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Journal homepage: <http://www.plantarchives.org>

DOI Url : <https://doi.org/10.51470/PLANTARCHIVES.2024.v24.no.1.194>

HIGH-YIELDING *STRIGA* RESISTANT MAIZE (*ZEA MAYS* L.) HYBRIDS: A REVIEW

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(Date of Receiving-24-01-2024; Date of Acceptance-02-04-2024)

ABSTRACT

Striga hermonthica (Del) Benth is an obnoxious parasitic weed that constitutes one of the devastating constraints in maize production. Many efforts have been made by crop protectionists, weed scientists, and agronomists using different methods to stem this obnoxious weed, however, these have yielded little or no positive results. Developing resistant hybrid host cultivars could have a major impact in reducing crop loss due to *Striga*. Though, the West and Central Africa Maize Network (WECAMAN) and IITA developed some maize varieties or hybrids that combine earliness or extra-earliness with resistance to *Striga hermonthica* through conventional breeding. Selection of parental lines from new source populations with different heterotic groups and appropriate breeding schemes becomes imperative to developing superior hybrids and breeding populations for *Striga* resistance. Combining ability analysis allows unbiased estimation of genetic parameters. Diallel mating design statistically separates parents and progenies performance into GCA and SCA components. This method offers a more effective method of developing high-yielding *Striga* resistance hybrid(s) in maize by crossing between *Striga*-resistant inbred lines and high-yielding but susceptible inbred lines from amongst the pools of parental lines in different heterotic groups.

Key words : Maize breeding, *Striga*, *Striga*-resistant.

Introduction

Maize (*Zea mays* L.) is a major staple food in developing countries. It is ranked third and one of the most important cereals in the world after wheat and rice (Kim *et al.*, 2021). The average yield per hectare of maize production in Southeast Asia and Nigeria is put at 4.8 and 1.69 metric tonnes per hectare respectively. This is far less than the world average yield per hectare of 5.82 metric tonnes (Dukhnytskyi, 2023). Plant breeders and other specialists globally have made tremendous efforts in maize crop improvement in the areas of improved production management, pest management and

development of hybrids with high-yielding potentials, however, arrays of constraints have continued to adversely affect maize production and productivity, especially in the tropics, Asia, Sub-Saharan Africa and other maize growing regions of the world. The most worrisome and devastating constraint is the problem of a parasitic weed, *Striga hermonthica* commonly called witch-weed; “wutawuta” (Hausa) northern Nigeria, which has reached an endemic status in maize growing ecologies of West and Central Africa and some parts of Asia like India, Myanmar, Indonesia, Thailand and the United States (Kim, 1994). The problem of *Striga* has resulted to an annual

yield loss of 20 - 100% in maize, millet and sorghum fields (Jamil *et al.*, 2011). The continued expansion of areas infested by this obnoxious parasitic weed in maize producing belt of the world in general and Nigeria in particular poses threat to meeting the ever-increasing demands for maize grain and achieving global food security. Most efforts made by crop protectionist, weed scientists and agronomist using different methods to stem out this obnoxious weed have yielded little or no positive results. Where positive results are obtained, they have no economic benefits to the poor farmers in the rural areas as they significantly increase the cost of production and impact negatively on the environment (Kanampiu *et al.*, 2018; Mrema *et al.*, 2020). Hence, the need to adopt a breeding scheme to develop high yielding *Striga* resistance hybrid maize varieties which could have a major impact in reducing crop loss due to *Striga*. In light of the above background, this review aims to present the genetic and genomic resources, research progress and opportunities in the genetic analysis of *Striga* resistance and yield components in maize. Information presented in this paper may guide new variety designs in maize for *Striga*-resistance and desirable product profiles.

Genetic variability of maize

Maize genetics is complex and better understood than any other plant species thus facilitated by controlled fertilizations. Maize has been an experimental model plant and the focus of in-depth genetic studies based on the many techniques developed in the field of genetics. A thousand loci which control the qualitative characters in maize have been analyzed, of which 575 have been carefully determined and mapped. All *Zea mays* species and sub species possess 10n chromosomes ($2n=20$) with exception of *Zea perennis*, which has 20n chromosomes ($2n = 40$) (Badu-Apraku and Fakorede, 2017). It has also been reported to possess an abnormal chromosome 10 and a supernumerary B chromosome called selfish chromosome which is believed is devoid of function does not pair or recombine with A chromosome but are transferred in a non-Mendelian manner thereby causing no obvious phenotypic variation (Huang *et al.*, 2016). However, it was discovered to influence A-genome transcription with stronger effect association with an increase in copy numbers of the B chromosomes. At least four 5kb sized genes are located on the B chromosome using Fluorescence *in situ* hybridization (FISH). The primary sequencing of the maize genome was completed in 2008 (Haberer *et al.*, 2005). The genome 85% of which is composed of transposons (jumping genes) was found to contain over 60,000 genes, which is much when compared to the human genome

containing about 26,000 genes (Kaeppeler, 2012). One hundred translocations between A and B chromosomes as well as more than a thousand reciprocal A-A translocations have also been mapped (Kaeppeler, 2012). According to Haberer *et al.* (2005) and Kaeppeler (2012), maize is likely to be an allotetraploid with $n=2x5$. Whitt *et al.* (2002) reported that the DNA amount in the nuclei of maize is as in autopolyploid which occur in steps that behave like 2:4:8:16. That is chromosome number before allotetraploid event was $n = 8$ then doubled to $n=16$ during allotetraploid event then reduced to $n=10$ by diploidization. Gaut *et al.* (2000) explained that genome rearrangement and diploidization followed the polyploidy event. He concluded that the maize genome has been replete with chromosomal duplication and repetitive DNA, a retro transposable element resulting from ancient polyploidy event millions of years after the divergence between sorghum and maize.

Association of characters

Correlation attempts to express the degree and type of association between a pair of variable (Matin *et al.*, 2017). When measuring correlation, it does not matter which variable is dependent and which is independent (Tucker *et al.*, 2020). It measures the magnitude (strong or weak, positive or negative) of association between two characters. The value of correlation (r) ranges from +1 (strong and positive association) through +0 (no association) to -1 (strong and negative association). The intermediate values are moderate association between characters (Kamal *et al.*, 2020).

Correlation studies between yield and yield components and *Striga* resistance parameters in maize have been reported by some workers. According to Jatto *et al.* (2015), yield in maize is highly dependent on the yielding contributing traits like 100 grain weight, cob length, cob weight and number of cob per plant. Selvaraj and Nagarajan (2011) also reported a significant positive association of grain yield per plant with plant height, ear height, ear length (0.87), ear girth (diameter), number of kernels per row (0.86), 100 kernel weights and non-significant positive association with days to tasseling and days to silking, however, a negative non-significant correlation on grain yield per plant with number of rows per ear and crude protein was recorded.

Grain yield per was reported to have a positive and significant phenotypic and genotypic correlation with days to maturity 0.78,0.61; ear length 0.71,0.45; number of kernels per row 0.67, 0.45; plant height 0.65,0.44; 1000-kernel weight 63, 0.50 and ear height 0.56, 0.37 respectively (Belay, 2018). In a similar studies conducted

by Khan *et al.* (2018), a positive genetic correlation between grain yield and plant, ear height, ear weight and kernel row per ear was recorded, however, the investigation revealed a negative correlation between grain yield and days to 50% silking and days to 50% tasseling.

According to the findings of Sangaré *et al.* (2019), significant positive correlation was found between grain yield, plant height and ear per plant while a significant negative correlation existed between grain yield and days to 50% tasseling, days to 50% silking, *Striga* damage rating at 10 WAP, however, the correlation of grain yield with ASI, ear height and *Striga* emergence (count) at 8 and 10 WAP were not significant. Olakojo and Olaoye (2011), reported significant positive phenotypic and genotypic correlation coefficients for *Striga* emergence count with maize agronomic traits whereas, *Striga* count was negatively correlated with *Striga* syndrome rating.

Combining ability in Maize

Combining ability analysis is employed to identify parents that are better combiners which can be hybridized to exploit heterosis and to select better crosses for direct use or further breeding work (Konate *et al.*, 2017; Murtadha *et al.*, 2018; Yao *et al.*, 2013). General combining ability (GCA) and specific combining ability (SCA) in crop experiments and their use in the analysis of diallel was introduced by Sprague and Tatum (1942), which help plant breeders to statistically separate the parents and progenies performances into GCA and SCA components. According to them, in an unselected material, genes with additive effects (general combining ability) are more common or produced greater effects than dominant and epistatic genes, thus making single cross tests most satisfactory in the determination of most specific combinations even though differences in the GCA are also revealed.

Fischer *et al.* (1932), recognized three components of hereditary variance:

- i) An additive portion describing the difference between homozygotes at any locus,
- ii) A dominance component arising from interactions of alleles (intra-allelic interaction),
- iii) An epistatic part associated with interactions of non-alleles (inter-allelic interaction or epistasis).

This classification has been proved useful both in describing types of gene action and in estimation of the magnitude of various types of gene action (Allard, 1960).

The information on the combining ability and gene action are not only important but very useful to breeders particularly if the inbred parents represent a selected elite

group of lines that are possible candidates as parent seed stock for the production of single cross hybrid (Hallauer *et al.*, 2010).

Plant breeders observe and measure phenotypes that are expression of genotypes in a particular set of environments. The environmental 'noise' is a very important parameter in maize breeding because the contrasts among genotypes may change and evidence shows that when they do, it becomes necessary to evaluate the genotypes in different environments (Hallauer *et al.*, 2010). Many authors have carried out Diallel experiments in varying environments in order to determine the extent to which combining ability and gene action influence the environment. Such influence could arise from difference in location, years, season, incidence of disease and pest.

Matzinger *et al.* (1959), conducted multi-locational maize diallel trial over years to determine the degree of genotype x environmental interaction. They observed significant differences in the general combining ability (GCA) × years, GCA × years × locations and specific combining ability (SCA) × locations in the traits studied. Kim and Ajala, (1996), investigated combining ability of ten inbred lines of tropical and temperate × tropical origins developed at IITA. The characters studied were grain yield, plant height, days to silking, ear aspect and root lodging. The forty-five single cross hybrids were evaluated in three environments in two seasons in the forest ecology. The third environment was in northern guinea savanna. Highly significant environment and entries mean squares were obtained for all traits and despite all the factors that were identified to possibly influenced heterosis and combining ability, the superiority of the savanna ecology for maize production in Africa was manifested (Bahari *et al.*, 2012) in their works on water melon reported a statistically significant GCA and SCA and their interactions suggesting that additive and non-additive gene effects were important in the inheritance of the characters studied and being greatly influenced by the environment.

Gene action and combining ability for disease and pests can be easily evaluated using diallel analytical technique. Sangaré *et al.* (2018), reported a significant GCA and SCA effects for most characters studied under *Striga*-free and *Striga* infested field, however the GCA effect had higher proportion of variance over the SCA effect thereby suggesting the control of additive gene effects on the inheritance of yield and *Striga* resistance. Similar results were also reported by Amiruzzaman *et al.* (2013), Fan *et al.* (2018), Badu-Apraku and Oyekunle (2012), Badu-Apraku and Fakorede (2017) in their

separate works. However, Olakojo and Olaoye (2005), Olaoye and Bello (2009) in their separate works reported low GCA and SCA effects on *Striga* related characters (*Striga* damage syndrome and *Striga* emergence counts) suggesting that both additive and dominant gene actions were involved in tolerance to *Striga hermonthica*. Kim (1994) used some inbred lines of maize investigated in research to study the genetics of maize tolerance to *Striga hermonthica*. His findings brought about far-reaching conclusions on the combining ability and gene action and how they are influenced by the environment to bring about the expression of resistance. These are:

- i) That the gene controlling tolerance to *Striga* were quantitatively inherited,
- ii) That two different types of gene action were responsible for the traits studied, with additive gene action playing a major role in *Striga* emergence,
- iii) That breeders could combine selection for host plant tolerance with low *Striga* emergence.

Heterosis

Heterosis or hybrid vigor is regarded as the converse of the deterioration that accompanies inbreeding. It is an aspect of heterozygosity, which is defined in terms of the superiority of F_1 hybrid over the better parent. Heterosis manifest in two directions i.e positive heterosis as in yield, ear weight, number of grains per row etc. or negative heterosis as in plant height and days to maturity (Vanipraveena *et al.*, 2022). The larger degree of heterosis according to Mackay *et al.* (2021) is encountered in cross pollinated crops than in self-pollinated crops. Nevertheless, the hybrid vigor in both cases is substantially increased on crossing of genetically diverse inbreds more than on the crossing closely related ones.

Most evidences in maize studies suggests that the genetics of heterosis is due to partial to complete dominance rather than over dominance (Akaogu *et al.*, 2020; Maioli *et al.*, 2020). The evolution of F_1 hybrid in the field of plant breeding did not only revolutionized maize breeding schemes, but has also constituted the foundation of the maize seed industry. The persistence of heterosis in the maize industry is necessary for commercial exploitation as the hybrid with significant heterosis could be recommended for commercialization. Past studies have revealed economic and standard heterosis for some desirable trait like earliness, grain yield, plant height, ear diameter, ear length etc.

In maize, the first studies on artificial hybridization

for yield was reported by Bearl in 1880 were 40% yield increase for the hybrids than the higher parents was reported (Kaeppler, 2012). Springer and Stupar (2007) reported 12 out of 15 maize hybrids exceeded their higher parent in yield and the mean of all the hybrids relative to their higher parent was 111.5 per cent. Amiruzzaman *et al.* (2013) in their work on diallel cross involving maize elite inbred lines reported heterosis value of -17.60 to 9.71% for grain yield, -2.44 to -42.11% for plant height and -0.10 to -4.42% for days to flowering. Meena *et al.* (2018) reported 56.65% economic heterosis for grain yield in dual purpose sorghum.

Striga Resistance in maize

Breeding for *Striga* resistance involves challenging crop germplasm with *Striga*, identifying and selecting the best performing genotypes in the pool through effective screening methods (Dossa *et al.*, 2023). The level of resistivity or susceptibility of *Striga* is determined by *Striga* counts and the extent of damage to the crop in breeding plots. This further determines whether a better performing variety is tolerant *i.e.* supports the same number of emerged *Striga* as the susceptible check with no damage, resistant *i.e.* fewer emerged *Striga* and no visible damage than susceptible check or immune *i.e.* no emerged *Striga* as well as no attachment and damage symptom. Immunity is not often durable because it frequently involves the function of just a few genes (oligogenic). This creates selection pressure for a corresponding virulence gene to overcome the immunity (Allard, 1960). Single gene immunity may thus become ineffective within a few years, canceling all progress made. Tolerance and resistance are usually based on larger number of genes and more durable in developing a resistance genotype. Identifying the specific genes controlling the trait can be very elusive because the expression of these genes can change with change in environment.

Sources of Resistance to *Striga* in maize

Sources of *Striga* resistance in maize have been reported in two *Striga* tolerant inbreds, TZI3 derived from Tuxpeno \times IITA streak resistance crosses and TZI 25 (9450 STR) derived from B73, a low stimulant producer from US Corn Belt germplasm, where tolerance is inherited quantitatively by multiline system (Menkirand Meseke, 2019). These two inbred lines have been used extensively for *Striga* resistance hybrid combination (Adetimirin *et al.*, 2000; Kolawole *et al.*, 2019). Crops' wild relatives have been reported in many studies to provide a broad genetic pool for breeding purposes. Wild relatives of maize and sorghum such as *Tripsacum*

dactyloides, *Zea diploperennis* and WSA-1, WSE-1, WSA-2 respectively and also N13, a sorghum land race have been identified to be useful in breeding maize and sorghum for *Striga* resistance (Mbuvi *et al.*, 2017; Yallou *et al.*, 2009). 5QTLs associated with *Striga* resistance through creation of barriers for attachments in WSA-1 WSE-1 and WSA-2 was reported by Mbuvi *et al.* (2017). Resistance to *S. hermonthica* has successfully been transferred from *Zea diploperennis* into maize, leading to the development of resistant inbred lines and synthetics (Yallou *et al.*, 2009). Hybridization between the above genotypes (sorghum) and maize have been reported to offer great potential as a source for *Striga* resistance in maize (Dawud, 2017).

Life cycle of *Striga hermonthica*

Striga seeds survive in the soil for more than ten years, but once the seed germinates, the endosperm can only support its life for only 3 to 7 days hence the germinated *Striga* seed must establish a parasitic relationship with a host, failure to which it dies (Fig. 1) (Konate *et al.*, 2017; Kountche *et al.*, 2013). The germination of *Striga* seeds is triggered by the emission of biochemical sesquiterpene lactone compounds from the root of the host plants called Strigolactone. The host produce Strigolactones for regulation of shoot and root branching as well as symbiotic relations with *Arbuscular mycorrhizal* fungi also known as bio-fertilizer which help in growth regulation and tolerant to environmental stress (Aslani *et al.*, 2019; Begum *et al.*, 2019; Piliarová *et al.*, 2019). Once the *Striga* seeds are in the proximity of the host plants roots, they encounter these stimulants (strigolactone) resulting to their germination. The root tips of germinating *Striga* seeds grow chemotropically in the direction of the host roots for attachment (Mutuku *et al.*, 2015) The minute root tip establishes contact with the host root, the host produces haustorium inducing factors which include various quinones, flavonoids and phenolic acids supporting the formation of the *Striga* haustorium (Yoshida *et al.*, 2019). The root tip develops swelling and forms haustorial hairs that act as attachment peg to the host root and penetrates the host cell, the host and parasite are connected via xylem-bridge (Yoshida and Shirasu, 2012).

Penetration is usually completed within 48 to 72 hours once contact has been made. *Striga* starts growing upwards and the developed adventitious roots may form a secondary attachment with other host roots. In 4 to 8 weeks, *Striga* emerges above the soil and starts photosynthesis (Yoshida and Shirasu, 2012). Although *Striga* carries out photosynthesis, the carbon fixation

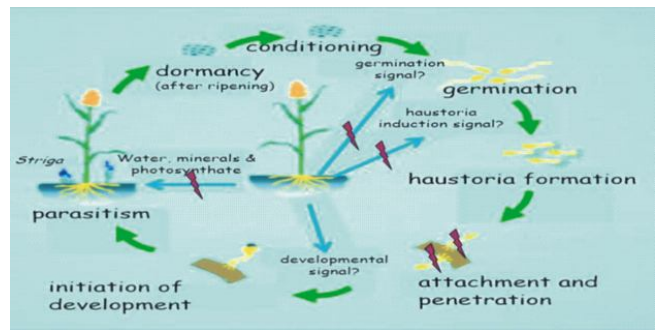


Fig. 1 : Illustrated *Striga* life cycle (Ejeta and Butler, 1993).

occurs at insufficient levels, so it continues depending on the host plant for sufficient carbon supply (Jamil *et al.*, 2011). According to Spallek *et al.* (2013) and Yoshida *et al.* (2019), *Striga* flowering occurs 4 weeks post-emergence, and pollination takes place, and the seeds mature in seed pods for 4 weeks, cracks and further deposit the seeds back to the soil. The host plant is significantly affected by *Striga* parasitism, and exhibits stunted growth, drought stress characteristics, wilting and low yield (Akaogu *et al.*, 2020).

Mechanism of Resistance

Striga parasitizes crops and propagates itself in a sequential process, germination, attachment, intoxication of its host, subterranean growth, emergence, flowering and seed production (Jamil *et al.*, 2022). Crop plant might be able to resist *Striga* at any of these stages. Combining different resistance mechanism through breeding may increase over all resistance and make the resistance more durable. Different genotypes react differently to *Striga* infestation. Genotypes with low stimulating efficiency may produce weak chemical stimulant, and less extensive root system to avoid contact with *Striga* seeds, though they may be severely damaged as the susceptible ones. Another genotype may produce stimulant to stimulate *Striga* seeds germination, allow its emergence and reduce its vigor hence, resistant genotype. Lastly, another genotype may stimulate *Striga* germination, allow it to attach, grow and reproduce normally, but do not suffer much from the intoxication effect. These genotypes are tolerant; this does not reduce parasitism in *Striga* seed production, which will attack the following crop. Genes responsible for the low production of strigolactone stimulants *lgs* genes have been identified in some genotypes of maize. Mutant alleles at the *lgs1* locus which codes an enzyme known as a sulfotransferase in a mutant sorghum (SRN39), a homozygous recessive genotype has been reported to be responsible for the change of dominant strigolactone (5-deoxystrigol) to orobanchol (strigolactone with opposite stereochemistry) which is also required for the normal growth and

development of the host plant (Gobena *et al.*, 2017). This drastically reduced germination of *Striga* and its infestation. However, other genotypes may produce stimulants to stimulate *Striga* seeds germination, allow its emergence and reduce its vigor, hence, resistant genotype. On the other hand, other genotypes may stimulate *Striga* germination, allow it to attach, grow and reproduce normally, but do not suffer much from the intoxication effect. These genotypes are tolerant; this does not reduce parasitism in *Striga* seed production, which will attack the following crop. However, it will be useful if the above mechanisms can be genetically combined in the right crosses and selection procedures into one genotype for maximum durable resistance (Amusan *et al.*, 2008).

Breeding of *Striga* Resistant Varieties and Conclusion

Breeding of genetically resistant crops to *Striga* weed constitutes the most economical, practical and reliable approach to solving this problem (Menkir and Meseka, 2019; Sangaré *et al.*, 2019). This approach has been successfully used in sorghum which produced low stimulant (Mbuvi *et al.*, 2017). The observation that different breeding lines of maize reacted differently to *Striga* indicates possible genetic differences in varietal susceptibility (Akaogu *et al.*, 2020). International Institute for Tropical Agriculture (IITA), Institute of Agricultural Research (IAR), ICRSAT and CYMMYT have all taken the challenge to develop lines that are resistant or tolerant to *Striga* through the adaption of various breeding strategies programs, which include conventional (Menkir and Meseka, 2019; Sangaré *et al.*, 2019) and Molecular Assisted Backcrossing (MAS) using Diversity Array Technology (DART) (Ali *et al.*, 2016), Simple sequence repeat (SSR) or microsatellites (Badu-Apraku *et al.*, 2020; Yohannes *et al.*, 2015), Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) to examine the genetic relationships among these lines and to determine the level of genetic diversity that exists within and between their source populations.

So far, efforts by researchers have yielded positive results with the discovery and identification of different *Striga* resistant lines. Open pollinated varieties ACR 97 TZL Comp-1-W and Sammaz 17 have been reported to show tolerance to *S. hermonthica* (Garba *et al.*, 2017), while TZL Comp1syn W-1 (Sammaz 16) and IWDC2Syn W-1 (Sammaz 15) have been reported to be resistant to *Striga*. Oba super 1 hybrid has also been reported to exhibit lower *Striga* count and damage when compared

to farmers local variety in Nigeria (Kureh *et al.*, 2003). Menkir and Meseka (2019), reported a marginal increase in productivity and remarkable linear reduction in *Striga* damage and emergence in 34 hybrids grown in *Striga* infested area. However, they do not show immunity to the parasite. The above materials may be sources of multigenic or polygenic and multi strain resistance. Reliance on resistance or tolerance alone for effective control of *Striga* in maize may be probably not possible as maize genotypes rely on many defense mechanisms to evade the parasite (Menkir and Meseka, 2019). Supplementing the use of resistant maize hybrid by control practices that preclude the presence of flowering to avoid re-infestation of the field becomes imperative.

Acknowledgements

I am grateful to the Nigeria government through Tertiary Education Trust Fund (TET fund) and my organization Federal College of Education, Yola, Adamawa Nigeria for granting me the scholarship to pursue my PhD program at University Putra, Malaysia (UPM). I am thankful to the Institute of Tropical Agriculture and Food Security (ITAFOS) and the Faculty of Agriculture, Universiti Putra, Malaysia for providing research supports and facilities.

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