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

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. asiatica*resistant cultivars by conventional breeding is slow and has 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 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.

Key words: Linkage map; molecular marker; S.*asiatica.*

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 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 finger printing 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 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 convectional 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, the aim of this review is 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].

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 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 are 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 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].

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 QLT are biological realities[14]

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 conversed DNA sequences flanking the SSR as primers. SSR markers have been used initially to detect polymorphism between the parent cultivars[27].

Although costly todevelop relative to some other classes of genetic markers, once developed, analysis by SSRmarkers 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	AGCCTATGTATGTGTTCGTCC
Xtxp065	CACGTCGTCACCAACCAA	GTTAAACGAAAGGGAAATGGC
Xcup033	GCGCTGCTGTGTGTTGTTC	ACGGGGATTAGCCTTTTAGG
Xtxp274	GAAATTACAATGCTACCCCTAAAAGT	ACTCTACTCCTTCCGTCCACAT
Xtxp013	TCTTTCCCAAGGAGCCTAG	GAAGTTATGCCAGACATGCTG
Xtxp197	CACGACGTTGTAAAACGACGCGTCAATTAATCCAAACAGCCTC	GAGTTCCTATTCCCGTTCATGGTGAT
Xtxp225	TTGTTGCATGTTGGTTATAG	CAAACAAGTTCAGAAGCTC
Xiabtp515	TGCCACATCGATCTTGTCAC	AGGCAGTCACCCACACTACC
XmsbCIR268	CACGACGTTGTAAAACGACGCTTCTATACTCCCCTCCAC	TTTATGGTAGGATGCTCTGC
Xcup037	CCCAGCCTTCCTCCTGATAC	GTACCGACTCCAATCCAACG
Xiabtp500	CACGACGTTGTAAAACGACTTGTGCTGGTAGACGTGGTC	GCATTGGTATCCAACTGCAA
Xtxp014	GTAATAGTCATGACCGAGG	TAATAGACGAGTGAAAGCCC
Xtxp56	TGTCTTCGTAGTTGCGTGTTG	CCGAAGGAGTGCTTTGGAC
Xtxp296	CACGACGTTGTAAAACGACCAGAAATAACATATAATGATGGGGTGAA	ATGCTGTTATGATTTAGAGCCTGTAGA GTT

Xtxp080	CACGACGTTGTAAAACGACGCTGCACTGTCCTCCCACAA	CAGCAGGCGATATGGATGAGC
Xtxp317	CCTCCTTTTCCTCCTCCTCCC	TCAGAATCCTAGCCACCGTTG
Xisep346	CACGACGTTGTAAAACGACCGCTCCTCAGGCTCCTCT	TCCTCGAGCACCTGGTTG
Xiabtp444	CACGACGTTGTAAAACGACCCTTCTTCCACCTCCGTTCTC	GGGAGAGAGAGAGGGTCCATA
XmsbCIR223	CACGACGTTGTAAAACGACCGTTCCAATGACTTTTCTTC	GCCAATGTGGTGTGATAAAT

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].

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 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 (*Panicummiliaceum* 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.

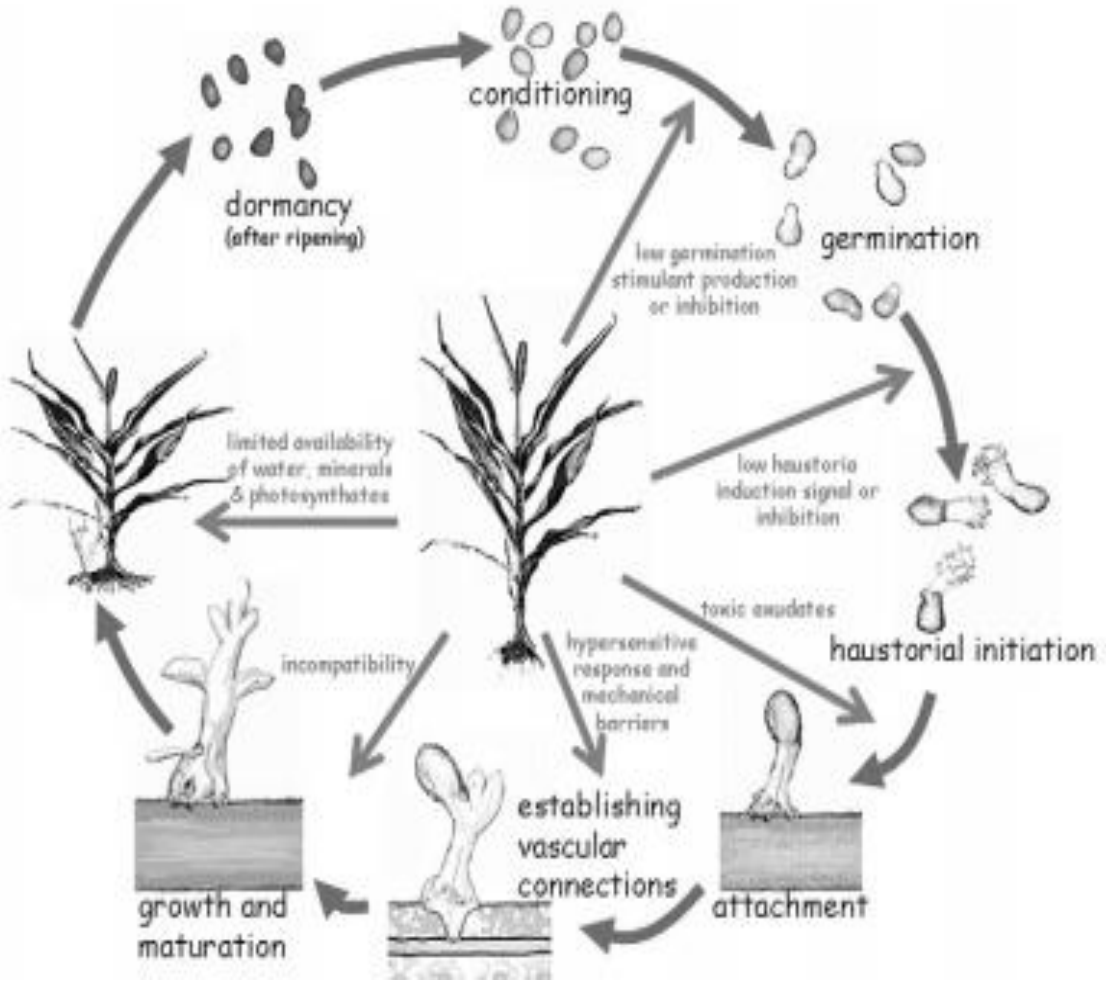

Figure 1. The *Striga* life cycle showing intricate association between the parasite, its hosts, and the environment with potential sites for genetic exploitation

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 necroticzones 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 versicolorand 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].

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 trigolactone [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].

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 betweenIS3620C 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 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.

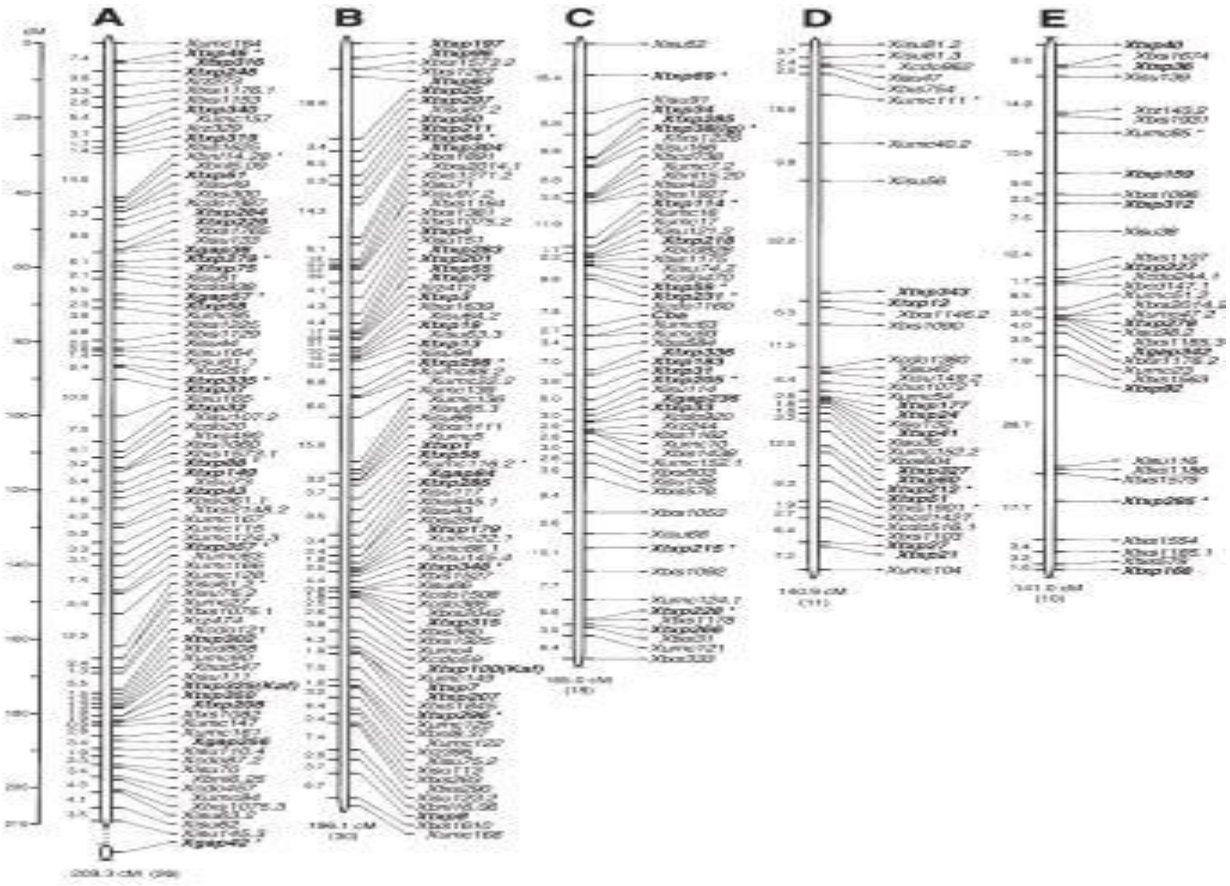

Fig. 2. Linkage map of the S. bicolor BTx623 × IS3620C recombinant inbred population

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].

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.

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 (R^2) and estimated additive effect (aI) 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

[b]Linkage grouped according to[24]

[c]Empirical LOD threshold values for QTL significance were 2.78 and 2.90 in sets 1 and 2, respectively (α=0.25);QTL with LOD scores below these thresholds are suggestive

[d]Additive effect: half of the difference between the two homozygotes. Positive values, resistance allele was contributed by resistance donorIS9830; negative values, resistance allele was derived from striga-susceptible parent E36-1

[e]Number of calibration runs in which the respective QTL was detected during the fivefold cross-validation

[f]Value corrected for QTL × environment interaction

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].

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

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