8	33.6	15.2	29.7	14.6	29.0	16.5	28.3	15.4	27.8	15.9	29.0	13.0		
23	33.0	15.0	34.0	14.5	30.1	15.3	28.4	16.3	28.5	18.2	18.5	16.0	29.0	17.0		
24	33.5	13.5	34.8	14.5	32.5	14.4	29.3	15.5	27.5	15.8	27.5	16.6	27.8	16.0		
25	33.9	16.0	32.5	16.6	34.2	14.4	28.1	17.8	30.0	17.0	27.5	15.5	29.0	15.0		
26	33.9	13.6	30.5	17.0	24.1	14.5	27.6	17.9	30.0	17.9	27.7	14.3	28.2	14.0		
27	34.5	15.3	32.2	16.5	33.5	14.4	27.0	17.4	28.5	17.2	28.2	13.0	30.0	13.7		
28	34.3	14.0	32.8	16.4	32.1	16.1	28.5	17.4	28.1	18.2	27.8	14.4	29.5	13.5		
29	35.5	14.4			31.9	17.9	30.0	16.5	27.9	17.5	27.5	14.5	28.5	14.4		
30	35.5	14.5			27.6	17.0	30.8	17.5	27.5	18.0	28.0	13.1	29.3	17.5		
31	30.0	14.9			31.7	19.5			28.0	16.2			29.5	15.0		
Mean	32.0	15.1	31.7	16.1	30.6	16.0	29	17.0	28.0	16.9	27.6	15.2	28.5	14.6		

Table 9. Mean monthly temperature (°C), Kibos Sugar Research Station.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1972	23.6	23.3	23.0	22.5	22.8	21.5	20.0	N/A	N/A	N/A	23.3	N/A
1973	22.5	24.4	N/A[a]	23.9	22.5	22.0	17.0	21.4	22.1	23.9	23.6	23.3
1974	23.6	23.9	23.0	22.5	22.8	21.4	20.0	22.0	21.7	22.0	24.2	22.8
1975	23.6	23.3	23.0	22.0	22.0	21.4	19.4	20.3	21.1	20.3	23.8	22.9
1976	23.1	22.6	22.7	22.5	22.2	22.0	21.7	N/A	N/A	N/A	N/A	22.9
1977	22.9	22.3	23.5	22.9	22.2	21.1	20.3	21.0	22.2	22.2	23.6	23.6
1978	21.8	N/A	21.9	22.0	22.2	20.3	18.4	20.8	21.2	22.0	22.2	23.7
Mean	23.0	23.4	22.8	22.6	22.3	21.3	19.5	21.1	21.8	22.0	23.4	23.2

Notes: N/A= not available

APPENDIX C

Supplementary Charts: Treatment Effects

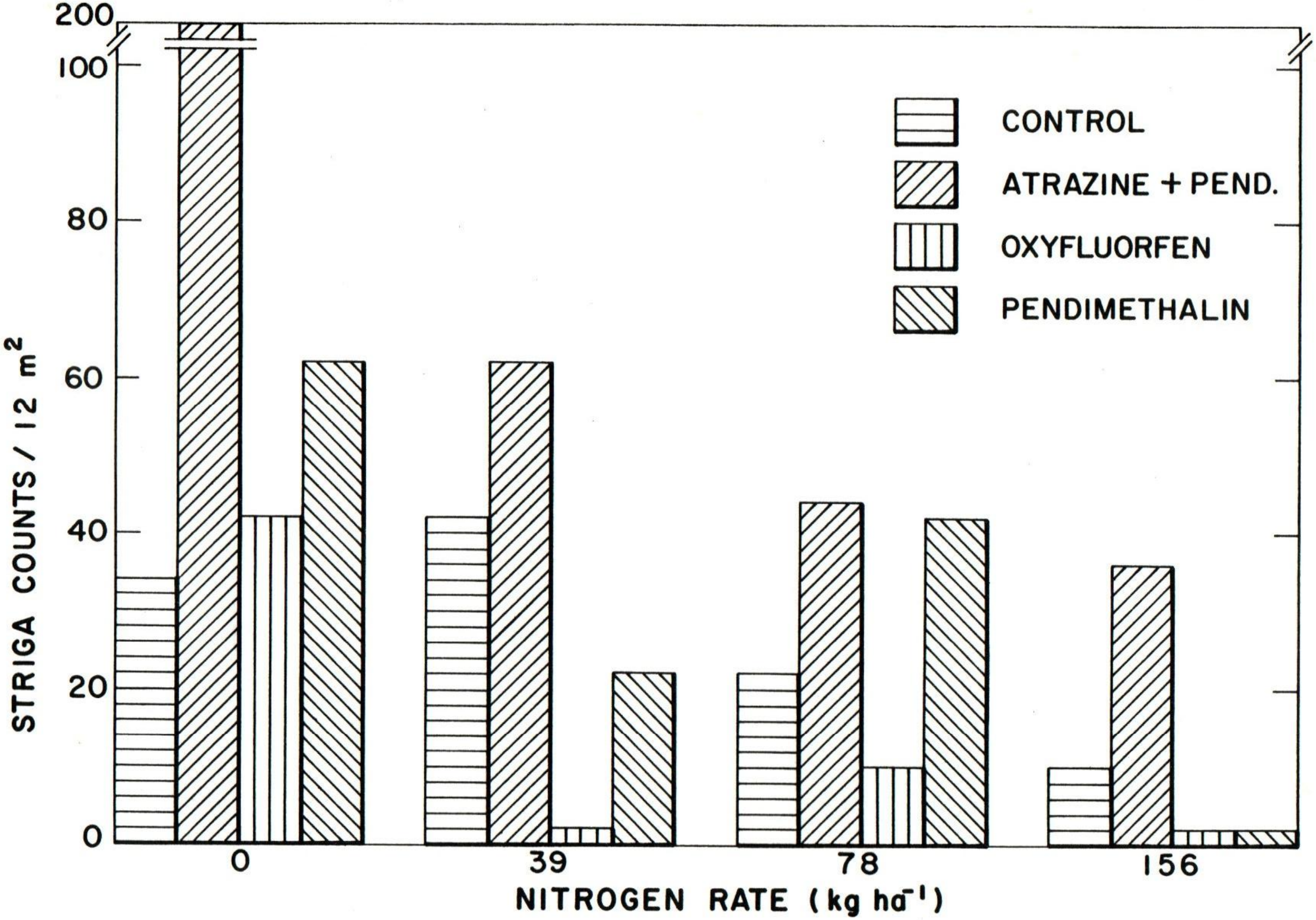

Figure 14. Striga counts in maize as influenced by herbicide and nitrogen.

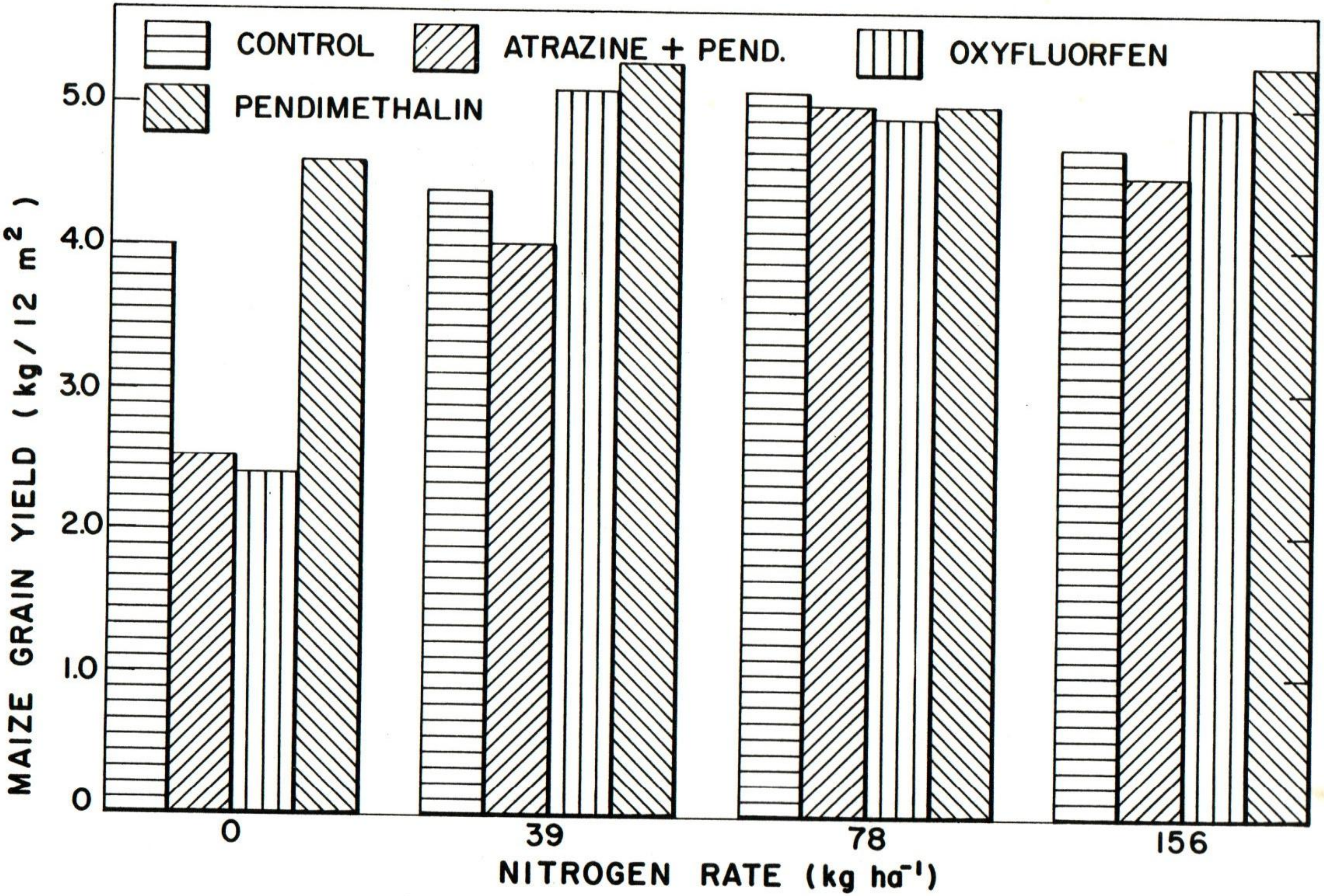

Figure 15.. Maize grain yield under *Striga* as influenced by herbicide and nitrogen.

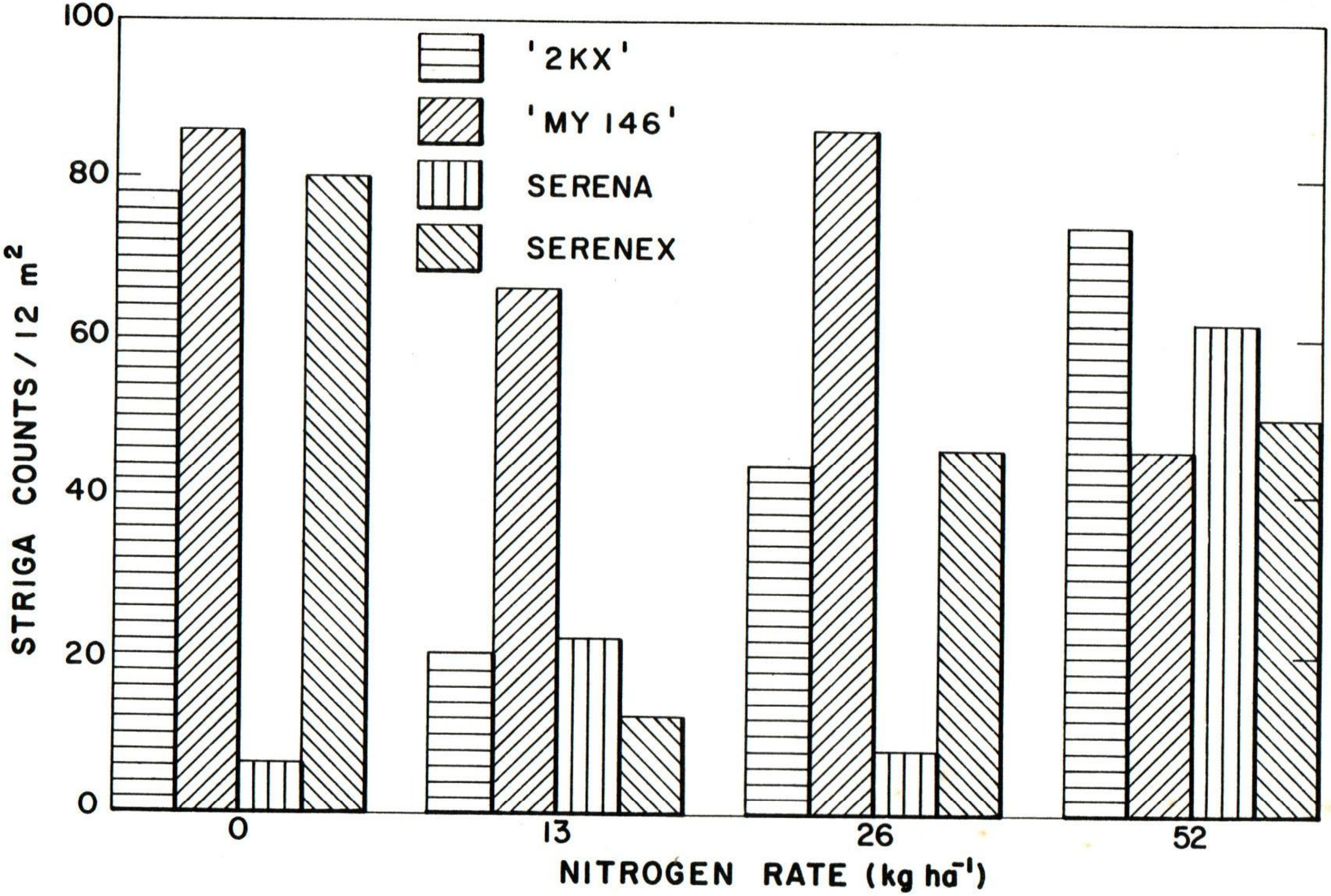

Figure 16. <u>Striga</u> counts in sorghum relative to cultivar and nitrogen.

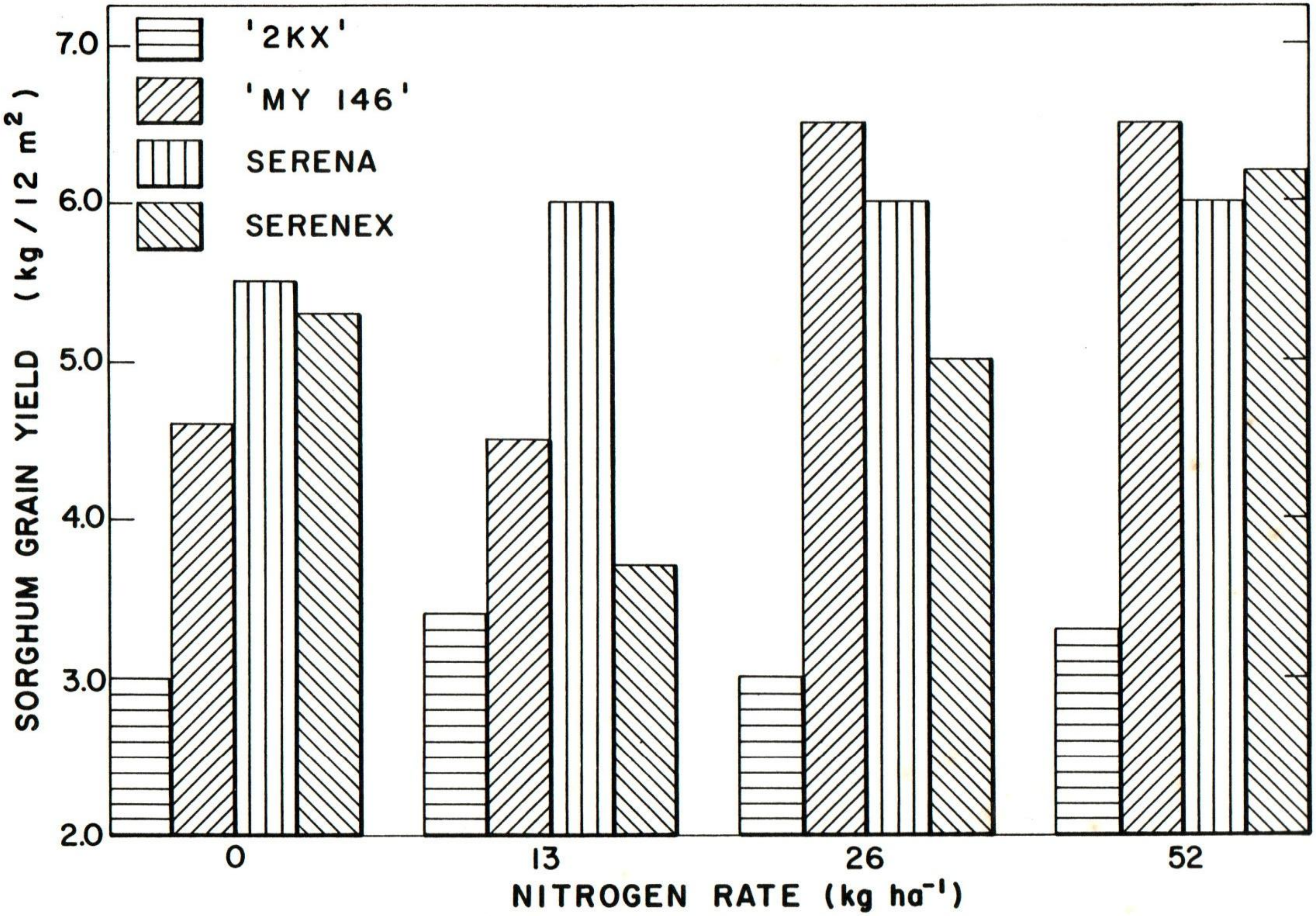

Figure 17. Sorghum grain yield under <u>Striga</u> relative to cultivar and nitrogen.