



Application of Marker Assisted Selection for Striga Hermonthica Resistance on Sorghum (*Sorghum bicolor* (L.) Moench

Habtamu Demelash Tamir^{1*}

¹*Ethiopian Institute of Agricultural Research (EIAR), Assosa Agricultural Research Center, Assosa, Ethiopia.*

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

Sorghum (*Sorghum bicolor* L. [Moench]) is a staple food crop for smallholder farmers in arid and semi-arid(ASALs) regions worldwide, feeding over 500 million of the world's most resource-poor. Development of *Striga Hermonthica* resistant cultivars by conventional breeding is slow and have been hampered by the lack of efficient and reliable screening techniques in breeding programs. Molecular markers that are linked to witchweed resistance can expedite the development of resistant cultivars through the adoption of appropriate marker-assisted selection (MAS) strategies. Marker-assisted selection involves the selection of genotypes carrying a desirable gene(s) via linked markers; through MAS more rapid transfer of traits from donor parents to more elite locally adapted crop cultivars is possible with simple-sequence repeat (SSR) markers which have been initially used to detect polymorphism between the parent cultivars. Although costly to develop relative to some other classes of genetic markers, once developed, analysis by SSR markers is both easy and inexpensive. The highly polymorphic nature (high information content) and other favorable characteristics make them excellent genetic markers for a number of studies including marker-assisted selection and fingerprinting of germplasm collections. In this review, we summarize the molecular markers that are linked to the inheritance trait or low germination stimulant production is one of the recognized mechanisms of witch weed resistance.

*Corresponding author: E-mail: habtedeme@gmail.com;

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1. INTRODUCTION

Sorghum is a diploid grass ($2n=20$) and it's emerging as a model crop species in a second position among the staple food grains in the ASLs [1]. It remains a critical component of food security for more than 300 million in Africa and it is a staple crop for more than countries [2]. It is a versatile crop used for food, feed, and fuel, building materials and alcoholic beverages to millions of people in the ASALs of the world [3]. Sorghum is also increasingly gaining importance as a source of livestock feed and biofuel [4]. Globally, it is grown in at least 86 countries, on an area of 47 million hectares (ha), with annual grain production of 69 million tonnes and average productivity of 1.45 t/ha (reference). Sorghum is ranked second, after maize as the most significant cereal crop in drought-prone areas, particularly in sub Saharan Africa where it originated [5].

Parasitic plants are a major threat to today's agriculture and provide an intriguing case of pathogenesis between species of relatively close evolutionary ancestry [6]. Almost all crop species are potential hosts for parasitic plants, but severe disease outbreaks are usually restricted to certain host-pathogen combinations [6]. Among the 23 species of *Striga spp* prevalent in Africa, *Striga hermonthica* is the most socio-economically important weed in eastern Africa. *S. hermonthica* is particularly harmful to sorghum, maize, millet infestation also increasingly being found in sugarcane and rice fields [7].

Molecular marker-assisted selection, often simply referred to as marker-assisted selection (MAS) involves the selection of plants carrying genomic regions that are involved in the expression of traits of interest through molecular markers [8]. MAS which is sometimes referred to as genomics is a form of biotechnology which uses genetic fingerprinting techniques to assist plant breeders in matching molecular profile to the physical properties of the variety [9]. It is the identification of DNA sequences located near genes that can be tracked to breed for traits that are difficult to observe [10].

The ability to associate quantitative phenotypic data with genetic maps has helped to increase the inheritance of complex agronomic traits in sorghum such as stay green, seed weight stability and yield stability [11], which is

beginning to lead to marker assisted in plant breeding. However, the application of this technology is still relatively new, and it may take some time before marker assisted selection (MAS) becomes a routine operation in most sorghum breeding programs [12].

Damage to crops is often severe because *Striga* has a remarkably bewitching effect on the host plant it invades [12]. Effective control of *Striga* has been difficult to achieve through conventional agronomic practices, since the parasite exerts its greatest damage before its emergence above ground provides evidence for host plant infection [12]. Estimates on the extent of crop damage in a country or region in the African continent vary depending on the crop cultivar and degree of infestation [13].

A number of control measures that have been tried are either not successful or are not feasible economically [14]. Integrated management strategies with host plant resistance as their backbone are believed to be the only solution [12]. However, this integrated approach had limited success, since efforts to identify germplasm with resistance to *Striga* parasitism generally failed [14]. This is due to the difficulty in selection for resistance in field tests, where unpredictable environmental factors influence *Striga* infestation [14]. Some *Striga* resistance genes are also recessive, increasing the time required for, and difficulty of conventional backcross schemes. Breeding for *Striga* resistance in the field is difficult because of the quantitative nature of the trait and strong influence of the environment on its expression [12]. Hence, this review aims to provide the summary of tightly linked to previously identified *Striga* resistance QTLs and the map and locate QTLs for *Striga* resistance by applying MAS breeding for *Striga* resistant sorghum varieties [15].

2. MARKER ASSISTED SELECTION AND MOLECULAR MARKER FOR CROP IMPROVEMENT

Marker-assisted selection involves the selection of genotypes carrying a desirable gene(s) via linked markers, through marker-assisted selection (MAS); more rapid transfer of traits from donor parents to more elite locally adapted crop cultivars is possible. Recently utilization of molecular markers in breeding programs has received considerable attention using different

crossing schemes [16]. The identification of the molecular markers for specific *Striga* resistance mechanisms facilitates faster introgression and pyramiding of genes controlling this important trait. In the few studies that relate to the other *Striga* resistance mechanisms, [17] identified and mapped QTLs associated with *Striga* resistance in the sorghum variety, N13, where the mechanical barrier is the suggested mechanism of *Striga* resistance.

Molecular markers are identifiable DNA sequence, found at specific locations of the genome and associated with the inheritance of a trait or linked gene [18], refer to molecular markers as naturally occurring polymorphism which include proteins and nucleic acids that are detectably different. Rapid advances in genome research and molecular biology as led to the use of DNA markers in plant breeding. Target genes in a segregating population can be identified with the assistance of DNA makers so as to accelerate traditional breeding programs [18].

Markers must be polymorphic they must exist in different forms so that the chromosome carrying the mutant gene can be distinguished from the chromosome with normal gene by form of the marker it carries [19]. Polymorphism can be detected at three levels morphological, biochemical or molecular [19].

The invention of molecular markers has significantly enhanced the effectiveness of breeding for *Striga* resistance [12]. Significant progress has been made to identify molecular markers associated with *Striga* resistance in sorghum under field conditions [14]. The theoretical advantages of using genetic markers and the potential value of genetic marker linkage maps and direct selection in plant breeding were first reported by [20]. However, it was not until the advent of DNA marker technology in the 1980s, that a large enough number of environmentally insensitive genetic markers were generated to adequately follow the inheritance of important agronomic traits and since then DNA marker technology has dramatically enhanced the efficiency of plant breeding [9]. The DNA-based molecular markers have acted as versatile tools and have found their own position in various fields like taxonomy, plant breeding, and genetic engineering [9].

3. MARKERS USED IN INTROGRESSION

In sorghum molecular genetics maps have been developed and positions of various DNA markers

have been reported [21]. Genetic linkage maps of sorghum harboring restriction fragment length polymorphism (RFLP) markers [22], AFLP [23], SSR [24], RAPD [11,25] and EST-SSR [19] markers have reported. The use of SSR markers for the genetic analysis and manipulation of important agronomic traits is becoming increasingly useful in sorghum improvement [19]. Molecular markers have been used in sorghum to identify quantitative trait loci QTL for many complex traits, including resistance to the parasitic weed *Striga* [20]. Five genomic regions (QTL) associated with stable *striga* resistance from resistant line N13 have been identified across a range of 10 field trials in Mali and Kenya and two independent samples of a mapping population involving this resistance source, indicating that the QTL are biological realities [14].

4. SIMPLE SEQUENCE REPEAT (SSR) MARKERS

Simple sequence repeats (SSR) are regions of DNA that consist of short, tandem repeated units (2-6 bp in length) found within the coding or noncoding regions of all eukaryotic organisms [26]. If nucleotide sequences in the flanking regions of the microsatellite are known, specific primers (generally 20–25 bp) can be designed to amplify the microsatellite by polymerase chain reaction (PCR). Different alleles can be detected at a locus by PCR using conserved DNA sequences flanking the SSR as primers. SSR markers have been used initially to detect polymorphism between the parent cultivars [27].

Although costly to develop relative to some other classes of genetic markers, once developed, analysis by SSR markers is both easy and inexpensive. The highly polymorphic nature (high information content) and other favorable characteristics make them excellent genetic markers for many types of investigations, including marker-assisted selection and fingerprinting of germplasm collections [28]. Different alleles can be detected at a locus by PCR using conserved DNA sequences flanking the SSR as primers. Combined, these maps include over 800 markers [29]. Based on a series of field evaluations of two independent recombinant inbred lines (RILs), [30] also confirmed the position and the stability of the identified the QTLs.

Table 1. SSR markers used for background selection in BC3S4& BC4F1 populations

Marker	Forward	Reverse
Xtxp050	TGATGTTGTTACCCTTCTGG	AGCCTATGTATGTGTTTCGTCC
Xtxp065	CACGTCGTCACCAACCAA	GTTAAACGAAAGGGAAATGGC
Xcup033	GCGCTGCTGTGTGTTGTTT	ACGGGGATTAGCCTTTTAGG
Xtxp274	GAAATTACAATGCTACCCCTAAAAGT	ACTCTACTCCTCCGTCCACAT
Xtxp013	TCTTTCCCAAGGAGCCTAG	GAAGTTATGCCAGACATGCTG
Xtxp197	CACGACGTTGTA AACGACGCGTCAATTAATCCAAACAGCCTC	GAGTTCCTATTCCCGTTCATGGTGAT
Xtxp225	TTGTTGCATGTTGGTTATAG	CAAACAAGTTCAGAAGCTC
Xiabtp515	TGCCACATCGATCTTGTCAC	AGGCAGTCACCCACACTACC
XmsbCIR268	CACGACGTTGTA AACGACGCTTCTATACTCCCCTCCAC	TTTATGGTAGGATGCTCTGC
Xcup037	CCCAGCCTTCCTCCTGATAC	GTACCGACTCCAATCCAACG
Xiabtp500	CACGACGTTGTA AACGACTTGTGCTGGTAGACGTGGTC	GCATTGGTATCCAAGTCAA
Xtxp014	GTAATAGTCATGACCGAGG	TAATAGACGAGTGAAAGCCC
Xtxp56	TGTCTTCGTAGTTGCGTGTTG	CCGAAGGAGTGCTTTGGAC
Xtxp296	CACGACGTTGTA AACGACCAGAAATAACATATAATGATGGGGTGAA	ATGCTGTTATGATTTAGAGCCTGTAGAGTT
Xtxp080	CACGACGTTGTA AACGACGCTGCACTGTCTCCACAA	CAGCAGGCGATATGGATGAGC
Xtxp317	CCTCCTTTTCCTCCTCCTCCC	TCAGAATCCTAGCCACCGTTG
Xisep346	CACGACGTTGTA AACGACCGCTCCTCAGGCTCCTCT	TCCTCGAGCACCTGGTTG
Xiabtp444	CACGACGTTGTA AACGACCCTTCTCCACCTCCGTTCTC	GGGAGAGAGAGGGGTCCATA
XmsbCIR223	CACGACGTTGTA AACGACCGTTCCAATGACTTTTCTTC	GCCAATGTGGTGTGATAAAT

Table 2. Linkage group (LG), position and support interval for a LOD decrease of 1.0 (sup. int.), flanking marker interval, LOD score, partial coefficient of determination (R²) and estimated additive effect (a) of the QTL detected in the two sets of RIP-1

LG ^b	Position in Centimorgans (sup. int)	Flanking Marker interval	LOD ^c	R ²	a ^d	C ^e
A	170(165-180)	33/50-561; txp 302	2.9	10.7	0.7	1
B1	15(5-30)	umc88; txp 1	2.7	10.3	0.7	2
B2	95(80-100)	txp296; 14/48-181	2.5	9.5	0.6	1
B2	5 (0–25)	txp197; txp 050	3	11.6	0.8	3
C	0 (0–15)	14/48-324; bnl 5.37	3.4	12.7	0.7	3
C	125 (115–130)	11/60-85; 14/48-173	3	11.2	0.7	4
D	110 (95–125)	txp327; bnl5.40	2.7	10.2	0.8	3
F	35 (20–50)	sbage03; 12/47-545	3.1	11.7	0.9	4
G	110 (90–125)	14/48-316; txp141	2.9	10.9	-0.8	2
I	15 (5–20)	txp6; 14/60-343	4.4	16	0.9	4
I	150 (145–150)	lgs_Bgu; lgs_Sko	6.4	22.5	1.1	5
Percentage of genetic variance explained by ^f			86.1			
A	170 (160–180)	33/50-561; txp302	4.9	18.8	1.4	4
B1	0 (0–10)	txp201; umc88	5.8	21.9	1.3	5
B2	90 (80–100)	txp296; 14/48-181	5	18.9	1.4	5
C	15 (0–20)	14/48-324; bnl5.37	3.5	14.1	1.1	3
C	70 (55–75)	12/61-313; 12/47-143	2.9	11.3	1	3
E	55 (50–65)	14/48-338; 14/50-288	2.8	11.1	1.1	2
E	145 (130–150)	isp 344; cup057	3.6	15.7	-1.4	4
I	60 (55–65)	12/61-53; txp145	4.2	16.2	-1.2	5
I	150 (145–150)	lgs_Bgu; lgs_Sko	12.7	41.5	2.4	5
Percentage of genetic variance explained by ^f			86.1			

Set 1, 116 F3:5 lines tested in 1997; set 2, independent sample of 110 F3:5 lines tested in 1998; ^bLinkage grouped according to [24]; ^cEmpirical LOD threshold values for QTL significance were 2.78 and 2.90 in sets 1 and 2, respectively ($\alpha=0.25$); QTL with LOD scores below these thresholds are suggestive; ^dAdditive effect: half of the difference between the two homozygotes. Positive values, resistance allele was contributed by resistance donor IS9830; negative values, resistance allele was derived from striga-susceptible parent E36-1; ^eNumber of calibration runs in which the respective QTL was detected during the fivefold cross-validation; ^fValue corrected for QTL × environment interaction

For foreground and background selection, markers have been investigated by [31] and [32] who reported a case that a QTL is an estimated gene with unknown position, introgression a favorable allele of the QTL by recurrent backcrossing could be powerful for improvement, provided that the expression of the gene(s) is not reduced in the recurrent genomic backgrounds. Generally, molecular markers can very effectively increase the efficiency of backcrossing by background selection for the genotype of the recurrent parent, with or without foreground selection for the donor parent alleles at markers in the region of the genome controlling the target trait [33].

5. BIOLOGY OF *STRIGA*

Striga seeds are very small and possess limited energy reserves compared to those produced by facultative parasites or free-living angiosperms [12]. Germination of *Striga* seeds appears to improve with long-term dry-seed storage. A chemical stimulus produced by host roots elicits parasitic seed germination, but an additional metabolic process needs to take place before the seed can respond to this external stimulus with germination. There is preparatory process known, as conditioning which requires exposure of the *Striga* seed to warm and moist environment so that the imbibed seed may respond to chemical stimulants of germination. Essential metabolic pathways appear to operate in the seed during the conditioning process leading to respiration and synthesis of proteins and hormones that would be involved in subsequent steps of parasitism [34]. *Striga* seeds that have after-ripened and conditioned will germinate in response to minute levels of exudates released by host roots. If the environmental conditioning has prepared seeds to germinate but no host stimuli is available in its proximity, *Striga* possesses an unusual but valuable capacity of entering "wet-dormancy," an ability to revert to a dormant state, which is reversible after desiccation [35].

Generally, *Striga* germination is controlled by a group of sesquiterpene derivatives including strigol, first isolated from cotton (*Gossypium* spp.) [36], which is not a *Striga* host [36].

reported the isolation of a sorgolactone as the major *Striga* germination stimulant exuded by sorghum roots. About the same time, [37] reported the identification of alectrol as the major germination stimulant from cowpea, and [38] isolated sorgolactones also from maize and proso millet (*Panicum miliaceum* L.). It is believed that endogenous ethylene plays a key role in the response of *Striga* to these germination stimulants [39]. Germinated *Striga* seeds attain a brief period of free-living state with an elongated radicle which may grow to a length of a few millimeters just on the small seed reserve.

6. *STRIGA* RESISTANCE MECHANISMS

Striga is an obligate parasite the interaction between *striga* and its host plant play a crucial role in the survival of the parasite. The following resistance mechanisms have been proposed [12]. Low production of germination stimulant, one of the better-understood mechanisms of resistance against *Striga* by sorghum is low production of compounds by the host root that *Striga* seeds require as stimulants for germination. Mechanical barriers (lignification of cell walls); e.g. with this mechanism is N13 and Framida [40]. Inhibition of germ tube exoenzymes by root exudates; Phytoalexin synthesis; kill the attached *Striga*, hence does not penetrate host tissues or develop further.

Post-attachment hypersensitive reactions or incompatibility: characterized by the appearance of necrotic zones around the site of attempted infection [41]. Death of host cells results in un successful establishment of the parasite hence its ultimate demise. Examples of sorghum genotypes with this mechanism are Framida, Dobbs, SAR 16, SAR 19, SAR 33, Sorghum Versicolor and wild sorghum accession P47121 [12,40]. Antibiosis, i.e., reduced *striga* development through Unfavorable phytohormone supply by the host, This mechanism is present in SRN 39 and N13, Insensitivity to *striga* toxin (maintenance of stomatal aperture and photosynthetic efficiency); Avoidance through root growth habit (fewer roots in the upper 15±20 cm). Absence of a haustorial induction compound in root exudates is unlikely to be a resistance mechanism in sorghum [42].

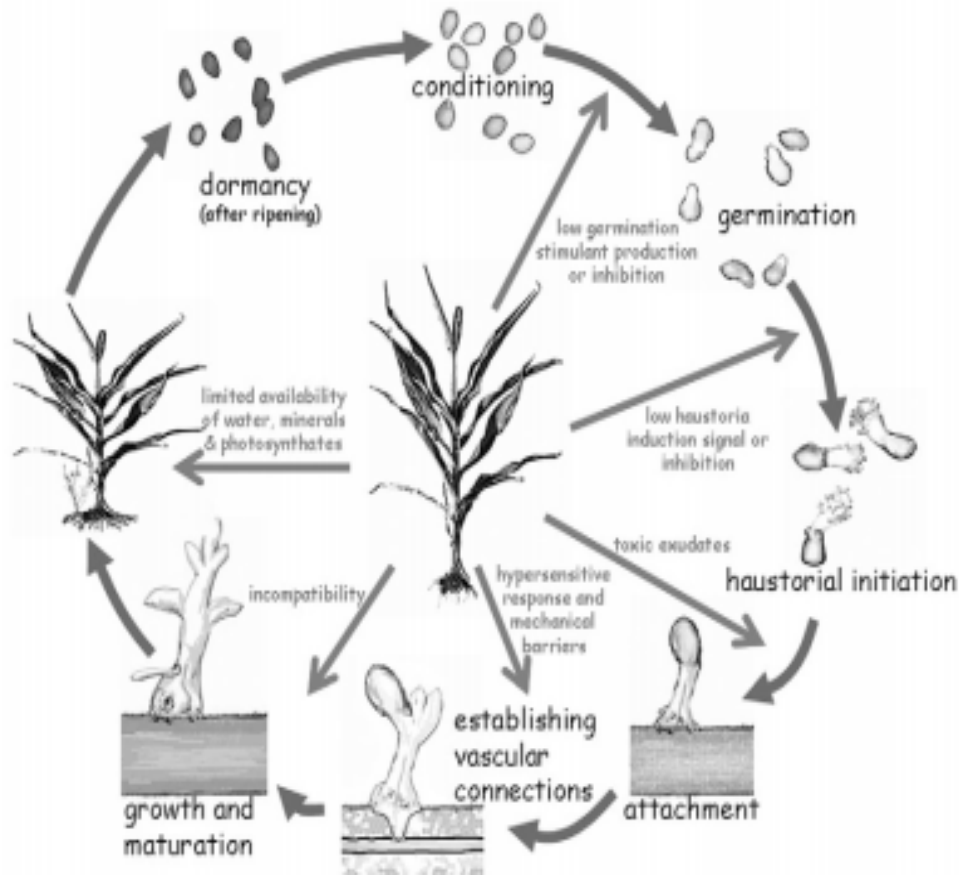


Fig. 1. The *Striga* life cycle showing intricate association between the parasite, its hosts and the environment with potential sites for genetic exploitation

7. GENETICS OF RESISTANCE OF *STRIGA*

strigolactones have a role in the development of root system architecture was the finding that *Arabidopsis* mutants in the strigolactone response or biosynthesis have more lateral roots than the wild type [43]. Accordingly, treatment of seedlings with GR24 (a synthetic and biologically active strigolactone [44] repressed lateral root formation in the wild type and the strigolactone-synthesis mutants (MAX3 and MAX4) but not in the strigolactone-response mutant (max2), suggesting that the negative effect of strigolactones on lateral root formation is (max2) dependent [45]. This negative effect on lateral root formation was reversed in *Arabidopsis* under phosphate deficiency [45]. Strigolactones are also suggested to regulate primary root length. GR24 led to elongation of the primary root and an increase in meristem cell number in an MAX2-dependent manner [45,46].

8. GENETIC MAPPING IN SORGHUM

The first group of genetic linkage maps of sorghum consisted primarily of RFLP markers derived from maize probes [47-49]. Comparison of these maps with those of maize revealed a high degree of synteny between the two genomes also noted that many of the probes which mapped to a single locus in sorghum were duplicated in maize, suggesting possible duplication events in the evolution of maize after its divergence from sorghum [47,49]. These early maps, however, did not contain enough markers to resolve ten linkage groups, which is the haploid chromosome number for sorghum.

[50] Published the first 'complete' linkage map of sorghum with ten linkage groups using mostly sorghum-derived RFLP probes, and some from maize. This map was based on an interspecific cross (*S. bicolor* BTx623 × *S. propinquum*), mapped in the F₂ generation. A 'composite' map

using the genotypic data from two recombinant inbred(RI) populations was published by [51] with linkage group designations following those of [52]. This map contained 199 markers on 13 linkage groups and was later supplemented in subsequent publications with the addition of more RFLP and AFLP markers [53], as well as with morphological markers, reducing the number of linkage groups to 11, with two very small unlinked clusters [23].

[54] also published a map of sorghum using RFLP probes primarily derived from sorghum, and some from maize. This map contained 190 markers on 10 major linkage groups, and four smaller ones. This map was based on the genotypes of 50F2 plants from a cross between IS3620C and BTx623. Several later studies improved upon this map by addition of more loci. Using 137 RI lines from this same cross generated a linkage map containing 323 mapped loci on 10 linkage groups. The total length of this map was 1,347 cM. [24] reported the addition of 147 SSR loci to this map using the same RI population, the total map length to 1,406 cM. Though these maps were useful tools for mapping of quantitative trait loci (QTL), the lack of agreement between maps from various research groups, as well as relatively poor map quality, made a comparison of results with other studies or research groups very difficult. Clearly, there arose a need among the sorghum research community for a consensus map.

More recently, two very dense genetic linkage maps of sorghum have emerged [55] added AFLP markers to the IS3620C × BTx623 map of [24] to create a very dense linkage map containing 2,926 loci on 10 linkage groups with a total genetic distance of 1,713 cM. Shortly thereafter, using the interspecific cross (*S. bicolor* BTx623 × *S. propinquum*) of [50], another dense linkage map was generated. This map contained 2,512 loci on 10 linkage groups, and is based entirely on RFLP probes [56]. Interestingly, the total genetic distance of this map was much shorter than the map by [55], at only 1,059.2 cM.

9. QTL IDENTIFICATION IN SORGHUM

Molecular markers have been used to identify and characterize QTL associated with many different traits in sorghum, including plant height

and maturity [57], traits associated with domestication [58], disease resistance, insect resistance [59], and drought tolerance. Identification of QTL often leads to further investigations to identify the underlying gene or genes through fine mapping and map-based cloning.

When successfully implemented, such studies provide valuable insight into the genetic mechanisms controlling complex, and often economically important, traits. However, from a practical plant breeding standpoint, QTL are usually identified for the purpose of finding linked molecular markers that can be utilized in trait introgression for crop improvement, and often the specific underlying genes are not identified. For the purposes of this review, examples of QTL identification for tolerance to biotic and abiotic stresses important in sorghum are highlighted [25].

10. IDENTIFICATION OF QTL FOR *Striga* RESISTANCE

Several parasitic plant species of the genus *Striga* are major pests of sorghum in parts of Africa, often causing complete loss of the crop in severe infestations [60]. Several investigations were done to control the pest through chemical or cultural means have been met with limited success and are often not practical in poor areas, developing crops with genetic resistance is currently the best strategy for dealing with *Striga* infestation. However, field resistance to *Striga* is a complex quantitative trait that has been difficult to address via conventional plant breeding approaches [61].

The identification of the molecular markers for specific *Striga* resistance mechanisms facilitates faster introgression and pyramiding of genes controlling this important trait. In the few studies that relate to the other *Striga* resistance mechanisms, [30] identified and mapped.

QTLs associated with *Striga* resistance in the sorghum variety, N13, where mechanical barrier is the suggested mechanism of *Striga* resistance. Based on a series of field evaluations of two independent RILs, [30] also confirmed the position and the stability of the identified the QTLs.

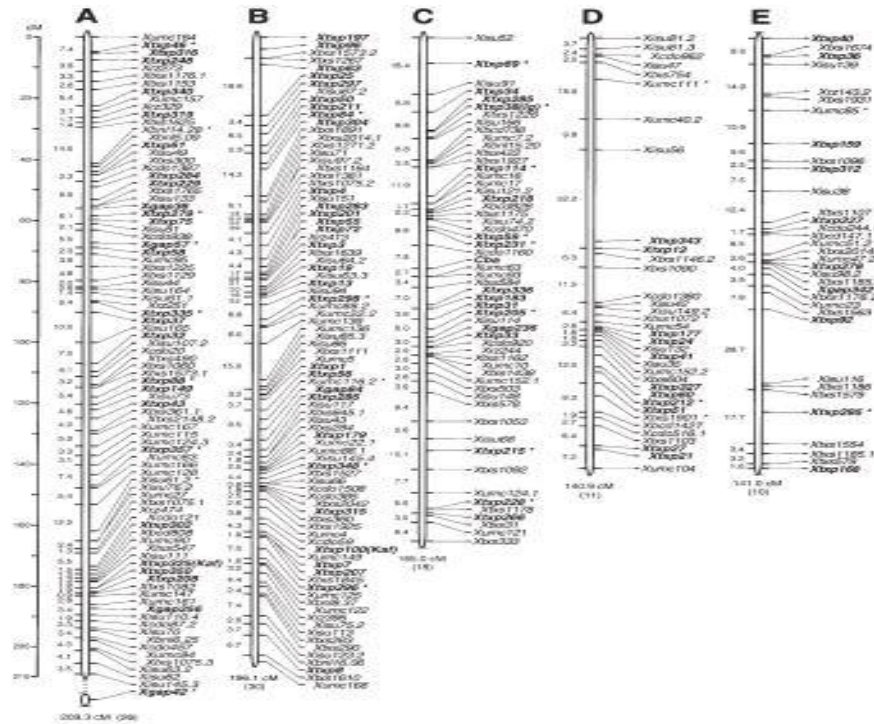


Fig. 2. Linkage map of the *S. bicolor* BTx623 x IS3620C recombinant inbred population

This ability to generate and process large amounts of genotypic data may permit large scale association mapping studies. Association mapping is based on the linkage disequilibrium (LD) within natural or assembled populations, and has been used by human geneticists to associate regions of the human genome with various diseases [62]. The greatest potential use of this technique for plant geneticists and breeders will be the ability to screen populations or collections of germplasm to identify potential QTL and genetic markers for MAS, without using traditional linkage mapping populations [63]. However, there are some disadvantages of this method compared to mapping in experimental populations [62].

11. CONCLUSION

Striga resistant sorghum cultivars have not been available until recently, as the complex nature of the host parasite relationship had hampered progress from selection in field-based breeding. The use of DNA-based markers for the genetic analysis and manipulation of important agronomic traits has become an increasingly useful tool in modern plant breeding. The

greatest potential of molecular markers is to improve precision and to accelerate selection gain of desirable genotypes of quantitative trait loci (QTLs) that condition complex important traits. Through (MAS), more rapid transfer of traits from donor parents to more elite locally-adapted

COMPETING INTERESTS

Author has declared that no competing interests exist.

REFERENCES

1. Aruna C, Visarada K, Bhat BV, Tonapi VA. Breeding sorghum for diverse end uses. Woodhead Publishing; 2018.
2. Mindaye TT, Mace ES, Godwin ID, Jordan DR. Heterosis in locally adapted sorghum genotypes and potential of hybrids for increased productivity in contrasting environments in Ethiopia. The Crop Journal. 2016;4(6):479-489.
3. Reddy D, Nagabhushanam P, Sukhija B, Reddy A, Smedley P. Fluoride dynamics in the granitic aquifer of the Wailapally watershed, Nalgonda District, India.

- Chemical Geology. 2010;269(3-4): 278-289.
4. Qiu H, Huang J, Yang J, Rozelle S, Zhang Y, Zhang Y, Zhang Y. Bioethanol development in China and the potential impacts on its agricultural economy. *Applied Energy*. 2010;87(1):76-83.
 5. Prakash R, Ganesamurthy K, Nirmalakumari A, Nagarajan P. Combining ability for fodder yield and its components in Sorghum (*Sorghum bicolor* L). *Electronic Journal of Plant Breeding*, 2010;1(2): 124-128.
 6. Spallek T, Mutuku M, Shirasu K. The genus *S triga*: A witch profile. *Molecular plant pathology*, 2013;14(9):861-869.
 7. Tekka HB. Advance research on Striga control: A review. *African journal of plant science*. 2014;8(11):492-506.
 8. Babu R, Nair SK, Prasanna B, Gupta H. Integrating marker-assisted selection in crop breeding—prospects and challenges. *Current Science*. 2004;607-619.
 9. Jonah P, Bello L, Lucky O, Midau A, Moruppa S. Moruppa Ω. Review: The importance of molecular markers in plant breeding programmes. *Global Journal of Science Frontier Research*. 2011;11(5): 4-12.
 10. Dunham I, Hunt A, Collins J, Bruskiwich R, Beare D, Clamp M, et al. The DNA sequence of human chromosome 22. *Nature*. 1999;402(6761):489-495.
 11. Tuinstra MR, Grote EM, Goldsbrough PB, Ejeta G. Genetic analysis of post-flowering drought tolerance and components of grain development in *Sorghum bicolor* (L.) Moench. *Molecular Breeding*. 1997;3(6):439-448.
 12. Ejeta G. Breeding for *Striga* resistance in sorghum: Exploitation of an intricate host–parasite biology. *Crop Science*. 2007;47:S-216-S-227.
 13. Parker C, Riches CR. Parasitic weeds of the world: biology and control. CAB international; 1993.
 14. Mohamed A, Ali R, Elhassan O, Suliman E, Mugoya C, Masiga CW, et al. First products of DNA marker-assisted selection in sorghum released for cultivation by farmers in sub-saharan Africa. *Journal of Plant Science and Molecular Breeding*. 2014;3(3):1-10.
 15. Yohannes T, Abraha T, Kiambi D, Folkertsma R, Hash CT, Ngugi K, et al. Marker-assisted introgression improves *Striga* resistance in an eritrean farmer-preferred sorghum variety. *Field Crops Research*. 2015;173:22-29.
 16. Varshney RK, Thudi M, May GD, Jackson SA. Legume genomics and breeding. *Plant breeding reviews*. 2010;33:257-304.
 17. Haussmann B, Hess D, Seetharama N, Welz H, Geiger H. Construction of a combined sorghum linkage map from two recombinant inbred populations using AFLP, SSR, RFLP, and RAPD markers, and comparison with other sorghum maps. *Theoretical and Applied Genetics*. 2002;105(4):629-637.
 18. Thottappilly G, Magonouna H, Omitogun O. The use of DNA markers for rapid improvement of crops in Africa. *African Crop Science Journal*. 2000;8(1):99-108.
 19. Ramu P, Billot C, Rami JF, Senthilvel S, Upadhyaya H, Reddy LA, et al. Assessment of genetic diversity in the sorghum reference set using EST-SSR markers. *Theoretical and Applied Genetics*. 2013;126(8):2051-2064.
 20. Crouch JH, Ortiz R. Applied genomics in the improvement of crops grown in Africa. *African journal of biotechnology*. 2004;3(10):489-496.
 21. Patil SA, Naik VH, Kulkarni AD, Badami PS. DNA cleavage, antimicrobial, spectroscopic and fluorescence studies of Co (II), Ni (II) and Cu (II) complexes with SNO donor coumarin Schiff bases. *SpectrochimicaActa Part A: Molecular and Biomolecular Spectroscopy*. 2010;75(1):347-354.
 22. Xu K, Xu X, Ronald P, Mackill D. A high-resolution linkage map of the vicinity of the rice submergence tolerance locus Sub1. *Molecular and General Genetics MGG*. 2000;263(4):681-689.
 23. Boivin K, Deu M, Rami JF, Trouche G, Hamon P. Towards a saturated sorghum map using RFLP and AFLP markers. *Theoretical and Applied Genetics*. 1999;98(2):320-328.
 24. Bhatramakki D, Dong J, Chhabra AK, Hart GE. An integrated SSR and RFLP linkage map of *Sorghum bicolor* (L.) Moench. *Genome*. 2000;43(6):988-1002.
 25. Tuinstra M, Grote E, Goldsbrough P, Ejeta G. Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. *Crop Science*. 1996;36(5):1337-1344.

26. Queller DC, Strassmann JE, Hughes CR. Microsatellites and kinship. *Trends in ecology & evolution*. 1993;8(8):285-288.
27. Klein R, Rodriguez-Herrera R, Schlueter J, Klein P, Yu Z, Rooney W. Identification of genomic regions that affect grain-mould incidence and other traits of agronomic importance in sorghum. *Theoretical and Applied Genetics*. 2001;102(2-3):307-319.
28. Kong L, Dong J, Hart G. Characteristics, linkage-map positions, and allelic differentiation of *Sorghum bicolor* (L.) Moench DNA simple-sequence repeats (SSRs). *Theoretical and Applied Genetics*. 2000;101(3):438-448.
29. Van Berloo R, Stam P. Comparison between marker-assisted selection and phenotypical selection in a set of *Arabidopsis thaliana* recombinant inbred lines. *Theoretical and Applied Genetics*. 1999;98(1):113-118.
30. Haussmann B, Hess D, Omany G, Folkertsma R, Reddy B, Kayentao M, et al. Genomic regions influencing resistance to the parasitic weed *Striga hermonthica* in two recombinant inbred populations of sorghum. *Theoretical and Applied Genetics*. 2004;109(5):1005-1016.
31. Groen A, Smith C. A stochastic simulation study of the efficiency of marker-assisted introgression in livestock. *Journal of Animal Breeding and Genetics*. 1995;112(1-6):161-170.
32. Visscher PM, Haley CS, Thompson R. Marker-assisted introgression in backcross breeding programs. *Genetics*. 1996;144(4):1923-1932.
33. Frisch M, Bohn M, Melchinger AE. Comparison of selection strategies for marker-assisted backcrossing of a gene. *Crop Science*. 1999;39(5):1295-1301.
34. Joel D, Bar H, Mayer A, Verdoucq V, Welbaum G, Westwood J. Characterization of a dioxygenase gene with a potential role in steps leading to germination of the root parasite *Orobanche aegyptiaca*. *Seeds: biology, development and ecology*. 2007:296.
35. Mohamed A, Ejeta G, Butler L, Housley T. Moisture content and dormancy in *Striga asiatica* seeds. *Weed research (Print)*. 1998;38(4):257-265.
36. Hauck C, Müller S, Schildknecht H. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a genuine host plant. *Journal of Plant Physiology*. 1992;139(4):474-478.
37. Müller S, Hauck C, Schildknecht H. Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. *Journal of Plant Growth Regulation*. 1992;11(2):77-84.
38. Siame BA, Weerasuriya Y, Wood K, Ejeta G, Butler LG. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. *Journal of Agricultural and Food Chemistry*. 1993;41(9):1486-1491.
39. Babiker AGT, Ejeta G, Butler LG, Woodson WR. Ethylene biosynthesis and strigol-induced germination of *Striga asiatica*. *Physiologia Plantarum*. 1993;88(2):359-365.
40. Haussmann B, Hess D, Reddy B, Mukuru S, Seetharama N, Kayentao M, et al. QTL for *Striga* resistance in sorghum populations derived from IS 9830 and N 13. in *Breeding for Striga resistance in cereals. Proceedings of a Workshop, IITA, Ibadan, Nigeria; 1999.*
41. Mohamed AH, Housley T, Ejeta G. An *In vitro* technique for studying specific *Striga* resistance mechanisms in sorghum. *African Journal of Agricultural Research*. 2010;5(14):1868-1875.
42. Frick E, Frahne D, Wegmann K. Biochemical synthesis of 2, 6-dimethoxy-para-benzoquinone-a haustorial stimulant of *Striga asiatica* (L.) Kuntze. *Natural Product Letters*. 1996;9(2):153-159.
43. Kapulnik Y, Delaux PM, Resnick N, Mayzlish-Gati E, Wininger S, Bhattacharya C, et al. Strigolactones affect lateral root formation and root-hair elongation in *Arabidopsis*. *Planta*. 2011;233(1):209-216.
44. Johnson A, Rosebery G, Parker C. A novel approach to *Striga* and *Orobanche* control using synthetic germination stimulants. *Weed Research*. 1976;16(4):223-227.
45. Ruyter-Spira C, Kohlen W, Charnikhova T, van Zeijl A, van Bezouwen L, De Ruijter N, et al. Physiological effects of the synthetic strigolactone analog GR24 on root system architecture in *Arabidopsis*: another belowground role for strigolactones? *Plant physiology*. 2011;155(2):721-734.
46. Koren D, Resnick N, Gati EM, Belausov E, Weininger S, Kapulnik Y, et al. Strigolactone signaling in the endodermis is sufficient to restore root responses and involves Short Hypocotyl 2 (SHY2) activity. *New Phytologist*. 2013;198(3):866-874.

47. Berhan AM, Hulbert S, Butler L, Bennetzen J. Structure and evolution of the genomes of *Sorghum bicolor* and *Zea mays*. *Theoretical and Applied Genetics*. 1993;86(5):598-604.
48. Hulbert SH, Richter TE, Axtell JD, Bennetzen JL. Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. *Proceedings of the National Academy of Sciences*. 1990;87(11):4251-4255.
49. Whitkus R, Doebley J, Lee M. Comparative genome mapping of Sorghum and maize. *Genetics*. 1992;132(4):1119-1130.
50. Chittenden L, Schertz K, Lin Y, Wing RA, Paterson A. A detailed RFLP map of *Sorghum bicolor* x *S. propinquum*, suitable for high-density mapping, suggests ancestral duplication of *Sorghum* chromosomes or chromosomal segments. *Theoretical and Applied Genetics*. 1994;87(8):925-933.
51. Dufour P, Deu M, Grivet L, D'Hont A, Paulet F, Bouet A, Lanaud C, Glaszmann JC, Hamon P. Construction of a composite sorghum genome map and comparison with sugarcane, a related complex polyploid. *Theoretical and Applied Genetics*. 1997;94(3-4):409-418.
52. Pereira M, Lee M, Bramel-Cox P, Woodman W, Doebley J, Whitkus R. Construction of an RFLP map in sorghum and comparative mapping in maize. *Genome*. 1994;37(2):236-243.
53. Vos P, Hogers R, Bleeker M, Reijans M, Lee TVD, Hornes M, et al. AFLP: A new technique for DNA fingerprinting. *Nucleic acids research*. 1995;23(21):4407-4414.
54. Xu XP, Needleman A. Numerical simulations of fast crack growth in brittle solids. *Journal of the Mechanics and Physics of Solids*. 1994;42(9):1397-1434.
55. Menz M, Klein R, Mullet J, Obert J, Unruh N, Klein P. A high-density genetic map of *Sorghum bicolor* (L.) Moench based on 2926 AFLP[®], RFLP and SSR markers. *Plant molecular biology*. 2002;48(5-6): 483-499.
56. Bowers JE, Nambeesan S, Corbi J, Barker MS, Rieseberg LH, Knapp SJ, et al. Development of an ultra-dense genetic map of the sunflower genome based on single-feature polymorphisms. *PLoS One*. 2012;7(12):e51360.
57. Pereira M, Lee M. Identification of genomic regions affecting plant height in sorghum and maize. *Theoretical and Applied Genetics*. 1995;90(3-4):380-388.
58. Paterson AH, Lin YR, Li Z, Schertz KF, Doebley JF, Pinson SR, et al. Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. *Science*. 1995;269(5231):1714-1718.
59. Nagaraj N, Reese JC, Tuinstra MR, Smith CM, Amand PS, Kirkham M, et al. Molecular mapping of sorghum genes expressing tolerance to damage by greenbug (Homoptera: Aphididae). *Journal of Economic Entomology*. 2005;98(2): 595-602.
60. Vogler R, Ejeta G, Butler L. Inheritance of low production of *Striga* germination stimulant in sorghum. *Crop science*. 1996;36(5):1185-1191.
61. Ejeta G, Knoll JE. Marker-assisted selection in sorghum, in genomics-assisted crop improvement. 2007; 187-205.
62. Collins AR, Ferguson LR. Nutrition and carcinogenesis. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis*. 2004;551(1-2):1-8.
63. Ramu P, Kassahun B, Senthilvel S, Kumar CA, Jayashree B, Folkertsma R, Reddy LA, Kuruvinashetti M, Haussmann B, Hash CT. Exploiting rice-sorghum synteny for targeted development of EST-SSRs to enrich the sorghum genetic linkage map. *Theoretical and Applied Genetics*. 2009;119(7):1193-1204.

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