INHERITANCE OF RESISTANCE TO *Striga hermonthica* (Del.) Benth. IN AN OPEN POLLINATED MAIZE POPULATION, TZL Composite-1 C1.

BY

LOUISE MODESTE AYA KOUAKOU AKANVOU

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(Breeding)

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DECLARATION

I hereby declare that the work herein now submitted as a thesis for the Doctor of Philosophy Degree in Crop Science (Breeding) is the result of my own investigations and has not been submitted for a similar degree in any other University.

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DEDICATION

This thesis is dedicated with love to my dear husband Remi Akanvou and to our lovely children Linda-Ann, Ghislain-Yves and Marie Louise.

May God bless my family always.

ABSTRACT

The parasitic weed *Striga hermonthica* (Del.) Benth. of the Scrophulariaceae family, constitutes one of the most economically important biological constraints in maize production in the sub-Saharan regions of Africa.

The type of gene action involved in the inheritance of resistance to *Striga hermonthica* was investigated using the open-pollinated population, TZLComposite-1 C1 in a North Carolina design 1 scheme. Recombination were done among the best families and also the poorest performing families selected. Realized heritabilities were thus computed for important *Striga* related variables. This study also elucidated the rate and the extent at which resistance to *Striga* can be increased by using conventional population improvement methods.

Comparison of the magnitude of the additive genetic variance (σ^2_a) and the dominance variance (σ^2_d) showed that additive genetic variance was a major portion of the genotypic variance for characters like ear *Striga* rating (σ^2_a = 0.41±0.15 and σ^2_d = -0.20±0.23), yield of infested plants (σ^2_a = 401564±172649 and σ^2_d = 57127±315131), anthesis-silking interval of infested plants (σ^2_a = 0.585±0.49 and σ^2_d = -0.38±0.93) and *Striga* rating at 8 weeks after planting (σ^2_a = 0.28±0.12 and σ^2_d = 0.03±0.21), whereas the number of *Striga* per host plants is controlled by non additive gene action (σ^2_a = 75.69±76.64 and σ^2_d = 211.47±134.48). Estimates of narrow-sense heritability (h^2_n) confirms the magnitude of the additive genetic variance in the total genetic variance for the traits ear *Striga* rating (h^2_n = 0.43±0.16), yield of infested plants (h^2_n = 0.31±0.13) and *Striga* rating (h^2_n = 0.33±0.15), which can be improved by selection. Estimates of realized heritability (h^2_r) were highest for ear *Striga* rating (h^2_r = 0.34±0.37), yield of infested plants (h^2_r = 0.32±0.48) and for *Striga* rating (h^2_r = 0.27±0.57). Genetic

correlations derived from the covariance of full-sib families (r_g) and also genetic correlations obtained from correlated responses to selection (R_g) were estimated between the yield of infested plants and ear *Striga* rating (R_g = -0.50±0.38; r_g = 0.88±1.28), *Striga* rating 1 (R_g = -0.52±0.43; r_g = -0.92±0.93), *Striga* count 1 (R_g = -0.26±0.56; r_g = -0.22±0.46) and anthesis-silking interval (R_g = 1.76±0.09; r_g = 1.05±1.30). Yield of infested plants was positively correlated to plant height of infested plants (r_g = 0.61±0.54), and also to the number of ear harvested for infested plants (r_g = 0.99±1.12). Anthesis-silking interval of infested plants had a positive but low correlation with days to silk (r_g = 0.45±0.85) and days to anthesis of infested plants (r_g = 0.09±0.73). Anthesis-silking interval was negatively correlated to *Striga* rating at 8 weeks after planting (r_g = 0.84±1.39).

The results of this study indicate that resistance to *Striga hermonthica* in open-pollinated maize varieties was shown to be controlled by polygenes . Recurrent selection (selection which involve recombination of superior genotypes to form a population for continued cyclic selection), using a selection index that includes the important traits with high level of additive genetic variance will lead to satisfactory results in selecting for *Striga* resistance in this open pollinated maize population.

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CHAPTER ONE

INTRODUCTION

Maize (*Zea mays* L.) is an important food crop grown and widely consumed in the major agro-ecological zones of West Africa. In Côte d'Ivoire, maize occupies 670,000 ha of cultivated land in diverse ecological systems and is the most widely grown cereal after rice. In the southern rain forest zone and the central forest-savanna region of Côte d'Ivoire, the rainfall distribution is bimodal, having two peaks per year. The early season (long rains) begins in late March and ends in late July, while the late season (short rains) occurs from September through November. Maize is generally planted during the early season as the rainfall is long and evenly distributed. However, in the late season, the rainfall duration is short with an erratic distribution , making it suitable for planting early maturing maize varieties only. However, in the savanna region of Côte d'Ivoire, there is only one rainfall peak per year. The rain begins in late May and ends in September. Maize is planted between May-July with an off season of nine months during which maize is obtained from stored grains. Savanna regions (Southern Guinea Savanna and Northern Guinea Savanna) have been reported to have the greatest potential for maize production in the West Africa (Kim *et al.*, 1994).

Worldwide open-pollinated varieties and hybrids occupy respectively 62% and 38% of the maize-growing area in developing countries (Shivaji *et al.*, 1991). The reasons for the limited use of hybrids in developing countries include the lack of improved germplasm for extraction of inbreds, limited financial resources to purchase farm inputs and lack of effective seed production and distribution systems (Sprague, 1981). However, use of open-pollinated maize varieties with satisfactory yield potential and greater variability permits better adjustment to the

more variable growing conditions in the tropics. Thus, growing open-pollinated maize varieties is advantageous under the low-input and variable maize-growing conditions in African countries.

Although maize is widely used for human consumption, animal feed and as industrial raw materials in most tropical countries, its production per unit of cultivated cropped land is not sufficient to meet population growth. The major factors limiting maize yields include poor use of cultural techniques such as field preparation, time of planting, use of fertilizers, weed control and unavailability of maize varieties resistant to diseases, insect pests and parasitic weeds. Among higher plants that are parasitic on the roots of other higher plants, *Striga* spp. (witchweed) and *Orobanche* spp. (Broomrape) cause severe damage to food crops. Both *Striga* and *Orobanche* root parasitic weeds belong to closely related families of dicotyledons, namely Scrophulariaceae and Orobanchaceae. *Striga* is a root parasitic plant of the Scrophulariaceae family, which is known as one of the major constraints to maize production in the northern and southern Guinea Savanna regions of Africa. In West Africa, *Striga. hermonthica* (Del.) Benth. is the most widespread *Striga* species in the drier savanna regions while *S. asiatica* is found in humid areas (Parker, 1991). *Striga* seeds are spread by farm machinery, livestock, animal waste, irrigation water and farmers (Bebawi *et al.*, 1981). *Striga* species are among the most serious constraints to food production in the semi-arid tropics (Ramaiah, 1987). The parasite attacks more than 60 species of crops and weeds of the Gramineae family, including corn (*Zea mays* L.), sorghum (*Sorghum bicolor* L.), sugarcane (*Saccharum officinarum* L.) (Shaw *et al.*, 1962). Crop loss due to *Striga* vary from 10% yield reduction to total crop failure (Smaling *et al.*, 1991). Efforts are still being made to identify

effective and practical means of *Striga* control.

Control methods using herbicides and nitrogen fertilizers are costly. Also, hoeing or hand pulling of is time consuming and very tedious for small-scale farmers. Breeding resistant varieties and use of cultural techniques such as crop rotation are among the few practical *Striga* control methods applicable to African countries. Better knowledge of the mechanism of *Striga* resistance and the mode of gene action controlling inheritance will improve screening methods and enhance development and identification of resistant crop varieties.

The objectives of this study are: (1) investigating the type of gene action involved in the inheritance of *S. hermonthica* resistance in the open-pollinated maize population TZL Composite-1 C1 and (2) providing information on the rate and the extent to which resistance to *Striga* can be increased using conventional population improvement methods.

CHAPTER TWO
LITERATURE REVIEW

2.1 *Striga* species and distribution

The genus *Striga* (witchweed), of the Scrophulariaceae family, is widespread throughout tropical Africa and South East Asia (Thalouarn and Fer, 1993). *Striga* species are known to cause serious economic losses to cereal crops like maize, millet, sorghum, rice, sugarcane and legumes (cowpea) which are the main staple food crops in some African countries. Among the 25 *Striga* species identified throughout the world, the most economically important ones are: *S. hermonthica*, *S. asiatica*, *S. densiflora*, *S. euphrasioides*, *S. aspera*, *S. forbesii* and *S. gesnerioides*. All of these *Striga* species are parasites on cereals except *S. gesnerioides* which is specific to dicotyledons (Ramaiah *et al.*, 1983). In Nigeria, *S. gesnerioides* is mostly found on cowpea in the central and southern parts of the country. A survey conducted in Nigeria, Togo and Benin revealed that *S. hermonthica* is the most widely distributed species in drier areas, causing severe losses in maize, sorghum and millet (Efron *et al.*, 1989). *S. hermonthica* is also one of the most important weeds observed on maize in the northern Guinea Savanna and Sudan Savanna of Nigeria. *S. aspera* is adapted to areas with higher humidity and was found in maize in the wetter parts of the savanna. *S. asiatica* is found in the eastern and southern part of Africa.

In Côte d'Ivoire, a low density of *S. hermonthica* was first located on millet, sorghum, maize and on rice in the north. *S. aspera* was found on rice, maize, sorghum and also on wild grass (Kouassi Ba, 1989). Initially, *Striga* did little damage to crops, and was therefore not given serious attention (Kouassi Ba, 1989). At present, however, the *Striga* population is

growing so fast that it is becoming a problem for farmers. *S. hermonthica* and *S. asiatica* are the most common and widespread species in Côte d'Ivoire. *S. hermonthica* was identified in the northern part of the country where sorghum, maize and millet were commonly grown. *S. asiatica* was also identified on maize and rice in the central part of the country. In Côte d'Ivoire, the *Striga* population will most likely increase with the movement of livestock from neighboring countries. *Striga* seeds dissemination may occur when animals graze on *Striga* infested fields. Furthermore, *Striga* seeds may be disseminated by farmers who harvest contaminated crop seeds.

2.2 *Striga* biology

Striga species are found not only on crops but on wild grasses. These alternative hosts have contributed in maintaining and spreading these endemic pests in the African savanna zone (Thalouarn and Fer , 1993). All *Striga* species are annual plants although they are sometimes referred to as perennials (Musselman, 1980). The *Striga* genus is characterized by opposite leaves and irregular flowers with a pronounced bend in the corolla tube (Musselman, 1980). The flowers are pink, white, purple or yellow depending on the species. *S. hermonthica*, *S. aspera* and *S. asiatica* are all hemiparasites whereas *S. gesnerioides* is a holoparasite of wild legumes or cowpea (Thalouarn and Fer, 1993). *Striga* species are obligate parasites whose roots are underdeveloped and which attach to host plants by means of a haustorium.

2.3 *Striga* seed production, dispersal and germination

2.3.1 *Striga* seed production

Striga plants produce an enormous number (400,000 to 500,000) of minuscule seeds, 200 to 400 μm in diameter (Doggett, 1984), which can remain dormant in the soil for approximately 20 years. The seeds are commonly spread by livestock, farm machinery, animal wastes, and farmers (Bebawi and El Hag, 1983; Berner *et al.*, 1994). *Striga* seeds may also be dispersed by the wind (Emechebe *et al.*, 1991) or transported on animal coats to noninfested areas (Bebawi, 1981 ; Berner *et al.*, 1994). Recent work at the International Institute of Tropical Agriculture (IITA) showed that wind was a poor disseminator of *Striga* seeds in the Guinea savannas (Berner *et al.*, 1994). The studies also showed that *Striga* spp. seeds were found in grain samples of cowpea, maize, millet and sorghum taken at different markets in Nigeria. Thus, man, through agriculture produce and animal movement, is the primary factor in the dispersal of *Striga* species (Berner *et al.*, 1994).

2.3.2 *Striga* seed germination

Striga seed germination requires three stages (Okonkwo, 1991): (1) an after-ripening period (dormancy), (2) a preconditioning period under moist conditions and (3) exposure of seeds to a chemical stimulant that triggers germination. *Striga* seeds require a period of after-ripening before they are able to germinate. Saunders (1933) reported a minimum after-ripening period of six months for *S. asiatica*. Vallane (1950) found similar behavior in *S. hermonthica*. The biochemical events occurring during that period are still unknown. Doggett (1984)

reported that the after-ripening period requirement is an adaptation of *Striga* to the arid tropical habitat. *Striga* seeds are thus unable to germinate upon harvest at the end of the rainy season.

Dormant *Striga* seeds require a preconditioning period in a warm, moist environment in the dark for several days before responding to a germination stimulant produced by the host root (Ramaiah *et al.*, 1983). The preconditioning time was two weeks for *S. hermonthica*, *S. densiflora* and *S. gesnerioides* (Reid and Parker, 1979). Cook *et al.* (1972) identified a natural exudate from cotton roots called 'strigol' which stimulates *Striga* germination. 'Strigol' analogs known as `GR compounds' were reported to stimulate *Striga* seed germination at low concentrations of 0.1 to 1 ppm (Johnson *et al.*, 1976). Germination stimulants called sorgoleones have been isolated from sorghum root exudates (Netzly *et al.*, 1988). Stewart and Press (1990) isolated a germination stimulant of *S. gesnerioides* from cowpea roots. In vitro experiments indicated that other substances such as cytokinins (kinetin, zeatin), gibberellins, methionin, inositol, and ethylene, not yet found in any crop root exudates, stimulate germination of *S. hermonthica* (Stewart and Press, 1990 and Babiker *et al.*, 1992).

At present, mechanisms involved in the stimulation of *Striga* germination are not yet fully elucidated. Thalouarn and Fer (1993) suggested that natural germination stimulants and other isolated substances act by eliciting the synthesis of ethylene which probably initiates the biochemical events leading to germination. Under ideal temperatures of 30-35^0 C, *Striga* seeds germinate and attach to host roots by way of a haustorium through which nutrients are transferred. After establishment of the haustoria, penetration of the host vascular tissue occurs (Musselman, 1980). Nickren and Musselman (1979) reported five stages of *Striga* parasitic development:

(1) *Striga* seed germination

(2) Haustorial initiation

(3) Penetration of host root tissues

(4) Physiological compatibility

(5) Parasite growth and maturity.

The mechanisms and structures involved in the fixation process and transport of nutrients between the parasite and the host are not yet elucidated. However, evidence of enzyme activity in the haustorium of *S. gesnerioides* and the contact zone with the cowpea host was reported by Okonkwo (1987). Enzymes released by the growing *Striga* root liberate quinonoid compounds like 2,6-dimethoxy-p-benzoquinone (2,6-DMBQ), a benzoquinone which triggers haustorial development (Lynn and Chang 1990).

2.4 *Striga* parasitic development

In general, *Striga* establishes itself directly on the root system of the host plant from which it extracts water and nutrients from the host. This results in yield losses of 15% to 75% depending on the severity of infestation (Thalouarn *et al.*, 1993). Okonkwo (1991) attributed the parasitic effects of *Striga* on sorghum to the diversion of photosynthates, mineral salts and water from the host to the parasite.

Striga always maintains its water potential at a value lower than that of its host. Thalouarn and Fer (1993) showed that *S. hermonthica* and *S. asiatica* had a rate of day-time transpiration which was 4 to 8 times higher than that of sorghum. Transpiration rates in parasitized sorghum plants are also 30% to 50% lower than that in unparasitized control plants.

Striga leaves have a large number of stomata on both sides but a low number of chloroplasts per cell (Tuohy *et al.*, 1986). In *S. hermonthica* and *S. asiatica*, the value of net photosynthesis is about 5 fold lower than that measured in the host plant. Due to its low photosynthetic activity and high transpiration rate, *Striga* exhibits a very low water use efficiency (Thalouarn *et al.*, 1993). These observations suggest that there is a requirement for host carbon to support the growth of the parasite. *Striga*, which is entirely dependent upon its host during its early underground development, receives additional carbon from the host plant after emergence. The parasite thereby induces a strong reduction in its host's photosynthetic activity (Shah *et al.*, 1987). *Striga* germination is affected by drought, temperature and soil fertility (Vasudeva *et al.*, 1987). Pietierse (1985) reported that light and gravely soils favor *Striga* infestation. *Striga* development is favored by well-drained, light soil texture with low moisture content (Saunders, 1933). Nelson (1958) found that at soil temperatures of 32^0c to 36^0c, *S. asiatica* developed to maturity when the soil texture was either sandy, light clay or peat. At lower soil temperatures, *Striga* growth occurred on lighter, sandier soils.

2.5 *Striga* syndromes and damage to host crops

Yield losses in farmers fields due to *Striga* infestation have not yet been assessed due to methodological constraints. Maize, a new crop in the savannas, is more vulnerable to *Striga* parasitism than sorghum and millet (Efron *et al.*, 1989). Maize plants parasitized by *Striga* are usually stunted, chlorotic and wilted, because of competition for light, moisture and nutrients. When the maize crop is heavily infested, no ears are formed. Under heavy *Striga hermonthica* infestation, Kim and Akintunde (1989) reported maize yield losses of up to 90% from on-

station trials. In cowpea, chlorosis is the first symptom of infestation by *S. gesnerioides*. Foliar desiccation and reduction in number and weight of pods occur later (Emechebe *et al.*, 1991). From visual observation, Emechebe *et al.* (1981) stated that yield losses in cowpea under heavy natural infestation of *S. gesnerioides* could be up to 100%. Under artificial infestation, Aggarwal *et al.* (1986) reported that yield loss of cowpea due to *S. gesnerioides* varied between 30% to 56% on susceptible varieties depending on the infestation intensity.

2.6 *Striga* cultural control

2.6.1 Hand pulling and hoe weeding

Hand pulling and hoe weeding are among the most common *Striga* control methods practiced by African farmers (Lagoke *et al.*, 1991). Weeding is carried out by farmers when *Striga* infestation is low. At very high infestation levels, fields are usually abandoned. Current information indicates that hand pulling can effectively control *Striga* seed production if *Striga* plants are pulled out with their haustorial connections (Doggett, 1988; Sallé and Raynal-Roques, 1989). Removal of the haustoria prevents subsequent *Striga* regrowth. Hand pulling could be effective in controlling a light *Striga* infestation, when done before or during the flowering of *Striga*, thereby preventing seed propagation (Pieterse, 1985). However, removal of *Striga* plants to create '*Striga*-free' plots cannot be fully satisfactory in the case of root parasites, because the damage to the host plant is done before parasites emerge from the soil (Parker, 1991). In most African countries, the practice of hoeing or hand pulling to control *Striga* is only partially effective, time consuming, labor intensive and an expensive operation which depletes the nutrients and moisture of the already infertile soils.

2.6.2 Crop rotation using trap and catch crops

Intercropping is an effective practice in reducing *Striga* emergence (Thalouarn and Fer, 1993). Interrow crops may induce abortive germination of *Striga* seeds, increase nitrogen in the soil, or cause inhibition of *Striga* seed germination (Carson, 1989). Effective control through the use of long fallow periods is unlikely, since several African savanna grass species are alternate hosts to *Striga*. Trap and catch crops are used as components of crop rotation systems to reduce *Striga* populations. Both trap and catch crops can induce the germination of *Striga* seeds. Trap crops however, are not parasitized by *Striga* whereas catch crops are and should therefore be destroyed (Lagoke et al., 1991). Several authors reported the beneficial use of 'trap crops' or 'false hosts' which stimulate germination of the root parasites without themselves being parasitized. Rotation with trap crops (groundnut, cowpea, cotton and sunflower) can reduce the amount of *Striga* seeds in the soil. In some West African countries, alternating sorghum or millet with groundnut resulted in low *Striga* infestation. However, a *Striga* population was not reduced in a field where sorghum and groundnut were intercropped in rows (Carson, 1985). Ramaiah (1981) observed that *S. hermonthica* did not grow well on various trap crops including groundnut and cotton. Such failure was attributed to the complex germination requirements of the parasites. Vallance (1950) and Reid and Parker (1979) suggested that when the preconditioning period exceeded the optimum period, germination declined and the parasite seeds fell into a second dormancy called 'wet dormancy'. Pieterse *et al.* (1984) reported that the phenomenon of 'wet dormancy' in *S. hermonthica* might be responsible for poor germination response when trap crops were not planted early in the wet season. Hsiao (1988 a,b) observed that germination stimulants (natural and synthetic) tended to

reduce germination of *S. asiatica* when they were present during the preconditioning phase, in the first two weeks after imbibition. Babiker and Handoun (1982 and 1983) earlier described the same phenomenon in *S. hermonthica*, but its scientific explanation is not yet clear. Parkinson *et al.* (1986) reported that groundnut is parasitized by *S. hermonthica* and therefore cannot be used to reduce the number of *Striga* seeds in the soil. Cotton, soybean and groundnut grown in rotation with a susceptible host can elicit *Striga* seed germination without acting as a host and reduce the number of deadly weed seeds in the soil. Crop rotation, however, is not very effective in solving the *Striga* problem when infestation is severe and besides, *Striga* seeds can remain viable in the soil without germinating for a long period (Okonkwo, 1987). Total eradication of *Striga* seeds underground is therefore difficult.

2.7 *Striga* chemical control

2.7.1 Use of herbicides

Striga control using herbicides is achieved in two ways:

a) by destruction of *Striga* plants before or after emergence above the soil surface and

b) by destruction of *Striga* seed stocks in the soil.

In non-crop growing areas, *Striga* plants are controlled by the use of non-selective herbicides such as Glyphosate and Paraquat. However, in crop growing fields, control of *Striga* is difficult since the herbicides used to reduce *Striga* species. emergence may also damage the host crop. Dicamba, Oxyfluorfen, metolachlore, chlorthal and 2,4-D were herbicides selectively effective on *Striga* foliage (Eplee and Norris, 1987). Babiker and Hamdoun (1982) reported that pre-emergence applications of atrazine were not toxic to *Striga* and that repeated applications were

required for *Striga* control. In the Gambia, use of paraquat was successful in reducing *Striga* flowering (Carson, 1988) but it was later discouraged for toxicological reasons (FAO, 1989). *Striga* plants, once established, can cause irreversible losses to the crop and herbicides cannot entirely prevent damage by *Striga* to the host crop. Moreover, the cost of herbicides is high for small scale farmers of Africa. Some herbicides are useful in controlling the development of *Striga* flowers and consequently *Striga* seeds. Research efforts should be directed towards identifying herbicides that stimulate *Striga* seed germination and kill seedlings before attachment to the host crops. Destruction of *Striga* seed stocks in soils was achieved by the use of ethylene or fumigants (methyl bromide). Use of soil-applied ethylene gas as a germination stimulant in the U.S. caused rapid depletion of *Striga* seed in soils where no host is available (Eplee and Norris, 1987). When no host is available, *Striga* seedlings die since they are unable to attach to a host root system through which water and nutrients for growth are obtained (Eplee and Norris, 1987). Use of ethylene gas to suppress *Striga* development is an effective method but requires special equipment and is expensive for African farmers.

2.7.2 Use of fertilizers

Heavy *Striga* infestation is usually associated with low soil fertility. Thus, application of nutrients in the form of inorganic fertilizer, or organic fertilizer such as farmyard manure may reduce *Striga* infestation and enhance crop yield. When ash was applied to sorghum fields, the *Striga* population was reduced (Kim, 1991). Off-season cattle grazing on farmlands provides dung which enhances soil fertility and reduces the *Striga* population (Kim, 1991). In the U.S.A, *S. asiatica* was controlled by using high rates of nitrogen (Shaw *et al.*, 1962). In India, nitrogen

applied to fields of pearl-millet reduced the effect of *Striga* on crop yield (Mathur and Mathur, 1967). Pieterse *et al*., (1984) also showed that urea and ammonium sulphate inhibited *Striga* germination in in-vitro experiments. Application of high levels of nitrogen reduces the host production of germination stimulant and prevents *Striga* emergence thus lowering *Striga* effects on host plants such as maize (Okonkwo, 1987). Despite all the beneficial effects of nitrogen fertilizer on the host plant and its adverse effects on *Striga*, use of nitrogen fertilizer to control *Striga* was criticized because of its high cost and unavaibility to small scale farmers. Furthermore, other reports show that nitrogen may increase infestation on highly infested *Striga* soils. This is contradictory to the belief that high nitrogen level can suppress *Striga* growth. Last (1960) indicated that on non fertile and heavily infested soils, nitrogen increased *Striga* population on sorghum varieties. In South Africa, Saunders (1933) found that nitrogen application to maize crop induced the appearance of more *Striga* plants above ground. A similar result was obtained in Nigeria where Butler *et al.* (1991) observed that sorghum plots treated with manure showed about 40% more *Striga* plants above ground compared to unmanured plots. Application of manure to fields increases soil fertility and therefore may enhance *Striga* growth in highly infested areas.

2.8 Biological control of *Striga*

During the past two decades, there has not been any decisive progress in biological control of *Striga* (Thalouarn and Fer, 1993). Several insects feeding on *Striga*, and fungi were used in *Striga* biological control. Attempts to use insects like *Smicronyx* , *Melanagromyza* and *Eurytoma* on *Striga* were not as successful as on *Cuscuta* (Greathead, 1984). Other insects

such as *Junonia orithya* which feed on the leaves, and *Eurytoma* which feed on the host stems, may be of interest in the biological control of *Striga*. Fungi, bacteria and even viruses are yet to be used as biological control agents.

2.9 Breeding strategies for *Striga* control

The cultivation of crop varieties that are resistant to *Striga* is among the most economical method to control *Striga*, especially in countries with limited resources. Most African farmers cannot afford the cost of fertilizers and herbicides. Therefore, breeding for crop varieties resistant to *Striga* and also, the use of some cultural control techniques are among the few economical strategies applicable to *Striga* control. For most of the literature consulted, success in breeding resistant varieties to *Striga* has been so far negligible for most of the crops affected. One of the reasons given by Parker (1991) is that *Striga* species are obligate parasites and that complicates the possibility of selecting crop varieties that have at least reduced susceptibility to *Striga* attack if not complete immunity. Therefore, the development of a simple and reliable screening technique is needed for a successful *Striga* resistance breeding program.

A major problem in breeding for *Striga* resistance is the specificity of resistance. For instance, sorghum genotypes identified as resistant to *S. hermonthica* and *S. asiatica* did not perform well when tested against *S. forbii* (Obilana, 1987). Resistant sorghum genotypes did not show stability of resistance and/or performance when tested with diverse *Striga* species over a range of geographical areas (Ejeta *et al.*, 1991).

Another constraint to consider when breeding for *Striga* resistance is the development of different 'strains' of the common *Striga* species (Bebawi, 1981). The development of

specific strains can be attributed to genetic recombination and mutation or geographical changes that occur over a number of years (Ramaiah, 1984). Thus, new gene recombinations in the parasite may induce stronger virulence that can overcome genetic protection in the host especially when resistance is simple and specific (Ejeta *et al.*, 1991). Wilson (1955) observed that when sorghum was planted on traditional millet fields, *S. hermonthica* did not emerge. Many authors (Kim and Winslow, 1991; Kim, 1991 and Efron, 1993) observed that maize plants often collapsed completely under *S. hermonthica* infestation, which affected *Striga* seed production. Since maize was introduced to the savanna zone not long ago, strains of *S. hermonthica* currently affecting maize evolved from sorghum, millet and intercrop sources (Kim *et al.*, 1994). Ramaiah (1984) reported the presence of intercrop and intracrop strains of *S. hermonthica*. The term 'intracrop specific' was used to describe strains that react differently to cultivars of a single host crop, whereas 'intercrop specific' are strains that react differently to various crops. To develop a breeding strategy for controlling *Striga*, it will be important to understand the range of variation of *S. hermonthica* strains that attack cereal crops (Kim *et al.*, 1994). Kim (1994) also suggested that a long-lasting way of combating *Striga* in Africa will be through breeding for tolerance or strain non-specific resistance (general resistance) based on polygenes and the use of cereal-legume rotations in which the legume acts as a trap crop.

2.9.1 Identification of *Striga* resistant germplasm

Initial attempts at selecting resistant sorghum varieties were made in South Africa (Saunders, 1933). A popular resistant sorghum variety 'Radar' was released but later, it failed to maintain its resistance to *Striga*. In India, Gadgil (1933) reported the existence of two

resistant sorghum varieties 'Bilichigan' and 'Boganhilo' which were later incorporated into four varieties CO-I, AS-60, N-1 and T-6 (Rao, 1985). Since 1970, The Institute for Agriculture Research (IAR), Samaru, Nigeria has developed sorghum varieties which exhibit resistance to *S. hermonthica*: L-187 (long season), RZI and YG-5760 (medium season) and BES (short season). Recently, two sorghum varieties SRN-39 and IS-9830, were found partially resistant to *S. hermonthica* and were released for use in Sudan (Anon, 1991). Williams (1959) reported that in selected sorghum lines and hybrid varieties, *Striga* resistance was related to 'low-stimulant' production. Sorghum variety SAR-1, which had the 'low-stimulant' type of resistance was released to farmers in India (Rao, 1985). Testing resistant sorghum varieties in field trials in Africa for resistance to both *S. asiatica* and *S. hermonthica* was encouraging. Results from Southern Africa showed that sorghum variety IS-7777 resistant to *S. asiatica* was also resistant to *S. hermonthica* (Obilana *et al.*, 1991). In millet, identification of resistant varieties was difficult, although 3/4HK showed some tolerance to *Striga* (Ramaiah, 1987).

Resistant cowpea varieties were selected in different countries including Burkina Faso (IITA, 1982, Aggarwal, 1991), Botswana and Southern Africa (Riches, 1987) and Nigeria (Emechebe *et al.*, 1991; Singh and Emechebe, 1990). The International Institute of Tropical Agriculture and the Semi Arid Food Grain Development (IITA/SAFGRAD) cowpea improvement program developed cowpea varieties such as SUVITA-2 and 58-57 that were resistant to *S. gesnerioides* in Burkina Faso and Mali but not in Niger and Nigeria (Aggarwal *et al.*, 1984, 1986). *S. gesnerioides*, like *S. hermonthica*, has different physiological strains that may alter the resistance of host plants from one location to another. Parker (1991) confirmed that the loss of resistance in cowpea was due to variation of virulence between different

populations of the parasite. Other cowpea varieties such as B-301 selected by Riches (1987) in Botswana, for its resistance to *Alectra vogelii* and IT82D-849 selected at IITA, have so far shown total resistance to all populations of *S. gesnerioides* (Parker, 1991). Resistance in cowpea is based on a single dominant gene which can be transferred to other cowpea varieties with other desirable characters (Aggarwal *et al.*, 1984; Singh and Emechebe, 1990). In maize, progress in breeding *Striga* resistant varieties is slow and no complete resistance has yet been identified. One of the possible reasons is that maize is a new crop in the savanna zone and it was not exposed to *Striga* in the course of its evolution. Over the past decade, scientists at IITA have successfully identified potentially valuable sources of *Striga* tolerance and resistance in some maize lines and hybrids, especially to *S. hermonthica*. A number of moderately resistant hybrid maize varieties such as 8322-13, 8321-18 and 9022-13 were identified at IITA. Inbred lines tolerant to *S. hermonthica* have also been developed: TZi11, TZi12, TZi25 and TZi30 (Kim and Akintunde, 1989). In maize, more effort has been devoted to the selection of inbred lines and hybrids rather than open-pollinated varieties. Considering that most small-scale farmers in Africa cannot afford to use hybrids, it is beneficial to improve screening and selection methods of open-pollinated and synthetic varieties for resistance or tolerance to *Striga*.

2.9.2 Mechanism of resistance/tolerance to *Striga*

Obilana (1984) earlier defined resistance as 'low total number of *Striga* per sorghum plant'. Later, in the context of field trials, Ramaiah (1987) defined resistance to *Striga* as the absence of emerged parasite plants or a very low number of infections compared to the

susceptible varieties. Partially resistant varieties would support few emerged parasites. A third term, tolerance to *Striga*, has been used to describe varieties which supported similar numbers of emerged parasites compared to those observed on the susceptible host, but which gave a significantly greater yield than susceptible varieties in *Striga* infested fields. Research on the mechanisms of resistance of sorghum to *S. asiatica* focused on 'low-stimulant' varieties (Ramaiah, 1987). However, a variety like N-13 stimulates germination of *S. asiatica* but supports fewer parasite stems than a susceptible variety (Lane and Bailey, 1992). This indicates that other mechanisms, probably not related to the 'low-stimulant' hypothesis, may be responsible for *Striga* resistance in crops. Maiti *et al.*(1984) reported that in sorghum, partially resistant varieties showed various changes in root cell anatomy which prevented or delayed penetration of the parasite. For instance, sorghum variety N-13 had thicker cell walls in the endodermis and pericycle than the susceptible variety and silica was also present in the endodermis cells (Maiti *et al.*, 1984). Another sorghum resistant variety IS-7777 accumulated cellulose-rich cell wall layers in the root cells in contact with invading parasite tissue (Olivier *et al.*, 1991b). These structural changes in the host root cell prevented parasite invasion. Sorghum resistant variety IS-5106 had similar root anatomy as susceptible varieties, confirming that other mechanisms may be responsible for host resistance (Maiti *et al.*, 1984). Olivier *et al.* (1991b) suggested that the changes in root cells of susceptible varieties occurred too slowly to stop penetration of host roots by *Striga*. Recently, after using an *in vitro* growth system, Lane and Bailey (1992) defined two mechanisms of *Striga* resistance in cowpea. The first resistance mechanism was observed on cowpea variety 58-57. This variety reacted to *Striga* penetration by the formation of necrotic cells surrounding the invading parasite radicles, a process

analogous to the response shown by plants invaded by fungi (Wood, 1982). A few days after inoculation, the parasite radicle turned black, indicating death. The second mechanism of resistance was more commonly observed on resistant variety B-301. After *Striga* seedlings penetrated the cortex and merged with cells of the host stele, tubercles developed on the host root surface but did not enlarge on the roots of B-301. This prevented any *Striga* stem development.

2.9.3 Selection of resistant germplasm

In sorghum, selection was based on the identification of 'low-stimulant' varieties. Among 20,000 lines screened at ICRISAT, about 4% 'low-stimulant' lines were identified as resistant to *Striga hermonthica* (Doggett, 1988).

In maize, selection for resistance and tolerance to *Striga* may also be based on 'low stimulant' production. At IITA, selection of *Striga* resistant varieties is essentially based on the use of parameters like *Striga* plant counts, host symptoms and yield loss (Kim and Akintunde 1989; Kim and Winslow 1991). However, some *Striga* seedlings attached to the host plant can fail to emerge above ground, but continue to compete for nutrients from the host as mentioned by Doggett (1984). Thus, the total number of the parasites which damage the host crop may be difficult to estimate from the number of green *Striga* plants above ground. In addition, *Striga* count is not highly correlated with tolerance (Kim *et al.*, 1985). Emechebe *et al.* (1991) also reported that the number of emerged *Striga* plants was not related to host plant resistance. For instance, severely affected host plants supported either no *Striga* above the soil level or numerous *Striga* plants. Besides, there are difficulties in counting the total number of *Striga*

above ground and the number attached to the maize host roots. Thus, a simple and reliable host *Striga* syndrome rating scale (1-9) developed at IITA (Kim and Winslow 1991), is used to assess the response of maize plants infected by *Striga*. The rating scale is based on the overall plant reaction to *Striga* (leaf scorching, plant height, ear and tassel development and stalk lodging): 1 corresponds to a highly tolerant host plant (very low *Striga* syndrome symptoms), whereas 9 corresponds to highly susceptible host plant (very high *Striga* syndrome symptoms). Any plant scoring below 5 is considered to be tolerant to the particular *Striga* species used in the screening experiment. Early infestation may cause severe reduction in plant height and complete yield loss. On the contrary, late infestation reduces plant height and yields to a lesser degree (Kim, 1991).

Recently, several scientists reported that resistance to *Striga* was not related to a 'low-stimulant' process which reduces parasite germination but rather, to the formation of structural barriers in the host root cells which prevent *Striga* attachment. Additional research is needed to understand host resistance mechanisms and to develop resistant crop varieties with certainty.

2.9.4 Genetic studies of resistance to *Striga*

Saunders (1933) earlier reported that resistance to *S. asiatica* was recessive in two sorghum crosses and partially dominant in a third genotype. Later, Kulkarni and Shinde (1985) confirmed that `field tolerance' to the same species, *S. asiatica*, was governed by non-additive gene action. Obilana (1984) suggested that gene action in *Striga* resistant sorghum was non-additive with overdominance of susceptibility, estimating that two to five genes control the resistance action. Ramaiah *et al.* (1990) and Ejeta *et al.* (1991) reported that a single recessive

gene was responsible for 'low-stimulant' production in three sorghum genotypes. After conducting a pot experiment using a known volume of *S. hermonthica*, Ejeta *et al.* (1991) reported that in the sorghum cultivar, SRN-39, resistance was inherited as a recessive trait controlled by one or two genes. Singh and Emechebe (1990) and Aggarwal (1991) indicated that resistance of cowpea variety B301 to the Burkina Faso race of parasite is controlled by a single dominant gene. Studies on the inheritance of resistance to *S. gesneriodes* in cowpea varieties Suvita-2 and 58-57 showed that resistance was controlled by single dominant genes (Aggarwal *et al.*, 1984; Aggarwal, 1991). Studies reported recently by Kim (1994) revealed that genetic control for tolerance and resistance to *S. hermonthica* in maize genotypes is polygenic and the inheritance is quantitative. Kim (1994) also pointed out that additive genes have a major role in controlling tolerance whereas non-additive genes have a major role in emergence. Information on the mode of inheritance of *Striga* resistance will help in identifying reliable screening methods for *Striga* resistance and appropriate breeding strategies.

CHAPTER THREE

MATERIAL AND METHODS

3.1 Experimental plant Material

The maize population of interest in this study is TZL Composite-1 c1 (TZLComp-1 c1), a broad-based population which is well adapted to different lowland savanna agroecologies. TZL Composite-1 c1 was developed from TZB-SR (Streak resistant population)and STR (*Striga* resistant) inbreds. TZLComp-1 c0 was formed by crossing TZB-SR to seven *Striga* resistant lines in 1988. The resistant lines used were as follow:

* 1188 (TZi 1)
* 5012 (TZi 9)
* 9030 (TZi 12)
* 9032 (TZi 13)
* 9091 (TZi 17)
* 9432 (TZi 24)
* 9848 (TZi 30)

This was followed by selection for agronomic traits and several recombination were done to generate TZLComp-1 c1. Hybrid maize varieties 9022-13 and 8338-1 were used as checks. Hybrid 9022-13 is resistant to *Striga* while 8338-1 is susceptible to *Striga*. Maize population TZLComp1-c1 and both hybrid checks 8338-1 and 9022-13 were all developed at IITA.

3.2 Experimental Design and Field Layout

3.2.1 1993 Experimental Design and Field Layout

In 1993, a bulk of maize population TZLComp-1 C1 was planted at IITA Ibadan and North Carolina design 1 crosses (also called nested design or hierarchical design) were

made by following Comstock and Robinson (1952) methodology. Eighty random plants designated as male or staminate parents were each crossed with four other random plants designated as female or pistillate parents. Each male plant was crossed with a different set of female plants. Seeds for plants used as males were planted 4 days after planting the female parents. Every plant used as a male parent was selfed. A set of four ears were produced (One ear for every female plant) for every male parent. One ear is equivalent to one full-sib family. As previously described by Hallauer and Miranda (1988), the genetic structure of the progenies obtained from design 1 crosses included full-sibs that have both parents in common and half-sibs that have a male parent in common. The matings were as follow:

Population TZLComp-1 c1

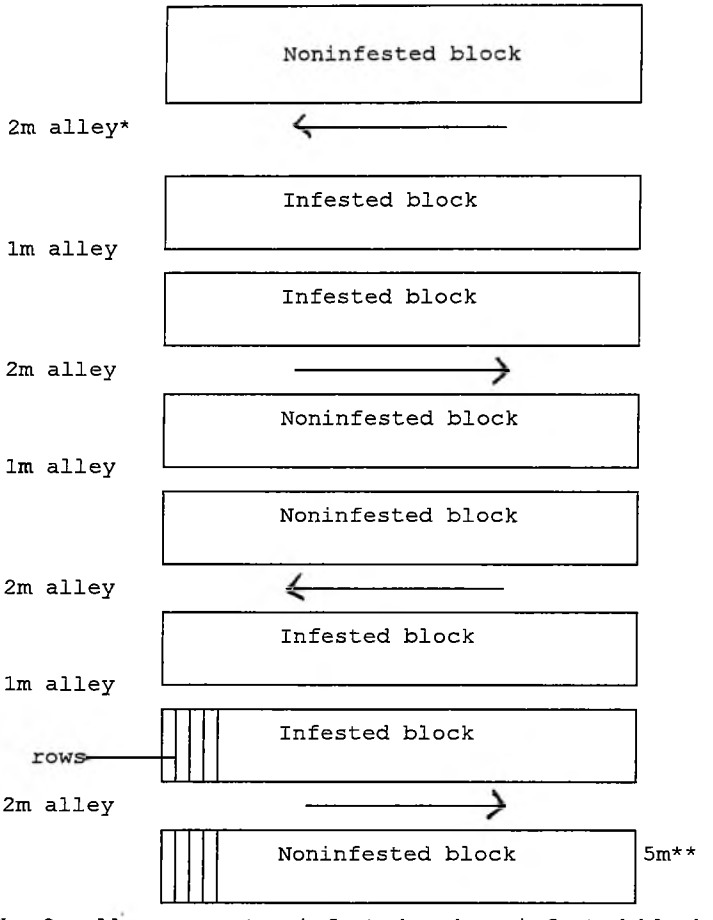
Randomly chosen Male parents		Randomly chosen Female parents
m_1	*	$f_1 = p_{11}$
		$f_2 = p_{12}$
		$f_3 = p_{13}$
		$f_4 = p_{14}$
m_2	*	$f_5 = p_{25}$
		$f_6 = p_{26}$
		$f_7 = p_{27}$
		$f_8 = p_{28}$
.		
.		
m_{80}	*	$f_{317} = p_{80\,317}$
	*	$f_{318} = p_{80\,318}$

* $f_{319} = p_{80\ 319}$
* $f_{320} = p_{80\ 320}$

Individual progenies p_{11}, p_{12} to $p_{80\ 320}$ are full-sib families (320 full-sib families were generated). However, progenies p_{11}, p_{12}, p_{13} and p_{14} collectively constitute a half-sib family because they have in common the male parent, m_1 in this case. Eighty male parents were used which resulted in formation of 80 groups of half-sib families.

From the different crosses, 320 full-sib progenies consisting of 80 groups of half-sib progenies were obtained within population TZLComp-1 c1. Those 320 full-sib families were divided into 20 sets of 4 male groups each. Each such set contained 16 full-sib families and also 2 hybrid checks (9022-13 and 8338-1) making up a total of 18 entries which were assigned to a block. A randomization of the 18 entries was made within each of two replications. Each plot consisted of two rows of 22 plants. One row of each plot was artificially infested with *S. hermonthica* while the other row remained noninfested. The 2 rows of a plot were arranged to face each other, the infested row on one side and the noninfested row on the opposite side of an alley within the same plot (Figure 1). The rows were 5m long and 0.75m apart. Plants were spaced 50 cm within rows. Three kernels per hill were planted and the stand was thinned to 2 plants per hill. Infested and non-infested blocks were separated by a 2m alley to avoid contamination.

Figure 1. Field layout used at IITA for screening open pollinated maize varieties under *Striga hermonthica* artificial infestation



* The 2m alley separates infested and noninfested blocks and the 1m alley separates infested blocks or noninfested blocks.

** Each block is 5m wide.

→ The arrow are followed for planting and for data collection.

3.2.2 1994 Experimental Design and Field Layout

In this study, several variables were measured (Table 1). Selections were based on the 1993 results of the combined statistical analysis of both locations (Abuja and Mokwa). Seven traits which were found to show significant genetic variation were subjected to divergent selection with a selection intensity of 5%. Selection was based on deviations from the means for families in each set. Thus, 16 promising families (5% of 320 families screened) and 16 poor families were selected for seven useful characters (Table 1): *Striga* emergence count 1, *Striga* symdrome rating 1, ear *Striga* rating, yield for infested plants, yield for noninfested plants, anthesis-silking interval for infested plants and delay in silking. The 16 best families and also the 16 poorest performing families selected for each trait were grouped and named according to the characters under study (Table 2).

For each of the seven characters studied, remnant seeds of the outstanding families were planted in blocks during the dry season. All of the 16 families selected for one trait were planted in the same block. Remnant seeds of poor families were also sowed in different blocks. Crosses were done between plants of different families within the same block. At harvest, seeds of selected families were bulked in each block. Thus, 14 groups of bulk seeds were formed. These were evaluated in 1994 by using a randomized complete block design with 6 replications. Two samples of the original population TZLComp-1 c1 and two hybrids, one resistant to *Striga* (9022-13) and one susceptible to *Striga* (8338-1) were used as checks. The field layout was similar to that used for the Design 1 experiment in 1993. The 18 entries were tested in 2 opposite areas of a field separated by 2 m (Figure 1). One area was infested with *S. hermonthica* while the opposite area was not infested. Plots consisted of two rows 5 m in length (one infested and one non infested), with 75 cm between rows. Plants were spaced 50 cm within rows. Infested and noninfested blocks were separated by a 2 m alley to avoid *Striga* contamination.

Table 1. Description of all variables measured

Variables	Description
VARIABLES MEASURED DIRECTLY	
Plant stand Count (inf. and noninf.)	Number of plants per row after thinning.
Mid-anthesis (inf. and noninf.)	Number of days from planting to the day when 50% of the plants have begun to shed pollen.
Mid-silking (inf. and noninf.)	Number of days from planting to the day when 50% of the plants have silks emerged.
Striga count	Number of *Striga* plants emerged per row at (inf.) 8 and 10 weeks after planting,including living and dead plants. *Striga* count 1: *Striga* plants emerged 8 weeks after planting. *Striga* count 2: *Striga* plants emerged 10 weeks after planting.
Striga plant rating (inf.)	Host plant reaction to *Striga* infestation which is rated on a scale of 1 (highly resistant) to 9 (highly susceptible). The overall rating of a row is an approximate average of the plants in the row. *Striga* plant rating 1: Host plant rating 8 weeks after planting. *Striga* plant rating 2: Host plant rating 10 weeks after planting.
Plant height	Measured in cm from the base of the plant (inf. and noninf.) to the base of the tassel (place where tassel begins branching). A representative plant(typical or approximately average for the plot as a whole) was measured. Plant height is measured 2-3 weeks after flowering.

Table 1. (continued)

Variables	Description
VARIABLES MEASURED DIRECTLY	
Ear height (inf. and noninf.)	Distance in cm from the base of the plant to the node which bears the top ear. Ear height is measured at 2-3 weeks after flowering. The same plant was used for plant height and ear height.
Plant aspect (noninf.)	Score for the general appearance of the plants in the row considering factors such as relative plant and ear heights, uniformity, reaction to disease and insects and lodging. A 1 to 5 scale is used: 1 = excellent and 5 = poor plant aspect.
Husk cover rating (noninf.)	Measured when the ears are fully developed and husk leaves are drying (1-3 weeks before harvest). Five to 10 plants are scored in the row and approximate average is taken. A 1 to 5 scale is used: 1 = excellent (husk extension is greater than the width of four fingers) and 5 = very poor husk cover (the tips of the cobs are exposed)
Stalk lodging (inf. and noninf.)	Indicates the number of plants in a row that are broken or severely bent (more than 45 degrees from the upright position) below the ear. It is taken at about one week before harvest.
Root lodging (inf. and noninf.)	Indicates the number of plants in a row that are leaning more than 45 degree (starting from the root base) from the upright position. It is taken at about one week before harvest.

Table 1. (continued)

Variables	Description
VARIABLES MEASURED DIRECTLY	
Plants at harvest (inf. and noninf.)	Total number of plants in the row at harvest time including barren plants and plants with ears.
Ear number (inf. and noninf.)	Total number of ears at harvest which bear kernels. It includes small second ears and top ears.
Striga ear rating (inf.)	Rating of 1 to 9 is used to indicate the level of damage to the ears caused by *Striga* (1= no damage 9= extensive damage). Ratings were taken by comparing ears of infested plants to the noninfested plants. Factors like size of cobs, grain fill and anticipated yield reduction were considered.
Ear aspect (noninf.)	Score (1 to 5) of the general appearance of all ears in a row. Fators considered are ear size, grain fill, disease and insect damage, uniformity of size, color and grain texture. Scale of 1= best ear aspect to 5= poorest ear aspect.
Ear rot (noninf.)	A 1 to 5 score is used to assess the proportion of the ears showing rot. The number of rotten ears and the degree of ear rot were considered.
Field weight (inf. and noninf.)	Weight in kg (to the nearest tenth of a kg) of all dehusked ears in a row.
% Moisture (inf. and noninf.)	Grain moisture content taken by a moisture tester (Dickey John) at harvest. Grains were sampled from the central part of a minimum of 5 representative ears. If the older model of Dickey John tester is used, a conversion of data is necessary to get the percentage moisture for maize. The newer models can be read directly to get the moisture for maize.

Table 1. (continued)

Variables	Description
DERIVED VARIABLES	
Anthesis-silking	Difference between the number of days interval to 50% anthesis and the number of days to midsilk.
% Height reduction	The difference between plant height of noninfested plants and plant height of infested plants divided by the plant height of noninfested plants. The result is multiplied by 100.
% Yield reduction	The difference between yield of noninfested plants and the yield of infested plants divided by the yield of noninfested plants. The result is multiplied by 100.
Delay silking	Difference between the days to midsilk of infested plants and day to midsilk of noninfested plants.
Ear harvest	Difference between the number of ears for reduction noninfested plants and the number of ears for infested plants.

Table 2. Divergent selection for seven *Striga* resistance characters in population TZL Composite-1 C1

Characters under study	Selection for promising families	Selection for poor performing families
Striga count 1	Low count	High count
Striga rating 1	Low rating	High rating
Ear *Striga* rating	Low rating	High rating
Yield infested plants	High yield	Low yield
Yield noninfested plants	High yield	Low yield
Anthesis-silking interval	Short interval	Long interval
Delay in silking	Short interval	Long interval

3.3 *Striga* infestation and Field Management

3.3.1 Field preparation and management

A good seedbed is needed to have a uniform *Striga* infestation. Screening for *Striga* resistance in population TZLcomp1-c1 began in 1993 on artificially infested fields at Abuja and Mokwa (Northern part of Nigeria). In both locations, maize was planted on ridges. Ridges provide a moist and well aerated seedbed and also reduce waterlogging. Fertilizer N.P.K (15:15:15) was applied to each row at a rate of 60 kg/ha. The low nitrogen rate which was half of the recommended rate for maize in Northern Nigerian soils was used to ensure maximum development of *S. hermonthica*. Half of the Nitrogen fertilizer (30 kg/ha) was applied at planting and the other half was top-dressed 4 to 5 weeks later. The experiment was kept free of weeds other than *S. hermonthica*.

3.3.2 *Striga* infestation with sand/*Striga* mixtures

Striga seeds are very small (200 to 400 µm, Doggett, 1970) and so, to achieve an effective infestation, *Striga* seeds were mixed with sieved sand (a 180 micron sieve was used to sieve the sand). The sieved sand was used as a carrier material to provide adequate volume for rapid and consistent infestation. The amount of sand and *Striga* seeds needed for artificial infestation was calculated by following the method outlined by IITA Berner *et al.*, 1993).

Prior to *Striga* infestation and planting of maize seeds, ethylene gas was used to stimulate suicidal germination of existing *Striga* seeds in the soil in non-infested areas. A scoop with a volume of approximately 5 ml was used for infestation. Holes of 10 cm in diameter and 8 cm in depth were dug out on the ridges. Infestation was then done by spreading the content of a scoop filled with *Striga* seed mixed with sieved sand in each of the holes of the infested rows. About 3,000 germinable *S. hermonthica* seeds were thus sowed in each hole. *Striga* seeds were then lightly covered with surrounding soil. Maize

seeds were planted the same day, both in the noninfested hills and infested hills above the *Striga* seeds.

3.4 Data collection

Data were collected on infested and noninfested rows for the parameters listed in Table 1. Data on the number of *Striga* plants emerged and *Striga* syndrome on host plants were taken on the entire infested row. Plant aspect was taken on host plants in noninfested rows only. Number of ears was counted from each infested and noninfested row. Moisture was measured on infested and noninfested rows. Estimates of moisture were determined on samples of grains shelled from the middle areas of at least 5 ears from each row. Moisture was measured with a moisture meter (Dicky-John Corp., U.S.A).

Yield of infested and noninfested rows was computerized in kg/ha by using the formula:

$$\text{Yield} = \text{Field weight} * (100 - \text{moisture}) * 22.82$$

where the field weight is the weight in kg of the total number of ears per row. The moisture used in computing the yield are the corrected values.

The *Striga* syndrome rating (1 = no symptoms, 9 = severe symptoms) used to measure tolerance of maize to *Striga* was based on several indicators listed in Appendix 1. This scale was designed at IITA by Kim *et al.*(1988).

3.5 Statistical Analysis

3.5.1 Analysis of variance

From data collected in 1993, the mean values for each plot were used to compute an analysis of variance (ANOVA) for each character for each location, Mokwa and Abuja, and also for both locations combined. The formats (Tables 3 and 4) used for the pooled analysis over sets in one location and for the combined analysis of variance for both

TABLE 3. General format of the analysis of variance of Design 1 experiment pooled across sets for one location (Abuja or Mokwa)

Source of Variation	DF	MS	EMS
Set	s-1		
Rep(Set)	s(r-1)		
Male(Set)	s(m-1)	M_1	$\sigma^2+r\sigma^2_f+rf+\sigma^2_m$
Female(MalexSet)	sm(f-1)	M_2	$\sigma^2+r\sigma^2_f$
Error	s(mf-1)(r-1)	M_3	$\sigma^2_e = \sigma^2$
Total	srmf-1		

s = number of sets = 20; r = replications per set = 2; m = male groups per set = 4; f = females mated to same male = 4; σ^2 = random plot to plot variation; σ^2_m = variance due to genetic differences among males; σ^2_f = variance due to genetic differences among females mated to the same male.

TABLE 4. General format of the combined analysis of variance of Design 1 experiment pooled across sets for two locations (Abuja and Mokwa)

Source of Variation	DF	MS	EMS
locations	l-1		
Set	s-1		
SetxLoc	(s-1)(l-1)		
Rep(SetxLoc)	sl(r-1)		
Male(Set)	s(m-1)	M_1	$\sigma^2+r\sigma^2_{fl}+rf\sigma^2_{ml}+rl\sigma^2_f+rlf\sigma^2_m$
Fem.(SetxMale)	sm(f-1)	M_2	$\sigma^2+r\sigma^2_{fl}+rl\sigma^2_f$
MalexLoc(Set)	s(m-1)(l-1)	M_3	$\sigma^2+r\sigma^2_{fl}+rf\sigma^2_{ml}$
Fem.xLoc(SetxMale)	sm(f-1)(l-1)	M_4	$\sigma^2+r\sigma^2_{fl}$
Error	ls(r-1)(mf-1)	M_5	$\sigma^2_e = \sigma^2$
Total	lsrmf-1		

l = locations = 2; s = number of sets = 20; r = replications per set = 2; m = male groups per set = 4; f = females mated to same male =4; σ^2 = random plot to plot variation; σ^2_m= variance due to genetic differences among males; σ^2_f = variance due to genetic differences among females mated to the same male; σ^2_{ml} = variance due to interaction of male genotypes with locations; σ^2_{fl}= variance due to interaction of female genotypes with locations.

locations followed the methods of Hallauer and Miranda, (1988). Because the mating design was nested, expected mean squares were obtained as for a hierarchical type of design. F-tests were made for males and females-within-male mean squares.

From data collected in 1994, the analysis of variance was done for each variable studied (Table 1). Analysis was done separately for each location Mokwa and Abuja, and also for the combined data from both locations. The general format of the analysis of variance is given in Table 5. F tests were made to compare the genotypes tested. Mean separation with the least significant difference (LSD) test was performed for any trait for which the F test showed significant differences among genotypes.

3.5.2 Estimates of the components of variance

By using the appropriate mean squares obtained from the analysis of variance in 1993, an estimate of the variance among males (σ^2_m), and variance among females mated to the same male (σ^2_f), were computed according to Comstock and Robinson (1948) formula by using the ANOVA general format in Table 3.

For a single location (Abuja or Mokwa):

$$\sigma^2_m = (M_1 - M_2)/rf \quad \text{and} \quad \sigma^2_f = (M_2 - M_3)/r$$

σ^2_m, σ^2_f and also the male by location interaction variance (σ^2_{ml}) and the female by location interaction variance (σ^2_{fl}) for the combined analysis of both locations (Abuja and Mokwa) were estimated from formulas given by Lindsey *et al.* (1962). The estimates were obtained from Table 4 as follows:

For the combined location analysis:

$$\sigma^2_m = (M_1 - M_2 - M_3 + M_4)/rlf$$

$$\sigma^2_f = (M_2 - M_4)/rl$$

$$\sigma^2_{ml} = (M_3 - M_4)/rf$$

$$\sigma^2_{fl} = (M_4 - M_5)/r$$

TABLE 5. General format of the analysis of variance for data collected from one location (Abuja or Mokwa) and both location combined in 1994 (fixed genotypes and random location)

Source of Variation	DF	MS	EMS
	Analysis for one location		
Replications	r-1		
Genotypes	g-1	M_1	$\sigma^2_e+r\sigma^2_{fg}$
Error	(r-1)(g-1)	M_2	σ^2_e
	Analysis for 2 locations		
Locations	l-1		
Rep(locations)	l(r-1)		
Genotypes	g-1	M_1	$\sigma^2_e+r\sigma^2_{lfg}+lr\sigma^2_{fg}$
Geno. x Location	(g-1)(l-1)	M_2	$\sigma^2_e+r\sigma^2_{lfg}$
Error	l(r-1)(g-1)	M_3	σ^2_e

r = number of replications = 6; g = number of genotypes = 18; l = number of locations = 2; f = fixed; σ^2_e= random plot to plot variation ; σ^2_g = variance due to genetic differences; σ^2_{lg} = variance due to genetic * location interaction.

where M_1, M_2, M_3 and M_4 are the mean squares from the analysis of variance (Table 3 and 4),

r = replication per block = 2,

l = number of locations = 2,

f = number of females mated to the same male = 4.

Under assumptions of a random mating population in linkage equilibrium with no inbreeding and epistasis (Comstock and Robinson, 1948), the estimate of variance due to male effects (σ^2_m) and the variance due to female effects (σ^2_f) were:

$$\sigma^2_m = [(1/4)\,\sigma^2_a]$$

and $$\sigma^2_f = [(1/4)\,\sigma^2_a] + [(1/4)\,\sigma^2_d].$$

Also, additive variances (σ^2_a) and dominance variances (σ^2_d) estimated from a nested mating design for intrapopulation crosses were:

$$\sigma^2_a = 4\sigma^2_m \quad \text{and} \quad \sigma^2_d = 4(\sigma^2_f - \sigma^2_m).$$

The genetic variance was estimated as follow for one location and both locations combined based on selection of full-sib families:

$$\sigma^2_g = [(1/2)\,\sigma^2_a] + [(1/4)\,\sigma^2_d].$$

The phenotypic variance was also estimated on the basis of the selection of full-sib families:

For one location (Abuja or Mokwa):

$$\sigma^2_p = [(1/2)\,\sigma^2_a] + [(1/4)\,\sigma^2_d] + [\sigma^2_e/r].$$

For both locations combined:

$$\sigma^2_p = [(1/2)\,\sigma^2_a] + [(1/4)\,\sigma^2_d] + [((1/2)\,\sigma^2_{al}) + ((1/4)\,\sigma^2_{dl})]/l + [\sigma^2_e/rl]$$

where σ^2_a, σ^2_d are the additive and dominance variance respectively and σ^2_{al}, σ^2_{dl} are the additive by location interaction variance and dominance by location interaction variance respectively.

The variances σ^2_{al} and σ^2_{dl} were estimated from Table 4:

$$\sigma^2_{al} = 4\sigma^2_m = [4(M_3-M_4)]/rf$$

$$\sigma^2_{dl} = 4(\sigma^2_f-\sigma^2_m) = 4\{[(M_4-M_5)/r]-[(M_3-M_4)/rf]\}$$

The environmental variance was taken from the ANOVA Table (3 and 4):

σ^2_e = M_3 for one location,

σ^2_e = M_5 for both locations combined.

3.5.3 Estimate of standard errors of components of variance

The general formula given by Anderson *et al.*(1952) was used to estimate the variance of the components of variance for data analyzed in 1993.

$$\hat{Var}(\sigma^2) = \frac{2}{k^2} \sum_i \frac{MS^2_i}{f_i+2}$$

Where k = Coefficient of the variance component being estimated,

MS^2_i = The i^{th} mean sguare used to estimate the variance component and

f_i = The degrees of freedom for the i^{th} mean square.

The standard error (S.E.) was obtained by taking the square root of the estimate of the variance.

$$S.E(\sigma^2) = \sqrt{Var(\sigma^2)}$$

By using the general formula given by Anderson *et al.*, (1952) standard errors of the additive genetic variance and dominance variance were estimated for one location (Abuja or Mokwa) and also for both location combined as follow:

For one location:

$$\hat{Var}(\sigma^2_a) = [(16*2)/r^2f^2] * \{[M_1^2/s(m-1)+2]+[M_2^2/sm(f-1)+2]\}$$

$$S.E(\sigma^2_a) = \sqrt{Var(\sigma^2_a)}$$

$$\widehat{Var}(\sigma^2 d) = (16*2/r^2)*\{M_2^2/[sm(f-1)+2]\}+\{M_3^2/[s(mf-1)(r-1)+2)]\}$$
$$+ (16*2/r^2f^2) * \{M_1^2/[s(m-1)+2]\}+\{M_2^2/[sm(f-1)+2]\}$$

$$S.E\ (\sigma^2_d) = \sqrt{Var}(\sigma^2_d).$$

For 2 locations combined:

$$\widehat{Var}\ (\sigma^2_a) = (16*2/r^2l^2f^2)\{M_1^2/[s(m-1)+2] + M_2^2/[sm(f-1)+2]+$$
$$M_3^2/[s(m-1)(l-1)+2]+ M_4^2/[sm(f-1)(l-1)+2]\}$$

$$S.E\ (\sigma^2_a) = \sqrt{Var}(\sigma^2_a)$$

$$\widehat{Var}\ (\sigma^2_d) = 16*2/(rl)^2\ \{M_2^2/[sm(f-1)+2]+M_4^2/[sm(f-1)(l-1)+2]\}$$
$$+ 16*2/r^2l^2f^2\{M_1^2/[s(m-1)+2]+M_2^2/[sm(f-1)+2]$$
$$+ M_3^2/[s(m-1)(l-1)+2] +M_4^2/[sm(f-1)(l-1)+2]\}$$

$$S.E\ (\sigma^2_d) = \sqrt{Var}(\sigma^2_d)$$

Where l, r, s, m and f referred to the number of locations, replications within sets, sets, males and females within males respectively.

3.5.4 Estimates of heritability

The heritability of a metric character is one of its most important properties. It expresses the reliability of the phenotypic value as a guide to the breeding value (Falconer, 1981). Heritability was defined by Lush (1945) and Robinson (1949) as the fraction of total variance within a segregating population attributable to additive genetic effects.

The components of variance can be used to estimate heritability on a single plant, a plot, or on an entry-mean basis. Heritability in a broad sense (h^2_b) is the ratio of total genetic variance to phenotypic variance (Hanson, 1963). Broad-sense heritability is the ratio of the total genotypic variance (which include additive variance, dominance and epistatic variance) to the phenotypic variance (Fehr, 1987).

$$\text{Thus, } h^2_b = \sigma^2_g/\sigma^2_p$$

Where σ^2_g is the genotypic variance and σ^2_p is the phenotypic variance.

Heritability in a narrow sense (h^2_n) is the ratio of the additive genetic variance to phenotypic variance. The Design 1 experiment allows one to estimate the additive genetic variance in a population (Dudley and Moll, 1969).

$$h^2_n = \sigma^2_a/\sigma^2_p$$

Where σ^2_g is the additive genetic variance and σ^2_p is the phenotypic variance.

The narrow-sense heritability measures the relative importance of the additive portion of the genetic variance that can be transmitted to the next generation of offspring (Fehr, 1987). This is important when heritability is used to predict the gain expected from selection for a character.

Heritability can be estimated by using one or two-factor mating designs (Cockerham, 1963). The most commonly used two-factor mating designs are Design 1, 2 and 3 (Comstock and Robinson, 1948).

For 1993, heritabilities of characters were estimated from a Design 1 experiment. Narrow-sense heritability (h^2_n) estimates were obtained by using the variance components derived from the analysis of variance. The estimates of narrow-sense heritability were based on the selection of full-sib families (Hanson, 1963).

The general formula is :

$$h^2 = \{[(1/2)(1+F)]\sigma^2_a\}/\ \sigma^2_p$$

Where F = the inbreeding coefficient of the full-sib families tested = 0.

For one location:

$$h^2 = [(1/2)\sigma^2_a]/\{[(1/2)\sigma^2_a]+[(1/4)\sigma^2_d]+(\sigma^2_e/r)\}$$

where $(1/2)\sigma^2_a = (1/2)(4*\sigma^2_m) = 2\sigma^2_m$ and

$$(1/2)\sigma^2_a+(1/4)\sigma^2_d+\sigma^2_e/r = [(1/2)(4\sigma^2_m)] + [(1/4)(4*\sigma^2_f-4\sigma^2_m)]+\sigma^2_e/r$$

$$= \sigma^2_m + \sigma^2_f + \sigma^2_e/r.$$

For the combined analysis of 2 locations:

$$h^2 = [(1/2)\sigma^2_a]/[(1/2)\sigma^2_a]+[(1/4)\sigma^2_d]+[(1/2)\sigma^2_{al}] + [(1/4)\sigma^2_{dl}/l]+[\sigma^2_e/rl]$$

where $(1/2)\sigma^2_a = (1/2)(4\sigma^2_m) = 2\sigma^2_m$

$$(1/2)\sigma^2_a + (1/4)\sigma^2_d = [(1/2)(4\sigma^2_m)]+[(1/4)(4\sigma^2_f-4\sigma^2_m)] = \sigma^2_m + \sigma^2_f \text{ and}$$

$$(1/2)\sigma^2_{al} + (1/4)\sigma^2_{dl} = [(1/2)(4\sigma^2_{ml})]+[(1/4)(4\sigma^2_{fl}-4\sigma^2_{ml})] = \sigma^2_{ml} + \sigma^2_{fl}.$$

Estimates of narrow-sense heritability (h^2_n) of each character for each location (Abuja or Mokwa).

$$h^2_n = (2\sigma^2_m)/[\sigma^2_m + \sigma^2_f + (\sigma^2_e)/r]$$

Estimates of narrow sense heritability (h^2n) based on the combined data analysis of both locations (Abuja and Mokwa) was:

$$h^2_n = (2\sigma^2_m)/[\sigma^2_m + \sigma^2_f + \sigma^2_{ml} + (\sigma^2_{fl})/l + \sigma^2/(rl)]$$

Where: σ^2_m and σ^2_f are the male and female variances respectively,

σ^2 = estimate of pooled error variability,

l = number of locations,

r = number of replication,

σ^2_{ml} and σ^2_{fl} are the variances due location by male and location by female interactions respectively.

$\sigma^2_{ml} = (M_3-M_4)/rf$ and $\sigma^2_{fl} = (M_4-M_5)/2$

Broad-sense heritabilities (h^2_b) were also estimated based on the selection of full-sib families for one location (Abuja or Mokwa) and for both locations combined (Hanson, 1963):

$$h^2_b = \sigma^2_g/\sigma^2_p$$

In this study broad-sense heritabilities were estimated on the basis of full-sib family selection.

The phenotypic variance (σ^2_p) was estimated for one location as follow:

$$\sigma^2_p = \sigma^2_g + \sigma^2_e/r$$

where the genotypic variance (σ^2_g) was:

$$\sigma^2_g = (1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d \text{ , then}$$

$$\sigma^2_p = (1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d) + \sigma^2_e/r = 4\sigma^2_f$$

For one location:

$$h^2_b = [(1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d] \;/\; [(1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d + (\sigma^2_e)/rl]$$

The phenotypic variance (σ^2_p) estimated for both locations combined:

$$\sigma^2_p = \sigma^2_g + \sigma^2_{gl}/l + \sigma^2_e/rl$$

$$\sigma^2_g = (1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d$$

$$\sigma^2_{gl} = (1/2)\,\sigma^2_{al} + [(1/4)\,\sigma^2_{dl}]/l$$

Then $\sigma^2_p = (1/2)\,\sigma^2_a + (1/4)\,\sigma^2_{dl} + (1/2)\,\sigma^2_{al} + [(1/4)\,\sigma^2_{dl}]/l + (\sigma^2_e)/rl$

For the combined analysis of two locations:

$$h^2_b = [(1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d] / \{(1/2)\,\sigma^2_a + (1/4)\,\sigma^2_d + (1/2)\,\sigma^2_{al} + [(1/4)\,\sigma^2_{dl})/l] + \sigma^2_e/rl\}$$

Where σ^2_a, σ^2_{al} and σ^2_e are the additive genetic variance, the genotype by location interaction variance and the environmental variance respectively,

r = number of replications

l = number of locations.

$$\sigma^2_{al} = 4\sigma^2_m = 4\,(M_3 - M_4)/rf$$

$$\sigma^2_{dl} = 4\,(\sigma^2_f - \sigma^2_m) = 4\,[(M_4 - M_5)/r] - [(M_3 - M_4)/rf]$$

3.5.5 Estimate of standard error of heritability

For the Design 1 experiment the formula used in estimating the standard errors of the estimate of the narrow sense heritability for one location and for the combined analysis of both locations (Abuja and Mokwa), were computed by an approximate procedure outlined by Hanson (1989).

$\hat{Var}(h^2) = (1/\sigma^2_x)^2 [\hat{Var}(\sigma^2_g) + \hat{Var}(\sigma^2_x)((h^2)^2 - 2h^2)]$.

The standard error (S.E) of the narrow-sense heritability (h^2_n) is the square root of:

$\hat{Var}(h^2_n) = (1/\sigma^2_x)^2 [\hat{Var}(\sigma^2_a) + \hat{Var}(\sigma^2_x)((h^2_n)^2 - 2h^2_n)]$

Where $\hat{Var}(h^2_n)$ is the estimate of the variance of the heritability,

h^2_n = narrow-sense heritability,

σ^2_x = phenotypic variance among family means,

$\hat{Var}(\sigma^2_a)$ = estimate of the variance of the additive variance and

$\hat{Var}(\sigma^2_x)$ = estimate of the variance of the phenotypic variance.

3.5.6 Estimates of the predicted response to selection (R) for the combined analysis.

Predicted response to selection was measured in 1993 for each of the seven studied traits across locations (Abuja and Mokwa). The formula used was derived from Hanson (1989):

The predicted response to selection (R) is the product of the selection differential $i\sigma_p$ (S) and the narrow-sense heritability estimate of full-sib families (H) (Hanson, 1963). The selection differential (S) is the product of the selection intensity (i) and the phenotypic standard deviation (σ_p). Thus, $R = (i\sigma_p)(h^2_n)$

$= (i\sigma_p)[(1/2)\ \sigma^2_a]/\sigma^2_p$

$= (i)[(1/2)\ \sigma^2_a]/\sqrt{\sigma^2_p}$

The selection intensity (i) depends on the selected fraction of a population. In this study, 5% of the population was selected. Tabulated values of selection intensity are available (Falconer, 1981). At 5% selection, i = 2.063.

h^2_n = narrow-sense heritability,

σ^2_a = additive variance,

σ^2_p = phenotypic variance,

σ_p = phenotypic standard deviation.

The standard error of the predicted response to selection (R) was computed by an approximate procedure outlined by Hanson (1989):

The standard error (S.E) of R is the square root of:

$$\hat{Var}(R) = i(1/\sigma^2_x)^2[\hat{Var}(\sigma^2_a) + \hat{Var}(\sigma^2_x)((h^2_n)^2/4) - h^2_n/^2)]$$

where $\hat{Var}(R)$ is the estimate of the variance of the predicted response to selection,

σ^2_x = phenotypic variance among family means,

$\hat{Var}(\sigma^2_a)$ = estimate of the variance of the additive variance,

$\hat{Var}(\sigma^2_x)$ = estimate of the variance of the phenotypic variance and

h^2_n = narrow-sense heritability.

3.5.7 Estimates of Realized heritability for the combined data from the two locations (Abuja and Mokwa).

The realized heritability is the heritability of a character that estimates the amount of genetic improvement realized by selection within a population (Falconer, 1981).

$$h^2_r = R/S$$

Where R is the response realized by selection, and S is the selection differential.

In the case of divergent selection as in this study, estimates of h^2_r were obtained from selection for high and low values of each character. Thus, the realized heritability was estimated as follow:

$$h^2_r = (X_{hRF} - X_{lRF})/(X_{hFS} - X_{lFS})$$

Where X_{hRF} = mean of the high-selected recombined families,

X_{lRF} = mean of the low-selected recombined families,

X_{hFS} = mean of the high-selected full-sib families,

and X_{lFS} = mean of the low-selected full-sib families.

The standard error of the realized heritability was computed by using the formula given by Prout (1962). The standard error (S.E) of h^2r is the square root of the variance of realized heritability:

$$\text{Var}(h^2_r) = 2[(1/D^2)((h^2_r(1- h^2_r)\ \sigma^2_p/N_s) + \sigma^2_x/N_1)$$
$$((N_sD^2/\sigma^2_p)/(N_s(D^2/\sigma^2_p)-1)]$$

Where $\text{Var}(h^2_r)$ is the variance of the realized heritability,

i = selection intensity = 2.063,

S = selection differential (equivalent to $X_{hRF} - X_{lRF}$),

h^2_r = realized heritability,

σ^2_p = phenotypic variance among family means,

σ^2_x = phenotypic variance in the selected population (Appendix 4),

N_s = number of selected parents (= 16 for this study),

and N_1 = number of measurements on selected population (= 12 for this study).

3.5.8 Estimates of genotypic and phenotypic correlations

The association between two characters that can be directly observed is the phenotypic correlation. The genetic correlation expresses the extent to which two measurements reflect what is genetically the same character (Falconer, 1981).

From the Design 1 experiment in 1993, genotypic correlations (r_g) between traits were computed for the male effects (r_{gm}) and female effects (r_{gf}). Also, phenotypic correlations were computed for the male (r_{pm}) and female effects (r_{pf}).

The phenotypic correlations (r_p) and genotypic correlations (r_g) were computed from the covariances of phenotypic and genotypic variances, respectively. Phenotypic and genotypic covariances were estimated by using the appropriate expected mean squares from the analysis of covariance.

Genetic correlations for male effects (r_{gm}) and female effects (r_{gf}) between two traits x, y were computed by using the formula:

$$r_{gm}(xy) = cov_{gm}(xy) / \sqrt{[\sigma^2_{gm}(x)][\sigma^2_{gm}(y)]}$$

$$r_{gf}(xy) = cov_{gf}(xy) / \sqrt{[\sigma^2_{gf}(x)][\sigma^2_{gf}(y)]}$$

Phenotypic correlations for male effects (r_{pm}) and female effects (r_{pf}) between two traits x, y were computed by using the formula:

$$r_{pm}(xy) = cov_{pm}(xy) / \sqrt{[\sigma^2_{pm}(x)][\sigma^2_{pm}(y)]}$$

$$r_{pf}(xy) = cov_{pf}(xy) / \sqrt{[\sigma^2_{pf}(x)][\sigma^2_{pf}(y)]}$$

where $cov_{gm}(xy)$ is the genotypic covariance for male effects between traits x and y, $cov_{gf}(xy)$ is the genotypic covariance for female effects between traits x and y, $cov_{pm}(xy)$ is the phenotypic covariance for male effects between traits x and y, $cov_{pf}(xy)$ is the phenotypic covariance for female effects between traits x and y, $\sigma^2_{gm}(xy)$ is the genotypic variance (σ^2_g) for male effects between traits x and y, $\sigma^2_{gf}(xy)$ is the genotypic variance (σ^2_g) for female effects between traits x and y, $\sigma^2_{pm}(xy)$ is the phenotypic variance (σ^2_p) for male effects between traits x and y, $\sigma^2_{pf}(xy)$ is the phenotypic variance (σ^2_p) for female effects between traits x and y.

$cov_{pm}(xy) = mcpm/ref$

$cov_{pf}(xy) = mcpf/re$

$cov_{gm}(xy) = (mcpm-mcpf-mcplm+mcplf)/ref$

$cov_{gf}(xy) = (mcpf-mcplf)/re$

$mcpm = scpm/dfm$

$mcpf = scpf/dff$

$mcplm = scplm/dflm$

$mcplf = scplf/dflf$

$\sigma^2_{pm}(x) = msxm/rlf$

$\sigma^2_{pf}(y) = msxf/rl$

$\sigma^2_{m}(y) = msym/rlf$

$\sigma^2_{pf}(y) = msyf/rl$

$\sigma^2_{gm}(x) = (msxm-msxf-msxlm+msxlf)/16$

$\sigma^2_{gf}(x) = (msxf-msxlf)/4$

$\sigma^2_{gm}(y) = (msym-msyf-msylm+msylf)/16$

$\sigma^2_{gf}(y) = (msyf-msylf)/4$

Where: x and y represent the variables studied, and

r = the number of replication per set = 2,

m = male groups per set = 4,

f = female mated to the same male = 4,

l = number of locations = 2,

mcp = mean cross product,

scp = sum cross product,

ss = sum of square,

The standard errors (S.E) of the genetic correlations are given by Scheinberg (1966). In general if $r = \sigma_{xy}/[\sigma^2_x * \sigma^2_y]^{1/2}$, then

$$V(r) = r^2\{[V(\sigma_{xy})/(\sigma_{xy})^2]+[V(\sigma^2_x)/(4\sigma^2_x)^2]+[V(\sigma^2_y)/(4\sigma^2_y)^2] - [cov(\sigma_{xy}, \sigma^2_x)/(\sigma_{xy})*\sigma^2_x)]-[cov(\sigma_{xy}, \sigma^2_y)/(\sigma_{xy})*\sigma^2_y)] + [cov(\sigma^2_x, \sigma^2_y)/2\sigma^2_x * \sigma^2_y)]\}.$$

To use this equation, Variances and covariances are estimated as follow:

$$V(\sigma^2) = (2/k^2)E[MS^2g/(fg+2)],$$

$$V(\sigma_{xy}) = (1/k^2)E[MS_xMS_y + MCP^2)/(fg+2)],$$

$$cov(\sigma^2_x, \sigma^2_y) = (2/k^2)E[MCP^2)/(fg+2)],$$

and $$cov(\sigma_{xy}, \sigma^2_x) = (2/k^2)EMS_xMCP/(fg+2)].$$

S.E(r) = square root of [V(r)].

In 1994, linear correlations between traits x and y were computed by using the formula:

$$r(xy) = cov(xy) / \sqrt{[\sigma^2(x)][\sigma^2(y)]}$$

where r(xy) is the correlation between studied traits x and y,

cov(xy) is the covariance between x and y,

$\sigma^2(x)$ is the variance of x,

$\sigma^2(y)$ is the variance of y.

3.5.9 Correlated response to selection.

The correlated responses, or the expected response of a character y when selection is made for another character x, were measured for pairs of characters selected. Selection was performed for *Striga* count 1, *Striga* rating 1, ear *Striga* rating, yield of infested plants, delay silking and anthesis silking interval of infested plants. In addition to the direct response to selection (R), predicted response (C) can be estimated for the yield of infested plants (y) when selecting for other *Striga* resistance traits (x) such as *Striga* count 1, *Striga* rating 1, ear *Striga* rating and anthesis-silking interval of infested plants. The formula used was

$$CR_y = i * h_x * h_y * r_g * \sigma_p \text{ (Falconer, 1981)}$$

Where CR_y = correlated response of character y,

i = selection intensity = 2.063,

h_x = square root of the heritability of character x,

h_y = square root of the heritability of character y,

r_g = genetic correlation between characters x and y,

and σ_p = phenotypic standard deviation.

Similarly, the correlated response in x to selection for y is CR_x. Falconer (1981) provided an estimate of the genetic correlation (r_g) between x and y:

$$r_g = \sqrt{[C_x C_y / Rr_x Rr_y]}$$

Where C_x, C_y = predicted correlation response of character x and y respectively, and Rr_x, Rr_y = response realized (X_{hRF} - X_{lRF}) when selecting for character x and y respectively.

$$V(R_g) = [(1-r^2_g)/4h^2_x h^2_y] \; [V(h^2_x) + V(h^2_y)]$$

$$S.E(R_g) = \sqrt{[V(R_g)]}.$$

CHAPTER FOUR

RESULTS

4.1 Response of maize populations to *Striga hermonthica* infection.

Striga emergence in Abuja and Mokwa showed tremendous plot to plot variability. However, counts of *Striga* plants emerged at 8 weeks after planting was more accurate than that of 10 weeks after planting because by 10 weeks, many *Striga* plants had died. Therefore, it was impossible to get an accurate count of the total number of *Striga* plants per row. *Striga* attack symptoms including leaf chlorosis, stunted plants and ear shoot growth and partial defoliation were clearly visible on susceptible plants on infested rows. Symptoms such as leaf chlorosis were seen on susceptible plants at about 4 to 5 weeks after planting.

Striga attack had some negative effects of on the infested plants: Number of days to silking increased (1.5 to 2 days) whereas, the days to anthesis decreased (about 1 day) (Table 6). Infested plants were shorter in height, fewer ears were harvested and the yields were lower than those of the noninfested plants. The results of the analysis of the derived data (Table 6) showed that the delay in silking was about 1.5 days, and the anthesis-silking interval was longer for infested families (about 1 day) compared to half a day for the noninfested families. The percent height reduction due to *Striga* effect was about 12%, the percent reduction in ears at harvest was about 4.8% and the percent yield reduction was about 40%. Similar results were obtained for the two locations Abuja and Mokwa (Table 7 and 8). Similar negative effects of *Striga* on the recombined families were obtained in 1994 for each location.

Across locations analysis of data collected in 1994 (Table 9) showed lower *Striga* counts compared to 1993 results. Also, a lower *Striga* rating was obtained in 1994.

Table 6. Design 1 mean squares for all variables analyzed across locations (Abuja and Mokwa)

Source of variation	d.f.	Mean Squares							
		Day silk inf.	Day silk Uninf.	Plt. Ht. inf.	Plt. ht Uninf.	*Striga* count1	*Striga* count2	*Striga* rating1	*Striga* rating2
Location	1	20.25	427.81	161685.15	18248.35	112725.11	144181.42	131.96	47.27
Sets	19	36.23	31.37	3095.21	1691.28	9496.93	8487.98	16.12	19.37
Set*Loc	19	16.57	19.63	1501.83	2080.33	8228.57	6288.30	3.99	4.64
Rep(set*loc)	40	11.22	6.03	1445.37	932.27	3299.90	3603.60	6.16	4.82
Male(set)	60	14.48**	14.74**	832.17**	686.56**	1381.57**	1594.33**	2.42**	1.39**
Fem(set*male)	240	6.75**	3.74**	427.52**	354.40**	991.01**	1113.24**	1.48**	1.02
Male*Loc(set)	60	5.11	2.43	210.75	259.43	791.62	957.27	0.95	0.91
Fem*loc(set*ma)	240	5.28	2.27*	283.61	162.31	703.84	1047.12*	1.15*	0.91
Error	600	4.85	1.87	269.65	200.52	687.25	841.45	0.93	0.91
Mean(320 full-sibs)		59.553	58.23	186.33	212.67	41.52	50.48	5.42	7.52
Mean(check 9022-13)		57.9	57.03	197.28	220.42	38.61	49.38	4.43	6.70
Mean(check 8338-1)		59.38	57.4	183.06	223.12	56.66	60.72	6.95	8.21
C.V%		3.70	2.35	8.81	6.65	63.13	57.46	17.79	12.70

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Pl. ht. = plant height.
inf. = infested.
Fem = female.
ma = male.
loc = location.

Table 6. (continued)

Source of variation	d.f.	Mean Squares						
		Ear harv. inf.	Ear harv. uninf.	Ear *Striga* Rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Location	1	49.61	14.45	24.75	2.45	52.02	141023390	34238713
Sets	19	138.65	27.97	21.38	22.99	20.91	22128670	26020221
Set*Loc	19	81.82	10.97	8.14	7.86	13.37	10791762	23165750
Rep(set*loc)	40	50.61	9.68	6.24	6.63	5.57	8811707	4212035
Male(set)	60	28.33**	11.32**	3.09**	8.93**	10.52**	3323548**	2915631**
Fem(set*male)	240	17.74*	7.14*	1.51	3.38**	3.14**	2267024**	1654592**
Male*Loc(set)	60	12.63	5.01	1.20	3.59**	2.91**	1258602	1978029**
Fem*loc(set*ma)	240	14.55	6.09	1.30	2.20	2.09*	1808333	1330311
Error	600	14.74	5.60	1.35	2.18	1.74	1711949	1183602
Mean(320 full-sibs)		14.93	19.76	5.93	58.37	57.83	3023.20	5833.52
Mean(check 9022-13)		17.15	19.85	5.03	57.97	57.2	4633	6601.65
Mean(check 8338-1)		8.22	17.51	7.35	58.81	57.41	1261.81	5569.50
C.V.%		25.71	11.97	19.64	2.53	2.28	43.27	18.64

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Anth. = Anthesis.
uninf. = uninfested.
inf. = infested.
Fem = female.
ma = male.
Loc. = location.

Table 6. (continue)

Source of variation	d.f.	Mean Squares (derived variables)				
		Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Location	1	8.61	15703.09	94.90	261.90	10.51
Sets	19	9.31	679.32	44676.29	12.21	104.81
Set*Loc	19	12.56	784.97	52455.76	31.40	97.36
Rep(set*loc)	40	6.68	191.73	8358.07	12.38	55.85
Male(set)	60	8.23*	111.26	4473.14	6.82	24.65
Fem(set*male)	240	6.25	92.71	3102.60	5.84	21.45
Male*Loc(set)	60	5.69	72.80	5558.54	7.88*	20.63
Fem*loc(set*ma)	240	6.05	77.255	3154.77	5.92	18.72
Error	600	5.80	85.14	5204.66	5.79	19.28
Mean(320 full-sibs)		1.180	12.07	41.67	1.31	4.83
Mean(check 9022-13)		0.31	10.56	29.98	0.86	2.7
Mean(check 8338-1)		1.17	17.92	77.44	1.98	9.29
C.V.%		204.15	76.39	173.11	182.38	90.77

*, ** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
inf. = infested.
ma = male.
Fem = female.

Table 7. Design 1 mean squares for all variables analysed for one location (Abuja)

Source of variation	d.f.	Mean Squares							
		Day silk inf.	Day silk uninf.	Plt. ht. inf.	Plt. ht. uninf.	*Striga* count1	*Striga* count2	Striga rating1	Striga rating2
Sets	19	32.414	17.230	3179.234	2721.008	14724.098	6688.726	8.454	11.135
Rep(sets)	20	15.201	5.631	1929.740	1207.515	5929.300	3457.335	7.657	5.931
Males(sets)	60	13.859**	8.827**	678.988**	527.778**	1682.643**	901.9**	1.282	0.935
Fem(set)*males	240	8.980	3.089**	513.162*	341.111*	1176.284	628.934*	1.543**	0.982
Error	300	7.828	2.127	417.510	266.675	865.573	478.075	0.947	0.981
Mean(320 full-sibs)		59.679	58.812	174.768	208.900	50.909	39.867	5.745	7.334
Mean(check 9022-13)		58.025	57.35	184.825	216.85	47.225	45.925	4.95	6.8
Mean(check 8338-1)		59.500	58.175	172.275	224.4	64.175	45.625	7.15	8.175
C.V%		4.68	2.48	11.69	7.81	57.79	54.84	16.94	13.50

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Plt. ht. = Plant height.
uninf. = uninfested.
inf. = infested.

Table 7. (continued)

Source of Variation	d.f.	Mean Squares						
		Ear harv. inf.	Ear harv. uninf.	Ear *Striga* rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Sets	19	136.088	17.884	19.123	21.747	20.612	17327661	14466652
Rep(sets)	20	66.021	9.196	10.045	8.967	6.684	12680497	4500596
Males(sets)	60	21.863	5.948	2.686**	9.425**	9.776**	2510015	2307305**
Fem(set)*males	240	18.825	6.384*	1.892	4.293*	3.336**	2704660	1762564**
Error	300	18.631	4.823	1.841	3.383	2.194	2219303	1275362
Mean(320 full-sibs)		15.128	19.875	5.795	58.417	58.040	3355.128	5997.077
Mean(check 9022-13)		19.025	20.175	5.1	57.675	56.900	5077.78	6931.856
Mean(check 8338-1)		8.8	17.159	7.3	58.5	57.625	1582.302	5670.662
C.V.%		28.53	11.05	23.41	3.14	2.55	44.40	18.83

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Anth. = Anthesis.
uninf. = uninfested.
inf. = infested.

Table 7. (continued)

Source of variation	d.f.	Mean Squares (derived variables) Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Sets	19	12.478	1334.557	5908.957	26.973	136.118
Rep(set)	20	9.440	329.815	4781.535	18.939	72.025
Males(set)	60	9.780	143.668	995.716	11.064	26.404
Fem.(set)*males	240	9.491	131.528	973.098	9.436	23.422
Error	300	9.310	139.229	880.093	9.319	21.261
Mean(320 full-sibs)		1.26	15.722	41.402	0.867	4.746
Mean(check 9022-13)		0.35	14.768	26.747	0.675	1.15
Mean(check 8338-1)		1	23.228	72.096	1.325	8.359
C.V.%		241.68	75.04	71.654	352.02	97.13

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.

Table 8. Design 1 mean squares for all variables analysed for one location (Mokwa)

		Mean Squares							
Source of variation	d.f.	Day silk inf	Day silk uninf	Plt. ht. inf	Plt. ht. uninf	*Striga* count1	*Striga* count2	*Striga* rating1	*Striga* rating2
Sets	19	20.398	33.782	1193.295	1050.606	3001.409	8087.555	11.661	12.372
Rep(sets)	20	7.250	6.437	1112.695	657.032	670.509	3749.878	4.668	3.721
Males(sets)	60	5.743**	8.345**	399.622**	418.230**	490.559	1649.709	2.093**	1.373**
Fem(set) * males	240	3.060**	2.923**	209.726	175.610*	518.575	1531.430	1.100	0.962
Error	300	1.883	1.62	176.195	134.366	508.92	1204.824	0.915	0.848
Mean (320 full-sibs)		59.425	57.656	197.570	216.451	32.140	61.093	5.103	7.718
Mean (check 9022-13)		57.775	56.725	209.75	224	30	52.85	3.925	6.615
Mean (check 8338-1)		59.275	56.625	193.85	221.85	49.15	75.825	6.75	8.25
C.V%		2.30	2.21	6.71	5.35	70.18	56.81	18.74	11.93

*,** Significant at 0.05 and 0.01 probability levels respectively.
d.f. = degree of freedom.
Pl. ht. = plant height.
inf. = infested.
uninf. = uninfested.

Table 8. (continued)

Source of variation	d.f.	Mean Squares						
		Ear harv. inf.	Ear harv. uninf.	Ear *Striga* rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Sets	19	84.389	21.064	10.405	9.110	13.675	15592771	34719320
Rep(sets)	20	35.215	10.168	2.451	4.295	4.471	4942916	3923474
Males(sets)	60	19.107**	10.393**	1.611**	3.099**	3.659**	2072135**	2586355**
Fem(set)*males	240	13.475*	6.851	0.923	1.291*	1.906**	1370697	1222339
Error	300	10.855	6.392	0.874	0.995	1.305	1204596	1091842
Mean(320 full-sibs)		14.734	19.662	6.073	58.329	57.637	2691.277	5669.975
Mean(check 9022-13)		15.275	19.275	4.975	58.275	57.5	4188.220	6271.451
Mean(check 8338-1)		7.65	17.875	7.4	57.925	57.2	941.321	5468.346
C.V.%		22.36	12.85	15.40	1.71	1.98	40.78	18.42

*,** Significant at 0.05 and 0.01 probability levels respectively.
d.f. = degree of freedom.
Anth. = Anthesis.
inf. = infested.
uninf. = uninfested.

Table 8. (continued)

Source of variation	d.f.	Mean Squares (derived variables)				
		Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Sets	19	9.402	131.186	91223.102	16.641	66.069
Rep (sets)	20	3.935	92.752	11934.609	5.825	39.693
Males(sets)	60	4.150**	41.372	9035.971	3.650**	18.881
Fem(set)*males	240	2.819*	43.390	5284.277	2.331	16.752
Error	300	2.305	41.82	9529.241	2.265	17.307
Mean(320 full-sibs)		1.098	8.576	41.944	1.771	4.928
Mean(check 9022-13)		0.275	6.361	33.217	1.05	4.25
Mean(check 8338-1)		1.35	12.621	82.786	2.65	10.225
C.V.%		138.24	75.40	232.73	84.93	84.41

*, ** Significant at 0.05 and 0.01 probability levels respectively.
d.f. = degree of freedom.

Table 9. Mean squares for all variables analysed in a Randomised complete block design across locations (Abuja and Mokwa)

Source of variation	d.f.	Mean Squares							
		Day silk inf.	Day silk uninf.	Plt. ht. inf.	Plt. ht. uninf.	*Striga* count1	*Striga* count2	*Striga* rating1	*Striga* rating2
Location	1	1176.00	1520.042	10347.338	49655.671	856.019	23312.667	51.042	85.630
Replication	10	3.665	8.464	1654.005	876.505	546.007	1583.387	9.831	8.602
Genotypes	17	1.041	1.336	433.286**	298.645*	378.087**	238.149	5.159**	4.313**
Geno*Loc	17	0.402	1.061	194.887	146.358	88.242	318.863	0.669	1.336
Error	170	0.692	0.801	169.740	150.132	163.274	258.199	1.072	1.088
Mean(rec.families)		56.70	56.79	204.04	248.80	13.60	26.83	4.32	6.77
Mean(TZLCompl-C1)		56.54	57.12	210.00	237.91	18.62	29.58	4.29	6.87
Mean(check 9022-13)		56.08	56.75	215.42	235.00	4.92	19.33	3.33	6.08
Mean(check 8338-1)		56.17	56.08	200.00	243.33	28.58	31.00	6.33	8.50
C.V%		1.47	1.58	6.35	5.25	88.07	59.62	23.66	15.24

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Plt. ht. = plant height.
inf. = infested.
uninf. = uninfested.
Loc = location.

Table 9. (continued)

Source of variation	d.f.	Mean Squares						
		Ear harv. inf.	Ear harv. uninf.	Ear *Striga* rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Locations	1	682.667	222.042	64.463	1589.796	2159.671	357116032	436143295
Replications	10	47.904	5.368	10.787	4.524	3.845	4330371	11287452
Genotypes	17	43.224**	12.956*	6.176**	2.117*	1.120	5637255**	2399340**
Geno*Loc	17	15.706	12.620	1.139	1.139	0.475	636839	1193122
Error	170	9.898	7.640	1.291	1.034	0.728	84201	954551
Mean(rec.families)		14.63	18.08	4.52	54.90	55.29	3590.19	5202.72
Mean(TZLComp1-C1)		14.16	18.00	4.58	55.04	55.58	1577.10	4923.16
Mean(check 9022-13)		17.58	17.58	2.92	55.50	56.00	4928.59	5248.07
Mean(check 8338-1)		8.83	15.58	6.50	54.00	55.00	1754.33	4897.55
C.V.%		21.56	15.43	24.94	1.85	1.54	27.57	18.94

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Plt. ht. = plant height.
inf. = infested.
uninf. = uninfested.

Table 9. (continue)

Source of variation	d.f.	Mean Squares (derived variables) Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Locations	1	31.130	1502.288	11974.806	6.338	111.192
Replications	10	3.419	551.183	3995.139	12.001	62.683
Genotypes	17	2.286**	112.857*	2004.761**	0.904	34.409
Geno*Loc	17	1.228	70.542	572.335	2.142	24.360
Error	170	1.054	61.580	511.849	1.440	17.911
Mean(rec.families)		1.79	11.43	34.06	0.28	3.29
Mean(TZLComp1-C1)		1.50	11.33	35.81	0.41	3.83
Mean(check 9022-13)		0.58	8.03	2.40	0.33	1.83
Mean(check 8338-1)		2.17	17.08	64.14	0.58	6.75
C.V.%		59.93	67.97	66.21	375.7	125.7

*, ** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Loc = location.

Table 6 and 9 show that the recombined families had a longer anthesis-silking interval (almost 2 days compared to 1.5 days for the full-sibs), a lower percent height reduction (11.5% compared to 12% for the full-sibs) and percent yield reduction (34% compared to 40% for the full-sibs) and a lower ear harvest reduction (3% compared to 5% for the full-sibs). Since the high selections and low selections would be expected to average out, the results may be related to the environmental effects on *Striga* growth or else to a high number of non germinable *Striga* seeds used to artificially infest the fields in 1994. Also, Table 9 showed that the high-selected recombined families had lower *Striga* counts, lower *Striga* ratings, and higher yields compared to the original population TZLComposite-1 C1.

4.2 Effect of *Striga hermonthica* attack on performance of maize populations

Tables 6, 7 and 8 show the ANOVA mean squares for all variables collected in one location (Abuja or Mokwa) and also for both locations combined. There were significant differences ($p < 0.01$) among the male groups for all of the characters except for *Striga* count 1 while female parents showed differences ($p < 0.05$) only for anthesis-silk interval (Table 10). At Abuja, the difference between male groups was significant for *Striga* count 1, ear *Striga* rating and yield for non-infested plants (Table 10). The female parents were significantly different for *Striga* count 1, *Striga* rating 1 and yield for non-infested plants (Table 10).

The analysis of variance pooled across locations (Table 11) showed significant differences among the males in sets (80 half-sib families) for all of the characters studies except for delay in silking. There were also significant differences among females (within males) in sets (320 full-sib families) for all characters except for ear *Striga* rating and anthesis-silking interval for infested plants. However, there was no interaction location by progeny effects for most of

Table 10. Design 1 mean squares for seven characters of male and female sets at Abuja (normal figures) and Mokwa (bold figures)

Source of variation	D.f.	MEAN SQUARES						
		Striga count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	Anthesis silking interval inf.plants	Delay in silking
Males in sets	60	**490.559**	**2.093****	**1.611****	**2072135****	**2586355****	**4.150****	**3.650****
		1682.643**	1.282	2.686**	2510015	2307305**	9.780	11.064
Females in males in sets	240	**518.575**	**1.10**	**1.923**	**1370697**	**1222339**	**2.819***	**2.331**
		1176.284**	1.543**	1.892	2704660	17662564**	9.491	9.436
C.V,%		**70.18**	**18.74**	**15.40**	**40.78**	**18.42**	***	**84.93**
		57.79	19.94	23.41	44.40	18.83	***	***

*, ** Significant at 0.05 and 0.01 levels respectively.
*** = C.V's are over 100 due to the environmental effects and the experimental material.
D.f. = Degree of freedom.

Table 11. Design 1 mean squares for seven characters of male and female sets at two locations (Mokwa and Abuja)

Source of variation	D.f.	Mean squares						
		Striga count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	ASI infested plants	Delay in silk
Male in sets	60	1381.579*	2.426**	3.090**	3323548	2915631	80236*	6.824
Females in male in sets	240	991.012**	1.485**	1.513	2267024**	1654592**	6.255	5.848
Male*loc in sets	60	791.699	0.950	1.208	1258602	1978029*	5.694	7.889*
Females in males*loc in sets	240	1.02	1.158*	1.302	1808333	1330311	6.054	5.920
C.V, %		63.13	17.79	19.64	43.27	18.64	***	***

*, ** Significant at 0.05 and 0.01 levels respectively.
*** = C.V's are over 100 due to the environmental effects and the experimental material.
D.f. = Degree of freedom.
ASI = Anthesis silking interval.

the characters studied except for the yield of non-infested plants and delay in silking of male parents and for *Striga* rating 1 for the female parents (Table 11).

Table 12 shows that at Abuja, there were significant differences among genotypes tested for *Striga* rating 1 (at 8 weeks after planting), ear *Striga* rating, yield infested plants and for anthesis-silk interval (ASI) infested plants. Differences among genotypes for *Striga* counts 1 (at 8 weeks after planting), yield uninfested plants and delay in silking were not significant. At Mokwa, significant differences were observed among genotypes for *Striga* rating 1, ear *Striga* rating, yield infested plants and yield uninfested plants (Table 12). The difference among genotypes obtained for the yield of uninfested plants might be due to natural *Striga* infestation of noninfested areas of the field. In most cases, *Striga* seeds are washed from infested areas to noninfested areas by heavy rains. There were no significant differences among genotypes for *Striga* counts 1, ASI infested plants and delay in silking.

The combined analysis of variance for both locations (Table 13) showed significant differences between genotypes (Table 13) for all variables studied except for delay in silking. The interaction of genotypes by locations was not significant for any of the variables studied. This indicates that there was no significant difference in the relative response of the genotypes tested in Mokwa and Abuja.

The analysis of variance was carried out for 7 traits which may be important in selecting for *Striga* resistance. For these traits, the results of the LSD test (probability level 0.05) which was used to compare each pair of genotypes selected in the high and low direction are shown in Tables 14 and 15 and Table 16. Two samples (entry, number 15 and 16) of population TZLComposite-1 C1 were used to test the different levels of selection. Entry 15 was used to compare to the low level selected genotypes and entry 16 was used to compare

Table 12. Mean squares of seven characters studied for 14 selected low and high families at Abuja (normal figures) and Mokwa (bold figures)

Source of variation	D.f.	MEAN SQUARES						
		Striga count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	Anthesis silking interval	Delay in silking
Genotypes	17	233.312	2.863**	2.421*	3723588**	1757652	3.196*	2.068
		233.118	**2.966***	**5.434****	**2550505****	**1834810**	**0.318**	**0.978**
Error	85	176.170	1.098	1.136	11239421	1026016	1.658	1.803
		150.378	**1.045**	**1.446**	**570459**	**883087**	**0.450**	**1.078**
C.V,%		106.0	26.95	26.58	22.92	15.40	96.56	***
		74.32	**21.03**	**23.57**	**36.79**	**25.15**	**32.06**	***

*,** Significant at 0.05 and 0.01 levels respectively.
*** = C.V's are over 100 due to the environmental effects and the experimental material.
D.f. = Degree of freedom.

Table 13. Mean squares of seven characters studied for 14 selected low and high families at two locations (Abuja and Mokwa)

		MEAN SQUARES						
Source of variation	D.f.	*Striga* count1	*Striga* rating	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	Anthesis silking interval	Delay in silking
Genotypes	17	378.087**	5.159**	6.716**	5637255**	2399340**	2.286**	0.904
Geno*loc	17	88.342	0.669	1.139	636839	1193122	1.228	2.142
Error	170	163.274	1.072	1.291	847201	954551	1.054	1.440
C.V,%		88.07	23.66	24.94	27.57	18.94	59.93	***

*,** Significant at 0.05 and 0.01 levels respectively.
*** = C.V's are over 100 due to the environmental effects and the experimental material.
Geno = Genotype
Loc = location.
D.f. = Degree of freedom.

Table 14. Means pair comparison (planned) of 7 characters studied for 14 selected low and high families at Abuja

Genotypes	*Striga* count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninf. plants	Anthesis silk interval	Delay in silking
Striga ct-H(High)	14.33	3.67	4.50	4199.34	7287.95	1.50	-0.50
Striga ct-L(Low)	11.83	4.50	3.83	4768.70	6218.64	1.83	-0.17
Difference		0.83 ns	0.67 ns	569.36 ns		0.33 ns	
Striga rat-H	7.00	3.83	4.00	4967.61	6663.67	1.50	-0.83
Striga rat-L	22.33	4.50	3.17	5009.86	6749.70	2.83	0.00
Difference		0.67 ns	0.83 ns	42.25 ns		1.33*	
Ear Striga rat-H	5.83	3.83	4.50	3901.38	6237.96	1.00	0.17
Ear Striga rat-L	5.33	3.67	3.83	5217.79	8100.34	0.00	-1.50
Difference		0.16 ns	1.12*	1316.41*		1.00 ns	
Yield inf plts-H	12.17	3.83	3.67	5081.44	6775.11	1.50	0.00
Yield inf plts-L	16.33	4.50	4.50	4167.62	6820.40	1.67	0.50
Difference		0.67 ns	0.83 ns	913.78 ns		0.17 ns	
Yield uninf plts-H	8.00	3.17	3.00	5780.88	6706.08	0.83	-1.00
Yield uninf plts-L	8.83	3.00	3.83	4546.47	6353.73	1.33	-1.00
Difference		0.17 ns	0.83 ns	1234.41*		0.25 ns	
Delay silk-S(short)	12.33	4.17	4.83	3551.17	6494.57	1.50	0.50
Delay silk-l(long)	13.83	4.17	3.67	4745.84	5910.38	2.00	-0.50
Difference		0.00 ns	1.16*	1194.67*		0.50 ns	
Anth-Silk interv-S	8.00	3.83	4.00	4760.48	5958.42	1.50	-0.17
Anth-Silk interv-l	10.17	3.17	4.17	4853.13	6145.46	1.50	-0.83
Difference		0.66 ns	0.17 ns	92.65 ns		0.00 ns	
TZLComposite1-c1(15)	13.50	3.33	3.83	4174.08	5800.96	0.67	-1.33
TZLComposite1-c1(16)	22.00	4.00	4.33	4470.89	6774.65	1.17	-0.67
9022-13(Resis.check)	6.00	3.00	3.00	6250.51	6620.31	0.33	-1.00
8338-1(Suscep.check)	27.50	5.83	5.50	2797.28	6789.37	2.00	-0.50
LSD (0.05)	**ns**	**1.006**	**1.02**	**1017.88**	**ns**	**1.23**	**ns**

*, Significant at 5% level.
(15), (16) Used to compare low and high selected traits respectively.

Table 15. Means pair comparison (planned) of 7 characters studied for 14 selected low and high families at Mokwa

Genotypes	*Striga* count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	Anthesis silking interval	Delay in silking
Striga ct-H(High)	20.17	4.67	5.83	1719.68	3419.39	2.50	0.17
Striga ct-L(Low)	19.50	5.17	5.67	1624.82	3886.70	2.17	0.00
Difference		0.50 ns	0.16 ns	94.18 ns	467.31 ns		
Striga rat-H	24.00	5.17	5.50	1580.59	3677.79	2.00	-0.33
Striga rat-L	18.00	4.50	4.67	2300.86	3415.09	2.00	-0.17
Difference		0.67 ns	0.83 ns	720.27 ns	262.7 ns		
Ear Striga rat-H	10.00	5.00	5.17	1817.99	4194.32	1.83	0.17
Ear Striga rat-L	11.50	4.50	4.00	2936.82	4750.48	2.00	0.00
Difference		0.50 ns	1.17*	1118.83*	556.16 ns		
Yield inf plts-H	9.67	4.00	4.67	2595.93	3798.85	2.33	0.67
Yield inf plts-L	20.00	5.50	5.83	1342.80	3985.89	2.33	0.50
Difference		1.5*	1.16*	1253.13*	187.04 ns		
Yield uninf plts-H	14.17	4.67	5.00	2709.61	5144.77	2.00	0.30
Yield uninf plts-L	13.67	4.33	5.33	1673.43	3515.92	2.00	0.50
Difference		0.34 ns	0.33ns	1036.18*	1628.85*		
Delay silk-S(short)	18.00	5.67	5.17	1998.04	2980.94	2.33	0.50
Delay silk-l(long)	9.00	4.33	4.17	2283.14	3119.19	2.00	-0.17
Difference		1.34*	1.00 ns	285.1 ns	138.25 ns		
Anth.Silk.int.-S	18.33	5.00	5.00	2169.61	3815.35	2.17	0.17
Anth.Silk.int.-l	18.50	4.67	5.33	1911.97	3549.16	2.00	0.33
Difference		0.33 ns	0.33 ns	257.64 ns	266.19 ns		
TZLComp-1 c1(1)	16.17	4.67	4.67	2235.30	3665.81	2.00	-0.83
TZLComp-1 c1(2)	22.83	5.17	5.50	1736.56	3451.26	2.17	0.50
9022-13(Resis.check)	3.83	3.67	2.83	3606.66	3875.82	1.50	-0.33
8338-1(Suscep.check)	29.67	6.83	7.50	711.38	3005.74	2.33	0.67
LSD (0.05)	**ns**	**0.98**	**1.15**	**725.16**	**902.25**	**ns**	**ns**

*, Significant at level 0.05.
(15), (16) Used to compare low and high selected traits respectively.

Table 16. Mean pair comparison (planned) of the means of 7 characters studied for 14 selected low and high families at two locations (Abuja and Mokwa)

Genotypes	*Striga* count1	*Striga* rating1	Ear *Striga* rating	Yield infested plants	Yield uninfested plants	Anthesis silking interval	Delay in silking
Striga ct-H(High)	17.25	4.17	5.17	2959.51	5353.67	2.00	0.33
Striga ct-L(Low)	15.67	4.83	4.75	3196.76	5052.67	2.00	0.08
Difference	1.58 ns	0.66 ns	0.42 ns	237.25 ns	301ns	0.00 ns	
Striga rat-H	15.50	4.835	4.75	3274.10	5170.73	1.75	0.25
Striga rat-L	20.17	4.165	3.92	3655.36	5082.39	2.42	-0.08
Difference	4.67 ns	0.67 ns	0.83 ns	381.26 ns	88.34 ns	0.67 ns	
Ear Striga rat-H	7.92	4.42	4.83	2859.69	5216.14	1.42	0.00
Ear Striga rat-L	8.42	4.08	3.92	4077.31	6425.41	1.00	0.75
Difference	0.5 ns	0.34 ns	0.91*	1217.62*	1209.27*	0.42 ns	
Yield inf plts-H	10.92	3.92	4.17	3838.69	5286.98	1.92	0.33
Yield inf plts-L	18.17	5.00	5.17	2755.21	5403.15	2.00	0.00
Difference	7.25 ns	1.08*	1.00*	1083.48*	116.17 ns	0.08 ns	
Yield uninf plts-H	11.08	3.92	4.00	4245.24	5925.42	1.42	0.67
Yield uninf plts-L	11.25	3.67	4.58	3109.95	4934.83	1.67	0.75
Difference	0.17 ns	0.25 ns	0.58 ns	1135.29*	990.59*	0.25 ns	
Delay silk-S(short)	15.17	4.92	5.00	2774.61	4737.76	1.92	0.00
Delay silk-l(long)	11.42	4.25	3.92	3514.49	4514.78	2.00	0.17
Difference	3.75 ns	0.67 ns	1.08 ns	739.88*	222.98 ns	0.08 ns	
Anth-Silk interv-S	13.17	4.42	4.50	3465.05	4886.88	1.83	0.17
Anth-Silk interv-l	14.33	3.92	4.75	3382.55	4847.31	1.75	0.58
Difference	1.16 ns	0.5 ns	0.25 ns	82.5 ns	39.57 ns	0.08 ns	
TZLComp-1 c1(15)	14.83	4.00	4.25	3204.69	4733.38	1.33	0.25
TZLComp-1 c1(16)	22.42	4.58	4.92	3103.73	5112.95	1.67	0.58
9022-13(Resis.check)	4.92	3.33	8.92	5248.07	5248.07	0.58	0.33
8338-1(Suscep.check)	28.58	6.33	6.50	4897.55	4897.55	2.17	0.58
LSD (0.05)	**8.096**	**0.704**	**0.919**	**687.419**	**940.912**	**0.954**	**ns**

*,Significant at 5% level.
(15), (16) Used to compare low and high selected traits respectively.

high level selected genotypes.

Table 14 shows that at Abuja, there were no significant differences among genotypes for the variable the *Striga* counts 1. For the variable ear *Striga* rating, there was a significant difference between pairs of genotypes selected for hight and low ear *Striga* rating and also for short and long delay in silking. However, the difference among both pairs of genotypes compared to the original population TZLComp-1 C1 was not significant. Since the high and low selections differed, some progress was achieved, but not significantly different from the initialpopulation for the variable ear *Striga* rating. For yield infested plants, the LSD test showed significant differences between pairs of genotypes selected for high and low ear *Striga* rating, high and low yield of uninfested plants and short and long delay in silking. For ASI infested plants, only the pair of genotypes selected for high and low *Striga* rating showed differences.

Table 15 shows that at Mokwa, the LSD test was significant for pair of genotypes selected for high and low yield under infestation and also for long and short delay silking when tested for the variable *Striga* rating 1. However, there was no significant difference among the pair selected for high and low *Striga* rating. This indicates that selection for *Striga* rating was not efficient enough to show any difference between genotypes selected for high and low *Striga* rating 1. For the variable ear *Striga* rating, the LSD test showed significant differences for pairs selected for high and low ear *Striga* rating and high and low yield under infestation. However, the high and low selection for ear *Striga* rating did not differ when compared to TZLComp1-C1. For the variable yield under infestation, genotypes selected for high and low ear *Striga* rating, yield infested and yield uninfested plants showed differences. The difference between the genotypes selected for high and low yield infested and population TZLComp1-C1

was significant. This indicates that significant progress was achieved in one cycle of selection from the original population.

In the case of the combined location analysis, the LSD test (Table 16) showed that for variable *Striga* count 1, there was no difference among the selected pairs of genotypes. Also, if when comparing the pair *Striga* count low and *Striga* count high to the original population TZLComp1-C1, the results show that there is no significant difference between *Striga* count high (difference of 5.17 from TZLComp1-C1 N°16), low (difference of 0.84 from TZLComp1-C1 N°15) and TZLComp-1 C1. Thus, no progress was accomplished by selection from the original population TZLComp1-C1. Thus, the significant differences between genotypes obtained for the analysis of variance may be due to the effects of the checks which were included in the analysis. For variable *Striga* rating 1, only the pair of genotypes selected for high and low yield infested showed differences. There was no significant difference between the pair of genotypes selected for high and low *Striga* rating and *Striga* rating or between those genotypes and the original population TZLComp-1 C1. For the variable ear *Striga* rating, pairs like *Striga* rating high and low, ear *Striga* rating high and low and yield infested high and low showed differences. For yield infested there were differences among pairs: ear *Striga* rating high and low, yield infested high and low and Delay silking short and long period. The difference between the pair yield infested high and low and population TZLComp-1 C1 was not significant. The LSD test which was performed on the recombined genotypes (in cycle 2) showed that very little progress was achieved by selecting from the original population. Further selection and recombination of genotypes is needed to achieve progress.

4.3 Estimate of the components of variance and their standard errors

Estimates of variance due to male effects (σ^2_m) and female effects (σ^2_f) were estimated for Abuja, Mokwa and for the combined data from both location combined (Table 17). Estimates of additive genetic variance (σ^2_a) and dominance variance (σ^2_d) were also done (Table 18 and 19).

The estimates of genetic variances for each location (Table 18) showed that in Mokwa, the estimates of additive genetic variance were greater than those of dominance variance for all of the characters studied except for *Striga* count 1. However in Abuja, The estimates of additive genetic variance were greater than that of the dominance variance only for ear *Striga* rating and delay in silking. In Mokwa, most of the dominance variance estimates were negative.

Comparison of the additive genetic variance and dominance variance estimates across locations (Table 19) showed that the estimates of additive genetic variance were lower than that of the dominance variance for *Striga* count 1, yield uninfested and delay in silking. Estimates of additive variance were greater than that of the dominance variance for *Striga* rating 1, ear *Striga* rating 1, yield of infested plants and for anthesis-silking interval of infested plants. The additive genetic variance and the dominance variance were almost of the same magnitudes for the yield of non-infested plants. Negative estimates of dominance variance for ASI and the additive genetic variance for delay silking were also obtained. The negative estimate of σ^2_d or σ^2_a may be due to either sampling error or lack of random mating in making the half-sib family groups.

Table 17. Estimates of variances due to male effects (σ^2m) and variances due to female effects (σ^2f) for seven characters characters across locations (Mokwa and Abuja) and at Mokwa (Mk) and Abuja (Ab) in 1993

	σ^2m			σ^2f		
Character	Mk	Ab	Across loc.	Mk	Ab	Across loc.
Striga count1	-3.502	63.29	18.92	4.825	155.35	71.79
Striga rating1	0.123	-0.032	0.071	0.092	0.298	0.081
Ear *Striga* rating	0.086	0.099	0.104	0.024	0.024	0.052
Yield inf.plts.	87679.75	-24330.71	100391	83050.65	242678.9	114672.76
Yield uninf.plts.	170502.112	68092.67	38332.53	65248.5	243601.2	81070.205
ASI inf. plts.	0.166	0.036	0.146	0.257	-3.850	0.050
Delay in silking	0.164	0.203	-0.062	0.033	0.058	-0.018

inf. = infested.
uninf. = uninfested.
plts. = Plants.

Table 18. Estimates of additive genetic variances (σ^2a), dominance variances (σ^2d) and ratios of additive variance to dominance variance to (σ^2d/σ^2a) at Abuja (Ab) and Mokwa (Mk)

	σ^2a		σ^2d		σ^2d/σ^2a	
Characters	Mokwa	Abuja	Mokwa	Abuja	Mokwa	Abuja
Striga count 1	-14.007±49.96	253.179±160.28	33.299±135.08	368.2±302.14	*	1.45
Striga rating 1	0.496±0.19	-0.130±0.13	-0.127±0.31	1.32±0.34	*	*
Ear *Striga* rating	0.344±0.15	0.397±0.25	-0.245±0.26	-0.296±0.52	*	*
yield infested plants	350719±196237	-97322±256753	-18516.4±372903	1068038±661980	*	*
Yield uninfested plants	682008±238815	272375±22215	-421014±371489	70229.4±441744	*	25.77
ASI infested plants	0.665±0.39	0.144±0.97	0.361±0.74	0.217±2.49	0.54	1.50
Delay in silking	0.659±0.34	0.813±1.08	-0.526±0.65	-0.577±2.53	*	*

* Negative ratio resulting from a negative additive genetic variance or dominance variance.

TABLE 19. Estimates of additive genetic variance (σ^2_a), dominance variance (σ^2_d), and ratios of additive variance to dominance variance for combined data

Character	σ^2_a	σ^2_d	σ^2_d/σ^2_a
Striga count1	75.69±76.64	211.47±134.48	2.79
Striga rating1	0.28±0.12	0.039±0.21	0.13
Ear *Striga* rating	0.417±0.15	-0.206±0.23	*
Yield infested plants	401564±172649	57127±315131	0.14
Yield non infested plants	153330±165395	170951±254178	1.11
Anthesis silking interval	0.585±0.49	-0.384±0.93	*
Delay in silking	-0.248±0.50	0.176±0.90	*

* Negative σ^2_d/σ^2_a ratio resulting from a negative additive genetic variance or a dominant variance estimate.

Table 19 shows that the ratio σ^2_d/σ^2_e was less than 1.0 for *Striga* rating 1 (0.135) and yield of infested plants (0.142) and was slightly greater than 1.0 for yield uninfested plant (1.114). On the other hand, the ratio was considerably greater than 1.0 for *Striga* count 1 (2.79) and for delay silking assuming σ^2_a was a value near zero.

Genotypic variances (σ^2_g) and phenotypic variances (σ^2_p) were also estimated for each location and both locations combined (Table 20 and 21). Table 20 shows that σ^2_g estimates were higher in Abuja than in Mokwa for all variables except for yield of uninfested plants and for ASI of infested plants. Likewise, σ^2_p estimates were also higher in Abuja than in Mokwa except for the variable yield uninfested plants. In both locations (Table 20), the estimates of σ^2_p were higher than those of σ^2_g for all variables. For the analysis across locations (Table 21) σ^2_g was higher than σ^2_{gl} for all variables except for yield non infested plants and for delay in silking. Also, the estimates of σ^2_p were higher than those of σ^2_g for all variables.

4.4 Estimates of heritability

Narrow sense heritability estimates (h^2_n) of the seven characters studied were based on the variance among full-sib families. The estimates of heritability (Table 22) were higher in Mokwa than in Abuja. Negative heritability estimates obtained in Abuja may be due to sampling error.

In the case of the combined analysis for both locations ear *Striga* rating had the highest heritability of 0.437 (Table 22). *Striga* rating 1 and yield infested plants had lower heritabilities compared to the variable ear *Striga* rating (h^2_n = 0.33 and 0.317, respectively). *Striga* count 1, yield non infested plants and ASI had a low heritability estimates (h^2_n = 0.139, 0.155 and 0.173,

Table 20. Estimates of genetic variances, phenotypic variances and broad sense heritability for seven characters at Mokwa (Mk) and Abuja (Ab)

	$\sigma^2 g$		$\sigma^2 e$		$\sigma^2 p$		$h^2 b$	
Character	Mk	Ab	Mk	Ab	Mk	Ab	Mk	Ab
Striga count 1	1.320	218.650	508.929	865.573	255.786	651.437	0.018	0.335
Striga rating 1	0.216	0.265	0.915	0.947	0.674	0.739	0.321	0.358
Ear *Striga* rating	0.110	0.124	0.874	1.841	0.54	1.045	0.202	0.119
Yld inf.plts	170730	218348	1204596	2219303	773029	1328000	0.220	0.164
Yld uninf. plts	235750	311695	1091842	1275362	781672	949376	0.301	0.328
ASI infested plants	0.423	0.126	2.305	9.310	1.576	4.781	0.268	0.026
Delay in silking	0.197	0.262	2.265	9.319	1.330	4.921	0.148	0.053

Yld = yield.
inf. = infested.
uninf. = noninfested.
plts = plants.

Table 21. Across locations (Abuja and Mokwa) estimates of genetic variances (σ^2_g), phenotypic variances (σ^2_p) and broad sense heritability (h^2_b) for seven characters in 1993

Characters	σ^2_g	σ^2_e	σ^2_{gl}	σ^2_p	h^2_b
Striga count1	90.715	687.25	9.635	272.163	0.333
Striga rating1	0.153	0.931	0.043	0.430	0.357
Ear *Striga* rating	0.157	1.358	-0.019	0.476	0.329
Yield infested plants	215064	1711949.744	-10262	632789	0.339
Yield non infested plants	119403	1183602.161	77159.7	492463	0.242
ASI infested plants	0.196	5.808	0.039	1.687	0.116
Delay in silking	-0.08	5.792	0.155	1.523	**

**, h^2_b not estimable because the genetic variance is negative.

Table 22. Estimates of the narrow-sense heritability for seven characters at two locations Mokwa (Mk) and Abuja (Ab) and also for the combined data

	h^2n		
Characters	Mokwa	Abuja	combined data
Striga count1	**	0.194±0.161	0.139±0.172
Striga rating1	0.368±0.137	**	0.330±0.152
Ear *Striga* rating	0.314±0.103	0.190±0.132	0.437±0.161
yield infested plant	0.226±0.164	**	0.317±0.130
Yield non infested plant	0.436±0.197	0.143±0.155	0.155±0.208
ASI infested plants	0.211±0.148	0.015±0.142	0.173±0.154
Delay in silking	0.247±0.142	0.082±0.144	**

** = Not estimable because σ^2a is negative.

respectively). The heritability of the variable delay silking was not estimable because the additive variance was negative.

Broad sense heritabilities (h^2_b) were estimated for each character for each location (Abuja and Mokwa) and both locations combined (Tables 20 and 21). Broad sense heritability estimates were higher for the combined analysis of both locations than for each location except for yield uninfested plants and ASI infested plants. Table 20 shows that h^2_b estimates were higher for traits *Striga* rating 1 and yield for non infested plants at Abuja and Mokwa (h^2_b = 0.358 and 0.321). Again, the variable delay in silking had the lowest estimate (h^2b = 0.053 and 0.148 for Abuja and Mokwa respectively). For the combined locations analysis (Table 21), variable *Striga* rating 1, yield of infested plants, ear *Striga* rating and *Striga* count 1 had the highest h^2b estimates (h^2_b = 0.357, 0.339, 0.329 and 0.33 respectively). Delay silking had the lowest estimate (h^2_b = 0.052).

4.5 Predicted response to selection and the realized heritability

Estimates of the predicted response to selection (R) were measured for seven important characters across locations (Abuja and Mokwa) (Table 23). The trait ear *Striga* rating (R = 0.62±0.30) had a higher estimate compared to *Striga* rating 1 (R = 0.45±0.28). Yield of infested plants (R = 520.70±0.25) had a higher estimate compared to yield of noninfested plants (R = 225.37±0.33). The predicted selection response of variable delay silking was not estimable because the additive variance was null and the heritability was therefore not estimable.

The estimates of the realized heritability (h^2_r) for the seven traits under study are given in Table 24. The results showed that h^2_r estimates were high for ear *Striga* rating, yield of

Table 23. Estimates of the additive variance (σ^2a), phenotypic variance (σ^2p) and the predicted response (R) for combined data from Abuja and Mokwa

Characters	σ^2a	σ^2p	R
Striga count 1	71.79±76.64	272.16±52.91	4.73±0.27
Striga rating 1	0.08±0.12	0.43±0.07	0.45±0.28
Ear *Striga* rating	0.05±0.15	0.47±0.09	0.62±0.30
Yield infested plants	114673±172649	632789±122749	520.70±0.27
Yield uninfested plants	81070±165395	492463±104462	225.37±0.33
Anthesis-silk infested plants	0.05±0.49	1.68±0.40	0.46±0.27
Delay in silking	-0.248±0.50	1.52±0.42	**

**, R not estimable because σ^2a is negative.

Table 24. Estimates of realized heritability, h^2_r across locations (Abuja and Mokwa) by using 1993 and 1994 data

Characters	Response ($X_{HRF} - X_{LRF}$)	Selection differential ($X_{HFS} - X_{LFS}$)	Realized Heritability (h^2_r)
Striga count 1	1.58	60.765	0.026±0.031
Striga rating 1	0.67	2.453	0.273±0.273
Ear *Striga* rating	0.91	2.672	0.340±0.195
Yield infested plants	1064.05	3240.729	0.328±0.227
Yield uninfested plants	990.59	3074.316	0.322±0.239
Anthesis silking infested plants	0.08	5.468	0.014±1.353
Delay in silking	0.17	3.499	0.048±0.907

X_{HRF} = mean of high-selected recombined families,
X_{LRF} = mean of low-selected recombined families,
X_{HFS} = mean of high-selected full-sib families,
X_{LFS} = mean of low-selected full-sib families.

infested plants and for yield of non infested plants (h^2_r = 0.340±0.195, 0.328±0.227 and 0.322±0.239 respectively). *Striga* rating had an unexpected low h^2_r estimate (h^2_r = 0.273±0.273). Variables like *Striga* count 1, ASI of infested plants and delay silking had very low estimates (h^2_r = 0.026±0.031, 0.014±1.353 and 0.048±0.907).

4.6 Estimates of phenotypic and genotypic correlations

Correlation coefficients (r) were computed to measure how closely the different traits were associated. The estimates of the genotypic and phenotypic coefficients of correlation (r_g and r_p respectively) computed in 1993 for pairs of characters are summurized in Table 25. Positive but low genotypic correlations were obtained between *Striga* count 1 and *Striga* rating 1 (r_g = 0.20±0.41), *Striga* count 1 and ear *Striga* rating (r_g = 0.036±0.50), *Striga* count 1 and day in silking for infested plants (r_g = 0.020±0.27) and *Striga* count 1 and days to mid-anthesis (r_g = 0.14±0.25). Positive and high genotypic correlations were obtained between *Striga* rating 1 and ear *Striga* rating (r_g = 1.08±0.71), *Striga* rating 2 and *Striga* rating 1 (r_g = 0.87±1.39) and days to mid-anthesis of infested plants and days to mid-silking of infested plants (r_g = 0.93±0.40). These high values of genotypic correlations indicated that there may be considerable genetic association between the tested characters. Yield showed a high genotypic correletion with plant height (r_g = 0.61±0.54) and with ears harvested for infested plants (r_g = 0.99±1.12); which is a component of yield. Negative correlations were obtained between *Striga* count 1 and yield (r_g = -0.227±0.46), *Striga* rating and yield (r_g = -0.92±0.93) and ear *Striga* rating and yield (r_g = -0.88±1.28). Such negative associations were expected since *Striga* affects the physiology and the yield of infested plants.

Table 25. Phenotypic and genotypic (bold) correlations among characters for the combined data from Mokwa and Abuja in 1993

	Day silk	Plant height	Ear height	*Striga* count 1	*Striga* count 2	*Striga* rating 1	*Striga* rating 2
Day silk	**0.18±0.28**	**0.15±0.02**	**0.02±0.27**	**-0.80±0.55**	**-0.30±0.30**	**0.03±0.31**
infested	-0.12	-0.13	0.11	0.01	0.15	0.12
Plant height		**0.89±0.52**	**-0.14±0.31**	**0.39±0.46**	**-0.68±0.45**	**-0.45±0.52**
infested		0.72	-0.27	-0.15	-0.49	-0.39
Ear height			**-0.03±0.28**	**0.17±0.31**	**-0.49±0.36**	**-0.12±0.41**
infested			-0.17	-0.08	-0.36	-0.27
Striga count 1				**1.44±1.75**	**0.20±0.41**	**0.21±0.60**
				0.67	0.36	0.38
Striga count 2					**0.08±0.63**	**0.57±1.28**
					0.27	0.33
Striga rating 1						**0.87±1.39**
						0.70

Table 25. (Continued)

	Ear harvested infested	Ear *Striga* rating	Anthesis infested plants
Day silking infested	**-0.35±0.33** -0.24	**0.29±0.32** 0.23	**0.93±0.40** 0.40
Plant height infested	**0.24±0.48** 0.38	**-0.33±0.54** -0.45	**0.003±0.25** -0.04
Ear height infested	**0.08±0.35** 0.26	**-0.23±0.39** -0.30	**0.12±0.25** -0.03
Striga count 1	**0.08±0.43** -0.32	**0.03±0.50** 0.36	**0.14±0.25** 0.06
Striga count 2	**0.24±0.71** -0.25	**0.04±0.08** 0.31	**0.48±0.36** 0.07
Striga rating 1	**-1.12±0.70** -0.64	**1.08±0.71** 0.70	**0.01±0.25** 0.07
Striga rating 2	**-1.64±1.10** -0.60	**1.73±1.90** 0.65	**-0.40±0.61** 0.04
Ear harvested infested		**-0.83±0.51** -0.65	**-0.48±0.22** -0.19
Ear *Striga* rating			**0.17±0.19** 0.09
Anthesis infested plants			
Yield infested plants			

Yield infested plants	Anthesis silking interval
-0.07±0.40	**0.45±0.85**
-0.27	0.74
0.61±0.54	**0.49±057**
0.54	-0.09
0.26±0.39	**0.11±0.39**
0.36	-0.11
-0.22±0.46	**-0.29±0.45**
-0.40	0.07
-0.09±0.75	**-0.34±0.67**
-0.31	-0.03
-0.92±0.93	**-0.84±1.39**
-0.73	0.10
-1.09±1.33	**1.06±0.80**
-0.66	0.09
0.99±1.12	**0.23±0.20**
0.77	-0.10
-0.88±1.28	**0.38±1.37**
-0.78	0.16
-0.52±0.28	**0.09±0.73**
-0.31	0.27
	1.05±1.30
	-0.13

In 1994, the means of the genotypes were used to compute the linear correlation coefficients (r) between characters under study for the combined analysis of two locations, Abuja

and Mokwa (Table 26). A positive but low correlation was found between days to mid-anthesis for infested plants and days to mid-silking for infested plants (r = 0.28**). *Striga* rating 1 had a significant but negative correlation with plant height of infested plants (r = -0.64**), and a positive and high correlation with *Striga* counts 1 (r = 0.81**). Root lodging for infested plants had a negative correlation with *Striga* counts 1 (r = -0.02) and also with *Striga* rating (r= -0.26). Ear *Striga* rating was significantly and positively correlated with *Striga* rating 1 (r = 0.74**). Ear harvest for infested plants had a significant and negative correlation with *Striga* count 1 (r = -0.75**) and with *Striga* rating 1 (r = -0.85**). As expected, yield of infested plants had a significant and negative correlation with *Striga* counts 1 (r = -0.74**), with *Striga* rating 1 (r = -0.81**), with ear *Striga* rating (r = -0.91**). The yield of infested plants had a positive and significant correlation with ear harvested for infested plants (r = -0.90**), since the ear harvested is a component of the yield.

4.7 Correlated response (CR_y) to selection

Estimates of the indirect response in the yield of infested plants (y) when selecting for other *Striga* resistance characters (x) were calculated (Falconer, 1981). Also, the indirect response in *Striga* resistance characters when selecting for the yield of infested plants were computed. The results showed that for improving the yield of infested plants, selecting indirectly for ear *Striga* rating (CR_y = 537.50) was more efficient than selecting directly for yield of infested plants (R = 520.70) (Table 23). Except for *Striga* count 1 (CR_y = 75.78)

Table 26. Linear correlations among characters for the combined data from Abuja and Mokwa in 1994

	2	3	4	5	6	7	8	9	10	11	12	13
1. Day silk inf.	0.28	-0.39	-0.10	0.02	-0.02	-0.02	0.24	0.15	-0.10	-0.13	0.36	-0.29
2. Anthesis infested		0.30	0.50	-0.45*	-0.61*	-0.14	-0.30	-0.45	0.44	0.56*	-0.78**	0.22
3. Plant height infested			0.65**	-0.44	-0.64**	0.43	-0.66**	-0.66**	0.60*	0.71**	-0.51*	0.38
4. Ear height infested				-0.60*	-0.68**	0.43	-0.48	-0.64**	0.69**	0.57*	-0.55*	0.11
5. *Striga* count 1					0.81*	-0.02	0.51*	0.72**	-0.75**	-0.74**	0.72**	0.10
6. *Striga* rating 1						-0.26	0.61**	0.74**	-0.85**	-0.81**	0.58*	-0.26
7. Root lodging infested							-0.41	-0.37	-0.28	0.15	0.12	-0.03
8. Stalk lodging infested								0.64**	-0.56**	-0.60*	0.45	-0.03
9. Ear *Striga* rating									-0.90**	-0.91**	0.54*	0.02
10. Ear harvested infested										0.90**	-0.49*	0.06
11. Yield infested											-0.63*	0.16
12. Anthesis-silking interval												-0.41
13. Delay silking												

*,** Significant at 0.05 and 0.01 levels respectively.

which had a low estimate, selecting indirectly for *Striga* rating 1 (CR_y = 488.31) and for anthesis silking interval (CR_y = 403.52) will also be efficient to improve the yield of infested plants. The indirect response in the yield (CR_y) when selecting for delay silking was not estimable. Since the additive variance was negative, the heritability could not be computed.

Estimates of the predicted response for *Striga* count 1, *Striga* rating 1, ear *Striga* rating and anthesis silking interval when selecting for yield infested plants are CR_x = -1.56, -0.39, -0.46 and 0.657 respectively. Genetic correlations (R_g) were then estimated from the predicted correlation responses (Falconer 1981) between yield of infested plants and *Striga* count 1 (R_g = -0.26±0.56), *Striga* rating 1 (R_g = -0.52±0.43), ear *Striga* rating (R_g = -0.50±0.38) and for anthesis-silking interval (R_g = 1.76±0.09).

CHAPTER FIVE

DISCUSSION

5.1 Comparative magnitude of the additive genetic variance and dominance variance

A two factor design (Design 1) which generated full-sib families within half-sib families was used in this study to detect the presence of genetic variability for traits associated with *Striga* resistance. Design 1 only permits the estimation of genetic components of variance such as additive genetic variance and dominance variance which might also contain epistatic variances if there is epistasis. However, several variance estimations studies, Compton *et al.*(1965); Eberhart *et al.*(1966) and Stuber and Moll(1969; 1971) suggested that epistatic variability is negligeable in maize, both within open-pollinated varieties and in varietal hybrids (F1 crosses of open-pollinated varieties).

Comstock and Robinson (1948) and Robinson *et al.*(1955) considered several assumptions in the genetic interpretation of variance components. The assumption of random mating of plants in the production of full-sib within half-sib family groups was important for the interpretation of the results obtained in 1993.

Table 19 shows that negative estimates of dominance variance (σ^2_d) were obtained for ear *Striga* rating and for anthesis-silk interval. Also, negative estimates of additive genetic variance (σ^2_a) were obtained for delay silking. Negative genetic variance component estimates may be due to experimental errors, inadequate sampling of reference populations or failure of the assumptions of the genetic or statistical models,

Gouesnard and Gallais (1992). A possible explanation for the negative σ^2_d estimate could be the lack of random mating. In Design 1, the estimate of σ^2_d is obtained by the difference between female-within-male and male variance components and the standard error of σ^2_d is usually quite large (Hallauer and Miranda, 1988). Lindsey *et al.*(1962) reported that estimates of σ^2_d were more often negative when male and female plants were sown at the same dates. This leads to assortive mating in making the full-sib family groups, the early flowering males will be crossed to early silking females, intermediate flowering males to intermediate silking females, and late flowering males to late silking females. The result of such assortive mating is an overestimation of σ^2_m, and an underestimation of σ^2_f. If the females crossed to the same male are correlated, the estimate of the male mean square increases and the female-within-male mean square decreases (Gouesnard *et al.*, 1992). Consequently, σ^2_m would be overestimated and σ^2_f would be underestimated. This would lead to upward bias in the estimate of the additive genetic variance and downward bias in the estimate of the dominance variance (Lindsey *et al.*, 1962). In our study, the assortive mating hypothesis may not be the factor responsible for the negative estimate of dominance variance for the characters such as ear *Striga* rating and anthesis-silking interval. During the 1993 experiment, seeds for plants designated as male were sown 4 days later than female parents. This should have allowed enough time for a greater range of maturity of female plants mated to a particular male to mature. Every plant designated as a male plant was crossed to 4 randomly chosen plants designated as female to avoid assortive mating. Another possible explanation for the negative dominance variance estimates was that of the sampling error, assuming the true

variances were positive but small. The negative values of σ^2_d were likely estimates of values near zero which is included in the standard error. Robinson *et al.*(1955) pointed out that variances by definition, are never negative. Therefore, true values of these negative variances are small positive quantities and negative estimates resulted from sampling error.

Comstock *et al.*(1948) and Robinson *et al.*(1955) discussed the implications of the ratios σ^2_d/σ^2_a relative to the type of gene action involved in the inheritance of quantitative characters. Their implications were applicable to this study. Estimates of the ratio σ^2_d/σ^2_a presented in Table 19 indicated partial to complete dominance for genes affecting *Striga* rating 1 and yield of infested plants, although the possibility of overdominance at some loci cannot be ignored. The ratio σ^2_d/σ^2_a value of 2.79 and 1.114 obtained for *Striga* count1 and yield of non-infested plants respectively, suggests that the average degree of dominance for genes affecting these characters were in the complete to overdominance range. Previous work by Lonnguist(1953) showed that dominant or partially dominant and overdominant gene action was indicated for grain yield. Results of the analysis of the data across locations (Table 19) showed that the proportion of the additive genetic variance was greater than that of the dominance variance (close to zero) for traits like ear *Striga* rating and anthesis-silking interval of infested plants. This suggested that the additive genetic variance is a high proportion of the total genetic variance for these characters. The estimates (Table 19) also indicated additive gene action with partial to complete dominance of genes controlling *Striga* rating 1, and yield of infested plants. The estimates of genetic variances indicate that within the population under study, σ^2_a represents a major portion of the total genotypic variance for characters

such as ear *Striga* rating, yield of infested plants, anthesis-silk interval of infested plants and *Striga* rating. Since for those traits, additive gene action appears to be the primary source of variation in the population TZLComp 1-C1, recurrent selection such as mass selection, S1 progeny testing, or half-sib family selection is suggested for improving that population for resistance to *S. hermonthica*. The number of *Striga* plants is however controlled by non-additive gene action which could be interpreted as dominance but, as no test for epistatic variation was made, such a distinction can not be drawn. Kim (1994), reported that in inbred maize lines, additive gene action plays a major role in inheritance of *Striga* tolerance and non-additive gene action plays a major role in *Striga* emergence.

5.2 Estimate of heritability

Estimates of heritability are of importance for the breeder, since they indicate to what extent selection is likely to be effective (Robinson *et al.*,1951; Dudley and Moll, 1969). The narrow-sense heritability measures the relative proportion of the additive portion of the genetic variance that can be transmitted to the next generation of offspring (Fehr, 1987). Use of genetic variance, as well as heritability estimates will enable us to provide information on the rate and extent to which resistance to *Striga* can be increased by using conventional population improvement methods.

In this study, estimates of narrow-sense heritability were low in general (Table 22). This indicates that at the early cycle of recombination (cycle 1) the proportion of the additive genetic variance, although present in the total genetic variance, was low for most of the characters under study. Also, narrow-sense heritability estimated on the basis of the

selection unit (full-sib families in our case) are generally lower than on a plant basis.

Estimates of narrow-sense heritability across locations (Table 22) were highest for ear *Striga* rating ($h^2_n = 0.437$), *Striga* rating ($h^2_n = 0.33$) and yield of infested plants ($h^2_n = 0.317$). These values indicated that a sufficient proportion of additive genetic variance might be available in the population under study. This is confirmed by the large additive variance estimates found for these characters (Table 19). Thus, these traits can be incorporated and improved in the germplasm that are being selected for *Striga* resistance. On the contrary, traits like *Striga* counts and delay in silking will be difficult to improve, since very little is inherited from one generation to the next generation. The results also showed that for the same characters, the magnitude of h^2_n estimates vary greatly from location to location. Thus, from a practical standpoint, it will be more appropriate and useful to work with estimates across a wide range of locations.

The realized response to selection (Table 24) was higher than that of the predicted response to selection (Table 23) for characters such as *Striga* rating, ear *Striga* rating and yield of infested plants and for yield of non infested plants. Thus, Some progress was achieved for those characters through selection.

The estimates of realized heritability (Table 24) were also higher for the same characters: *Striga* rating, ear *Striga* rating and yield of infested plants and for yield of non infested plants. These traits are of economic interest because they have a great potential to be improved by selection in a short time.

5.3 Genetic association among characters

Genotypic and phenotypic correlations between characters are of importance because they indicate the correlated response of other characters that may occur during selection of a single trait. Some characters of economic importance like yield, are complex in inheritance and may involve several related characters (Stuber *et al.*, 1966).

Genetic correlations (r_g) for characters measured in 1993 showed that yield was negatively correlated with *Striga* count 1 (r_g = -0.22), *Striga* rating 1 (r_g = -0.92) and with ear *Striga* rating (r_g = -0.88) as expected. The yield of infested plants was genetically correlated to the number of ears harvested on infested plants (r_g = 0.99). Plant height and ear height of infested plants were genetically correlated (r_g = 0.89). Similar results were reported by Stuber *et al.*, (1966) who revealed the presence of genetic interrelationships between yield and number of ears; plant height and ear height. A low correlation was found between *Striga* count 1 and *Striga* rating 1 (r_g = 0.20). This indicates that the number of *Striga* plants is not linearly related to the ability of the host plants to tolerate *Striga* effects. For instance, a host plant can support few *Striga* plants or no *Striga* plants at all above ground, but show heavy *Striga* symptoms. The estimates of genetic correlations between plant height and *Striga* count 1, *Striga* rating 1 and ear *Striga* rating were negative values (r_g = -0.14, -0.68 and -0.33 respectively). However, genetic correlations between plant height and yield (r_g = o.61) and also plant height and ear height (r_g = 0.89) showed high and positive values. The transformed trait, ASI of infested plants had an unexpected negative genetic correlation with *Striga* rating (r_g = -0.84), and a positive correlation with plant height (r_g = 0.49). Genetic correlation values above one

may be due to sampling variation.

The linear correlations estimated between characters of importance in 1994 (Table 19) confirmed 1993 results. Yield was significantly but negatively correlated to *Striga* rating 1 ($r = -0.81^{**}$), ear *Striga* rating ($r = -0.91^{**}$), and to *Striga* counts ($r = -0.74^{**}$). Yield was also negatively correlated to stalk lodging of infested plants ($r = -0.60^{*}$), as previously reported by Kim (1991 and 1994) who reported that grain yield was negatively correlated to stalk lodging ($r = -0.34^{**}$). Stalk lodging of infested plants positively correlated to *Striga* count 1 ($r = 0.51^{*}$), and to *Striga* rating 1 ($r = 0.61^{**}$). The yield of infested plants was not correlated to root lodging of infested plants ($r = 0.15$). *Striga* rating 1 was also correlated to *Striga* count 1, but the correlation value was higher ($r = 0.81^{**}$) than the estimate obtained previously. Root lodging of infested plants showed very little or no correlation with the characters studied. It indicates that perhaps, this trait is not related to any of the characters studied in the population TZLComp-1 C1.

Estimates of the indirect response in the yield of infested plants (C_y) when selecting for *Striga* resistance traits showed that selecting for low ear *Striga* rating, low *Striga* rating and short anthesis-silking interval will be efficient for improving the yield of infested plants.

Estimates of the genetic correlations (R_g) between the yield of infested plants and ear *Striga* rating ($R_g = -0.50 \pm 0.38$; $r_g = -0.88 \pm 1.28$), *Striga* rating 1 ($R_g = -0.52 \pm 0.43$; $r_g = -0.92 \pm 0.93$), *Striga* count 1 ($R_g = -0.26 \pm 0.56$; $r_g = -0.22 \pm 0.46$) and anthesis-silking interval ($R_g = 1.76 \pm 0.09$; $r_g = 1.05 \pm 1.30$). These estimates were lower than the genetic correlation estimates (r_g) derived from the covariance of full-sib families between the same

characters. Generally, realized genetic correlations are more precise than estimates of correlations derived from the covariance of full sib families. R_g and r_g were of the same magnitude for *Striga* count 1. These results confirm the fact that the level of host plant damage is not well correlated with *Striga* emergence. Thus, resistance to *Striga* is not controlled by the number of *Striga* plants that emerge above ground. To improve the level of *Striga* resistance, therefore the yield of infested plants, it will be more efficient to select for low *Striga* rating, low ear *Striga* rating and short anthesis-silking interval.

CHAPTER SIX

SUMMARY AND CONCLUSION

Striga hermonthica (Del.) Benth. is a root parasite of the Scrophulariaceae family that attacks most cereal crops including sorghum (*Sorghum bicolor* (L.) Moench), pear millet (*Pennisetum americanum* (L.) Leeke), cowpea (*Vigna unguiculata* (L.) Walpers) and maize (*Zea mays* (L.)). *Striga hermonthica* is most widespread in the savanna regions of Africa. It is one of the most damaging 'pests' of food crop production, especially maize, in sub-Saharan Africa. Crop loss due to *Striga* varies from 10% yield reduction to total crop failure in heavily infested field when susceptible maize varieties are planted (Smaling *et al.*, 1991). The use of resistant varieties to *Striga* species provides the most pratical and economical strategy to control the parasite.

The choice of an effective breeding scheme to use for the genetic improvement to *Striga* resistance in open-pollinated maize varieties, depends upon the type of gene action involved. Estimates of genetic variances and heritability and also the mode of gene action controlling inheritance to *Striga* resistance were of interest in this study. A Design 1 scheme was used to estimate the magnitude of additive and non-additive genetic variances present in the population under study, TZLComposite-1 C1. Seven characters (*Striga* count 1, *Striga* rating 1, ear *striga* rating, yield of infested plants, yield of non-infested plants, anthesis-silking interval of infested plants and delay in silking due to *Striga* effects) descriptive of the inheritance of *Striga* resistance were studied.

Results of this study showed that Estimates of additive genetic variance were larger than dominance variance for *Striga* rating 1, ear *Striga* rating and yield of infested

plants. Additive variance and dominance variance were about the same magnitude for yield of non-infested plants. Although epistasis, linkage and genotype-environment interaction are potential sources of bias, all operate to increase the estimate of dominance variance proportionately more than that of the additive genetic variance as indicated by several authors (Robinson *et al.*, 1955; Compton *et al.*, 1965; and Stuber and Moll, 1971).

Narrow-sense heritability estimates indicated that the additive variance was a major proportion of the genotypic variance for characters such as *Striga* rating 1, ear *Striga* rating and yield of infested plants. On the contrary, *Striga* counts, delay in silking and anthesis-silking interval had a lower proportion of additive variance in the total genetic variance. The realized heritability estimates were also higher for *Striga* rating 1, ear *Striga* rating and yield of infested plants as previously indicated from the results of the estimates of the genetic variances. These results indicate that these characters are controlled by additive gene action and therefore they have a great potential to be improved by selection. However, *Striga* counts, delay in silking and anthesis-silking interval are controlled by non-additive gene action. Estimates of genotypic correlations indicated that grain yield was negatively correlated to *Striga* rating, ear *Striga* rating, number of ear harvested, anthesis-silk interval of infested plants and to a lesser extent to *Striga* counts. Yield of infested plants was positively correlated to plant height of infested plants and also to the number of ears harvested for infested plants. Anthesis-silking interval of infested plants had a positive but low correlation with days to silk and days to anthesis of infested plants. Anthesis-silking interval was negatively correlated to *Striga* rating 1.

Since additive gene action appears to be an important source of variation for *Striga* rating 1, ear *Striga* rating and yield of infested plants, recurrent selection (selection which involves recombination of superior genotypes to form a population for continued cyclic selection) would be effective in improving level of *Striga* resistance. This should take the form of mass selection, S1 progeny testing or full-sib family selection is suggested for improving the level of *Striga* resistance of open-pollinated maize varieties. The choice of the selection scheme will depend on the length of time and the amount of effort required to complete a selection cycle. Other traits such as plant height, ear height and the number of ears, which were shown to be genetically correlated to yield, should be incorporated in the breeding scheme to achieve satisfactory results. The improvement of each character separately will lead to unsatisfactory results since all of the traits involved in resistance to *Striga* are genetically linked. The construction of a selection index including these important traits will be appropriate for more effective selection to improve the level of resistance in open-pollinated maize varieties.

This study showed that the level of host plant damage is not well correlated with *Striga* emergence. Thus, resistance to *Striga* is not controlled by the number of *Striga* plants emerged above ground but rather, it is controlled by quantitative characters with interactions between them: the ratings of *Striga* effects on the host plants influence other traits like the days to silk, the plant height and the number of ears which are all related to the yield. In the open-pollinated maize population under study, inheritance of resistance to *Striga* is therefore controlled by quantitative characters which are polygenic (more stable and durable).

To increase the level of screening efficiency for resistance to *Striga* in open-pollinated maize varieties, the artificial infestation technique used now must be improved so that an acceptable level of infestation is achieved.

The use of resistant maize varieties combined with the use of cereal-legume rotation (which has long been practiced by African farmers), is one of the most economical ways to solve the *Striga* problem in sub-Saharan Africa. In addition, farmers should be educated about of how to avoid spreading *Striga* seeds since man was shown to play a key role in *Striga* seed dispersal (Berner *et al.*, 1993). This can be done with the help of the national programs.

Most of all of the strategies and recommendations, collaborative research between national and international institutions should be strengthened to permit the establishment of programs involving systematic screening of germplasm collections, and identification of new genes that can be incorporated in the germplasm to improve the level of resistance.

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Appendix 1: *Striga* syndrome ratings (1-9) used for measurement of tolerance of maize to *Striga* based on *Striga* damage symptoms to the host plant (1 = highly tolerant; 9 = highly susceptible)

Rating	Description
1	No chlorosis, no blotching, and no leaft scorching (firing) and normal plant growth.
2	Mild leaf blotching and scorching on about 10% of leaves with purplish-brown necrotic spots, almost normal plant growth. No stunting and no ear size reduction.
3	Mild definite leaf blotching and scorching on about 20% of leaves with some purplish-brown necrotic spots. Mild stunting and ear size reduction.
4	Some definite leaf scorching on about 30% of leaves with some purplish-brown necrotic spots; some stunting and ear and tassel size reduction.
5	Definite leaf scorching on about 40% of leaves with gray brown necrotic spots; some stunting and ear and tassel size reduction.
6	Definite leaf scorching on about 50% of leaves with mostly brown necrotic spots. Definite stunting. Stem diameter, ear size and tassel size reduction.
7	Definite leaf scorching on about 60% of leaves with severe gray necrotic spots and leaf wilting and rolling. Definite stunting. Stem diameter, ear size and tassel size reduction, often cause severe stalk lodging and husk opening at late growing stage.
8	Definite leaf scorching on about 70% of leaves with definite gray necrotic spots. Conspicuous stunting, leaf wilting and rolling. Stem diameter, ear size and tassel size reduction.
9	Complete leaf scorching of all leaves causing premature death of host plant and no ear formation.

Appendix 2. Mean squares for all variables analysed in a Randomised complete block design for Abuja

Source of variation	d.f.	Mean Squares							
		Day silk inf	Day silk uninf	Plt. ht inf	Plt. ht uninf	*Striga* count1	*Striga* count2	*Striga* rating1	*Striga* rating2
Replication	5	4.276	10.756	1630.370	1099.861	598.437	884.320	8.933	10.254
Genotypes	17	0.839	1.686	297.168**	342.770*	233.312	144.630	2.863**	2.800*
Error	85	0.837	0.991	133.508	163.489	176.170	139.838	1.098	1.473
Mean(rec.families)		59.08	59.45	211.36	246.369	11.16	15.46	4.10	6.07
Mean(TZLCompl-C1)		58.75	59.75	215.83	254.16	17.75	21.66	3.66	6.25
Mean(check 9022-13)		58.33	59.33	221.67	250.00	6.00	15.00	3.00	6.17
Mean(check 8338-1)		58.33	58.83	204.17	265.00	27.50	23.33	5.83	8.17
C.V%		1.55	1.67	5.45	5.15	106.0	71.39	26.95	19.54

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Plt. = plant height.
ht. = height.
uninf. = uninfested.
inf. = infested.
Rec. = recombined.

Appendix 2. (continued)

Source of variation	d.f.	Mean Squares: Ear harv. inf.	Ear harv. uninf.	Ear *Striga* rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Replications	5	62.459	3.993	9.854	6.720	1.987	5987951	18047957
Genotypes	17	12.442	4.318	2.421*	2.682	1.009	3723588**	1757652
Error	85	10.581	7.083	1.136	1.673	0.940	1123942.33	1026016.563
Mean(rec.families)		16.67	19.03	3.96	57.60	62.61	4682.26	6601.6
Mean(TZLComp1-C1)		15.41	18.08	4.08	57.83	58.91	4322.48	6287.80
Mean(check 9022-13)		17.83	19.67	3.00	58.67	59.33	6250.51	6620.31
Mean(check 8338-1)		12.50	19.67	5.50	56.33	58.33	2797.28	6789.37
C.V.%		19.87	14.06	26.58	2.24	1.66	22.92	15.40

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Anth. = Anthesis.
uninf. = uninfested.
inf. = infested.
Rec. = recombined.

Appendix 2. (continued)

Source of variation	d.f.	Mean Squares (derived variables)				
		Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Replications	5	6.556	635.380	3308.666	22.520	71.594
Genotypes	17	3.196*	125.091*	1040.158**	2.068	8.960
Error	85	1.658	62.301	393.689	1.803	17.744
Mean(rec.families)		1.52	13.69	25.94	-0.28	2.47
Mean(TZLComp1-C1)		0.92	14.88	28.76	-1.00	2.66
Mean(check 9022-13)		0.33	11.19	3.40	-1.00	1.83
Mean(check 8338-1)		2.00	22.62	56.93	-0.50	5.83
C.V.%		96.56	55.65	74.24	***	***

*, ** Significant at 0.05 and 0.01 levels respectively.
*** = C.V.'s are over 100 due to environmental effects.
d.f. = degree of freedom.
Rec. = recombined.

Appendix 3. Mean squares for all variables analysed in a Randomised complete block design for Mokwa

Source of variation	d.f.	Mean Squares							
		Day silk inf	Day silk uninf	Plt. Ht inf	Plt. Ht uninf	*Striga* count1	*Striga* count2	*Striga* rating1	*Striga* rating2
Replication	5	3.054	6.172	1677.639	653.148	493.578	2282.454	10.728	6.950
Genotypes	17	0.604	0.711	331.005	102.233	233.118	412.382	2.966**	2.848**
Error	85	0.548	0.611	205.972	136.776	150.378	376.560	1.045	0.703
Mean(rec.families)		54.33	54.14	196.72	217.26	16.03	38.25	4.79	7.47
Mean(TZLComp1-C1)		54.33	54.50	204.16	221.66	19.5	37.50	4.92	7.50
Mean(check 9022-13)		53.83	54.17	209.17	220.00	3.83	23.67	3.67	6.00
Mean(check 8338-1)		54.00	53.33	195.83	221.67	29.67	38.00	6.83	8.83
C.V%		1.36	1.44	7.24	5.36	74.32	51.97	21.03	11.22

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Plt. = plant height.
ht. = height.
uninf. = uninfested.
inf. = infested.
Rec. = recombined.

Appendix 3. (continued)

Source of variation	d.f.	Mean Squares						
		Ear harv. inf.	Ear harv. uninf.	Ear *Striga* rating	Anth. inf.	Anth. uninf.	Yield inf.	Yield uninf.
Replications	5	33.348	6.743	11.720	2.328	5.704	2672790	4526948
Genotypes	17	46.488**	21.258**	5.434**	0.574	0.586	2550505**	1834810*
Error	85	9.215	8.197	1.446	0.394	0.515	570459	883087
Mean(rec.families)		9.44	17.14	5.09	59.64	52.17	2047.52	3803.86
Mean(TZLComp1-C1)		12.92	17.92	5.08	52.25	52.25	1985.93	3558.53
Mean(check 9022-13)		17.33	15.50	2.83	52.33	52.67	3606.66	3875.82
Mean(check 8338-1)		55.30	12.83	7.50	51.67	51.67	711.38	3005.40
C.V.%		23.69	16.94	23.57	1.20	1.38	36.79	25.15

*,** Significant at 0.05 and 0.01 levels respectively.
d.f. = degree of freedom.
Anth. = Anthesis.
uninf. = uninfested.
inf. = infested.
Rec. = recombined.

Appendix 3. (continued)

Source of variation	d.f.	Mean Squares (derived variables)				
		Anthesis silk interval	Percent height reduction	Percent yield reduction	Delay in silking	Ear harvest reduction
Replications	5	0.281	466.987	4681.613	1.481	53.772
Genotypes	17	0.318	58.307	1536.937**	0.978	49.809**
Error	85	0.450	60.859	630.010	1.078	18.078
Mean(rec.families)		2.08	9.170	42.18	0.18	4.18
Mean(TZLComp1-C1)		2.08	7.77	42.86	-0.16	5.00
Mean(check 9022-13)		1.50	4.86	1.40	-0.33	1.83
Mean(check 8338-1)		2.33	11.55	71.34	0.67	7.67
C.V.%		32.06	87.58	60.31	***	***

*, ** Significant at 0.05 and 0.01 levels respectively.
*** = C.V.'s are over 100 due to environmental effects.
d.f. = degree of freedom.
Rec. = recombined.

Appendix 4. Across location (Abuja and Mokwa) estimates of phenotypic variance for high and low selected families in 1994.

Characters	Selected population		
	high	low	mean
Striga count 1	244.734	166.616	205.675
Striga rating 1	1.909	1.364	1.636
Ear *Striga* rating	1.423	1.175	1.299
Yield infested plants	2496763.413	3384010.427	2940386.920
Yield uninfested plants	2368813.419	3791735.829	3080274.624
Anthesis-silking interval	0.697	0.568	0.632
Delay silking	1.243	0.908	1.075