MARKER ASSISTED INTROGRESSION OF *STRIGA* RESISTANT AND DROUGHT TOLERANT QUANTITATIVE TRAIT LOCI INTO POPULAR ETHIOPIAN SORGHUM CULTIVARS

A THESIS SUBMITTED
TO
THE SCHOOL OF GRADUATE STUDIES
COLLEGE OF NATURAL AND COMPUTATIONAL SCIENCES
ADDIS ABABA UNIVERSITY

BY
TEKLAY ABEBE TEFERI

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY (PhD) IN MICROBIAL, CELLULAR AND MOLECULAR BIOLOGY
(APPLIED GENETICS)

ADDIS ABABA MARCH 2021

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(APPLIED GENETICS)

SUPERVISORS: DR. GURJA BELAY
DR. TAYE TADESSE
DR. GEMECHU KENENI

ADDIS ABABA MARCH 2021

DEDICATION

This thesis is dedicated to my beloved mother, Roman Hailemariam and my father, Abebe Teferi who are naturally wise, humble and kind to all; undefeated by the vagaries of poverty, they have raised me with determination, affection and great discipline. They are my icon of high integrity, ethics and humanity.

DECLARATION

I declare that the thesis hereby submitted for the Degree of Doctor of Philosophy (PhD) in Microbial, Cellular and Molecular Biology (Applied Genetics) to the School of Graduate Studies of Addis Ababa University is my own independent work and has not previously been submitted by me or anybody else at another University. The materials obtained from other sources have been duly acknowledged in the thesis.

Signed on March 2021, to the School of Graduate Studies, College of Natural and Computational Sciences, Addis Ababa University, Arat Kilo.

PhD Candidate ______________________________

Teklay Abebe

Supervisor ______________________________

Gurja Belay

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ACRONYMS AND ABBREVIATIONS

AAU	Addis Ababa University
AGA	Agar gel assay
AGP-II	Agricultural growth program phase two
ANOVA	Analysis of variance
ARC	Agricultural research center
AUSNPC	Area under *Striga* number progress curve
AUSSPC	Area under *Striga* severity progress curve
BC_1F_1	First backcross, first filial generation
BC_2F_1	Second backcross, first filial generation
BC_2F_2	Second backcross, second filial generation
BC_2F_3	Second backcross, third filial generation
BLs	Backcrossed lines
BM	Biomass
CSA	Central statistical agency
CV	Coefficient of variation
DSI	Drought susceptibility index
DTF	Number of days to flowering
DTM	Number of days to maturity
EIAR	Ethiopian Institute of Agricultural Research
FAO	Food and Agriculture Organization (of the United Nations)
GA	Genetic advance from selection

GI	Germination index
GLAB	Green leaf area at booting
GLAM	Green leaf area at maturity
GMP	Geometric mean productivity
GR	Germination rate
HM	Harmonic mean
HRM	Human resource management
KASP	Kempetetive allele specific polymerase chain reaction
lgs	Low germination stimulant
LS	Leaf senescence
LSD	Least significant difference
MABC	Marker assisted backcrossing
MARC	Melkassa agricultural research center
MAS	Marker assisted selection
MGD	Maximum germination distance
MoA	Ministry of agriculture
MP	Mean productivity
MRP	Mean relative performance
NABRC	National agricultural biotechnology research center
PCA	Principal component analysis
PGLAM	per cent of green leaf area preserved at maturity
PGLM	per cent of green leaves retained at maturity
PL	Panicle length

PLHT	Plant height
PW	Panicle width
PWt	Panicle weight
QTL	Quantitative trait locus
RLS	Rate of leaf senescence
SAPDB	Chlorophyll values (SPAD) at booting
SAPDM	Chlorophyll values (SPAD) at maturity
sddH2O	Sterilized double distilled water
SSI	Stress susceptible index
Stg	Stay green markers
STI	Stress tolerance index
TARI	Tigray agricultural research institute
TOL	Tolerance index
TSW	Thousand seeds weight
v/v	Volume to volume ratio
w/v	Weight to volume ratio
YI	Yield index
YLD	Grain yield
Yp	Yield in irrigated conditions
Ys	Yield in stress conditions
YSI	Yield stability index

ABSTRACT

Sorghum (Sorghum bicolor (L.) Moench) is the fifth important dryland cereal crop worldwide, and a dietary staple food for more than half a billion poor and food-insecure people dwelling in the semi-arid tropics of Africa and Asia. Sorghum is one of the strategic crops in Ethiopia, which provides more than one third of the cereal diet and is almost entirely grown by subsistence farmers to meet needs for food, feed, income, beverage, house and fuel purposes. Despite the multiple uses, its productivity is constrained at least partly by the intense Striga infestation and frequent drought, which causes up to 100% crop loss. The possible approaches to overcome the two prevailing constraints include genetic manipulation of the crop and the growing environment. The use of host-plant resistance offers a potentially cost-effective and environmentally sound complementary management strategy for incorporation into integrated management of Striga and drought.

The studies were, therefore, designed to introgress Striga resistance and drought tolerance genes/quantitative trait loci (QTLs) into popular and farmer-preferred cultivars through marker assisted backcrossing (MABC). One-hundred-eighteen and 61 backcrossed lines were developed for Striga and drought, respectively. The 118 backcrossed lines and 15 parental lines were evaluated for Striga resistance based on low Striga seed germination stimulant activity in the agar gel assay (AGA) and under field condition. The AGA study was conducted at Holetta national agricultural biotechnology research center (NABRC) arranged in completely randomized design with four replications, while the field evaluation was conducted at two selected Striga hotspots and two non-infested locations layout in α-lattice design with triplicates. The 61 drought tolerant converted and nine parental lines were evaluated under two-contrasting (optimum vis-à-vis stress) environments in α-lattice design with three replications. The well-watered experiment was irrigated throughout the season, while the water-limited trial was irrigated well during the early growth stages with irrigation withheld at anthesis in order to allow moisture stress during grain-filling stage.

The results from the AGA indicated that genotypes significantly differed ($P<0.01$) for their low production of Striga germination stimulant activity (lgs). The mean maximum germination distance (MGD) and germination rate (GR) ranged from 0.0 mm to 29.45 mm and 0.0% to 72.4% in the agar, respectively. Of the 118 backcrossed lines, 22.9% showed less than 10 mm of MGD and GR of <30%, revealing provision of low germination stimulant/strigolactones production (lgs). There were significant positive (r = 0.4-0.81) correlations showing the roles of these parameters as selection criteria in breeding for resistance. The existence of higher heritability (h^2_b = 77-83%) and genetic advance (GA = 62-93%) for the germination parameters indicated possibilities for improving resistance against Striga through selection.

The results from the field evaluation also revealed that genotypes significantly differed ($P<0.01$) for both agronomic traits and reaction to Striga. About 21.2% of the backcrossed lines were promising with relatively good level of resistance to Striga and yield ranging from 773.3 to 1220 kg ha^{-1}. Grain yield showed highly significant negative associations with all the studied Striga characters indicating severe damage. The heritability and genetic advance ranged from 37.7 to 88.7% and 7.72 to 52.9%, respectively, in which their values are greater for agronomic than Striga resistance traits. The aspects of interaction with heterogeneity of natural Striga infestation, pathogenicity, and concomitant environmental effects may have increased genotype by environment interactions resulted relatively low heritability.

Genotypes that carry different QTLs showed different capacity to produce Striga germination stimulants in the AGA and agronomic performances under natural Striga infestation. The combined effect of both QTL (lgs2_SBI-05_60404021 and lgs_3_60629027) at a time showed lower Striga germination stimulant activity and better field resistance indicating existence of possible cumulative effects. The pre-attachment traits (MGD and GR) based on the AGA and emerged Striga under field condition showed significant positive relationships. This indicated that the AGA proved to be a useful, precise and fast *indirect selection method to screen for sorghum lines with the low production of Striga germination stimulants resistance mechanism.*

The analysis of variance (ANOVA) for the stay-green (drought tolerant) experiment revealed that the developed backcrossed lines significantly differed for most of the agronomic and physiological characters. The mean grain yield of the genotypes under full-water (2069.2 to 5704.2 kg ha^{-1}*) and water-limited (923 to 4585 kg ha*$^{-1}$*) conditions were 3633 and 1991 kg ha*$^{-1}$*, respectively. Out of the 61 backcrossed lines, only 9.8% showed superior performance in yield ranging from 2831-4585 kg ha*$^{-1}$*, under water-limited condition indicating the potential to withstand drought after anthesis. They were also characterized by high chlorophyll content, leaf area and greenness at physiological maturity. Relatively high heritability (35.4-79.5%; 35.1-76.3%) and genetic advance (1.7-35.5%; 1.4-42.7%) was obtained for most agronomic and physiological characters under full-irrigation and water-limited regimes, respectively, indicating that selection for such characters could be fairly easy. Grain yield showed significant positive association with chlorophyll content (r = 0.24 & 0.45), green leaves (r = 0.31 & 0.29) and leaf area (r = 0.29 & 0.27) both at booting and maturity under the former and later moisture regimes, respectively. This indicated that the presence of greater green leaf area with high chlorophyll content at booting and maturity contributed higher photosynthesis, better availability of food reserves for grain-filling and enhanced yield.*

Of the 13 groups of QTLs, the cumulative effect of stg1+stg2+stg3a+stg4, stg1+stg2+stg3a+stg3b, stg1+stg3a+stg3b+stg4, and *stg2+stg3b+stg4 showed overall superior performance in most of the agronomic and physiological characters under both moisture regimes.*

Thus, the study provided useful evidence that the MABC transfer of lgs and drought tolerance genes from donor into popular cultivars have the potential to enhance tolerance/resistance to Striga and drought in sorghum, respectively, and could be used as noble tools supporting effective future sorghum breeding.

1. INTRODUCTION

1.1. Background and Justification

Sorghum [*Sorghum bicolor* (L.) Moench], 2n = 2x = 20] is the fifth most important dryland cereal crop widely produced worldwide for food, feed, and industrial purposes (Hariprasanna and Rakshit, 2016). Sorghum is among the top ten crops that feed the world, cultivated in more than 100 countries and a dietary staple food crop for more than 500 million people in over 30 countries (Kumar, 2016; FAO, 2017; Reddy, 2017; Visarada and Aruna, 2019). Globally sorghum is cultivated on 43.7 million ha of land from which 66 million tons of grain is produced annually, the average productivity being 1.5 t ha^{-1} (FAO, 2017). The highest area (80%) lays in developing countries on the African and Asian continents and the remaining 16-20% placed in developed world. Africa and Asia together account for approximately 56 % of global sorghum production and USA contributes nearly 38 % of global output (FAO, 2017). The top 10 sorghum-producing countries are United States, India, Mexico, Nigeria, Sudan, Ethiopia, Australia, Brazil, China, and Burkina Faso (Kumar, 2016).

Sorghum is one of the strategic crops in Ethiopia, which provides more than one-third of the cereal diet and is almost entirely grown by subsistence farmers to meet needs for food, feed, income, beverage, construction and fuel purposes (MoA, 2018) and the country is considered as one of the Vavilovian centers of genetic diversity (Doggett, 1988; Mekbib, 2008). Sorghum is adapted to a wide range of agro-ecologies and hence, produced in the highland, midland, and lowland areas with altitude ranging from 400 m to 2500 m. Ethiopia is the third largest sorghum producing country next to Nigeria and Sudan in Africa and sixth in the world behind USA, Nigeria, Mexico, Sudan and India both in terms of area coverage and volume of total production (FAO, 2017). Sorghum takes the third largest share of all cereals grown in Ethiopia only after tef [*Eragrostis tef* (Zucc.) Trotter] and maize (*Zea mays* L.) be it in hectarage or volume of total annual national production (CSA, 2018). Presently, about 5.3 million smallholders produce sorghum and its production is estimated to be 5.2 million tons from nearly 1.9 million hectares of land giving the national average yield of around 2.7 t ha^{-1} (CSA, 2018).

Although sorghum has shown significant increment in area coverage, productivity, and total volume of production in the last two decades, the productivity of the crop is still very low (CSA, 2018) compared to the developed world average (FAO, 2017) and genetic potential (MoA, 2018) because of a number of biotic and abiotic factors. The major biotic constraints include; *Striga* spp., insect pests (stalk borer, midge, shoot fly, fall armyworm), and disease (grain mold, anthracnose, and smuts). Paramount among the abiotic constraints; drought and low soil fertility are the major production challenges. Although these constraints cause significant grain yield loss, the relative importance varied spatially and temporally. Among which, *Striga* weed (Ejeta, 2007a, b; Reda *et al.,* 2010; AATF, 2011; Abate *et al*., 2014; Gebretsadik *et al.* 2014) and drought (Amelework *et al*., 2015; Mera, 2018; Teshome and Zhang,

2019) have been found to be the most important constraints in sorghum production.

Parasitic weeds, particularly members of the genus *Striga* (*Orobanchaceae* family), are economically important obligate root hemiparasitic plants that attach themselves to the roots of cereals and other crops. These not only compete for water and nutrients but also secrete toxins from their roots to the host thereby inhibiting normal growth and development of the host plant (Gurney *et al.*, 2000; Rank *et al.*, 2004; Kanampiu *et al.*, 2018). *Striga hermonthica* has long been recognized as the most persistent biological constraint to food production as it infects important staple crops such as sorghum, maize, finger millet (*Eleusine coracana* L.), pearl millet (*Pennisetum glaucum* L.), and rice (*Oryza sativa* L.) (Ejeta, 2007a, b; Scholes and Press, 2008; Chemisquy *et al.*, 2010; Atera *et al.*, 2012; Parker, 2012; Spallek *et al.*, 2013; Badu-Aprakuet *et al.*, 2013). During the past decade or so, this parasitic weed has expanded its host-range, becoming increasingly important on other crops including tef (Reda *et al.*, 2010; AATF, 2011; Welsh and Mohamed, 2011), barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) (Reda *et al.*, 2010).

It is estimated that more than 50 million ha of the sub-Saharan African arable land is infested with *Striga*, causing enormous yield losses (Ejeta, 2007a; Parker, 2012; Westwood *et al.*, 2012; Kountche *et al.*, 2019) and affecting livelihoods of millions of poor rural families in the semiarid and sub-tropical regions (Kountche *et al.*, 2016). The global yield losses attributable to *Striga* are immense, ranging from 30% to 90% on average, with a total crop failure under worst situations from which >300 million people are affected (Ejeta, 2007b; Pennisi, 2010; Westwood *et al.*, 2012; Kountche *et al.*, 2019). In Africa, the average annual yield loss has been estimated to exceed 40% (Ejeta, 2007a, b; Joel *et al.*, 2007; Venne *et al.*, 2009; AATF, 2011; Parker, 2012; Westwood *et al.*, 2012; Pennisi, 2015; Kountche *et al.*, 2019). The yield loss attributable to *Striga* infestation in Ethiopia ranged from 65 to 100% depending on the *Striga* infestation, soil fertility and moisture conditions (Tesso *et al.*, 2007).

Drought is also a major constraint to sorghum production worldwide (Kassahun *et al.*, 2010; Sabadin *et al.*, 2012; Reddy *et al.*, 2014; Amelework *et al.*, 2015; Mera, 2018; Teshome and Zhang, 2019), although sorghum by its nature is considered as a highly drought tolerant cereal crop (Kassahun *et al.*, 2010; Sabadin *et al.*, 2012; Reddy *et al.*, 2014). Yield loss due to drought in the tropics alone exceeds 17% of well-watered production, reaching up to 60% in severely affected regions (Ribaut *et al.*, 2002; Sharma and Lavanya, 2002).

In Ethiopia, where more than 50% of the total area is semi-arid/drought-prone, insufficient, unevenly distributed, and unpredictable rainfall is usually experienced in drier parts of the country (Amelework *et al.*, 2015; Mera, 2018; Teshome and Zhang, 2019) in which nearly 40% of the population lives (EMA, 1988). It is manifested by either of the delay in onset, dry spell after sowing, and drought during critical crop growth stage such as flowering and grain filling (early withdrawal of rain). Moisture stress during later growth stages (grain filling) is the common phenomenon facing subsistence farmers in the country. The effects of drought stress on grain yield depend, among other factors, on the occurrence and intensity of drought as well as the stage of development in which the water deficit occurs and the complete failure which is frequent, leading to hunger and even famine.

It is frequently observed that drought is occurring at more frequent intervals- every two years during recent years. For instance, between 1960 and 1990 there were six drought episodes in the country, but between 1990 and 2014 the episodes increased to nine (USGS, 2017; Mera, 2018) causing up to complete loss of sorghum and other crops affecting millions of people. This shows drought is becoming very challenging for production and productivity of sorghum and many other crops, perhaps due to changing and variable climates. Reports also declare that the intensity and frequency of droughts are expected to increase, resulting in decreased food production and food security and increased vulnerability of the crop to drought (Bates *et al.*, 2008; Wassmann *et al.*, 2009; Mera, 2018; Teshome and Zhang, 2019).

The large loss of sorghum yield is also related to the poor *Striga* resistance and drought tolerance level of the available cultivars/varieties. Hence, the control and/or management of the two constraints through different options are an important factor and priority to ensuring food security in Africa in general and in Ethiopia in particular.

The possible approaches to overcome the problem of *Striga* and drought include manipulation of the genetic of the crop and growing environment or both. The genetic manipulation of the crop to improve resistance to *Striga* (Ejeta, 2007a; Abate *et al.*, 2014) and tolerance to drought (Kassahun *et al.*, 2010; Amelework *et al.*, 2015) is preferred to the continual manipulation of the growing environment because of sustainability and cost particularly to the resource-poor farmers. The hitherto sorghum breeding made to address *Striga* and drought problems facing poor farmers in Ethiopia has been entirely based on the conventional approaches. As the result of the breeding efforts made up to now, limited varieties resistant to *Striga* (Ejeta *et al.*, 2007; Tesso *et al.*, 2007; MoA, 2018) and tolerant to drought (Geremew *et al.*, 2004; MoA, 2018) have been released and made available to producers. Nonetheless, in relation to the desire, it is difficult to conclude that the conventional breeding approach has boosted the resistance/tolerance to *Striga* and drought as anticipated because of technical difficulties encountered in making major advances.

Experiences elsewhere show that when modern biotechnological tools are properly applied with the conventional breeding system, it is obvious that the long backcrossing cycles to transfer specific genes of interest would be shortened, gene pyramiding would be simpler and the release of high yielding varieties and their subsequent use as improved seeds would be enhanced and hastened (Collard and Mackill, 2007; Satish *et al.*, 2012). The conventional sorghum breeding efforts supported by molecular assisted tools have scored remarkable successes in identifying and incorporating genes for resistance to *Striga* (Grenier e*t al.*, 2007; Satish *et al.*, 2012; Gamar and Mohamed, 2013; Yohannes *et al.*, 2015) and tolerance to drought (Subudhi *et al.*, 2000; Tao *et al.*, 2000; Xu *et al.*, 2000a; Haussmann *et al.*, 2002; Sanchez *et al.*, 2002; Kassahun *et al.*, 2010).

On the other hand, the application of marker-assisted methods for resistance to *Striga* and tolerance to drought is at rudimentary stages in Ethiopia and thus, leading to an inadequate marker system for the genetic improvement of the crop. Creating an integrated population specific gene-based map of the sorghum genome onto which the loci conferring resistance to the parasitic weed and drought is time taking. In this regard, as an immediate option, it is advisable to validate, refine and adopt molecular markers developed elsewhere for *Striga* resistance and drought tolerance to better serve the needs in Ethiopia. This approach is believed to offer opportunities to Ethiopian breeders thereby proffering better solutions for these top priority constraints in sorghum and may even be replicated in other crops like maize.

The Ethiopian local sorghum varieties are highly preferred by the farming communities mostly for their yield, biomass and other morpho-agronomic attributes. Nonetheless, most of these varieties are not desirable, among others, because of susceptibility to *Striga* and drought. To this effort, limited works have been made so far to improve the major limitations (such as susceptibility to *Striga* and drought) of the popular and farmers' preferred cultivars. Therefore, it is strategically advisable that breeding efforts should build on the popular improved varieties or landraces to deliver established varieties with protection against *Striga* infestation and drought afforded through a few genes as a stopgap measure to farmers through a marker-assisted backcrossing. Thus, the conversion of the popular varieties or landraces into their *Striga* resistant and drought tolerant versions through incorporation of responsible genes employing marker-assisted backcrossing seems to be the best strategy in terms of time saving, effectiveness and efficiency. Therefore, this study was designed with the following general and specific objectives.

1.2. General Objective

- To validate and deploy molecular markers developed elsewhere for breeding *Striga* resistant and drought tolerant sorghum varieties in Ethiopia

1.3. Specific Objectives

- To introgress *Striga* resistance genes (QTLs) into popular Ethiopian sorghum cultivars/varieties;
- To introgress drought tolerance genes (QTLs) into popular Ethiopian sorghum cultivars/varieties;
- To identify and evaluate *Striga* resistant and drought tolerant sorghum backcross progeny developed through marker-assisted backcrossing for potential release thereby validate the markers for future application in sorghum breeding.

2. LITERATURE REVIEW

2.1. The Sorghum Crop

2.1.1. Origin

The origin and early domestication of sorghum is hypothesized to have taken place in northeastern quadrant of Africa comprising Ethiopia, Sudan and east Africa or at the Egyptian-Sudanese border around 5,000-8,000 years ago (de Wet, 1977; Mann *et al.*, 1983; Doggett, 1988). Thus, there seems to be no argument against the African origin of sorghum (Kimber, 2000), which is also supported by the largest diversity of the cultivated and wild sorghum in Africa (de Wet, 1977; Doggett, 1988; Ejeta, 2007b). The great diversity of *S. bicolor* has been created through disruptive selection, geographic isolation and recombination in the extremely varied habitats of northeast Africa, leading to the creation of a large number of types, varieties and races of sorghum.

2.1.2. Taxonomy and classification

Sorghum was first described by Linnaeus in 1753 under the name *Holcus* and later Moench separated the genus *Sorghum* from the genus *Holcus* (Celarier *et al.*, 1959; Clayton *et al.*, 1961). The name of cultivated sorghum, *Sorghum bicolor* (L.) Moench was proposed by Clayton and is currently being used (Clayton *et al.*, 1961). Subsequently, several authors have discussed the systematics, origin, and evolution of sorghum since Linnaeus (de Wet and Harlan, 1971; Dahlberg, 2000). The most detailed classification of sorghum was made by Snowden, (1955) (31 cultivated species and 17 related wild species) and other classifications proposed since then have been the modifications of the Snowden system (Doggett, 1970).

2.1.3. Cultivated sorghum

The cultivated races are placed in *S. bicolor* subsp. *bicolor* and represented by diverse agronomic types (Berenji and Dahlberg, 2004). Harlan and de Wet, (1972) have developed a simplified, informal classification useful to plant breeders for the cultivated sorghums and their closest wild relatives. The cultivated taxa, covering 28 (out of 31) species of Snowden's series *Sativa* belonging to a primary gene pool, are partitioned into five basic races (*Bicolor, Guinea, Caudatum, Kafir* and *Durra*) and 10 intermediate races (*Guinea-bicolor, Caudatum-bicolor, Kafir-bicolor, Durra-bicolor, Guinea-caudatum, Guinea-Kafir, Guinea-durra, Kafir-caudatum, Durra-caudatum* and *Kafir-durra*) based on fundamental spikelet types. All the 15 races can be identified by mature spikelets and head type (Hariprasanna and Patil, 2015; Kumar, 2016).

2.1.4. Cytogenetics

Sorghum comprises three known ploidy levels: $x = 5$, $x = 10$ and $x = 20$ (Rooney *et al.*, 2000; Price *et al.*, 2005; Reddy and Patil, 2015). Important sorghum species are: *S. bicolor* (Linn.) Moench ($2n = 2x = 20$), *S. propinquun* (Kunth) Hitche ($2n = 2x = 20$), and *S. halepense* (Linn.) Pers ($2n = 4x = 40$). Of these three, the most important to crop production is *S. bicolor*. Grassy species such as *S. arundinuceuin, S. verticillijlorum,* and *S. aethiopicum,* have the same chromosome number ($2n = 2x = 20$) and can be crossed with *S. bicolor*.

Cultivated races are readily crossable with each other to produce fertile hybrids. In sorghum production, natural interspecific crossing between *S. bicolor* and *S. halepense* is a common source of off-types in the field. Two types of products arise from this type of cross - sterile plants with 30 chromosomes and fertile plants with 40 chromosomes, the later often persisting in the field as perennial weeds. Cytogenetic male sterility and fertility restoration systems have been discovered in sorghum and are used in hybrid sorghum production.

2.1.5. Genome

Sorghum genome is estimated about 730 mbp with a small diploid genome and low level of gene duplication. DNA transposons constitute 7.5% of the sorghum genome (Paterson *et al.*, 2005). Gene order and density are similar to those of rice and the retrotransposon accumulation explains more than 75% of the whole genome size compared to rice. The number and size of sorghum gene families are similar to those of Arabidopsis and rice. The 58% of sorghum gene families were shared among all species. Nearly 94% of high-confidence sorghum genes have orthologues in rice and Arabidopsis, and all together these gene set define 11502 ancestral angiosperm gene families. About 24% gene families have members only in sorghum and rice, while only 7% are sorghum specific. The conservation of grass gene structures and order facilitate the development of DNA markers in order to perform crop improvement (Paterson *et al.*, 2009).

2.2. Sorghum Production and Importance

2.2.1. Global production and importance

Sorghum is the fifth most important cereal crop both in terms of total volume of production and area harvested behind wheat, maize, rice and barley worldwide (Hariprasanna and Rakshit, 2016; Reddy, 2017). It is one of the most important dryland food crops grown in marginal lands in more than 100 countries and stable food for about half a billion peoples living in the tropical and subtropical regions of Africa and Asia (Hariprasanna and Rakshit, 2016; Kumar, 2016; Reddy, 2017).

Globally, sorghum is growing in two contrasting situations based on production and utilization patterns. In the developed world, there is intensive and commercialized production with average yields of 3-5 t ha^{-1} predominantly used for feed. Conversely, in most of the developing world, sorghum is cultivated in low-input, extensive production systems, where mainly for food with productivity of being around 1 t ha^{-1} (Kumar, 2016; FAO, 2017; Reddy, 2017). Globally sorghum is cultivated on 43.69 million ha to produce 66 million tons (average from 2014-2016) (Figure 1). The top six leading producers of sorghum in the world are the Americas (United States), Nigeria, Mexico, India, Sudan, and Ethiopia (FAO, 2017).

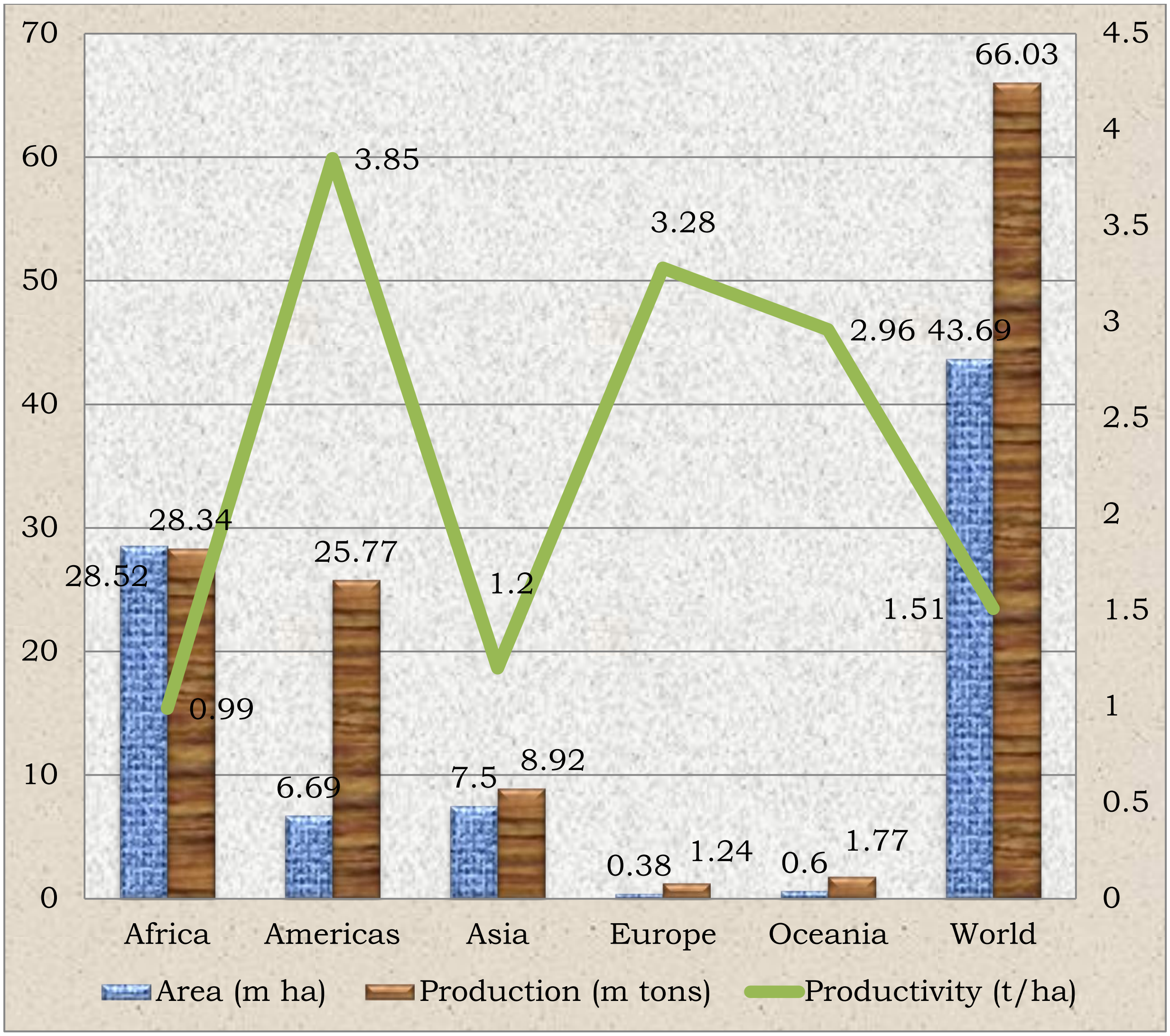


Figure 1. The area, production and productivity of sorghum worldwide

Source: FAO, 2017

2.2.2. Production and importance in Ethiopia

Ethiopia is among the top six sorghum-producing countries and the third largest producer of sorghum in Africa (FAO, 2017), with sorghum contributing 16.89% of the total annual cereal grain production and 14.96% of the total area allocated for cereals (CSA, 2018). Sorghum stands third next to tef and maize both in area and total volume of production (CSA, 2018).

Sorghum is cultivated over a wide range of elevation (400 m to 2700 m) and rainfall conditions in the country (MoA, 2018). It grows in many of the hot, arid, lowland parts, while some forms are also cultivated in the cooler and wetter highland areas up to 2,700 m elevation. It is more widely produced than any other crops, in the areas with moisture stress (dry lowland environments) which accounts for nearly 66% of the cultivated land (Geremew *et al.*, 2004). The major sorghum producing regions of the country are Oromia (38.8%), Amhara (35.5%), Tigray (13.4%), and Southern Nations and Nationalities People (5.9%), Benshangul Gumuz (3.1%), and Somali (2.2%) in area coverage and 40.5%, 35.5%, 14.05%, 3.1% and 1.8% in total production, respectively (CSA, 2018).

The area covered by sorghum showed an oscillating pattern over the last 18 years, while its production and productivity showed an increasing trend (Figure 2). The overall increase in productivity could be related to the genetic potential of farmers' selected/adopted varieties (Mekbib, 2006) and use of improved management practices such as row spacing and tie-ridge to conserve moisture.

Sorghum provides more than one third of the cereal diet and it is used in various ways (McGuire, 2005; MoA, 2018). It is the second most important crop for injera quality next to tef. The grain is also used for the preparation of locally prepared beverages ("*Tella*" and "*Arekie*"), Porridge, Nefro (boiled and roasted), infant food, and syrup. In addition, the stover is equally valued as animal feed, fuel wood and construction purposes.

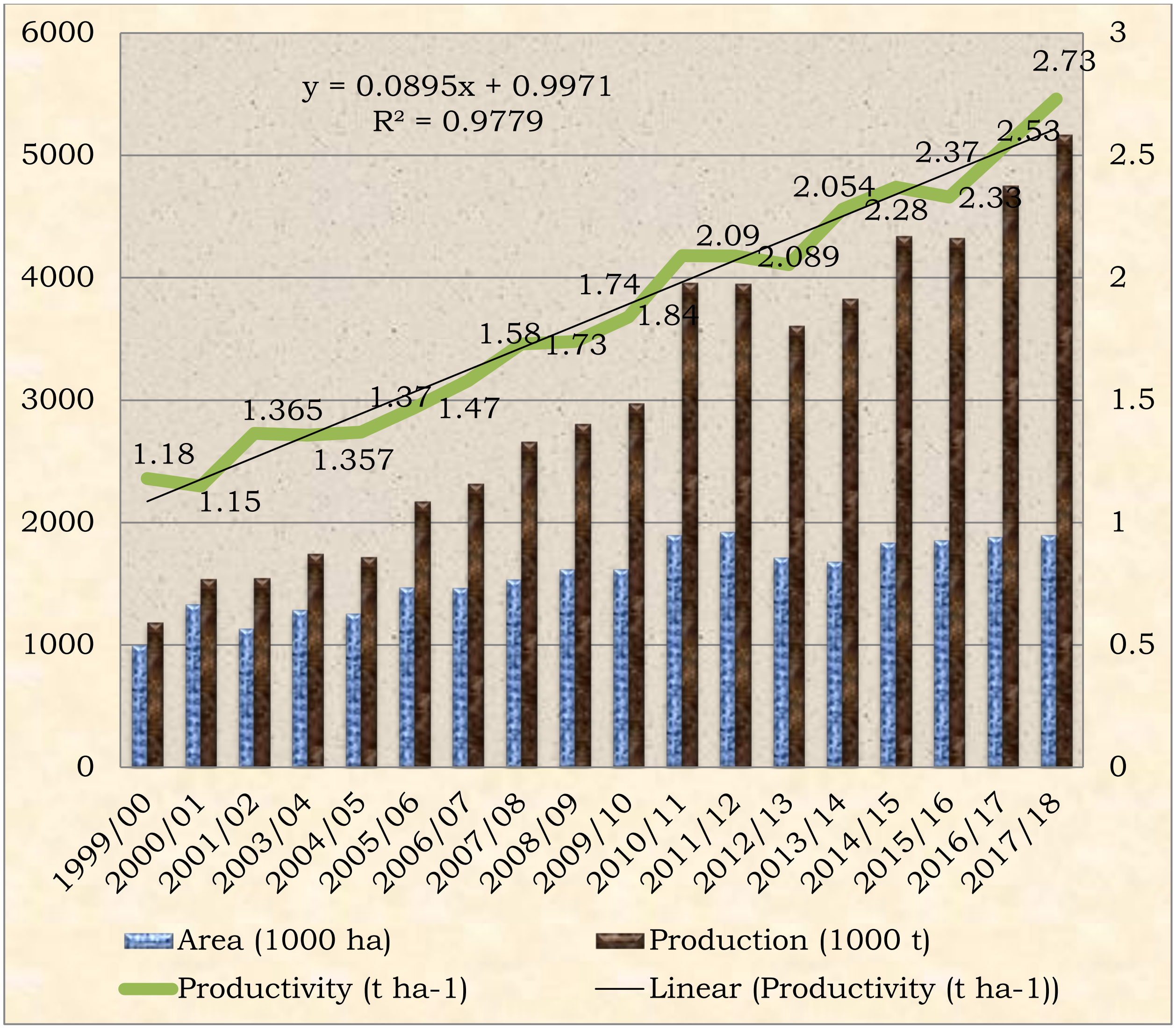


Figure 2. Area, production and productivity of sorghum in Ethiopia (CSA, 1999-2018)

2.2.3. Nutritional importance of sorghum

Sorghum is one of the major food crops in the world and has a predominant role in meeting the dietary energy and micronutrient requirements particularly in the low-income group populations dwelling in the arid and semi-arid regions of the world (Ng'uni *et al.*, 2012; USDA, 2016; Ratnavathi, 2019). More than half of all sorghum produced in the world is used for human consumption. Sorghum is a principal source of energy, proteins, vitamins and minerals for people lives in such environments (Table 1).

Table 1. Nutritional composition of sorghum (100 g) edible portions

Composition	Quantity	Composition	Quantity
Nutrients		Chlorine (mg)	44
Protein (g)	11.3	Sulfur (mg)	54
Fat (g)	3.3	Sodium (mg)	7.3
Carbohydrate (g)	75	Moldybnium (mg)	0.039
Crude fiber (g)	6.3	Manganese (mg)	1.6
Ash (g)	1.6	**Vitamin**	
Energy (kJ)	1419	Thiamine (B1) (mg)	0.4
Minerals		Niacin(B3)(mg)	4.3
Calcium (mg)	28	Riboflavin(B2)(mg)	0.2
Iron (mg)	5.4	B6 (mg)	0.26
Phosphorus (mg)	287	**Fats**	
Potassium (mg)	363	Saturated fatty acids (g)	0.46
Magnesium (mg)	171	Monounsaturated fatty acid (g)	0.99
Zinc (mg)	1.7	Polyunsaturated fatty acid (g)	1.37
Copper (mg)	0.46		

Source: USDA, 2016; Ratnavathi, 2019

2.3. Sorghum Production Constraints

The national average sorghum productivity in Ethiopia is 2.7 t ha^{-1} (CSA, 2018) which is far below the USA average of 3.85 t ha^{-1} (FAO, 2017) owing to various biotic and abiotic production constraints. The major biotic production constraints include; insects (stalk borer complex, midge, shoot fly, and fall armyworm (Tegegne *et al.*, 2008; Assefa and Ayalew, 2019), parasitic weeds (*Striga* spp.) (Ejeta, 2007a, b; Tesso *et al.*, 2007; Teka, 2014; Abate *et al.*, 2014), and disease (grain mold, anthracnose, smuts, downy mildew, and leaf blight (Eshte *et al.*, 2015; Teklay and Muruts, 2015). In addition, drought, poor soil fertility and soil salinity are the most important abiotic constraints affecting sorghum production (Reynolds *et al.*, 2015; Amelework *et al.*, 2016).

Paramount among the biotic and abiotic factors are the parasitic weed (*Striga* spp.) and drought, respectively. These production constraints are the major challenges across regions and cause significant grain yield loss, even to the point of total loss. It is, therefore, noteworthy that *Striga* and drought are serious threat to agricultural production and usually occur together in Ethiopia and hence this study tried to address to both challenges.

2.3.1. The *Striga* species

The genus *Striga* belongs to the *Orobanchaceae* family (ex *Scrophulariaceae*) and are obligate root hemi-parasitic plants (Olmstead *et al.*, 2001; Tank *et al.*, 2006; Spallek *et al.*, 2013). The family *Orobanchaceae* contains the highest number of parasitic species (Bennett and Mathews, 2006). The genus *Striga* comprises of 42 species worldwide, of which 11 species are considered parasitic on agricultural crops (Ejeta, 2007b). Out of the parasitic species, *S. hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze (henceforth denoted as *Striga*) are deemed to be the most economically important weeds parasitizing cereals (Haussmann *et al.*, 2000a, b; Gressel *et al.,* 2004; Ejeta, 2007b; Spallek *et al.*, 2013; Kountche *et al.*, 2016). *Striga* possibly originates from a region between the Semien Mountains of Ethiopia and the Nubian Hills of Sudan (Mohamed *et al.*, 2001; Ejeta, 2007b; Atera *et al.*, 2011). This region is also the origin of domesticated sorghum (de Wet, 1977; Mann *et al.*, 1983; Doggett, 1988), which is a major host species for several *Striga* species. Geographically, *Striga* are widely distributed in tropical and semi-arid regions of Africa, Middle East, Asia, and Australia (Cochrane and Press, 1997; Teka, 2014), and have been reported in more than 40 countries (Ejeta, 2007b).

2.3.1.1. Economic importance of *Striga* weed

The root hemiparasitic weed is among the most devastating pests attacking cereal production in many of sub-Saharan Africa and parts of Asia (Babiker, 2007; Ejeta, 2007b; Scholes and Press, 2008; Chemisquy *et al.*, 2010; Atera *et al.*, 2012; Parker, 2012; Spallek *et al.*, 2013; Badu-Aprakuet *et al.*, 2013; Kountche *et al.*, 2016; 2019). The major cereals attacked by *Striga* are sorghum, maize, finger millet, pearl millet, upland rice, tef, wheat, and barley which represent the staple food and fodder crops of millions of poor rural families in the tropical and semiarid regions of their cultivation. Therefore, they are of utmost significance to subsistence farmers (Chemisquy *et al.*, 2010; Reda *et al.*, 2010; AATF, 2011; Welsh and Mohamed, 2011; Atera *et al.*, 2012; Parker, 2012; Kountche *et al.*, 2016; 2019).

Striga species present the largest challenge to food security in the region where an estimated over 50 million hectares of arable land are infested leading to an estimated yield loss of about 40%. As a result, farmers have been reported to be eventually forced to abandon highly *Striga*-infested fields (Atera *et al.*, 2011). *Striga* infestation and damage are expected to be aggravated by the predominant low soil fertility, irregular rains and low-input (subsistence farming) conditions (Babiker, 2007; Ejeta, 2007a; Parker, 2009; AATF, 2011; Welsh and Mohamed, 2011). In Ethiopia and elsewhere, land pressure cause farmers needing to feed their families to opt for continuous cropping of the higher yielding cereal crops without rotation or moving to other land. In these regions, *Striga* is favoured by declining soil fertility and low soil moisture stress conditions. This compounds the problem for the small-scale farmers who can least afford input on unproductive land.

2.3.1.2. The life cycle of *Striga*

Life cycle of *Striga* is synchronized to that of the host (Figure 3) and a number of mechanisms ensure the co-ordination of the parasites life cycle and that of its host (Bouwmeester *et al.*, 2003). Seed dormancy, germination, attachment to its host, haustoria formation and penetration into the plants vascular system, establishment of the vascular connections, absorption and accumulation of the host's nutrients, flowering and seed production; marks the most important developmental stages of *Striga* (Parker and Riches, 1993). Each of these complex processes has been reported to be stimulated independently by different specific host signals (Yoshida and Shirasu, 2009; Estep *et al.*, 2011).

2.3.1.2.1. Seed dormancy, conditioning and germination

Striga seeds pass through a period of dormancy and generally cannot germinate in the season in which they are produced (Rich and Ejeta, 2007). They are released from dormancy through a process called conditioning or preconditioning during which species specific temperature and moisture requirements must be met so that the imbibed seed may respond to chemical stimulants of germination. Once conditioned, germination of *Striga* proceeds in response to signals derived from host plants (true and/or false non-host derived signal) (Bouwmeester *et al.*, 2003; Matusova *et al.*, 2005; Zwanenburg *et al.*, 2009).

2.3.1.2.2. Haustorial initiation

The germinated radicle cells differentiate into distinctly parasitic organs called haustoria, which are round shaped organs, specialized in host attachment and penetration (Agrios, 2005). The formation of haustoria also requires host derived signals compounds such as 2, 6-dimethoxy-1, 4-benzoquinone (DMBQ) (Ejeta, 2007b; Rich and Ejeta, 2007). Formation of haustorium is the start of the parasitic process, as the parasite begins to tap water and nutrients from the host plant (Joel *et al.*, 2007; Rich and Ejeta, 2007).

2.3.1.2.3. Attachment and penetration

The haustorium begins its function in attachment and after attachment or penetration develops into an organ of acquisition and metabolism of host-derived nutrients and water (Albrecht *et al.*, 1999). Connection to the vascular core of the host root is aided by enzymatic activity that breaks down the wall components of host cortical cells. After penetration of the xylem, haustorial cells lose their protoplast transforming them into water-conducting elements that are continuous with host xylem.

2.3.1.2.4. Maturity and seed production

The parasitic seedling develops a tubercle to assist with accumulation of nutrients soon after its attachment to host tissue. The cotyledenous *Striga* leaves emerge from the seed coat after vascular connections have been established with the host (Hood *et al.*, 1998). After six weeks of above ground emergence it forms flowers that later mature to seeds after two weeks of pollination. Survival of *Striga* as a parasite and its successful development as a plant depends on its interactions with the host plant; and shoot development follows and *Striga* eventually emerges above the ground, matures and sets seeds (Parker and Riches, 1993; Berner *et al.*, 1997).

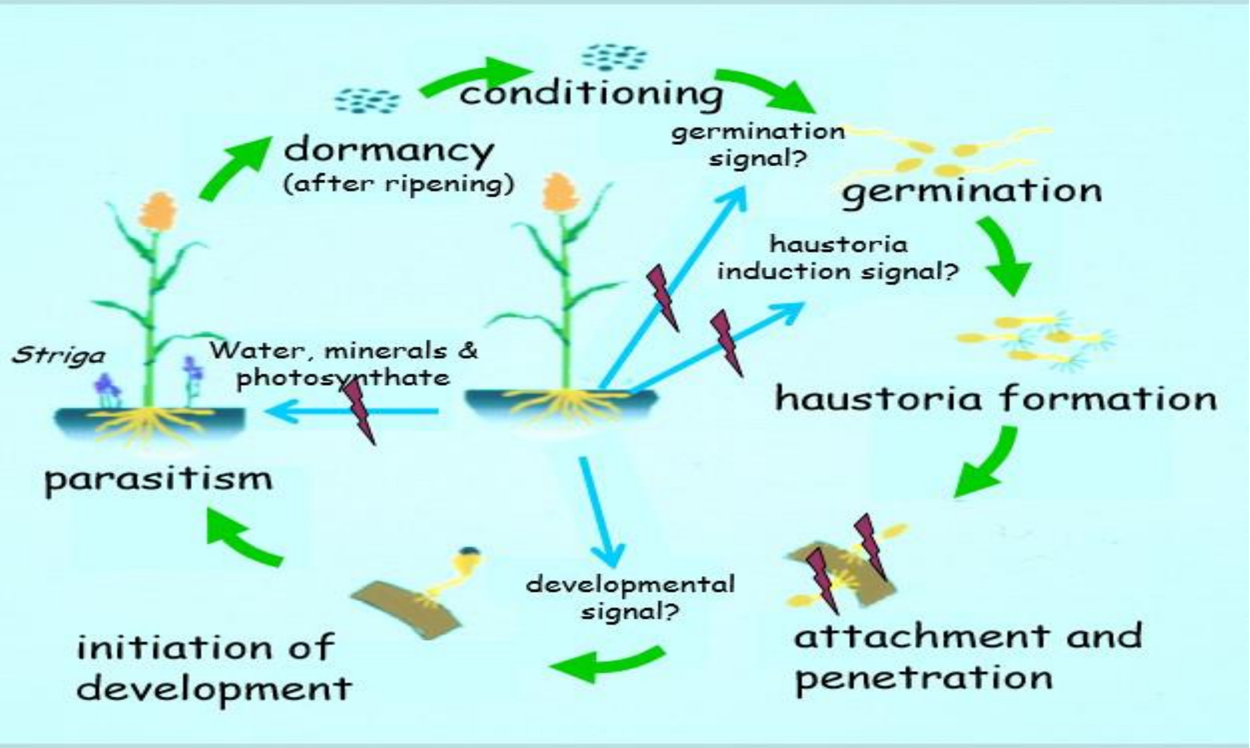


Figure 3. The *Striga* life cycle showing complex association between the parasite, its hosts, and the environment with potential sites for genetic exploitation (?) (Ejeta *et al.*, 1993).

2.3.1.3. Germination stimulants of *Striga*

A number of different classes of secondary metabolites (benzoquinones e.g. dihydrosorgoleone, strigolactones, sesquiterpene lactones, and isoflavanone) have been described to have germination stimulant activity (Keyes *et al*., 2001; Bouwmeester *et al*., 2003; Tsanuo *et al*., 2003). The best explored secondary metabolites with germination stimulants are the strigolactones from both hosts and non-hosts. The first germination stimulants, strigol and strigyl acetate were isolated from non-host cotton (*Gossypium hirsutum L.*) (Cook *et al*., 1972) and latter it was detected from hosts of maize (*Zea mays L.*), proso millets (*Panicum miliaceum* L.) and sorghum (Hauck *et al*., 1992; Siame *et al*., 1993). Alectrol was identified in cowpea (Muller *et al*., 1992) and together with orobanchol also isolated from *Orobanche* host, red clover (Yokota *et al*., 1998). An isomer of strigol, named sorghumol, was detected in sorghum (Awad *et al*., 2006). 5-Deoxystrigol, which was first isolated from *Lotus japonicus* (Regel) root exudates was later reported to be the major strigolactone present in maize, millet, and sorghum (Akiyama *et al*., 2005). Recently, several strigolactones were detected from tomato (*Solanum lycopersicum L.)*, tobacco (*Nicotiana tabacum L.)*, spinach (*Spinacia oleracea* L.), and white lupin (*Lupinus albus* L.) (Yoneyama *et al*., 2010) suggesting that strigolactones are structurally diverse and are produced by many plant species. Around 25 different strigolactones have been isolated from the root exudates of different plants, all acting with varying efficiency as *Striga* and other parasitic seed germination stimulants (Xie *et al*., 2008; 2016; Yoneyama *et al*., 2010; Mohemed *et al*., 2018; Kountche *et al*., 2019).

2.3.2. Drought as production constraint

In the semi-arid tropics, drought is often the main production constraint causing a significant yield loss (Amelework *et al.*, 2015; Mera, 2018; Teshome and Zhang, 2019). Several authors have given their version of the definition of drought (Tallaksen and Van Lanen, 2004; Wilhite *et al.*, 2007; Mishra and Singh, 2010; Van Loon, 2015). However, the simplest definition of drought from agricultural point of view is as a meteorological event manifested in inadequate precipitation to meet crop water requirements, causing loss of yield below that expected under optimal water supply (Kramer, 1983). It is a normal recurrent feature of climate that can occur in virtually all climatic zones; however, its feature varies significantly from region to region. In the semi-arid tropics where dryland farming is practiced, drought is a common phenomenon that occurs at different periods during the growing season (Blum, 1988). There is also a high season-to-season variability of rainfall, temperature, and radiation in the tropics.

Drought can have major consequences on growth, development and yield of plants by affecting several physiological, morphological and biochemical processes (Simpson, 1981). It is the major cause of poor crop performance and low yield, and sometimes it causes total crop failure. Drought can occur at seedling, pre-flowering and post-flowering stages of development and has the most adverse effect on yield (Xin *et al*, 2008; Reddy *et al.*, 2009; Amelework *et a1.*, 2015; Mera, 2018; Teshome and Zhang, 2019). Yield loss due to drought in the tropics alone exceeds 20 million tons of grains per year or 17% of well-watered production, reaching up to 60% in severely affected regions (Edmeades *et al.*, 1989; Ribaut *et al.*, 2002).

In Ethiopia, where more than 50% of the total area is semi-arid, insufficient, unevenly distributed, and unpredictable rainfall is usually experienced in drier parts of the country. At one point, rain may be abundant and perhaps wasted through runoff; in some years much rain may fall completely outside the growing season. In other years, the amount of rain may be low after the crops have germinated, soil moisture may be severely depleted. Consequently, in almost all lowland areas crops are prone to periodic moisture stress in one way or another. It is frequently observed that drought is occurring at more frequent intervals-every two years during recent years (USGS, 2017; Mera, 2018) affecting millions. Recent evidences also declare that the intensity and frequency of droughts are expected to increase, resulting in decreased food production and food security and increased vulnerability of the crop to drought (Bates *et al.*, 2008; Wassmann *et al.*, 2009; Mera, 2018; Teshome and Zhang, 2019).

2.4. *Striga* Management Options

Ever since the weed became a menace in semi-arid tropics including Ethiopia, efforts were made to manage the weed by different methods ranging from cultural measures, chemical or soil fumigation, biological and use of resistant varieties. Nevertheless, so far, effective control of *Striga* has been difficult to achieve through conventional cultural, chemical as well as biological control. These methods have one or more limitations, including high cost, impracticability, environmental safety, and temporary relief. The difficulty in *Striga* control is also aggravated by the parasite exerts its greatest damage bewitching the crop before its emergence above the ground.

The reliable management option, among others is, development and use of resistant crop cultivars resistant to *Striga* has proven to be both effective and durable as well as economical and practical for low-input farming systems (Joel, 2000; Ejeta and Gressel, 2007). This option is a potentially acceptable *Striga* control strategy to resource-poor farmers (Badu-Apraku and Akinwale, 2011).

2.4.1. Breeding and screening for *Striga* resistance

Host plant defense against *Striga* spp. constitutes two complementary mechanisms: resistance, the opposite of susceptibility and tolerance, the opposite of sensitivity and there has been considerable confusion in use of the terms resistance and tolerance in host plant response to *Striga*. *Striga* resistance refers to the ability of the host plant to stimulate significantly reduced *Striga* germination or prevent the attachment and establishment of the parasite under *Striga* infestation than susceptible crop plant grown under similar infestation, while tolerance shows smaller yield reductions than susceptible cultivars under the same level of infestation (Haussmann *et al.*, 2000b; Rodenburg *et al.*, 2006; Rodenburg and Bastiaans, 2011). The resistant genotype supports significantly fewer *Striga* plants and produces relatively higher yield than a susceptible genotype. Yet, complete resistance, or immunity, against *Striga* has not been found to date because of the complexity of host-parasite interaction. Because few *Striga* infections can already seriously harm the host plant, resistance alone may not be enough to prevent crop losses. It is therefore, recommended to direct breeding efforts towards finding varieties with high levels of resistance (Haussmann *et al.*, 2001a; Rodenburg and Bastiaans, 2011). *Striga* tolerant genotype stimulates germination and supports as many *Striga* plants as the sensitive genotype but produces more grain and shows fewer damage symptoms (Rodenburg and Bastiaans, 2011).

Breeding for resistance and tolerance requires suitable selection criteria. Many different selection measures have been developed for resistance and tolerance. Haussmann *et al.,* (2000a, b) and Rodenburg *et al.,* (2006) reported resistance and tolerance of the various genotypes can be estimated based on the field observations using the following criteria: (1) number of aboveground *Striga* plants at harvest, (2) maximum number of aboveground *Striga* plants, (3) area under *Striga* number progress curve (AUSNPC), (4) area under *Striga* severity progress curve (AUSSPC) and (5) field resistance.

Similarly, different measures of tolerance have been proposed taking sorghum yield from *Striga*-free plots as a control representing the maximum attainable yield. The attainable yield is the yield that could be obtained under the specific environmental conditions, in the absence of biotic stresses including *Striga* (Adetimirin *et al.*, 2000; Gurney *et al.*, 2002; Kim *et al.*, 2002). Tolerance is measured by comparing such yield with the sorghum yield from adjacent *Striga*-infested plots. Hence, selecting a host variety that combines superior levels of resistance and tolerance has been proposed in many studies as an obvious breeding objective (Haussmann *et al.*, 2001a; Pierce *et al.*, 2003; Showemimo, 2003; Rodenburg *et al.*, 2005; Rodenburg and Bastiaans, 2011).

2.4.1.1. Resistance mechanisms for *Striga*

Several resistance mechanisms to *Striga* have been described, which include resistance associated with low germination stimulant *(lgs)* production, low production of the haustorial initiation factor (*lhf*), germination inhibitors, hypersensitive response, incompatible response (Ejeta *et al.*, 2000a), mechanical barriers and antibiosis (Ejeta and Butler, 1993).

2.4.1.1.1. Low germination stimulant (*lgs*) production

The most thoroughly studied mechanism of resistance to *Striga* is decreased production of germination stimulants by host roots. It is well understood that *Striga* seeds require a chemical signal from the roots of a potential host in order to germinate. Sorghum genotypes that produce very low levels of the germination stimulants have been found to be resistant to *Striga* in field tests (Ramaiah, 1987, Hess *et al.*, 1992; Vogler *et al.*, 1996), while, susceptible sorghum genotypes appear to be abundant producers of the germination stimulant (Ejeta, 2007a). Several sorghum genotypes were found with *lgs* production; Framida, SRN39, 555, IS9830, SAR lines, IS15401, ICSV1006 and a wild accession *S. bicolor subspecies drummondii* (Ejeta and Butler, 1993, Heller and Wegmann, 2000, Haussmann *et al.*, 2000b; Ejeta *et al.*, 2007). Many authors reported that *lgs* is controlled by a single recessive gene inheritance (Vogler *et al.*, 1996) while others reported quantitative gene inheritance (Haussmann *et al.*, 2000a, b).

2.4.1.1.2. Low production of haustorial initiation factor (*lhf*)

Once germinated, *Striga* also requires the presence of an additional factor to initiate formation of a haustorium. Germinated *Striga* near the roots of sorghum genotypes that exhibits decreased production of the haustorial initiation factor mechanism do not form haustoria and therefore, die from their inability to attach to their potential host (Mohamed, 2002). Mohamed, (2002) suggest that a single nuclear gene with dominant gene action controlled the haustoria initiation trait, and proposed the gene symbol *lhf* for low haustoria initiation factor. Example of sorghum with this mechanism is accession P-78 of *S. drummondii* (Haussmann *et al.*, 2000b, Ejeta, 2007a).

2.4.1.1.3. Hypersensitive response (HR)

HR resistance involves localized necrosis of host tissues surrounding the site of attempted parasite attachment (Agrios, 2005), presumably coupled with release of reactive oxygen species, phytoalexins and other phenolic compounds, and pathogenesis-related proteins that kill the attached *Striga*, hence does not penetrate host tissues or develop further (Mohamed *et al.*, 2003). HR expression has been studied extensively in a number of host-parasite system, it is generally characterized by the appearance of necrotic zones around the site of attempted infection (Agrios, 2005) and by slowing the further advance of attached *Striga*, which does not develop normally and eventually dies on the host (Ejeta *et al.*, 2007). The HR in sorghum roots is conferred by two dominant genes, designated *Hrs1* and *Hrs2* (Mohamed, 2002). This phenomenon has been observed in sorghum genotypes; Framida, Dobbs, Serena, CK32, KP33, SAR 16, SAR 19, SAR 33, *Sorghum versicolor* and wild accession P47121, *S. bicolor s.p. drummondii*, *S. hewisonni* and *S.b. verticilliflorum* (Ejeta, 2007a, Haussmann *et al.*, 2000b; Rich *et al.*, 2004).

2.4.1.1.4. Incompatible response (IR)

The resistance mechanism confer by the IR is characterized as *Striga* seedlings attach to host roots, but discourages further development beyond attachment (Grenier *et al.*, 2001; Mohamed, 2002). There is no apparent necrosis in host root tissue surrounding the attachment site rather *Striga* seedlings that succeed in penetrating host tissue may not develop beyond emergence of the first leaves (Mohamed, 2002). IR reactions may develop because of failure to establish adequate vascular connections caused by lack of vital factors or because of the production of toxic factors that disrupt growth and development of the parasite. Sorghum cultivars; SRN39, ICSV761 and wild accession *S. verticilliflorum* possess this trait (Haussmann *et al.*, 2000b; Rich *et al.*, 2004; Ejeta, 2007a).

2.4.1.1.5. Mechanical barriers

Mechanical barrier to penetration has been reported in certain host-parasite associations by increased lignification (Maiti *et al.*, 1984), deposition of cellulose layers (Olivier *et al.*, 1991) and encapsulation (Labrousse *et al.*, 2001). Example of varieties with this mechanism is N13 and Framida (Haussmann *et al.*, 2000b; Ejeta, 2007a).

2.4.1.1.6. Antibiosis

Antibiosis reduces *Striga* development through unfavourable phytohormones supply by the host. This mechanism is present in SRN39 and N13, while insensitivity to *Striga* toxin through maintenance of stomatal aperture and photosynthetic efficiency and avoidance through root growth habit is achieved by having fewer roots in the upper 15 to 20 cm (Haussmann *et al.*, 2000b).

2.4.2. Screening techniques for *Striga* resistance

Precise and reliable screening techniques are indispensable prerequisites to breeding for resistance to *Striga* species (Vasudeva Rao, 1985). The presence of individual mechanisms conferring resistance to *Striga* may be examined in the laboratory, pot and field conditions (Haussmann *et al.*, 2000b; Omanya *et al.*, 2004).

2.4.2.1. Laboratory screening

Laboratory screening is commonly used in *Striga* research and a large number of methods have been developed and used including the agar-gel assay (Hess *et al.*, 1992), paper roll assay (Ejeta *et al.*, 2000a), sand-packed titer plate assay (Ejeta *et al.*, 2007), and extended agar gel assay (Mohamed *et al.*, 2010) methods that allow observation of early resistance reactions during *Striga* seed germination, radicle formation, attachment, penetration and haustorium production. According to Haussmann *et al.*, (2000a, b) and Omanya *et al.*, (2004) this is a useful, fast, indirect selection method used to screen for low stimulant character, but correlation analysis showed that this resistance mechanism was ineffective in some environments, pointing to the necessity of field evaluation.

2.4.2.2. Pot screening

Pot screening involves growing the host in pots artificially infested with *Striga* seeds. It is useful technique because of the ease of managing controlled over the environment, the inoculum density and its origin. Furthermore, unlike in the field, cross- inoculation studies, i.e. screening of genotypes against range of *Striga* eco-biotypes is possible.

2.4.2.3. Field screening

Conventional plant breeding for *Striga* resistance has traditionally involved field evaluation of germplasm under artificial or natural infestation. Field screening allows evaluation of genotypes for their reaction to *Striga* infestation and for other important agronomic traits such as grain yield. According to Haussmann *et al.*, (2000a, b) and Omanya *et al.*, (2004) field screening is still the most reliable technique to produce stable resistance to *Striga*. However, field screening for *Striga* field resistance is hampered by the heterogeneity of natural field infestations, large environmental effects on *Striga* emergence, and complex interactions between host-parasite-environment affecting the parasite's establishment and reproductive success (Ejeta, 2007a; Amusan *et al.*, 2008). Therefore, Kim, (1991) and Haussmann, (2000b) suggested that improved field testing methodologies should include; field artificial inoculation and appropriate experimental design (more replications, appropriate layout, inclusion of susceptible and resistant checks at regular intervals, evaluation in adjacent infested and uninfected plots and use of appropriate selection indices).

2.4.2.4. Establishing sickplots

Experiments can be undertaken under field conditions using heavily infested plots. However, the trials under field conditions are hampered by the heterogeneity of naturally infested soils. It is, therefore, crucial to ensure uniform distribution of the parasite seeds in the soil to prevent selection of genotypes that merely remain unchallenged. For small-scale tests, the plots can be artificially inoculated mixing parasite seeds with sand and applying them to the row with the crop seeds when sowing or two weeks ahead of sowing. Because *Striga* seeds are so small, soil infestations are most easily accomplished if the *Striga* seeds are mixed with a carrier material to increase volume. Sand is a good material, but it should be sieved so that only particles of the same size as *Striga* seed are used.

2.5. Drought Management Options

It is obvious that adoption of suitable moisture conservation practices in crop production is proving to be an effective means in mitigation water stress and increase crop productivity. In Ethiopia, different moisture conservation strategies such as mulching, tie-ridging, rainwater harvesting (spate irrigation), and improving soil fertility are the common practices in the drought prone areas to improve sorghum and other crops production.

In addition to the agronomic moisture conservation methods, breeding for more productive crop cultivars is one of the sound strategies in increasing crop yields in drought-prone environments. This is because better environmental manipulation with moisture-conserving agronomic practices alone may not lead to better yields from inferior genotypes unless they are integrated with crop genotypes that are capable of efficiently exploiting the limited moisture conserved (Singh, 2002). Furthermore, once drought tolerant cultivars become available, their adoption by the resource-poor farmers in the dry areas should be rapid because their use may not necessarily involve additional costs apart from the initial seed cost, and the existing cropping systems and soil and water management practices may not necessarily be affected (Keneni, 2012). Experience also shows that seed-based technologies are easier to transfer to farmers than more complex knowledge based agronomic practices (Edmeades *et al.*, 1996). Therefore, improving drought tolerance of sorghum is one of the most important objectives of plant breeders.

2.5.1. Drought tolerance or resistance

Drought is recognized as a condition where the water requirement of the plants, at different crop growth stages, exceeds the available water by more than 50% in the root zone because of inadequate precipitation leading to perceptible reduction in crop growth and economic yield (Reddy *et al.*, 2009). Drought tolerance refers to physiological or biochemical adaptations that enable plant tissues to withstand water deficits (Clarke and Durley, 1981), or the ability of plant tissues to function under stress or adapt to low tissue water potential (Blum, 1979). In agricultural context, drought tolerance is defined as stability of crop yield under a specific target drought stress environment. According to Turner (1986), Wenzel, (1999) and Mitra, (2001) drought resistance is the ability of the plants to produce satisfactory yield under limited soil water or drought stress conditions. In addition, Blum, (2005) stated that when a genotype yields better than another under a severe strain of drought, it is relatively more drought resistant. According to Ribaut *et al.*, (2002) genotypes vary in their ability to withstand or tolerate drought stress. Although sorghum is more drought tolerant compared to other cereals improving drought resistance in sorghum would further increase and stabilize grain production in low rainfall and harsh environmental regions of the world and contribute to food security to millions of poor depending on it.

2.5.2. Mechanism of drought resistance

The complete exploitation of genetic diversity for genetic improvement of crops for stress tolerance requires identification of mechanisms that ameliorate internal stresses and those that minimize drought injury (Steponkus *et al.*, 1980). The mechanisms of drought resistance can be described as escape, tolerance at high tissue water potential and tolerance (Levitt, 1972; Blum, 1979; Ludlow, 1993).

2.5.2.1. Drought escape

Drought escape is defined as a mechanism by which plants grow and complete their life cycle before severe drought stress occurs (Rosenow and Clark, 1981; Krieg and Hutmacher, 1982; Mitra, 2001). In regions where end-of-season drought stress is common, the most effective way to reduce losses due to drought is through the development of early-maturing genotypes to enable them escape end off-season drought (Blum, 1979; Turner, 1979). Drought escape involves rapid phenological development, developmental plasticity and remobilization of pre-anthesis assimilates to the grains while good soil water content conditions prevail (Krieg and Hutmacher, 1982; Turner, 1986; Mitra, 2001). Developmental plasticity is the ability of plants to halt growth during drought stress periods hence it is an important aspect for drought resistance.

Different sorghum improvement programs are most successful in exploiting a “drought-escape” mechanism and have breed specific maturity cultivars that match the available soil moisture. Early maturing is a well-known drought-escape mechanism through which the crop matures before experiencing water stress and is often associated with reduced yield potential (Blum *et al.*, 1992). Early sorghum genotypes compared to late ones have lower evapotranspiration rates due to smaller leaf area and smaller root density (Blum, 1979) as well as reduced seasonal transpiration due to a shorter life cycle. Of course, it is evident that while exploiting drought escape as a solution, some of the potential grain yield must be sacrificed in return for improved stability under moisture stress. Drought escape is, however, not drought tolerance per se. Therefore, breeding for early maturity may not be always associated with higher yield in regions with erratic rainfall pattern. Concerted breeding for tolerance to a given pattern of drought in a target region is the best way to improve grain yield under moisture-limited conditions.

2.5.2.2. Tolerance at high tissue water potential

Drought tolerance at high tissue water potential also called dehydration postponement or drought avoidance is the mechanism by which plants are able to maintain high water level within the tissues despite increasing soil and atmospheric water deficits (Blum *et al.*, 1978; Stout and Simpson, 1978; Krieg and Hutmacher, 1982; Blum, 2005). According to Krieg and Hutmacher, (1982) and Chaves *et al.*, (2003) green plants have two options for maintaining high tissue water status during soil water deficit periods, i.e. reduction of transpirational water loss and increasing water absorption.

2.5.2.2.1. Reduced water loss

To reduce the effects of soil water deficit, plants have to control transpirational water loss from the aboveground parts. This can be accomplished by changes in the surface area of transpiring parts such as leaves, physical changes in transpiring surface and by regulating the opening and closing of stomata (Passioura, 1976; Simpson, 1981) through reduction of stomatal and lenticular conductance (Tuinstra *et al.*, 1997; Mitra, 2001).

2.5.2.2.2. Increased water uptake or absorption

By maintaining and absorbing water more efficiently from the soil through increased roots depth, efficient root system and increased hydraulic conductance can help plants to maintain high tissue water content (Jordan and Monk, 1980; Seetharama *et al.*, 1982; Turner, 1986; Tuinstra *et al.*, 1997).

2.5.2.3. Drought tolerance at low tissue water potential

Drought tolerance at low water potential is the ability of plants to endure or withstand water deficits and maintain physiological processes even though low tissue water potential develops (Jordan and Monk, 1980; Rosenow and Clark, 1981). According to Tuinstra *et al.*, (1997) this mechanism functions within the tissues, since it protects and stabilizes cellular and metabolic processes during tissue dehydration. Jordan and Monk, (1980) stated that drought tolerance at low water potential could be accomplished by accumulation of solutes (osmotic adjustment), an increase in cellular elasticity and decreasing cell size. Osmotic adjustment refers to net increase of solute concentration due to metabolic processes as triggered by drought stress (Babu *et al.*, 1999; Hopkins and Hüner, 2004). Hinckley *et al.,* (1981) and Babu *et al.*, (1999) mentioned that osmotic adjustment is able to increase water-absorbing power of the foliage, delay wilting and stomatal closure and protect protoplasm from desiccation and maintaining turgor pressure.

Drought tolerance mechanisms mostly depend on the developmental stage of the plants at the time of drought stress occurrence (Stout and Simpson, 1978; Tuinstra *et al.*, 1997). According to Tuinstra *et al.*, (1997) drought stress tolerance has been identified and susceptibility symptoms have been categorized into three different growth stages (early seedling and vegetative stage, pre-flowering and post-flowering). Rosenow and Clark, (1981) stated that sorghum cultivars that have good drought tolerance during pre-flowering developmental stage are usually found to be susceptible to drought stress during post-flowering growth stage. Some genotypes have been found to possess moderate levels of drought tolerance at both pre and post-flowering stages (Rosenow and Clark, 1981). Pre-flowering response period starts during head differentiation until flowering (Tuinstra *et al.*, 1997), while post-flowering resistance is indicated by the stay green trait during grain filling stage, which makes plants resistant to premature senescence (Crasta *et al.*, 1999).

Stay green in sorghum is characterized by the plant's ability to tolerate post-flowering drought stress, thereby delaying the premature leaf and plant death (Subudhi *et al.*, 2000; Xu *et al.*, 2000a; Harris *et al.*, 2007; Kassahun *et al.*, 2010). Stay green lines produce two to three more basal tillers per plant at black layer, have a greater stem diameter, higher sugar concentrations at the base of the stem, maintain greater green leaf area longer, greater leaf area index, higher leaf relative water content, higher specific leaf nitrogen, contain a higher level of cytokinins, and have enhanced transpiration efficiency than senescent lines (Duncan *et al.*, 1981; Ambler *et al.*, 1987; Dahlberg, 1992; Borrell and Hammer, 2000). Moreover, stay green genotypes do not show reduced yield under well-watered conditions, thus stay green genotypes are productive on both irrigated and non-irrigated condition (Borrell *et al.*, 2000b).

2.5.3. Empirical screening method for drought tolerance

Breeding for drought-tolerant crops largely depends on the availability of the genetic resources for tolerance, reliable screening techniques, identification of genetic components of tolerance (Blum, 2011), successful genetic manipulation of the desired genetic backgrounds, and ultimate development of drought-tolerant cultivars with acceptable agronomic and quality-related traits (Araus and Cairns, 2014). The relative yield performance of genotypes under drought stressed and non-stressed environments can be used as an indicator to identify drought resistant varieties to drought (Raman *et al.*, 2012; Mohammadi, 2016).

Based on their comparative yield performance in stress and non-stress environments genotypes were categorized in four groups; genotypes with high performance under both moisture regimes (group A), high yield in non-stress (B), high yield in stress (C), and low yield under both moisture regimes (D) (Fernandez, 1992). Several drought indices that are based on drought resistance/susceptibility of genotypes have been suggested for screening to drought and computed between yield under stress and optimal conditions. These includes: stress tolerance index (STI) and geometric mean productivity (GMP) (Fernandez, 1992), stress susceptibility index (SSI) (Fischer and Maurer, 1978), tolerance index (TOL) (Hossain *et al.*, 1990), mean productivity (MP) (Rosielle and Hamblin, 1981), yield index (YI) (Gavuzzi *et al.*, 1997), yield stability index (YSI) (Bouslama and Schapaugh, 1984), harmonic mean (HM) (Kristin *et al.*, 1997), and mean relative performance (MRP) (Osmanzai, 1994).

2.6. Genetic Markers

The discovery of the structure of DNA by Watson and Crick has enhanced traditional breeding techniques by allowing breeders to pinpoint the particular gene responsible for a particular trait and to follow its transmission to subsequent generations (Xu, 2010). Genetic markers are biological features that are determined by allelic forms and can be used as experimental probes or tags to keep track of an individual, a tissue, cell, nucleus, chromosome or gene. Genetic markers used in genetics and plant breeding can be classified as: classical markers (morphological, cytological and biochemical markers) and DNA markers (Xu, 2010; Jiang, 2013). Morphological markers are based on visible/phenotypic characteristics, whereas biochemical markers are based on gene products. Molecular markers are identifiable DNA sequences found at specific locations of the genome (DNA sequence variation) and transmitted from one generation to the next, following standard laws of inheritance (Collard *et al.*, 2005, Semagn *et al.*, 2006; Jiang, 2013).

Morphological and biochemical markers are limited in number and are influenced by environmental conditions, developmental stage/ tissue type, while molecular markers are virtually unlimited in number and are not affected by environment or tissue type, making them valuable tools in various analyses in plant breeding. They are used in early generation selection, in choosing donor parents in backcrossing, recovering of recurrent parent genotype in backcrossing, germplasm characterization/fingerprinting, among other uses

(Varshney *et al.*, 2009). DNA based markers can be utilized effectively in marker assisted selection (MAS) for tracing favourable alleles (dominant or recessive) across generations and identifying the most suitable individuals among the segregating progeny based on allelic composition across a part or the entire genome. The utility of DNA markers in resistance breeding depends on the existence of tight linkage between these markers and the resistance genes/QTLs of interest (in this case, *Striga* and drought resistance genes).

Different types of molecular markers have been developed and evolved. Molecular markers are grouped after their different abilities of showing homozygosity (dominant marker) or heterozygosity (co-dominant marker) (Hartl, 1988). The most commonly used dominant DNA markers are: Random Amplified Polymorphic DNA (RAPD) (Welsh and McClelland, 1990; Williams *et al.*, 1990), DNA amplification fingerprinting (DAF) (Caetano-Anolles *et al.*, 1991), arbitrarily primed polymerase chain reaction (AP-PCR) (Welsh and McClelland, 1990), inter-simple sequence repeat (ISSR) (Zietkiewicz *et al.*, 1994) and amplified fragment length polymorphisms (AFLP) (Vos *et al.*, 1995), whereas the most common used co-dominant markers are: restriction fragment length polymorphisms (RFLP) (Botstein *et al.*, 1980), microsatellites (SSR) (Tautz and Renz, 1984; Akkaya *et al.*, 1992), sequence characterized amplified regions (SCAR) (Paran and Michelmore, 1993), cleaved amplified polymorphic sequence (CAPS) (Konieczny and Ausubel, 1993), expressed sequence tag (EST) (Adams *et al.*, 1991) and single nucleotide polymorphism (SNP) (Jordan and

Humphries, 1994), sequence tagged sites (STS) (Olsen *et al.*, 1989), diversity arrays technology (DArT) (Jaccoud *et al.*, 2001; Wenzel *et al.*, 2004) and Kompetitive allele specific PCR (KASP) (He *et al.*, 2014).

Each marker system has its own merits and demerits. The various factors to be considered in selecting one or more of these marker systems have been described as: (i) high level of genetic polymorphism; (ii) codominance; (iii) clear distinct allele features; (iv) even distribution on the entire genome; (v) neutral selection; (vi) easy detection; (vii) low cost of marker development and genotyping; and (viii) high duplicability (Collard and Mackill, 2007; Doveri *et al.*, 2008; Xu, 2010; Jiang, 2013). Different markers were greatly exploited for mapping of different traits in sorghum including *Striga* resistance (Haussmann *et al.*, 2004; Satish *et al.*, 2012) and drought tolerance (Subudhi *et al.*, 2000; Tao *et al.*, 2000; Xu *et al.*, 2000a; Kebede et al., 2001; Sanchez et al., 2002; Kassahun *et al.*, 2010). DNA markers, which are related to this study, are described hereunder as subtitles.

2.6.1. Single nucleotide polymorphism (SNP)

Single nucleotide polymorphism (SNP) is a DNA sequence variation occurring when a single nucleotide (A, T, G or C) differs among members of a species. SNPs can be categorized according to nucleotide substitution as either transitions (C/T or G/A) or transversions (C/G, A/T, C/A or T/G) (Xu, 2010). SNP is the most abundant marker system both in animal and plant genomes and has recently emerged as the new generation molecular markers for various applications. Being binary or co-dominant status, they are able to efficiently discriminate between homozygous and heterozygous alleles. Moreover, unlike microsatellites their power comes not from the number of alleles but from the large number of loci that can be assessed (Foster *et al.*, 2010). Most importantly, SNPs are amenable to high throughput automation, allowing rapid and efficient genotyping of large numbers of samples (Tsuchihashi and Dracopoli, 2002).

2.6.2. Kompetitive Allele Specific PCR (KASP)

Single nucleotide polymorphism (SNP) data can be obtained using one of the numerous uniplex or multiplex SNP genotyping platforms that combine a variety of chemistries, detection methods, and reaction formats (Semagn *et al.*, 2013). Although multiplexing offers greater throughput with less reagent consumption, it restricts researchers to the use of a multiplexed set of several thousand SNPs per assay. As the multiplex level rises, this becomes increasingly problematic for crop improvement applications that require low to medium marker density because highly multiplexed platforms have relatively high per-sample cost and may require substantial time for initial assay development. For this reason, chip based platforms may be less suitable for applications requiring small to moderate numbers of SNPs for a large number of samples. This may be the case for quality control analysis where few SNPs may be required (Semagn *et al.*, 2012), and for QTL mapping, MABC, and marker-assisted recurrent selection applications where polymorphism and hence genetic significance of SNP varies from population to population.

In such cases, uniplex (single-plex) SNP genotyping platforms, such as KASP, may be more suitable (Neelam *et al.*, 2013). KASP is a homogeneous, fluorescence-based genotyping technology, initially developed by KBioscience for in-house genotyping and eventually evolving into a global benchmark technology. The technology is based on allele-specific oligo extension and fluorescence resonance energy transfer (FRET) for signal generation (Kumpatla *et al.*, 2012). The application of the KASP assay is preferred as genotyping technology, because of its ease of use, consistency, and cost effectiveness (Semagn *et al.*, 2013; He *et al.*, 2014; Rosas *et al.*, 2014). KASP chemistry has been documented to be an effective method for medium throughput genotyping projects previously in maize (Semagn *et al.*, 2013) and recently in other economically important cereal crops. In sorghum, MABC using KASP can expedite the development of backcrossed lines to 3 years compared to 5-6 years using conventional method of backcrossing and improved overall efficiency both in terms of cost and accuracy of introgression (Burow *et al.*, 2019).

2.7. Marker-Assisted Selection (MAS)

MAS involves selection of plants with genomic regions involved in expression of trait of interest (Collard and Mackill, 2007; Choudhary *et al.*, 2008; Vogel, 2014). It is possible for traits controlled by major genes as well as quantitative trait loci (QTL) due to the availability of an array of molecular markers and dense molecular genetic maps (Semagn *et al.*, 2006). MAS is gaining importance as it would improve the efficiency of plant breeding through precise transfer of genomic regions of interest (Semagn *et al.*, 2006; Choudhary *et al.*, 2008; Ibitoye and Akin-Idowu, 2011). There are many MAS breeding schemes including marker-assisted backcrossing (MABC), early generation marker assisted selection, marker-assisted recurrent selection (MARS), and marker-assisted gene pyramiding (MAGP). Of the MAS schemes, MABC is frequently used to improve the existing elite varieties, which is the target of this study.

2.7.1. Marker-assisted backcrossing (MABC)

MABC is a plant breeding method most commonly used to incorporate one or a few genes into an adapted or elite variety (Jiang, 2013; 2015). In most cases, the parent used for backcrossing has a large number of desirable attributes but is deficient in only a few characteristics (Allard, 1999). MABC can be efficiently used to improve an existing variety for a specific trait, because it reduces both the time needed to breed a variety and the risk of undesirable linkage drag with unwanted genes (e.g. those that reduce yield) from the trait donor (Xu, 2010; Vogel, 2014; Akshay *et al.*, 2015). DNA markers are now increasingly used in backcross breeding to increase the efficiency of selection at three levels, viz. foreground selection, background selection and recombinant selection (Holland 2004; Collard and Mackill, 2007; Akshay *et al.*, 2015; Jiang, 2015).

In foreground selection, the selection is made only for the marker allele(s) of the donor parent at the target locus to maintain the target locus in a heterozygous state until the final backcrossing is completed. Then the selected plants are selfed and the progeny plants with homozygous donor parent allele(s) of selected markers are harvested for further evaluation and release.

In background selection, however, the selection is made for the marker alleles of recurrent parent in all genomic regions of desirable traits except the target locus, or selection against the undesirable genome of donor parent to hasten the restoration of the recurrent parent genome and eliminate undesirable genes brought in by the donor parent. In addition, the linkage drag also can be efficiently addressed by background selection using DNA markers, although it is difficult to overcome in a traditional backcrossing program (Jiang, 2015).

Foreground selection and background selection are usually conducted in the same program, either simultaneously or successively. The individuals that have the desired marker alleles for target trait are selected first (foreground selection) and then the selected individuals are screened for other marker alleles again for the recurrent parent genome (background selection).

Marker-assisted recombinant selections reduce the size of the donor segment of the genome containing the target locus. This approach is important because the decrease of donor fragment size reduce the deleterious effect of many undesirable genes, linked to the target gene, that negatively affect crop performance, this is referred to as 'minimization of linkage drag' (Hospital, 2005; Collard and Mackill, 2007).

2.7.3. Quantitative trait loci for *Striga* resistance

MAS can greatly accelerate breeding progress for *Striga* resistance, because screening for complex resistance under field conditions is difficult and sometimes unreliable. In addition, some *Striga* resistance genes are recessive (Ramaiah *et al.*, 1990; Vogler *et al.*, 1996; Haussmann *et al.*, 2002) making selection during backcrossing schemes more difficult. A single recessive gene (*lgs*) controls low *Striga* germination stimulant activity, a well-known resistance mechanism in sorghum (Satish *et al.*, 2012).

A population of recombinant inbred lines (RILs) generated from a cross between SRN39 (*lgs*), a *Striga* resistant line and Shanqui Red a susceptible Chinese sorghum cultivar was developed through the single seed descent which resulted in the identification of six resistance QTL and four were shared between the two species. The gene mapped to one of the QTL regions, supporting the hypothesis that resistance to *Striga* is the product of one or a combination of several mechanisms that influences the development of parasitism (Ejeta *et al.*, 1997).

Results revealed that the predicted responses were higher with MAS for *S. hermonthica* resistance, where selection is solely based on genetic markers (24%) more efficient and MAS based on marker loci information plus phenotype (41%) than with phenotypic selection signifying the importance of molecular markers for enhancing efficiency of breeding for *Striga* resistance in sorghum.

In other studies, two populations of RILs from crosses: IS9830 (partially resistant with *lgs*) x E36-1 (RIP-1) (susceptible to *Striga* but possesses a certain degree of drought resistance) and N13 (stimulates abundant *Striga* seed germination but possesses a resistance mechanism through mechanical) x E36-1 (RIP-2) were evaluated. The final maps revealed lengths of about 1550 cM in the two recombinant inbred populations, and contained relatively few gaps. In the RIP-1 (IS9830 x E36-1) population, 11 and 9 QTL were identified for area under the *Striga* number progress curve (AUSNPC) in Sets 1 and 2, together explaining 77% and 60% of the genetic variance, respectively (Haussmann et al., 2004). Five of the QTL were common to both sets. Several QTL were identified in the two genotypic sets of RIP-2 (N13 × E36-1) and explained about 80% of the genetic variance for AUSNPC. Again, five QTL were common to both sets. A five-fold cross-validation of the results revealed a low genotype dependency of the QTL results for the N13 population. Because of the successful QTL validation across locations, years, and genotype samples, the five stable QTL identified in this population may serve as candidates for marker-assisted transfer into other cultivars via MABC. These QTL analyses affirm that *Striga* resistance under field conditions is a quantitative trait affected by many genes. The results of these studies based on the two populations seem to suggest that several linkage groups may be involved in the expression of *Striga* resistance. Some loci probably have a stronger role in host-parasite interaction and may therefore be more stable across test locations and years (Haussmann *et al.*, 2004).

Recently, Satish *et al.*, (2012) fine-mapped four QTLs of low germination stimulants (*lgs*) genes from 354 recombinant inbred lines derived from SRN39 (low stimulant) x Shanqui Red (high stimulant) on SBI-05. The three markers (SB3344, SB3346 and SB3343) are flanking on the same side with genetic distances of 0.5, 0.7 and 1.5 cM, respectively, from the lgs gene. The fourth marker SB3352 flanked the lgs gene on the opposite side with a genetic distance of 1.5 cM.

2.7.4. Quantitative trait loci for drought tolerance

The use of molecular markers and QTL analysis has the potential to alleviate the problems associated with inconsistent and unpredictable onset of moisture stress or the confounding effect of other related stresses, such as heat (Ejeta *et al.*, 2000b). Many researchers (Tuinstra *et al.*, 1996; 1997; 1998; Crasta *et al.*, 1999; Ejeta *et al.*, 2000b; Subudhi *et al.*, 2000; Tao *et al.*, 2000; Xu *et al.*, 2000a; Kebede *et al.*, 2001; Sanchez *et al.*, 2002) have identified and deployed QTLs associated with pre and post-flowering drought tolerance in sorghum.

The molecular genetic analysis of QTL influencing the stay green (characterized by the plant's ability to maintain functional photosynthetic leaf area during the grain-filling stage even under severe post-flowering drought stress) trait, which is an important post-flowering drought tolerance character resulted in the identification several QTLs on different linkage groups. Comparison of the stay green QTLs from Tuinstra *et al.*, (1997), Xu *et al.*, (2000a), Subudhi *et al.*, (2000), Tao *et al.*, (2000) and Haussmann *et al.*, (2002) using B35 as source resulted in the consistent identification of six major stay-green QTLs, *stgC* (SBI-01), *stg3A* and *stg3B* (on SBI-02), *stg1* and *stg2* (on SBI-03), and *stg4* (on SBI-05) have been detected across several studies, which together accounted up to 53.5% phenotype variance.

The ranking of stay green QTL based on their contribution to the stay green phenotype in BTx642 × RTx7000 population is *Stg2* > *Stg1* > *Stg3* > *Stg4* (Xu *et al.*, 2000a). Recently, *Stg2, Stg3*, and *StgB* were identified to be the three key QTLs for MAS to improve terminal drought tolerance (Reddy *et al.*, 2014). Stay green QTL individually reduced leaf senescence in introgression lines and may contribute significantly towards breeding drought tolerance (Harris *et al.*, 2007; Kassahun *et al.*, 2010). More recently, the potential use of stay green QTL in improving transpiration efficiency and water extraction capacity in sorghum for terminal drought tolerance (Vadez *et al.*, 2011), colocation with nodal root angle (Mace *et al.*, 2012), and grain yield particularly under low-yield environments has been demonstrated (Jordan *et al.*, 2012).

2.8. Status of Sorghum Breeding and Genetics Research in Ethiopia

Ethiopia is probably the original home of sorghum and is the source of many wild and cultivated forms (diversity) adapted to a wide range of growing conditions. Having this huge natural endowment, the country is a valuable reservoir of diverse genetic material for sorghum improvement throughout the world (Mekbib, 2008). Sorghum research in Ethiopia started in 1953 at the then Jimma agricultural and technical school, which is now called Jimma University. The program moved to the then Alemaya College of agriculture and technical arts now called Haramaya University in 1957, where a formal research was started (Mekbib, 2008). The establishment of the Ethiopian sorghum improvement project (ESIP) in 1972 in Adama (the then Nazareth) can be considered as the landmark for the establishment of formal research on sorghum in Ethiopia. In 1982, ESIP assimilated to the Ethiopian institute of agricultural research (EIAR) (the then institute of agricultural research, IAR) and founded as one of the national program. As of then, sorghum-breeding activities were done in the different ecological parts of the country by different national and international organizations. Since the establishment of the program, about 56 sorghum varieties have released for different ago-ecologies (MoA, 2018) (Table 2). Among which, the *Striga* resistant varieties (Gobiye and Birhan) used in this crossings as pollen source and improved varieties with high yielding potential (Melkam, Dekeba, Meko, Macia, Debir, Gambella 1107, and Teshale) used as seed parents are amongst the popular released varieties under production (MoA, 2018).

Table 2. List of sorghum varieties released in Ethiopia

No.	Variety	Pedigree	Year of release	Center	Agro-ecologies Zones	Yield (kg/ha)	Selected traits
1	Alemaya-70	-	1970	HU	Highland(>1900 m)	4250	High yield
2	76T1#23	954062 x 73pp9	1976	MARC/EIAR	Lowlands (<1600)	3500	Early maturing
3	Gambella 1107	Landrace	1976	MARC/EIAR	Lowlands	4000	High yield & good quality
4	IS9302	-	1981	MARC/EIAR	Intermediate (1600-1900 m)	4500	High yield
5	Seredo	Seredo	1986	MARC/EIAR	Low lands	3000	Bird tolerance
6	Dinkimash	Dinkimash	1986	MARC/EIAR	Low lands	6600	High yield
7	Birmash	80LPYT-1#433 x IS9302	1989	MARC/EIAR	Intermediate	3520	High yield
8	Baji(85MW5334)	RS/R-20-86142 x IS9293	1996	M/J/ARC/EIAR	Intermediate	4500	High yield
9	Chiro	Coll#4	1996	MARC/EIAR	Highlands	5000	Sugary stalk
10	Meko	M-36121	1997	MARC/EIAR	Low lands	4500	Earliness & good quality grain
11	Muyra-1	EST-1005	2000	HU	Highland	5130	High yield and early maturing
12	Muyra-2	EST-567	2000	HU	Highland	4820	Early maturing
13	Gobiye	P-9401	2000	MARC/EIAR	Low lands	4000	*Striga* resistant
14	Abshir	P-9403	2000	MARC/EIAR	Low lands	3000	*Striga* resistant
15	Aba-Melko	SARTU	2001	JARC/EIAR	intermediate	6800	Stalk borer & grain disease resistant
16	Yeju	ICSV 111INC	2002	SARI/ARARI	Lowlands	5000	Disease resistant
17	Teshale	3443-2-OP	2002	SARC/ARARI	Low lands	6100	High yield
18	Birhan	Key#8566	2002	SARC/ARARI	Lowlands	4000	*Striga* resistant
19	Abuare	90MW 5353	2003	SARC/ARARI	Lowlands	4000	Disease resistant
20	Chelenko	ETS1176	2005	MARC/EIAR	Highland	4600	High yield

No.	Variety	Pedigree	Year of release	Center	Agro-ecologies Zones	Yield (kg/ha)	Selected traits
21	Hormat	ICSV 1112 BF	2005	SARC/ARARI	Lowlands	2400	*Striga* resistant
22	Dano	BRC-378	2006	BARC/OARI	Intermediate	4500	High yield
23	Lalo	BRC-245	2006	BARC/OARI	Intermediate	4600	High yield
24	Geremew	87MW5325 x IS-158(ETS-2113)3	2007	MARC/EIAR	Intermediate	5750	High yield
25	Red Swazi	Red Swazi	2007	MARC/EIAR	Low lands	3150	Malting type
26	Macia	Macia	2007	MARC/EIAR	Low lands	4300	Malting type
27	Gedo	Gambella1107 x P9403	2007	SARI/ARARI	Low lands	3400	High yield, *Striga* resistant, early maturing
28	Emahoy	PW01-092	2007	PARC/EIAR	Humid lowlands	4200	High yield & tannin (bird resistant)
29	Miskir	E#69441 x P9401	2007	SARI/ARARI	Low lands	4070	High yield & early maturing
30	Girana-1	35DJ1195 x N-13	2007	SARC/ARARI	Lowlands	4100	High yield, early maturing & good injera making
31	Lalo	BRC-245	2007	BARC/OARI	Intermediate	4600	High yield & stay green
32	Raya	PGRC/EX222878XKAT369-1	2007	SARC/ARARI	Lowlands	3000	Disease & pest resistant
33	Melkam	WSV-387	2009	MARC/EIAR	Low lands	5150	High yield
34	ESH-1	P-9501A x ICSR14	2009	MARC/EIAR	Low lands	5300	High yielding hybrid
35	ESH-2	ICSA21 x ICSR50	2009	MARC/EIAR	Lowlands	5200	High yielding hybrid
36	Dagim	97MW6130	2011	MARC/EIAR	Intermediate	4000	Grain mold & leaf resistant
37	Chare	PGRC/E#222880	2011	DBARC/ARARI	Highland	2589	
38	Mesay	Meko x Gobye-2	2011	SARC/ARARI	Lowlands	2637	
39	Dekeba	ICSR24004	2012	MARC/EIAR	Low lands	4100	High yield, earliness, & stay green

No.	Variety	Pedigree	Year of release	Center	Agro-ecologies Zones	Yield (kg/ha)	Selected traits
40	Gemedi	ACC-BCC-5	2013	BACK/OARI	Intermediate	3300	High yield, resistance to anthracnose, leaf bight & smuts
41	Chemeda	Acc-BRC-18	2013	BACK/OARI	Intermediate	3200	High yield and resistance to anthracnose, leaf bight & smuts
42	PAC537	-	2013	GCT/MARC	Lowlands	3820	High yield
43	ESH-3	ICSA-15 X M-5568	2014	MARC/EIAR	Lowlands	5410	High yield hybrid
44	Fendisha-1	-	2015	HU	Highlands	4935	High yield
45	Assosa-1	Bambasi no-9	2015	AARC/EIAR	Humid lowlands	3950	High yield
46	Adukara	-	2015	AARC/EIAR	Lowlands	4016	High yield
47	Dibaba	ETS639/SRN-39	2015	MARC/EIAR	Lowlands	4120	High yield
48	Jiru	ETS-2752	2016	MARC/EIAR	Lowlands	3800	High yield
49	Adele	ACC#70583	2016	MARC/EIAR	Lowlands	2253	High yield
50	ESH-4	PU209A/PU304	2016	MARC/EIAR	Lowlands	4860	High yield hybrid
51	Argeti (2005M15064)	WSV387/P9404	2017	MARC/EIAR	Lowlands	4500	High yield & early maturing
52	Bonsa	97BK6129/85MW4138	2017	MARC/EIAR	Lowlands	4450	High yield
53	Alene	WSV-387 x E-36-2	2017	SARC/ARARI	Lowlands	4717	High yield
54	ESH-5 (9058)	P9511A/PRL020817	2018	MARC/EIAR	Lowlands	5760	High yield & tolerant major to disease
55	Mentebteb/Debir	Debir	2018	MARC/EIAR	Lowlands	4780	Malt type & tolerant to major insect & diseases
56	Tilahun	-	2019	MARC/EIAR	Lowlands	4560	High yield & early maturing

GCT-Advanta seed International, HU- Haramaya University, SARC- Srinka Agricultural Research Center, ARARI- Amhara regional Agricultural Research Institute, MARC-Melkassa Agricultural Research Center, EIAR-Ethiopian Institute Agricultural Research, JARC- Jimma Agricultural Research Center, AARC-Assosa Agricultural Research Center, DBARC-Debre Birhan Agricultural Research Center

2.9. The Rationale and Relevance of the Study

In Ethiopia, sorghum is the third most important and widely grown cereal crop for food, feed, beverages and fuel. It is largely grown in the marginal, where annual rainfall is very low, erratic and poorly distributed, intense *Striga* infestation and soils are of low fertility. In these marginal areas, the grain yields of sorghum are very low and unstable predominantly due to frequent drought stress and intense *Striga* weed infestations and most importantly they frequently occur together. With changing climatic conditions and erratic rainfall patterns, the recurrence of drought along with *Striga* in these regions rather complicated the problem due to the interaction between the two.

To overcome the two challenges, genetic control is the most feasible means of crop protection from the economic standpoint and sustainability. In this regard, plant breeders have utilized molecular markers/QTLs for stay green and *Striga* resistance on sorghum. From the practical viewpoint and urgency, the validation, refining and adoption of molecular markers developed elsewhere for drought tolerant and *Striga* resistance are advisable, effective and efficient to better serve the needs of Ethiopia. This approach is believed to offer opportunities to Ethiopian sorghum breeders to take control of breeding solutions for this top priority constrain in sorghum.

3. MATERIALS AND METHODS

3.1. Introgression of *Striga* Resistant Genes into Popular Ethiopian Sorghum Genotypes

3.1.1. Plant materials

The parental pure lines used for this crossing and backcrossing were three donor parents and twelve recurrent parents selected from among the released varieties and known farmers' cultivars (Table 3). The donor parents are known for their low *Striga* germination stimulant activity as reported for Framida (Mohamed *et al.*, 2010; Satish *et al.*, 2012; Mohemed *et al.*, 2018), Gobiye and Birhan (Ejeta *et al.*, 2007; Grenier *et al.*, 2007; Tesso *et al.*, 2007; Satish *et al.*, 2012). The male parents were used as sources of resistant genes to *Striga* by the national sorghum breeding programs. The recurrent parents are both high yielding and popular amongst the farmers but susceptible to *Striga hermonthica*. The description of the test genotypes is given in Table 3.

Table 3. The parental lines used in marker-assisted backcrossing for *Striga* resistance

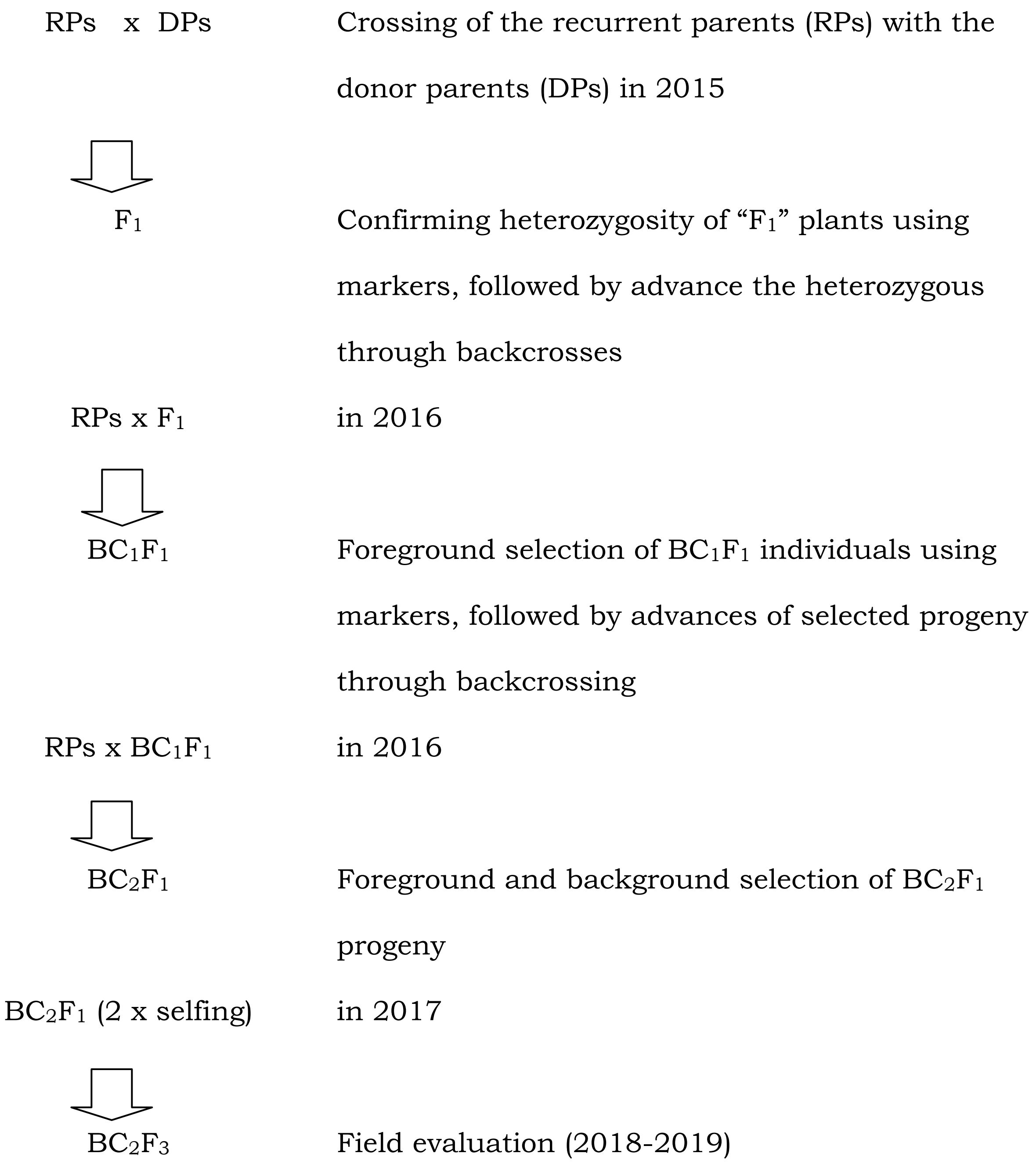
No	Variety	Breeder's code	Year of release	Center of release	Parental lines
1	AbaAre-1	Local	-	-	RP
2	America-1	Local	-	-	RP
3	Berjokecoll#1	Local	-	-	RP
4	Birhan	Key#8566	2002	Srinka	DP
5	Debir	Debir	2018	Melkassa	RP
6	Dekeba	ICSR24004	2012	Melkassa	RP
7	Framida	87441	1991	-	DP
8	Gambella1107	Gambella1107	1976	Melkassa	RP
9	Gobiye	P-9403	2000	Melkassa	DP
10	Jamiyu	Local	-	-	RP
11	Jigurti	Local	-	-	RP
12	Teshalle	3443-2-OP	2002	Srinka & Melkassa	RP
13	Tseadachimure	Local	-	-	RP
14	Wediaker	Local	-	-	RP
15	Wetetbegunche	Local	-	-	RP

RP = Recurrent parent, and DP = Donor parent

3.1.2. Development of backcross lines

Two diagnostic markers mapped on chromosome five (SBI-05) (Satish *et al.*, 2012) grouped *Striga* resistance and susceptible sorghum genotypes representing the breeding population were identified. The Ethiopian popular cultivars and farmers preferred cultivars (recurrent parents) were crossed with donor parents to generate 328 F_1 plants using hand pollination method at Melkssa Agricultural Research Center (MARC), Ethiopia. Crossing was done by emasculation of selected plant panicles (recurrent parents) and dusting of pollen from identified plants (donor parents). The resultant 176 F_1 plants (out of the 328) with desired quantitative trait loci (QTLs) were backcrossed to the respective recurrent parents to generate 153 BC_1F_1 progeny. BC_1F_1 progeny were screened for the presence of donor parent allele and selected progeny were backcrossed to generate 131 BC_2F_1. The BC_2F_1 conferring the targeted donor parent allele and recovered the genetic background of the recurrent parent were selected and advanced to 118 BC_2F_3 stage.

Off-season nursery at Werer agricultural research center, Ethiopia was used to reduce the time to advance the generation. The schematic diagram for crossing, backcrossing, selfing and marker-assisted selection to generate converted progeny for *Striga* resistance is given in Figure 4.



RPs x DPs	Crossing of the recurrent parents (RPs) with the donor parents (DPs) in 2015
F_1	Confirming heterozygosity of “F_1” plants using markers, followed by advance the heterozygous through backcrosses
RPs x F_1	in 2016
BC_1F_1	Foreground selection of BC_1F_1 individuals using markers, followed by advances of selected progeny through backcrossing
RPs x BC_1F_1	in 2016
BC_2F_1	Foreground and background selection of BC_2F_1 progeny
BC_2F_1 (2 x selfing)	in 2017
BC_2F_3	Field evaluation (2018-2019)

Figure 4. Scheme of crossing, backcrossing, selfing and MABC to generate sorghum lines converted for *Striga* resistance

3.1.3. DNA extraction, genotyping and KASP assay

The parental lines and backcross progeny (F_1, BC_1F_1, BC_2F_1) planted in the crossing block at Melkassa research center were tagged to collect tissue for polymorphic and confirmation of the targeted markers. Plant tissue samples were collected using a puncher at fourth stages (leaves) from eight to ten plants from each backcrossed family. The leaf tissues were packed in a labeled waterproof envelope and then sent to LGC Genomics Ltd, Unit 1-2 Trident Industrial Estate, Pinar Road, Hoddesdon, Herts, EN11 0ZW, UK for KASP molecular analysis.

The leaf samples from each genotype were grinded to fine powder using Qiagen® Tissue Lyser II followed by genomic DNA extraction using MagAttract® 96 DNA plant Kit (Qiagen). An ultraviolet/visible spectrophotometer was used for the quantification of genomic DNA (He *et al.*, 2014; Burow *et al.*, 2019). The reaction mix (~10 µl total) for each sample in KASP genotyping was comprised of the following reagents per reaction: 1 µl of gDNA, 5 µl of KASP 2xMaster mix (KASP MM), 0.14 µl of KASP SNP primer (competitive two forward primers i.e. a wild type allele and mutant allele primers and a common reverse primer), and 4µl of PCR water. Centrifuge was done at 3787 rpm for 5 min.

The specific KASP assay genotyping was done in Roche 480 Light Cycler with the following programs: (i) enzyme activation at 94°C for 15 min, 1 cycle; (ii) touchdown PCR consisting of a denaturation step at 94°C followed by actual touch down steps from 65°C to 57°C, dropping at 0.6°C per cycle for 10 cycles; (iii) thermocycling, consisting of a denaturation step at 94°C for 20 second followed by rapid decline to a target temperature of 55°C for 1 min for annealing and elongation for 30 cycles; (iv) complete the KASP PCR assay with a quantification step consisting of 37°C for 3 min, followed by 37°C single data acquisition for 1 second. Then allele calls was done based on fluorescence data using allele calling software embedded within the endpoint genotyping suite of Roche LC480 (www.lgcgenomics.com).

3.1.4. Description of the markers

The parental and backcrossed lines were genotyped for polymorphic and incorporation of the desired KASP SNP alleles, namely *lgs2_SBI-05_60404021* (TTAGAGATTGAGATTTGAGACTGAAGATGACCGATTGCGTGTTCACCGACTGAATAAGCTTCGGAACTTGCTGCAGATTCAGAGATGAAGAAAAACACA[**T/A**]GCGTAATAGCTGGCTGTTGCGTGTAATCGCCGCTTAACAGTCATCGATCA GATGCGGCCCGGATACCAAGGCCCGATGCAACGAAACCAGCCCAATTCGTC) & *lgs_3_60629027*) CGAACAGGGGTACGGTGGTGCGGCGGTTCAGGCACGGCGCC GTGGTGGACGTCGTGTTCCAGAGCACCGCCATGCTGCAGAGCGACTCCAACCC GATGCA[**T/C**]CTCCATGGACACGACATGTTCGTGCTCGCGCAGGGGATCGGCAACTACGACGCGGCAAGGGACGAGGCCAAGTTCAACCTGGTGAACCCGGCGAGGAAGA) markers. The markers were identified from 354 recombinant inbred lines (RILs) developed by crossing SRN39 (low stimulant) and Shanqui Red (high stimulant) (Satish *et al.*, 2012).

3.2. *In-vitro* Evaluation of Converted Lines and their Parents for *Striga* Resistance

Striga bioassay based on the agar-gel method developed by Hess *et al.*, (1992) was conducted at the National Agricultural Biotechnology Research Center (NABRC), Holetta, Ethiopia. A total of 134 genotypes including the parental lines (3: donor parents + 12: recurrent parents), their backcross progeny (118: BC_2F_3) and one resistant check (SRN39) were screened for *Striga* resistance based on the capacity of *Striga* germination stimulants production in agar-gel assay (Table 4).

Table 4. List of sorghum backcrossed lines and their parental lines evaluated against *Striga hermonthica* under agar-gel bioassay and field condition

SN	Genotypes	Pedigree /Breeder's code	QTL
1	AbaAre-1	AbaAre-1	Recurrent parent
2	America-1	America-1	Recurrent parent
3	BC_2F_3_ETSC_17001	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2† & lgs3‡
4	BC_2F_3_ETSC_17002	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
5	BC_2F_3_ETSC_17003	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
6	BC_2F_3_ETSC_17004	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
7	BC2F3_ETSC_17005	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
8	BC_2F_3_ETSC_17006	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
9	BC_2F_3_ETSC_17007	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
10	BC_2F_3_ETSC_17008	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
11	BC_2F_3_ETSC_17009	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
12	BC_2F_3_ETSC_17010	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
13	BC_2F_3_ETSC_17011	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
14	BC_2F_3_ETSC_17012	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
15	BC_2F_3_ETSC_17013	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
16	BC_2F_3_ETSC_17014	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
17	BC_2F_3_ETSC_17015	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
18	BC_2F_3_ETSC_17016	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
19	BC_2F_3_ETSC_17017	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
20	BC_2F_3_ETSC_17018	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
21	BC_2F_3_ETSC_17019	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
22	BC_2F_3_ETSC_17020	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
23	BC_2F_3_ETSC_17021	Jamiyu/Birhan///Jamiyu	lgs_3
24	BC_2F_3_ETSC_17022	Jigurti/Birhan///Jigurti	lgs2 & lgs3
25	BC_2F_3_ETSC_17023	Jigurti/Birhan///Jigurti	lgs2 & lgs3
26	BC_2F_3_ETSC_17024	Jigurti/Birhan///Jigurti	lgs2 & lgs3
27	BC_2F_3_ETSC_17025	Jigurti/Birhan///Jigurti	lgs2 & lgs3
28	BC_2F_3_ETSC_17026	Jigurti/Birhan///Jigurti	lgs2 & lgs3
29	BC_2F_3_ETSC_17027	Jigurti/Birhan///Jigurti	lgs2 & lgs3

SN	Genotypes	Pedigree /Breeder's code	QTL
30	BC_2F_3_ETSC_17028	Jigurti/Birhan///Jigurti	lgs2 & lgs3
31	BC_2F_3_ETSC_17029	Teshale/Framida///Teshale	lgs2
32	BC_2F_3_ETSC_17031	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
33	BC_2F_3_ETSC_17032	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
34	BC_2F_3_ETSC_17033	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
35	BC_2F_3_ETSC_17034	Wetetbegunchie/Birhan///Wetetbegunchie	lgs3
36	BC_2F_3_ETSC_17035	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
37	BC_2F_3_ETSC_17036	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
38	BC_2F_3_ETSC_17037	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
39	BC_2F_3_ETSC_17038	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
40	BC_2F_3_ETSC_17039	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
41	BC_2F_3_ETSC_17040	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
42	BC_2F_3_ETSC_17041	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
43	BC_2F_3_ETSC_17042	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
44	BC_2F_3_ETSC_17043	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
45	BC_2F_3_ETSC_17044	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
46	BC_2F_3_ETSC_17045	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
47	BC_2F_3_ETSC_17046	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
48	BC_2F_3_ETSC_17047	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
49	BC_2F_3_ETSC_17048	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
50	BC_2F_3_ETSC_17049	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
51	BC_2F_3_ETSC_17050	Wetetbegunchie/Gobiye///Wetetbegunchie	lgs2 & lgs3
52	BC_2F_3_ETSC_17051	AbaAre-1/Gobiye///AbaAre-1	lgs3
53	BC_2F_3_ETSC_17052	AbaAre-1/Gobiye///AbaAre-1	lgs2 & lgs3
54	BC_2F_3_ETSC_17053	AbaAre-1/Gobiye///AbaAre-1	lgs3
55	BC_2F_3_ETSC_17054	AbaAre-1/Gobiye///AbaAre-1	lgs2 & lgs3
56	BC_2F_3_ETSC_17055	AbaAre-1/Gobiye///AbaAre-1	lgs2 & lgs3
57	BC_2F_3_ETSC_17056	America-1/Birhan///America-1	lgs2 & lgs3
58	BC_2F_3_ETSC_17057	America-1/Birhan///America-1	lgs2 & lgs3
59	BC_2F_3_ETSC_17058	America-1/Birhan///America-1	lgs2 & lgs3
60	BC_2F_3_ETSC_17059	America-1/Birhan///America-1	lgs2 & lgs3
61	BC_2F_3_ETSC_17060	America-1/Birhan///America-1	lgs2 & lgs3

SN	Genotypes	Pedigree /Breeder's code	QTL
62	BC_2F_3_ETSC_17061	America-1/Framida///America-1	lgs2 & lgs3
63	BC_2F_3_ETSC_17062	America-1/Framida///America-1	lgs2 & lgs3
64	BC_2F_3_ETSC_17063	America-1/Framida///America-1	lgs2 & lgs3
65	BC_2F_3_ETSC_17064	America-1/Framida///America-1	lgs2 & lgs3
66	BC_2F_3_ETSC_17065	America-1/Framida///America-1	lgs2 & lgs3
67	BC_2F_3_ETSC_17066	America-1/Framida///America-1	lgs2
68	BC_2F_3_ETSC_17067	America-1/Framida///America-1	lgs2 & lgs3
69	BC_2F_3_ETSC_17068	America-1/Framida///America-1	lgs2 & lgs3
70	BC_2F_3_ETSC_17069	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
71	BC_2F_3_ETSC_17070	Berjokecoll#1/Birhan///Berjokecoll#1	lgs2 & lgs3
72	BC_2F_3_ETSC_17071	Berjokecoll#1/Framida///Berjokecoll#1	lgs2 & lgs3
73	BC_2F_3_ETSC_17072	Debir/Birhan///Debir	lgs2 & lgs3
74	BC_2F_3_ETSC_17073	Debir/Birhan///Debir	lgs2 & lgs3
75	BC_2F_3_ETSC_17074	Debir/Birhan///Debir	lgs2
76	BC_2F_3_ETSC_17075	Debir/Birhan///Debir	lgs2 & lgs3
77	BC_2F_3_ETSC_17076	Debir/Birhan///Debir	lgs2 & lgs3
78	BC_2F_3_ETSC_17077	Debir/Gobiye///Debir	lgs3
79	BC_2F_3_ETSC_17078	Debir/Gobiye///Debir	lgs3
80	BC_2F_3_ETSC_17079	Debir/Gobiye///Debir	lgs3
81	BC_2F_3_ETSC_17080	Debir/Gobiye///Debir	lgs2 & lgs3
82	BC_2F_3_ETSC_17081	Debir/Gobiye///Debir	lgs2 & lgs3
83	BC_2F_3_ETSC_17082	Debir/Gobiye///Debir	lgs2 & lgs3
84	BC_2F_3_ETSC_17083	Debir/Gobiye///Debir	lgs2 & lgs3
85	BC_2F_3_ETSC_17084	Dekeba/Framida///Dekeba	lgs2
86	BC_2F_3_ETSC_17085	Gambella1107/Birhan///Gambella1107	lgs3
87	BC_2F_3_ETSC_17086	Gambella1107/Birhan///Gambella1107	lgs3
88	BC_2F_3_ETSC_17087	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
89	BC_2F_3_ETSC_17088	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
90	BC_2F_3_ETSC_17089	Jamiyu/Birhan///Jamiyu	lgs2 & lgs3
91	BC_2F_3_ETSC_17090	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
92	BC_2F_3_ETSC_17091	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
93	BC_2F_3_ETSC_17092	Jamiyu/Framida///Jamiyu	lgs2 & lgs3

SN	Genotypes	Pedigree /Breeder's code	QTL
94	BC_2F_3_ETSC_17093	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
95	BC_2F_3_ETSC_17094	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
96	BC_2F_3_ETSC_17095	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
97	BC_2F_3_ETSC_17096	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
98	BC_2F_3_ETSC_17097	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
99	BC_2F_3_ETSC_17098	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
100	BC_2F_3_ETSC_17099	Jamiyu/Framida///Jamiyu	lgs2 & lgs3
101	BC_2F_3_ETSC_17100	Jigurti/Birhan///Jigurti	lgs3
102	BC_2F_3_ETSC_17101	Jigurti/Birhan///Jigurti	lgs2 & lgs3
103	BC_2F_3_ETSC_17102	Jigurti/Birhan///Jigurti	lgs2 & lgs3
104	BC_2F_3_ETSC_17103	Jigurti/Birhan///Jigurti	lgs2 & lgs3
105	BC_2F_3_ETSC_17104	Jigurti/Birhan///Jigurti	lgs3
106	BC_2F_3_ETSC_17105	Jigurti/Gobiye///Jigurti	lgs2 & lgs3
107	BC_2F_3_ETSC_17106	Tseadachimure/Birhan///Tseadachimure	lgs2 & lgs3
108	BC_2F_3_ETSC_17107	Tseadachimure/Birhan///Tseadachimure	lgs2 & lgs3
109	BC_2F_3_ETSC_17108	Tseadachimure/Birhan///Tseadachimure	lgs2 & lgs3
110	BC_2F_3_ETSC_17109	Tseadachimure/Birhan///Tseadachimure	lgs2 & lgs3
111	BC_2F_3_ETSC_17111	Wediaker/Birhan///Wediaker	lgs2
112	BC_2F_3_ETSC_17112	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
113	BC_2F_3_ETSC_17113	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
114	BC_2F_3_ETSC_17114	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
115	BC_2F_3_ETSC_17115	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
116	BC_2F_3_ETSC_17116	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
117	BC_2F_3_ETSC_17117	Wetetbegunchie/Birhan///Wetetbegunchie	lgs2 & lgs3
118	BC_2F_3_ETSC_17119	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
119	BC_2F_3_ETSC_17120	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
120	BC_2F_3_ETSC_17121	Wetetbegunchie/Framida///Wetetbegunchie	lgs2 & lgs3
121	Berjokecoll#1	Local	Recurrent parent
122	Birhan	Key#8566	Donor parent
123	Debir	DEBIR	Recurrent parent
124	Dekeba	ICSR24004	Recurrent parent
125	Framida	87441	Donor parent

SN	Genotypes	Pedigree /Breeder's code	QTL
126	Gambella1107	GAMBELLA1107	Recurrent parent
127	Gobiye	P-9403	Donor parent
128	Jamiyu	Local	Recurrent parent
129	Jigurti	Local	Recurrent parent
130	SRN39	-	Resistant check
131	Teshalle	3443-2-OP	Recurrent parent
132	Tseadachimure	Local	Recurrent parent
133	Wediaker	Local	Recurrent parent
134	Wetetbegunche	Local	Recurrent parent

†lgs2 (lgs2_SBI-05_60404021) with allele AT, ‡lgs3: (lgs_3_60629027) with allele of CT

NB: The donor parents contain both QTLs

3.2.1. Surface sterilization of *Striga* seeds

Striga seeds collected by MARC from Humera areas in northern Ethiopia, Tigray Regional State, were kindly provided by the NABRC. The *Striga* seeds were surface sterilized following the procedure described by Amusan *et al.,* (2011) and Rich and Gobena, (2016) with minor modifications as necessary. On lab bench, an aliquot of cleaned S*triga* seeds was taken from bulk to a 50 ml flask. About six smidgen/scoops of *Striga* seeds were picked and put in 50 ml size of flask enough for 50 plates (with size of 100 mm). More than six scoops of *Striga* seeds were used to incorporate more plates at a time and the surface sterilization was performed in 125 ml by doubling the volume of the sterilants, washes, and conditioning solutions (Rich and Gobena, 2016). The flask with *Striga* seeds was transferred to laminar hood for surface sterilization processes. The surface sterilization of *Striga* seeds was accomplished by sonicating in 25 ml 75% (v/v) ethanol to the flask and agitated for 2 min by sucking the solution with a sterile glass pipette equipped with an amber bulb. The seeds were allowed to settle in the flask. The mixtures that floated (debris, immature seeds, grasses etc.) were removed by gently pouring over the waste flask filter funnel. The remaining liquid was sucked with pipette fitted with amber bulb by squeezing the bulb before putting into the seed slurry and pressing the tip against the inside bottom of the flask.

The *Striga* seed was again washed by adding 25 ml of activated MetriCide. The MetriCide (MERICIDE®-Glutaraldehyde 2.5%, a 28-day sterilizing and disinfecting solution, Metrex®Research, USA) was activated by adding the entire contents (35.8 g) of the Activator Plus activator into 946 ml of MetriCide followed by shaking for a minute. The activation date was labeled on the container and the solution was active only for 28 days (as indicated on the tag). The solution was agitated for 2 min by sucking seeds and sterilant in and out of the pipette under the surface of the liquid. The bubbles from the surface of the MetriCide solution was removed with the pipette before emptying the liquid to the waste flask in the same manner as the alcohol was removed, pouring off most, and then sucking the remainder with the pipette. In the same way, floating seeds and debris were removed. The *Striga* seeds were also washed twice through rinsing in sterile double distilled water (sddH2O) with each rinse approximately lasting 2 min. After sonication, the remaining sand/debris and water was removed by pipette.

3.2.2. Preconditioning of *Striga* seeds

First, a Benomyl 10 x stock solution was prepared by dissolving 0.15 g benomyl wettable powder [methyle-1-(butylcarbomyl) - 2- benzimidazolecarbamate] in 10 ml activated dimethyl sulfoxide (DMSO: C_2H_6OS, Fisher Chemical, China). Then the resultant solution was heated at 50-70 ^oC for 5 min to dissolve the fungicide in the solvent and stored at room temperature for subsequent uses but not for more than three months. Then after, a working solution was prepared by adding 0.5 ml of benomyl solution (from stock solution) in 49.5 ml of sddH2O only active for a week.

Surface sterilized *Striga* seeds were preconditioned by keeping them in 14.5 ml of sddH_2O and 1.5 ml of a 0.015% benomyl in 50 ml flask. Then flasks were enclosed with aluminum foil and placed in dark in an incubator with a temperature adjusted at 29°C for 5 days. During these days, the Benomyl solution was changed after one day and then at every two-three days until the seeds was embedded in agar under a laminar flow hood chamber. After the *Striga* seed was placed in liquid for five days (sddH_2O and Benomyl), agar (Bacto™ Agar) was prepared to embed *Striga* seeds. A Pyrex bottles (1 L), each containing 700 ml water plus 4.9 Bacto Agar (0.7% w/v) enough for about 20 plates was prepared and autoclaved for 20 min and allowed to cool in containment room water bath to 50 °C. After changing the Benomyl solution, as much seed into the pipette was sucked from the conditioning flask as possible with aid of an amber bulb and allowed to settle to the narrow tip. A drop of *Striga* seeds (about size of sorghum seed) was added from the pipette by touching it to the center of each of the opened plate bottom through barely squeezing the bulb. About 35 ml sterilized agar cooled to 50°C was poured over a drop of *Striga* seeds to evenly distribute the seeds in the agar to embed it and allow the conditioning to finish in the agar. The plates with poured *Striga* seeds were allowed to cool before covering and stacking in petri-dish bag. Then the seeds were conditioned in this agar in the dark at 29°C for an additional 5-7 days.

3.2.3. *Striga* seed germination test

Plates containing only *Striga* seeds (but not sorghum) were sprayed on the agar surface with a solution of 10^{-7} M of the synthetic strigolactone, GR24. The GR24 was prepared by adding 0.012 g of GR24 in 10 mm DMSO. From this solution, 250µ GR24 +100 ml ddH_2O was prepared (10^{-7}M) and sprayed for each *Striga* containing plates. Sprayed plates were incubated in the dark at 29°C for 72 hours and plates were observed for germination under binocular stereo microscope (10× magnification) fitted with a digital camera. The *Striga* seed was considered to have germinated if it showed a protruded radicle through the seed coat (Prandi *et al.*, 2011). The total number of seeds and germinated seeds were counted and germination percentage was determined from the ratio of the number of germinated to the total number of seeds and expressed in percentage. Mean germination percentage was obtained by calculating the average germination from 16 plates and was ranged from 45-70% indicating that *Striga* was responsive to the stimulant (GR24) so that procced to the actual bioassay.

3.2.4. Surface sterilization of sorghum seed and pre-germination test

One-hundred thirty-four sorghum seeds (118 BC_2F_3, 15 parental lines, and SRN39) were surface sterilized and pre-germinated according to the method described by Amusan *et al.*, (2011) with minor modification such as replacement of consumables. Twenty cleaned sorghum seeds were counted from each entry and placed in labeled individual glass vial.

Once all entries were placed in vials, seeds were soaked by adding 5 ml of freshly prepared 50% bleach / 0.2% Tween 20/ solution from a squirt bottle (for 500 ml, 250 ml household bleach [5% NaOCl] + 250 ml ddH_2O + 1 ml of Tween 20) for 30 min and shaken three times to break surface tension of sorghum seeds. After the 30 min soak, bleach solution was poured off gently (not to pour the seeds) into a waste container followed by rinsing in $sddH_2O$ for three times to completely washing of bleach.

Then after, seeds were soaked in a non-systemic fungicide, 5% (w/v) Travo (active ingredient: Azoxystrobin: methyl (E)-2-{2-[6-(2-cyanophenoxy) pyrimidin-4-yloxy]phenyl}-3- methoxyacrylate, 22.9%) and left overnight or at least for more than five hours. The 5% (w/v) Travo solution was prepared by adding 25 g Travo powder to 500 ml $sddH_2O$ and shaking to form slurry. Then, 5 ml of Travo solution was added to each vial and left overnight to imbibe. Next day, Travo solution was poured off after shaking the tube to suspend the Travo. About 5 ml of $sddH_2O$ was added to each vial.

Each entry was poured into labeled sterile petri plates containing double filter paper (Whatman #1 90 mm circles) at uniform distribution. The plates were covered by wetted paper towels to retain high humidity but also allow air flow. Sorghum containing plates were placed in warm (30 °C) dark incubator for 30 hours or until the seed had germinated and the radicles were averagely around 1 cm long (as germination varies among genotypes). After protrusion of both radicle and plumule, only healthy germinated seeds was selected and gently picked up with the forceps and planted on the preconditioned *Striga* seeds.

3.2.5. Agar gel assay (AGA)

The agar gel assay method developed by Hess *et al.*, (1992) was used to measure *Striga* germination stimulant activity and germination inhibition activity for screening resistant host genotypes. The experiment was conducted in a completely randomized design with four replications. One healthy germinated sorghum seedling (average 1.5 cm length) from each genotype was gently picked and inserted into the plates containing conditioned *Striga* seeds for 10 days. Seedlings were planted deeply such that the root reaches beneath the agar to where the *Striga* seeds were embedded and that it points toward the center of the plate. The plates were covered and placed into an incubator for incubation set at 29^0C in the dark for 3 days. During each cycle, the same batch(s) of *Striga* blank (no sorghum) and *Striga* batch sprayed with GR24 were included as control.

3.2.6. Data scoring

After three days of incubation, the plates were observed under a zoom stereomicroscope at about 10× magnification through the bottom of the plate to determine *Striga* germination stimulant activity. Before going to the sorghum planted plates, the germination rate was calculated from the GR24 treated plates to confirm the germination rate and *Striga* seed is responsive enough at least 30% (Rich and Gobena, 2016) to give a meaningful measure of germination stimulant activity of sorghum genotypes. In this regard, *Striga* germination rate was more than 45%. A standard area of 2 cm × 2.5 cm was selected along the main sorghum root beginning 2 cm away from the kernel and moving toward the root apex in which to make counts to determine near host root *Striga* germination rates. For all observed seedlings, comparisons of *Striga* germination stimulant activity as well as any possible germination inhibition was made. The maximum germination distance and germination rate was taken. And then each plates were treated with 10^{-7} M GR24 to remove any difference in host root for *Striga* germination stimulant activity and incubated for additional two days and observed under the microscope (10× magnification) for germination inhibition activity.

3.2.6.1. Maximum germination distance (MGD)

Three furthest germinated *Striga* seeds from sorghum root were measured at 3 days of incubation through transparent ruler. MGD is the average of these three measurements on each seedlings/plates. Seedlings with MGD $\geq$ 10 mm have high *Striga* germination stimulant activity, while those with MGD < 10 mm have low *Striga* germination stimulant activity (Hess *et al.*, 1992; Haussmann *et al.*, 2001a,b; Mohamed *et al.*, 2010).

3.2.6.2. Germination rate (GR)

The GR was obtained from the ratio of number of germinated *Striga* seeds in the image of selected area of microscopic field (2 cm x 2.5 cm) to the total number of seeds expressed as percentage at three days of incubation.

3.2.6.3. Germination index (GI)

Two images for each plate were taken after GR24 treatment (the day 5 images) was used to determine germination index for each plate. First, the same area used to count *Striga* seeds in determination of germination rate "near host root" and secondly a 2 cm × 2.5 cm area was selected "far from host". The germination rates were determined by dividing the number of germinated *Striga* seeds in the areas by the total number of *Striga* seeds there. The germination index was obtained from the ratio of germination rate calculated for the "near-host-root" area to germination rate of the "far-from-host" area. A germination index, that widely deviated from the one that could indicate some inhibition of the sorghum genotype on *Striga* germination. This is analogous to the exudate assay in those wells that are concurrently added GR24 and exudate (Rich and Gobena, 2016).

3.3. *In-vivo* Evaluation of Converted Lines and their Parents for *Striga* Resistance

3.3.1. Description of the study area

The developed BC_2F_3 lines and their parents were evaluated under *Striga* infested and non-infested locations of Ethiopia. The study locations were Kafta Humera, Tahitay Adiyabo, and Raya Azebo districts of Tigray regional state and Fedis district of Oromia regional state (Figure 5). The former two sites from Tigray were found to be naturally infested by *Striga hermonthica*. The remaining two-specific locations in the two regional states were, free of the parasitic weed during the season. The data obtained from the *Striga* free locations was used to determine the relative reduction of traits *per se*. The details of the district characteristics are given in Table 5.

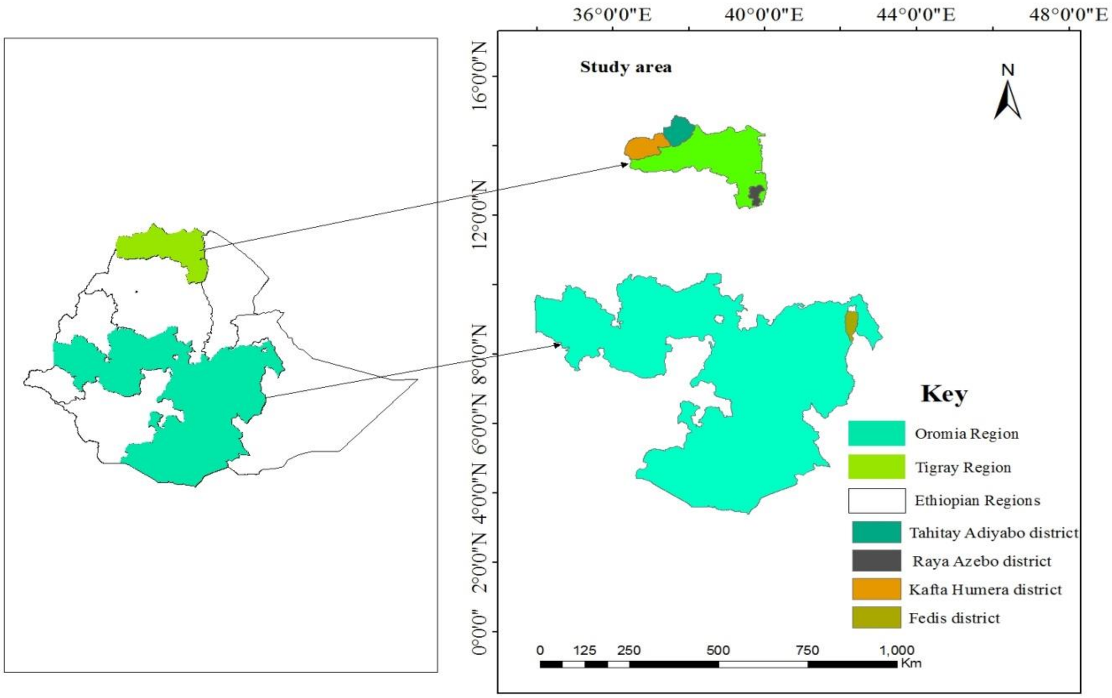


Figure 5. Map of study districts in Tigray and Oromia Regional States, Ethiopia

Table 5. Details of field experiments

Site characteristics	Tigray			Oromia
	Infested fields		Non-infested fields	
	Kafta Humera	Tahitay Adiyabo	Raya Azebo	Fedis
Altitude (m)	607	1018	1578	1400
Latitude (N)	14° 16'	14° 24'	12° 42’	8°22’
Longitude (E)	36° 38'	37° 46	39° 42’	42°02’
Dominant soil types	Chromic vertisols, Eutric regosols, Calcic xerosols, Eutric cambisols	Vertic, Eutric, Calcis cambisols and Orthic solonchaks	Chromic vertisols, Eutric cambisols, Haplic xerosols	Vertic, Calcic, Eutric cambisols,
Rainfall (mm)	400-650	400-500	250-539	400-804
Temp. Min (°C)	33	28	15	22
Temp. Max (°C)	41.7	40.5	33	32

3.3.2. Experimental design and treatments

A total of 135 sorghum genotypes, including; 118 BC_2F_3, three donor parents, 12 recurrent parents, one resistant check (Table 4) and one local cultivar were considered for the study. The experiments were executed at four locations in the main growing season of 2018/2019. The entries were arranged in α-lattice design with three replications. Each entry was planted on an area of two rows of 5 meters long, with a spacing of 75 cm between rows and 15 cm between plants. Fertilizer (NPS) was applied at a rate of 100 kg ha^{-1} at planting. Nitrogen fertilizer was applied at a rate of 50 kg ha^{-1} in two splits, half applied at planting and the other half four weeks after planting. All recommended agronomic practices were applied uniformly to ensure good crop stand. Weeds other than *Striga* were controlled by hand weeding.

The crop was protected from leaf feeding/sucking insect pests such as aphids, stem borers and fall armyworm using pesticides (Karate 5% EC, Darate 5%, and Bestfield 360 EC) following research recommendations.

3.3.3. Data collection

Both plant and *Striga* related data were collected based on random sample plants or whole plot basis depending on the characters under consideration.

3.3.3.1. Agronomic traits

The following crop agronomic characters were recorded:

(i) **Days to 50% flowering:** the number of days from emergence to 50% of the plants flowered in each plot.

(ii) **Days to 75% maturity**: the number of days from emergence to 75% of the plants in each plot reached physiological maturity i.e. number of days from emergence to form a black tip on seed at the junction between seed and plant at the base of the head.

(iii) **Plant height:** measured from the soil surface to the tip of the main head as an average of randomly chosen five plants at physiological maturity.

(iv) **Panicle length:** The main spikes from five sampled plants of each plot were measured in cm and averaged to represent the spike length in cm.

(v) **Biomass:** total above ground biomass weight of each plot, which was later converted to kg ha^{-1} for statistical analysis.

(vi) **Grain yield**: harvested from a plot, which was later converted to kg ha^{-1} for statistical analysis.

3.3.3.2. *Striga* related traits

With regard to *Striga,* the following traits were assessed:

(i) ***Striga* emergence:** number of *Striga* plants counted in two-week intervals during the course of the season beginning one week after *Striga* appearance.

(ii) ***Striga* vigor:** scored based on the scale of 0 to 9 as suggested by Haussmann *et al.*, (2000b). The value of 0 = no emerged *Striga* plants, 1 = average height of *Striga* plants 5 cm without branches, 2 = average height of *Striga* plants 6-20 cm without branches, 3 = average height of *Striga* plants 6-20 cm with branches, 4 = average height of *Striga* plants 21-30 cm with 5 branches, 5 = average height of *Striga* plants 21-30 cm with >5 branches, 6 = average height of *Striga* plants 31-40 cm with 10 branches, 7 = average height of *Striga* plants 31-40 cm with >10 branches, 8 = average height of *Striga* plants >40 cm without branches, and 9 = average height of *Striga* plants >40 cm with >10 branches) for four consecutive times at 14-day intervals during each counts.

(iii) ***Striga* severity:** determined from the index of multiplying the *Striga* count with the average *Striga* vigor of each plot as suggested by Haussmann *et al.*, (2000b).

(iv) **Field resistance:** scored according to Hausmann *et al.*, (2000b) scale (1-5: 1 = very resistant, 2 = fairly resistant, 3 = average, 4 = below average and 5 = very susceptible).

(v) **Area under the *Striga* number progress curve (AUSNPC):** calculated from four successive counts or numbers at 14-day intervals

(vi) **Area under the *Striga* severity progress curve (AUSSPC):** calculated from four consecutive severity records at 14-day intervals

AUSNPC and AUSSPC were computed using the formula for area under diseases progress curves (Shaner and Finney, 1977) as follows:

$$\text{AUSN/S/PC} = \sum_{i=o}^{n-1} [0.5(Y_{i+1} + Y_i)]\,[t_{i+1} - t_i]$$

Where, n = the number of *Striga* assessment dates, Yi = the *Striga* count at the i^{th} assessment date, t_i = the days after planting at the i^{th} assessment date, t_0= the days after planting to *Striga* emergence minus 1 and Y_0 = is 0. Similarly, AUSSPC was also calculated as AUSNPC instead '*S*' represents the *Striga* severity.

3.3.3.3. Estimation of relative yield loss

The relative yield loss was calculated from yield obtained under *Striga* infected and non-infected fields as follows:

$$RYL(\%) = \frac{Yc - Ys}{Yc} x100$$

Where, RYL = relative yield loss in percent, Yc = yield from *Striga* free fields and Ys = yield from *Striga* infested fields (Omanya *et al.*, 2004; Rodenburg *et al.*, 2005).

3.4. Introgression of Drought Tolerant Genes into Popular Ethiopian Sorghum Genotypes

3.4.1. Plant materials

The parental sorghum progeny used for this backcrossing program were one donor parent “B35” and eight recurrent parents which are released varieties and known farmers’ cultivars (Table 6). The donor parent is known for post-flowering drought tolerant and it has been used as a source of tolerant genes to drought by the national sorghum-breeding program. B35 is a 3-gene dwarf genotype, BC_1 derivative of IS12555 accession, a durra from Ethiopian and is known for its stay green behavior (Rosenow *et al.*, 1983), more specifically a type-A stay-green-delayed onset of leaf senescence (Thomas and Smart, 1993; Thomas and Howarth, 2000). As characterized by several research groups (Tuinstra *et al.*, 1997; Crasta *et al.*, 1999; Subudhi *et al.*, 2000; Xu *et al.*, 2000b; Sanchez *et al.*, 2002), it was identified as a source of a number of stay green QTLs involving B35. B35 is also known for a number of other characteristics including early maturing, long stature, short compact panicle with copious number of infertile branches; purple genotype with small seeds covered by glumes, dry leaf midrib and relatively low yield potential (Srinivas *et al.*, 2009; Kassahun *et al.*, 2010). The recurrent parents are generally high yielding under optimum moisture conditions (MoA, 2018) and popular amongst the farmers but susceptible to terminal drought.

Table 6. Sorghum genotypes used in marker-assisted backcrossing for drought tolerance

No	Variety	Breeders' code	Year of release	Center of release	Parental lines
1	Melkam	WSV-387	2009	Melkassa	RP
2	Teshale	3443-2-0P	2002	Srinka & Melkassa	RP
3	Gambella 1107	Gambella1107	1976	Melkassa	RP
4	Dekeba	ICSR 24004	2012	Melkassa	RP
5	Macia	Macia	2007	Melkassa	RP
6	Meko	M-36121	1997	Melkassa	RP
7	Tseadachimure	Local	-	-	RP
8	Wediaker	Local	-	-	RP
9	B35	IS12555	-	-	DP

RP = Recurrent parent, DP = Donor parent

3.4.2. Development of backcross progeny

The popular and farmers preferred Ethiopia sorghum pure lines (improved and/or local) were crossed with B35 (with stay green genes). The crossings were made using hand pollination method to generate 147 F1 progeny and subsequent generations at MARC, Ethiopia. Crossing is done by emasculation of selected plant panicles (recurrent parents) and dusting of pollen from identified plants (donor parent). After analysis for the presence of the desired donor parent alleles and recurrent parents' genome, selected heterozygous 147 F_1 plants were backcrossed with respective recurrent parents to generate 106 BC_1F_1 progeny. Then after the individuals selected based on desired marker(s) were backcrossed to generate 77 BC_2F_1. After each series of backcrossing marker-assisted foreground (donor allele) and background (recurrent parent's recovery potential) selections were made to fix through twice selfing and generated 61 BC_2F_3 (Figure 4). The generated 61 BC_2F_3 progeny and nine parental lines were evaluated for drought tolerance and other desirable agronomic characteristics.

3.4.3. DNA extraction, genotyping and KASP Assay

The parental lines (Table 6) and developed backcrossed lines (Table 7) were genotyped for polymorphic and confirmation of the targeted markers. The extraction of DNA and the KASP assay was outsourced (www.lgcgenomics.com). The detail of the molecular analysis is presented in section 3.1.3.

3.4.4. Description of the markers

Five stay green QTLs (*stg3A* and *stg3B* (SBI-02), *stg1* and *stg2* (SBI-03), and *stg4* (SBI-05) associated with the stay green character and located on three linkage groups were selected as the targets for marker-assisted backcrossing (MABC). The QTLs were previously identified from 354 recombinant inbred lines (F_7 RILs) developed from the cross of two inbred lines B35 (stay green) and Tx7000 (non-stay green) (Tuinstra *et al.*, 1997; Crasta *et al.*, 1999; Subudhi *et al.*, 2000; Tao *et al.*, 2000; Xu *et al.*, 2000; Haussmann *et al.*, 2002; Sanchez *et al.*, 2002; *Harris et al.*, 2007). The developed progeny were selected based on containing of at least three QTLs at a time in each progeny (Table 7).

3.5. Field Evaluation of Backcross Lines and Parents for Drought Tolerance

3.5.1. Description of the study area

Field experiments were conducted in Rama Kebele of Mereblekhe District in central zone of Tigray (Figure 6). The location was selected based on the potential of sorghum growing and availability of irrigation for imposing a managed level of stress. Rama kebele is situated at 14°23’39″ N latitude and 038°48’90″ E longitude. Rama is found at an altitude of 1389 meter above sea level, with average minimum and maximum temperatures ranging from 22 °C to 38 °C, respectively, during the study time (December 2018 to May 2019). The district is characterized by eutric cambisols, haplic xerosols, orthic solonchaks, calcic xerosols, chromic cambisols, eutric nitisols, and orthic luvisols soil types. The specific site was characterized by eutric cambisols soil type.

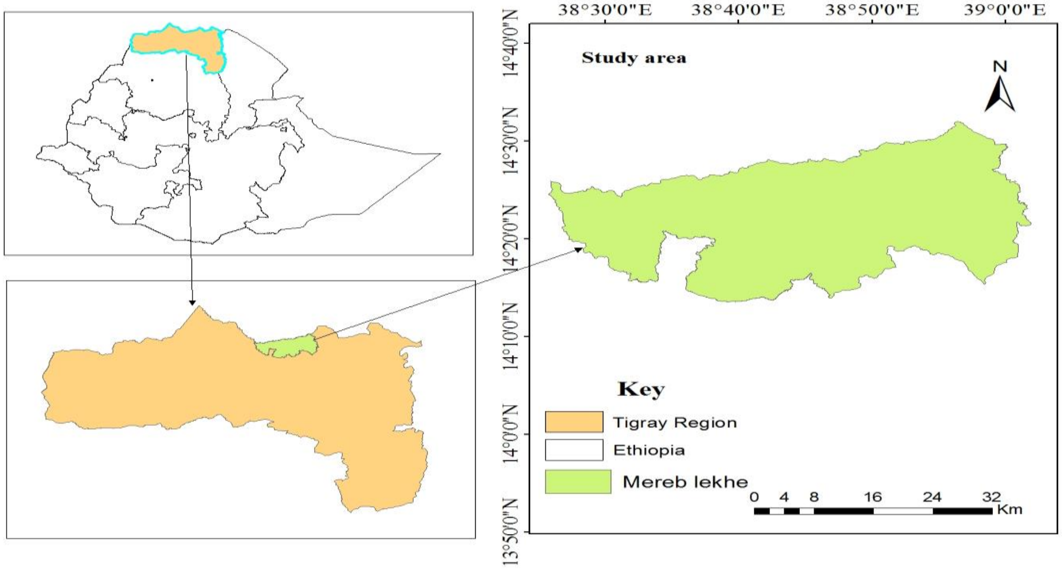


Figure 6. Map of Mereblekhe district in Tigray Regional State, Ethiopia

3.5.2. Experimental setup and treatment combinations

The field trials consisted of 61 BC_2F_3, one donor parent and eight recurrent parents (Table 7) which were evaluated under well-watered and water-limited conditions arranged in α-lattice design with three replications. The well-watered trial was irrigated throughout the season, so that, essentially, no moisture stress occurred at any stage of the crop development. Conversely, the limited irrigation (stress) trial was irrigated well during the early growth stages but irrigation was withheld after anthesis. The trials were planted on the same date and the same field in adjacent blocks. The experimental units were two-rows of 4 m long with 0.15 m plant to plant spacing and 0.75 m row to row spacing. Fertilizer (NPS) was applied at the rate of 100 kg ha^{-1} at planting and urea at rate of 50 kg ha^{-1} split two times, half at planting and the remaining half as knee height. All other agronomic management and protection practices were applied uniformly to all plots as recommended.

Table 7. Developed BC_2F_3 and parental lines evaluated under two-contrasting moisture regimes

SN	Genotype	Pedigree/breeder's code	QTL/Markers
1	BC_2F_3_ETSC_16139	Dekeba/B35///Dekeba	*stg1+stg2+stg3a+stg3b*
2	BC_2F_3_ETSC_16140	Dekeba/B35///Dekeba	*stg2+stg3a+stg3b*
3	BC_2F_3_ETSC_16141	Dekeba/B35///Dekeba	*stg2+stg3a+stg3b*
4	BC_2F_3_ETSC_16142	Gambella1107/B35///Gambella1107	*stg2+stg3a+stg3b+stg4*
5	BC_2F_3_ETSC_16143	Gambella1107/B35///Gambella1107	*stg2+stg3a+stg3b*
6	BC_2F_3_ETSC_16144	Gambella1107/B35///Gambella1107	*stg1+stg2+stg3a+stg3b*
7	BC_2F_3_ETSC_16145	Gambella1107/B35///Gambella1107	*stg1+stg2+stg4*
8	BC_2F_3_ETSC_16146	Gambella1107/B35///Gambella1107	*stg2+stg3a+stg3b+stg4*
9	BC_2F_3_ETSC_16147	Gambella1107/B35///Gambella1107	*stg1+stg2+stg3b+stg4*
10	BC_2F_3_ETSC_16148	Gambella1107/B35///Gambella1107	*stg1+stg2+stg3b+stg4*
11	BC_2F_3_ETSC_16149	Gambella1107/B35///Gambella1109	*stg2+stg3a+stg3b+stg4*
12	BC_2F_3_ETSC_16150	Gambella1107/B35///Gambella1113	*stg2+stg3a+stg3b+stg4*
13	BC_2F_3_ETSC_16210	Macia/B35///Macia	*stg1+stg3a+stg3b*
14	BC_2F_3_ETSC_16211	Macia/B35///Macia	*stg1+stg3a+stg3b*
15	BC_2F_3_ETSC_16212	Macia/B35///Macia	*stg2+stg3a+stg3b+stg4*
16	BC_2F_3_ETSC_16213	Meko/B35///Meko	*stg1+stg2+stg3a+stg4*
17	BC_2F_3_ETSC_16214	Meko/B35///Meko	*stg1+stg2+stg3a+stg3b+stg4*
18	BC_2F_3_ETSC_16215	Meko/B35///Meko	*stg1+stg2+stg3a*
19	BC_2F_3_ETSC_16216	Meko/B35///Meko	*stg1+stg2+stg4*
20	BC_2F_3_ETSC_16217	Meko/B35///Meko	*stg1+stg2+stg4*
21	BC_2F_3_ETSC_16218	Meko/B35///Meko	*stg1+stg2+stg4*
22	BC_2F_3_ETSC_16219	Meko/B35///Meko	*stg1+stg2+stg3a*
23	BC_2F_3_ETSC_16220	Melkam/B35///Melkam	*stg3a+stg3b+stg4*
24	BC_2F_3_ETSC_16221	Melkam/B35///Melkam	*stg2+stg3a+stg3b*
25	BC_2F_3_ETSC_16222	Melkam/B35///Melkam	*stg2+stg3a+stg3b+stg4*
26	BC_2F_3_ETSC_16223	Melkam/B35///Melkam	*stg2+stg3b+stg4*
27	BC_2F_3_ETSC_16224	Teshale/B35///Teshale	*stg3a+stg3b+stg4*
28	BC_2F_3_ETSC_16225	Teshale/B35///Teshale	*stg2+stg3a+stg3b*
29	BC_2F_3_ETSC_16226	Teshale/B35///Teshale	*stg2+stg3a+stg3b+stg4*
30	BC_2F_3_ETSC_16227	Teshale/B35///Teshale	*stg3a+stg3b+stg4*
31	BC_2F_3_ETSC_16228	Teshale/B35///Teshale	*stg2+stg3a+stg4*
32	BC_2F_3_ETSC_16229	Teshale/B35///Teshale	*stg2+stg3a+stg4*
33	BC_2F_3_ETSC_16230	Teshale/B35///Teshale	*stg2+stg3a+stg4*
34	BC_2F_3_ETSC_16231	Teshale/B35///Teshale	*stg1+stg2+stg3a+stg3b*

SN	Genotype	Pedigree/breeder's code	QTL/Markers
35	BC_2F_3_ETSC_16232	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3b+stg4*
36	BC_2F_3_ETSC_16233	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3b+stg4*
37	BC_2F_3_ETSC_16234	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3b+stg4*
38	BC_2F_3_ETSC_16235	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3a+stg3b+stg4*
39	BC_2F_3_ETSC_16236	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3b+stg4*
40	BC_2F_3_ETSC_16237	Tseadachimure/B35///Tseadachimure	*stg2+stg3b+stg4*
41	BC_2F_3_ETSC_16238	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3b+stg4*
42	BC_2F_3_ETSC_16239	Tseadachimure/B35///Tseadachimure	*stg2+stg3b+stg4*
43	BC_2F_3_ETSC_16240	Tseadachimure/B35///Tseadachimure	*stg2+stg3a+stg3b+stg4*
44	BC_2F_3_ETSC_16241	Tseadachimure/B35///Tseadachimure	*stg2+stg3a+stg3b+stg4*
45	BC_2F_3_ETSC_16242	Tseadachimure/B35///Tseadachimure	*stg2+stg3a+stg4*
46	BC_2F_3_ETSC_16243	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg4*
47	BC_2F_3_ETSC_16244	Tseadachimure/B35///Tseadachimure	*stg1+stg2+stg3a+stg3b+stg4*
48	BC_2F_3_ETSC_16245	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
49	BC_2F_3_ETSC_16246	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
50	BC_2F_3_ETSC_16247	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
51	BC_2F_3_ETSC_16248	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
52	BC_2F_3_ETSC_16249	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
53	BC_2F_3_ETSC_16250	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
54	BC_2F_3_ETSC_16251	Wediaker/B35///Wediaker	*stg3a+stg3b+stg4*
55	BC_2F_3_ETSC_16252	Wediaker/B35///Wediaker	*stg3a+stg3b+stg4*
56	BC_2F_3_ETSC_16253	Wediaker/B35///Wediaker	*stg1+stg3a+stg3b+stg4*
57	BC_2F_3_ETSC_16254	Wediaker/B35///Wediaker	*stg1+stg2+stg3a+stg3b+stg4*
58	BC_2F_3_ETSC_16255	Wediaker/B35///Wediaker	*stg1+stg2+stg3a+stg3b+stg4*
59	BC_2F_3_ETSC_16256	Wediaker/B35///Wediaker	*stg3a+stg3b+stg4*
60	BC_2F_3_ETSC_16257	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
61	BC_2F_3_ETSC_16258	Wediaker/B35///Wediaker	*stg2+stg3b+stg4*
62	Macia	Macia	Recurrent parent
63	Wediaker	Local	Recurrent parent
64	Dekeba	ICSR 24004	Recurrent parent
65	Gambella 1107	Gambella 1107	Recurrent parent
66	Meko	M-36121	Recurrent parent
67	Melkam	WSV-387	Recurrent parent
68	Tseadachimure	Local	Recurrent parent
69	Teshale	3443-2-0P	Recurrent parent
70	B35	IS12555	Donor parent (5 QTLs)

3.5.3. Data collection

Data were collected on important morpho-agronomic and morpho-physiological parameters on either pre-tagged random sample plants or whole plot basis depending on the trait under consideration.

3.5.3.1. Agronomic traits of sorghum

The important agronomic traits recorded in this study include:

(i) **Days to flowering (DTF):** number of days from emergence to 50% flowering of the plot plants.

(ii) **Days to maturity (DTM):** number of days from emergence to form a black tip on seed at the junction between seed and plant at the base of the head.

(iii) **Plant height (PLHT):** the height of the plant from the bottom to the tip of the panicle at maturity.

(iv) **Biomass yield (BM):** sun dried weight of all above ground part from a plot (g) and later converted to kg ha^{-1}.

(v) **Grain yield (YLD):** the grain yield (g) harvested from a plot and later converted to kg ha^{-1}.

(vi) **Panicle length (PL):** measured from the bottom to tip of the panicle.

(vii) **Panicle width (PW):** measured at the middle of panicle diameter.

(viii) **Panicle weight (PWt):** measured from five randomly selected heads.

(ix) **Thousand seed weight (TSW):** weight of 100 seeds in grams and later converted to thousand seed weight (g).

3.5.3.2. Physiological or stay green characters

The following physiological characters were collected:

(i) **Leaf senescence:** the leaf senescence expression of individual converted lines and their parental lines were estimated visually on a scale of 1 to 5 based on the degree of premature leaf and plant death at physiological maturity from five pre-tagged plants, i.e. 1 = very slight senescent, 2 = 25% leaves senescent, 3 = 50% leaves senescent, 4 = 75% leaves senescent, and 5 = 100% or complete senescent as suggested by Wanous *et al.*, (1991).

(ii) **Chlorophyll content:** the total were measured with a Minolta Chlorophyll Meter SPAD-502 (Konica-Minolta Camera Co., Ltd Tokyo, Japan) both at booting (SPADB) and physiological maturity (SPADM). The SPAD readings were taken from the middle of the leaf lamina of the second and fourth leaves from the top on five random pre-tagged sample plants at three places and averaged for analysis (Xu *et al.*, 2000b).

(iii) **Number green leaves:** the total number of green leaves at booting (NGLB) and maturity (NGLM) were counted and used to determine per cent of green leaves retained at maturity (PGLM), obtained as ratio between NGLM to NGLB expressed in percentage (Srinivas *et al.*, 2009).

(iv) **Green leaf area:** green leaf area at booting (GLAB in cm^2) and maturity (GLAM in cm^2) were measured from the length and the width of five green leaves from the top to bottom five pre-tagged plants and the area of each leaf was estimated using a correction factor of 0.70 (Mahalakshmi, 2002; Srinivas *et al.*, 2009) as: Leaf area = leaf length × leaf width × 0.70. The total green leaf area of each tagged plant was calculated as the sum of all the measured leaves from that particular plant. The upper six leaves were considered for measuring the green leaf area (Haussmann *et al.*, 2002), as the upper leaves are photosynthetically active at the stage of anthesis and direct assimilate mostly to the grain (Joshi *et al.*, 2003). The average percentage green leaf area preserved at maturity (PGLAM) from each plot was calculated by dividing the total green leaf area of each plot at maturity (GLAM) by the total green leaf area of that plot at anthesis (GLAB) (Srinivas *et al.*, 2009).

(v) **Rate of leaf senescence:** The rate of leaf senescence (RLS in cm^2 day^{-1}) was determined as: RLS = [GLAB - GLAM]/number of days taken from booting and maturity (Reddy *et al.*, 2014).

3.5.3.3. Determination of drought indices

Yield results obtained from both the stressed and non-stressed plots were used to calculate the following drought indices:

1. Stress susceptibility index (SSI) (Fischer and Maurer, 1978)

Stress susceptibility index (SSI) = $\frac{[1-\left(\frac{Ys}{Yp}\right)]}{1-SI}$;

$$SI=[1-\left(\frac{\bar{Y}s}{\bar{Y}p}\right)]$$

2. Mean relative performance (MRP) (Osmanzai, 1994)

$$MRP=\frac{Ys}{\overline{Ys}}+\frac{Yp}{\overline{YP}}$$

3. Tolerance index (TOL) (Hossain *et al.*, 1990)

Yp-Ys

4. Mean productivity (MP) (Rosielle and Hamblin, 1981)

$$\mathrm{MP} = \frac{\mathrm{Yp} + \mathrm{Ys}}{2}$$

5. Harmonic mean (HM) (Kristin *et al.*, 1997)

$$\mathrm{HM} = \frac{2(\mathrm{Yp} * \mathrm{Ys})}{\mathrm{Yp} + \mathrm{Ys}}$$

6. Geometric mean productivity (GMP) (Fernandez, 1992)

$$\mathrm{GMP} = \sqrt{(\mathrm{Yp})(\mathrm{Ys})}$$

7. Stress tolerance index (STI) (Fernandez, 1992)

$$STI = \frac{(Yp)(Ys)}{(\overline{Yp})^2}$$

8. Yield index (YI) (Gavuzzi *et al.*, 1997)

$$\mathrm{YI} = \frac{\mathrm{Ys}}{\overline{\overline{Ys}}}$$

9. Yield stability index (YSI) (Bouslama and Schapaugh, 1984)

$$\mathrm{YSI} = \frac{\mathrm{Ys}}{\mathrm{Yp}}$$

Where, Ys = yield in stress conditions, Yp = yield in irrigated conditions, $\bar{Y}$s= mean yield of all genotypes under stress conditions, $\bar{Y}$p = mean yield of all genotypes in irrigated conditions and SI = Stress intensity.

3.6. Data Analyses

3.6.1. Data preparation

The R software package (R Core Team, 2019) was used to test for presence of outliers and normality of residuals in all the cases. The variance of *Striga* related characters and rate of leaf senescence (stay green component) have been found to increase with the mean; therefore a log transformation [log (counts + 1)] was used to reduce the heterogeneity of variance. Before proceeding with the combined analysis of variance for each variable, tests were made for homogeneity of variances using the F_{max} test which is based on the ratio of the larger mean square of error (MSE) from the separate analysis of variance to the smaller mean square of error as given by the following formula:

$$F - ratio = \frac{larger\ MSE}{Smaller\ MSE}$$

If the larger error mean square is not three-fold larger than the smaller error mean square, the error variance was considered homogeneous (Gomez and Gomez, 1984) and thus it was appropriate to proceed with combined analysis of variance.

3.6.2. Analysis of variance

All the collected data were subjected to statistical analysis using R software version 3.6.1 (R Core Team, 2019). Genotype differences for low *Striga* germination stimulants, agronomic performance, *Striga* resistance or tolerance and stay green physiological characters were analyzed by residual maximum likelihood algorithm as suggested by Patterson and Thompson, (1971).

The total variability for each trait was quantified using analysis of variance according to the following models:

Bioassay: $Y_i = m + G_i + e_i$

For field experiment (single location): $Y_{ijk} = m + G_i + R_j + B_k (R_j) + e_{ijk}$

Where m = grand mean, Y_i denotes response for their capacity to produce *Striga* stimulants for the i^th^ genotype, Y_{ijk} denotes the value of the observed trait for i^{th} genotype in the k^{th} block within j^{th} replicate (superblock), G_i is the fixed effect of the i^{th} genotype ($i = 1,2,\ldots,g$); R_j is the effect of the j^{th} replicate (superblock) ($j = 1,2,\ldots,r$); B_{jk} is the effect of the k^{th} incomplete block within the j^{th} replicate ($k = 1,2,\ldots s$), is experimental error related to i^{th} genotype, e_i is the experimental error for the i^{th} genotype and e_{ijk} is an experimental error associated with the observation of the i^{th} treatment in the k^{th} incomplete block within the j^{th} complete replicate.

For combined over locations analysis, the following linear model was used:

$$Y_{ijkn} = m + G_i + R_j + B_k (R_j) + L_n + (G \times L)_{in} + e_{ijkn}$$

where Y_{ijkn} denotes the phenotypic observation of a trait for i^{th} genotype in the k^{th} block within j^{th} replicate (superblock) in n^{th} location; L_n is the effect of the n-th location (n=1,2,…,l); $(GxL)_{in,}$ is the interaction effect between genotype and location and e_{ijkn} is an experimental error associated with the observation of the i^{th} genotype in the k^{th} incomplete block within the j^{th} complete replicate in n^{th} location.

3.6.3. Interrelationships between characters

Correlation coefficients between characters were estimated based on the standard procedure as:

$$\mathrm{r} = \frac{Covxy}{\sqrt{\sigma \mathrm{x}^2 \; + \; \sigma \mathrm{y}^2}}$$

Where Cov(xy)= co-variance of traits x and y, σx^2= variance of x and σy^2 = variance of y. The level of significance of correlation coefficients was determined from the correlation Table at appropriate degrees of freedom and probability levels following Gomez and Gomez, (1984).

3.6.4. Estimation of heritability in broad sense

Broad sense heritability (H^2b) was estimated as described by Allard (1960) as follows:

$H^2b = \left(\frac{\sigma^2 g}{\sigma^2 p}\right)$, where $\sigma^2 p = \sigma^2 g + \frac{\sigma^2 e}{r} = H^2 b = \left(\frac{\sigma^2 g}{\sigma^2 g + (\frac{\sigma^2 e}{r})}\right) \times 100$, for single location;

$\sigma^2 p = \sigma^2 g + (\frac{\sigma^2 ge}{l} + \frac{\sigma^2 e}{lr}) = \; H^2 b = \left(\frac{\sigma^2 g}{\sigma^2 g + (\frac{\sigma^2 ge}{l}) + (\frac{\sigma^2 e}{lr})}\right) \times 100,$ for combined of the two locations. Where $\sigma^2{}_{\mathrm{g}}$ = genotypic variance, σ^2ge = genotype by environment variance, σ^2e = environmental variance, l = number of locations and r = number of replications.

3.6.5. Estimation of genetic advance

Genetic advance (GA) was calculated with the method suggested (Allard, 1960; Singh and Chaudhury, 1985; Falconer, 1989), assuming the selection intensity of 5%, as:

$$GA = K \times \sigma ph \times H^2_b$$

Where, GA= expected genetic advance from selection, K= the constant differential (K=2.063 at 5% selection intensity), σph = square root of phenotypic variance or its standard deviation and H^2b = broad-sense heritability.

The genetic advance as percentage of the mean (GA %) was calculated as described by Johnson et al., (1955) and Falconer, (1989) as follow:

$$GA(\%) = \frac{GA}{\bar{x}} \times 100$$

GA = genetic advance, and x = grand mean of a character.

3.6.6. Multivariate analysis

Before undertaking a series of multivariate analysis, data were standardized to a mean of zero and a variance of unity to avoid differences in scales used for recording data on different characters (Sneath and Sokal, 1973).

3.6.6.1. Principal component analysis

Principal component analysis (PCA) was performed using R software version 3.6.1 on the average values for each trait to identify the group of traits that accounted for most of the variance in the data.

3.6.6.2. Cluster analysis

The number of clusters in the data set was determined by an R package NbClust, available from the comprehensive R archive network (CRAN) at http://CRAN.R-project.org/package=NbClust (Charrad *et al.*, 2014).

4. RESULTS AND DISCUSSION

4.1. Introgression of *Striga* Resistant Genes into Popular Ethiopian Sorghum Genotypes

A total of 118 backcrossed progeny that containing one or two *lgs* gene(s) were developed through marker assisted backcrossing and subjected to evaluation in agar-gel assay for *Striga* pre-attachment resistance and field evaluation for agronomic performance and *Striga* resistance. The average crossing success of sorghum for *Striga* resistance in this study was 39.9%. The average of breeding success was determined from the ratio of generated progeny with target quantitative trait loci or marker to those all developed progeny.

4.2. *In-vitro* Performance of Backcross Lines and their Parents for *Striga* Germination Stimulant Activity

4.2.1. Analysis of variance

Analysis of variance (ANOVA) showed that the introgessed progeny and their parents significantly differed ($p<0.01$) for all the measured variables (Table 8). This unveils the existence of considerable variation in the pre-attachment of *Striga* resistance mechanisms among the developed and parental lines as discussed trait by trait below (Table 9). The variability for the pre-attachment *Striga* related traits were accounted by the variability in response of the test progeny/genotypes as indicated by high coefficient of determination (R^2) ranged from 78.4 to 85.9%.

Table 8. Analysis of variance for measured pre-attachment *Striga* traits

Source of variation	Degree of freedom	Mean square		
		Germination distance	Germination rate	Germination index
Genotypes	133	90.6**	852.7**	13.65**
Residual	402	20.9	190.3	2.25
R^2		85.9	78.4	82.6

4.2.2. Maximum germination distance (MGD)

The mean MGD of the converted lines and their parents ranged from the lowest of 0.0 mm to the highest of 29.45 mm in the agar-gel assay (Table 9). Out of the 134 genotypes screened for *Striga hermonthica* resistance, 32 showed low germination stimulant activity (MGD <10 mm), while the remaining 102 showed high germination stimulant activity (MGD $\geq$10 mm). Considering the introgressed 118 lines alone, 22.9% of them showed less than 10 mm of MGD values, while the remaining 77.1% showed MGD values of more than 10 mm. Interestingly, the lowest germination stimulant activity (0.0 mm) were recorded from the resistant check, SRN39, followed by the donor parents (Framida, Birhan and Gobiye) which showed MGD values of less than 5 mm. In agreement with this study, a number of previous studies also established the *Striga* germination stimulant activity to be low in Framida (Mohamed *et al.*, 2010; Mohemed *et al.*, 2018), Gobiye and Birhan (Ejeta *et al.*, 2007; Grenier *et al.*, 2007; Tesso *et al.*, 2007; Satish *et al.*, 2012), and, SRN39 (Mohamed *et al.*, 2010; Satish *et al.*, 2012; Gobena *et al.*, 2017; Mohemed *et al.*, 2018). It was re-confirmed in this study that the donor parents could further serve as potential sources of genes under the Ethiopian condition for incorporation of resistance genes into the popular sorghum varieties susceptible to *Striga*, but otherwise desirable for other attributes including grain yield and biomass. In fact, the two donor parents (Gobiye and Birhan), not only serve as parents but they have also been in the production system as released varieties in the country (Grenier *et al.*, 2007; Tesso *et al.*, 2007).

Based on the dividing line of germination stimulant activity of less than 10 mm of MGD, 28 backcrossed lines were found to be resistant to *Striga* (Table 9). The low germination distance of these introgressed progeny revealed their better resistance to the parasitic weed based on the low *Striga* germination stimulants activity. In addition to the low production stimulant activity of these converted progeny and their donor parents, the resistance may also be caused by the altered production of the strigolactone orobanchol over 5-deoxystrigol, a mutation on sulfotransferase gene (*lgs1*) which reduces the germination of *S. hermonthica* as reported by Yoneyama *et al., (*2010) and Gobena *et al.*, (2017). They confirmed that *lgs* sulfotransferase is absent in SRN39 and this is associated with loss of function which results in the production of high orobanchol but low 5-deoxystrigol profile, simulating less *Striga* seed germination. These observations suggest that *S. hermonthica* seeds may distinguish the different variants or composition of strigolactones.

Generally, the practicality of agar-gel assay and the use of MGD in *Striga* resistance breeding is well-established (Ejeta *et al.*, 1992; 2000a; Haussmann *et al.*, 2000a; Omanya *et al.*, 2004; Ejeta *et al.*, 2007; Yoder and choles, 2010). Thus, the low *Striga* germination stimulant activity has been an important resistance trait in sorghum improvement programs. To this effect, this useful *in-vitro* assay has resulted in the development and release of several *Striga*-resistant sorghum varieties with low germination stimulant activity (Ejeta, 2007b; Ali *et al.*, 2016). According to Ejeta (2007b), not all sorghum lines showing field resistance to *Striga* had low *Striga* germination stimulant activity due to other means of resistance mechanisms. However, based on previous research, all low-stimulant sorghums that were field-tested showed *Striga* resistance, indicating the positive correlations between the amount of germination stimulant produced and *Striga* infection levels in the field as reported by several authors (Ramaiah, 1987; Vasudeva Rao, 1987; Hess *et al.*, 1992; Haussmann *et al.*, 2004; Rich *et al.*, 2004; Mohemed *et al.*, 2016).

On the other hand, 77.1% of the developed progeny were predicted to have higher production of stimulant activity due to their genetic background and associated marker. It is also important to note that, the recurrent parents (83.3%) were found to be have high *Striga* germination stimulants activity that varied from 10.7 to 23.9 mm and this confirmed their susceptibility as anticipated. The high germination distance of those genotypes indicated that abundant production of germination stimulant activity stimulated the germination of seeds that were further away from the host root than did sorghum genotypes that caused only a few *Striga* seeds to germinate.

4.2.3. Germination rate (GR) of *Striga* near sorghum root

The GR of *Striga* seeds from the different batch or cycle of bioassay treated with GR24 (a synthetic analog of strigolactones) ranged from 45% to 70% the average being 60%, indicating the responsiveness of the seeds to the germination stimulant (GR24) in each batch of bio-assaying or screening.

The results from the screening of sorghum backcrossed lines along with their parents revealed that there were significant variation in *Striga* GR around the sorghum roots in the AGA. The result showed that none of the introgressed progeny were as *Striga* resistance or tolerance as the donor parents, which may be only a result of the transfer of selected low germination stimulant *(lgs)* QTL rather than the full complement of *lgs* QTL in the donor parents. The GR of *Striga* seed in response to the stimulant from the host plant ranged from 0.0% to 72.38%, indicating the clear difference in the production of germination stimulant activity among the backcrossed and parental lines. Of the total (118) converted lines, nearly 22.9% stimulated germination rate of less than 30% and germination distance of less than 10 mm (Table 9). Such low *Striga* germination percent may indicate a potential for resistance to *Striga*. The resistant check, SRN39 (0.0%), followed by the donor parent, Gobiye (1.76%) initiated the lowest germination stimulant activity. Even though these backcross lines did not show total immunity against *Striga* seed germination, as there is no reported complete resistance to *Striga* so far in sorghum (Ejeta, 2007a), the expression of low percentage level of stimulant production was an indication of their high level of resistance to the parasitic weed suggests to the low germination stimulant production. Consequently, the low level of germination stimulant produced by host plant may result in reduced number of germinated *Striga* seeds. This study is in agreement with previous reports, which recommended selection of sorghum variants with low production of strigolactones as the sound strategy in resistance breeding, based on the relation that sorghum genotypes with low stimulant production have also low germination-inducing activity in their root exudates (Haussmann *et al.*, 2001a, Omanya *et al.*, 2004; Ejeta, 2007a; 2007b; Rich and Ejeta, 2008; Satish *et al.*, 2012; Tokuma, 2016; Gobena *et al.*, 2017; Gwatidzo *et al.*, 2020).

On the other hand, 65% of the introgressed lines showed higher *Striga* GR that ranged from 20% to 72.4%, indicating that these backcrossed lines produce higher amount of germination stimulant activity depending on the genetic background (epistasis interaction) or additionally might be related to the incomplete conversion of the generated progeny (87.5%). The recurrent parents showed high GR ranged from 11% to 40% reflecting their high production of *Striga* germination stimulants. Earlier reports showed that not only the amount of exudates they produce but also the type of stimulant (strigolactones) might have resulted in the differences of *Striga* seed GR (Xie *et al.*, 2010; Yoneyama *et* *al*., 2015; Mohemed *et al*., 2016; Tsuchiya *et al*., 2018) among the sorghum genotypes. For instance, sorghum produces at least five different strigolactones, including 5-deoxystrigol, sorgolactone, strigol, strigyl acetate, and sorgomol, which varied in *Striga* germination initiation activity (Awad *et al*., 2006; Xie *et al*., 2008; Satish *et al*., 2012 Gwatidzo *et al*., 2020). Other studies, also reported that *Striga* GR might vary with the composition, quantity and nature of the signaling molecules (Yoneyama *et al*., 2010; 2015; Mohemed *et al*., 2018).

It is noteworthy that, genotypes classified as having low *Striga* germination stimulant activity based on the MGD values also showed low GR near their roots in the AGA and *vice-versa*. Previous reports declared that low germination stimulant (*lgs*) gene has been successfully introduced into high yielding and adapted sorghum varieties that have been deployed into several African countries (Ejeta *et al*., 1997; 2007; Grenier *et al*., 2007) including Ethiopia (Tesso *et al*., 2007). Although sorghum genotypes that produce little germination stimulants have been shown to be resistant to *Striga* in field tests (Haussmann *et al*., 2000a, 2001; Omanya *et al*., 2004; Rodenburg *et al*., 2006) it is, however, important to note that there exist other *Striga* resistant genotypes without low stimulant but yet resistant due to other resistant mechanisms (Ejeta *et al*., 2007; Mohamed *et al*., 2010). It was also observed that the germination of preconditioned *Striga* seeds might be influenced by the position, nature or architecture of the root of sorghum and distribution of *Striga* seeds in the agar (Figure 7).

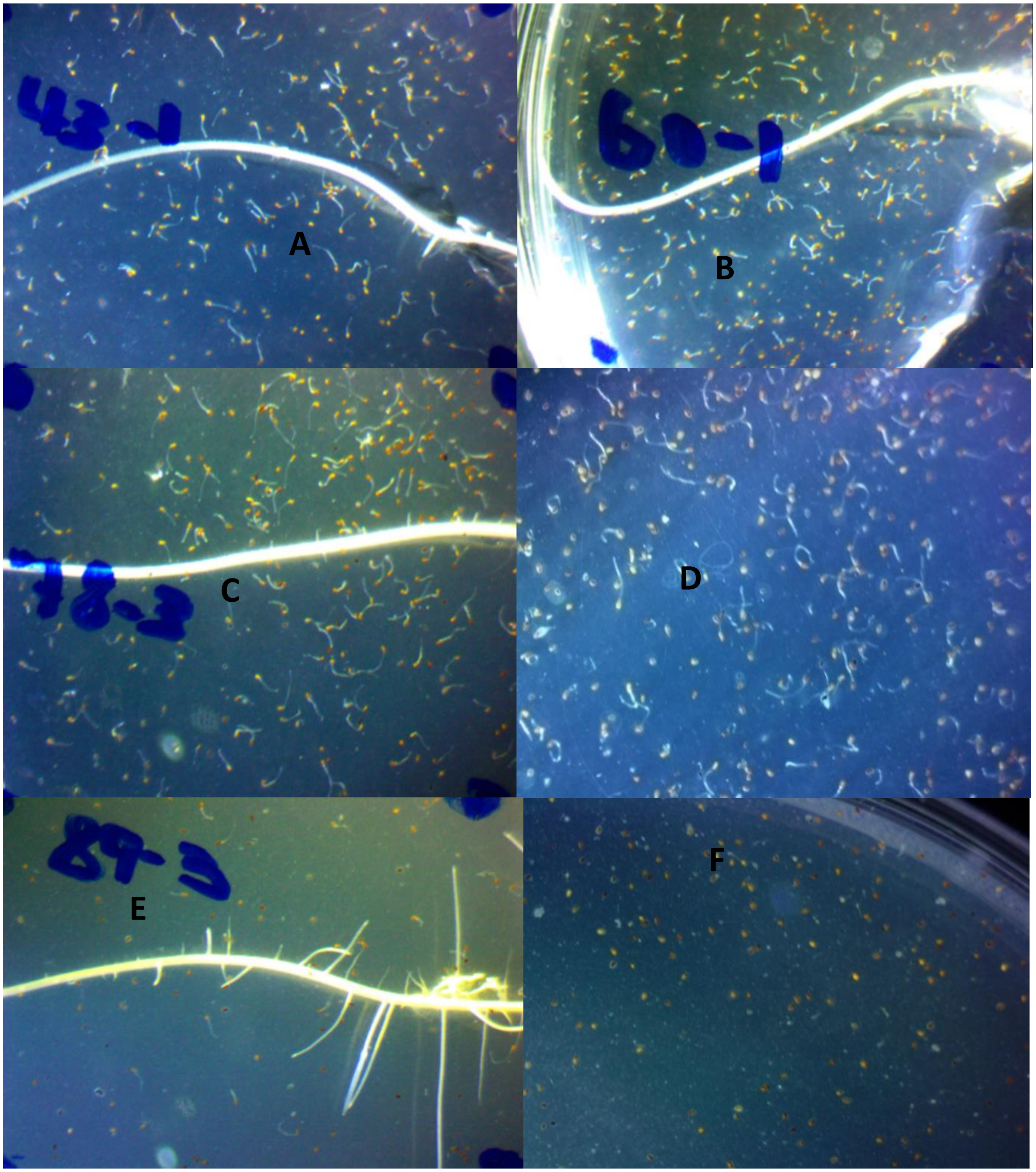


Figure 7. Germination of preconditioned *Striga* seeds embedded in agar surrounding the sorghum root after treatment with GR24. High *Striga* germination stimulant genotypes (A-C); treated with GR24 (D), low *Striga* germination stimulant genotype (E), and pre-conditioned *Striga* seeds with no treatments.

4.2.4. Germination index (GI)

The GI values were determined from the ratio of germination rate in the close (within one cm sorghum near root) to germination rate of the distance (2 cm away from any sorghum roots). The GI values of converted progeny included in this study varied from the lowest of 0.08 to the highest of 16.2. Of the 118 backcrossed lines, only nine (7.6%) of them shows GI values of less than unity (Table 9). In addition, two donor parents (Birhan and Gobiye) also showed GI values less than one. It is logical to assume that inhibitors being exuded from the host root might affect *Striga* seeds close to the host root more than those at a distance, thereby resulting in the germination indices of less than one. Therefore, the low germination events after GR24 spraying could be due to some germination-inhibitory compounds produced by the sorghum genotypes that may interfere with the germination response sequence of conditioned *Striga* seeds. GI values of one indicate that the GRs of the artificially stimulated *Striga seeds* in the proximal position equaled those at the distal positions. Conversely, 92.4% of the introgressed lines and recurrent parents shows germination indices of greater than one suggesting more germination events at the proximal than those at the distal positions and hence no-inhibitory induction activity form the host (Table 9).

Table 9. The response of converted lines and parents lines for their capacity of production *Striga* stimulants

Genotypes	Pedigree	QTL	MGD	GR	GI	Resistant level
AbaAre-1	AbaAre-1	Recurrent parent	$10.67^{\text{o-H}}$	$11.3^{\text{x-H}}$	$1.08^{\text{w-F\#}}$	S††
America-1	America-1	Recurrent parent	$8.33^{\text{v-I}}$	$19.64^{\text{l-H}}$	$1.17^{\text{v-F}}$	R‡‡
BC2F3_ETSC_17001	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2† & lgs3	$12.56^{\text{i-G}}$	$28.41^{\text{f-H}}$	$1.078^{\text{w-F}}$	S
BC2F3_ETSC_17002	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3‡	$13.94^{\text{g-E}}$	$33.68^{\text{d-D}}$	$2.3^{\text{j-F}}$	S
BC2F3_ETSC_17003	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	$13.78^{\text{g-E}}$	$28.1^{\text{f-H}}$	$1.78^{\text{p-F}}$	S
BC2F3_ETSC_17004	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	$10^{\text{r-H}}$	$20.76^{\text{j-H}}$	$0.88^{\text{x-F}}$	S
BC2F3_ETSC_17005	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	$8.67^{\text{u-I}}$	$14.31^{\text{u-H}}$	$1.41^{\text{t-F}}$	R
BC2F3_ETSC_17006	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	$14.33^{\text{f-E}}$	$38.61^{\text{c-y}}$	$3.42^{\text{f-D}}$	S
BC2F3_ETSC_17007	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	$11.22^{\text{n-G}}$	$9.47^{\text{z-H}}$	$0.72^{\text{z-F}}$	S
BC2F3_ETSC_17008	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$6.89^{\text{z-I}}$	$9.21^{\text{z-H}}$	$2.64^{\text{h-F}}$	R
BC2F3_ETSC_17009	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$6.05^{\text{D-I}}$	$6.72^{\text{B-H}}$	$0.35^{\text{C-F}}$	R
BC2F3_ETSC_17010	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$9.11^{\text{t-I}}$	$16.64^{\text{r-H}}$	$1.03^{\text{w-F}}$	R
BC2F3_ETSC_17011	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$14.39^{\text{e-E}}$	$19.17^{\text{m-H}}$	$1.57^{\text{s-F}}$	S
BC2F3_ETSC_17012	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$13.61^{\text{g-E}}$	$28.44^{\text{e-H}}$	$4.09^{\text{e-w}}$	S
BC2F3_ETSC_17013	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$12.5^{\text{i-G}}$	$9.87^{\text{y-H}}$	$1.04^{\text{w-F}}$	S
BC2F3_ETSC_17014	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$9.33^{\text{s-I}}$	$20.61^{\text{k-H}}$	$2.64^{\text{h-F}}$	R
BC2F3_ETSC_17015	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$20.44^{\text{a-n}}$	$10.35^{\text{y-H}}$	$3.4^{\text{g-D}}$	S
BC2F3_ETSC_17016	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$6.55^{\text{B-I}}$	$14.9^{\text{t-H}}$	$1.2^{\text{u-F}}$	R
BC2F3_ETSC_17017	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$13.33^{\text{h-F}}$	$26.22^{\text{h-H}}$	$4.88^{\text{e-p}}$	S
BC2F3_ETSC_17018	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$12.44^{\text{i-G}}$	$12.64^{\text{w-H}}$	$2.7^{\text{h-F}}$	S
BC2F3_ETSC_17019	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$12.5^{\text{i-G}}$	$34.29^{\text{d-C}}$	$2.74^{\text{g-F}}$	S
BC2F3_ETSC_17020	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$13.45^{\text{h-E}}$	45.03a-r	$1.9^{\text{n-F}}$	S
BC2F3_ETSC_17021	Jamiyu/Birhan///Jamiyu	lgs3	$11.72^{\text{k-G}}$	$33.94^{\text{d-C}}$	6.78^{cde}	S
BC2F3_ETSC_17022	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$12.78^{\text{i-G}}$	68.78^{ab}	$5.4^{\text{d-j}}$	S
BC2F3_ETSC_17023	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$16.44^{\text{b-A}}$	$29.51^{\text{e-H}}$	$2.05^{\text{m-F}}$	S
BC2F3_ETSC_17024	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$7.06^{\text{y-I}}$	$14.04^{\text{v-H}}$	$1.5^{\text{s-F}}$	R
BC2F3_ETSC_17025	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$21.22^{\text{a-l}}$	$30.85^{\text{e-G}}$	$4.64^{\text{e-s}}$	S
BC2F3_ETSC_17026	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$21.61^{a\text{-}j}$	$46.89^{a\text{-}o}$	$5.5^{\text{d-i}}$	S

Genotypes	Pedigree	QTL	MGD	GR	GI	Resistant level
BC2F3_ETSC_17027	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	14.3^{f-E}	8.98^{z-H}	1.64^{r-F}	S
BC2F3_ETSC_17028	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	8.3^{v-I}	9.55^{y-H}	1.98^{n-F}	R
BC2F3_ETSC_17029	Teshale/Framida///Teshale	lgs2	18^{b-v}	48.28^{a-l}	2.17^{l-F}	S
BC2F3_ETSC_17031	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	$15.2d^{-D}$	35.93^{d-A}	5.2^{d-l}	S
BC2F3_ETSC_17032	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	10.06^{r-H}	21.81^{j-H}	4.8^{e-q}	S
BC2F3_ETSC_17033	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	7.55^{w-I}	18.44^{o-H}	2.64^{h-F}	R
BC2F3_ETSC_17034	Wetetbegunchie/Birhan///Wetetbegunchie	lgs3	20^{b-q}	60.76^{a-d}	3.6^{f-B}	S
BC2F3_ETSC_17035	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	14.3^{f-E}	49.75^{a-j}	5.14^{d-m}	S
BC2F3_ETSC_17036	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	18.89^{b-s}	52.2^{a-i}	16.2^{a}	S
BC2F3_ETSC_17037	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	9.78^{r-I}	17.81^{p-H}	5.75^{d-h}	R
BC2F3_ETSC_17038	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	17.67^{b-v}	40.82^{b-w}	7.94^{cd}	S
BC2F3_ETSC_17039	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	8.44^{v-I}	3.64^{E-H}	1.78^{p-F}	R
BC2F3_ETSC_17040	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	15.67^{d-D}	6.58^{C-H}	2.58^{i-F}	S
BC2F3_ETSC_17041	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	17.44^{b-v}	34.15^{d-C}	6.44^{def}	S
BC2F3_ETSC_17042	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	11.3^{m-G}	34.88^{d-C}	9.27^{bc}	S
BC2F3_ETSC_17043	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	26^{ab}	53.18^{a-h}	4.79^{e-r}	S
BC2F3_ETSC_17044	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	15.78^{c-C}	34.13^{d-C}	3.44^{f-C}	S
BC2F3_ETSC_17045	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	24.22^{a-d}	64.65^{abc}	5.83^{defg}	S
BC2F3_ETSC_17046	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	17.56^{b-v}	37.77^{c-z}	3^{g-F}	S
BC2F3_ETSC_17047	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	14.22^{g-E}	51.98^{a-i}	2.73^{g-F}	S
BC2F3_ETSC_17048	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	10.56^{o-H}	23.28^{i-H}	2.2^{l-F}	S
BC2F3_ETSC_17049	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	15.55^{d-D}	44.41^{a-s}	3.84^{e-z}	S
BC2F3_ETSC_17050	Wetetbegunchie/Gobiye///Wetetbegunchie	Lgs2 & lgs3	17^{b-w}	39.49^{c-x}	3.94^{e-y}	S
BC2F3_ETSC_17051	AbaAre-1/Gobiye///AbaAre-1	lgs3	14^{g-E}	34.72^{d-C}	2.97^{g-F}	S
BC2F3_ETSC_17052	AbaAre-1/Gobiye///AbaAre-1	Lgs2 & lgs3	29.45^{a}	42.71^{b-v}	1.94^{n-F}	S
BC2F3_ETSC_17053	AbaAre-1/Gobiye///AbaAre-1	lgs3	19.89^{b-q}	43.33^{b-u}	3.15^{g-F}	S
BC2F3_ETSC_17054	AbaAre-1/Gobiye///AbaAre-1	Lgs2 & lgs3	17.5^{b-v}	35.74^{d-B}	4.3^{e-v}	S
BC2F3_ETSC_17055	AbaAre-1/Gobiye///AbaAre-1	Lgs2 & lgs3	10.72^{o-H}	18.54^{n-H}	1.08^{w-F}	S
BC2F3_ETSC_17056	America-1/Birhan///America-1	Lgs2 & lgs3	11.56^{l-G}	8.65^{z-H}	1.9^{n-F}	S

Genotypes	Pedigree	QTL	MGD	GR	GI	Resistant level
BC2F3_ETSC_17057	America-1/Birhan///America-1	Lgs2 & lgs3	11.44^{m-G}	18.85^{m-H}	5.44^{d-j}	S
BC2F3_ETSC_17058	America-1/Birhan///America-1	Lgs2 & lgs3	21.3^{a-k}	34.95^{d-C}	2.48^{i-F}	S
BC2F3_ETSC_17059	America-1/Birhan///America-1	Lgs2 & lgs3	9.67^{r-I}	15.44^{s-H}	1.7^{q-F}	R
BC2F3_ETSC_17060	America-1/Birhan///America-1	Lgs2 & lgs3	16.89^{b-x}	26.92^{g-H}	5^{e-o}	S
BC2F3_ETSC_17061	America-1/Framida///America-1	Lgs2 & lgs3	20.22^{b-o}	43.06^{b-v}	4.6^{e-t}	S
BC2F3_ETSC_17062	America-1/Framida///America-1	Lgs2 & lgs3	24^{a-e}	28.47^{e-H}	1.7^{p-F}	S
BC2F3_ETSC_17063	America-1/Framida///America-1	Lgs2 & lgs3	8.89^{t-I}	9.5^{z-H}	1.25^{u-F}	R
BC2F3_ETSC_17064	America-1/Framida///America-1	Lgs2 & lgs3	6.78^{A-I}	4.3^{E-H}	0.61^{A-F}	R
BC2F3_ETSC_17065	America-1/Framida///America-1	Lgs2 & lgs3	6.56^{B-I}	3.27^{FGH}	0.24^{DEF}	R
BC2F3_ETSC_17066	America-1/Framida///America-1	lgs2	18.89^{b-s}	22.07^{j-H}	0.89^{x-F}	S
BC2F3_ETSC_17067	America-1/Framida///America-1	Lgs2 & lgs3	11.44^{m-G}	19.75^{l-H}	2.1^{l-F}	S
BC2F3_ETSC_17068	America-1/Framida///America-1	Lgs2 & lgs3	23.22^{a-g}	59.96^{a-d}	1.98^{n-F}	S
BC2F3_ETSC_17069	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	19.39^{b-r}	43.72^{b-t}	1.62^{s-F}	S
BC2F3_ETSC_17070	Berjokecoll#1/Birhan///Berjokecoll#1	Lgs2 & lgs3	16.16^{c-B}	48.87^{a-k}	2.1^{m-F}	S
BC2F3_ETSC_17071	Berjokecoll#1/Framida///Berjokecoll#1	Lgs2 & lgs3	9.94^{r-H}	16.47^{r-H}	1.29^{u-F}	R
BC2F3_ETSC_17072	Debir/Birhan///Debir	Lgs2 & lgs3	7.22^{x-I}	6.8^{A-H}	1.63^{r-F}	R
BC2F3_ETSC_17073	Debir/Birhan///Debir	Lgs2 & lgs3	20.94^{a-m}	32.25^{d-F}	1.3^{u-F}	S
BC2F3_ETSC_17074	Debir/Birhan///Debir	lgs2	15.45^{d-D}	25.43^{h-H}	1.36^{u-F}	S
BC2F3_ETSC_17075	Debir/Birhan///Debir	Lgs2 & lgs3	21.89^{a-i}	42.56^{b-v}	2.2^{l-F}	S
BC2F3_ETSC_17076	Debir/Birhan///Debir	Lgs2 & lgs3	15.44^{d-D}	30.93^{e-G}	5.03^{e-n}	S
BC2F3_ETSC_17077	Debir/Gobiye///Debir	lgs3	17.2^{b-w}	40.91^{b-w}	2.93^{g-F}	S
BC2F3_ETSC_17078	Debir/Gobiye///Debir	lgs3	18.94^{b-s}	46.11^{a-q}	2.1^{l-F}	S
BC2F3_ETSC_17079	Debir/Gobiye///Debir	lgs3	24.1^{a-d}	72.38^{a}	2.6^{i-F}	S
BC2F3_ETSC_17080	Debir/Gobiye///Debir	Lgs2 & lgs3	18.61^{b-t}	57.34^{a-e}	2.8^{g-F}	S
BC2F3_ETSC_17081	Debir/Gobiye///Debir	Lgs2 & lgs3	21.55^{a-j}	56.53^{a-f}	1.9^{n-F}	S
BC2F3_ETSC_17082	Debir/Gobiye///Debir	Lgs2 & lgs3	15.67^{d-D}	25.78^{h-H}	3.76^{e-A}	S
BC2F3_ETSC_17083	Debir/Gobiye///Debir	Lgs2 & lgs3	22.56^{a-h}	53.39^{a-h}	1.6^{s-F}	S
BC2F3_ETSC_17084	Dekeba/Framida///Dekeba	lgs2	26^{ab}	64.93^{abc}	1.8^{p-F}	S
BC2F3_ETSC_17085	Gambella1107/Birhan///Gambella1107	lgs3	17.1^{b-w}	47.6^{a-m}	3.1^{g-F}	S

Genotypes	Pedigree	QTL	MGD	GR	GI	Resistant level
BC2F3_ETSC_17086	Gambella1107/Birhan///Gambella1107	lgs3	25.3^{abc}	$55.75^{a\text{-}g}$	$1.79^{p\text{-}F}$	S
BC2F3_ETSC_17087	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$15^{d\text{-}D}$	$24.38^{h\text{-}H}$	$1.82^{p\text{-}F}$	S
BC2F3_ETSC_17088	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$9.78^{r\text{-}I}$	$26.1^{h\text{-}H}$	$2.35^{i\text{-}F}$	R
BC2F3_ETSC_17089	Jamiyu/Birhan///Jamiyu	Lgs2 & lgs3	$15.2^{d\text{-}D}$	$42.7^{b\text{-}v}$	$1.6^{r\text{-}F}$	S
BC2F3_ETSC_17090	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$15.4^{d\text{-}D}$	$29.03^{e\text{-}H}$	$2.4^{i\text{-}F}$	S
BC2F3_ETSC_17091	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$21^{a\text{-}m}$	$47.88^{a\text{-}m}$	$1.48^{s\text{-}F}$	S
BC2F3_ETSC_17092	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$14.06^{g\text{-}E}$	$12.48^{w\text{-}H}$	$3.2^{g\text{-}F}$	S
BC2F3_ETSC_17093	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$5.17^{E\text{-}I}$	$4.66^{D\text{-}H}$	$2.5^{i\text{-}F}$	R
BC2F3_ETSC_17094	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$5^{E\text{-}I}$	$8.16^{A\text{-}H}$	$1.8^{p\text{-}F}$	R
BC2F3_ETSC_17095	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$16.55^{b\text{-}z}$	$13.26^{w\text{-}H}$	$1.5^{t\text{-}F}$	S
BC2F3_ETSC_17096	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$14.17^{g\text{-}E}$	$40.49^{b\text{-}w}$	$2.05^{m\text{-}F}$	S
BC2F3_ETSC_17097	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$17.56^{b\text{-}v}$	$47.47^{a\text{-}o}$	$3.1^{g\text{-}F}$	S
BC2F3_ETSC_17098	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$10^{r\text{-}H}$	$14.52^{u\text{-}H}$	$3.15^{g\text{-}F}$	S
BC2F3_ETSC_17099	Jamiyu/Framida///Jamiyu	Lgs2 & lgs3	$10.45^{p\text{-}H}$	$8.23^{A\text{-}H}$	$0.5^{B\text{-}F}$	S
BC2F3_ETSC_17100	Jigurti/Birhan///Jigurti	lgs3	$14.3^{f\text{-}E}$	$29.61^{e\text{-}H}$	$1.4^{t\text{-}F}$	S
BC2F3_ETSC_17101	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$20.1^{b\text{-}p}$	$55.22^{a\text{-}g}$	$1.99^{m\text{-}F}$	S
BC2F3_ETSC_17102	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$14.2^{g\text{-}E}$	$28.54^{e\text{-}H}$	11.5^{b}	S
BC2F3_ETSC_17103	Jigurti/Birhan///Jigurti	Lgs2 & lgs3	$12^{j\text{-}G}$	$13.28^{w\text{-}H}$	$1.84^{p\text{-}F}$	S
BC2F3_ETSC_17104	Jigurti/Birhan///Jigurti	lgs3	$13.3^{h\text{-}F}$	$32.73^{d\text{-}E}$	$3.28^{g\text{-}E}$	S
BC2F3_ETSC_17105	Jigurti/Gobiye///Jigurti	Lgs2 & lgs3	$8.55^{v\text{-}I}$	$9.76^{y\text{-}H}$	$1.36^{u\text{-}F}$	R
BC2F3_ETSC_17106	Tseadachimure/Birhan///Tseadachimure	Lgs2 & lgs3	$8.78^{u\text{-}I}$	$20.59^{k\text{-}H}$	$1.2^{u\text{-}F}$	R
BC2F3_ETSC_17107	Tseadachimure/Birhan///Tseadachimure	Lgs2 & lgs3	$6.89^{z\text{-}I}$	$12.53^{w\text{-}H}$	$0.77^{y\text{-}F}$	R
BC2F3_ETSC_17108	Tseadachimure/Birhan///Tseadachimure	Lgs2 & lgs3	$7.56^{w\text{-}I}$	$8.58^{A\text{-}H}$	$1.1^{w\text{-}F}$	R
BC2F3_ETSC_17109	Tseadachimure/Birhan///Tseadachimure	Lgs2 & lgs3	$12.4^{i\text{-}G}$	$28.73^{e\text{-}H}$	$2.7^{h\text{-}F}$	S
BC2F3_ETSC_17111	Wediaker/Birhan///Wediaker	lgs2	$10.3^{q\text{-}H}$	$28.21^{f\text{-}H}$	$1.47^{s\text{-}F}$	S
BC2F3_ETSC_17112	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	$9.78^{r\text{-}I}$	$16.78^{r\text{-}H}$	$1.5^{s\text{-}F}$	R
BC2F3_ETSC_17113	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	$17.2^{b\text{-}w}$	$25.57^{h\text{-}H}$	$1.8^{p\text{-}F}$	S
BC2F3_ETSC_17114	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	$18.3^{b\text{-}u}$	$32.5^{d\text{-}E}$	$4.35^{e\text{-}u}$	S
BC2F3_ETSC_17115	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	$15.78^{c\text{-}C}$	$30.31^{e\text{-}H}$	$4.4^{e\text{-}u}$	S

Genotypes	Pedigree	QTL	MGD	GR	GI	Resistant level
BC2F3_ETSC_17116	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	9.1^{t-I}	10.15^{y-H}	0.98^{w-F}	R
BC2F3_ETSC_17117	Wetetbegunchie/Birhan///Wetetbegunchie	Lgs2 & lgs3	6.2^{C-I}	17.69^{q-H}	2.51^{i-F}	R
BC2F3_ETSC_17119	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	11.78^{k-G}	27.08^{g-H}	3.98^{e-x}	S
BC2F3_ETSC_17120	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	16.67^{b-y}	46.76^{a-p}	2.27^{k-F}	S
BC2F3_ETSC_17121	Wetetbegunchie/Framida///Wetetbegunchie	Lgs2 & lgs3	17.67^{b-v}	40.93^{b-w}	4.35^{e-u}	S
BERJOKECOLL#1	Local	Recurrent parent	11.67^{k-G}	27.24^{g-H}	1.85^{o-F}	S
Birhan	Key#8566	Donor parent	3.2^{GHI}	9.13^{z-H}	0.15^{EF}	R
Debir	DEBIR	Recurrent parent	15.4^{d-D}	27.81^{f-H}	1.83^{p-F}	S
Dekeba	ICSR24004	Recurrent parent	21^{a-m}	60.35^{a-d}	2.2^{l-F}	S
Framida	87441	Donor parent	3.72^{F-I}	12.68^{w-H}	1.16^{v-F}	R
Gambella1107	GAMBELLA1107	Recurrent parent	23.89^{a-f}	65.6^{abc}	2.01^{m-F}	S
Gobiye	P-9403	Donor parent	1.3^{HI}	2.76^{GH}	0.09^{F}	R
Jamiyu	Local	Recurrent parent	10.1^{r-H}	17.75^{p-H}	5.38^{d-k}	S
Jigurti	Local	Recurrent parent	19.2^{b-r}	43.27^{b-u}	2.5^{i-F}	S
SRN39	-	Recurrent parent	0.0^{I}	0.0^{H}	1.54^{s-F}	R
Teshalle	3443-2-OP	Recurrent parent	16.1^{c-B}	29.24^{e-H}	1.12^{u-F}	S
Tseadachimure	Local	Recurrent parent	17.89^{b-v}	47.58^{a-n}	2.06^{m-F}	S
Wediaker	Local	Recurrent parent	15^{d-D}	25.91^{h-H}	1.19^{u-F}	S
Wetetbegunche	Local	Recurrent parent	13.67^{g-E}	28.65^{e-H}	2.29^{k-F}	S
Mean			14.18	29.46	2.68	
LSD(0.05)§			4.5	13.5	4.45	
CV (%) ¶			14.5	19.3	25.2	

†lgs2_SBI-05 (lgs2_SBI-05_60404021) with allele AT, ‡lgs_3: (lgs_3_60629027) with allele CT, § least significant difference, ¶ coefficient of variation, #treatments with the same letter are not significantly different, ††Susceptible lines, ‡‡ Resistant line, LSD = Least significant difference, CV = Coefficient of variation

NB: The donor parents contain both QTLs

4.2.5. Comparison of introgressed progeny with QTLs and their parents for *Striga* stimulant activity

The donor parents consistently showed lowest *Striga* germination stimulant activity followed by 32.4% of backcrossed progeny with double QTLs. Of the 118 developed lines, 86.44%, 9.32%, and 4.24%, were comprised of QTLs (*lgs2_SBI-05_60404021 + lgs_3_60629027), lgs_3_60629027,* and *lgs2_SBI-05_60404021*, respectively (Table 9). About 32.4% of the converted progeny consisted of both markers at a time showed low *Striga* germination stimulants as explained by less than 10 mm MGD and low germination rate indicating the cumulative effects of the two QTLs in reducing the stimulation of *Striga* seeds germination. This clearly showed that these progeny had *lgs* resistance genes from the donor parents. Earlier reports also showed that the identification of different genes controlling low stimulation of *Striga* seed germination and their introgression into a single genotype enhanced not only the degree but also the durability of resistance to *Striga* (Ramaiah *et al.*, 1990; Yohannes *et al.*, 2015). Conversely, none of the backcrossed progeny with individual QTL showed resistance to the parasitic weed as revealed by the high production of *Striga* germination stimulants, perhaps due to the genetic background (epistasis interaction). Likewise, the seed parents were dominantly high producers of *Striga* stimulant activity.

4.2.6. Interrelationships among *Striga* pre-attachment traits

Correlation coefficients (r) showed positively significant association among the three traits studied. MGD maintained significantly strong positive correlations ($p<0.01$) with GR ($r = 0.81$) and GI ($r = 0.4$). This indicated that the use of low levels of MGD and/or GR values could be considered as the best selection criteria for improving *Striga* resistance in sorghum. It is also interesting to note that the phenotype could reflect the genotype for these traits. GR also showed significant and positive ($r = 0.48$) correlation with GI. This might indicate that low germination rate could be associated with the induction of inhibitory compounds from the host roots. Previous reports also revealed existence of high positive correlation ($r = 0.93$) between percent of germinated *Striga* and the distance from the host root to the furthermost germinated *Striga* seeds (Hess *et al.*, 1992).

4.2.7. Heritability and expected genetic advance from selection

The results clearly revealed the presence of genetic variation among the sorghum genotypes for stimulation of *S. hermonthica* seeds germination activity in the agar-gel assay. Broad-sense heritability (H^2b) for the traits; MGD, GR, and GI were 77%, 79%, and 83% in that order. The magnitude of broad sense heritability was generally high for the characters studied. According to Singh, (2002), heritability values greater than 80% were considered as very high, values from 60-79% were moderately high, values from 40-59% were medium and values less than 40% were low. Accordingly, the estimate of H^2b for GI was very high and values for MGD and GR were moderately high. This indicated that germination distance, germination rate and germination index in the agar gel assay had high heritability values as reported by others (Haussmann *et al.*, 2001a, b) and, hence, progress from selection based on these traits can be attained for the development of *Striga* resistance.

It is normally concluded that heritability coupled with genetic advance is more useful and effective for selection of superior individuals than either of them alone (Johnson *et al.*, 1955). In this study, the genetic advance for the characters MGD, GR, and GI were 62%, 93.2% and 71.3% in that order. According to Johnson *et al.*, (1955) characters with > 20% indicates high GA and this could be imply selection based on the pre-attachment *Striga* traits is fairly encouraging.

4.2.8. Principal component analysis

Principal component (PC) analysis showed that the first two PCs accounted for 92.89% of the total variation with PC_1, and PC_2 contributing 65.85 and 27.04% of the total variation, respectively (Table 10). The first PC that accounted for the highest total variation had high and positive load values for GR (0.921) and MGD (0.894). The second PC shows high and positive weight score for GI (0.819). The variables with eigenvector of large absolute magnitude (close to unity) more dictated the magnitude and pattern of the variation than those with small magnitude (near zero) and lower influence (Chahal and Gosal, 2002).

Table 10. Principal component analysis for three traits of 134 genotypes tested in agar gel bioassay

PC	1	2
Eigen value	1.976	0.811
Proportion	65.85	27.04
Cumulative	65.85	92.89
Eigen vectors		
MGD	0.894	-0.316
GR	0.921	-0.202
GI	0.573	0.819

MGD = Maximum germination distance, GR = germination rate and germination index

4.2.9. Cluster analyses

Cluster analysis grouped the 134 sorghum genotypes into three distinct clusters (Figure 8). It is generally assumed that members within a cluster are more closely related to the traits studied than genotypes in different clusters. The first cluster (C_1) was characterized by low MGD, GR and GI values. This cluster consisted of resistance backcrossed lines and donor parents with low *Striga* germination stimulant activity as a means of resistance mechanism. The second cluster (C_2) consisted of genotypes with intermediate mean values of MGD, GR, and GI. The final cluster (C_3) was characterized by high MGD, GR, and GI values showing high *Striga* production stimulant activity and hence reflecting their susceptibility.

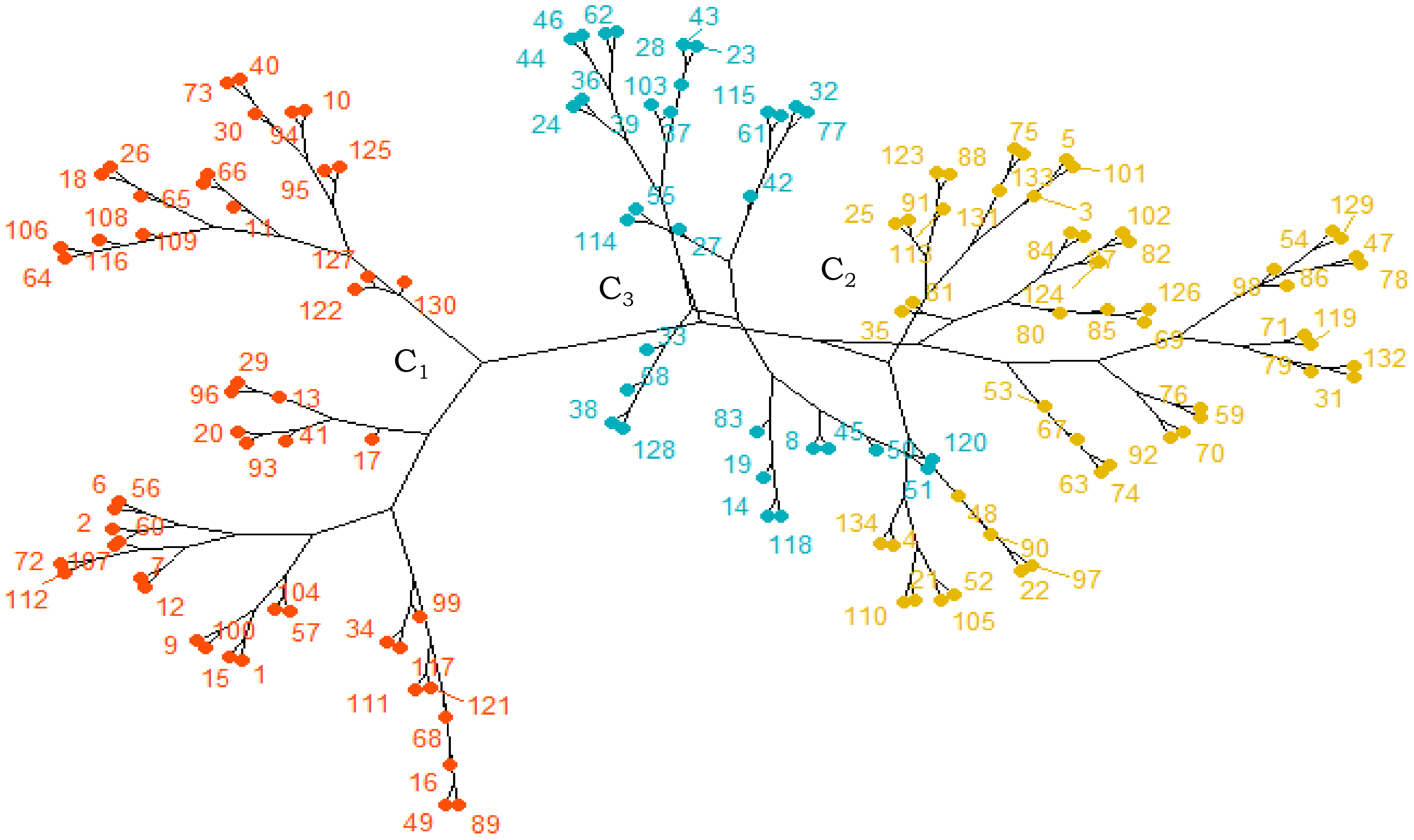


Figure 8. The cluster of sorghum converted and parental lines based on *Striga* germination stimulant production (refer to Table 9 for the names of genotypes corresponding to the serial numbers).

4.3. *In-vivo* Performances of Converted Lines and their Parents under Natural *Striga* Infestation

4.3.1. Analysis of variance

The independent ANOVA for the two locations indicate that there was a significant difference (P<0.01) among genotypes for all traits (Table 11, Appendix 1 & 2). The effect of genotypes on the response variables were relatively large as explained by the coefficient of determination (R^2) ranging from 62.4 to 84.8% & 60.9 to 90.1% in Kafta Humera and Tahitay Adiyabo, respectively.

Table 11. The specific location ANOVA of agronomic and *Striga* related traits

Traits	Kafta Humera			Tahitay Adiyabo		
	Mean square		R^2	Mean square		R^2
	Genotype	Residual		Genotype	Residual	
Degree of freedom	134	277		134	277	
Days to flowering	58.3**	32.66	65.5	110.7**	12.7	81.6
Plant height	2364.3**	353.9	84.8	4321.4**	683.2	74.5
Panicle length	37.6**	7.5	77.4	69.6**	20.9	63.4
Days to maturity	128.6**	28.4	73.56	648.1**	46.4	90.1
Biomass	10730302**	2909961	66.6	6538533**	2219625	61.2
Yield	197820**	38782	77.2	509855**	59619	81.5
Striga number	0.11**	0.04	67.91	0.112**	0.054	63.3
Striga No. max	0.11**	0.028	68.1	0.099**	0.05	62.6
Vigor	0.01**	0.004	67.8	0.018**	0.01	60.9
Severity	0.124**	0.051	62.4	0.24**	0.11	65.5
AUSNPC	0.132**	0.037	65.5	0.11**	0.053	64.9
AUSSPC	0.19**	0.054	64.2	0.22**	0.11	65.4
Field resistance	0.032**	0.007	54.7	0.011**	0.008	61.4

** = significant at P<0.01, AUSN/SPC = area under *Striga* number/severity progress curve

The combined ANOVA also showed significant difference among the location, genotypes, and genotype by location interaction (P<0.01/0.05) for most of the characters (Table 12). However, the magnitude of the genotype by location interaction variation was small compared to that of genotypes. The effect of location, genotype, and genotype by location interaction, combined together explained R^2 of that range from 61.7% to 82.1%.

Table 12. The combined ANOVA of agronomic and *Striga* related characters

Traits	Mean square				R^2
	Genotype (G)	Location (L)	G*L	Residual	
Degree of freedom	134	1	134	556	
Days to flowering	135.94 **	684.45**	14.78 NS	23.01643	74.4
Plant height	3804.3**	3821.2**	821.7**	5.501993	82.1
Panicle length	47.74 **	1973.75**	14.33**	7.420426	76.9
Days to maturity	95.192**	67.2 NS	79.314*	35.13649	78.2
Biomass	6813833**	8434089NS	10450750*	26028632	61.7
Yield	483416**	40202461**	224259**	51004	79.7
Striga count	0.13 **	17**	0.096**	0.051	76.3
Striga count(max)	0.12**	26.3**	0.091**	0.042	71.6
Vigor	0.013**	0.001NS	0.014**	0.008	61.7
Severity	0.204 ***	18.01**	0.16**	0.09	70.9
AUSNPC	0.139 **	43.45 *	0.1* *	0.051	69.8
AUSSPC	0.23**	40.9**	0.18*	0.094	69.2
Field resistance	0.027**	0.15**	0.015*	0.01	71.3

*, ** = significant at P<0.01 and P< 0.05, respectively, NS = non-significant difference, AUSN/SPC = area under *Striga* number/severity progress curve

4.3.2. Agronomic performances

The combined ANOVA revealed that the genotypes significantly ($P < 0.001$) differed for all characters studied (Table 12). The number of days to flowering for donor parents, converted progeny and recurrent parents ranged from 66.3 to 78.7, 63.2 to 86.7, and 73.5 to 85.8 with a population mean of 78 days (Table 13). About 36.4% of the backcrossed progeny showed a delay in flowering (80-86 days) compared to the population mean and donor parents depending on the genomic behavior of the seed parent. On the other hand, the increase in days to flowering could exposed to high *Striga* infestation with great effects on the physiology of plants from vegetative to flowering as it was observed on recurrent parents and explained by the significant positive correlation between days to flowering and emerged *Striga* plants.

A significant difference was observed in plant height among genotypes in which the susceptible are poorly developed and stunted, although genotypes with resistance genes had normal development and long height (Figure 9). This showed that plant height is considered as one of the most sensitive parameters that indicate the effects of *Striga* on plants as reported by Mignouna *et al*., (2013). Plant height ranged from 121.2 to 247 cm with an average being 190.6 cm (Table 13). There were about 117 cm plant height differences between the shortest and the longest converted progeny attributed to the variation of the genetic background of recurrent parents. It is generally known that the plant height of donor parents and improved released varieties range from short to medium (MoA, 2018), while the local cultivars are commonly characterized by long plant height (Mekbib, 2006; Mindaye *et al*., 2016). Among the backcrossed progeny, 56.8% showed superior performances in plant height more than the donor parents, population mean, and most of the recurrent parents. This signifies that the successful genome recovery from the seed parents and a good level of resistance from the pollen parents. The greater plant height of the resistant backcross progeny than the seed parents indicates the presence of resistance genes that would help to withstand the noxious effect of the parasitic weed.

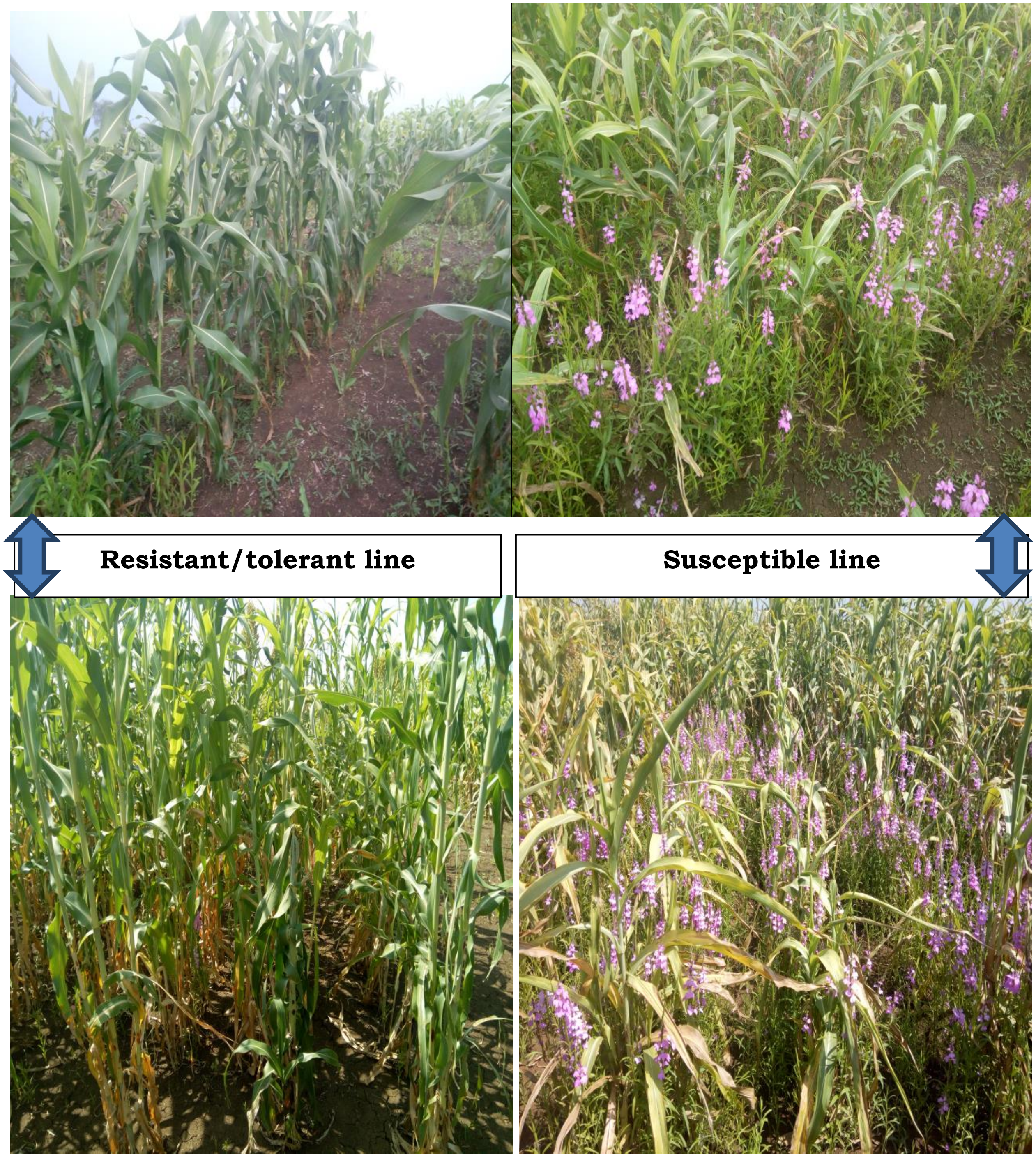


Figure 9. The difference in plant height among the resistant/tolerant and susceptible lines

The highest panicle length was recorded from the BC_2F_3_ETSC_17035 (31.6 cm), while the shortest was measured from BC_2F_3_ETSC_17085 (14.8 cm) depending on the genetic background and markers present. It was observed in this study that genotypes with a good level of resistance/tolerance showed long panicle length than the respective seed parent.

The days to maturity of the sorghum genotypes showed significant variation that ranged from 98.7 to 139.7 days. The recurrent parents had longer days to maturity; AbaAre-1 (139.7), Berjokecoll#1 (139.5), and Wetetbegunche (139.2) as expected (Mekbib, 2006; Mindaye *et al.*, 2016). This study showed that 12.7% of introgressed progeny took long days to maturity (132-138 days) revealing the successful genome recovery of the seed parents through successive backcrossing. However, genotypes with long days to maturity could also be a reason for the exposure of *Striga* infestation as it was observed in this study that the seed parents were found susceptible with the increase in maturity.

It was observed in this study that, in general, *Striga* reduced the above ground dry biomass of sorghum genotypes, implying that the parasite had the ability to affect the allocation of photoassimilates. Mabasa, (2003), reported that, under *Striga* infestation, the parasite channeled all photoassimilates to itself rather than the host plant. The biomass weight of sorghum genotypes under *Striga* infestation ranged from 2133 kg ha^{-1} for BC_2F_3_ETSC_17075 to 7245 kg ha^{-1}

for BC_2F_3_ETSC_17107. About 39.8% of the converted progeny had high biomass that ranged from 5161.7 to 7000 kg ha^{-1} compared to the donor parents and comparable to the recurrent parents. This indicated that the higher biomass accumulation could be related to the successful recovery of the genome of the recurrent parents through backcrossing, which are known for high biomass and grain yield under *Striga*-free environments (Mekbib, 2006; Abate *et al*., 2014; Mindaye *et al*., 2016). Furthermore, these progeny also had the resistance genes from their donor parents that exhibit a good level of resistance/tolerance under *Striga* infection.

The result for grain yield revealed that there were promising lines with acceptable yield and *Striga* resistance indicating the magnitude of the shift in the backcrosses towards the respective recurrent parents for yield potential and resistance towards their donor parents. The highest grain yield was obtained from five converted progeny with yield ranging from 1093.3 to 1220 kg ha^{-1}, and two donor parents, Birhan (1121.7) and Gobiye (1083.3 kg ha^{-1}). Furthermore, 17.8% of the backcrossed progeny showed good yield ranging from 785 to 1066.7 kg ha^{-1}. These converted progeny were observed to closely resemble their respective recurrent parents for morpho-agronomic characteristics, indicating successful genome recovery through the successive backcrossing generations. In addition, the relative high grain yield in the converted progeny implies the consolidation of resistance genes from their donor parents and thus, would help in maintaining a high photosynthetic rate, leading to more photoassimilates being allocated to the host. Gamar and Mohamed, (2013) and Yohannes *et al*., (2015) also observed a clear reduction in *Striga* emergence and sorghum yield increments after introgressing *Striga* resistance quantitative trait loci from donor parents to recurrent parents.

Conversely, the lowest grain yield was obtained from BC_2F_3_ETSC_17083 (110), BC_2F_3_ETSC_17072 (153.3) from the seed parent (Debir). This might be associated with the genetic background (epistasis interaction). The recurrent parents were consistently highly susceptible to *Striga* with a significant yield reduction potential of up to 97% despite their yielding potential under non-infested fields (Appendix 3). It is well known that heavy infestation by the notorious hemiparasites *Striga* has caused farms to be abandoned in tropical and sub-tropical regions of Africa (Lagoke *et al*., 1991; Atera *et al*., 2011; Mandumbu *et al*., 2016).

Table 13. The combined mean agronomic performance of sorghum genotypes under *Striga* infestation from two locations

Genotypes	QTL	DTF	PLHT	PL	DTM	BM	YLD
AbaAre-1	-	83.2	193.7	18.7	139.7	5848.3	333.3
America-1	-	77.2	182.8	25.7	131.0	4431.7	581.7
BC_2F_3_ETSC_17001	lgs2 & lgs3	74.5	204.3	20.4	127.7	5985.0	528.3
BC_2F_3_ETSC_17002	lgs2 & lgs3	76.7	204.5	22.7	126.8	6146.7	671.7
BC_2F_3_ETSC_17003	lgs2 & lgs3	85.0	190.0	16.0	130.3	6148.3	180.0
BC_2F_3_ETSC_17004	lgs2 & lgs3	85.5	199.3	16.9	134.5	6515.0	335.0
BC_2F_3_ETSC_17005	lgs2 & lgs3	85.8	247.1	20.4	137.0	5721.7	211.7
BC_2F_3_ETSC_17006	lgs2 & lgs3	83.8	195.9	22.6	131.5	5186.7	231.7
BC_2F_3_ETSC_17007	lgs2 & lgs3	86.7	185.1	15.6	136.2	5000.0	340.0
BC_2F_3_ETSC_17008	lgs2 & lgs3	76.0	208.0	30.2	127.5	5541.7	855.0
BC_2F_3_ETSC_17009	lgs2 & lgs3	81.2	200.0	29.0	128.0	6603.3	756.7
BC_2F_3_ETSC_17010	lgs2 & lgs3	80.5	194.2	29.0	129.5	5445.0	758.3
BC_2F_3_ETSC_17011	lgs2 & lgs3	79.5	213.6	29.1	127.3	6078.3	785.0
BC_2F_3_ETSC_17012	lgs2 & lgs3	78.2	199.4	28.3	127.8	6015.0	808.3
BC_2F_3_ETSC_17013	lgs2 & lgs3	79.2	181.1	30.1	126.2	4943.3	1180
BC_2F_3_ETSC_17014	lgs2 & lgs3	78.0	195.9	28.5	129.8	6683.3	973.3
BC_2F_3_ETSC_17015	lgs2 & lgs3	78.8	188.4	23.3	128.7	5815.0	565.0
BC_2F_3_ETSC_17016	lgs2 & lgs3	79.0	180.3	25.2	126.7	4966.7	608.3
BC_2F_3_ETSC_17017	lgs2 & lgs3	78.5	214.6	25.2	125.3	5183.3	640.0
BC_2F_3_ETSC_17018	lgs2 & lgs3	79.8	198.7	24.5	128.7	4910.0	418.3
BC_2F_3_ETSC_17019	lgs2 & lgs3	83.7	192.2	22.7	125.7	4371.7	560.0
BC_2F_3_ETSC_17020	lgs2 & lgs3	77.8	192.9	25.1	126.0	5055.0	565.0
BC_2F_3_ETSC_17021	lgs3	78.2	206.8	27.1	127.3	5000.0	620.0
BC_2F_3_ETSC_17022	lgs2 & lgs3	74.7	226.8	22.0	122.0	5480.0	690.0
BC_2F_3_ETSC_17023	lgs2 & lgs3	75.2	224.7	22.8	124.2	5476.7	791.7
BC_2F_3_ETSC_17024	lgs2 & lgs3	75.0	217.5	21.4	125.0	4965.0	705.0
BC_2F_3_ETSC_17025	lgs2 & lgs3	76.3	221.8	24.9	128.7	5200.0	733.3
BC_2F_3_ETSC_17026	lgs2 & lgs3	76.2	222.6	20.3	125.0	5870.0	750.0
BC_2F_3_ETSC_17027	lgs2 & lgs3	75.0	217.5	21.7	125.8	4810.0	413.3
BC_2F_3_ETSC_17028	lgs2 & lgs3	74.3	227.8	27.2	125.8	5578.3	1093
BC_2F_3_ETSC_17029	lgs2	77.7	186.9	20.1	105.7	7000.0	435.0
BC_2F_3_ETSC_17031	lgs2 & lgs3	84.7	198.8	24.2	137.2	4416.7	303.3
BC_2F_3_ETSC_17032	lgs2 & lgs3	81.5	211.3	26.7	126.5	5976.7	580.0
BC_2F_3_ETSC_17033	lgs2 & lgs3	84.2	216.0	23.7	126.0	5736.7	251.7
BC_2F_3_ETSC_17034	lgs3	82.8	179.1	25.6	129.8	3983.3	348.3
BC_2F_3_ETSC_17035	lgs2 & lgs3	80.2	180.6	31.6	122.0	3818.3	310.0

Genotypes	QTL	DTF	PLHT	PL	DTM	BM	YLD
BC$_2$F$_3$_ETSC_17036	lgs2 & lgs3	79.8	187.7	25.6	129.8	4078.3	335.0
BC$_2$F$_3$_ETSC_17037	lgs2 & lgs3	82.3	175.4	20.9	125.5	3595.0	290.0
BC$_2$F$_3$_ETSC_17038	lgs2 & lgs3	83.5	194.3	23.9	133.0	4520.0	313.3
BC$_2$F$_3$_ETSC_17039	lgs2 & lgs3	80.5	218.0	25.3	126.5	4318.3	383.3
BC$_2$F$_3$_ETSC_17040	lgs2 & lgs3	81.5	183.3	26.0	128.2	5991.7	628.3
BC$_2$F$_3$_ETSC_17041	lgs2 & lgs3	83.0	188.0	26.5	126.2	4963.3	591.7
BC$_2$F$_3$_ETSC_17042	lgs2 & lgs3	84.8	177.0	24.2	132.2	3928.3	246.7
BC$_2$F$_3$_ETSC_17043	lgs2 & lgs3	78.0	177.7	23.1	127.8	4063.3	396.7
BC$_2$F$_3$_ETSC_17044	lgs2 & lgs3	78.5	177.6	24.9	130.3	4988.3	523.3
BC$_2$F$_3$_ETSC_17045	lgs2 & lgs3	79.8	188.4	23.5	131.7	3375.0	476.7
BC$_2$F$_3$_ETSC_17046	lgs2 & lgs3	78.8	194.5	22.6	127.3	5833.3	870.0
BC$_2$F$_3$_ETSC_17047	lgs2 & lgs3	81.2	185.8	20.3	128.0	4731.7	436.7
BC$_2$F$_3$_ETSC_17048	lgs2 & lgs3	80.2	202.5	22.4	132.0	4605.0	591.7
BC$_2$F$_3$_ETSC_17049	lgs2 & lgs3	82.2	198.1	23.5	134.0	3916.7	508.3
BC$_2$F$_3$_ETSC_17050	lgs2 & lgs3	83.5	191.9	20.9	129.7	4403.3	246.7
BC$_2$F$_3$_ETSC_17051	lgs3	80.2	201.9	20.6	127.8	5088.3	508.3
BC2F$_3$_ETSC_17052	lgs2 & lgs3	83.3	191.5	20.8	128.7	4666.7	431.7
BC$_2$F$_3$_ETSC_17053	lgs3	80.8	200.9	20.7	127.8	5076.7	618.3
BC$_2$F$_3$_ETSC_17054	lgs2 & lgs3	78.7	220.1	22.1	128.2	5370.0	453.3
BC$_2$F$_3$_ETSC_17055	lgs2 & lgs3	78.2	202.1	18.9	128.5	5476.7	525.0
BC$_2$F$_3$_ETSC_17056	lgs2 & lgs3	75.8	190.1	28.1	126.7	5161.7	838.3
BC$_2$F$_3$_ETSC_17057	lgs2 & lgs3	71.2	207.8	28.3	123.3	4540.0	1007
BC$_2$F$_3$_ETSC_17058	lgs2 & lgs3	71.5	211.7	29.2	125.8	5720.0	1030
BC$_2$F$_3$_ETSC_17059	lgs2 & lgs3	73.7	183.1	25.3	123.5	4171.7	761.7
BC$_2$F$_3$_ETSC_17060	lgs2 & lgs3	72.3	172.3	25.1	128.7	4206.7	638.3
BC$_2$F$_3$_ETSC_17061	lgs2 & lgs3	74.5	204.1	28.0	124.0	5353.3	700.0
BC$_2$F$_3$_ETSC_17062	lgs2 & lgs3	77.0	210.6	27.4	127.3	4206.7	1098
BC$_2$F$_3$_ETSC_17063	lgs2 & lgs3	75.3	213.7	26.3	124.7	6456.7	1067
BC$_2$F$_3$_ETSC_17064	lgs2 & lgs3	74.5	207.4	24.5	126.5	5523.3	790.0
BC$_2$F$_3$_ETSC_17065	lgs2 & lgs3	79.5	187.8	26.1	124.8	3850.0	523.3
BC$_2$F$_3$_ETSC_17066	lgs2	81.2	185.7	26.8	123.8	3765.0	453.3
BC$_2$F$_3$_ETSC_17067	lgs2 & lgs3	78.2	194.5	24.0	127.7	3338.3	355.0
BC$_2$F$_3$_ETSC_17068	lgs2 & lgs3	81.0	177.6	20.0	126.7	3850.0	446.7
BC$_2$F$_3$_ETSC_17069	lgs2 & lgs3	79.3	181.7	25.0	126.2	4908.3	548.3
BC$_2$F$_3$_ETSC_17070	lgs2 & lgs3	79.2	187.8	20.4	127.7	5610.0	565.0
BC$_2$F$_3$_ETSC_17071	lgs2 & lgs3	85.8	189.5	17.3	137.7	3461.7	166.7
BC$_2$F$_3$_ETSC_17072	lgs2 & lgs3	75.3	181.6	21.5	107.0	3821.7	153.3
BC$_2$F$_3$_ETSC_17073	lgs2 & lgs3	68.3	188.4	19.1	106.2	4043.3	221.7
BC$_2$F$_3$_ETSC_17074	lgs2	71.3	175.9	20.8	110.0	6666.7	531.7

Genotypes	QTL	DTF	PLHT	PL	DTM	BM	YLD
BC$_2$F$_3$_ETSC_17075	lgs2 & lgs3	73.7	165.7	18.0	108.5	2133.3	165.5
BC$_2$F$_3$_ETSC_17076	lgs2 & lgs3	78.2	154.6	17.6	109.3	5090.0	219.3
BC$_2$F$_3$_ETSC_17077	lgs3	65.8	184.3	22.4	106.8	4711.7	368.3
BC$_2$F$_3$_ETSC_17078	lgs3	71.7	172.1	17.8	104.5	4733.3	325.0
BC$_2$F$_3$_ETSC_17079	lgs3	76.0	146.1	18.8	105.5	3066.7	177.5
BC$_2$F$_3$_ETSC_17080	lgs2 & lgs3	79.0	168.3	20.2	108.0	5665.0	181.7
BC$_2$F$_3$_ETSC_17081	lgs2 & lgs3	74.5	152.5	19.5	101.7	2311.7	256.7
BC$_2$F$_3$_ETSC_17082	lgs2 & lgs3	73.7	151.1	19.5	100.0	3800.0	358.3
BC$_2$F$_3$_ETSC_17083	lgs2 & lgs3	78.2	130.1	15.1	107.5	2733.3	110.0
BC$_2$F$_3$_ETSC_17084	lgs2	73.5	167.1	18.3	104.0	3713.3	506.7
BC$_2$F$_3$_ETSC_17085	lgs3	83.5	170.3	14.8	108.5	5066.7	241.2
BC$_2$F$_3$_ETSC_17086	lgs3	72.0	180.6	18.6	102.0	6311.7	968.3
BC$_2$F$_3$_ETSC_17087	lgs2 & lgs3	78.0	220.5	25.9	126.8	4505.0	446.7
BC$_2$F$_3$_ETSC_17088	lgs2 & lgs3	79.5	215.6	25.0	126.5	5763.3	526.7
BC$_2$F$_3$_ETSC_17089	lgs2 & lgs3	80.3	207.1	24.8	129.2	5186.7	466.7
BC$_2$F$_3$_ETSC_17090	lgs2 & lgs3	76.2	199.4	28.3	125.8	5575.0	1017
BC$_2$F$_3$_ETSC_17091	lgs2 & lgs3	85.5	202.1	18.9	132.5	5938.3	190.0
BC$_2$F$_3$_ETSC_17092	lgs2 & lgs3	83.0	181.2	23.7	129.8	5276.7	488.3
BC$_2$F$_3$_ETSC_17093	lgs2 & lgs3	84.8	173.2	22.7	133.0	5313.3	268.3
BC$_2$F$_3$_ETSC_17094	lgs2 & lgs3	77.7	200.4	24.3	129.7	5378.3	730.0
BC$_2$F$_3$_ETSC_17095	lgs2 & lgs3	74.2	202.9	28.8	123.5	4408.3	1050
BC$_2$F$_3$_ETSC_17096	lgs2 & lgs3	75.2	220.2	26.6	126.5	4930.0	1025
BC$_2$F$_3$_ETSC_17097	lgs2 & lgs3	72.2	207.9	25.4	129.2	5221.7	995.0
BC$_2$F$_3$_ETSC_17098	lgs2 & lgs3	72.5	225.4	28.0	126.0	4876.7	816.7
BC$_2$F$_3$_ETSC_17099	lgs2 & lgs3	74.7	191.8	23.1	122.3	2665.0	696.7
BC$_2$F$_3$_ETSC_17100	lgs3	72.3	223.9	21.0	122.3	3965.0	488.3
BC$_2$F$_3$_ETSC_17101	lgs2 & lgs3	68.5	194.7	20.2	120.8	2971.7	821.7
BC$_2$F$_3$_ETSC_17102	lgs2 & lgs3	69.0	199.9	22.8	123.5	4166.7	598.3
BC$_2$F$_3$_ETSC_17103	lgs2 & lgs3	72.5	218.1	22.2	122.5	4166.7	488.3
BC$_2$F$_3$_ETSC_17104	lgs3	76.0	229.0	22.0	121.3	3390.0	463.3
BC$_2$F$_3$_ETSC_17105	lgs2 & lgs3	72.3	233.5	26.9	124.8	5256.7	1220
BC$_2$F$_3$_ETSC_17106	lgs2 & lgs3	63.2	189.6	23.8	100.8	4666.7	743.3
BC$_2$F$_3$_ETSC_17107	lgs2 & lgs3	73.7	212.9	25.9	103.7	7245.0	1150
BC$_2$F$_3$_ETSC_17108	lgs2 & lgs3	75.8	212.4	23.9	107.0	6088.3	926.7
BC$_2$F$_3$_ETSC_17109	lgs2 & lgs3	73.5	190.6	20.7	101.5	5211.7	786.7
BC$_2$F$_3$_ETSC_17111	lgs2	71.3	138.1	18.9	98.7	4668.3	998.3
BC$_2$F$_3$_ETSC_17112	lgs2 & lgs3	81.7	192.4	24.2	130.8	3838.3	381.7
BC$_2$F$_3$_ETSC_17113	lgs2 & lgs3	82.3	187.1	26.8	125.5	3261.7	326.7
BC$_2$F$_3$_ETSC_17114	lgs2 & lgs3	81.5	189.0	23.0	128.3	2945.0	345.0

Genotypes	QTL	DTF	PLHT	PL	DTM	BM	YLD
BC$_2$F$_3$_ETSC_17115	lgs2 & lgs3	84.3	184.5	23.6	128.8	3728.3	245.0
BC$_2$F$_3$_ETSC_17116	lgs2 & lgs3	84.3	171.3	19.0	132.2	3183.3	316.7
BC$_2$F$_3$_ETSC_17117	lgs2 & lgs3	82.5	173.0	19.3	125.7	3628.3	283.3
BC$_2$F$_3$_ETSC_17119	lgs2 & lgs3	83.0	170.1	21.6	127.5	2905.0	253.3
BC$_2$F$_3$_ETSC_17120	lgs2 & lgs3	85.8	150.0	19.0	131.5	3338.3	230.0
BC$_2$F$_3$_ETSC_17121	lgs2 & lgs3	81.3	182.3	27.9	130.5	4296.7	273.3
Berjokecoll#1	-	85.8	195.6	21.5	139.5	4408.3	160.0
Birhan	lgs2 & lgs3	66.3	140.2	23.7	107.8	4217.5	1122
Debir	-	78.0	155.3	17.0	110.2	3332.0	185.0
Dekeba	-	77.6	127.3	19.5	102.6	2400.0	236.7
Framida	lgs2 & lgs3	78.7	180.7	18.0	111.3	5764.2	475.0
Gambella1107	-	80.8	162.4	15.9	112.3	5100.0	246.7
Gobiye	lgs2 & lgs3	66.6	143.5	23.4	107.2	3053.3	1083
Jamiyu	-	81.0	192.6	28.5	131.0	4680.0	523.3
Jigurti	-	75.5	224.6	23.3	128.0	4630.0	661.7
local	-	71.8	170.8	19.8	122.2	3538.3	780.0
SRN39	lgs2 & lgs3	72.3	136.5	19.9	122.5	3458.3	751.7
Teshale	-	74.2	189.7	18.8	101.7	3853.3	525.0
Tseadachimure	-	73.5	188.2	22.1	105.8	4088.3	606.7
Wediaker	-	76.3	121.2	16.8	98.8	3890.0	478.3
Wetetbegunchie	-	83.2	179.2	21.9	139.2	4205.0	160.0
Mean		78	190.6	22.9	123.2	3200	550
LSD (0.05)		4.8	62.9	5.7	11.3	1860.7	269.2
CV (%)		6.11	12.36	16.7	4.97	26.8	33.2
Genotype (G)		***	***	***	***	***	***
Location (L)		*	***	***	NS	NS	***
G*L		NS	***	***	**	**	***

lgs2 (lgs2_SBI-05_60404021) with allele AT, *lgs*_3 (lgs_3_60629027) with allele CT, *, **, *** = significant at 0.05, 0.01 and 0.001, respectively. DTF = days to 50% flowering, PLHT = plant height (cm), PL = panicle length (cm), BM = biomass (kg ha^{-1}), YLD= yield (kg ha^{-1}), QTL = Quantitative trait locus, LSD = Least significant difference, CV = Coefficient of variation

4.3.3. *Striga* resistance/tolerance

The combined ANOVA showed highly significant ($P < 0.01$) for all *Striga* related traits studied (Table 12). The result revealed that none of the converted progeny and their parental lines were immune to *Striga*, despite the relative differences in terms of infestation levels by the parasite (Table 14). Parker and Riches, (1993) and Rodenburg *et al.*, (2005) reported that it is very unlikely to have immune genotypes for resistance to *Striga*. A number of other workers also considered relative rather than absolute resistance i.e. when genotypes grown under conditions of *Striga* infestation supported significantly fewer *Striga* plants and gave higher yields (Ejeta *et al.*, 1992; Haussmann *et al.*, 2000b; Mbuvi *et al.*, 2017). On the other hand, tolerant genotypes showed smaller yield reductions than susceptible cultivars under a reasonable level of *Striga* infestation (Parker and Riches, 1993; Haussmann *et al.*, 2000b; Rodenburg *et al.*, 2006; Rodenburg and Bastiaans, 2011; Mbuvi *et al.*, 2017). In the absence of complete immunity or resistance to *Striga*, resistance and tolerance are often confused and each genotype likely combines a certain degree of resistance and tolerance. Therefore, the preservation of yield under *Striga* infection is the result of the combined effects of resistance and tolerance (Rodenburg *et al.*, 2005).

4.3.3.1. *Striga* emergence

The days to first *Striga* emergence among genotypes varied from 40 to 47 days after planting showing at least one-week differences. *Striga* infestation was generally intense at both sites (Kafta Humera and Tahitay Adiyabo) while the former was severely affected (Appendix 1 & 2). The combined mean numbers of emerged *Striga* at physiological maturity ranged from relatively light infestation 36.8 to heavy infestation 179 *Striga* plants m^{-2} (Table 14). In the same way, the mean maximum *Striga* count ranged from 44.4 to 176.2 *Striga* plants m^{-2}. The maximum number of *Striga* plants was recorded 47, 61, 75, or 89 days after planting, depending on the genotypes and associated mechanism of resistance. About 29.7% of the converted progeny were found with a relatively low number of emerged *Striga* and comparable to donor parents. *Striga* emergence was generally earlier and immense on susceptible such as recurrent parents compared to resistant genotypes such as donor parents and nearly 30% of the introgressed progeny (Table 14). This result is a clear indication that resistance to *Striga* has been successfully introgressed into the backcross progeny. Besides their resistance or tolerance to *Striga* as explained by the few numbers of *Striga* plants they supported, these progeny also showed good agronomic adaptability in the environments with a good grain yield.

The present study clearly showed genetic variation among the genotypes for a number of *Striga* plants, with relatively lower counts being associated with the donor parents and 29.7% the converted progeny. These converted progeny and donor parents showed only a few *Striga* plants emerged at 47 days after planting (delayed emergence), which was probably associated with the production of very little *Striga* seed germination stimulant activity or altered strigolactones composition (Gebremedhin *et al.*, 2000; Gurney *et al.*, 2000; Haussmann *et al.*, 2000b; Ejeta, 2007; Robert *et al.*, 2011; Yohannes *et al.*, 2015; Gwatidzo *et al.*, 2020). Genetic differences in time of parasite attachment, with resistant varieties showing later attachment and parasite emergence than susceptible cultivars were also reported from previous studies in sorghum (Ezeaku and Gupta, 2004; Rodenburg *et al.*, 2006). Delaying the time of the first infection not only influences *Striga* parasitism and reproduction but also strongly reduces its damaging effects on host plant (Oswald *et al.*, 2001; Van Ast and Bastiaans, 2006). It is interesting to note that the donor parents consistently supported significantly lower *Striga* plants throughout the season, signifying their superior resistance level and potential sources of resistance for breeding programs (Tesso *et al.*, 2007; Satish *et al.*, 2012). It was also observed that a reduction on emerged *Striga* plants in some sorghum genotypes revealed the parasitism was not progressing. The Framida (donor parent) and 17 of the developed progeny show such characteristics. It can possibly suggested that the donor parent and 17 backcrossed progeny might have more than one mechanism of resistance as evidenced by relatively high *Striga* emergence but otherwise poor *Striga* vigor and severity and associated relatively good yield. This indicated that genotypes with high stimulants production activity otherwise with other means of resistances. This study has been found corroborates with previous reports (Haussmann *et al.*, 2000b; Grenier *et al.*, 2001, Mohamed *et al.*, 2003; Omanya *et al.*, 2004; Ejeta *et al.*, 2007a; Robert *et al.*, 2011).

Conversely, the recurrent parents supported high (51.5 to 130.5 plants m^{-2}) *Striga* population indicating abundant *Striga* germination stimulant activity and successful parasitism of the host and the parasite as anticipated. It was also evidenced by early *Striga* appearance at least one week earlier than resistance lines. In addition, the emerged *Striga* was high (76 to 179 *Striga* plants m^{-2}) and progressive for 47.5% of the introgressed progeny, which was not expressing the low germination stimulant QTLs. This might be probably associated with the genetic background (epistasis interaction) (Liao *et al.*, 2001), QTL x environment interaction (Li *et al.*, 2003), and transfer of a segment of the genome rather than the full complement the donor parents.

4.3.3.2. *Striga* vigor

The average *Striga* vigor based on 0-9 scoring scale ranged from 5 to 9. Based on this result, 16.1% of the converted progeny showed relatively less progressive and poor vigor (5 to 6) of *Striga* plants throughout the growing season (Table 14). This may probably indicate that the parasitic weed is not deriving adequate nourishment from its host and there could be some incompatible reactions from the host. On the other hand, eight converted progeny showed less number emerged *Striga* but more vigorous indicating their lower stimulant production from the root with otherwise a compatible reaction. *Striga* vigor score offers a quick, effective, non-destructive approximation of *Striga* development and average biomass in each field plot (Hausemann *et al.*, 2000a, b; Omanya *et al.*, 2004). *Striga* vigor influences the mortality and seed production capacity (Rodenburg *et al.*, 2006).

4.3.3.3. *Striga* severity

There was significant difference in *Striga* sensitivity (P < 0.01) among the converted progeny and their parental lines. The severity of *Striga* ranged from 228.5 to 1396.3. High *Striga* severity shows successful parasitism in susceptible genotypes while low severity indicates low or unsuccessful parasitism, which happens in resistant genotypes (Robert *et al.*, 2011). About 25.4% of the backcrossed lines exhibited *Striga* severity that ranged from 228.5 to 464 and was statistically similar to their donor parents. The mean *Striga* number, vigor, and severity increased throughout the growing season (47 to 89 recording days after planting) (Figure 10).

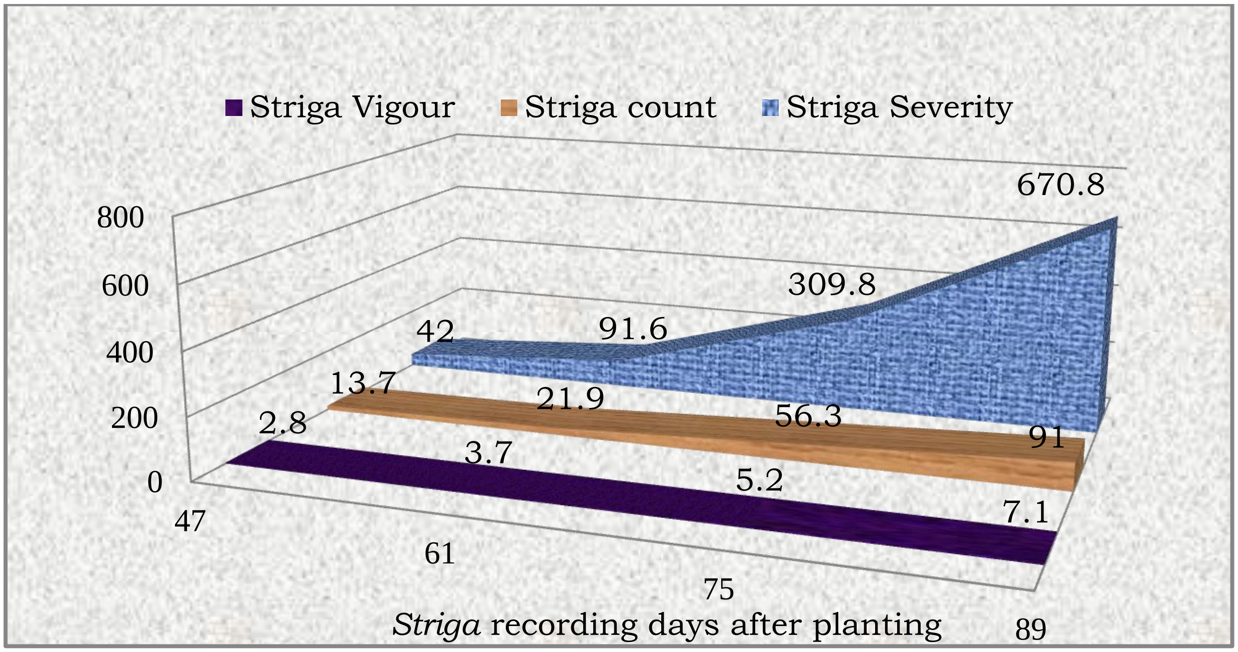


Figure 10. The interrelationships of *Striga* number, vigor and severity with time

4.3.3.4. Area under *Striga* number progress curve

AUSNPC offered useful measures of progressive *Striga* development in the field as it incorporates emergence time and numbers of emerged *Striga* (Haussmann *et al*., 2000a; 2001a, b; Omanya *et al*., 2004). The combined mean AUSNPC ranged from the lowest of 764.4 to the highest of 4552.8. Significantly lower AUSNPC were obtained from Gobiye (764.4) and 12 backcrossed lines with values that ranged from 929.1 to 1405.8. This showed that these genotypes had the targeted resistant genes responsible for resistance or tolerance to the parasitic weed. Conversely, 55.1% of the developed progeny and recurrent parents showed significantly higher AUSNPC (2041 to 4352) indicating their susceptibility as evidenced by supporting high number of emerged *Striga* though time (Figure 11).

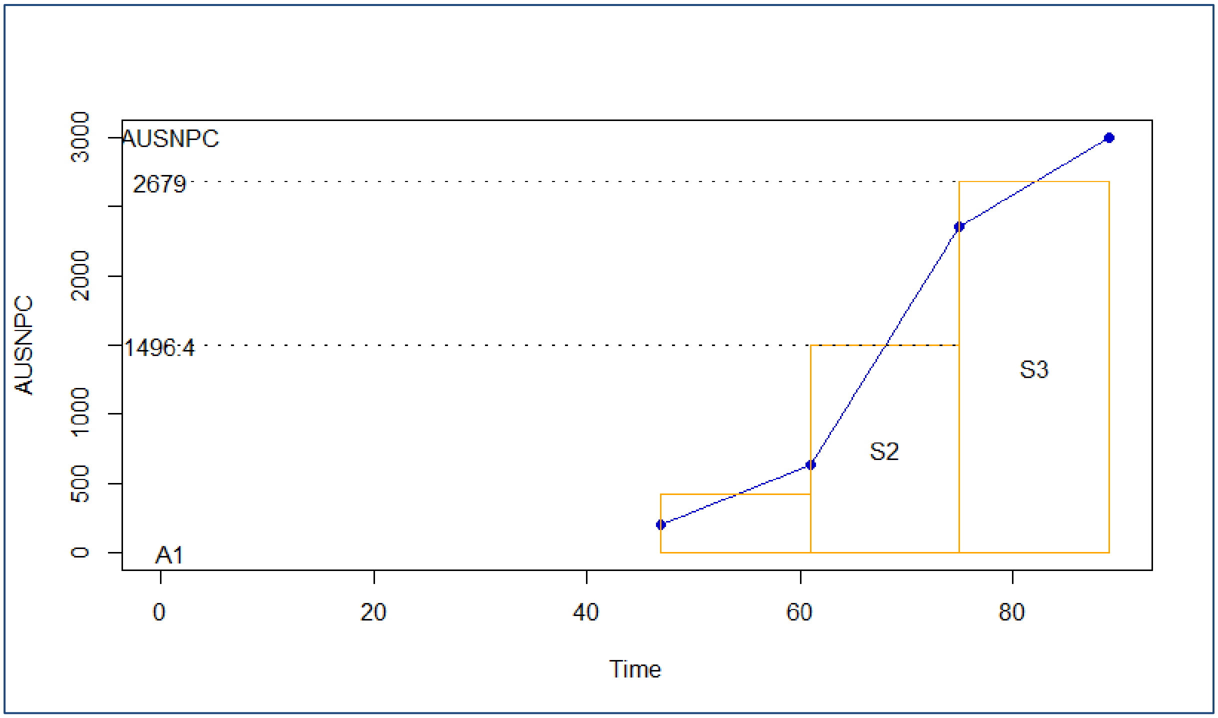


Figure 11. Area under *Striga* number progress curve

4.3.3.5. Area under *Striga* severity progress curve

The AUSSPC of the genotypes ranged from the lowest of 3264 to the highest of 25446.5. About 23.7% of the introgressed progeny and donor parents showed relatively lower AUSSPC values ranging from 4370.8 to 8919.3 (Table 14). This revealed that these progeny incorporated responsible genes for *Striga* resistance agreeing with previous reports (Haussmann *et al.*, 2000a; Omanya *et al.*, 2004; Yohannes *et al.*, 2015). In most of the cases, sorghum genotypes that exhibited low AUSSPC also showed similar pattern of AUSNPC indicating their close relationships among these indicators. On the other hand, it was observed that 76.3% of the developed progeny and recurrent parents exhibited higher AUSSPC depending on the genetic background and QTLs contained. The AUSSPC showed a progressive trend showing the severity and vigor of *Striga* increase with time (Figure 12).

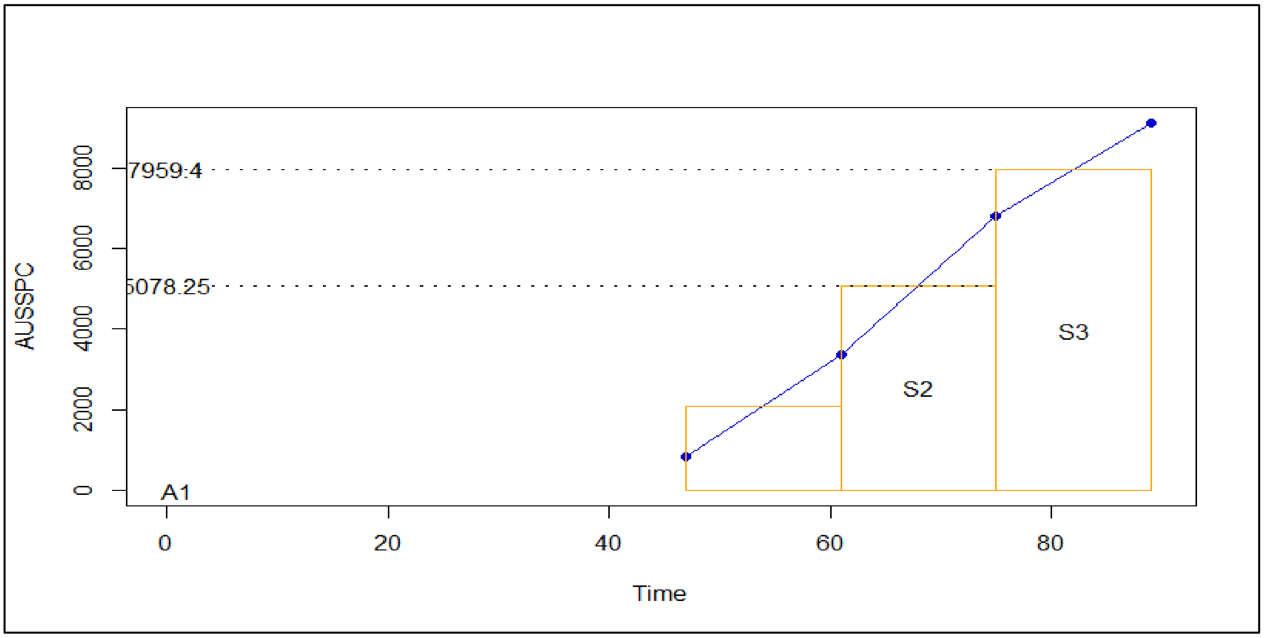


Figure 12. Area under *Striga* severity progress curve

4.3.3.6. Field resistance score

The overall mean of field resistance score varied from 2 (fairly-resistant) to 5 (very susceptible). The donor parents consistently showed good performance under field conditions, ranging from fairly resistant to average resistance/tolerance (score of 2 to 3). In the same manner, 25.4% of the converted progeny exhibited fairly resistant to average field resistance score (2 to 3), indicating a good potential of resistance or tolerance to the parasitic weed (Table 14). It is generally shown that progeny with lower values for *Striga* number and poor vigor also showed lower AUSNPC, AUSSPC, and field resistance and *vice versa* (Haussmann *et al.*, 2000b).

Table 14. Combined mean response of sorghum genotypes to *Striga* resistance or tolerance characters

Genotypes	SN	SN$_{max}$	Vigor	Severity	AUSNPC	AUSSPC	FR
AbaAre-1	1.99(106.8)	2.05(132.2)	0.91(7.2)	2.84(718.6)	3.34(2713.4)	4.12(16301.8)	0.7(4)
America-1	1.93(121.7)	1.97(125.2)	0.89(6.8)	2.75(774.8)	3.26(2605.6)	4.02(15920.9)	0.71(4)
BC$_2$F$_3$_ETSC_17001	1.63(46.5)	1.81(81.5)	0.88(6.8)	2.44(319.)	3.09(1709.7)	3.85(10390)	0.7(4)
BC$_2$F$_3$_ETSC_17002	1.7(54.3)	1.97(104.5)	0.91(7.3)	2.54(391.3)	3.19(1917.8)	3.93(11805.6)	0.69(4)
BC$_2$F$_3$_ETSC_17003	1.75(59.3)	1.96(96.3)	0.93(7.7)	2.63(475.7)	3.22(1753.8)	4(10733.7)	0.65(4)
BC$_2$F$_3$_ETSC_17004	2.1(142.8)	2.07(142.8)	0.92(7.5)	2.93(1035)	3.34(2734.6)	4.14(17549.3)	0.69(4)
BC$_2$F$_3$_ETSC_17005	1.94(96.7)	2.03(123.2)	0.93(7.7)	2.82(730.5)	3.28(2196.8)	4.03(12207.2)	0.7(4)
BC$_2$F$_3$_ETSC_17006	2.15(179)	2.12(176.2)	0.93(7.7)	3.03(1396.3)	3.45(3847.2)	4.24(25446.5)	0.78(5)
BC$_2$F$_3$_ETSC_17007	2.1(134.5)	2.11(143.3)	0.91(7.2)	2.91(925.8)	3.35(2728.5)	4.16(17759.7)	0.69(4)
BC$_2$F$_3$_ETSC_17008	1.75(87.7)	1.77(89)	0.85(6.3)	2.51(651.8)	3.05(1887.2)	3.72(11465.6)	0.7(4)
BC$_2$F$_3$_ETSC_17009	1.92(113.2)	1.97(124.3)	0.87(6.5)	2.72(738.7)	3.25(2476.7)	3.97(13657.3)	0.65(4)
BC$_2$F$_3$_ETSC_17010	1.87(96)	2.01(115.5)	0.86(6.8)	2.64 (678.7)	3.15(2041.7)	3.83(12708.5)	0.69(4)
BC$_2$F$_3$_ETSC_17011	1.82(91.7)	1.86(106.7)	0.8(5.7)	2.53(580.9)	3.14(2420)	3.79(13628.6)	0.69(4)
BC$_2$F$_3$_ETSC_17012	1.76(91)	1.81 (95.2)	0.89(7)	2.58(669.6)	3.11(2073.9)	3.8(11251)	0.66(4)
BC$_2$F$_3$_ETSC_17013	1.58(53.2)	1.59(54.3)	0.86(6.7)	2.35356.5 ()	2.86(1229.3)	3.52(6828.8)	0.67(4)
BC$_2$F$_3$_ETSC_17014	1.80(102.3)	1.81(103.2)	0.85(6.3)	2.55(691.8)	3.07(2041.3)	3.71(10571.9)	0.59(3)
BC$_2$F$_3$_ETSC_17015	1.94(104)	1.99(122)	0.89(6.8)	2.76(692.8)	3.21(2043.5)	3.95(11296.3)	0.66(4)
BC$_2$F$_3$_ETSC_17016	1.87(91.2)	2.03(135.8)	0.87(6.5)	2.67(569.8)	3.33(3074.1)	4.08(19405.6)	0.71(4)
BC$_2$F$_3$_ETSC_17017	1.85(79.5)	1.97(110.5)	0.89(7)	2.67(580.8)	3.24(2184.5)	3.97(13183.4)	0.66(4)
BC$_2$F$_3$_ETSC_17018	1.92(88.8)	2.03(126.8)	0.95(8)	2.81(690.8)	3.37(3080.1)	4.18(19611.8)	0.73(4)
BC$_2$F$_3$_ETSC_17019	1.84(80.8)	1.94(113.2)	0.91(7.5)	2.69(611.1)	3.22(2280)	4(15323)	0.71(4)
BC$_2$F$_3$_ETSC_17020	1.86(80.2)	1.95(111.7)	0.91(7.3)	2.71(595.8)	3.22(2227.1)	3.99(14231.7)	0.63(4)
BC$_2$F$_3$_ETSC_17021	1.66(57.8)	1.76(79)	0.91(7.3)	2.49(426.5)	3.03(1524.2)	3.75(8919.3)	0.57(3)
BC$_2$F$_3$_ETSC_17022	1.89(79)	2.15(152.3)	0.91(7.2)	2.73(555.8)	3.46(3496.3)	4.22(19653.5)	0.65(4)
BC$_2$F$_3$_ETSC_17023	1.73(74.8)	1.94(108.3)	0.87(6.8)	2.52(501.3)	3.26(2521.8)	3.99(14664.3)	0.63(3)
BC$_2$F$_3$_ETSC_17024	1.86(76.3)	2.01(118.5)	0.95(8)	2.74(570.2)	3.31(2595.6)	4.08(15134)	0.68(4)
BC$_2$F$_3$_ETSC_17025	1.73(58.8)	1.86(88.5)	0.87(6.5)	2.52(386.7)	3.19(2050.1)	3.94(12233)	0.63(3)
BC$_2$F$_3$_ETSC_17026	1.87(102.7)	1.94(114.7)	0.85(6.2)	2.65(621.9)	3.28()2689.8	4.01(14808.7)	0.62(3)
BC$_2$F$_3$_ETSC_17027	2.06(119.2)	2.15(160)	0.92(7.3)	2.92(876.4)	3.44(3378.8)	4.21(20175.3)	0.69(4)
BC$_2$F$_3$_ETSC_17028	1.63(48)	1.89(92)	0.85(6.2)	2.4 (295.7)	3.14(1665.7)	3.83(8145.3)	0.59(3)
BC$_2$F$_3$_ETSC_17029	1.79(60.7)	1.83(67.8)	0.93(7.7)	2.65(475.2)	3.24(1915.3)	3.89(8245.8)	0.62(3)
BC$_2$F$_3$_ETSC_17031	1.8(71.7)	1.95(114.7)	0.91(7.3)	2.65(547.3)	3.27(2614.1)	4.03(16984.8)	0.74(5)
BC$_2$F$_3$_ETSC_17032	1.89(90.8)	2.01(120)	0.87(6.5)	2.7(568.4)	3.24(2235.7)	4(13657.8)	0.72(4)
BC$_2$F$_3$_ETSC_17033	1.88(78.5)	1.94(88.2)	0.91(7.2)	2.73(564.4)	3.2(1671.9)	3.95(9721.4)	0.66(4)
BC$_2$F$_3$_ETSC_17034	1.77(72.)	2.05(132.5)	0.89(6.8)	2.59(498.2)	3.31(2411.6)	4.05(13954.9)	0.75(5)
BC$_2$F$_3$_ETSC_17035	1.89(80.7)	2.03(115.3)	0.95(8)	2.79(644.4)	3.33(2283.3)	4.15(14776.8)	0.78(5)
BC$_2$F$_3$_ETSC_17036	2.06(120.8)	2.12(139.8)	1(9)	3.01(1086.7)	3.39(2687.3)	4.22(18136.1)	0.73(4)
BC$_2$F$_3$_ETSC_17037	1.85(77.7)	2.06(140.8)	0.92(7.5)	2.7(545.8)	3.4(3453.8)	4.17(20627)	0.75(5)
BC$_2$F$_3$_ETSC_17038	1.82(75.5)	1.95(116.2)	0.9(7.3)	2.64(578.3)	3.23(2504.4)	3.99(15483.1)	0.73(4)

Genotypes	SN	SN$_{max}$	Vigor	Severity	AUSNPC	AUSSPC	FR
BC$_2$F$_3$_ETSC_17039	1.66(47)	1.94(95.7)	0.91(7.2)	2.5(356.5)	3.21(1852.9)	3.99(11337.9)	0.75(5)
BC$_2$F$_3$_ETSC_17040	1.75(69.7)	1.88(95)	0.92(7.3)	2.6(501.9)	3.17(1956.5)	3.9(10389)	0.66(4)
BC$_2$F$_3$_ETSC_17041	1.8(74.2)	1.91(99.5)	0.91(7.5)	2.65(608.3)	3.23(2182)	3.99(13655.8)	0.7(4)
BC$_2$F$_3$_ETSC_17042	1.85(81.8)	2.03(122)	0.89(6.8)	2.67(569.4)	3.36(2948.3)	4.13(18114.5)	0.75(5)
BC$_2$F$_3$_ETSC_17043	1.87(81.8)	2.03(121.3)	0.92(7.5)	2.73(612)	3.3(2363.2)	4.09(14840.6)	0.75(5)
BC$_2$F$_3$_ETSC_17044	1.8(65.7)	1.95(98.8)	0.89(7)	2.62(451.3)	3.18(1778.7)	3.9(10208.9)	0.72(4)
BC$_2$F$_3$_ETSC_17045	1.7(57.3)	1.83(69.8)	0.92(7.3)	2.55(429.6)	3.14(1532.7)	3.85(8128.6)	0.73(4)
BC$_2$F$_3$_ETSC_17046	1.61(49)	1.72(62.2)	0.86(6.7)	2.39(360.7)	3.06(1525.4)	3.73(8467.6)	0.68(4)
BC$_2$F$_3$_ETSC_17047	1.71(70)	1.84(93.2)	0.88(7)	2.52(514.5)	3.14(2117.2)	3.81(11832.6)	0.72(4)
BC$_2$F$_3$_ETSC_17048	1.72(76)	1.86(125.5)	0.82(6)	2.45(493.9)	3.18(3035.6)	3.9(18043.8)	0.7(4)
BC$_2$F$_3$_ETSC_17049	1.77(67.8)	1.86(91)	0.87(6.7)	2.57(478)	3.09(1646.8)	3.82(9472)	0.68(4)
BC$_2$F$_3$_ETSC_17050	1.69(52.3)	1.88(92.8)	0.98(8.5)	2.61(427.3)	3.17(1994.9)	3.98(12686.8)	0.71(4)
BC$_2$F$_3$_ETSC_17051	1.89(79.8)	2.01(114.3)	0.93(7.7)	2.76(617.5)	3.25(2126.9)	4(11698.8)	0.66(4)
BC$_2$F$_3$_ETSC_17052	1.86(75.2)	1.91(85.7)	0.93(7.7)	2.73(564.6)	3.2(1716)	3.93(9199.8)	0.58(3)
BC$_2$F$_3$_ETSC_17053	1.76(62.5)	1.89(85.3)	0.95(8)	2.64(523.8)	3.17(1647.4)	3.88(8736.8)	0.62(3)
BC$_2$F$_3$_ETSC_17054	1.9(79.8)	2.01(106.5)	0.95(8)	2.79(617.3)	3.3(2149.5)	4.05(11992.9)	0.65(4)
BC$_2$F$_3$_ETSC_17055	1.98(102.5)	2.01(109.5)	0.94(7.8)	2.86(764.1)	3.3(2139.2)	4.11(13784.5)	0.68(4)
BC$_2$F$_3$_ETSC_17056	1.68(56.5)	1.74(64.5)	0.94(7.8)	2.55(435.2)	3.02(1331.5)	3.78(7716.8)	0.59(3)
BC$_2$F$_3$_ETSC_17057	1.64(43.7)	1.79(65)	0.9(7.2)	2.47(303.7)	3.07(1329.8)	3.77(7234.4)	0.62(3)
BC$_2$F$_3$_ETSC_17058	1.75(63.8)	1.81(74.7)	0.92(7.7)	2.61(518.3)	3.11(1507.4)	3.84(8825)	0.56(3)
BC$_2$F$_3$_ETSC_17059	1.81(73.5)	2.09(165.5)	0.95(8)	2.7(580.3)	3.4(3766.3)	4.2(25073.2)	0.75(5)
BC$_2$F$_3$_ETSC_17060	1.89(82.2)	2.01(111.5)	0.91(7.2)	2.73(599)	3.32(2234.5)	4.08(13162.1)	0.75(5)
BC$_2$F$_3$_ETSC_17061	1.65(50.5)	1.78(75.3)	0.92(7.5)	2.5(403.8)	3.07(1536.7)	3.77(8610.5)	0.66(4)
BC$_2$F$_3$_ETSC_17062	1.86(86.5)	2(132.2)	0.91(7.3)	2.71(702.2)	3.31(2856.9)	4.04(16871.6)	0.63(3)
BC$_2$F$_3$_ETSC_17063	1.55(36.8)	1.7(62.5)	0.88(7)	2.35(267.7)	2.95(1242.8)	3.59(6289.1)	0.51(2)
BC$_2$F$_3$_ETSC_17064	1.6(48.8)	1.92(104.3)	0.88(6.8)	2.4(372.9)	3.17(1938.3)	3.84(10746.8)	0.62(3)
BC$_2$F$_3$_ETSC_17065	1.89(93.3)	1.98(117.7)	0.93(7.7)	2.75(684)	3.25(2281.6)	4.03(14468.3)	0.73(4)
BC$_2$F$_3$_ETSC_17066	1.93(85.5)	2.07(135.8)	0.93(7.7)	2.79(660.4)	3.3(2605.3)	4.05(15741.1)	0.66(4)
BC$_2$F$_3$_ETSC_17067	2.04(112.3)	2.15(148.8)	0.92(7.5)	2.9(808.9)	3.43(2915.5)	4.23(17602.4)	0.73(4)
BC$_2$F$_3$_ETSC_17068	1.63(54)	1.86(81.8)	0.95(8)	2.49(386.9)	3.12(1543.8)	3.89(9408.6)	0.72(4)
BC$_2$F$_3$_ETSC_17069	1.7(63.2)	2(114.8)	0.91(7.5)	2.55(535.7)	3.22(1979.2)	3.96(12164.7)	0.75(5)
BC$_2$F3_ETSC_17070	1.72(58.3)	1.76(65.8)	0.86(6.3)	2.5(380.8)	3.05(1316.4)	3.74(7019.8)	0.65(4)
BC$_2$F$_3$_ETSC_17071	1.8(64.3)	1.88(81.3)	0.98(8.7)	2.73(563.3)	3.22(1863.3)	3.97(10715.4)	0.78(5)
BC$_2$F$_3$_ETSC_17072	1.83(73.7)	1.89(82)	0.98(8.7)	2.76(647.5)	3.34(2743.8)	4.03(11953.8)	0.68(4)
BC$_2$F$_3$_ETSC_17073	1.75(58.5)	1.92(83.5)	0.97(8.3)	2.66(475.7)	3.29(2239.5)	4(10797.5)	0.69(4)
BC$_2$F$_3$_ETSC_17074	1.81(66.2)	1.87(79)	0.93(7.7)	2.68(499.3)	3.28(2151)	3.97(10711.3)	0.66(4)
BC$_2$F$_3$_ETSC_17075	1.87(79.2)	1.88(81.3)	0.98(8.7)	2.8(697.2)	3.33(2840.7)	4.01(11804.7)	0.76(5)
BC$_2$F$_3$_ETSC_17076	1.73(66.5)	1.8(73.7)	0.9(7)	2.56(487.5)	3.17(1943.8)	3.81(8128.7)	0.71(4)
BC$_2$F$_3$_ETSC_17077	1.76(64.3)	1.83(75)	0.9(7.2)	2.59(463.5)	3.22(1924.8)	3.86(8550.5)	0.56(3)
BC$_2$F$_3$_ETSC_17078	1.71(54.3)	1.8(67.5)	0.92(7.5)	2.57(426.2)	3.19(1913.7)	3.83(8413.2)	0.66(4)
BC$_2$F$_3$_ETSC_17079	1.89(84.5)	1.93(91.5)	0.98(8.5)	2.81(735.5)	3.35(2933.5)	4.05(13336)	0.67(4)
BC$_2$F$_3$_ETSC_17080	1.94(91.2)	1.97(96.2)	0.97(8.3)	2.85(736.5)	3.36(2533.5)	4.1(12764.8)	0.68(4)

Genotypes	SN	SN$_{max}$	Vigor	Severity	AUSNPC	AUSSPC	FR
BC$_2$F$_3$_ETSC_17081	1.96(108.5)	2.03(122.3)	0.97(8.3)	2.87(932.2)	3.52(4352.8)	4.23(19884.5)	0.69(4)
BC$_2$F$_3$_ETSC_17082	1.85(76.8)	1.88(81.5)	0.98(8.7)	2.78(677.3)	3.32(2451.3)	4.04(12375.3)	0.61(3)
BC$_2$F$_3$_ETSC_17083	1.93(90.7)	1.93(90.7)	0.98(8.7)	2.86(804.3)	3.36(2972.8)	4.09(14378.2)	0.69(4)
BC$_2$F$_3$_ETSC_17084	1.84(69.5)	1.89(78.5)	0.92(7.3)	2.69(504.7)	3.18(1642.5)	3.92(8818.3)	0.58(3)
BC$_2$F$_3$_ETSC_17085	1.94(89.7)	1.95(91.8)	0.93(7.7)	2.81(661)	3.28(1990.2)	3.97(9795.2)	0.62(3)
BC$_2$F$_3$_ETSC_17086	1.82(69.8)	1.84(71.8)	0.94(7.7)	2.69(544.2)	3.27(2285.7)	3.93(9678)	0.61(3)
BC$_2$F$_3$_ETSC_17087	1.6(51.8)	1.77(83.2)	0.88(7.2)	2.41(439.8)	2.93(1233.1)	3.6(7017.8)	0.55(3)
BC$_2$F$_3$_ETSC_17088	1.76(62.2)	1.93(111.5)	0.92(7.7)	2.61(515.2)	3.19(2153.5)	3.92(13268.8)	0.74(5)
BC$_2$F$_3$_ETSC_17089	1.78(80)	1.89(107.3)	0.87(7)	2.56(674.3)	3.2(2360.3)	3.86(14261.9)	0.68(4)
BC$_2$F$_3$_ETSC_17090	1.52(41.2)	1.59(47.2)	0.77(5)	2.19(228.5)	2.86(929.1)	3.46(4370.8)	0.53(2)
BC$_2$F$_3$_ETSC_17091	1.88(87.3)	2(109.7)	0.91(7.3)	2.73(709)	3.25(2115.6)	4.01(13084.7)	0.72(4)
BC$_2$F$_3$_ETSC_17092	1.75(62.8)	1.84(84.3)	0.87(7)	2.54(499.8)	3.12(1767.2)	3.8(10665.3)	0.7(4)
BC$_2$F$_3$_ETSC_17093	1.91(87.7)	1.96(96)	0.94(7.8)	2.79(735.1)	3.2(1672.8)	3.93(9724.9)	0.65(4)
BC$_2$F$_3$_ETSC_17094	1.89(83)	2.08(142.3)	0.9(7.2)	2.72(602.2)	3.29(2376.2)	4.05(13949.1)	0.6(3)
BC$_2$F$_3$_ETSC_17095	1.71(65.7)	1.78(70)	0.84(6.2)	2.47(454.3)	3.06(1330.3)	3.72(6659.8)	0.52(2)
BC$_2$F$_3$_ETSC_17096	1.62(73.5)	1.65(75.8)	0.82(6.2)	2.34(498.5)	2.95(1617.3)	3.57(8699.2)	0.58(3)
BC$_2$F$_3$_ETSC_17097	1.74(72.2)	1.75(72.8)	0.78(5.2)	2.44(412.7)	3.06(1685.4)	3.65(8521.8)	0.54(3)
BC$_2$F$_3$_ETSC_17098	1.79(65.8)	1.86(75.7)	0.89(6.8)	2.62(455.8)	3.2(1827.2)	3.95(10315.8)	0.67(4)
BC$_2$F$_3$_ETSC_17099	1.72(57.7)	1.72(57.7)	0.94(7.8)	2.61(481.3)	2.93(970.6)	3.68(5372.8)	0.66(4)
BC$_2$F$_3$_ETSC_17100	1.88(83.2)	2.03(108.7)	0.91(7.2)	2.72(578.3)	3.32(2235.3)	4.07(12920.7)	0.62(3)
BC$_2$F$_3$_ETSC_17101	1.41(43.7)	1.48(51.2)	0.93(7.8)	2.27(382.9)	2.66(954.2)	3.34(6345.5)	0.5(3)
BC$_2$F$_3$_ETSC_17102	1.9(84.3)	1.97(103.5)	0.91(7.2)	2.74(575.5)	3.28(2281.1)	4.03(12823.5)	0.6(3)
BC$_2$F$_3$_ETSC_17103	2.03(112.8)	2.06(122.5)	0.96(8.3)	2.94(926.9)	3.36(2581.6)	4.17(16053.4)	0.64(4)
BC$_2$F$_3$_ETSC_17104	1.96(117.3)	1.96(117.3)	0.91(7.8)	2.8(1041.2)	3.24(2342.1)	3.99(16796.7)	0.68(4)
BC$_2$F$_3$_ETSC_17105	1.66(53.5)	1.74(61.2)	0.97(8.3)	2.57(464)	3.1(1608.1)	3.83(9595.9)	0.54(3)
BC$_2$F$_3$_ETSC_17106	1.83(84.2)	1.87(88.3)	0.88(6.7)	2.63(627.8)	3.28(2845.2)	3.89(11414.5)	0.68(4)
BC$_2$F$_3$_ETSC_17107	1.62(49.3)	1.74(59.5)	0.89(6.8)	2.44(346.3)	3.1(1405.8)	3.73(6083)	0.56(3)
BC$_2$F$_3$_ETSC_17108	1.82(75.8)	1.85(80.3)	0.92(7.5)	2.67(600.3)	3.19(1888)	3.87(9455.2)	0.58(3)
BC$_2$F$_3$_ETSC_17109	1.75(61.5)	1.78(64)	0.89(7)	2.56(458)	3.14(1837.2)	3.78(8237.3)	0.59(3)
BC$_2$F$_3$_ETSC_17111	1.69(54.5)	1.82(71.3)	0.92(7.3)	2.54(429)	3.18(1778.2)	3.85(8816)	0.58(3)
BC$_2$F$_3$_ETSC_17112	1.76(62.8)	1.92(106.5)	0.93(7.7)	2.63(499.3)	3.2(2073.9)	3.98(13271.6)	0.72(4)
BC$_2$F$_3$_ETSC_17113	1.85(71.5)	1.91(84.7)	0.93(7.7)	2.71(548.8)	3.23(1808.5)	3.99(10774.1)	0.69(4)
BC$_2$F$_3$_ETSC_17114	1.93(84)	1.94(86.3)	0.96(8.2)	2.83(689.8)	3.06(1216.3)	3.88(8402.3)	0.75(5)
BC$_2$F$_3$_ETSC_17115	1.95(94.8)	1.99(103.7)	0.92(7.5)	2.81(661.2)	3.25(1897.7)	4.07(12441.1)	0.76(5)
BC$_2$F$_3$_ETSC_17116	1.77(80.5)	1.91(100.5)	0.9(7.3)	2.58(579)	3.2 (2093.1)	3.91(12079.2)	0.75(5)
BC$_2$F$_3$_ETSC_17117	1.85(80.2)	1.87(83.3)	0.95(8)	2.73(688.8)	3.18(1837.7)	3.94(12325.9)	0.74(5)
BC$_2$F$_3$_ETSC_17119	1.82(72.7)	1.88(85.7)	0.89(7)	2.64(523.5)	3.16(1727.2)	3.94(10928.5)	0.73(4)
BC$_2$F$_3$_ETSC_17120	2.09(129)	2.1(133)	0.95(8)	2.98(1015.9)	3.4 (2674.2)	4.18(16743)	0.75(5)
BC$_2$F$_3$_ETSC_17121	2.03(120.8)	2.12(141.2)	0.92(7.5)	2.89(842.8)	3.44(3183.1)	4.24(19864.8)	0.7(4)
Berjokecoll#1	1.92(89.3)	1.92(89.3)	0.92(7.5)	2.79(634.5)	3.18(1711.3)	3.96(9895.8)	0.71(4)
Birhan	1.48(51.9)	1.59(59.7)	0.78(5.3)	2.15(300.5)	2.94(1422.5)	3.5(6446.3)	0.53(3)
Debir	1.86(73.8)	1.88(77.6)	0.98(8.6)	2.79(637.6)	3.32(2139.6)	4.03(10964.6)	0.7(4)

Genotypes	SN	SN_{max}	Vigor	Severity	AUSNPC	AUSSPC	FR
Dekeba	1.81(71.7)	1.88(81.6)	0.97(8.4)	2.73(618)	3.22(1888.3)	3.93(9456.4)	0.72(4)
Framida	1.71(63.8)	1.77(69.7)	0.86(6.5)	2.5(469)	3.07(1334)	3.7(6915.8)	0.63(3)
Gambella1107	1.94(88.2)	1.96(93.2)	0.99(8.8)	2.88(773.8)	3.37(2581.5)	4.08(12394)	0.66(4)
Gobiye	1.34(42.3)	1.43(44.4)	0.8(5.7)	2.03(293.2)	2.67(764.4)	3.22(3264)	0.51(2)
Jamiyu	1.87(88.8)	1.96(109.8)	0.93(7.7)	2.74(727.5)	3.3(2670.7)	4.08(17584.3)	0.67(4)
Jigurti	2.05(130.5)	2.12(156.2)	0.91(7.2)	2.89(867.3)	3.48(3726.8)	4.26(22120.1)	0.69(4)
local	1.79(72.7)	1.79(72.7)	0.87(6.7)	2.59(502.3)	3.1(1537.2)	3.83(8935)	0.68(4)
SRN39	1.82(76.2)	1.87(80.3)	0.92(7.5)	2.68(618.7)	3.15(1730.9)	3.89(10636.8)	0.68(4)
Teshale	1.71(52.5)	1.82(69.5)	0.84(6.2)	2.47(325.8)	3.11(1443.2)	3.7(6119)	0.63(3)
Tseadachimure	1.8(64.2)	1.81(66)	0.96(8.2)	2.7(536.8)	3.15(1516)	3.86(7894.5)	0.62(3)
Wediaker	2(104)	2.02(107.2)	0.93(7.7)	2.87(767.7)	3.34(2380)	4.01(10722.2)	0.69(3)
Wetetbegunchie	1.99(109.5)	2.01(111.8)	0.92(7.5)	2.85(750.7)	3.31(2309)	4.08(13497.2)	0.78(5)
MEAN	1.81	1.91	0.91	2.66	3.21	3.94	0.67
LSD (0.05)	0.33	0.32	0.12	0.42	0.33	0.44	0.13
CV (%)	10.2	8.8	7.9	8.7	5.3	5.8	10.7
Genotype (G)	***	***	***	***	***	***	***
Location (L)	***	***	NS	***	***	***	***
G*L	***	***	**	***	***	**	**

, * = Significant at 0.01 and 0.001, respectively, NS =Non-significant, SN = *Striga* count at harvest, SN_{max} = maximum *Striga* count, AUSNPC = area under *Striga* number progress curve, AUSSPC = area under *Striga* severity progress curve, FR = field resistance, data on *Striga* related traits were subjected to log (x+1) transformation, numbers in parenthesis are original mean values (non-transformed), LSD = Least significant difference, CV = Coefficient of variation

4.3.4. Effects of locations on traits performances

The two locations have shown significant differences for most of the agronomic and *Striga* related traits by affecting the way in which the genotypes performance agronomically and reaction to *Striga* (Appendix 1 and 2). It was generally observed that most of the agronomic characters showed relatively better performance in Tahitay Adiyabo district compared to Kafta Humera district attributed to relatively light *Striga* infestation in the former than the later. The mean days to flowering, maturity, grain yield, biomass, plant height, and panicle length were 78.3 and 77.5 days, 123.6 and 122.6 days, 771.4 and 329.1 kg ha^{-1}, 4840.3 and 4595.4 kg ha^{-1}, 227.8 and 153.3 cm and 27.4 and 18.4 cm, in the former and later locations, respectively (Appendix 1 and 2).

On the other hand, the mean for *Striga* number, *Striga* maximum, vigor, severity, AUSNPC, AUSSPC, and field resistance were 101.3 and 55.1 plants m^{-2}, 134.7 and 62.5 plants m^{-2}, 7.3 and 7.2, 729 and 444.4, 3124.5 and 1147.2, 17106.7 and 7170.3, and 3.9 and 3.7 for Kafta Humera and Tahitay Adiyabo sites, respectively (Appendix 1 and 2). This showed that heavy *Striga* infestation resulted in poor performance of the genotypes observed at Kafta Humera compared to Tahitay Adiyabo. These variations could be due to differences in *Striga* population existing in the soil, in which intense natural infestation was observed in the former than the latter locations. The problem of heterogeneity of natural field infestation is a common phenomenon in African soils (Haussmann *et al.*, 2001a, b, c; Ngugi, 2014).

4.3.5. Genotype by location interaction effects

Genotype by environment interaction is a well-documented fact that the phenotype is a combined contribution of both genes/genotype and the environments (Falconer and Mackey, 1996; Ceccarelli, 1996; Annicchiarico, 2002). As presented in the combined analysis of variance (Table 12) above, there was significant genotypes by environment for the entire agronomic and *Striga* related traits with exception of days to flowering. This revealed that any change in the environment of a particular genotype does not produce an equivalent change in phenotype and the effect of a particular environment is not exactly the same on the mean performances of two or more genotypes and even ranking of the genotypes varies across environments. In this regard, the aspects of interaction with the heterogeneity of natural *Striga* infestation, variation in pathogenicity of *Striga* population, microvariability of soils, and concomitant large environmental effects may have increased the genotype by environment interactions.

4.3.6. Relative reduction of yield and its attributes

The overall agronomic performances of sorghum genotypes were significantly reduced in *Striga* infested fields compared to non-infested once. The average relative reduction was determined on population-based i.e recurrent parents, donor parents, introgressed lines, and selected 10% (high yield) of the introgressed lines. The average reduction of at least by 9.6%, 18.1%, 12%, 78.6%, and 75.6% in days to flowering, plant height, days to maturity, dry biomass weight, and grain yield, respectively in the infested field as opposed to non-infested fields (Table 15). The relative yield loss of donor parents, recurrent parents, and backcross lines varied from 39.2 to 85.1%, 78.6 to 97.4%, and 71.5 to 92.9%, respectively. The donor parents showed lower yield reduction. Similarly, the converted progeny showed better resistance to *Striga* and associated lower yield reduction compared to seed parents. Sorghum yield increments after introgressing *Striga* resistance QTL from donor parents to recurrent parents was reported (Gamar and Mohamed, 2013 and Yohannes *et al*., 2015). On the contrary, the recurrent parents suffered the highest *Striga* damage with potential loss estimates of up to 97.4% yield loss. This study was found to be in line with previous reports that *Striga* infestation reduces the overall host growth through the impairment of photosynthesis and competition for carbon (Parker and Riches, 1993; Tenebe and Kamara, 2002; Oswald, 2005; Ayangowa *et al*., 2010; Satish *et al*., 2012; Traore, 2016; Akomolafe *et al*., 2018).

It was observed in this study that, plant height, biomass, and grain yield showed the most important characters that were severely damaged by the parasitic weed (Table 15). According to Mignouna *et al.*, (2013), plant height is considered as one of the most sensitive plant parts that severely bewitched by *Striga* through changes in host growth regulators (Mandumbu *et al.*, 2017; Nyakurwa *et al.*, 2018) and this led to reduction in photosynthesis and cell enlargement. The greatest damage to biomass and yield could be due to the intricate bewitching of the parasitic weed in assimilates production, leaf area, and light interception during host growth (Botanga and Timko, 2006), leaf arrangement and growth, subsequently reducing photosynthesis and dry matter allocation (Chitagu *et al.*, 2014).

Table 15. The relative reduction (%) of agronomic performance of sorghum genotypes under *Striga* infested fields compared to the non-infested fields

Population category	DTF	PLHT	DTM	BM	YLD
Recurrent parents (12)	10.7	23.9	9.4	81	86.2
Donor parents (3)	4.3	4.7	12.7	78.1	60.9
Backcrossing lines (118)	7.99	23.5	10.8	78.2	81.9
10% high yield backcross lines (12)	15.3	20.4	15.2	77.1	73.4
Mean	9.6	18.1	12	78.6	75.6

DTF = days to 50% flowering, DTM = days to 75% maturity, PLHT = plant height, BM = biomass weight, YLD= yield, number in parenthesis indicates the number of individuals or lines within the category

4.3.7. Interrelationships among characters

There were significant positive and negative correlations for a number of characters showing their direct and indirect associations, respectively (Table 16). Among the agronomic characters, grain yield showed significant positive relationships with plant height (r = 0.32), panicle length (r = 0.54) and biomass (r = 0.36). This implies that when one is improved, the other also improves in the same direction and they are useful for indirect selection for the targeted trait. Grain yield showed significant negative association with days to flowering (r = -0.54) showing the long period of vegetative growth may be exposed to *Striga* infestation and damage. This may be also an indication that genotypes with faster developmental switch to reproductive growth earlier and had a better comparative advantage of escaping the damage from *Striga* infestation and better yield. Grain yield was not correlated with days to maturity. Days to flowering showed significant positive association with day to maturity indicating some delay to flowering may be due to high vegetative growth that enforced their reproductive growth to an end and *vice versa*. Similarly, plant height and panicle length showed significant positive association with all agronomic characters and each other indicating their indirect selection based on these traits could be effective.

There was significant ($P < 0.05/0.01$) negative correlation between all the *Striga* parameters studied and most of the agronomic characters. This showed that most of the agronomic characters were significantly affected by *Striga* infestation. This exemplified that the grain yield of sorghum showed highly significant negative associations with all the measured *Striga* characters. Low grain yield was more strongly associated with high *Striga* number, severity, AUSNPC, and AUSSPC as would be expected (Kim *et al*., 1997; Omanya *et al*., 2000; Mbuvi *et al*., 2017). In the same manner, biomass showed significant negative association with *Striga* vigor and field resistance. It is noted that days to flowering and maturity showed close significant positive association with most of the *Striga* related characters. This showed that as the days to flowering and maturity delayed, the probability of emerging *Striga* seeds available in the soil also increased resulting in significant yield loss. This result is in agreement with previous reports (Talleyrand *et al*., 1991; Kureh *et al*., 1999; Ngugi, 2014).

It was also clearly shown that *Striga* infestation was significantly higher during the early stage of crop development in terms of *Striga* vigor and severity. The present finding seems to support the previous observations by a significant positive correlation being observed between *Striga* infestation and sorghum damage at the early stages of growth (Babiker, 2007). There were highly significant (P<0.01) positive associations among *Striga* related traits, indicating that *Striga* emergence increased the severity, vigor, AUSNPC, and AUSSPC (Rodenburg *et al*., 2006).

Table 16. Correlation coefficients (r) between agronomic and *Striga* related traits on 135 sorghum genotypes

Traits	DTF	PLHT	PL	DTM	BM	YLD	*Striga* count	*Striga* vigor	Severity	AUSNPC	AUSSPC
DTF	1										
PLHT	0.03NS	1									
PL	-0.09NS	0.43**	1								
DTM	0.61**	0.47**	0.35**	1							
BM	0.05NS	0.48**	0.22*	0.15NS	1						
YLD	-0.54**	0.32**	0.54**	-0.05NS	0.36**	1					
Striga count	0.42**	0.26*	0.1NS	0.56**	-0.23*	-0.3**	1				
Striga vigor	0.33**	-0.28*	-0.37**	-0.17*	-0.36**	-0.67**	0.41**	1			
Severity	0.44**	0.11NS	-0.32**	0.47**	-0.18*	-0.38**	0.95**	0.68**	1		
AUSNPC	0.26*	0.14NS	-0.27**	0.47**	-0.13NS	-0.38**	0.95**	0.52**	85**	1	
AUSSPC	0.36**	0.13NS	-0.22*	0.33**	-0.19*	-0.36**	0.87**	0.58**	0.88**	0.97**	1
FR	0.55**	-0.22*	-0.13NS	0.34**	-0.33**	-0.63**	0.5**	0.35**	0.61**	0.61**	0.54**

*, ** = significant at 0.05 and 0.01, respectively, NS = non-significant difference, DTF = days to flowering, PLHT = plant height, PL = panicle length, DTM = days to maturity, BM = biomass, YLD= yield, AUSNPC = area under *Striga* number progress curve, AUSSPC = area under *Striga* severity progress curve, FR = field resistance

4.3.8. Heritability and genetic gain from selection

Broad-sense heritability and expected genetic gains from selection for traits of agronomic and *Striga* related characters are presented in Figure 13. From among the agronomic characters, the highest broad-sense heritability values ranging from 83.5 to 88.7% were obtained for plant height, days to flowering, and days to maturity. According to Singh, (2002), selection for a trait with a high heritability (≥ 80%) can be effective because of close correspondence between genotype and phenotype due to a relatively smaller contribution of the environment to the phenotype. Grain yield and panicle length had heritability of 58.9 and 69.6% in that order, while biomass exhibited lower broad-sense heritability. Among the *Striga* resistance/tolerance indicators, sorghum field resistance (51.2%), *Striga* severity (49.7%), *Striga* vigor (42.5%) and *Striga* number/count at harvest (41.3%) exhibited medium heritability, while the remaining characters showed less heritability (< 40%). Selection could be difficult for a trait with low heritability (< 40%) due to the environment confounding genotypic effects (Keneni, 2012). In general, heritability was greater for agronomic sorghum traits than for *Striga* resistance traits agreeing with the report of Hess and Ejeta, (1992). This indicates that selection in this population is possible but it would be more efficient for agronomic characters than for *Striga* resistance traits *per se*. The aspects of interaction with different natural *Striga* infestation existing in the soil, variation in pathogenicity and environmental factors may have increased genotype by environment interactions that resulting in low heritability (Haussmann *et al.*, 2000 a, b; Omanya *et al.*, 2004).

The genetic gain from selection ranged from 7.7% to 52.9. The agronomic characters like plant height, panicle length, and grain yield had high GA (> 20%), while, days to flowering and maturity, *Striga* number at harvest, maximum *Striga* number, severity, AUSNPC, AUSSPC, and field resistance exhibited moderate (10-20%).

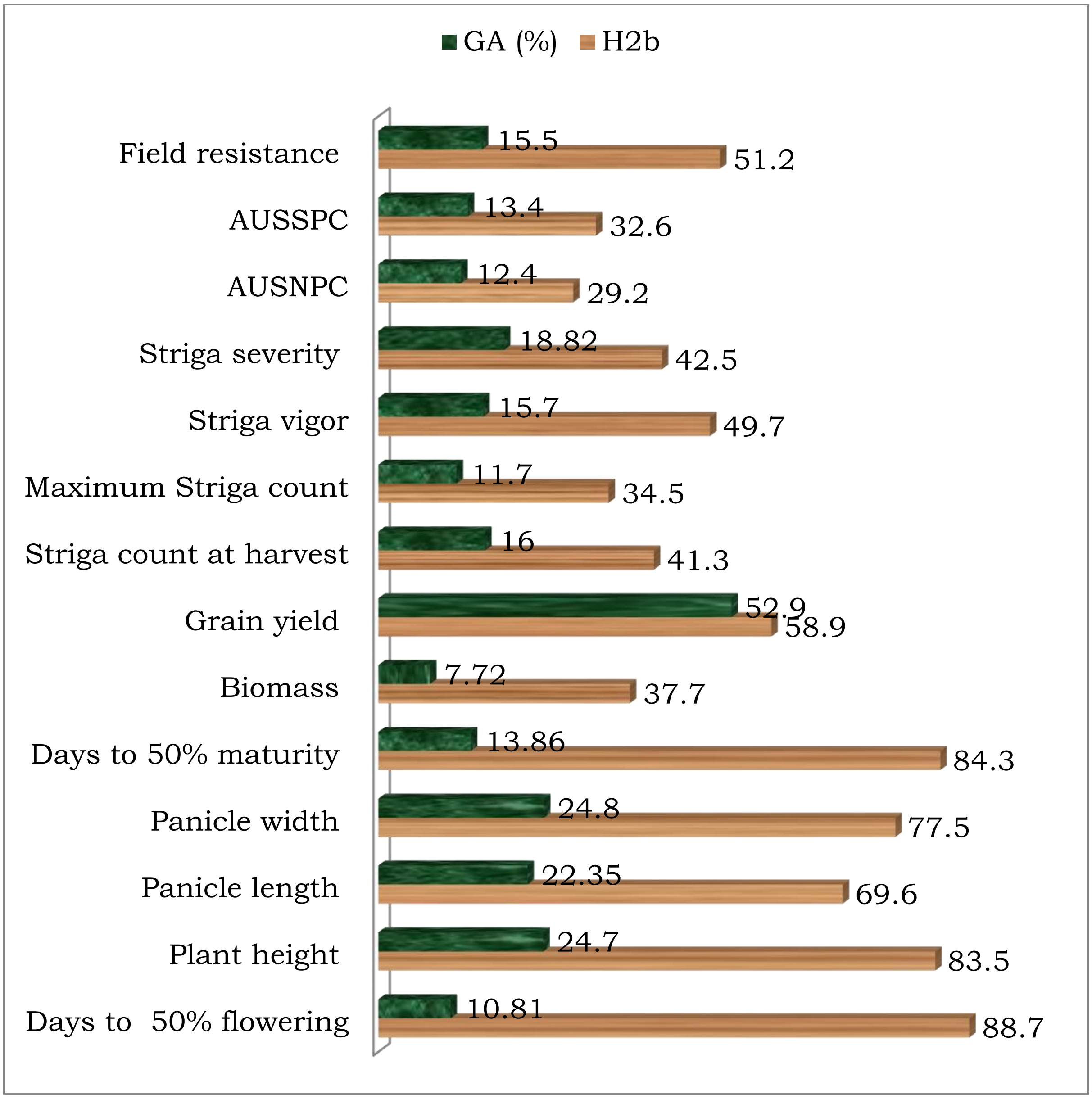


Figure 13. Estimates of broad-sense heritability (H^2b) and expected genetic advance from selection on 135 sorghum genotypes

4.3.9. The expression of QTLs on the agronomic and *Striga* related characters

Genotypes that carry different QTLs showed significant difference in agronomic performances and *Striga* related traits (Figure 14). The developed 118 progeny consisted of 5, 11, and 102 individuals with *lgs2, lgs3* and cumulative (*lgs2+lgs3*), respectively. The two QTLs (*lgs2+lgs3*) contained about 86.4% of the developed progeny. Thus, the comparison of QTL/gene expression was based on the selected top 20 high yielding lines having *lgs2 and lgs3* and with progeny developed with *lgs2, lgs3* and that of their parental lines.

The donor parents showed relatively superior performance in grain yield (862.3 kg ha^{-1}) and resistance or tolerance to *Striga* than either of the introgressed lines and recurrent parents agreeing with previous reports (Grenier *et al.*, 2007; Tesso *et al.*, 2007; Satish *et al.*, 2012). The mean *Striga* number per m^{-2} was 51 plants. When the mean performance of the top 20 progeny with both QTL (*lgs2* and *lgs3*) was compared with recurrent parents, individuals QTLs showed superior agronomic performance and better reaction to *Striga* comparable to donor parents. The mean grain yield and emerged *Striga* of the 20 progeny were 840.2 kg ha^{-1} and 63 m^{-2}, respectively. This showed that the integration of many putative QTLs could also be considered as a potential means of developing resistant lines by pulling together the cumulative effects of different genes responsible for *Striga* resistance. The progeny with *lgs2* showed better yield (591.3 kg ha^{-1}) and low *Striga* number (70 plants m^{-2}) than *lgs3* (466 kg ha^{-1}) and emerged

Striga (77 plants m^{-2}), respectively. The mean of agronomic traits and reaction to *Striga* of backcrossed progeny were significantly better compared to recurrent parents indicating the introgression of responsible genes from the donor parents and important genome recovery from the seed parents. The recurrent parents were generally susceptible to *Striga* with poor overall field performance.

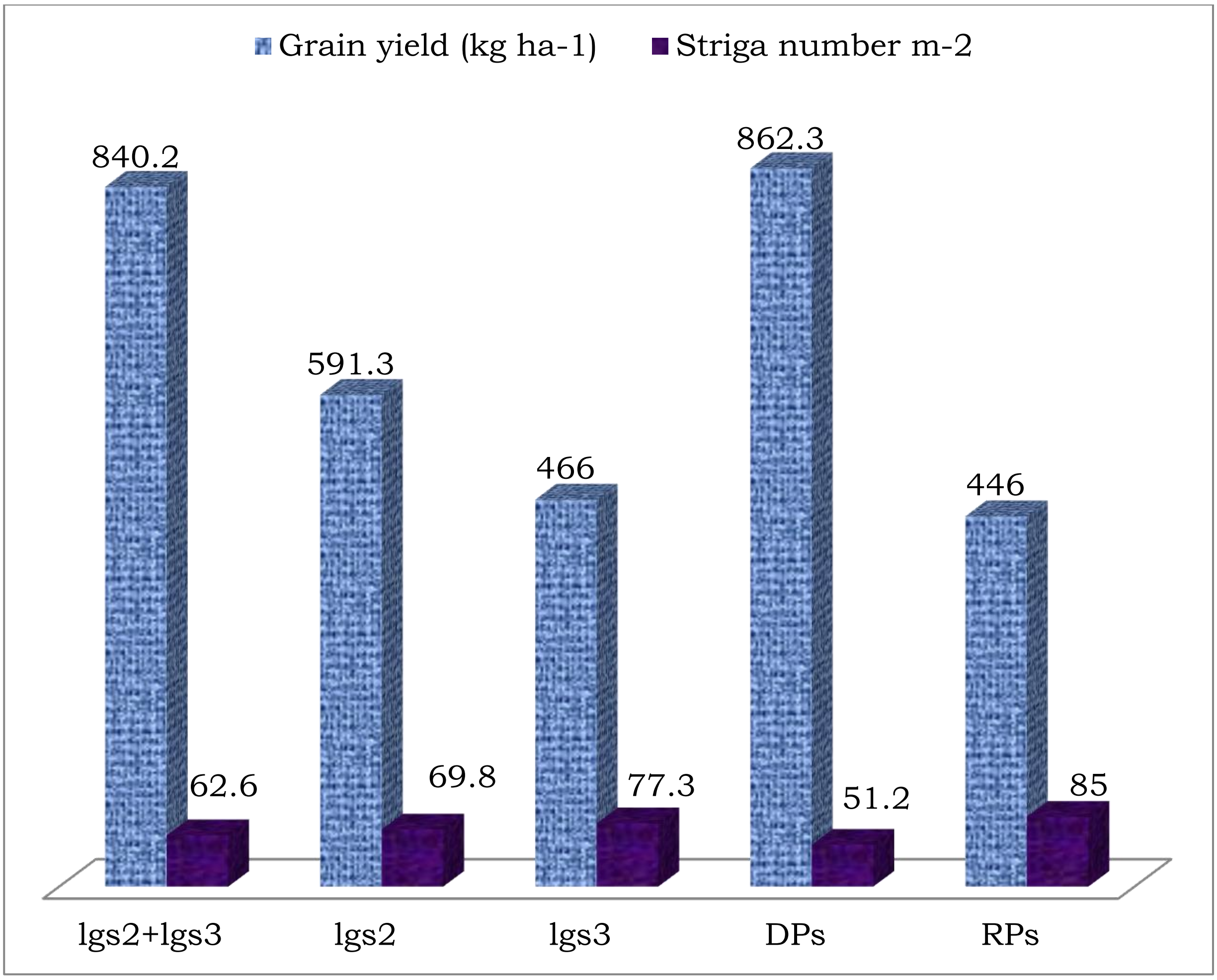


Figure 14. Comparison of mean grain yield and *Striga* number of backcrossed progeny and parental lines

4.3.10. Interrelationship between agar gel bioassay and field evaluation

The interrelationship between results obtained from the agar gel bioassay and emerged *Striga* related characters under field conditions showed highly significant positive correlation (Table 17). The MGD and GR in the agar showed significant positive relationships with all *Striga* resistance/tolerance characters under field conditions. This revealed that genotypes with high production of *Striga* germination stimulant activity also repeat the same tendency under field conditions enabling the germination of *Striga* seeds available in soil (Figure 15).

It was interestingly observed that grain yield showed highly significant negative correlations with all characters in the agar gel bioassay (MGD and GR) and under field condition (*Striga* number, vigor, severity, AUSNPC, AUSSPC, and FR). This may not be surprising due to the fact that susceptible genotypes are also high producers of *Striga* germination stimulants (Vogler *et al.*, 1996; Ejeta, 2007a). It is well known that sorghum genotypes vary in the amount and type of the germination stimulants they produce (Rich *et al.*, 2004; Gobena *et al.*, 2017; Mohemed *et al.*, 2018; Kountche *et al.*, 2019). In agreement with this study, positive correlations between the amount of germination stimulant produced and *Striga* infection levels in the field were reported in different times by several authors (Hess *et al.*, 1992; Rich *et al.*, 2004; Mohemed *et al.*, 2016; Mbuvi *et al.*, 2017) depending on the genetic material evaluated (Haussmann *et al.*, 2000a; Haussmann *et al.*, 2004; Omanya *et al.*, 2004). It was also observed that some progeny with high production of stimulant in the agar-gel assay showed some resistance under field condition probably due to other resistance mechanisms agreeing with previous studies (Bapat, 1982; Haussmann *et al.*, 2000a, b; Omanya *et al.*, 2004; Ejeta, 2007a, b; Mohamed *et al.*, 2010).

The results from the bioassay may provide the unique opportunity to minimize environmental variations and ensure that the resistance rankings that were observed could be confidently associated with the genotype reaction under field conditions. This provided a relatively easy and fast way of getting reliable results with high heritability. This may probably have the advantage of the possibilities to forecast the performance of genotypes under one condition on the basis of performance obtained under another and can assist breeders in deciding variety development and allocation of the scarce resources (Omanya *et al.*, 2004; Keneni, 2007). However, the exclusive selection for low germination distances could result in the loss of valuable materials possessing resistance mechanisms other than low-stimulant production. Therefore, it is advisable that the bioassay should always be complemented with multi-location field evaluation or available methods to handle other mechanism of resistances (Haussmann *et al.*, 2000b; Ejeta, 2007a, b; Mohamed *et al.*, 2010).

Table 17. Correlation coefficients (r) between agar-gel bioassay and *Striga* resistant characters in field conditions

Traits	Germination rate	*Stirga* number	*Striga* vigor	Severity	AUSNPC	AUSSPC	FR	Yield
Germination distance	0.92**	0.53**	0.51**	0.45**	0.55**	0.49**	0.46**	-0.54**
Germination rate	1	0.5**	0.42**	0.46**	0.46**	0.49**	0.39**	-0.48**
Stirga number		1	0.58**	0.82**	0.84**	0.59**	0.66*	-0.62**
Striga vigor			1	0.65**	0.5**	0.59**	0.77*	-0.49**
Severity				1	0.6**	0.54**	0.63**	-0.54**
AUSNPC					1	0.45**	0.5**	-0.54**
AUSSPC						1	0.5**	-0.57**
FR							1	-0.71**

** = significant at 0.01, AUSNPC = Area under *Striga* number progress curve, AUSSPC = Area under Striga severity progress curve, and FR = field resistance

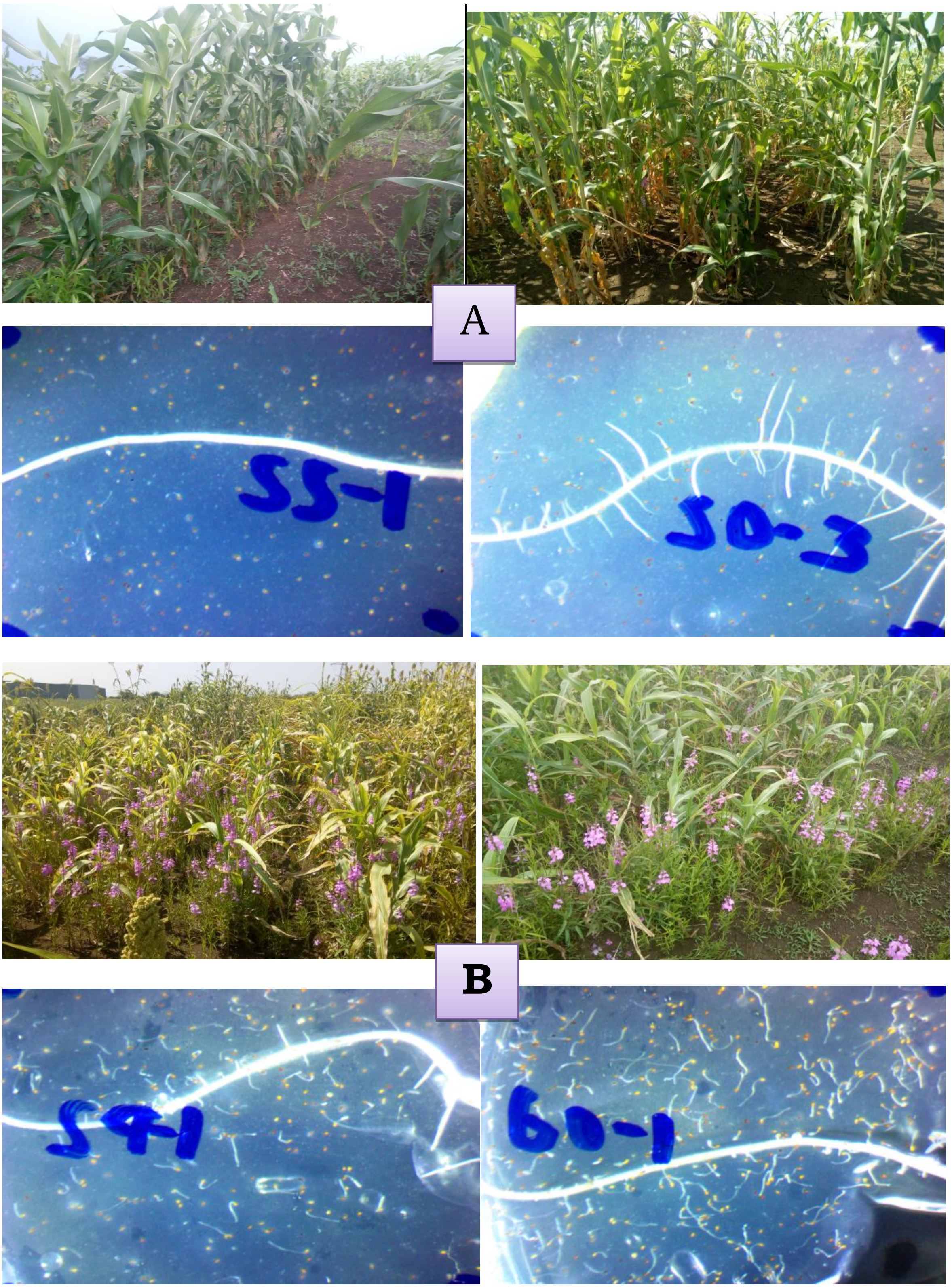


Figure 15. Sorghum backcross progeny with low germination stimulant and field resistance (A) and high germination stimulant and field susceptiblity (B)

4.3.11. Principal component analysis (PCA)

PCA is important to observe the interrelationship in the whole set of data that explains the largest proportion of the variance which could be exploited to execute a breeding program aimed at improving *Striga* resistance/ tolerance. Principal component (PC) analysis showed the first five of the thirteen PCs (PC_1-PC_5) contributed for 85.25% of the total variation (Table 18). It was reported that eigenvalues greater than one are considered significant and component loadings greater than ± 0.3 were considered to be meaningful, while an eigenvalue of less than 1 should be eliminated so that fewer components are dealt with (Chatfied & Collins,1980; Hair *et al.*, 1998).

The first and the second PC constituted 40.4% and 20.42% of the gross variation, respectively. The first PC that accounted for the highest total variation was biomass (-0.669), grain yield (+0.831), *Striga* number at harvest (+0.858), *Striga* vigor (+0.859), severity (+0.823), AUSNPC (+0.881), AUSSPC (+0.682), and field resistance (+0.542). Earlier reports also suggested that variation of genotypes in the first PC was due *Striga* related traits under *Striga*- infested conditions (Menkir, 2006; Badu-Apraku, 2007; Abate *et al.*, 2014). The second PC showed high load for plant height (+0.775), panicle length (+0.689) and panicle width (+0.657). Most of the useful characters showed greater absolute values of eigenvectors in the first and/or second PCs. This indicated that these traits had higher contributions to the total differentiation of the populations into clusters indicating selection based on these characters may be more effective. Grouping of sorghum genotypes under *Striga* infested condition based on yield and its attributes and *Striga* related traits are highly desirable in sorghum breeding for *Striga* resistance/tolerance varieties.

Table 18. Eigenvalue, variances and eigenvectors on the first five PC for 13 agronomic and *Striga* characters of the 135 sorghum genotypes

PCs	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Eigenvalue	5.25	2.65	1.54	0.94	0.71
Variance (%)	40.4	20.42	11.83	7.24	5.43
Cumulative variance (%)	40.4	60.79	72.62	79.85	85.28
Characters			**Eigenvectors**		
Days to 50% flowering	0.542	0.164	-0.70	0.216	-0.164
Plant height	-0.091	0.775	-0.039	0.153	0.486
Panicle length	-0.230	0.689	0.024	-0.512	0.074
Panicle width	0.321	0.657	-0.566	-0.112	-0.035
Days to 50% maturity	-0.226	0.602	0.058	0.627	0.014
Biomass	-0.669	0.470	0.392	-0.150	-0.053
Grain yield	0.831	0.160	0.264	0.163	-0.230
Final *Striga* count	0.858	0.367	0.171	-0.052	-0.020
Maximum *Striga* count	0.457	-0.549	-0.087	0.062	0.609
Striga vigor	0.859	-0.023	0.236	0.148	-0.050
Striga severity	0.823	0.069	0.432	-0.062	0.051
Area under *Striga* number progress curve	0.881	0.246	0.253	-0.136	0.059
Area under *Striga* severity progress curve	0.682	-0.105	-0.395	-0.320	0.013
Sorghum field resistance	0.542	0.164	-0.700	0.216	-0.164

4.3.12. Cluster analysis

Cluster analysis of the 135 genotypes distinguished three different groups of genotypes (Figure 16). This reflects that members within a single cluster are considered similar showing more close relationships than those in different cluster or significantly distant clusters (Keneni, 2012). Characterization of the clusters based on cluster mean performance showed varying response of member genotypes in each cluster to the agronomic and infestation by *Striga*. Cluster C_1 (n = 36) constituted genotypes with short days to flowering (73.7), long plant height (192.3 cm) and panicle length (23.5 cm), short days to maturity (117), higher biomass (5036.7 kg ha^{-1}) and grain yield (787.7 kg ha^{-1}) and least values of *Striga* number (58 m^{-2}), maximum *Striga* count (72 m^{-2}), poor vigor (6), severity (427), AUSNPC (1601.4), AUSSPC (11274.1), and average level of field resistance (3). This showed that this cluster (C_1) consisted of desirable genotypes that can be even promoted for further evaluation and for potential release.

On the other hand, cluster C_2 (n = 42) constituted genotypes with the long days to flowering (79.4), plant height (199.4 cm) and panicle length (24 cm), late maturity (128.2), intermediate biomass (4868.8 kg ha^{-1}) and yield (524 kg ha^{-1}), highest *Striga* number (94 m^2), highest severity (688), AUSNPC (2555.5) , AUSSPC(15571.9) and poor field resistance (4.1). The final cluster (C_3, n = 57) consisted of longest days to flowering (80.5) and plant height (175.2 cm), short panicle length (20.6 cm), lowest biomass (4066.8 kg ha^{-1}) and yield (310 kg ha^{-1}), high *Striga* number (76.7 m^{-2}) highest *Striga* vigor (8), AUSNPC (2094), AUSSPC (11274) and poor field resistance (4.1).

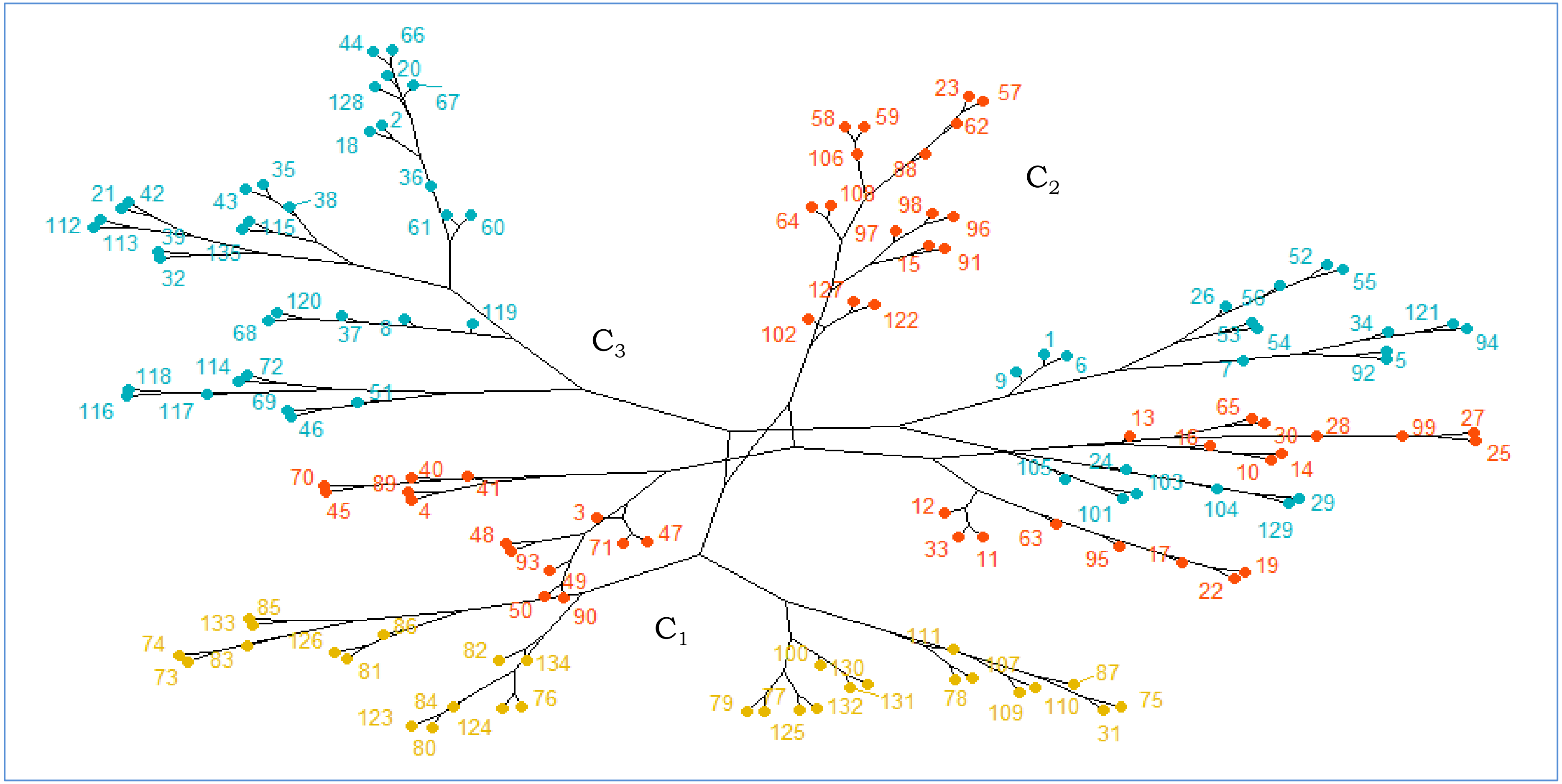


Figure 16. Dendrogram of hundred thirty five sorghum genotypes developed using mean of 18 agronomic and *Striga* related characters (refer to Table 13/14 for the names of genotypes corresponding to the alphabetical order)

4.4. Introgression of Drought Tolerant Genes into Popular Ethiopian Sorghum Genotypes

In this study, 61 converted progeny that containing three or more stay-green (*stg*) QTLs were developed and evaluated under both non-stress (full irrigation) and stress (water-limited) moisture conditions. The average crossing success for drought tolerance in this study was 44%. The breeding success, in this case, was determined from the ratio of QTLs contained progeny to those all developed progeny and expressed as percentage.

4.5. The Phenotypic and Physiological (Stay-Green) Traits Performance under Contrasting Moisture Regimes

4.5.1. Analysis of variance

The analysis of variance for both sets of experiments showed that there was significant difference ($P<0.05/0.01$) among the tested lines for all the traits studied under both non-stress and water-stress conditions (Table 19 and 20). The effect of the genotypes on the response variables was high under both water conditions, ranging from 68.6 to 87.9% under full-water and 69.4% to 91.5% under water-stressed conditions as expressed by the coefficient of determination (R^2). This means that 68.6 to 87.9% of the variability in the traits studied under full-water conditions and 69.4% to 91.5% under water-stressed conditions were accounted for by the variability in the test lines/genotypes.

Table 19. The ANOVA of agronomic and stay green traits under moisture stress and well-watered condition

Traits	Stress condition				Well-watered			
	Mean square		Mean	R^2	Mean square		Mean	R^2
	Genotype	Residual			Genotype	Residual		
DTF	26.3 **	16.3	82	79.9	35.6**	14	85.2	85.1
PLHT	1188.2**	345.1	136.4	85.2	1704.6**	613.6	157.9	88.7
DTM	15.7 *	10.5	118.2	74.5	14.3**	8.1	125.4	75.8
PL	16.7**	7.9	20.3	87.9	18.3**	4.1	21.7	91.5
PW	0.98*	0.61	5.5	70.5	0.81*	0.53	6.6	69.4
PWt	9776.1**	4309.2	220	71.8	10574.6**	7190.8	333.7	74.9
TSW	40.5**	17.8	30.1	81	47.5**	18.6	35.3	83.2
BM	8029.6**	3256.6	5110.9	79	1511.6**	5822.1	8951.8	81
Yield	951.3 *	331.4	1991.4	80.7	1423.4**	870.9	3633.1	78.3
SPADB	31.9**	13.1	48.6	84.2	32.5**	14.3	49.4	75.2
SAPDM	43.6**	22.6	29	82.5	49.4**	20.9	36.6	81.6
PGLM	311.8**	75.8	38.8	81.5	191.6**	114.2	48.7	69.4
GLAB	136807**	77343	1520.2	84.9	94537**	50396	1821.6	82.5
GLAM	41681**	21650	1085.7	81.4	53676*	34582	1543.3	79
PGLAM	264.9**	156.5	73.6	68.6	151.1**	68.1	85.4	79.7
LS	0.93**	0.4	3.3	75.6	0.75**	0.38	2.95	69.7
RLS	2.44**	1.3	3.3	75	2.1**	1.1	2.6	74.9

*, ** = significant at 0.05 and 0.01, respectively, DTF = days to flowering, PLHT = plant height, PL = panicle length, PW = panicle length, DTM = days to maturity, TSW = thousand seeds weight, PWt = panicle weight, BM = biomass, SPADB = chlorophyll content at booting, SPADM = chlorophyll content at maturity, PGLM = percent green leaf at maturity, GLAB = green leaf at booting (cm^2 plant^{-1}), GLAM = green leaf area at maturity (cm^2 plant^{-1}), RLS = rate of leaf senescence (cm^2 day^{-1}), PGLAM = percent of green leaf area preserved at maturity and LS = leaf senescence, RLS = rate of leaf senescence.

4.5.2. Phenotypic trait performances

Differences among the genotypes were significant (P<0.05) for all traits studied under both moisture regimes (Table 20). The comparison of the converted progeny with their parents showed superior performances agronomic attributes mainly under water-limited condition. The overall mean of days to flowering (DTF) was 85.2 and 82 days under full and water-limited conditions, respectively. It is assumed that the difference in DTF was attributed to the genetic background as each set was subjected to uniform irrigation until the induction of stress after flowering. Plant height of the genotypes under full-water and water-stressed conditions were 157.9 and 136.4 cm, respectively, showing that the exposure of stress from anthesis significantly reduced plant height.

Plant height of the converted progeny and recurrent parents ranged from 100.3 to 192.6 cm and 104.1 to 163.8 cm under water-limited, while under well-watered ranged from 115.7 to 211 cm and 128.3 to 183.8 cm, respectively. This showed that the converted progeny performed well in both moisture conditions revealing the amalgamation of the targeted genes from their parents. The shortest plant height was recorded from B35 in both moisture with values of 93.5 and 107.4 cm, respectively as it was expected (Kassahun *et al.*, 2010).

Days to maturity (DTM) were 125.4 and 118.7 days under full and water-limited conditions respectively. The mean DTM of backcrossed progeny and recurrent parents varied from 120.6 to 131.7 and 122 to 128 for full-irrigation and 114 to 126.7 and 114.8 to 119.9 for water-limited conditions and that of B35 was 118.8 and 116.9, respectively. Generally, about 23% and 42.6% of converted progeny showed some delay for DTM under moisture stress and well-watered, respectively. This might be due to high vegetative growth and deferring of relatively longer part of their reproductive growth to an end-of-season, which is the behavior of the donor parent 'stay green'. The maintenance of grain filling in the last stage of plant maturity has been considered as key to the success of stay green genotypes (Luche *et al.*, 2015).

When looking at the yield components such as panicle length, panicle width, and panicle weight ranged from 14.6 to 27.1 cm, 4 to 7 cm, and 116.7 to 465.4 g in stressed and 17 to 26.6 cm, 5 to 8.24 cm, and 221.2 to 500.3 g in non-stress, respectively. In the same manner, the values for recurrent parent ranged from 20.2 to 23.5 cm, 5.6 to 6.3 cm, and 147.3 to 367.2 g and from 19 to 29 cm, 5.7 to 8.5 cm, and 293.4 to 525.3 g in that order. Under full-irrigation, the highest panicle length (29 cm), width (8.5 cm), and weight (525.3 g) was obtained from the recurrent parent 'Dekeba' followed by 11.5%, 18%, and 26.2% of the developed backcrossed lines. Similarly, about 6.6%, 9.8%, and 13.1% of the backcrossed lines showed good performance under moisture stress (Table 20).

The mean biomass (BM) of the genotypes ranged from 1634 to 11010 kg ha^{-1} and 4015 to 16315 kg ha^{-1} under water-limited and well watered, respectively. The highest biomass was obtained from the converted progeny under both moisture regimes indicating the potential of the introgressed progeny and performing well in such environments, as they contain stay-green trait. It is clear that biomass accumulation is a function of water use efficiency by plants (Balota *et al.*, 2008). On the other hand, the main effect of moisture deficit is the reduction of biomass accumulation (Tsuji *et al.*, 2003; Castro-Nava *et al.*, 2012) through drought induced inhibition of leaf and stem elongation, which differs among species (Pelleschi *et al.*, 1997), and a reduction of relative growth and net CO_2 assimilation rates (Younis *et al.*, 2000). Therefore, the yield reduction under water deficit is at least partly due to variations in total biomass accumulation (Craufurd and Peacock, 1993) among the genotypes. It was observed that about 27.9% and 19.7% of the developed converted progeny showed high biomass ranging from 6128.3 to 11010 and 12000 to 16320 kg ha^{-1} under water-limited and fully irrigated, respectively. It is imperative to consider that backcrossed lines with high biomass could be recommended for livestock feed as dual-purpose, but also affected by drought episodes.

Similarly, thousand seeds weight (TSW) of the genotypes ranged from 20.8 to 41.7 g, and 23.8 to 45.6 g under moisture stress and full irrigation. The results showed that nearly 36.1% and 37.7% of the converted progeny showed superior seed weight ranging from 33.8 to 41.7 g and 37.2 to 45.6 g, under the former and later conditions, respectively.

The mean grain yield of the genotypes under full-irrigation (2069.2 to 5704.2 kg ha^{-1}) and water-stressed (923 to 4585 kg ha^{-1}) conditions were 3633 and 1991 kg ha^{-1}, respectively. The mean grain yield of converted progeny ranged from 2069.2 to 5453 kg ha^{-1} and 923 to 4585 kg ha^{-1} and that of recurrent parents ranged from 3049 to 5704 kg ha^{-1} and 2160 to 2796 kg ha^{-1} under the former and later moisture conditions. The result showed that the highest yield was obtained from the recurrent parent Dekeba (5704 kg ha^{-1}) followed by the converted progeny BC_2F_3_ETSC_16142 (5453 kg ha^{-1}) under full-irrigation. On the other hand, in water-limited condition, the highest yield was obtained from BC_2F_3_ETSC_16258 (4585 kg ha^{-1}) followed by five backcrossed progeny namely BC_2F_3_ETSC_16216 (3538 kg ha^{-1}), BC_2F_3_ETSC_16257 (3107 kg ha^{-1}), BC_2F_3_ETSC_16213 (2924 kg ha^{-1}), BC_2F_3_ETSC_16248 (2886 kg ha^{-1}), and BC_2F_3_ETSC_16141 (2831 kg ha^{-1}).

It may imply that converted progeny may have better structural and functional fitness to apt well on the water use efficiency, water extraction, growth, and good seed-sink interaction during grain filling period under water deficit environments than the seed parents. This confirmed that the developed progeny had the target genes responsible for the stay-green trait from the donor parent and yield potential from their respective recurrent parents. Although there was no single genotype that exhibiting consistent superiority for grain yield and other desirable characters under both moisture regimes, six progeny were among the best performers compared to parental lines for many attributes. These backcrossed lines displayed the best character in grain yield and biomass under the two-contrasting moisture regimes and hence, it is, therefore, needs further evaluation for potential release.

On the other hand, about 67.2 % of progeny show significant yield reduction attributed to terminal drought depending on the genetic background with yield ranging from 923 to 1987 kg ha^{-1}. The yield reduction of the developed progeny could be attributed to the expression of QTLs that might be affected by the genetic background (epistasis interaction) and incomplete conversion of the generated progeny (BC_2F_3) i.e. 87.5%. Previous reports showed that the diminishing in yield under water stress usually resulted from reduction in starch accumulation during grain development (Barnabás *et al.*, 2008) and grain number (van Oosterom and Hammer, 2008). It is also clear that grain yield and other traits reduction depends on the phenological stage on which the stress occurs and this varies depending on the resistance level of the genotypes (Kassahun *et al.*, 2010; Castro-Nava *et al.*, 2012).

Table 20. Mean traits performance of 70 sorghum genotypes tested under full-irrigation and water-stressed conditions at Mereblekhe district in 2018/19

Genotypes	Full irrigation									Water-limited								
	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD
B35	71.8	107.4	118.7	24.4	5.1	206.6	5106	34.6	2069	78.03	93.5	116.9	24	4.4	205.2	3427	31.5	1318
BC$_2$F$_3$_ETSC_16139	83.7	139.5	127.0	24.6	7.3	396.6	12417	38.4	4560	88.21	112.4	120.3	27.1	5.7	235.0	5304	32.4	1722
BC$_2$F$_3$_ETSC_16140	86.6	124.8	122.3	26.5	7.0	341.2	7260	29.2	3478	85.17	102.7	114.1	21.7	6.2	201.8	2839	28.0	1493
BC$_2$F$_3$_ETSC_16141	85.7	129.5	131.7	20.4	6.2	313.6	12909	33.6	3725	85.93	116.7	119.2	22.1	5.9	465.4	5451	31.6	2831
BC$_2$F$_3$_ETSC_16142	85.3	149.2	128.3	19.4	8.2	500.3	9810	40.4	5453	84.49	124.8	116.2	17.2	6.4	262.4	5057	27.9	2309
BC$_2$F$_3$_ETSC_16143	86.4	173.1	127.3	17.0	5.9	232.0	11998	38.6	2671	83.95	150.4	116.5	17.3	4.7	235.9	4970	26.5	1921
BC$_2$F$_3$_ETSC_16144	80.8	164.2	126.8	20.4	6.7	348.3	10668	40.9	3935	82.54	127.3	117.1	18.6	6.0	220.6	7670	32.4	2469
BC$_2$F$_3$_ETSC_16145	86.0	145.6	126.4	17.9	5.7	247.8	10143	37.6	2920	83.79	129.6	117.9	15.9	4.9	147.4	8930	36.4	1812
BC$_2$F$_3$_ETSC_16146	89.0	161.0	126.4	19.9	6.3	298.0	11397	36.6	3381	85.48	160.5	120.8	20.3	5.6	206.9	5798	29.2	1558
BC$_2$F$_3$_ETSC_16147	83.6	147.8	126.9	18.4	6.5	321.5	8195	36.2	3612	83.44	134.6	117.6	16.6	5.2	199.9	5134	38.3	1631
BC$_2$F$_3$_ETSC_16148	83.7	152.1	125.8	18.8	6.5	341.5	7687	39.7	3474	83.14	135.2	116.6	16.6	5.4	208.3	5732	36.2	2015
BC$_2$F$_3$_ETSC_16149	83.2	156.2	121.6	18.9	6.1	264.3	8082	33.9	3138	81.70	141.6	114.2	20.3	5.4	192.3	3206	25.4	2064
BC$_2$F$_3$_ETSC_16150	80.5	163.3	125.5	19.4	6.6	274.4	11924	39.6	3113	81.29	137.4	118.9	18.3	4.7	135.7	4000	23.4	923
BC$_2$F$_3$_ETSC_16210	82.6	127.7	125.8	24.0	6.4	286.4	8373	33.9	3333	82.54	100.3	120.0	18.2	4.8	183.0	4117	20.8	1427
BC$_2$F$_3$_ETSC_16211	82.8	124.8	126.6	20.3	6.0	245.4	6020	36.4	2759	77.72	111.3	118.0	20.1	5.2	181.2	4237	28.6	1866
BC$_2$F$_3$_ETSC_16212	86.1	134.7	124.2	25.9	7.2	383.4	12983	28.9	4197	78.75	121.2	114.7	22.7	5.2	219.2	4446	27.2	1942
BC$_2$F$_3$_ETSC_16213	86.3	141.9	128.0	21.9	6.9	351.7	11291	33.1	3803	85.13	114.0	126.0	21.1	6.0	307.2	7167	30.5	2924
BC$_2$F$_3$_ETSC_16214	86.6	167.1	124.7	24.8	7.1	443.0	14328	45.6	4878	81.64	115.0	118.4	20.7	5.2	177.6	6833	33.3	2149
BC$_2$F$_3$_ETSC_16215	85.8	131.8	124.1	19.1	5.7	221.2	8110	29.4	2270	84.43	114.0	116.0	19.4	5.0	152.6	3676	23.6	1333
BC$_2$F$_3$_ETSC_16216	86.6	152.9	127.6	24.2	6.6	443.7	9842	42.2	4727	84.96	127.1	119.7	20.9	5.7	325.1	9725	36.4	3538
BC$_2$F$_3$_ETSC_16217	85.5	161.1	120.6	22.7	5.9	302.5	8269	38.0	3971	79.86	127.2	116.0	21	6.0	219.3	4486	27.3	1671
BC$_2$F$_3$_ETSC_16218	84.3	136.5	122.7	20.1	6.0	300.7	8660	37.2	3362	84.69	124.4	115.8	17.9	4.7	153.5	4757	28.4	1082
BC$_2$F$_3$_ETSC_16219	80.1	147.4	126.4	22.8	6.9	375.0	12989	31.9	4268	80.51	130.3	115.7	20.9	4.9	190.9	4918	32.6	1751
BC$_2$F$_3$_ETSC_16220	81.2	141.1	121.3	26.6	7.2	362.3	6259	35.5	3973	79.54	129.6	115.7	26.5	5.6	222.4	5482	29.1	1854
BC$_2$F$_3$_ETSC_16221	83.5	140.0	123.1	23.4	6.4	300.0	6900	34.8	3317	82.44	135.3	117.4	25	6.3	249.0	4953	25.4	2465

Genotypes	Full irrigation									Water-limited								
	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD
BC$_2$F$_3$_ETSC_16222	84.6	129.0	124.7	24.3	6.0	310.2	7043	32.7	3317	82.06	105.2	117.4	21.9	4.7	178.7	3697	34.2	1490
BC$_2$F$_3$_ETSC_16223	87.9	165.0	128.9	23.1	6.7	411.9	16315	35.9	4282	86.75	146.5	117.6	22.5	5.4	192.6	4625	29.2	1837
BC$_2$F$_3$_ETSC_16224	89.6	174.6	128.2	20.8	6.7	365.5	8621	37.3	3663	86.82	145.3	119.0	17.7	4.4	151.2	2650	27.6	1096
BC$_2$F$_3$_ETSC_16225	88.0	195.7	126.0	19.0	7.3	306.6	12613	38.5	3363	87.99	158.6	118.3	22	5.8	190.2	6365	29.6	1745
BC$_2$F$_3$_ETSC_16226	86.8	188.4	126.1	20.7	7.6	383.8	8509	29.4	4172	85.06	155.9	122.9	17.1	6.4	231.6	8209	33.8	2179
BC$_2$F$_3$_ETSC_16227	88.0	211.0	125.7	20.4	6.2	266.2	7270	29.4	2675	85.14	175.5	120.2	20.1	5.6	208.1	4881	30.0	1987
BC$_2$F$_3$_ETSC_16228	91.0	177.5	123.4	19.8	6.7	389.9	10495	31.3	4248	86.39	131.2	125.1	15.3	4.9	170.8	3465	31.6	1885
BC$_2$F$_3$_ETSC_16229	88.0	173.9	127.1	21.2	7.2	314.8	7270	32.3	3178	87.79	172.9	123.8	17.7	5.7	316.9	6054	26.5	2417
BC$_2$F$_3$_ETSC_16230	91.7	176.6	129.3	19.4	7.1	289.9	7108	23.8	2764	84.28	134.6	126.2	19.5	5.8	158.9	6277	25.5	1799
BC$_2$F$_3$_ETSC_16231	84.5	192.7	125.3	22.9	6.6	277.4	6908	31.5	2704	84.81	153.7	119.0	20.8	5.8	190.7	6128	28.4	1985
BC$_2$F$_3$_ETSC_16232	87.3	170.9	123.6	19.5	6.9	349.8	5965	37.8	2676	83.84	173.5	118.1	21.2	6.0	228.7	3614	29.1	1749
BC$_2$F$_3$_ETSC_16233	90.2	189.4	125.8	19.7	6.7	308.8	12119	33.8	3125	87.58	192.6	115.7	18.4	5.5	203.1	9179	34.0	1211
BC$_2$F$_3$_ETSC_16234	85.8	195.0	126.0	17.5	7.1	301.6	5982	33.1	3410	83.58	142.2	118.6	18.1	5.9	214.0	1634	30.0	1625
BC$_2$F$_3$_ETSC_16235	85.8	203.3	123.7	23.7	7.1	419.2	11171	41.7	4671	83.05	174.0	116.0	19.1	5.7	209.5	5620	34.5	1314
BC$_2$F$_3$_ETSC_16236	85.6	183.1	125.4	20.3	5.9	340.3	9372	38.1	3351	83.12	143.5	115.1	17.3	4.9	194.3	3112	31.5	1368
BC$_2$F$_3$_ETSC_16237	95.0	200.4	129.2	23.1	6.8	358.1	9786	37.2	3516	83.12	147.8	118.2	19.5	5.1	187.4	4442	30.7	1343
BC$_2$F$_3$_ETSC_16238	90.7	198.1	125.7	20.0	7.0	293.4	9671	36.5	3259	76.35	142.4	117.5	16.1	4.0	116.7	3415	33.1	1128
BC$_2$F$_3$_ETSC_16239	88.8	203.6	127.8	20.8	6.1	295.1	10152	36.1	2840	76.74	186.0	121.0	21.8	6.7	239.1	5321	28.5	2090
BC$_2$F$_3$_ETSC_16240	86.9	186.0	128.0	21.9	6.4	330.6	10931	39.2	3611	78.37	178.8	117.8	23.4	5.7	233.0	8343	41.7	1951
BC$_2$F$_3$_ETSC_16241	83.0	175.5	129.2	24.6	7.1	327.2	10983	34.5	3473	78.72	144.1	118.5	19.2	5.8	180.8	3708	27.1	1930
BC$_2$F$_3$_ETSC_16242	82.3	182.2	126.7	24.9	6.9	385.4	6538	43.5	4265	78.24	153.6	116.2	20.1	4.7	162.3	2774	33.6	1564
BC$_2$F$_3$_ETSC_16243	87.3	172.1	127.4	20.9	6.0	251.7	5858	38.4	2690	79.12	146.0	117.0	18.9	4.8	165.6	1676	32.9	1869
BC$_2$F$_3$_ETSC_16244	85.5	181.5	124.4	21.1	6.5	284.6	7490	40.7	3120	82.19	159.8	118.1	22.4	4.9	157.9	3532	29.8	1265
BC$_2$F$_3$_ETSC_16245	88.5	148.7	122.5	22.7	6.2	341.9	8033	31.7	3637	82.13	128.0	117.3	21	5.2	198.2	5109	26.1	1655
BC$_2$F$_3$_ETSC_16246	79.7	166.7	121.5	24.0	6.5	344.5	8501	36.8	3721	78.54	139.0	114.8	23	6.0	243.2	4114	32.3	1533
BC$_2$F$_3$_ETSC_16247	82.8	125.3	123.2	20.3	6.1	233.9	4015	35.6	2559	78.49	122.8	114.8	23.3	6.2	302.0	3732	28.7	2374
BC$_2$F$_3$_ETSC_16248	78.1	115.9	121.6	18.8	6.1	271.1	6660	31.6	3193	80.95	132.4	120.0	22.1	6.5	313.4	3554	31.6	2886
BC$_2$F$_3$_ETSC_16249	83.8	154.4	127.9	19.3	6.2	334.2	8663	32.5	3638	79.42	110.4	120.1	14.6	4.7	146.0	4931	23.5	1386

Genotypes	Full irrigation									Water-limited								
	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD
BC$_2$F$_3$_ETSC_16250	79.7	143.1	122.1	18.9	6.6	290.2	6401	33.5	3381	78.50	113.1	116.3	17.8	5.1	164.4	5710	24.5	1474
BC$_2$F$_3$_ETSC_16251	82.1	161.2	122.2	24.4	6.8	419.5	11672	31.1	4640	76.52	159.2	117.3	19	5.6	242.6	6423	31.2	2278
BC$_2$F$_3$_ETSC_16252	79.4	126.6	125.4	21.2	6.2	274.1	6814	33.3	3040	74.10	121.2	117.6	20.6	5.8	215.7	6298	27.2	2368
BC$_2$F$_3$_ETSC_16253	81.2	137.4	121.9	23.9	6.5	309.7	5150	30.9	3474	75.19	118.6	115.4	18.5	5.0	246.2	4274	28.4	2549
BC$_2$F$_3$_ETSC_16254	79.8	135.1	123.3	20.9	5.9	238.5	7181	28.2	2511	79.42	123.8	118.4	19.5	5.0	174.7	6368	27.3	1492
BC$_2$F$_3$_ETSC_16255	84.0	115.7	128.2	21.4	6.9	352.6	6225	36.0	3611	77.60	109.8	119.3	19.8	5.2	183.4	3708	27.4	1510
BC$_2$F$_3$_ETSC_16256	82.2	140.0	124.4	22.0	6.6	326.4	9979	35.5	3642	83.80	114.1	120.3	20.5	5.5	198.4	6276	29.9	2107
BC$_2$F$_3$_ETSC_16257	84.2	155.3	124.0	24.2	6.8	409.1	9044	35.3	4506	79.57	144.9	118.3	24.8	6.2	305.1	7812	26.9	3107
BC$_2$F$_3$_ETSC_16258	87.4	163.0	129.2	23.9	7.1	375.9	12361	35.6	4649	81.98	149.7	122.0	23.8	7.0	392.7	11010	33.3	4585
Dekeba	86.4	139.6	126.2	29.0	8.5	525.3	10369	36.0	5704	81.82	104.1	116.8	23.5	6.3	296.7	4819	29.8	2796
Gambella1107	91.7	155.3	124.4	18.7	6.2	360.4	11366	40.8	4088	84.13	148.2	119.6	20.9	6.4	367.2	6063	33.7	2751
Macia	87.9	128.3	126.3	26.2	6.9	408.7	8063	33.3	4679	82.33	115.5	119.6	20.2	5.7	311.0	5084	31.4	2679
Meko	86.5	146.6	125.4	21.1	6.9	411.6	8036	39.9	4641	81.39	142.0	117.6	20.9	6.3	290.1	5364	31.5	2759
Melkam	82.5	136.5	122.5	27.7	6.3	358.2	6318	34.4	4207	82.68	123.7	114.8	23.2	5.6	147.8	3663	30.4	2160
Teshale	89.4	180.7	126.1	18.9	6.3	293.5	5684	30.9	3049	85.68	160.5	119.9	21.9	5.9	258.4	4369	27.8	2651
Tseadachimure	85.7	183.8	128.2	23.2	7.1	382.1	7045	34.4	4135	80.37	163.8	118.4	21.7	5.9	236.4	3977	28.0	2698
Wediaker	86.8	146.4	126.4	20.9	6.7	436.7	9254	36.9	5151	77.58	126.1	119.9	21	6.1	186.0	4065	39.1	2700
Mean	85.17	157.9	125.4	21.8	6.6	333.7	8951	35.3	3633	82.04	136.4	118.2	20.3	5.5	219.9	5111	30.1	1991
LSD (0.05)	6.4	41.19	5.13	3.54	1.3	150.4	4360	7	1670	7.16	33.56	5.9	4.89	1.4	120.6	3300	7.1	1040
CV (%)	4.4	15.69	2.3	9.3	11	25.41	26.95	12.2	25.69	4.99	13.61	2.75	13.8	14	29.84	35	14	28.9

DTF = days to 50% flowering, PLHT = plant height (cm), DTM = days to 75% maturity, PL = panicle length (cm), PW = panicle width (cm), PWt = panicle weight of five heads (g), BM = biomass (kg ha^{-1}), TSW = thousand seeds weight (g), YLD = grain yield (kg ha^{-1}), LSD = Least significant difference, CV = Coefficient of variation

4.5.3. Relative trait mean performance reduction due to water-stress

Drought stress affects all phenological growth stages, reduces the normal growth and development periods, dry matter production and final yield. Relative reduction due to moisture stress for different population categories is given in Table 21. The relative reduction was determined on population bases i.e the parents (recurrent and donor) and developed introgressed lines (whole and 10% selected based on high yield). All the traits considered in this study were affected by terminal water-stress, although at different magnitude. In general, the mean relative traits performance reduction ranged from 5.7% to 38.9%. The mean relative reduction of plant height, days to maturity, panicle length, panicle width, panicle weight, biomass, thousand seed weight, and grain yield were 13.6%, 5.7%, 6.9%, 16.7%, 34.1%, 43.3%, 14.7%, and 38.9%, respectively. The relative reduction of grain yield was ranging from 34.8% to 43.2% with a mean of 38.9%. The highest relative reductions in grain yield were recorded for the overall developed progeny (43.2%) followed by the recurrent parent (40%) depending on the genetic background and QTLs/genes expression. The relative reduction for the 10% selected converted progeny was intermediate (34.8%), indicating the presence of some promising lines that better tolerate the effects of water-stress as compared to the recipient parents.

In general, panicle weight, dry biomass weight and grain yield was amidst the severely affected by the terminal drought or stress.

Table 21. Mean traits performance relative reduction due to terminal stress of 70 sorghum genotypes tested under full-irrigation and water-stressed conditions at Mereblekhe district in 2018/19

Genotypes category	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD
				Relative reductions (%)				
B35 (donor parent)	12.9	1.5	1.6	13.7	0.7	33.3	9.0	38.1
Backcrossed lines	13.9	5.8	6.5	16.7	34.4	42.9	15.3	43.2
10% high yield backcrossed lines	12.3	4.8	3.6	17.8	23.2	35.1	9.1	34.8
Recurrent parents	10.9	5.9	6.5	13.0	34.1	43.4	12.0	40.0
Mean	13.6	5.7	6.9	16.7	34.1	43.3	14.7	38.9

PLHT = plant height (cm), DTM = days to 75% maturity, PL = panicle length, PW = panicle width, PWt = panicle weight, BM = biomass, TSW = thousand seeds weight, YLD = grain yield

4.5.4. The morpho-physiological trait performance

Differences among genotypes were significant ($P<0.05$) for all stay-green characters under both moisture regimes (Table 19). The comparison of converted progeny with their parents revealed that the existence of superior performance for stay-green characters (Table 22). In order to determine if the introgression of the B35 stay-green markers into the recurrent parents background also affected chlorophyll content, two SPAD measures were made at booting (SPADB) and maturity (SPADM). In this context, the highest SPADB values were observed for B35 in both irrigation conditions indicating high chlorophyll concentration index (Kassahun *et al.*, 2010; Reddy *et al.*, 2014). The overall mean of SPADB were comparable in both moisture regimes (49.4 and 48.6) because each experiment was received similar irrigation until the induction of stress after anthesis. At booting or flowering stage, almost all genotypes showed a good leaf health and chlorophyll concentration index (40-60) showing a good indicator of the transfer of energy to the reaction center of the photosystems (Mullan and Mullan, 2012).

The overall mean of SPADM was 36.6 and 29 under full and water-limited conditions, respectively. The highest mean SPADM values were registered from progeny BC_2F_3_ETSC_16258 (43.5), BC_2F_3_ETSC_16225 (39), BC_2F_3_ETSC_16253 (36.9) and BC_2F_3_ETSC_16139 (35.6) under water-limited condition. This showed that the introgression of responsible genes enhanced the relative amount of total chlorophyll present in plant leaves enabling structural and functional fitness under water-limited condition. In addition, the recurrent 'Wediaker' contains high chlorophyll content at maturity (40) and this might need further confirmation in order to utilize in the breeding process. B35 showed significantly better records of SPADM than the recurrent parents did as it was expected. This corroborates with previous reports (Xu *et al.*, 2000b; Kassahun *et al.*, 2010; Reddy *et al.*, 2014), B35 showed much higher chlorophyll content than the recurrent parents at physiological maturity.

The mean percent of green leaves at maturity (PGLM) under full and water-limited conditions was 48.7% and 38.8% in that order. The highest mean PGLM was observed for recurrent parent 'Tseadachimure' (71.9%) under full-water irrigation followed by four backcrossed progeny BC_2F_3_ETSC_16255 (65.51%), BC_2F_3_ETSC_16244 (62.5%), BC_2F_3_ETSC_16213 (61.61%), BC_2F_3_ETSC_16247 (60.8%). On the other hand, the highest mean PGLM under water-stressed was observed for BC_2F_3_ETSC_16139 (64.01%) followed by 11 converted progeny with values that ranged from 50 to 60.6%. This indicated that the presence of more green leaves (stay green) at maturity stage may contribute to higher photosynthesis and better availability of food reserves for grain filling (Kassahun *et al.*, 2010; Vadez *et al.*, 2011; Jordan *et al.*, 2012).

The mean green leaf area at booting (GLAB) was 1821.6 and 1520.2 in cm^2 $plant^{-1}$ under full and water-limited conditions, respectively. The highest GLAB were measured from BC_2F_3_ETSC_16223 (2366.3 cm^2 $plant^{-1}$) followed by seven converted progeny with values ranging from 2043.8 to 2270.3 cm^2

plant^{-1} under full-irrigation. Under water-limited, the highest GLAB was measured from line BC$_2$F$_3$_ETSC_16229 (2070.1 cm^2 plant^{-1}) followed by seven progeny with values ranging from 1814.8 to 2043 cm^2 plant^{-1}.

Equally, the green leaf area at maturity (GLAM) was high for the converted progeny under both moisture regimes. The highest GLAM was measured for BC$_2$F$_3$_ETSC_16224 (1878.3 cm^2 plant^{-1}) followed by 18 converted progeny (1644.1-1820.4 cm^2 plant^{-1}) under full-irrigation and for BC$_2$F$_3$_ETSC_16223 (1407.2 cm^2 plant^{-1}) followed by four progeny (1283.2-1325.3 cm^2 plant^{-1}) under water-limited condition.

Similarly, the percent of green leaf area preserved at maturity (PGLAM) ranged from 67.97% to 98.2% and 51% to 96.3% for converted progeny, 75.99 to 90.2% and 67.4 to 78.98% for recurrent parents, and that of B35 was 81.6 and 80.8% under full and water-limited, respectively. The highest PGLAM was obtained consistently from the 24 and 15 converted progeny under the former and the later moisture conditions indicating their potential in maintaining high green leaf area in the entire growth stage. This study was found in agreement with previous reports that green leaf area at physiological maturity has proved to be an excellent indicator of stay green, and has successfully been used to select drought resistant sorghums (Rosenow *et al.*, 1983; Henzell *et al.*, 1992; Borrell *et al.*, 2014). Likewise, Kassahun *et al.*, (2010) and Pask and Pietragalla, (2012), reported that maintaining prolonged green area at maturity stage of the sorghum genotypes contributed for higher photosynthesis enhanced grain yield.

The score of leaf senescence (LS) and rate of leaf senescence (RLS) were more pronounced for water-limited compared to well-watered condition. This is to mean that the induction of drought had significantly hastened both characters. Under water-limited, the LS of the genotypes ranged from lowest (stay-green) 1.85 to the highest 4.6 (leaf drying). Among the developed progeny, 34.4% of them exhibit delayed or reduced LS with values ranged from 1.85 to 3. The donor parent (B35) had LS score of 2.25.

In the same manner, the mean RLS under water-limited condition was 1.1 cm^2 day^{-1}. Among the converted progeny, 15 had lower RLS ranged from 0.35 to 0.85 cm^2 day^{-1} under water-stressed and comparable with B35. In most cases, those genotypes with stay-green (LS) trait also had lower RLS.

The results showed that there were six potential progeny that exhibits good stay-green characters, which can be recommended for further evaluation so as to release particularly in environments in which available water during grain filling is not adequate to support potential transpiration. It is a fact that LS is associated with the balance between hormones such as cytokinins and ethylene, and the over expression or suppression of these hormones show changes in the timing of senescence, accelerating and retarding the process (Buchanan-Wollaston *et al.*, 2003; Gregersen *et al.*, 2013).

Genotypes with stay-green characteristics have been found to contain higher cytokinin levels (Reguera *et al.*, 2013; Ambler *et al.*, 1987); more stem sugars (Duncan *et al.*, 1981; Dahlberg, 1992; Borrell *et al.*, 1999; 2000b; Zwack and

Rashotte, 2013) and more nitrogen possibly associated with a higher transpiration efficiency (Borrell and Hammer, 2000; Borrell *et al.*, 2001; Mahalakshmi and Bidinger, 2002) than senescent genotypes. In addition, drought increases the C/N ratio and this C/N imbalance is associated with various senescence-related symptoms, including decreases in photosystem II efficiency and chlorophyll content, and up-regulation of senescence-related genes (Reguera *et al.*, 2013; Chen *et al.*, 2015).

Furthermore, the stay-green phenotype may be achieved via the modification of root architecture (nodal root angel) (Mace *et al.*, 2012), canopy development (Borrell *et al.*, 2000a), or both. Mace *et al.*, (2012) reported that nodal root angle in sorghum influences vertical and horizontal root distribution in the soil profile and is thus relevant to drought adaptation. The same report also indicates that colocation of the QTLs between nodal root angle and the stay-green drought response in sorghum.

About 9.8% of the progeny showed a good tolerance to terminal stress. Generally, characters such as GLAM, LS, and subsequent RLS are important factors determining greater green leaf area during grain-filling (Van Oosterom *et al.*, 1996; Borrell *et al.*, 2000a; Mahalakshmi and Bidinger, 2002). It is believed that a stay-green plants photosynthesize for a longer period (Hörtensteiner, 2006; Tian *et al.*, 2013; Borrell *et al.*, 2014; Abdelrahman *et al.*, 2017) through C-N transition point is delayed, or the transition occurs on time but subsequent yellowing and N remobilization run slowly (Yoo *et al.*, 2007; Thomas and Ougham, 2014).

Table 22. Mean performance of 70 sorghum genotypes tested under full-water and water-stress conditions at Mereblekhe (Rama site) in 2018/19

Genotypes	Full irrigation								Water-limited							
	SAPDB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS	SPADB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS
B35	61.1	44.3	40.1	1711.2	1348.0	0.89	81.6	1.3	57.1	34.6	48.0	1359.9	1068.2	0.9	80.8	2.2
BC_2F_3_ETSC_16139	50.8	41.2	54.3	1907.6	1721.0	0.77	90.3	2.1	45.3	35.6	64.0	1572.7	1182.4	1.1	77.3	2.5
BC_2F_3_ETSC_16140	51.6	28.2	47.4	1927.2	1648.2	0.95	87.3	3.6	47.6	29.9	49.8	1462.6	1213.2	1.0	81.6	3.3
BC_2F_3_ETSC_16141	49.0	41.3	51.8	2010.1	1446.4	1.08	73.6	1.8	49.2	26.8	60.6	1320.8	1099.4	1.0	78.6	3.5
BC_2F_3_ETSC_16142	50.5	40.0	57.3	2023.1	1531.1	1.08	77.3	2.5	51.9	27.4	45.4	1656.0	1032.7	1.3	59.7	2.7
BC_2F_3_ETSC_16143	45.9	31.9	37.3	1759.2	1460.2	0.92	83.4	2.1	49.2	24.4	43.3	1522.5	1134.9	1.1	73.2	3.3
BC_2F_3_ETSC_16144	46.9	32.6	54.2	2085.0	1484.3	1.21	71.2	3.1	47.4	31.3	51.9	1731.0	1271.2	1.1	74.8	3.1
BC_2F_3_ETSC_16145	46.4	35.2	53.9	1773.6	1379.7	1.05	77.4	3.1	43.1	27.7	46.4	1612.7	1038.4	1.2	65.3	3.4
BC_2F_3_ETSC_16146	44.7	26.9	39.9	2224.3	1760.7	1.35	78.3	3.2	43.6	23.3	53.3	1499.8	1141.1	1.0	80.0	3.9
BC_2F_3_ETSC_16147	48.3	37.6	48.0	1840.5	1744.1	0.73	95.2	3.0	41.4	28.2	40.1	1880.8	1227.1	1.3	65.6	3.4
BC_2F_3_ETSC_16148	46.0	31.7	52.0	1937.5	1630.0	0.89	84.3	4.0	46.7	23.4	37.1	1814.8	1138.7	1.3	64.8	3.2
BC_2F_3_ETSC_16149	48.8	25.5	44.8	1672.5	1518.2	0.66	91.1	3.4	46.7	24.5	37.8	1538.6	1124.4	1.1	73.4	3.9
BC_2F_3_ETSC_16150	50.3	37.4	44.3	1945.8	1717.1	0.77	88.3	3.1	47.1	28.8	50.6	1396.3	1110.5	0.9	78.4	3.4
BC_2F_3_ETSC_16210	52.1	37.8	53.1	1924.5	1785.8	0.63	94.4	2.9	50.6	29.6	34.6	1745.9	1312.7	1.1	71.6	3.2
BC_2F_3_ETSC_16211	53.4	44.3	60.2	1782.3	1610.6	0.66	90.2	1.9	54.5	31.9	29.9	1350.7	1014.6	1.1	68.7	3.7
BC_2F_3_ETSC_16212	54.8	38.3	43.4	1849.5	1577.0	0.86	85.4	3.4	52.3	32.8	35.3	1298.8	997.6	1.0	74.0	3.2
BC_2F_3_ETSC_16213	48.2	40.3	61.7	2079.6	1666.3	1.10	80.2	2.2	45.6	31.0	48.5	1713.4	1209.0	1.2	68.9	2.9
BC_2F_3_ETSC_16214	47.4	38.3	45.4	2043.8	1675.8	0.92	82.0	2.5	46.5	26.7	20.5	1412.2	975.4	1.1	68.5	3.5
BC_2F_3_ETSC_16215	44.5	32.3	34.7	1772.9	1665.2	0.47	92.1	3.3	48.3	28.4	25.1	1412.7	1126.9	1.0	78.0	4.6
BC_2F_3_ETSC_16216	45.4	34.8	56.6	1711.2	1585.0	0.63	93.1	2.7	45.5	32.7	49.7	1546.9	1039.0	1.2	69.8	2.6
BC_2F_3_ETSC_16217	50.2	35.6	31.5	1837.8	1738.0	0.66	94.3	4.1	47.5	25.1	29.1	1308.7	1083.4	0.8	83.6	3.7
BC_2F_3_ETSC_16218	53.0	34.7	38.5	1762.5	1730.6	0.17	98.2	3.1	43.7	22.1	36.7	1406.8	882.1	1.2	69.0	2.6
BC_2F_3_ETSC_16219	46.9	35.0	37.4	1715.0	1574.9	0.63	91.6	2.9	46.4	24.4	34.3	1492.6	1060.5	1.0	77.9	3.9
BC_2F_3_ETSC_16220	54.0	33.4	50.5	1790.4	1593.6	0.73	89.3	3.3	50.8	30.1	29.7	1479.6	1079.3	1.0	77.8	3.7
BC_2F_3_ETSC_16221	52.8	28.2	34.4	2156.9	1704.8	1.08	81.7	3.8	50.0	29.0	29.6	1626.4	1207.9	1.0	78.7	3.8

Genotypes	Full irrigation								Water-limited							
	SAPDB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS	SPADB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS
BC_2F_3_ETSC_16222	55.2	38.2	33.1	1936.8	1468.7	1.05	79.0	3.4	51.2	32.0	30.0	1796.8	1133.2	1.3	62.8	3.3
BC_2F_3_ETSC_16223	50.9	35.5	42.6	2366.3	1723.9	1.25	72.4	3.4	49.9	24.8	37.0	1818.7	1407.2	1.2	76.1	2.7
BC_2F_3_ETSC_16224	44.4	39.6	53.3	1979.0	1878.3	0.51	94.2	2.6	43.7	28.0	47.0	1618.2	1001.1	1.3	63.7	3.4
BC_2F_3_ETSC_16225	47.1	37.7	44.9	1621.7	1588.2	0.43	96.5	3.1	43.2	39.0	59.7	1738.8	1168.7	1.3	68.6	4.1
BC_2F_3_ETSC_16226	43.8	37.0	42.1	2045.5	1480.9	1.27	71.7	2.9	50.6	31.0	43.3	2043.0	1187.4	1.4	57.0	3.1
BC_2F_3_ETSC_16227	41.0	34.9	52.2	1709.8	1270.8	1.12	73.7	3.2	40.8	25.8	53.0	1573.6	1016.9	1.2	67.6	3.6
BC_2F_3_ETSC_16228	46.1	34.8	37.5	1918.6	1703.9	0.92	88.7	3.1	41.8	28.4	53.7	1956.9	1325.3	1.2	69.7	3.2
BC_2F_3_ETSC_16229	43.2	43.2	48.7	1957.5	1400.1	1.25	71.3	3.2	44.1	32.5	50.4	2070.1	1138.5	1.4	58.7	2.7
BC_2F_3_ETSC_16230	47.7	41.4	48.7	2013.3	1448.2	1.27	71.1	3.1	39.1	23.3	48.5	1742.2	1032.1	1.3	59.8	4.0
BC_2F_3_ETSC_16231	50.2	37.9	57.9	1795.7	1446.2	0.95	81.1	2.7	45.7	31.5	26.7	1861.9	1001.7	1.4	59.0	3.4
BC_2F_3_ETSC_16232	50.9	38.0	40.7	1732.2	1572.5	0.73	89.2	2.9	51.9	28.4	35.7	1424.3	1088.8	0.8	79.7	3.2
BC_2F_3_ETSC_16233	48.0	29.7	41.9	1769.1	1291.8	1.17	75.5	3.0	48.2	24.6	45.1	1761.2	1242.9	1.3	69.1	3.3
BC_2F_3_ETSC_16234	48.4	36.2	50.3	1595.0	1288.9	0.80	82.1	3.1	48.7	25.5	40.7	1346.0	1250.0	0.6	91.5	2.0
BC_2F_3_ETSC_16235	47.4	26.8	44.8	1670.0	1480.5	0.70	88.8	2.7	49.3	27.4	28.4	1986.7	893.8	1.5	51.0	3.6
BC_2F_3_ETSC_16236	48.7	40.8	47.2	1590.8	1436.4	0.73	90.3	2.9	48.4	24.6	33.4	967.9	795.4	0.7	81.7	4.1
BC_2F_3_ETSC_16237	52.1	41.9	53.0	1586.1	1469.7	0.77	92.6	2.5	43.7	30.0	31.4	1794.3	913.3	1.4	53.8	4.4
BC_2F_3_ETSC_16238	49.4	39.7	54.4	1856.1	1737.8	0.59	93.8	2.7	53.5	24.5	39.2	1193.0	1171.6	0.3	96.3	4.4
BC_2F_3_ETSC_16239	51.8	39.3	51.3	1676.1	1492.8	0.70	90.2	2.0	54.5	31.9	24.5	1606.6	927.5	1.2	57.6	3.7
BC_2F_3_ETSC_16240	50.2	39.2	48.3	1539.0	1442.9	0.55	93.2	2.5	49.7	29.5	39.1	1513.2	857.3	1.2	59.2	3.6
BC_2F_3_ETSC_16241	53.3	42.1	53.4	1941.1	1820.4	0.51	93.7	2.2	48.6	29.6	48.2	1547.0	1064.5	1.1	67.4	2.8
BC_2F_3_ETSC_16242	53.1	40.5	47.1	1856.3	1655.5	0.70	89.6	2.9	47.4	29.7	35.8	1288.9	921.0	1.1	69.3	2.7
BC_2F_3_ETSC_16243	50.8	40.8	56.7	1592.3	1492.9	0.77	93.4	3.5	52.6	22.4	28.3	1107.5	953.6	0.7	86.1	3.3
BC_2F_3_ETSC_16244	50.1	33.4	62.5	1760.5	1378.5	1.12	78.2	2.9	50.3	26.6	25.7	1211.2	952.5	0.8	81.8	3.3
BC_2F_3_ETSC_16245	48.5	41.9	44.7	2270.3	1532.5	1.46	68.0	3.3	50.0	28.3	35.1	1393.2	1283.2	0.4	94.9	2.6
BC_2F_3_ETSC_16246	51.1	36.7	40.0	1454.5	1320.9	0.63	91.4	2.6	48.7	28.2	32.0	1356.0	934.2	0.9	80.4	4.0
BC_2F_3_ETSC_16247	50.2	35.9	60.8	1644.5	1387.2	0.97	83.0	3.1	53.4	31.2	21.9	1464.8	1179.1	0.8	84.0	2.9
BC_2F_3_ETSC_16248	45.7	37.2	42.9	1376.2	1215.1	0.63	86.8	3.1	52.3	33.7	31.8	1437.7	1207.2	0.8	86.4	2.3
BC_2F_3_ETSC_16249	50.8	36.4	57.6	1918.5	1599.7	0.66	85.0	3.1	51.9	30.5	28.8	1158.8	895.8	0.9	73.9	3.7

Genotypes	Full irrigation								Water-limited							
	SAPDB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS	SPADB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS
BC$_2$F$_3$_ETSC_16250	52.5	32.3	40.2	1921.7	1427.4	1.08	75.9	4.1	49.1	25.1	27.3	1260.4	891.8	1.0	75.0	4.1
BC$_2$F$_3$_ETSC_16251	52.1	37.7	47.6	1484.5	1408.4	0.51	94.4	3.1	49.9	25.7	29.0	1231.0	1056.6	0.9	82.4	3.8
BC$_2$F$_3$_ETSC_16252	50.2	33.5	57.4	1684.8	1538.4	0.51	92.5	3.2	48.2	26.6	22.1	1227.0	1035.3	0.6	88.0	2.7
BC$_2$F$_3$_ETSC_16253	52.9	37.8	50.4	1630.9	1571.8	0.51	95.7	3.1	49.8	36.9	35.0	1291.4	1130.3	0.7	85.3	2.8
BC$_2$F$_3$_ETSC_16254	48.9	43.4	55.7	1557.1	1318.0	0.83	85.8	3.0	48.5	30.6	36.5	1438.1	1118.0	0.9	81.9	2.9
BC$_2$F$_3$_ETSC_16255	48.5	40.4	65.5	1641.0	1451.7	0.66	89.2	2.0	48.6	28.2	51.1	1333.1	949.5	0.9	78.4	3.0
BC$_2$F$_3$_ETSC_16256	51.8	37.7	51.2	1939.6	1418.8	1.19	73.4	3.5	49.8	24.6	19.3	1324.4	1096.5	0.7	87.9	2.9
BC$_2$F$_3$_ETSC_16257	49.8	37.8	50.9	1683.2	1635.1	0.47	94.7	2.2	51.5	29.2	32.1	1351.5	1014.7	0.9	76.3	1.9
BC$_2$F$_3$_ETSC_16258	48.4	33.1	49.0	1711.3	1673.1	0.39	96.9	2.2	52.9	43.5	48.7	1622.2	1142.5	1.0	73.4	2.2
Dekeba	57.3	38.1	48.5	1950.9	1609.8	1.23	76.0	3.1	50.0	28.4	39.0	1796.9	1181.0	1.3	67.6	4.4
Gambella1107	46.6	30.2	42.6	1907.6	1478.9	1.14	79.2	3.3	45.9	28.1	27.1	1568.1	1276.1	0.9	77.8	3.6
Macia	51.6	38.1	53.6	1618.9	1443.6	0.77	89.9	2.1	51.5	30.6	46.1	1571.0	1158.1	1.1	72.9	2.3
Meko	44.4	37.4	60.9	2042.6	1626.4	0.95	82.9	3.6	49.0	25.0	38.8	1657.5	1087.1	1.2	67.4	3.3
Melkam	50.1	35.9	30.8	1912.5	1619.2	0.95	84.5	4.1	55.3	28.1	45.8	1654.3	1193.2	1.1	72.2	3.7
Teshale	38.6	31.3	44.1	1812.5	1390.6	1.12	79.3	4.0	45.2	31.5	41.6	1575.7	1048.5	1.2	67.4	4.0
Tseadachimure	50.1	34.1	60.5	1776.9	1456.1	0.89	83.0	3.0	52.8	35.0	46.9	1288.5	1008.0	0.8	79.0	3.6
Wediaker	53.2	42.8	57.7	1819.9	1644.1	0.66	90.2	3.2	50.0	40	42.9	1278.3	896.6	1.0	71.0	3.1
Mean	49.4	36.6	48.5	1821.6	1543.3	0.89	85.4	2.9	48.6	29	38.8	1520.2	1085.7	1.1	73.59	3.3
LSD (0.05)	6.83	7.83	18.5	387.93	323.99	0.64	14.4	1.1	6.47	8.47	14.2	485.3	266.1	0.7	20.7	1.1
CV (%)	7.6	12.5	21.9	12.3	12	19.6	9.7	20.8	7.5	16.41	22.5	18.3	13.6	20.9	17	19.2

SPAD = chlorophyll content at booting, SPADM = chlorophyll content at maturity, PGLM = percent green leaf at maturity, GLAB = green leaf at booting (cm^2 plant^{-1}), GALM = green leaf area at maturity (cm^2 plant^{-1}), RLS = rate of leaf senescence (cm^2 day^{-1}), PGLAM = percent of green leaf area preserved at maturity and LS = leaf senescence. The RLS was subjected to log (x + 1) transformation, LSD = Least significant difference, CV = Coefficient of variation

4.5.5. Interrelationships among traits

A total of 81 and 88 significant correlation coefficients ($P < 0.05/ 0.01$) (Table 23) were observed among the traits under full and water-limited conditions, respectively. The correlation coefficients among traits ranged from 0 to 0.93 under well-watered and from 0 to 0.96 in water-limited condition.

Under water-stressed conditions, DTF showed significant positive correlation only with DTM, while significant positive correlation with most of stay green characters (PGLM, GLAB, GLAM, and RLS). On the other hand, PLHT and DTM revealed significant positive correlation with almost all of the agronomic traits and most of stay green characters, while, negatively correlated with PGLAM and LS. The characters PL and PW had significant positive correlation with most of the agronomic and physiological characters. Similarly, PWt showed significant positive correlation with all characters except with DTF and RLS, while negatively correlated with PGLAM and LS. BM also showed significant positive correlation with the majority of the character under study except for PGLAM and LS that was significant negative correlation. TSW showed significant correlation with most of the agronomic and some of physiological traits. Grain yield showed significant positive correlation with almost all morpho-agronomic and stay green characters, while, negatively correlated with LS.

The SPADB had significant positive correlation with SPADM and GLAM and negative correlation with PGLM and LS. Similarly, SPADM showed significant positive correlation with PGLM and negative correlation with LS. PGLM showed no significant difference for the entire stay green components except SPADB and LS. GLAB showed significant positive correlation with, GLAM, and RLS, while negatively correlated with PGLAM and LS. GLAM showed significant and positive correlation with SPADB, GLAB, and RLS and negatively correlated with LS. PGLAM had significant negative correlation with GLAB and RLS and negative correlation with GLAM.

Interestingly, LS showed significantly and negatively correlated with all stay-green characters except for RLS indicating that the scale of stay-green character with lower score is advantageous and higher is disadvantageous for drought screening. This showed that as the leaf starts drying or yellowing (high LS), the protein is degraded and amino acids are transported out of the leaf resulting loss of chlorophyll from the pigment-protein complexes of the photosynthetic apparatus. For instance, Xu *et al.*, (2000b) reported that the chlorophyll content was significant negative correlation to stay green rating ($r = -0.90$). Similarly, grain yield significant negative association with leaf senescence rate ($r = -0.74$) were identified in stress conditions. In this regard, converted progeny with reduced RLS and delayed LS may have the advantage of high photosynthetic activities resulted a good yield under moisture stress conditions. In agreement with this, Pask and Pietragalla, (2012) reported that genotypes with prolonged green leaf area duration through delayed LS allows photosynthetic activity to continue and enables the crop continue producing assimilates. Wanous *et al.*, (1991) and Borrell *et al.*, (2014) reported that GLAM was correlated with both green leaf retention and green leaf number for sorghum grown under drought and has successfully been used to select drought-resistant sorghums (Rosenow *et al.*, 1983; Henzell *et al.*, 1992).

Grain yield showed significant and positive correlation with SPADB, SPADM, GLAB and GLAM in both moisture regimes. This indicated that the presence of more green leaves, greater green leaf area and higher chlorophyll content either at booting or at maturity stage might contribute to higher photosynthesis, better availability of food reserves for grain-filling and associated enhanced yield. Grain yield showed significant negative correlation with LS and its rate of progress (RLS) indicating as the leaf senescence accelerated the yield significantly decreased. Conversely, delayed LS or reduced RLS resulted higher grain yield due to the higher translocation of food reserve from leaves for better grain filling (Reddy *et al.*, 2014). Previous report suggested that delayed LS in sorghum has been associated with improved grain yield, particularly in environments in which available water during grain filling is not adequate to support potential transpiration (Rosenow *et al.*, 1983; Henzell *et al.* 1992; Borrell and Douglas, 1996; Borrell *et al.*, 2014; Jordan *et al.,* 2012).

In summary, the analyses of direct and indirect effects provide an effective means of association between agronomic and physiological traits. The characters like leaf area, LS, and SPAD values had positive direct effect on yield under stress condition. Therefore, simple indirect selection based on these traits for grain would be effective. The correlation of traits under full-irrigation followed the same trend with minor exceptions (Table 15).

Table 23. The correlation coefficients (r) for 20 morpho-agronomic and physiological traits of 70 sorghum genotypes tested at Mereblekhe district under full-water conditions (above diagonal) and water-limited (below diagonal)

Traits	DTF	PLHT	DTM	PL	PW	PWt	BM	YLD	TSW	SPADB	SPADM	PGLM	GLAB	GLAM	RLS	PGLAM	LS
	Full-irrigation																
DTF	1	**0.28**	**0.23**	-0.11	0.08	0.05	0.09	0.01	0.05	**-0.21**	-0.06	-0.06	0.12	0.07	**0.23**	-0.07	0.05
PLHT	0.01	1	**0.22**	-0.05	**0.3**	**0.19**	**0.31**	**0.14**	**0.16**	-0.13	0.00	0.04	0.02	0.01	0.01	0.03	**-0.14**
DTM	**0.24**	**0.14**	1	-0.03	**0.23**	**0.24**	**0.32**	**0.23**	**0.21**	-0.08	**0.2**	**0.43**	0.12	**0.16**	-0.11	0.06	**-0.53**
PL	-0.06	**0.36**	0.09	1	**0.48**	**0.58**	**0.24**	**0.56**	0.02	**0.5**	**0.22**	0.05	**0.26**	**0.25**	0.09	-0.01	-0.12
PW	0.03	**0.47**	**0.39**	**0.61**	1	**0.79**	**0.47**	**0.75**	0.1	**0.33**	**0.29**	**0.23**	**0.42**	**0.31**	**0.15**	-0.12	**-0.23**
PWt	-0.04	**0.38**	**0.41**	**0.48**	**0.77**	1	**0.56**	**0.96**	**0.26**	**0.41**	**0.31**	**0.25**	**0.48**	**0.42**	0.08	-0.02	**-0.34**
BM	0.12	**0.41**	**0.44**	**0.31**	**0.56**	**0.5**	1	**0.56**	**0.19**	**0.18**	**0.22**	**0.16**	**0.34**	**0.3**	0.05	-0.03	**-0.4**
YLD	-0.06	**0.32**	**0.45**	**0.45**	**0.73**	**0.8**	**0.6**	1	**0.28**	**0.4**	**0.31**	**0.26**	**0.47**	**0.43**	0.05	0	**-0.34**
TSW	0.07	**0.15**	**0.17**	0.03	**0.14**	**0.24**	**0.27**	**0.25**	1	0.06	-0.03	0.11	0.01	0.12	**-0.16**	**0.16**	**-0.26**
SPADB	**-0.22**	**0.18**	-0.05	**0.38**	**0.31**	**0.28**	0.08	**0.24**	0.00	1	**0.38**	0.04	**0.29**	**0.29**	0	0.03	-0.12
SPADM	-0.09	0.04	**0.39**	**0.27**	**0.4**	**0.42**	**0.27**	**0.45**	0.12	**0.29**	1	**0.3**	0.13	**0.17**	-0.03	0.07	**-0.36**
PGLM	**0.32**	-0.05	**0.28**	-0.03	0.04	**0.15**	**0.18**	0.11	0.1	**-0.2**	**0.31**	1	0.08	0.07	-0.03	-0.02	**-0.41**
GLAB	**0.33**	**0.42**	**0.19**	**0.28**	**0.47**	**0.33**	**0.42**	**0.29**	0.08	0.06	0.11	0.12	1	**0.64**	**0.49**	**-0.39**	-0.01
GLAM	**0.22**	**0.32**	0.06	**0.35**	**0.38**	**0.24**	**0.33**	**0.27**	-0.04	**0.16**	0.07	0.1	**0.63**	1	**-0.23**	**0.4**	**-0.18**
RLS	**0.4**	**0.22**	0.06	0.06	**0.22**	0.13	**0.23**	0.07	0.08	-0.11	0.01	0.12	**0.76**	0.06	1	**-0.89**	**0.28**
PGLAM	**-0.23**	**-0.17**	**-0.17**	0	**-0.19**	**-0.15**	**-0.2**	-0.07	-0.12	0.11	-0.05	-0.07	**-0.59**	**0.22**	**-0.93**	1	**-0.22**
LS	-0.08	-0.08	**-0.41**	**-0.18**	**-0.36**	**-0.37**	**-0.32**	**-0.46**	-0.13	**-0.16**	**-0.36**	**-0.19**	**-0.16**	**-0.21**	0.02	-0.03	1
	Water-limited																

DTF = days to flowering, PLHT = plant height, DTM = days to maturity, PL = panicle length, PW = panicle width, PWt = panicle weight, BM = biomass, YLD = grain yield, TSW = thousand seeds weight, SPADB = SPAD reading at flowering, SPADM = SPAD reading at maturity, NGLB = number green leaf at booting, NGLM = number green leaf at maturity, PGLM = per cent green leaf retained at maturity, GLAB = green leaf area at booting, GLAM = green leaf area at maturity, RLS = rate of leaf senescence, PGLAM = per cent green leaf area preserved at maturity, LS = leaf senescence, **bold** number = significant at P<0.05/0.01.

4.5.6. Estimates of heritability

Heritability is the percentage of phenotypic variance that is attributed to genetic variance. The estimates of heritability (H^2b) for the traits studied ranged from 35.4% to 79.5% under full-irrigation and 34.8% to 76.3% under water-limited condition (Table 24). The majority of the characters showed medium to moderately high H^2b (40-79.5%) under both moisture conditions. As bench mark, heritability values greater than 80% were grouped as very high, values from 60-79% were moderately high, values from 40-59% were medium and values less than 40% were low (Singh, 2001). In this regard, the estimate of H^2b on most of the characters was categorized as medium or moderately high. The characters having very high heritability (≥80%) indicated relative small contribution of the environment factors to the phenotype and selection for such characters could be effective (Singh, 2002; Keneni, 2012). Conversely, characters that exhibited lower broad-sense heritability (below 40%), selection could be difficult or virtually impractical due to the environment concealing genotypic effects (Vinodhana *et al.*, 2009; Keneni, 2012).

4.5.7. Genetic advance from selection

Heritability together with genetic advance has a greater role to play in determining the effectiveness of selection of a character. Genetic advance (GA) under selection referred to the improvement of characters in genotypic value for the new population compared with the base population under one cycle of selection at given selection intensity (Singh, 2001; Hamdi *et al.,* 2003). GA was high for PLHT (18.98 and 23.86%), PL (19.5 and 13.87%), PWt (13.31 and 34.11%), BM (33.11 and 44.1%), YLD (17.27 and 42.53), SPADM (14.02 and 14.69%), PGLM (13.21 and 40.7%), GLAB (10.34 and 13.58%), RLS (35.52 and 26.42), and LS (19.24 and 22.6%) under full and water-limited condition, respectively (Table 24). Based on this finding, it could be concluded that selection will be effective in the tested lines used in this study. GA is categorized as high (> 20%), moderate (10-20%), and low (<10%) as described by Johnson *et al.*, (1955). Based on this borderline, characters categorized as high of GA include BM and RLS under full-irrigation and PLHT, PWt, BM, YLD, PGLM, RLS and LS in stressed condition. The majority of characters (ten) under full-irrigation were categorized for having moderate GA and six characters under-water stressed were having moderate GA. The result showed that the GA values were generally high under water-stressed condition than in optimum irrigation. In summary, these characters exhibited high H^2b, high GA with high genotypic co-efficient of variation indicating importance of additive genetic variance for these characters which could be used for selection and improvement of genotypes.

Table 24. Estimates of broad-sense heritability (H^2b) and genetic gain (GA) of 17 agronomic and physiological traits of 70 sorghum genotypes tested under full and water-limited conditions at Mereblekhe district in 2018/19

Trait	Full-irrigation		Water-limited	
	H^2b (%)	GA (%)	H^2b (%)	GA (%)
DTF	62.71	5.41	35.05	2.85
PLHT	63.87	18.98	74.67	23.86
DTM	45.21	1.66	34.78	1.42
PL	79.49	19.48	56.11	13.87
PW	35.66	5.93	43.03	9.50
PWt	35.44	13.31	60.51	34.11
BM	61.36	33.11	63.48	44.1
YLD	42.92	17.27	69.34	42.71
TSW	61.37	13.96	56.33	14.53
SPADB	58.73	8.46	62.56	9.08
SPADM	60.96	14.02	52.45	14.69
PGLM	40.01	13.21	76.33	40.70
GLAB	49.95	10.34	45.92	13.58
GLAM	37.83	6.59	50.58	11.79
RLS	50.66	35.52	47.00	26.42
PGLAM	57.33	10.19	41.11	10.67
LS	52.67	19.24	60.81	22.03

DTF = days to flowering, PLHT = plant height, DTM = days to maturity, PL = panicle length, PW = panicle width, PWt = panicle weight, BM = biomass, YLD = grain yield, TSW = thousand seeds weight, SPADB = SPAD reading at flowering, SPADM = SPAD reading at maturity, PGLM = percent green leaf retained at maturity, GLAB = green leaf area at booting, GLAM = green leaf area at maturity, RLS = rate of leaf senescence, PGLAM = percent green leaf area preserved at maturity, LS = leaf senescence

4.5.8. Comparison of cumulative expression of QTLs on agronomic and physiological traits

Under water-limited condition, the performance of the introgressed progeny with markers showed better performance for most of the agronomic trait compared to their seed parents (Figure 17). The backcrossed progeny with *stg1+stg2+stg3a+stg4, stg1+stg2+stg3a+stg3b* and *stg1+stg2+stg4* markers yielded highest biomass compared either of the parents. Similarly, the highest yield was obtained from backcrossed progeny with QTL *stg1+stg2+stg3a+stg4* (2800 kg ha^{-1}) and *stg1-stg3a-stg3b-stg4* (2500 kg ha^{-1}).

Stay green characters also showed significant difference between developed progeny and parental lines. The highest SPADB was measured from B35 followed by those progeny that contain *stg1+stg3a+stg3b* and *stg2+stg3b+stg4,* while the highest SPADM was recorded from *stg1+stg3a+stg3b+stg4.* The highest GLAB and GLAM were measured from converted progeny consisting of *stg1+stg2+stg3a*+stg4 QTL (Figure 18). The converted progeny with *stg1+stg2+stg3a+stg4*, *stg1+stg2+stg3a+stg3b* and *stg1+stg3a+stg3b+stg4* QTLs showed delayed LS. It was generally observed that the different combination of QTLs revealed clear evidence of an interaction between the stay-green QTLs.

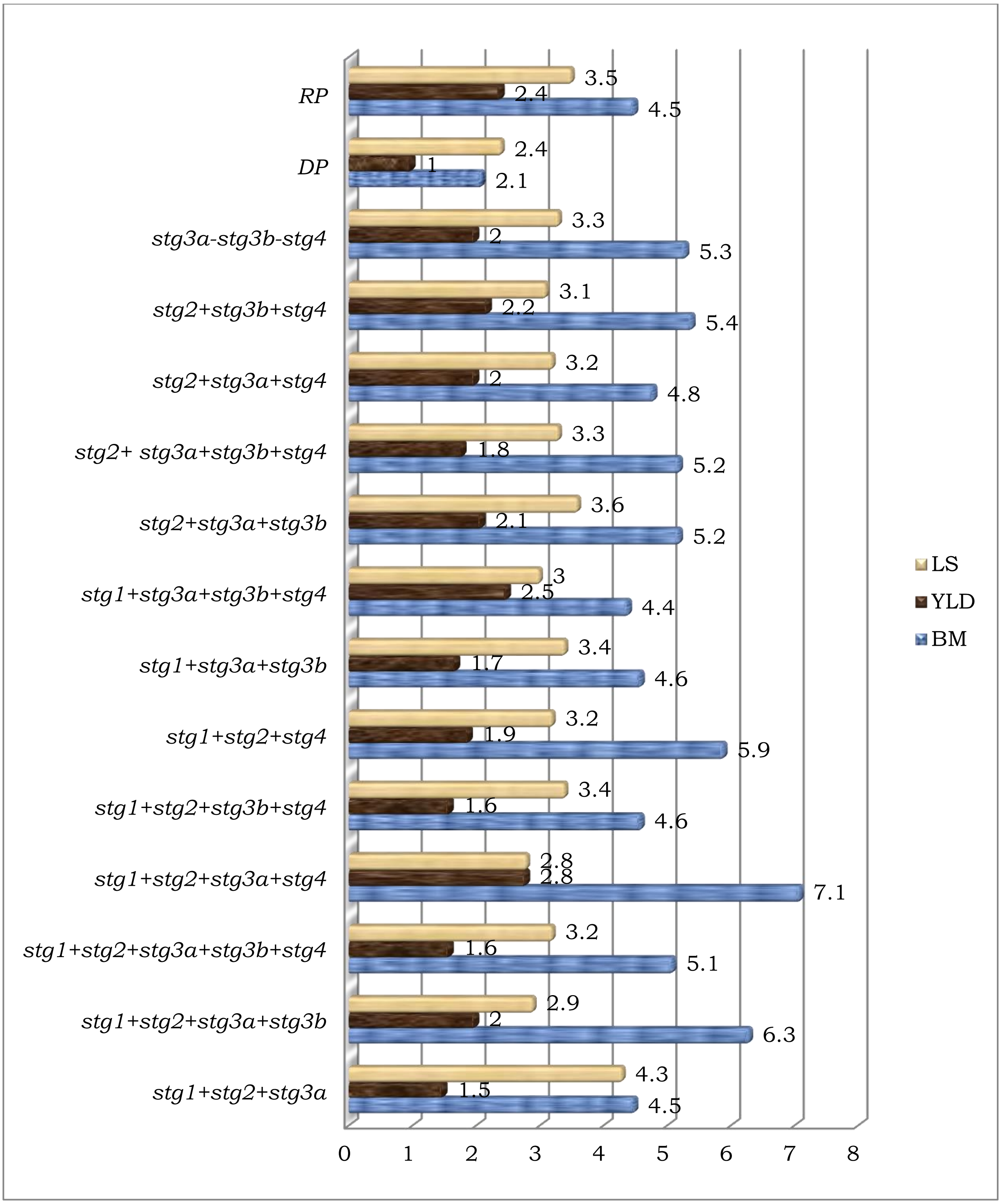


Figure 17. The effect of QTLs on the leaf senescence (LS), yield (YLD) and biomass (BM) t ha^{-1} under water-limited condition

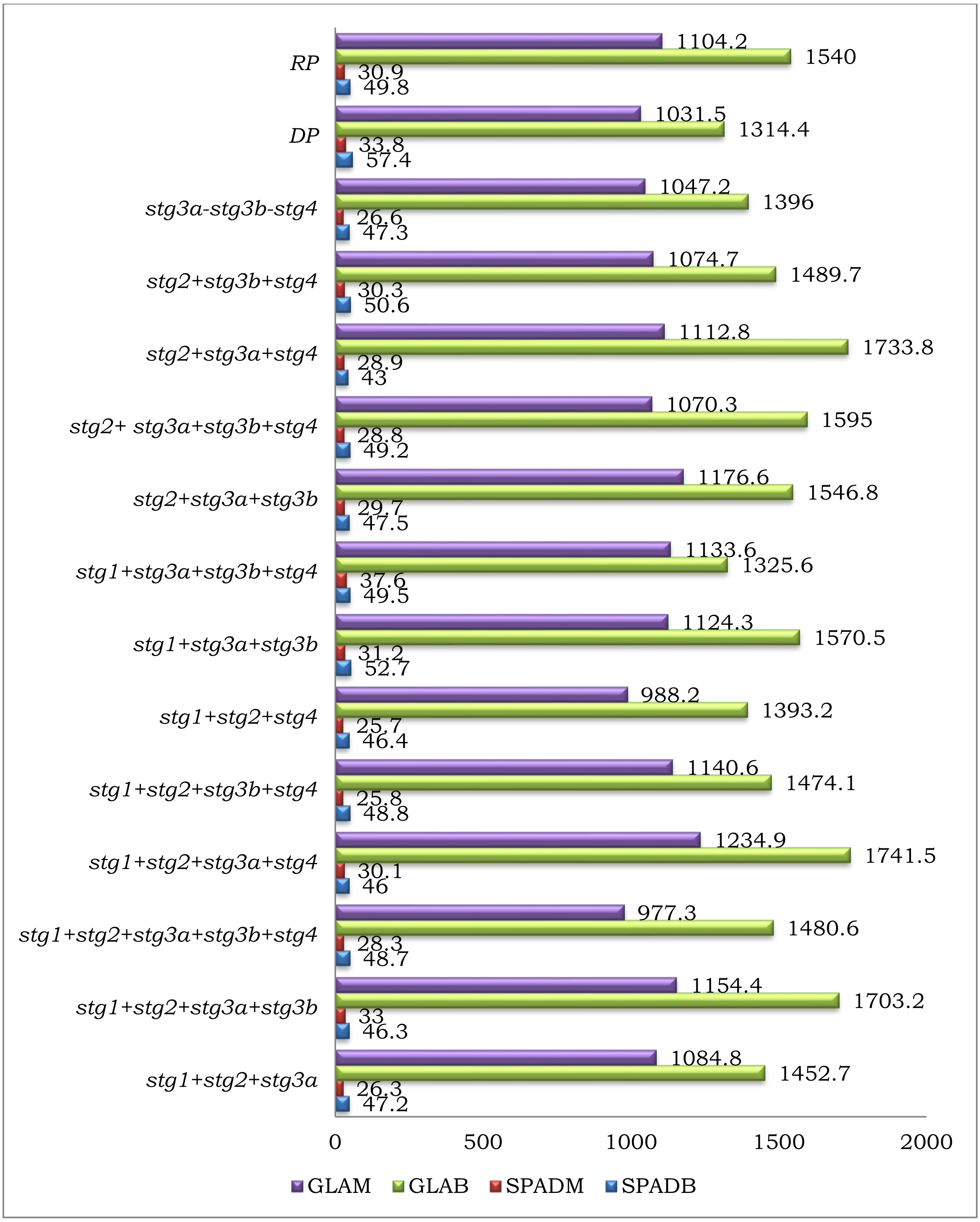


Figure 18. The expression of QTLs on the green leaf area and chlorophyll content under water-limited condition

GLAB = Green leaf area at booting, GLAM = Green leaf area at maturity, SPADB = Chlorophyll content (SPAD values) at boating, SPADM = Chlorophyll content (SPAD values) at maturity, RP = recurrent parents, DP = donor parent

4.5.9. Principal component analysis

Principal component (PC) analysis indicated that the first vectors were more important than the second and all the other vectors. The first five PCs accounted for about 72% and 68.8% of the total variation under full-irrigation and water-limited conditions, respectively. The corresponding values for the first five principal components (PC_1-PC_5) were 22.1%, 17.8%, 13.5%, 10.98% and 7.75% for full-irrigation and 25.3%, 19.3%, 10.7%, 6.9%, and 6.7% for water-limited that contributed to the entire variation, respectively (Table 25).

Under full-irrigation, the first PC that accounted for the highest total variation with high and positive weights for DTF, PW, PWt, BM, TSW, and YLD. Similarly, under water-limited condition, the seven top important characters responsible for genetic divergence include DTF, DTM, BM, PGLM, GLAB, RLS and GLAM. The second PC contributed with high weights for PL, SPADB, and GLAM and RLS under full-irrigation and PL, PW, PWt, yield, SPADB and LS under water-limited condition. Plant height, DTM, and PGLM under full-irrigation and GLAM under water-limited were also important in the third principal component. The fourth PC was associated with the high weights for SPADM and PLHT under water-limited and SPADM under full-irrigation. Finally, TSW under full-irrigation, GLAB and GLAM under water-limited were the least contributor.

Based on these results, it is possible to find out causes of the variation associated with a particular PC by examining the coefficients of linear combination of original variables. The variables with eigenvector of large absolute magnitude (close to unity) dictated the magnitude and pattern of the variation while those of small magnitude reflect little influence (Chahal and Gosal, 2002).

Table 25. Eigenvalue, percentage and cumulative variances and eigenvectors on the first five principal components for 17 agronomic and morpho-physiological traits of 70 genotypes at Mereblekhe under stressed and unstressed conditions

	Under full-watered condition					Under water-stressed condition				
Parameter	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Eigen value	3.759	3.026	2.298	1.866	1.317	4.298	3.275	1.814	1.167	1.134
Proportion	22.11	17.80	13.52	10.98	7.75	25.28	19.26	10.67	6.867	6.672
Cumulative	22.11	39.91	53.43	64.41	72.15	25.28	44.54	55.21	62.08	68.75
DTF	0.478	-0.459	0.379	-0.198	-0.049	0.634	-0.348	0.413	0.214	0.069
PLHT	0.257	-0.347	0.523	-0.298	-0.295	0.323	-0.181	-0.403	0.409	-0.254
DTM	0.523	-0.182	0.612	0.237	0.243	0.558	0.008	0.260	-0.148	-0.328
PL	0.337	0.525	-0.490	0.179	-0.160	0.060	0.622	-0.122	0.071	0.398
PW	0.770	0.078	-0.057	0.114	-0.352	0.524	0.594	-0.173	0.327	0.152
PWt	0.865	0.235	-0.183	-0.001	-0.298	0.472	0.692	0.001	0.243	-0.047
BM	0.623	-0.049	0.123	-0.224	0.240	0.603	0.207	-0.220	0.069	-0.315
TSW	0.349	0.233	0.192	-0.278	0.143	0.309	0.087	-0.372	-0.167	-0.400
YLD	0.824	0.275	-0.250	-0.058	-0.253	0.471	0.747	-0.092	0.079	-0.116
SAPDB	-0.058	0.629	-0.360	0.324	0.128	-0.432	0.562	-0.195	-0.136	0.289
SPADM	0.057	0.340	0.282	0.643	0.158	0.276	0.487	-0.068	-0.628	0.172
PGL	0.154	0.160	0.498	0.512	-0.067	0.495	-0.063	0.460	-0.278	-0.184
GLAB	0.495	-0.466	-0.412	0.121	0.550	0.815	-0.291	0.080	-0.001	0.342
GLAM	0.445	0.279	-0.146	-0.376	0.635	0.279	0.163	0.731	0.226	0.235
RLS	0.208	-0.780	-0.346	0.403	0.008	0.755	-0.467	-0.256	-0.143	0.292
PGLAM	-0.129	0.766	0.293	-0.494	0.045	-0.677	0.425	0.448	0.235	-0.214
LS	-0.115	-0.407	-0.511	-0.404	-0.185	-0.141	-0.476	-0.334	0.324	0.227

DTF = days to flowering, PLHT = plant height, DTM = days to maturity, PL = panicle length, PW = panicle width, PWt = panicle weight, BM = biomass, YLD = grain yield, TSW = thousand seeds weight, SPADB = SPAD reading at flowering, SPADM = SPAD reading at maturity, NGLB = number green leaf at booting, NGLM = number green leaf at maturity, PGLM = per cent green leaf retained at maturity, GLAB = green leaf area at booting, GLAM = green leaf area at maturity, RLS = rate of leaf senescence, PGLAM = per cent green leaf area preserved at maturity, LS = leaf senescence

4.5.10. Cluster analyses

The cluster analysis has grouped the seventy sorghum genotypes into five and six distinct groups under full-irrigation and water-limited condition, in that order (Table 26, Figures 19 & 20). Each cluster comprises different number of genotypes; C_1-C_5 and C_1-C_6 consisted of 10, 12, 19, 13, and 16 under full-irrigation and 9, 5, 13, 20, 6, and 17 under water-limited conditions. Each cluster has its own a peculiar characteristics.

The first cluster (C_1) was characterized by intermediate overall agronomic performance and high SPADB, GLAB, GLAM, RLS and LS, while, low SPADM and PGLM under full-irrigation. Conversely, C_2 contains those genotypes with poor agronomic performance and a good level of stay green characteristics such as SPADB, SPADM, PGLM, PGLAM and LS. Similarly, the third cluster (C_3) showed slight good agronomic performance compared to C_2 and high GLAB, RLS and LS and lowest PGLAM. The fourth cluster consisted of relatively better agronomic performance than C_2 with almost similar stay green traits. The members in C_5 comprised best genotypes in agronomic traits with intermediate leaf area, reduced RLS, and delayed LS. This cluster was also superior to grand mean of all other traits averaged over all clusters, indicating this cluster contained desirable genotypes under optimum environments.

In the same manner, under water-stressed condition, cluster 1 (C_1=9) characterized by high morpho-agronomic (DTM, PW, PWt, BM, TSW, YLD) and intermediate values for most of the physiological character and high

SPADB and SPADM. This cluster comprised genotypes with superior to grand mean of all other traits averaged over all clusters, indicating that this cluster contained desirable genotypes according to physiological and agronomic characters. This indicated that those genotypes within the cluster could be possibly recommended for moisture areas and incorporations in the breeding programs. In contrast, C_2 constituted genotypes with overall inferior agronomic performance (YLD) and intermediate physiological character (SPADM, PGLM, and GLAB), small GLAM and high leaf drying (RLS and LS). The third cluster (C_3) had intermediate leaf area and SAPD values but high RLS and RS. Similarly, C_4 had characterized by lowest agronomic and stay green components, with correspondingly accelerated RLS and LS. The fifth and six clusters consisted of intermediate agronomic performance and stay green characteristics with exception of leaf area, RLS and LS was higher in C_4. In general, for further improvement through breeding, selection should be focused on the clusters and individuals within clusters with high mean for desirable agronomic traits and good stay green characteristics.

Table 26. Number of elements in each cluster their mean trait performances of seventy sorghum genotypes grouped into different clusters under the full-water and water-limited conditions

Cluster	No. of Genotypes	DTF	PLHT	DTM	PL	PW	PWt	BM	TSW	YLD	SPADB	SPADM	PGLM	GLAF	GLAM	RLS	PGLAM	LS
		Full-irrigation																
C1	10	83.7	140.0	122.5	22.8	6.3	305.1	7300	33.9	3400	51.3	32.4	38.6	1869.1	1611.4	0.5	87.3	3.6
C2	12	80.9	131.8	124.6	21.0	6.2	279.0	7000	34.1	3100	51.0	38.8	53.0	1721.4	1524.0	0.5	89.0	2.7
C3	19	87.4	164.2	126.4	20.2	6.5	328.0	9900	34.5	3500	46.2	35.5	47.8	1980.1	1505.0	0.7	76.6	3.1
C4	13	87.7	187.5	126.6	20.8	6.6	318.2	8500	36.8	3300	49.6	38.4	52.4	1700.1	1513.9	0.5	89.1	2.8
C5	16	84.6	157.0	125.9	24.2	7.1	412.1	10600	37.0	4600	50.8	37.6	49.2	1777.6	1584.8	0.5	89.1	2.7
		Water-limited																
C1	9	83.7	129.5	119.7	20.6	6.2	326.9	7000	32.1	3000	48.8	30.7	46.3	1598.5	1146.1	0.7	71.5	2.9
C2	5	81.2	168.1	118.4	20.9	5.8	211.9	5900	32.8	1700	48.6	30.1	30.0	1752.5	918.7	0.7	56.1	3.7
C3	13	85.7	150.3	120.4	19.1	5.6	210.4	6100	31.6	1900	44.1	28.8	48.9	1757.1	1145.2	0.7	67.0	3.4
C4	20	81.1	130.5	117.4	18.9	4.9	169.9	4100	28.3	1500	48.6	27.0	35.7	1392.4	1028.8	0.6	75.4	3.5
C5	6	83.1	123.7	116.1	23.7	5.9	218.4	4400	28.7	2100	50.6	28.4	38.5	1639.8	1213.6	0.6	75.7	3.6
C6	17	79.4	131.7	117.4	21.3	5.7	232.6	4600	29.6	2100	51.1	30.5	33.3	1337.2	1079.1	0.5	82.0	3.0

NB: the RLS was subjected to log (x + 1) transformation

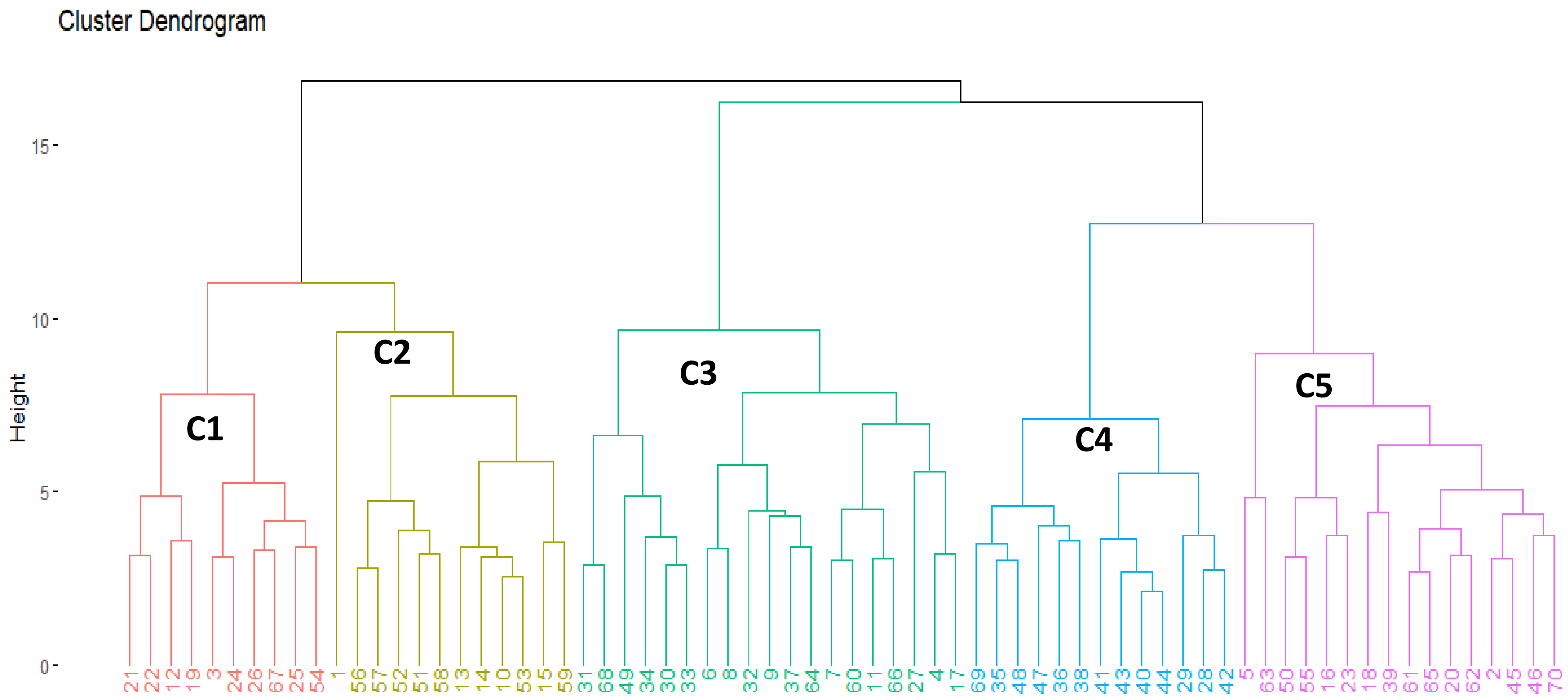


Figure 19. Dendrogram of sorghum backcrossed lines and their parental lines under full-irrigation conditions ((refer to Table 20/22 for the names of genotypes corresponding to the serial numbers)

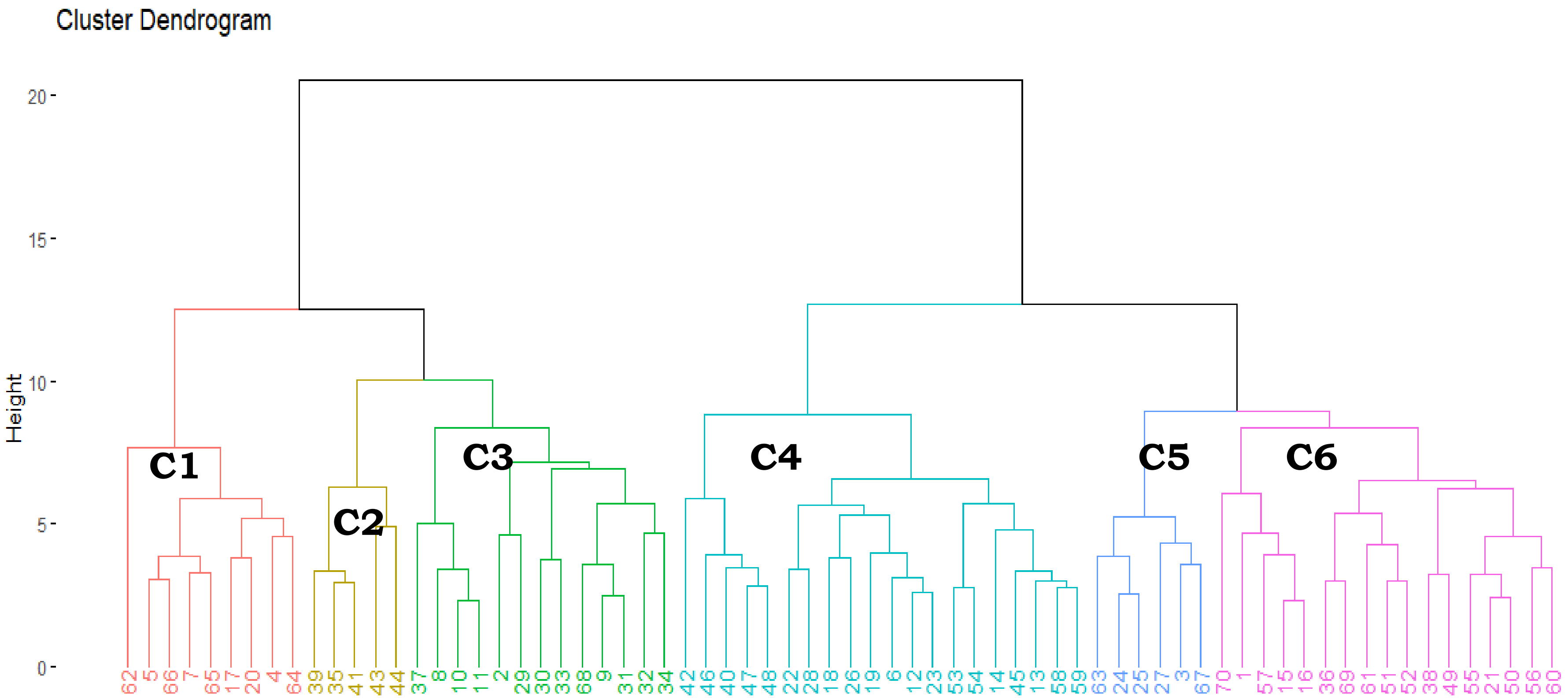


Figure 20. Dendrogram of sorghum backcrossed lines and their parental lines under water-limited conditions (refer to Table 20/22 for the names of genotypes corresponding to the serial numbers)

4.5.11. Efficiency of yield based drought tolerance indices to identify superior genotypes

4.5.11.1. Yield performance

The ANOVA for grain yield obtained from both moisture regimes showed differential responses, thereby suggesting the possibility of selecting better-performing genotypes under both production environments. Mean grain yields that varied widely in water-limited (923 to 4585 kg ha^{-1}) and full-irrigation conditions (2069 to 5704 kg ha^{-1}) were 1991 and 3633 kg ha^{-1}, respectively (Table 27). This showed that an increase of 45.2 % in yield productivity under the later compared to the former moisture condition. The grain yield under optimum condition (Yp) was high for recurrent parents compared to the majority of the developed progeny as it was expected. It was also observed that some of the converted progeny showed higher yield under full-irrigation. Among the developed progeny with higher yield and statistically similar to the recurrent parents were BC_2F_3_ETSC_16214, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16251, BC_2F_3_ETSC_16235, BC_2F_3_ETSC_16139, BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16257, BC_2F_3_ETSC_16242, and BC_2F_3_ETSC_16223 indicating the potential of these progeny under optimum production environments.

On the other hand, the converted progeny that showed highest grain yield under stressed condition (Ys) include; BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16257, and BC_2F_3_ETSC_16213 with a yield of 4585, 3538, 3107, and 2924 kg ha^{-1}, respectively. The yield under water-stressed condition (Ys) had good association with yield obtained under non-stressed condition (Yp), indicating the possibilities of obtaining potential lines for both moisture regimes. For example, converted progeny with a good yield performance under both irrigation conditions were BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16257, BC_2F_3_ETSC_16251, and BC_2F_3_ETSC_16141 (Table 27).

The consistence performances of these progeny in the two contrasting (non-stress *vis-à-vis* stress) environments represent very nearly the same character, determined nearly by the same set of genes (Falconer, 1989). This may probably have the advantage of the possibilities to forecast the performance of genotypes under one condition on the basis of performance obtained under another and can assist breeders in deciding variety development and allocation of the scarce resources (Keneni, 2007). Therefore, indirect selection for such conditions based on the results of optimum conditions may be efficient (Brennan and Byth, 1979; Rosielle and Hamblin, 1981). However, this needs to be supported by a large data from the multi-location-year experiments as many authors disproved the concept that stipulates cultivars selected under favorable environments also suit to the unfavorable ones (Ceccarelli and Grando, 1996; Banziger and Edmeades, 1997; Banziger *et al.*, 1997; Banziger and Lafitte, 1997). This is because of it is practically impossible to collect together genes responsible for superior performance in all environments into a single genotype (Annicchiarico, 2002).

4.5.11.2. Drought tolerance indices

The ANOVA for the quantitative selection indices significantly differed for all indices namely SSI, MRP, MP, HM, GMP, STI, YI, TOL and YSI (Table 27). The mean values of each tolerance indices was ranged from 1.61 to 0.12, 3.48 to 1.19, 4.5 to 1.7, 4.52 to 1.47, 4.52 to 1.58, 1.72 to 0.18, 2.22 to 0.54, 3.33 to 0.42, and 4.27 to 0.98, respectively. The highest values of SSI and TOL belonged to backcrossed progeny of BC_2F_3_ETSC_16235, BC_2F_3_ETSC_16218, BC_2F_3_ETSC_16238, BC_2F_3_ETSC_16249, BC_2F_3_ETSC_16242, BC_2F_3_ETSC_16217 and BC_2F_3_ETSC_16139, whereas lower values related to BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16229, BC_2F_3_ETSC_16247, BC_2F_3_ETSC_16213, BC_2F_3_ETSC_16252, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16149, BC_2F_3_ETSC_16239, BC_2F_3_ETSC_16230, and BC_2F_3_ETSC_16227. For instance, progeny BC_2F_3_ETSC_16235 with both greater SSI and TOL values had grain yield of 4671 and 1314 kg ha^{-1} under full-irrigation and water-limited, respectively. This signified that the progeny was highly sensitive to moisture stress after anthesis. In contrast, the lower value of SSI and TOL belonged to BC_2F_3_ETSC_16258 with grain yield of 4649 t ha^{-1} under full-irrigation and 4585 kg ha^{-1} in water-limited condition, and therefore, this line is less sensitive to stress. This means that the greater SSI and TOL values, the greater sensitivity to stress, thus a smaller value of these indices is favored, agreeing with other reports (Rosielle and Hamblin, 1981; Ghasem and Farshadfar, 2015). On the other hand, selection based on TOL with minimum yield reduction under stress condition in comparison with non-stress condition failed to identify the most tolerant genotypes (Farshadfar *et al.,* 2014). Similar to TOL, stress susceptibility index (SSI), genotypes with highest values were considered as genotypes with high drought susceptibility and poor yield stability in both moisture regimes. With regard to yield stability index (YSI) backcrossed progeny with higher values were BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16229, BC_2F_3_ETSC_16143, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16249, BC_2F_3_ETSC_16141, BC_2F_3_ETSC_16247, and BC_2F_3_ETSC_16221 and were also the most stable under stress and non-stress conditions. The lowest values of SSI and TOL as well as the highest values of YSI indicated that SSI, TOL, and YSI indices were able to identify genotypes with higher yields under drought stress rather than under non-stress conditions.

The tolerance indices MRP, GMP, STI, HM, MP and YI measure the higher stress tolerance and yield potential. Accordingly, the highest and consistent values across all indices belonged to the four converted progeny BC_2F_3_ETSC_16258, BC_2F_3_ETSC_16216, BC_2F_3_ETSC_16257, and BC_2F_3_ETSC_16142 and therefore, they were the most tolerant progeny based on all quantitative indices. These lines were the most tolerant genotypes and had lower values of SSI and TOL (Table 19). Conversely, the lowest values for all quantitative indices related to B35, BC_2F_3_ETSC_16215, BC_2F_3_ETSC_16150, BC_2F_3_ETSC_16254, BC_2F_3_ETSC_16238, BC_2F_3_ETSC_16218, BC_2F_3_ETSC_16233 and BC_2F_3_ETSC_16244. This showed that some of them were stress sensitive and the other stress tolerant (B35) but with low yield potential under both moisture regimes. Generally, this study confirmed that quantitative indices (MRP, GMP, STI, HM, MP, and YI) were comparable for identifying superior sorghum genotypes under both environments. Different studies have also used different indices for selecting tolerant genotypes in various crops. For instances, SSI and GMP were preferable in common bean (Ramirez and Kelly, 1998), STI and GMP in maize (Khallili *et al.*, 2004) and mung bean (Fernandez, 1992), durum wheat (Nouri *et al.*, 2011; Mohammadi, 2016), safflower (Majidi *et al.*, 2011; Bahrami *et al.*, 2014), HM, YI, MP, GMP, STI in bread wheat (Khakwani *et al.*, 2011; Dorostkar *et al.*, 2014; Ghasemi and Farshadfar, 2015; Amare *et al.*, 2019), Barley (Nazari and Pakniyat, 2010) and sorghum (Sory *et al.*, 2017) implies that they were useful in identifying lines that yield well under well-watered and also relatively well in water-limited condition.

Table 27. Estimates of stress tolerance attributes based on the yield obtained from non-stressed and stressed of seventy sorghum genotypes

SN	Genotypes	Yp	Ys	SSI	TOL	MRP	MP	HM	GMP	STI	YI	YSI
1	B35	2069	1318	1.11	1.12	1.19	1.70	1.47	1.58	0.25	0.56	0.50
2	BC$_2$F$_3$_ETSC_16139	4560	1722	1.32	2.99	2.12	3.15	2.30	2.67	0.57	0.83	0.40
3	BC$_2$F$_3$_ETSC_16140	3478	1493	1.35	2.04	1.73	2.51	2.02	2.25	0.45	0.74	0.39
4	BC$_2$F$_3$_ETSC_16141	3725	2831	0.82	1.68	2.34	3.23	3.08	3.16	0.88	1.24	0.63
5	BC$_2$F$_3$_ETSC_16142	5453	2309	1.20	3.15	2.69	3.91	3.15	3.49	0.91	1.18	0.46
6	BC$_2$F$_3$_ETSC_16143	2671	1921	0.70	0.87	1.72	2.32	2.27	2.30	0.43	0.96	0.68
7	BC$_2$F$_3$_ETSC_16144	3935	2469	0.88	1.63	2.28	3.16	2.86	3.01	0.77	1.19	0.60
8	BC$_2$F$_3$_ETSC_16145	2920	1812	0.77	1.10	1.71	2.37	2.20	2.28	0.37	0.89	0.66
9	BC$_2$F$_3$_ETSC_16146	3381	1558	1.09	1.86	1.69	2.45	1.94	2.17	0.39	0.76	0.51
10	BC$_2$F$_3$_ETSC_16147	3612	1631	1.24	2.06	1.80	2.60	2.11	2.33	0.45	0.81	0.44
11	BC$_2$F$_3$_ETSC_16148	3474	2015	0.98	1.65	1.91	2.69	2.42	2.54	0.57	0.95	0.56
12	BC$_2$F$_3$_ETSC_16149	3138	2064	0.58	1.06	1.93	2.62	2.49	2.56	0.54	1.07	0.74
13	BC$_2$F$_3$_ETSC_16150	3113	923	1.32	1.89	1.39	2.05	1.48	1.72	0.30	0.56	0.40
14	BC$_2$F$_3$_ETSC_16210	3333	1427	1.11	1.70	1.68	2.41	2.07	2.23	0.41	0.77	0.50
15	BC$_2$F$_3$_ETSC_16211	2759	1866	0.82	1.01	1.71	2.32	2.24	2.29	0.43	0.95	0.63
16	BC$_2$F$_3$_ETSC_16212	4197	1942	1.08	2.27	2.14	3.06	2.63	2.83	0.68	1.00	0.51
17	BC$_2$F$_3$_ETSC_16213	3803	2924	0.46	1.27	2.47	3.32	3.03	3.15	0.80	1.42	0.79
18	BC$_2$F$_3$_ETSC_16214	4878	2149	1.25	2.98	2.36	3.44	2.78	3.08	0.82	1.03	0.43
19	BC$_2$F$_3$_ETSC_16215	2270	1333	1.10	1.26	1.26	1.76	1.57	1.66	0.18	0.64	0.50
20	BC$_2$F$_3$_ETSC_16216	4727	3538	0.52	1.31	3.05	4.11	3.93	4.02	1.32	1.76	0.77
21	BC$_2$F$_3$_ETSC_16217	3971	1671	1.32	2.56	1.89	2.78	2.13	2.41	0.47	0.80	0.40
22	BC$_2$F$_3$_ETSC_16218	3362	1082	1.48	2.24	1.47	2.23	1.64	1.90	0.28	0.54	0.33
23	BC$_2$F$_3$_ETSC_16219	4268	1751	1.25	2.42	2.07	3.02	2.39	2.67	0.58	0.88	0.44
24	BC$_2$F$_3$_ETSC_16220	3973	1854	1.18	2.03	2.08	2.98	2.52	2.74	0.57	0.95	0.47
25	BC$_2$F$_3$_ETSC_16221	3317	2465	0.58	0.85	2.18	2.93	2.80	2.86	0.64	1.24	0.74
26	BC$_2$F$_3$_ETSC_16222	3317	1490	0.98	1.61	1.68	2.42	2.05	2.22	0.41	0.75	0.56
27	BC$_2$F$_3$_ETSC_16223	4282	1837	1.15	2.35	2.13	3.10	2.53	2.79	0.64	0.93	0.48
28	BC$_2$F$_3$_ETSC_16224	3663	1096	1.36	2.42	1.58	2.40	1.63	1.95	0.29	0.59	0.39
29	BC$_2$F$_3$_ETSC_16225	3363	1745	1.07	1.61	1.80	2.56	2.22	2.38	0.45	0.87	0.52
30	BC$_2$F$_3$_ETSC_16226	4172	2179	0.95	1.87	2.28	3.22	2.76	2.97	0.73	1.11	0.57
31	BC$_2$F$_3$_ETSC_16227	2675	1987	0.70	0.94	1.71	2.36	2.09	2.21	0.43	0.90	0.68

SN	Genotypes	Yp	Ys	SSI	TOL	MRP	MP	HM	GMP	STI	YI	YSI
32	BC_2F_3_ETSC_16228	4248	1885	1.17	2.26	2.17	3.12	2.60	2.85	0.62	0.98	0.47
33	BC_2F_3_ETSC_16229	3178	2417	0.36	0.59	2.09	2.79	2.70	2.74	0.56	1.24	0.84
34	BC_2F_3_ETSC_16230	2764	1799	0.68	0.98	1.67	2.30	2.13	2.21	0.36	0.89	0.69
35	BC_2F_3_ETSC_16231	2704	1985	1.00	1.37	1.65	2.34	2.05	2.18	0.39	0.81	0.55
36	BC_2F_3_ETSC_16232	2676	1749	0.75	1.02	1.58	2.18	2.03	2.10	0.32	0.85	0.66
37	BC_2F_3_ETSC_16233	3125	1211	1.05	1.71	1.52	2.21	1.73	1.94	0.35	0.65	0.53
38	BC_2F_3_ETSC_16234	3410	1625	1.10	1.82	1.78	2.56	2.11	2.32	0.43	0.80	0.50
39	BC_2F_3_ETSC_16235	4671	1314	1.61	3.33	1.98	3.03	2.00	2.45	0.55	0.67	0.27
40	BC_2F_3_ETSC_16236	3351	1368	1.34	2.02	1.62	2.37	1.91	2.13	0.40	0.69	0.39
41	BC_2F_3_ETSC_16237	3516	1343	1.32	2.17	1.66	2.45	1.88	2.13	0.38	0.68	0.40
42	BC_2F_3_ETSC_16238	3259	1128	1.48	2.28	1.44	2.16	1.61	1.86	0.29	0.55	0.33
43	BC_2F_3_ETSC_16239	2840	2090	0.62	0.86	1.80	2.45	2.31	2.37	0.53	1.00	0.72
44	BC_2F_3_ETSC_16240	3611	1951	1.07	1.76	1.96	2.76	2.47	2.60	0.62	0.96	0.52
45	BC_2F_3_ETSC_16241	3473	1930	1.01	1.61	1.93	2.70	2.42	2.56	0.54	0.98	0.54
46	BC_2F_3_ETSC_16242	4265	1564	1.33	2.83	1.91	2.87	2.19	2.50	0.49	0.75	0.40
47	BC_2F_3_ETSC_16243	2690	1869	0.85	1.16	1.64	2.28	2.05	2.16	0.34	0.86	0.62
48	BC_2F_3_ETSC_16244	3120	1265	1.39	1.93	1.50	2.20	1.75	1.95	0.33	0.63	0.38
49	BC_2F_3_ETSC_16245	3637	1655	1.18	1.89	1.83	2.63	2.24	2.42	0.46	0.83	0.47
50	BC_2F_3_ETSC_16246	3721	1533	1.22	2.07	1.84	2.66	2.16	2.39	0.52	0.80	0.45
51	BC_2F_3_ETSC_16247	2559	2374	0.45	0.48	1.87	2.47	2.39	2.43	0.47	1.11	0.80
52	BC_2F_3_ETSC_16248	3193	2886	0.74	1.20	2.26	3.08	2.84	2.95	0.78	1.22	0.66
53	BC_2F_3_ETSC_16249	3638	1386	1.36	2.29	1.74	2.56	1.91	2.18	0.43	0.71	0.38
54	BC_2F_3_ETSC_16250	3381	1474	1.27	1.95	1.68	2.45	2.00	2.20	0.41	0.73	0.42
55	BC_2F_3_ETSC_16251	4640	2278	1.21	2.48	2.44	3.49	2.99	3.23	0.86	1.14	0.46
56	BC_2F_3_ETSC_16252	3040	2368	0.46	0.70	2.04	2.74	2.58	2.65	0.58	1.17	0.79
57	BC_2F_3_ETSC_16253	3474	2549	0.83	1.43	2.11	2.94	2.70	2.81	0.63	1.13	0.62
58	BC_2F_3_ETSC_16254	2511	1492	0.92	0.95	1.42	1.97	1.85	1.90	0.29	0.76	0.58
59	BC_2F_3_ETSC_16255	3611	1510	1.29	2.05	1.74	2.56	2.04	2.27	0.44	0.74	0.42
60	BC_2F_3_ETSC_16256	3642	2107	1.06	1.69	2.04	2.88	2.46	2.64	0.70	1.01	0.52
61	BC_2F_3_ETSC_16257	4506	3107	0.75	1.37	2.77	3.77	3.63	3.69	1.20	1.55	0.66
62	BC_2F_3_ETSC_16258	4649	4585	0.12	0.14	3.48	4.49	4.52	4.52	1.72	2.22	0.95
63	Dekeba	5704	2796	1.07	2.89	3.01	4.29	3.72	3.98	1.16	1.42	0.52
64	Gambella1107	4088	2751	1.26	2.38	2.40	3.45	2.98	3.21	0.87	1.10	0.43
65	Macia	4679	2679	0.92	2.11	2.60	3.66	3.32	3.48	0.95	1.32	0.58
66	Meko	4641	2759	0.88	2.29	2.59	3.67	3.27	3.46	0.92	1.28	0.60

SN	Genotypes	Yp	Ys	SSI	TOL	MRP	MP	HM	GMP	STI	YI	YSI
67	Melkam	4207	2160	1.12	2.32	2.20	3.17	2.68	2.91	0.64	1.00	0.49
68	Teshale	3049	2651	0.79	1.15	2.09	2.84	2.74	2.79	0.65	1.15	0.64
69	Tseadachimure	4135	2698	0.75	1.65	2.45	3.40	3.13	3.25	0.83	1.28	0.66
70	Wediaker	5151	2700	1.04	2.57	2.74	3.88	3.53	3.71	1.07	1.34	0.53
	Mean	3633	1991	1	1.8	1.99	2.8	2.4	2.6	0.6	0.97	0.54
	LSD (0.05)	1560	1030	0.67	1.7	0.73	1	1.02	0.98	0.48	0.52	0.3
	CV (%)	23.6	29.5	37.4	30.4	20	19.7	23.2	20.7	20.7	29.6	31.2

Yp = yield in full irrigation, Ys = yield in water-limited, STI = stress tolerance index, MRP = mean relative performance, GMP = geometric mean productivity, HM = harmonic mean, MP = mean productivity, TOL = tolerance index, SSI = stress susceptible index, YSI = yield stability index and YI = yield index, LSD = Least significant difference, CV = Coefficient of variation

4.5.11.3. Interrelationships of the drought tolerance indices

To determine the most desirable drought tolerance criteria, the correlation coefficient between grain yield from both moisture conditions (Yp and Ys) and the quantitative indices of drought tolerance were determined (Table 28). Thus, the correlation analysis showed both positive and negative associations, showing that some of the indices are generally similar and dissimilar in genotypic ranking, respectively. The correlation coefficients of grain yield obtained from Yp showed significant positive correlation with Ys and all of the selection indices except for SSI and YSI. The significant positive correlations between Yp and Ys indicated that genotypes that performed well under non-stress also performed well under stress and *vice versa*. No significant correlation was observed between Yp and that of SSI and YSI. Ys was significantly and positively correlated with all of the indices except for SSI and TOL, which were significant negatively correlated (Figure 23). A positive correlation between TOL and Yp and the negative correlation between TOL and Ys suggested that selection based on TOL will lead to reduction of yield under well-watered conditions.

Among the drought tolerant indices that showed strong positive correlation under both non-stress and stress irrigation include; MRP (r = 0.82; 0.91), MP (r = 0.91; 0.83), HM (r = 0.71; 0.96), GMP (r = 0.81; 92), STI (r = 0.76; 0.92) and YI (r = 0.52; 1.00), respectively. This indicated that the six indices were comparably effective for selecting and predicting better grain-yielding genotypes under both moisture regimes, corroborating with previous reports (Ezatollah *et al.*, 2012; Farshadfar *et al.*, 2013; Sardouie-Nasab *et al.*, 2015; Darzi-Ramandi *et al.*, 2016). The negative associations of SSI and TOL with Ys indicated that genotypes with low SSI and TOL values had lower yield differences between non-stress and stress environments (Ceccarelli *et al.*, 1998; Rizza *et al.*, 2004; Mehammadi, 2016). SSI showed significant negative correlation with all selection indices except for TOL that showed significant positive association. Moreover, SSI showed a negative correlation with Ys while no significant correlation was detected between Yp and SSI. Thus, SSI index is suitable for identification of genotypes with low yield and tolerance to drought stress (Kharrazi and Rad, 2011). TOL had significant positive association with MP and significant negative correlation with YI and YSI. TOL had poorly correlated with indices MRP, GMP, HM, YI, MP and STI. Thus, TOL and SSI ranked differently from the other selection indices.

MRP showed strong significant correlation with MP, HM, GMP, STI, YI and YSI. MP, YI, STI, GMP, MRP, and HM showed strong positive correlation among themselves implying their similarity for genotypes ranking. According to Farshadfar *et al.*, (2001) most suitable indices for selecting stress-tolerant cultivars are those which have a relatively strong correlation with the seed yield under both moisture conditions. Therefore, evaluating correlations between stress tolerance indices and the seed yield in both environments can lead to identification of the most suitable indices. The perfect correlation between MRP and GMP (r = 1.0) that indicates these two indices are identical in genotypes ranking. YSI had strong and positive correlation with HM, GMP, STI and YI but negatively with SSI and TOL. Likewise, a perfect correlation (r = 1.00) was observed between Ys and YI. So that consistent correlations were also found between SSI and TOL, showing they can be used interchangeably for screening under stress condition. In conclusion, the strong significant positive correlations between HMP, GMP, MP and STI indices showed genotypes with a good performance in both conditions (Yp and Ys) indicating that they are the best indices for identification of superior genotypes agreeing with reports of Golabadi *et al.,* (2006) and Farshadfar *et al.,* (2014).

Table 28. Correlation coefficients (r) between grain yield of sorghum genotypes under non-stressed and stressed conditions and among selection indices

Traits	Ys	SSI	TOL	MRP	MP	HM	GMP	STI	YI	YSI
YP	0.52**	0.18ns	0.66**	0.82**	0.91**	0.71**	0.81**	0.76**	0.52**	0.18*
Ys	-	-0.7**	-0.29*	0.91**	0.83**	0.96**	0.92**	0.92**	1**	0.76**
SSI		-	0.82**	-0.38**	-0.23*	-0.52**	-0.4**	-0.4**	-0.7**	-1.0**
TOL			-	0.12ns	0.28*	-0.14ns	0.12ns	0.04ns	-0.29*	0.82**
MRP				-	0.99**	0.98**	1.00**	0.98**	0.91**	0.38**
MP					-	0.94**	0.98**	0.95**	0.83**	0.23*
HM						-	0.99**	0.97**	0.96**	0.52**
GMP							-	0.98**	0.92**	0.4**
STI								-	0.92**	0.4**
YI									-	0.71**

*, ** = significant at 0.05 and 0.01, respectively, ns = non-significant difference, STI = stress tolerance index, MRP = mean relative performance, GMP = geometric mean productivity, HM = harmonic mean, MP= mean productivity, TOL = tolerance index, SSI = stress susceptible index, YSI = yield stability index YI = yield index, Yp = mean grain yield under full-irrigation, Ys = mean grain yield underwater-limited condition.

4.5.11.4. Principal components analyses

Principal components (PC) of the grain yield under water-limited and well-watered conditions as well as drought tolerance indices of the sorghum lines are given in Table 29. The PC analysis was performed to assess the relationships between all attributes to identify superior genotypes under the two-contrasting environments. The results showed that the first two principal components (PC_1-PC_2) accounted for 98.8% of the entire variation (Figure 21). The PC_1 alone contributed the largest component score of 70.3% with high positive weight due to grain yield in the stress (Ys) (0.977), MRP (0.978), MP (0.93), HM (0.995), GMP (0.982), STI (0.972), and YI (0.977). Therefore, characters with relatively larger absolute values of eigenvector weights in PC_1 had the largest contribution to the differentiation of the genotypes into clusters. It is normally assumed that characters with larger absolute values closer to unity within the first PC influence the clustering more than those with lower absolute values closer to zero (Chahal and Gosal, 2002).

The second PC explained 28.4% of the total variation and with high weight corresponding to Yp (0.719), SSI (0.804) and TOL (0.988) due to lower value is preferred for the lower sensitivity to moisture stress and YSI (-0.820), therefore, it was grouped as drought sensitive. This study was in agreement with earlier reports that stated more than 99% of the total variation was explained by the first two principal components (Drikvand *et al.*, 2012; Nouraein *et al.*, 2013; Amare *et al.*, 2019). They also pinpointed the high association of STI, MRP, GMP, HM, MP, and YI with higher grain yield under both conditions. Therefore, selection efforts based on these indices may be more effective.

PC_1 and PC_2 were explained for grain yield potential under both irrigation conditions and stress susceptibility under stressed condition, respectively. This indicates that selecting genotypes with high PC_1 and low PC_2 is suitable for both moisture regimes. Accordingly genotypes; 4 (BC_2F_3_ETSC_16141), 17 (BC_2F_3_ETSC_16213), 20 (BC_2F_3_ETSC_16216), 52 (BC_2F_3_ETSC_16248), 61(BC_2F_3_ETSC_16257) and 62 (BC_2F_3_ETSC_16258) with high PC_1 and low PC_2 (low sensitivity and high yield) are likely better genotypes in both environments. These genotypes also showed high values of STI, MP, MRP, YI, MP, GMP and HM as well as low values of SSI and TOL. Whereas, genotypes 5 (BC_2F_3_ETSC_16142), 18 (BC_2F_3_ETSC_16214), 55 (BC_2F_3_ETSC_16251), 63 (Dekeba), 64 (Gambella1107), 65 (Macia), 66 (Meko), and 70 (Wediaker) with both high PC_1 and PC_2 are suitable in non-stress condition because they are sensitive to terminal drought. On the other side, sorghum genotypes with both low PC_1 and PC_2 had low sensitivity to stress condition but with low yield potential and can be used in breeding programs for drought tolerance (eg. B35).

Conversely, genotypes with low PC_1 and high PC_2 exhibited inferior yield performance and high sensitivity to end-season drought and therefore their cultivation and incorporating in the breeding programs may not encouraged. Finally, the two first PCs ascertained that their discrimination and correlation between yield potential and drought sensitively agreeing with earlier reports (Thomas *et al.*, 1995; Kaya *et al.*, 2002; Nazari and Pakniyat, 2011; Nouri *et al.*, 2011; Dorostkar *et al.*, 2014; Ghasemi and Farshadfar, 2015).

Table 29. Eigenvalue, variances and eigenvectors on the first five principal components for seventy sorghum genotypes to different drought tolerant selection indices grown in under full water and stressed water condition

	Principal components (PCs)	
Parameter	PC_1	PC_2
Eigenvalue	7.736	3.129
Proportion (%)	70.3	28.4
Cumulative (%)	70.3	98. 8
Yp	0.690	0.719
Ys	0.977	-0.207
SSI	-0.558	0.804
MRP	0.978	0.205
TOL	-0.084	0.988
MP	0.930	0.364
HM	0.995	0.037
GMP	0.982	0.182
STI	0.972	0.148
YI	0.977	-0.206
YSI	0.560	-0.820

Stress susceptibility index (SSI), yield stability index (YSI), stress tolerance (TOL), mean productivity (MP), mean relative performance (MRP), geometric mean productivity (GMP), stress tolerance index (STI), harmonic mean (HM), yield index (YI), and seed yield of sorghum genotypes under non-stress (Yp) and stress (Ys) conditions.

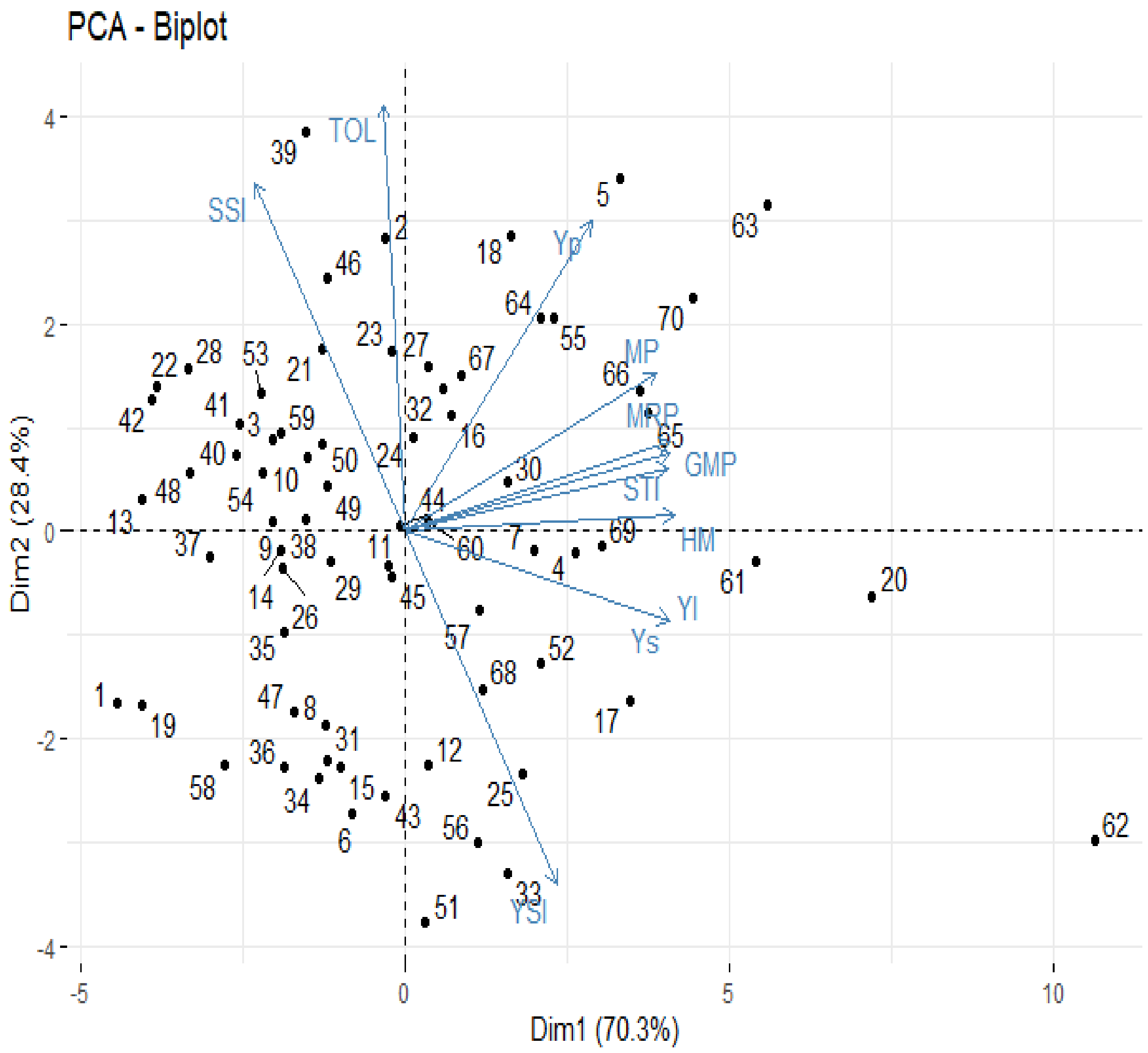


Figure 21. Biplot based on first and second components obtained from PC analysis (refer to Table 27 for the names of genotypes corresponding to the serial numbers)

4.5.11.5. Cluster analyses

Cluster analysis based on grain yield obtained from Ys and Yp conditions and drought tolerance indices were classified into three clusters (Figure 22). Clustering indices was performed to verify the accuracy of conclusions based on their similarity by average linkage method. Clusters I, II, and III encompassed 64.3%, 20%, and 15.7% of the genotypes, respectively. The first cluster (C_1, n = 45) had the largest number of genotypes characterized by high and lowest Yp and Ys, respectively. This cluster also showed lowest values of MRP, GMP, MP, STI, HM, YI and YSI, while higher values of SSI and TOL. The cluster constituted those genotypes characterized by overall inferior performances. The second cluster (C_2, n = 14) classified as intermediate in mean yield under both irrigation conditions and high vales of MRP, GMP, MP, STI, HM, YI, and YSI with lower values of TOL and SSI. Genotypes in cluster III (C_3, n = 11) had high grain yield both under non-stressed (4.52-4.76 t ha^{-1}) and stressed (3.1-4.42 t ha^{-1}) conditions and had the highest value of MRP, GMP, MP, STI, HM, YI and YSI, while lower values of SSI and TOL. This cluster consisted of desirable genotypes with overall superior performances. This study is in line with previous reports that stated genotypes can be classified adapted to moisture-stressed and non-stressed conditions using cluster analysis in various crops (Eivazi *et al.*, 2013; Johari-Pireivatlou, 2014; Bahrami *et al.*, 2014; Sory *et al.*, 2017). Generally, this study showed that selection can be improved though MRP, MP, GMP, STI, and HM.

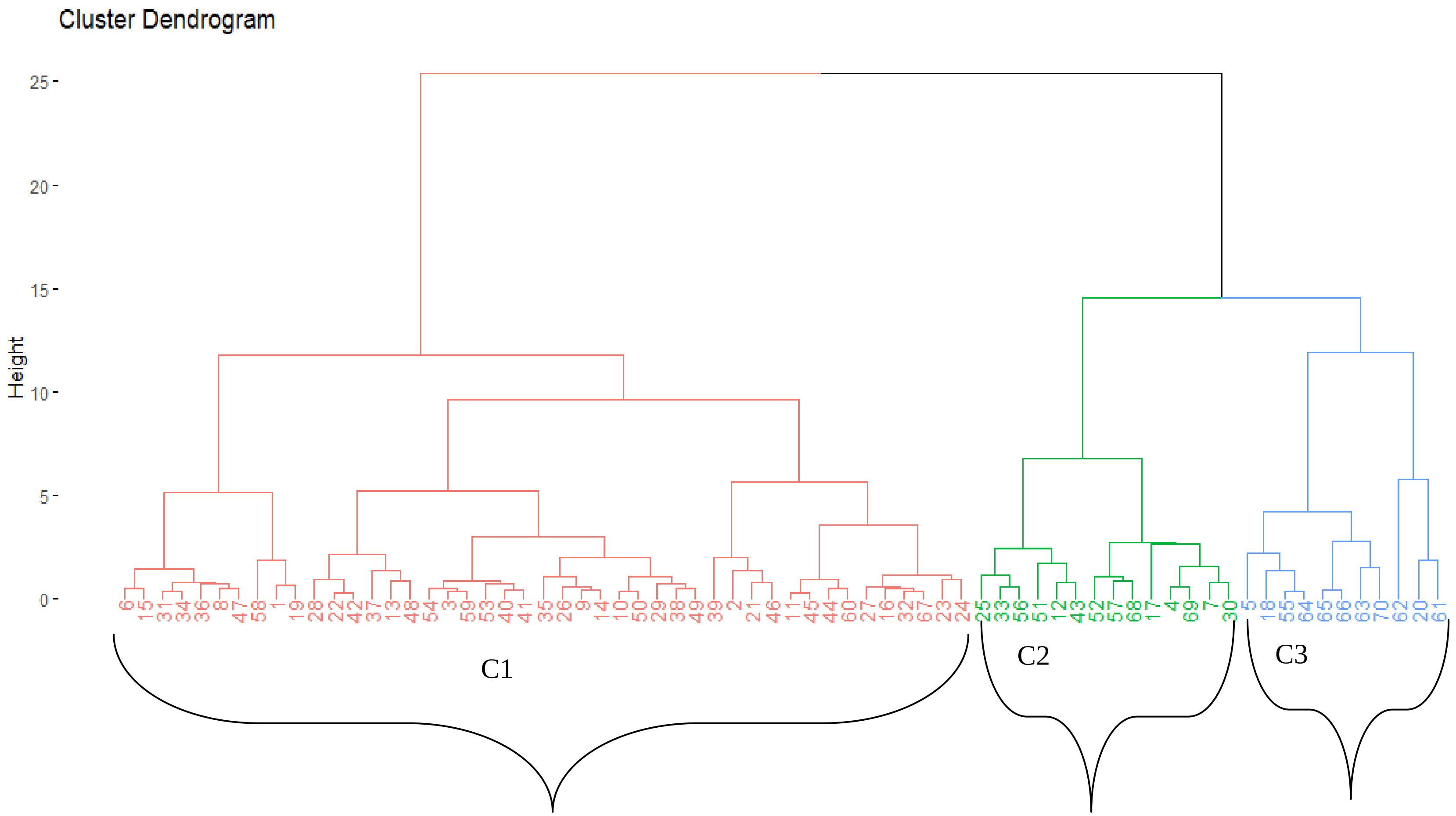


Figure 22. Cluster analysis of seventy sorghum converted progeny and their parental lines (refer to Table 27 for the names of genotypes corresponding to the serial numbers)

5. CONCLUSION AND RECOMMENDATIONS

Sorghum has been cultivated for centuries as a staple food crop for millions of people in sub-Saharan Africa and Asia. As the major cereal crop in Ethiopia, it contributes to the incomes of more than 5.3 million smallholders and contributes nutritional values to millions of consumers. Despite the potential and importance of the crop, the average national yield of the crop has remained very low due to wide array of production constraints, notably severe drought stress and intense *Striga* infestation.

Although methods in classical plant breeding have contributed immensely towards genetically insulating crops from various biotic/abiotic stresses during the last decades, classical breeding alone does not seem to be an effective approach in the current scenario of crop production wherein multiple and new threats have arisen. Modern molecular breeding approaches have emerged as a savior towards developing improved varieties in a fast & effective manner. In this regard, MAS has emerged as a powerful tool for breeders for enhancing genetic gain in crop breeding in less time and more accuracy.

This study clearly showed that markers developed elsewhere for improving traits like *Striga* and drought resistance could possibly be utilized in our breeding program to develop varieties. The introgression of *Striga* and drought resistance or tolerance gene (s) from respective donor parents to well adapted and potential varieties using MABC has resulted in generation of acceptable resistant or tolerant to both menaces and high yielding. These converted progeny could be further used for selection and release as a variety for the target environments. The introgression of new resistance genes from other sources into the breeding scheme in addition to retaining and maintaining the already available ones at least for integrated use with other control methods may also be advisable. To these efforts, 118 and 61 converted progeny were developed for *Striga* and drought resistance, respectively using MABC and subjected to evaluation in the target environments.

It may be concluded from this study that the donors (Framida, Gobiye and Birhan) were promising sources of resistance to *Striga* as logically expected and can be recommended for future use in breeding programs. The result also indicated that low MGD and GR values in the AGA could be effective for selection of resistant genotypes, as these traits were found to be indicative for existence of low germination stimulant mode of resistance mechanism. Of the 118 test backcrossed progeny, 23% showed <10 mm of MGD and germination rates of <30%, revealing provision of low germination stimulant (*lgs*).

In the same manner, the field evaluation for *Striga* resistance of these backcrossed progeny confirmed that there seems a tendency to shift the resistance of progeny towards that of the resistant parents (donor parents) while retaining the phenotype of the recurrent parents. About 21.2% of the progeny were found with both very good field resistances to *Striga* and valuable agronomic attributes like yield. Therefore, resistant/tolerant progeny selected based on the results of such evaluation can be combined with other management options to control the parasite in areas that are severely infested with *S. hermonthica.*

The stacking of several genes controlling each component of resistance into a single genotype is a preferred strategy to deliver more durable resistance to *Striga hermonthica* by pulling together the cumulative effects of different genes responsible for *Striga* resistance. The significant positive associations between *Striga* seeds germination stimulant activity in the AGA and *Striga* plant counts in the field suggested that indirect selection based on AGA would be effective for resistance based on low stimulant production (*lgs*).

The results from stay-green QTL introgression from donor parent (B35) have been successfully introgressed into the recurrent parents. It was observed that some of the converted progeny exhibit stay-green characteristics (greater leaf area, delayed and low leaf senescence, and high chlorophyll content) and outperform in economical traits like grain yield, thousand seeds weight and biomass. Of the thirteen QTLs, progeny that contained *stg1+stg2+stg3a+stg4* markers showed overall superior performance in most of the agronomic and physiological characters under both moisture regimes. Based on the yield tolerance indices measurements, the correlation and principal component analysis revealed drought tolerance indices MRP, MP, GMP, STI and HM are superior indices to identify genotypes that yield well under stressed and optimal moisture conditions.

It is believed that a substantial variation in *Striga* resistance and drought tolerance is available in sorghum gene pool globally including Ethiopia. The deployment of such genes into the already adapted varieties is expected to generate *Striga* resistance and drought tolerance breeding materials. Thus, creating an integrated population specific gene-based map of the sorghum genome onto which the loci conferring resistance to *Striga* and drought in Ethiopia, remains the subject of future investigation.

In general, the introgression of quantitative trait loci into popular and farmers preferred cultivars resulted in the generation of promising backcrossed lines for *Striga* resistance and drought tolerance. Hence, those backcross lines should be included in variety evaluation and release process for the target environments so as farmers could get a new version of his preferred varieties with a good level of resistance or tolerance to both constraints.

Although selection for low germination distance based on the AGA is advantageous, valuable materials possessing resistance mechanisms other than low stimulant production may be lost if these traits are not additionally assessed. Therefore, the use of further assays such as extended AGA and paper roll assay that targeted both the pre- and post-attachment stages of parasitic development, respectively (Ejeta *et al.*, 2000a; 2007), which allow the non-destructive, quick and inexpensive evaluation of individual plants for resistance mechanisms other than the low stimulant character is essential.

While marker assisted selection has been effective for the manipulation of large effect alleles with known association to a marker, it has been at an impasse when many alleles of small effect segregate and no substantial, reliable effects can be identified (Zhong *et al.*, 2006; Wang and Chee, 2010). Thus, breeding effort should gear towards the use of genomic selection or genome-wide association selection that simultaneously estimates many (hundreds or thousands) markers, which cover the entire genome in a dense manner so that all genes are expected to be in linkage disequilibrium with at least some of the markers.

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Appendix 1. The mean performance of backcrossed and their parental lines for agronomic traits and reaction to *Striga hermonthica* at Kafta Humera during 2018/2019 cropping season

Genotype	DTF	PLHT	PL	DTM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
AbaAre-1	81.3	157.6	15.5	134.0	6250	233.3	2.17(148)	2.29(198.7)	0.85(6)	2.95(887.5)	3.63(4283.5)	4.39(25325.5)	0.65(3.5)
America-1	75.7	149.4	18.3	126.3	3750	243.3	2.31(204.7)	2.31(204.7)	0.85(6)	3.09(1226.5)	3.63(4331.5)	4.42(26690.5)	0.69(4)
BC2F3_ETSC_17001	72.3	148.2	16.6	125.3	3750	230.0	1.73(54.7)	2.10(124.7)	0.87(6.7)	2.54(348)	3.45(2833)	4.23(17215)	0.74(4.5)
BC2F3_ETSC_17002	75.7	158.6	19.2	124.7	5850	233.3	1.82(65.7)	2.18(150)	0.92(7.7)	2.69(494.5)	3.47(2971)	4.27(18830.5)	0.69(4)
BC2F3_ETSC_17003	83.7	157.8	17.6	126.7	5850	200.0	1.72(56.7)	2.10(126.7)	0.9(7)	2.56(425)	3.35(2241.5)	4.12(13316)	0.54(2.5)
BC2F3_ETSC_17004	83.3	166.4	14.7	130.3	6250	253.3	2.30(202.7)	2.30(202.7)	0.87(6.7)	3.11(1343)	3.59(3900.5)	4.38(24075)	0.60(3)
BC2F3_ETSC_17005	83.7	248.7	16.8	133.7	5000	200.0	2.14(138.7)	2.26(180.7)	0.9(7)	2.98(1001)	3.51(3253)	4.23(17118)	0.65(3.5)
BC2F3_ETSC_17006	80.7	142.2	17.2	129.0	4150	213.3	2.44(276.7)	2.44(276.7)	0.92(7.7)	3.31(2136.5)	3.79(6274)	4.60(42150)	0.78(5)
BC2F3_ETSC_17007	84.0	150.7	15.3	134.0	5000	246.7	2.25(180)	2.27(188)	0.85(6)	3.03(1078.5)	3.57(3749)	4.36(23080)	0.69(4)
BC2F3_ETSC_17008	74.0	162.7	24.1	125.3	3750	350.0	2.17(150.7)	2.17(150.7)	0.95(8)	3.07(1174)	3.50(3223)	4.31(20554.5)	0.78(5)
BC2F3_ETSC_17009	81.3	167.6	23.3	125.3	6250	393.3	2.2(167.7)	2.26(184.7)	0.85(6)	2.98(1004)	3.58(3915)	4.32(21383)	0.65(3.5)
BC2F3_ETSC_17010	81.3	158.2	22.5	127.0	5000	256.7	2.1(135)	2.10(135)	0.92(7.7)	2.95(915)	3.41(2923)	4.18(17374)	0.69(4)
BC2F3_ETSC_17011	79.7	169.6	22.7	124.7	4600	330.0	2.18(151.7)	2.26(181.7)	0.87(6.7)	2.99(989.5)	3.63(4305)	4.39(24418.5)	0.78(5)
BC2F3_ETSC_17012	80.0	161.6	22.6	126.7	6250	306.7	2.16(151)	2.16(151)	0.93(7.7)	3.02(1103.5)	3.51(3391.5)	4.25(18341)	0.69(4)
BC2F3_ETSC_17013	80.0	133.1	26.0	123.3	3000	636.7	1.72(68.7)	1.73(71)	0.92(7.7)	2.55(435)	3.11(1884)	3.86(10625.5)	0.74(4.5)
BC2F3_ETSC_17014	79.7	153.1	22.7	128.3	6700	400.0	2.2(168.7)	2.20(168.7)	0.92(7.7)	3.06(1157)	3.52(3491)	4.23(18297.5)	0.59(3)
BC2F3_ETSC_17015	75.7	163.8	19.3	126.3	5850	243.3	2.17(151.7)	2.28(187.7)	0.85(6)	2.95(909)	3.48(3041)	4.19(16032)	0.59(3)
BC2F3_ETSC_17016	77.7	124.5	19.0	122.7	4600	233.3	2.14(140.7)	2.34(219.7)	0.85(6)	2.92(843)	3.72(5259.5)	4.53(33853.5)	0.78(5)
BC2F3_ETSC_17017	77.0	179.7	20.7	121.3	4200	246.7	2.07(117)	2.23(168.7)	0.92(7.7)	2.94(893.5)	3.54(3472)	4.34(22017.5)	0.65(3.5)
BC2F3_ETSC_17018	77.3	155.0	18.5	127.3	4600	236.7	2.07(117)	2.28(193)	0.93(7.7)	2.93(865.5)	3.70(5001.5)	4.49(31034)	0.7(4.5)4
BC2F3_ETSC_17019	82.7	154.3	17.3	122.0	3300	230.0	2.05(112)	2.25(176.7)	0.92(7.7)	2.91(813.5)	3.58(3774)	4.41(25555)	0.69(4)
BC2F3_ETSC_17020	76.3	154.0	20.0	124.0	5000	290.0	2.03(105.7	2.20(168.7)	0.92(7.7)	2.89(783)	3.48(3431.5)	4.26(22192)	0.56(3)
BC2F3_ETSC_17021	77.0	179.7	20.0	123.3	5000	236.7	1.91(81)	2.05(122)	0.92(7.7)	2.76(579)	3.34(2475)	4.07(14331)	0.54(2.5)
BC2F3_ETSC_17022	73.3	162.6	15.2	118.0	5850	303.3	1.94(89)	2.29(196.7)	0.85(6)	2.71(532)	3.72(5234)	4.46(28895)	0.60(3)
BC2F3_ETSC_17023	75.0	163.8	17.3	123.0	5400	463.3	1.89(107.7)	2.18(156)	0.87(6.7)	2.69(656.5)	3.56(3912)	4.31(21977)	0.60(3)
BC2F3_ETSC_17024	74.0	167.4	16.5	121.0	4600	276.7	1.99(99.7)	2.25(180)	0.92(7.7)	2.85(703)	3.60(4144.5)	4.37(23837)	0.65(3.5)
BC2F3_ETSC_17025	76.3	166.4	21.2	126.0	5400	403.3	1.8(71)	1.96(106)	0.85(6)	2.57(425)	3.36(2884.5)	4.09(16494)	0.59(3)

Genotype	DTF	PLHT	PL	DTM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17026	76.0	165.8	15.5	123.0	5850	316.7	2.23(172.7)	2.28(191)	0.85(6)	3.01(1034.5)	3.65(4566.5)	4.39(25151)	0.60(3)
BC2F3_ETSC_17027	73.0	174.7	16.1	122.7	5400	260.0	2.15(140)	2.32(216)	0.90(7)	2.99978.5)	3.68(5037)	4.43(28523.5)	0.65(3.5)
BC2F3_ETSC_17028	73.3	166.6	23.8	123.7	4600	650.0	1.62(53)	2.14(141)	0.85(6)	2.38(319)	3.41(2581)	4.10(12683.5)	0.54(2.5)
BC2F3_ETSC_17029	79.3	193.9	17.5	113.0	10890	290.0	1.83(66.3)	1.90(78)	0.97(8.3)	2.74(553.7)	3.44(2742.7)	4.02(10506)	0.60(3)
BC2F3_ETSC_17031	83.7	124.7	17.8	132.7	2500	230.0	1.99(99)	2.23(180.7)	0.92(7.7)	2.86(785)	3.59(4291.5)	4.38(28604)	0.78(5)
BC2F3_ETSC_17032	79.7	156.6	17.8	123.3	5400	233.3	2.11(132.7)	2.24(173.7)	0.85(6)	2.89(794.5)	3.54(3481)	4.34(21801)	0.78(5)
BC2F3_ETSC_17033	83.0	154.4	21.5	123.0	6250	163.3	1.9(82)	1.99(97)	0.85(6)	2.67(493.5)	3.28(1937.5)	3.98(9957.5)	0.59(3)
BC2F3_ETSC_17034	82.3	124.1	19.3	127.3	3300	233.3	1.81(64)	2.26(179.7)	0.85(6)	2.59(384)	3.54(3497.5)	4.30(20044.5)	0.74(4.5)
BC2F3_ETSC_17035	77.7	126.7	32.3	120.0	3750	193.3	1.96(93)	2.18(151.7)	0.90(7)	2.80(674.5)	3.45(2876.5)	4.24(17839.5)	0.78(5)
BC2F3_ETSC_17036	77.7	158.9	20.3	129.3	4600	203.3	2.18(152)	2.26(179.7)	1.0(9)	3.13(1369)	3.55(3569)	4.37(23576.5)	0.74(4.5)
BC2F3_ETSC_17037	80.7	97.1	15.5	123.0	3300	196.7	2.01(105)	2.33(218)	0.87(6.7)	2.82(665.5)	3.73(5679.5)	4.49(33204)	0.78(5)
BC2F3_ETSC_17038	82.0	148.6	23.3	129.3	4150	163.3	2.01(100.7)	2.26(182)	0.92(7.7)	2.87(738)	3.62(4199.5)	4.41(25468.5)	0.74(4.5)
BC2F3_ETSC_17039	79.0	172.1	19.6	123.0	3750	206.7	1.57(37.7)	2.10(128.7)	0.85(6)	2.34(227)	3.42(2654.5)	4.18(15520.5)	0.78(5)
BC2F3_ETSC_17040	82.7	110.8	19.0	127.3	6650	210.0	1.99(101.7)	2.17(148)	0.93(7.7)	2.86(741.5)	3.49(3104)	4.21(16537)	0.6(4)9
BC2F3_ETSC_17041	82.7	123.4	20.5	123.3	3750	203.3	1.97(102)	2.18(152.7)	0.92(7.7)	2.85(846.5)	3.52(3380)	4.32(20961)	0.74(4.5)
BC2F3_ETSC_17042	83.0	110.0	19.2	128.7	3300	163.3	1.95(99)	2.17(151)	0.85(6)	2.73(595.5)	3.61(4309)	4.38(25523)	0.74(4.5)
BC2F3_ETSC_17043	77.3	115.6	18.1	124.3	3350	203.3	1.98(95.7)	2.23(167)	0.87(6.7)	2.79(628)	3.54(3497)	4.34(22103.5)	0.78(5)
BC2F3_ETSC_17044	75.7	114.8	20.4	124.7	4200	240.0	1.92(84.7)	2.13(137)	0.92(7.7)	2.78(605.5)	3.40(2625)	4.16(15879.5)	0.74(4.5)
BC2F3_ETSC_17045	78.0	141.5	17.3	128.0	1750	210.0	1.57(41.7)	1.83(66.7)	0.90(7)	2.39(268.5)	3.26(1868)	3.93(8788.5)	0.74(4.5)
BC2F3_ETSC_17046	77.7	119.6	16.0	123.3	5000	410.0	1.86(72)	1.95(88.7)	0.92(7.7)	2.73(548)	3.35(2295.5)	4.10(12863.5)	0.74(4.5)
BC2F3_ETSC_17047	79.7	109.1	11.0	126.3	3350	203.3	1.93(102)	2.17(147)	0.93(7.7)	2.79(730)	3.55(3529)	4.29(19923.5)	0.78(5)
BC2F3_ETSC_17048	80.0	117.7	14.5	130.7	2100	203.3	2.07(116)	2.32(210.7)	0.85(6)	2.84(693.5)	3.70(5266.5)	4.47(30760)	0.78(5)
BC2F3_ETSC_17049	82.0	111.5	14.0	132.7	2500	203.3	1.91(79.7)	2.08(125.7)	0.85(6)	2.68(476)	3.38(2466.5)	(13526)	0.69(4)
BC2F3_ETSC_17050	82.7	137.7	19.0	127.0	3750	166.7	1.7(54.7)	1.96(124)	0.95(8)	2.58(405.5)	3.30(2845.5)	4.08(17389.5)	0.70(4)
BC2F3_ETSC_17051	78.3	168.7	15.8	123.7	5400	270.0	1.88(75.7)	2.13(144.7)	0.92(7.7)	2.75(561)	3.49(3156.5)	4.19(16111)	0.60(3)
BC2F3_ETSC_17052	82.0	155.3	20.6	126.3	5000	273.3	1.98(95)	2.04(111)	0.93(7.7)	2.84(699.5)	3.35(2276)	4.05(11486)	0.46(2)
BC2F3_ETSC_17053	80.3	158.7	16.0	125.0	4600	236.7	1.82(73)	2.06(115)	1.0 (9)	2.76(655)	3.36(2270.5)	4.07(11711)	0.54(2.5)
BC2F3_ETSC_17054	77.7	179.7	19.9	126.0	5850	240.0	1.94(87)	2.14(139)	0.92(7.7)	2.80(625.5)	3.47(2975)	4.20(15948.5)	0.60(3)
BC2F3_ETSC_17055	76.7	166.7	15.9	127.7	5400	303.3	2.03(115)	2.04(119.7)	0.87(6.7)	2.83(718.5)	3.42(2759)	4.18(16587)	0.60(3)
BC2F3_ETSC_17056	76.3	160.9	26.5	126.3	4600	383.3	1.55(40)	1.63(51.7)	0.98(8.7)	2.47(350)	2.91(1211)	3.67(7238.5)	0.51(2.5)

Genotype	DTF	PLHT	PL	DTM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17057	72.3	169.2	20.9	122.0	3300	573.3	1.60(39.7)	1.88(79.7)	0.92(7.7)	2.45(283)	3.21(1750)	3.91(9262.5)	0.64(3.5)
BC2F3_ETSC_17058	70.7	172.3	24.8	122.0	4550	666.7	1.97(92.7)	2.05(111.7)	0.98(8.7)	2.89(785.5)	3.33(2200.5)	4.09(12918)	0.48(2)
BC2F3_ETSC_17059	74.3	146.8	19.1	121.0	2900	283.3	2.01(101.7)	2.43(272.7)	0.92(7.7)	2.88(763.5)	3.81(6462)	(43411)	0.74(4.5)
BC2F3_ETSC_17060	74.0	125.8	20.2	129.0	3750	246.7	1.92(83)	2.11(131)	0.85(6)	2.70(496)	3.44(2765)	4.18(15252.5)	0.78(5)
BC2F3_ETSC_17061	72.0	161.3	22.4	120.3	4150	260.0	1.76(62)	1.99(105.7)	1.0(9)	2.71(559)	3.33(2226)	4.09(13267)	0.69(4)
BC2F3_ETSC_17062	75.7	170.3	20.7	125.0	3300	1200.0	2.02(113.7)	2.29(200)	0.92(7.7)	2.9(937)	3.62(4465.5)	4.36(26077.5)	0.60(3)
BC2F3_ETSC_17063	75.0	177.5	20.4	123.7	5800	573.3	1.63(42)	1.88(90)	0.92(7.7)	2.48(301)	3.16(1828.5)	3.83(9205.5)	0.46(2)
BC2F3_ETSC_17064	74.3	174.9	19.3	124.3	4600	353.3	1.73(53)	2.18(150.7)	0.92(7.7)	2.59(387.5)	3.46(2862)	4.18(15472)	0.60(3)
BC2F3_ETSC_17065	79.3	148.9	19.9	123.3	1700	203.3	2.14(140.7)	2.27(185.7)	0.92(7.7)	3(992)	3.55(3537.5)	4.35(22488)	0.74(4.5)
BC2F3_ETSC_17066	82.0	156.0	21.8	121.3	3750	230.0	1.99(96)	2.26(196.7)	0.92(7.7)	2.85(718.5)	3.58(4110.5)	4.30(23786.5)	0.59(3)
BC2F3_ETSC_17067	78.0	177.1	20.6	126.7	2900	240.0	2.12(132.7)	2.30(198.7)	0.85(6)	2.9(793.5)	3.60(3941)	4.32(21110.5)	0.70(4)
BC2F3_ETSC_17068	79.7	134.1	14.1	123.7	1700	163.3	1.58(61)	2.00(108)	0.92(7.7)	2.4(375.5)	3.27(2064.5)	4.00(11793.5)	0.74(4.5)
BC2F3_ETSC_17069	76.7	101.0	21.4	122.7	4150	200.0	1.71(54.7)	2.17(149)	0.92(7.7)	2.59(448)	3.44(2832)	4.23(17883)	0.78(5)
BC2F3_ETSC_17070	79.3	148.0	16.1	126.0	5000	196.7	1.89(77.7)	1.89(77.7)	0.85(6)	2.66(466.5)	3.22(1712.5)	3.92(8435.5)	0.60(3)
BC2F3_ETSC_17071	84.0	136.1	17.8	135.0	1700	166.7	1.85(73.7)	2.02(107.7)	1.0(9)	2.8(661)	3.39(2609)	4.15(15086.5)	0.78(5)
BC2F3_ETSC_17072	75.0	179.7	16.8	111.0	4887	120.0	1.91(92.3)	2.02(107)	1.0(9)	2.86(832)	3.62(4333.7)	4.20(16418.3)	0.67(3.7)
BC2F3_ETSC_17073	66.3	191.0	17.3	113.3	5330	140.0	1.84(69)	1.95(91)	0.94(7.7)	2.71(522)	3.42(2962)	4.03(11788.7)	0.66(3.7)
BC2F3_ETSC_17074	72.3	170.1	15.8	114.3	9557	386.7	1.87(76)	1.92(87.7)	0.89(7)	2.7(521.3)	3.41(2743.7)	4.00(10931)	0.63(3.3)
BC2F3_ETSC_17075	75.3	135.5	12.7	113.3	1777	124.3	2.01(104)	2.03(108.3)	1.0(9)	2.96(936.3)	3.66(4663)	4.23(17354.7)	0.78(5)
BC2F3_ETSC_17076	80.3	134.4	12.8	114.7	6003	118.7	1.93(95.7)	1.98(102)	0.94(7.7)	2.81(733.3)	3.48(3123.3)	4.07(12334.3)	0.69(4)
BC2F3_ETSC_17077	68.3	179.8	21.8	113.0	6223	320.0	1.83(77)	1.95(97.7)	0.87(6.7)	2.63(498)	3.40(2753.3)	3.92(10632)	0.56(3)
BC2F3_ETSC_17078	74.3	175.6	17.0	112.3	6890	233.3	1.72(55.3)	1.82(69)	0.88(6.7)	2.53(393)	3.34(2558.3)	3.86(8742)	0.63(3.3)
BC2F3_ETSC_17079	78.7	124.3	12.3	113.3	3780	128.3	2.04(110.7)	2.09(124)	0.98(8.7)	2.97(969.7)	3.67(4739)	4.29(19611)	0.72(4.3)
BC2F3_ETSC_17080	81.0	174.3	16.8	110.7	8220	160.0	2.07(116.7)	2.09(121.3)	0.94(7.7)	2.95(883)	3.55(3555.7)	4.16(14701.3)	0.66(3.7)
BC2F3_ETSC_17081	80.7	134.3	13.6	112.3	2220	130.0	2.17(160)	2.19(166)	0.97(8.3)	3.08(1379.3)	3.81(6846.7)	4.39(26384.3)	0.72(4.3)
BC2F3_ETSC_17082	74.3	144.1	15.7	111.0	5110	330.0	1.95(94.3)	2.00(101)	1.0(9)	2.9(848.7)	3.53(3454.3)	4.17(14791.7)	0.63(3.3)
BC2F3_ETSC_17083	79.7	95.3	10.0	112.7	3110	26.7	2.08(121)	2.08(121)	1.0(9)	3.03(1088)	3.66(4689)	4.30(20314)	0.78(5)
BC2F3_ETSC_17084	73.3	160.7	15.9	112.3	5113	540.0	1.91(82.7)	1.95(89)	0.9(7)	2.75(579)	3.29(2077.3)	3.97(9783.3)	0.56(2.7)
BC2F3_ETSC_17085	85.3	167.4	12.0	112.0	7110	192.3	2.03(107.3)	2.03(107.3)	0.86(6.3)	2.82(671.3)	3.37(2388.3)	3.95(9302.7)	0.52(2.3)
BC2F3_ETSC_17086	73.0	180.4	15.1	110.7	9777	1206.7	1.98(94.3)	1.98(94.3)	0.94(7.7)	2.85(733.7)	3.54(3506)	4.11(13296.3)	0.56(2.7)

Genotype	DTF	PLHT	PL	DTM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17087	76.3	192.1	21.2	123.7	2900	203.3	1.89(81.7)	2.15(141.7)	1.0(9)	2.84(735.5)	3.31(2106.5)	4.07(12355)	0.46(2)
BC2F3_ETSC_17088	77.7	162.3	19.1	123.7	3750	203.3	1.87(78)	2.22(176.7)	1.0(9)	2.82(702)	3.53(3495)	4.32(21732.5)	0.78(5)
BC2F3_ETSC_17089	79.7	156.7	20.1	124.3	4150	233.3	2.03(105.3)	2.19(156)	1.0(9)	2.93(962.5)	3.53(3446)	4.31(21132.5)	0.74(4.5)
BC2F3_ETSC_17090	75.7	154.4	24.1	124.7	4150	570.0	1.80(62.7)	1.85(70)	0.85(6)	2.57(373)	3.14(1395.5)	3.85(7111)	0.54(2.5)
BC2F3_ETSC_17091	82.7	163.4	17.4	129.7	7100	163.3	1.88(90)	2.11(131.7)	0.92(7.7)	2.76(764)	3.44(2929.5)	4.21(17890)	0.69(4)
BC2F3_ETSC_17092	82.0	139.3	18.5	128.7	5000	163.3	1.90(81.7)	2.09(124)	0.95(8)	2.8(676)	3.43(2728)	4.20(16384.5)	0.74(4.5)
BC2F3_ETSC_17093	84.7	163.4	20.3	131.3	5850	163.3	1.95(93.7)	2.03(107)	0.95(8)	2.86(781.5)	3.28(1924)	3.99(10115.5)	0.54(2.5)
BC2F3_ETSC_17094	76.3	169.5	20.6	127.0	4200	236.7	2.04(110)	2.28(209.7)	0.92(7.7)	2.91(810)	3.47(3349)	4.23(19537.5)	0.54(2.5)
BC2F3_ETSC_17095	74.3	174.4	23.1	121.0	4150	586.7	2.02(104)	2.02(104)	0.92(7.7)	2.89(778)	3.30(1982.5)	4.01(10502.5)	0.48(2)
BC2F3_ETSC_17096	74.3	162.7	20.4	122.7	3750	496.7	2.09(128.7)	2.09(128.7)	0.92(7.7)	2.94(887)	3.44(2787.5)	4.19(15428)	0.60(3)
BC2F3_ETSC_17097	72.0	162.2	18.9	128.7	5000	593.3	2.05(115.7)	2.05(115.7)	0.85(6)	2.83(692)	3.40(2801.5)	4.10(15060)	0.51(2.5)
BC2F3_ETSC_17098	72.0	181.8	22.4	124.0	3750	280.0	1.87(74)	1.96(90)	0.85(6)	2.64(442.5)	3.42(2690)	4.16(14606)	0.74(4.5)
BC2F3_ETSC_17099	74.0	145.5	16.8	119.7	1000	163.3	1.75(60.7)	1.75(60.7)	0.95(8)	2.65(517)	2.97(1032.5)	3.73(5832.5)	0.65(3.5)
BC2F3_ETSC_17100	72.3	177.5	17.0	121.3	4150	240.0	1.95(97)	2.04(112.7)	0.85(6)	2.72(581)	3.37(2502.5)	4.09(13559)	0.54(2.5)
BC2F3_ETSC_17101	69.0	176.7	12.7	119.0	2500	596.7	0.97(12.7)	1.01(12.7)	0.87(6.7)	1.73(94.5)	2.13(191)	2.66(832)	0.30(1)
BC2F3_ETSC_17102	69.0	174.6	17.7	121.3	5000	290.0	2.04(110.7)	2.18(149)	0.85(6)	2.81(664)	3.54(3453.5)	4.26(18549)	0.54(2.5)
BC2F3_ETSC_17103	71.7	182.1	17.5	120.7	5000	333.3	2.16(147.7)	2.22(167)	0.92(7.7)	3.04(1151.5)	3.57(3685.5)	4.33(21578.5)	0.59(3)
BC2F3_ETSC_17104	76.0	202.5	16.8	120.3	1000	163.3	2.14(138.7)	2.14(138.7)	1.0(9)	3.09(1245)	3.44(2778.5)	4.30(20102)	0.70(4)
BC2F3_ETSC_17105	73.0	205.6	24.5	124.0	5400	1066.7	1.74(62)	1.73(59.7)	1.0(9)	2.69(558)	3.17(1905.5)	3.90(11230.5)	0.46(2)
BC2F3_ETSC_17106	63.3	172.3	21.7	113.0	6667	696.7	2.12(134.3)	2.13(137)	0.94(7.7)	3(1057.3)	3.61(4803.7)	4.20(18933.3)	0.63(3.3)
BC2F3_ETSC_17107	75.0	219.6	22.8	114.7	12000	1326.7	1.79(69.3)	1.83(73.3)	0.88(6.7)	2.61(467.3)	3.26(1899)	3.81(7109.7)	0.42(1.7)
BC2F3_ETSC_17108	77.0	231.6	20.1	114.7	9777	1393.3	1.93(99.7)	1.93(99.7)	0.87(6.7)	2.73(751.3)	3.30(2469.7)	3.86(10307.7)	0.53(2.7)
BC2F3_ETSC_17109	76.0	187.8	14.5	114.3	7667	910.0	1.84(75.7)	1.84(75.7)	0.84(6.3)	2.6(555.3)	3.21(2446.7)	3.74(9500)	0.49(2.3)
BC2F3_ETSC_17111	75.3	138.1	16.5	111.3	6667	1156.7	1.77(68)	1.79(70.3)	0.90(7)	2.6(531.3)	3.20(2026.3)	3.78(8297)	0.49(2.3)
BC2F3_ETSC_17112	79.7	117.3	17.0	130.0	2900	163.3	1.90(79.7)	2.22(167)	0.92(7.7)	2.77(626.5)	3.51(3280.5)	4.32(21179.5)	0.74(4.5)
BC2F3_ETSC_17113	80.0	132.2	22.9	123.7	3300	163.3	1.93(83.7)	1.99(98)	0.92(7.7)	2.79(620)	3.33(2172)	4.07(12169.5)	0.69(4)
BC2F3_ETSC_17114	79.0	142.0	17.9	126.0	1000	203.3	1.91(81.7)	1.91(81.7)	0.95(8)	2.81(655)	3.01(1021)	3.82(6670)	0.74(4.5)
BC2F3_ETSC_17115	81.7	129.5	20.9	125.0	2900	236.7	2.11(127.7)	2.11(127.7)	0.85(6)	2.88(765)	3.38(2424)	4.18(15051.5)	0.78(5)
BC2F3_ETSC_17116	82.0	113.9	17.5	129.7	1700	200.0	1.91(103)	2.14(140)	0.92(7.7)	2.75(659)	3.45(3023.5)	4.17(16349)	0.78(5)
BC2F3_ETSC_17117	79.0	89.9	11.5	119.3	1700	163.3	2.06(114.7)	2.08(119)	1.0(9)	3.01(1031)	3.43(2686)	4.26(18487.5)	0.78(5)

Genotype	DTF	PLHT	PL	DTM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17119	81.7	104.2	17.3	124.0	1700	163.3	1.79(69.7)	1.84(83)	0.81(5.7)	2.53(402)	3.19(1837)	3.92(10886)	0.74(4.5)
BC2F3_ETSC_17120	83.7	99.1	14.5	129.0	2900	163.3	2.15(142)	2.17(150)	0.92(7.7)	3.01(1027.5)	3.48(3032)	4.27(18679)	0.74(4.5)
BC2F3_ETSC_17121	78.0	141.8	22.3	127.3	4150	163.3	2.22(164)	2.27(187.7)	0.85(6)	2.99(986)	3.65(4604.5)	4.43(27972.5)	0.65(3.5)
Berjokecoll#1	83.0	154.1	21.4	137.0	4150	163.3	2.05(112.7)	2.05(112.7)	0.85(6)	2.82(676)	3.38(2441.5)	4.11(12959.5)	0.65(3.5)
Birhan	68.2	136.4	19.4	115.0	5167	675.0	1.87(90.3)	1.94(101.2)	0.81(5.5)	2.6(527.2)	3.33(2450.9)	3.91(11269.8)	0.53(2.6)
Debir	80.3	154.7	15.4	113.7	4220	183.3	1.88(77.7)	1.88(77.7)	0.97(8.3)	2.79(655.3)	3.37(2407.3)	3.96(9462)	0.69(4)
Dekeba	82.7	111.1	16.1	109.3	2310	226.7	1.90(93.7)	1.94(98)	0.97(8.3)	2.81(821)	3.39(2621.7)	3.97(10355.3)	0.75(4.7)
Framida	79.5	167.9	13.6	111.3	6783	375.0	1.90(90.7)	1.94(95.3)	0.86(6.5)	2.69(680)	3.22(1778.3)	3.84(9183.3)	0.63(3.4)
Gambella1107	84.0	171.4	13.2	112.7	7443	236.7	1.96(92.7)	2.00(102.7)	0.98(8.7)	2.89(792.3)	3.52(3498.7)	4.13(13980.7)	0.65(3.7)
Gobiye	68.0	125.8	20.3	113.2	3605	920.0	1.70(72.5)	1.70(72.8)	0.87(6.8)	2.49(531.6)	2.97(1256.2)	3.56(5533.5)	0.43(1.8)
Jamiyu	79.7	166.9	22.5	127.7	4250	203.3	2.07(123.7)	2.21(162)	0.92(7.7)	2.95(996)	3.61(4114)	4.43(27117)	0.65(3.5)
Jigurti	75.0	156.9	18.9	126.7	4150	250.0	2.28(191.7)	2.33(210.7)	0.85(6)	3.06(1149.5)	3.73(5441)	4.49(31083.5)	0.69(4)
local	72.0	109.6	13.3	118.7	3300	326.7	1.96(90.7)	1.96(90.7)	0.85(6)	2.74(545)	3.31(2065)	4.06(11377)	0.69(4)
SRN39	74.3	104.3	18.3	121.3	3750	230.0	2.05(112.7)	2.05(112.7)	1.00(9)	3(1014)	3.42(2664.5)	4.25(17868)	0.78(5)
Teshale	76.0	187.5	15.6	110.7	5220	490.0	1.79(62.3)	1.87(76.3)	0.79(5.3)	2.5(352.3)	3.23(1837)	3.74(6405)	0.59(3)
Tseadachimure	75.3	181.7	18.6	113.3	5600	696.7	1.86(74.3)	1.86(74.3)	0.95(8)	2.75(619)	3.20(1757.7)	3.83(7914.7)	0.55(2.7)
Wediaker	77.7	121.0	15.3	111.7	5113	356.7	2.1(125.3)	2.10(125.3)	0.89(7)	2.93(869.7)	3.50(3272.3)	4.06(12125.3)	0.66(3.7)
Wetetbegunchie	80.7	107.5	14.0	135.7	3300	163.3	2.2(157)	2.20(157)	0.85(6)	2.97(943)	3.52(3336)	4.27(18642)	0.78(5)
Mean	77.5	153.3	18.4	122.6	4595.4	329.1	1.95(101.3)	2.1(134.7)	0.91(7.3)	2.8(729)	3.44(3124.5)	4.16(17106.7)	0.65(3.9)
LSD(P<0.05)	8.4	30	4.3	8.2	2584.9	309.4	0.31	0.26	0.1	0.35	0.29	0.35	0.13
CV (%)	7.4	12.3	14.8	4.34	32.1	28.6	10.1	8.1	6.9	8.1	5.6	5.7	12

DTF = days to 50% flowering, PLHT = plant height (cm), PL = panicle length (cm), DTM = days to maturity, BM = biomass (kg ha^{-1}), YLD= yield (kg ha^{-1}), LSD = Least significant difference, CV = Coefficient of variation, SN = *Striga* count at harvest, SN$_{max}$ = maximum *Striga* count, AUSNPC = area under *Striga* number progress curve, AUSSPC = area under *Striga* severity progress curve, FR = field resistance, data on *Striga* related traits were subjected to log (x+1) transformation, numbers in parenthesis are original mean values (non-transformed).

Appendix 2. The mean performance of backcrossed and parental lines for agronomic traits and reaction to *Striga hermonthica* at Tahitay Adiyabo during 2018/19 cropping season

Genotype	DTF	PLHT	PL	DM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
AbaAre-1	85.0	229.7	21.8	145.3	5446.7	433.3	1.82(65.7)	1.82(65.7)	0.97(8.3)	2.73(549.7)	3.05(1143.3)	3.85(7278)	0.75(4.7)
America-1	78.7	216.3	33.2	135.7	5113.3	920.0	1.55(38.7)	1.62(45.7)	0.93(7.7)	2.41(323)	2.89(879.7)	3.61(5151.3)	0.73(4.3)
BC2F3_ETSC_17001	76.7	260.5	24.3	130.0	8220.0	826.7	1.53(38.3)	1.53(38.3)	0.89(7)	2.35(290)	2.73(586.3)	3.46(3565)	0.66(3.7)
BC2F3_ETSC_17002	77.7	250.3	26.2	129.0	6443.3	1110.0	1.57(43)	1.76(59)	0.89(7)	2.39(288)	2.9(864.7)	3.59(4780.7)	0.69(4)
BC2F3_ETSC_17003	86.3	222.2	14.3	134.0	6446.7	160.0	1.79(62)	1.81(66)	0.97(8.3)	2.7(526.3)	3.09(1266)	3.89(8151.3)	0.75(4.7)
BC2F3_ETSC_17004	87.7	232.2	19.1	138.7	6780.0	416.7	1.83(83)	1.83(83)	0.97(8.3)	2.74(727)	3.1(1568.7)	3.9(11023.7)	0.78(5)
BC2F3_ETSC_17005	88.0	245.4	24.0	140.3	6443.3	223.3	1.74(54.7)	1.81(65.7)	0.97(8.3)	2.65(460)	3.04(1140.7)	3.84(7296.3)	0.75(4.7)
BC2F3_ETSC_17006	87.0	249.7	28.0	134.0	6223.3	250.0	1.87(81.3)	1.8(75.7)	0.94(7.7)	2.74(656)	3.12(1420.3)	3.88(8743)	0.78(5)
BC2F3_ETSC_17007	89.3	219.6	15.8	138.3	5000.0	433.3	1.88(89)	1.94(98.7)	0.97(8.3)	2.79(773)	3.13(1708)	3.96(12439.3)	0.69(4)
BC2F3_ETSC_17008	78.0	253.2	36.4	129.7	7333.3	1360.0	1.32(24.7)	1.37(27.3)	0.75(4.7)	1.96(129.7)	2.61(551.3)	3.13(2376.7)	0.63(3.3)
BC2F3_ETSC_17009	81.0	232.3	34.6	130.7	6956.7	1120.0	1.64(58.7)	1.68(64)	0.89(7)	2.46(473.3)	2.91(1038.3)	3.63(5931.7)	0.65(3.7)
BC2F3_ETSC_17010	79.7	230.3	35.5	132.0	5890.0	1260.0	1.65(57)	1.93(96)	0.79(6)	2.34(442.3)	2.9(1160.3)	3.48(8043)	0.69(4)
BC2F3_ETSC_17011	79.3	257.7	35.4	130.0	7556.7	1240.0	1.46(31.7)	1.46(31.7)	0.72(4.7)	2.06(172.3)	2.65(535)	3.2(2838.7)	0.59(3)
BC2F3_ETSC_17012	76.3	237.2	33.9	129.0	5780.0	1310.0	1.37(31)	1.45(39.3)	0.85(6.3)	2.13(235.7)	2.72(756.3)	3.36(4161)	0.62(3.3)
BC2F3_ETSC_17013	78.3	229.1	34.1	129.0	6886.7	1723.3	1.44(37.7)	1.44(37.7)	0.79(5.7)	2.14(278)	2.62(574.7)	3.17(3032)	0.59(3.3)
BC2F3_ETSC_17014	76.3	238.7	34.3	131.3	6666.7	1546.7	1.39(36)	1.42(37.7)	0.77(5)	2.05(226.7)	2.61(591.7)	3.19(2846.3)	0.59(3)
BC2F3_ETSC_17015	82.0	212.9	27.3	131.0	5780.0	886.7	1.71(56.3)	1.71(56.3)	0.93(7.7)	2.57(476.7)	2.95(1046)	3.7(6560.7)	0.72(4.3)
BC2F3_ETSC_17016	80.3	236.1	31.5	130.7	5333.3	983.3	1.6(41.7)	1.71(52)	0.89(7)	2.43(296.7)	2.93(888.7)	3.63(4957.7)	0.63(3.3)
BC2F3_ETSC_17017	80.0	249.4	29.7	129.3	6166.7	1033.3	1.63(42)	1.72(52.3)	0.85(6.3)	2.41(268)	2.94(897)	3.59(4349.3)	0.67(3.7)
BC2F3_ETSC_17018	82.3	242.5	30.4	130.0	5220.0	600.0	1.78(60.7)	1.78(60.7)	0.97(8.3)	2.69(516)	3.04(1158.7)	3.86(8189.7)	0.73(4.3)
BC2F3_ETSC_17019	84.7	230.1	28.2	129.3	5443.3	890.0	1.63(49.7)	1.63(49.7)	0.9(7.3)	2.46(408.7)	2.86(786)	3.59(5091)	0.73(4.3)
BC2F3_ETSC_17020	79.3	231.7	30.1	128.0	5110.0	840.0	1.7(54.7)	1.7(54.7)	0.89(7)	2.53(408.7)	2.97(1022.7)	3.71(6271.3)	0.69(4)
BC2F3_ETSC_17021	79.3	233.9	34.1	131.3	5000.0	1003.3	1.41(34.7)	1.46(36)	0.89(7)	2.23(274)	2.71(573.3)	3.44(3507.7)	0.6(3)
BC2F3_ETSC_17022	76.0	291.1	28.8	126.0	5110.0	1076.7	1.84(69)	2(108)	0.97(8.3)	2.75(579.7)	3.21(1758.7)	3.98(10412)	0.7(4)
BC2F3_ETSC_17023	75.3	285.5	28.3	125.3	5553.3	1120.0	1.56(42)	1.7(60.7)	0.87(7)	2.34(346)	2.96(1131.7)	3.68(7351.7)	0.67(3.7)
BC2F3_ETSC_17024	76.0	267.6	26.3	129.0	5330.0	1133.3	1.73(53)	1.76(57)	0.97(8.3)	2.64(437.3)	3.01(1046.7)	3.79(6431)	0.7(4)
BC2F3_ETSC_17025	76.3	277.1	28.6	131.3	5000.0	1063.3	1.65(46.7)	1.76(71)	0.89(7)	2.48(348.3)	3.02(1215.7)	3.8(7972)	0.67(3.7)

Genotype	DTF	PLHT	PL	DM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17026	76.3	279.5	25.0	127.0	5890.0	1183.3	1.51(32.7)	1.59(38.3)	0.86(6.3)	2.29(209.3)	2.91(813)	3.63(4466.3)	0.63(3.3)
BC2F3_ETSC_17027	77.0	260.3	27.4	129.0	4220.0	566.7	1.98(98.3)	1.99(104)	0.94(7.7)	2.85(774.3)	3.2(1720.7)	3.99(11827)	0.72(4.3)
BC2F3_ETSC_17028	75.3	289.0	30.6	128.0	6556.7	1536.7	1.63(43)	1.63(43)	0.86(6.3)	2.42(272.3)	2.87(750.3)	3.55(3607)	0.63(3.3)
BC2F3_ETSC_17029	76.0	180.0	22.7	98.3	3110.0	580.0	1.74(55)	1.77(57.7)	0.89(7)	2.57(396.7)	3.04(1088)	3.76(5985.7)	0.63(3.3)
BC2F3_ETSC_17031	85.7	272.9	30.6	141.7	6333.3	376.7	1.62(44.3)	1.67(48.7)	0.9(7)	2.45(309.7)	2.95(936.7)	3.68(5365.7)	0.7(4)
BC2F3_ETSC_17032	83.3	266.0	35.6	129.7	6553.3	926.7	1.67(49)	1.77(66.3)	0.9(7)	2.5(342.3)	2.95(990.3)	3.66(5514.7)	0.67(3.7)
BC2F3_ETSC_17033	85.3	277.6	25.9	129.0	5223.3	340.0	1.87(75)	1.89(79.3)	0.97(8.3)	2.78(635.3)	3.12(1406.3)	3.93(9485.3)	0.73(4.3)
BC2F3_ETSC_17034	83.3	234.0	31.9	132.3	4666.7	463.3	1.73(80)	1.85(85.3)	0.94(7.7)	2.6(612.3)	3.08(1325.7)	3.81(7865.3)	0.75(4.7)
BC2F3_ETSC_17035	82.7	234.5	30.8	124.0	3886.7	426.7	1.82(68.3)	1.88(79)	1(9)	2.77(614.3)	3.21(1690)	4.05(11714)	0.78(5)
BC2F3_ETSC_17036	82.0	216.6	31.0	130.3	3556.7	466.7	1.94(89.7)	1.98(100)	1(9)	2.89(804.3)	3.22(1805.7)	4.07(12695.7)	0.72(4.3)
BC2F3_ETSC_17037	84.0	253.7	26.3	128.0	3890.0	383.3	1.68(50.3)	1.79(63.7)	0.97(8.3)	2.59(426)	3.06(1228)	3.86(8050)	0.73(4.3)
BC2F3_ETSC_17038	85.0	240.1	24.5	136.7	4890.0	463.3	1.63(50.3)	1.63(50.3)	0.87(7)	2.42(418.7)	2.85(809.3)	3.58(5497.7)	0.72(4.3)
BC2F3_ETSC_17039	82.0	263.9	31.1	130.0	4886.7	560.0	1.74(56.3)	1.78(62.7)	0.97(8.3)	2.65(486)	2.99(1051.3)	3.8(7155.3)	0.73(4.3)
BC2F3_ETSC_17040	80.3	255.8	33.0	129.0	5333.3	1046.7	1.51(37.7)	1.59(42)	0.9(7)	2.34(262.3)	2.85(809)	3.58(4241)	0.63(3.3)
BC2F3_ETSC_17041	83.3	252.6	32.5	129.0	6176.7	980.0	1.63(46.3)	1.63(46.3)	0.9(7.3)	2.46(370)	2.93(984)	3.66(6350.7)	0.66(3.7)
BC2F3_ETSC_17042	86.7	244.1	29.3	135.7	4556.7	330.0	1.75(64.7)	1.89(93)	0.93(7.7)	2.61(543.3)	3.12(1587.7)	3.88(10706)	0.75(4.7)
BC2F3_ETSC_17043	78.7	239.9	28.1	131.3	4776.7	590.0	1.76(68)	1.83(75.7)	0.97(8.3)	2.67(596)	3.05(1229.3)	3.83(7577.7)	0.73(4.3)
BC2F3_ETSC_17044	81.3	240.5	29.5	136.0	5776.7	806.7	1.67(46.7)	1.78(60.7)	0.86(6.3)	2.46(297)	2.96(932.3)	3.64(4538.3)	0.69(4)
BC2F3_ETSC_17045	81.7	235.4	29.6	135.3	5000.0	743.3	1.84(73)	1.84(73)	0.94(7.7)	2.71(590.7)	3.02(1197.3)	3.77(7468.7)	0.73(4.3)
BC2F3_ETSC_17046	80.0	269.5	29.1	131.3	6666.7	1330.0	1.37(26)	1.49(35.7)	0.79(5.7)	2.06(173.3)	2.77(755.3)	3.36(4071.7)	0.62(3.3)
BC2F3_ETSC_17047	82.7	262.6	29.7	129.7	6113.3	670.0	1.49(38)	1.51(39.3)	0.84(6.3)	2.24(299)	2.74(705.3)	3.33(3741.7)	0.67(3.7)
BC2F3_ETSC_17048	80.3	287.3	30.2	133.3	7110.0	980.0	1.38(36)	1.4(40.3)	0.79(6)	2.06(294.3)	2.66(804.7)	3.32(5327.7)	0.62(3.3)
BC2F3_ETSC_17049	82.3	284.7	33.0	135.3	5333.3	813.3	1.63(56)	1.64(56.3)	0.9(7.3)	2.45(480)	2.8(827)	3.54(5418)	0.66(3.7)
BC2F3_ETSC_17050	84.3	246.1	22.9	132.3	5056.7	326.7	1.69(50)	1.79(61.7)	1(9)	2.63(449)	3.05(1144.3)	3.89(7984)	0.73(4.3)
BC2F3_ETSC_17051	82.0	235.2	25.4	132.0	4776.7	746.7	1.9(84)	1.9(84)	0.94(7.7)	2.77(674)	3.02(1097.3)	3.82(7286.7)	0.73(4.3)
BC2F3_ETSC_17052	84.7	227.6	20.9	131.0	4333.3	590.0	1.74(55.3)	1.78(60.3)	0.94(7.7)	2.62(429.7)	3.05(1156)	3.81(6913.7)	0.69(4)
BC2F3_ETSC_17053	81.3	243.0	25.3	130.7	5553.3	1000.0	1.7(52)	1.72(55.7)	0.89(7)	2.52(392.7)	2.98(1024.3)	3.69(5762.7)	0.69(4)
BC2F3_ETSC_17054	79.7	260.5	24.2	130.3	4890.0	666.7	1.86(72.7)	1.87(74)	0.97(8.3)	2.78(609)	3.12(1324)	3.9(8037.3)	0.7(4)
BC2F3_ETSC_17055	79.7	237.4	21.9	129.3	5553.3	746.7	1.94(90)	1.99(99.3)	1(9)	2.89(809.7)	3.18(1519.3)	4.03(10982)	0.75(4.7)
BC2F3_ETSC_17056	75.3	219.3	29.6	127.0	5723.3	1293.3	1.81(73)	1.84(77.3)	0.89(7)	2.64(520.3)	3.13(1452)	3.89(8195)	0.67(3.7)

Genotype	DTF	PLHT	PL	DM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17057	70.0	246.3	35.7	124.7	5780.0	1440.0	1.68(47.7)	1.7(50.3)	0.87(6.7)	2.48(324.3)	2.93(909.7)	3.62(5206.3)	0.6(3)
BC2F3_ETSC_17058	72.3	251.0	33.5	129.7	6890.0	1393.3	1.53(35)	1.57(37.7)	0.87(6.7)	2.32(251)	2.89(814.3)	3.59(4732)	0.63(3.3)
BC2F3_ETSC_17059	73.0	219.3	31.5	126.0	5443.3	1240.0	1.61(45.3)	1.74(58.3)	0.97(8.3)	2.52(397)	2.99(1070.7)	3.76(6735.3)	0.75(4.7)
BC2F3_ETSC_17060	70.7	218.7	30.1	128.3	4663.3	1030.0	1.86(81.3)	1.92(92)	0.97(8.3)	2.77(702)	3.2(1704)	3.98(11071.7)	0.73(4.3)
BC2F3_ETSC_17061	77.0	246.9	33.6	127.7	6556.7	1140.0	1.54(39)	1.57(45)	0.84(6)	2.29(248.7)	2.82(847.3)	3.45(3954)	0.63(3.3)
BC2F3_ETSC_17062	78.3	250.8	34.1	129.7	5113.3	996.7	1.7(59.3)	1.72(64.3)	0.89(7)	2.52(467.3)	3(1248.3)	3.71(7665.7)	0.66(3.7)
BC2F3_ETSC_17063	75.7	249.9	32.3	125.7	7113.3	1560.0	1.47(31.7)	1.51(35)	0.84(6.3)	2.22(234.3)	2.75(657)	3.35(3372.7)	0.56(2.7)
BC2F3_ETSC_17064	74.7	239.9	29.7	128.7	6446.7	1226.7	1.47(44.7)	1.66(58)	0.83(6)	2.21(358.3)	2.88(1014.7)	3.5(6021.7)	0.63(3.3)
BC2F3_ETSC_17065	79.7	226.7	32.3	126.3	6000.0	843.3	1.65(46)	1.68(49.7)	0.93(7.7)	2.51(376)	2.96(1025.7)	3.71(6448.7)	0.72(4.3)
BC2F3_ETSC_17066	80.3	215.3	31.8	126.3	3780.0	676.7	1.87(75)	1.87(75)	0.93(7.7)	2.73(602.3)	3.01(1100)	3.8(7695.7)	0.72(4.3)
BC2F3_ETSC_17067	78.3	211.9	27.4	128.7	3776.7	470.0	1.95(92)	1.99(99)	1(9)	2.9(824.3)	3.27(1890)	4.13(14094.3)	0.75(4.7)
BC2F3_ETSC_17068	82.3	221.0	25.9	129.7	6000.0	730.0	1.67(47)	1.73(55.7)	0.97(8.3)	2.58(398.3)	2.96(1023)	3.77(7023.7)	0.7(4)
BC2F3_ETSC_17069	82.0	262.4	28.7	129.7	5666.7	896.7	1.69(71.7)	1.83(80.7)	0.9(7.3)	2.51(623.3)	2.99(1126.3)	3.68(6446.3)	0.72(4.3)
BC2F3_ETSC_17070	79.0	227.7	24.6	129.3	6220.0	933.3	1.55(39)	1.64(54)	0.87(6.7)	2.34(295)	2.88(920.3)	3.56(5604)	0.69(4)
BC2F3_ETSC_17071	87.7	242.9	16.9	140.3	5223.3	166.7	1.74(55)	1.74(55)	0.97(8.3)	2.65(465.7)	3.05(1117.7)	3.79(6344.3)	0.78(5)
BC2F3_ETSC_17072	75.7	183.5	26.2	103.0	2756.7	186.7	1.74(55)	1.76(57)	0.97(8.3)	2.65(463)	3.06(1154)	3.87(7489.3)	0.69(4)
BC2F3_ETSC_17073	70.3	185.7	20.9	99.0	2756.7	303.3	1.65(48)	1.88(76.7)	1(9)	2.6(429.3)	3.17(1517)	3.98(9806.3)	0.73(4.3)
BC2F3_ETSC_17074	70.3	181.7	25.8	105.7	3776.7	676.7	1.75(56.3)	1.82(70.3)	0.97(8.3)	2.66(477.3)	3.15(1558.3)	3.93(10491.7)	0.69(4)
BC2F3_ETSC_17075	72.0	196.0	23.3	103.7	2490.0	206.7	1.73(54.3)	1.73(54.3)	0.97(8.3)	2.64(458)	3(1018.3)	3.78(6254.7)	0.75(4.7)
BC2F3_ETSC_17076	76.0	174.8	22.3	104.0	4176.7	320.0	1.52(37.3)	1.63(45.3)	0.86(6.3)	2.3(241.7)	2.86(764.3)	3.55(3923)	0.73(4.3)
BC2F3_ETSC_17077	63.3	188.9	23.0	100.7	3200.0	416.7	1.69(51.7)	1.7(52.3)	0.93(7.7)	2.55(429)	3.03(1096.3)	3.8(6469)	0.56(2.7)
BC2F3_ETSC_17078	69.0	168.7	18.7	96.7	2576.7	416.7	1.7(53.3)	1.78(66)	0.97(8.3)	2.61(459.3)	3.04(1269)	3.81(8084.3)	0.68(4)
BC2F3_ETSC_17079	73.3	167.9	25.3	97.7	2353.3	226.7	1.75(58.3)	1.76(59)	0.97(8.3)	2.66(501.3)	3.04(1128)	3.82(7061)	0.62(3.3)
BC2F3_ETSC_17080	77.0	162.2	23.5	105.3	3110.0	203.3	1.81(65.7)	1.85(71)	1(9)	2.76(590)	3.18(1511.3)	4.03(10828.3)	0.69(4)
BC2F3_ETSC_17081	68.3	170.8	25.3	91.0	2403.3	383.3	1.76(57)	1.87(78.7)	0.97(8.3)	2.67(485)	3.24(1859)	4.06(13384.7)	0.65(3.7)
BC2F3_ETSC_17082	73.0	158.1	23.4	89.0	2490.0	386.7	1.75(59.3)	1.77(62)	0.97(8.3)	2.66(506)	3.11(1448.3)	3.91(9959)	0.59(3)
BC2F3_ETSC_17083	76.7	164.9	20.2	102.3	2356.7	193.3	1.77(60.3)	1.77(60.3)	0.97(8.3)	2.68(520.7)	3.07(1256.7)	3.87(8442.3)	0.59(3.3)
BC2F3_ETSC_17084	73.7	173.6	20.8	95.7	2313.3	473.3	1.76(56.3)	1.83(68)	0.94(7.7)	2.63(430.3)	3.07(1207.7)	3.86(7853.3)	0.59(3)
BC2F3_ETSC_17085	81.7	173.1	17.5	105.0	3023.3	290.0	1.85(72)	1.88(76.3)	1(9)	2.79(650.7)	3.19(1592)	3.99(10287.7)	0.72(4.3)
BC2F3_ETSC_17086	71.0	180.8	22.1	93.3	2846.7	730.0	1.66(45.3)	1.7(49.3)	0.94(7.7)	2.53(354.7)	3.01(1065.3)	3.74(6059.7)	0.66(3.7)

Genotype	DTF	PLHT	PL	DM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17087	79.7	248.9	30.7	130.0	6110.0	690.0	1.31(22)	1.39(24.7)	0.77(5.3)	1.97(144)	2.55(359.7)	3.12(1680.7)	0.63(3.3)
BC2F3_ETSC_17088	81.3	268.9	30.9	129.3	7776.7	850.0	1.65(46.3)	1.65(46.3)	0.84(6.3)	2.4(328.3)	2.85(812)	3.51(4805)	0.69(4)
BC2F3_ETSC_17089	81.0	257.4	29.5	134.0	6223.3	700.0	1.72(53)	1.59(58.7)	0.73(5)	2.2(386)	2.88(1274.7)	3.4(7391.3)	0.62(3.3)
BC2F3_ETSC_17090	76.7	244.5	32.5	127.0	7000.0	1463.3	1.24(19.7)	1.34(24.3)	0.69(4)	1.81(84)	2.59(462.7)	3.08(1630.7)	0.52(2.3)
BC2F3_ETSC_17091	88.3	240.9	20.5	135.3	4776.7	216.7	1.87(84.7)	1.9(87.7)	0.89(7)	2.7(654)	3.07(1301.7	3.81(8279.3)	0.75(4.7)
BC2F3_ETSC_17092	84.0	223.0	28.8	131.0	5553.3	813.3	1.59(44)	1.6(44.7)	0.79(6)	2.28(323.7)	2.82(806.3)	3.41(4946)	0.65(3.7)
BC2F3_ETSC_17093	85.0	183.0	25.2	134.7	4776.7	373.3	1.86(81.7)	1.9(85)	0.93(7.7)	2.73(688.7)	3.11(1421.7)	3.88(9334.4)	0.75(4.7)
BC2F3_ETSC_17094	79.0	231.3	27.9	132.3	6556.7	1223.3	1.73(56)	1.87(75)	0.87(6.7)	2.54(394.3)	3.12(1403.3)	3.87(8360.7)	0.66(3.7)
BC2F3_ETSC_17095	74.0	231.5	34.4	126.0	4666.7	1513.3	1.4(27.3)	1.55(36)	0.75(4.7)	2.05(130.7)	2.82(678)	3.42(2817)	0.56(2.7)
BC2F3_ETSC_17096	76.0	277.7	32.7	130.3	6110.0	1553.3	1.15(18.3)	1.21(23)	0.72(4.7)	1.73(110)	2.45(447)	2.95(1970.3)	0.56(2.7)
BC2F3_ETSC_17097	72.3	253.6	31.9	129.7	5443.3	1396.7	1.43(28.7)	1.45(30)	0.72(4.3)	2.05(133.3)	2.71(569.3)	3.2(1983.7)	0.56(2.7)
BC2F3_ETSC_17098	73.0	268.9	33.5	128.0	6003.3	1353.3	1.72(57.7)	1.76(61.3)	0.94(7.7)	2.59(469)	2.97(964.3)	3.75(6025.7)	0.6(3)
BC2F3_ETSC_17099	75.3	238.1	29.4	125.0	4330.0	1230.0	1.7(54.7)	1.7(54.7)	0.94(7.7)	2.57(445.7)	2.9(908.7)	3.63(4913)	0.67(3.7)
BC2F3_ETSC_17100	72.3	270.3	25.0	123.3	3780.0	736.7	1.8(69.3)	2.01(104.7)	0.97(8.3)	2.71(575.7)	3.27(1968)	4.06(12282.3)	0.7(4)
BC2F3_ETSC_17101	68.0	212.7	27.8	122.7	3443.3	1046.7	1.85(74.7)	1.94(89.7)	1(9)	2.8(671.3)	3.19(1717.3)	4.03(11859)	0.69(4)
BC2F3_ETSC_17102	69.0	225.2	27.9	125.7	3333.3	906.7	1.76(58)	1.76(58)	0.97(8.3)	2.68(487)	3.02(1108.7)	3.8(7098)	0.67(3.7)
BC2F3_ETSC_17103	73.3	254.1	26.8	124.3	3333.3	643.3	1.89(78)	1.89(78)	1(9)	2.84(702.3)	3.15(1477.7)	4.01(10528.3)	0.69(4)
BC2F3_ETSC_17104	76.0	255.5	27.3	122.3	5780.0	763.3	1.78(96)	1.78(96)	0.83(6.7)	2.51(837.3)	3.03(1905.7)	3.68(13491.3)	0.67(3.7)
BC2F3_ETSC_17105	71.7	261.3	29.3	125.7	5113.3	1373.3	1.58(45)	1.76(62.7)	0.94(7.7)	2.45(370)	3.02(1310.7)	3.76(7961.3)	0.63(3.3)
BC2F3_ETSC_17106	63.0	206.9	25.8	88.7	2666.7	790.0	1.53(34)	1.61(39.7)	0.82(5.7)	2.27(198.3)	2.95(886.7)	3.58(3895.7)	0.73(4.3)
BC2F3_ETSC_17107	72.3	206.1	29.1	92.7	2490.0	973.3	1.45(29.3)	1.65(45.7)	0.89(7)	2.27(225.3)	2.94(912.7)	3.66(5056.3)	0.7(4)
BC2F3_ETSC_17108	74.7	193.3	27.7	99.3	2400.0	460.0	1.7(52)	1.76(61)	0.97(8.3)	2.61(449.3)	3.08(1306.3)	3.88(8602.7)	0.63(3.3)
BC2F3_ETSC_17109	71.0	193.3	26.8	88.7	2756.7	663.3	1.66(47.3)	1.71(52.3)	0.94(7.7)	2.53(360.7)	3.06(1227.7)	3.81(6974.7)	0.69(4)
BC2F3_ETSC_17111	67.3	138.2	21.3	86.0	2670.0	840.0	1.6(41)	1.84(72.3)	0.94(7.7)	2.47(326.7)	3.16(1530)	3.91(9335)	0.66(3.7)
BC2F3_ETSC_17112	83.7	267.5	31.4	131.7	4776.7	600.0	1.62(46)	1.62(46)	0.93(7.7)	2.48(372)	2.9(867.3)	3.63(5363.7)	0.7(4)
BC2F3_ETSC_17113	84.7	242.0	30.8	127.3	3223.3	490.0	1.77(59.3)	1.83(71.3)	0.93(7.7)	2.64(477.7)	3.12(1445)	3.91(9378.7)	0.69(4)
BC2F3_ETSC_17114	84.0	235.9	28.1	130.7	4890.0	486.7	1.94(86.3)	1.96(91)	0.97(8.3)	2.85(724.7)	3.12(1411.7)	3.95(10134.7)	0.75(4.7)
BC2F3_ETSC_17115	87.0	239.5	26.2	132.7	4556.7	253.3	1.79(62)	1.88(79.7)	1(9)	2.74(557.3)	3.11(1371.3)	3.97(9830.7)	0.75(4.7)
BC2F3_ETSC_17116	86.7	228.7	20.4	134.7	4666.7	433.3	1.62(58)	1.69(61)	0.87(7)	2.4(499)	2.96(1162.7)	3.65(7809.3)	0.72(4.3)
BC2F3_ETSC_17117	86.0	256.2	27.1	132.0	5556.7	403.3	1.63(45.7)	1.66(47.7)	0.89(7)	2.46(346.7)	2.93(989.3)	3.62(6164.3)	0.69(4)

Genotype	DTF	PLHT	PL	DM	BM	YLD	SN	SNmax	Vigor	Severity	AUSNPC	AUSSPC	FR
BC2F3_ETSC_17119	84.3	236.0	26.0	131.0	4110.0	343.3	1.85(75.7)	1.92(88.3)	0.97(8.3)	2.76(645)	3.14(1617.3)	3.95(10971)	0.72(4.3)
BC2F3_ETSC_17120	88.0	200.8	23.5	134.0	3776.7	296.7	2.03(116)	2.03(116)	0.97(8.3)	2.94(1004.2)	3.33(2316.3)	4.1(14807)	0.75(4.7)
BC2F3_ETSC_17121	84.7	222.9	33.6	133.7	4443.3	383.3	1.85(77.7)	1.97(94.7)	1(9)	2.8(699.7)	3.23(1761.7)	4.05(11757)	0.75(4.7)
Berjokecoll#1	88.7	237.0	21.6	142.0	4666.7	156.7	1.8(66)	1.8(66)	1(9)	2.75(593)	2.98(981)	3.82(6832)	0.78(5)
Birhan	64.3	144.1	28.1	100.5	3268.3	1568.3	1.08(13.5)	1.25(18.2)	0.75(5)	1.7(73.8)	2.55(394)	3.1(1622.8)	0.53(2.5)
Debir	72.0	166.7	21.1	101.0	2223.3	186.7	1.82(65.7)	1.86(72)	0.97(8.3)	2.73(550.3)	3.14(1446.7)	3.97(10362.7)	0.73(4.3)
Dekeba	76.0	123.5	21.2	99.0	2400.0	246.7	1.73(53.3)	1.84(72)	1(9)	2.68(478)	3.15(1496.3)	3.98(10159.3)	0.67(3.7)
Framida	77.8	193.6	22.4	111.2	4745.0	575.0	1.53(36.8)	1.61(44)	0.86(6.5)	2.31(258)	2.91(889.8)	3.56(4648.3)	0.64(3.5)
Gambella1107	77.7	153.3	18.6	112.0	2756.7	256.7	1.93(83.7)	1.93(83.7)	1(9)	2.88(755.3)	3.22(1664.3)	4.02(10807.3)	0.67(3.7)
Gobiye	65.2	161.2	26.5	101.2	2501.7	1246.7	0.99(12)	1.16(16)	0.72(4.5)	1.57(54.8)	2.37(272.7)	2.89(994.5)	0.59(3.2)
Jamiyu	82.3	218.2	34.4	134.3	5110.0	843.3	1.67(54)	1.7(57.7)	0.93(7.7)	2.53(459)	2.99(1227.3)	3.72(8051.7)	0.69(4)
Jigurti	76.0	292.2	27.7	129.3	5110.0	1073.3	1.81(69.3)	1.92(101.7)	0.97(8.3)	2.72(585)	3.22(2012.7)	4.02(13156.7)	0.69(4)
local	71.7	232.0	26.4	125.7	3776.7	1233.3	1.62(54.7)	1.62(54.7)	0.9(7.3)	2.45(459.7)	2.89(1009.3)	3.61(6493)	0.67(3.7)
SRN39	70.3	168.8	21.5	123.7	3166.7	1273.3	1.59(39.7)	1.68(48)	0.84(6)	2.35(223.3)	2.87(797.3)	3.52(3405.7)	0.58(3)
Teshale	72.3	191.8	22.1	92.7	2486.7	560.0	1.63(42.7)	1.76(62.7)	0.89(7)	2.45(299.3)	2.98(1049.3)	3.66(5833)	0.67(3.7)
Tseadachimure	71.7	194.7	25.6	98.3	2576.7	516.7	1.74(54)	1.77(57.7)	0.97(8.3)	2.65(454.7)	3.1(1274.3)	3.88(7874.3)	0.69(4)
Wediaker	75.0	121.3	18.3	86.0	2666.7	600.0	1.9(82.7)	1.94(89)	0.97(8.3)	2.82(665.7)	3.17(1487.7)	3.97(9319)	0.73(4.3)
Wetetbegunchie	85.7	250.9	29.8	142.7	5110.0	156.7	1.79(62)	1.81(66.7)	1(9)	2.73(558.3)	3.09(1281)	3.9(8352.3)	0.78(5)
Mean	78.3	227.8	27.4	123.6	4840.3	771.4	1.7(55.1)	1.73(62.5)	0.91(7.4)	2.5(444.4)	2.98(1147.2)	3.72(7170.3)	0.68(3.7)
LSD(P<0.05)	5.5	39.4	7.3	10.4	2009.4	340.5	0.34	0.33	0.15	0.46	0.31	0.45	0.13
CV (%)	4.6	11.5	16.7	5.5	31.1	31.4	14	12.9	11.7	13.4	7.8	9	13.2

DTF = days to 50% flowering, PLHT = plant height (cm), PL = panicle length (cm), DTM = days to maturity, BM = biomass (kg ha^{-1}), YLD= yield (kg ha^{-1}), LSD = Least significant difference, CV = Coefficient of variation, SN = *Striga* count at harvest, SN$_{max}$ = maximum *Striga* count, AUSNPC = area under *Striga* number progress curve, AUSSPC = area under *Striga* severity progress curve, FR = field resistance, data on *Striga* related traits were subjected to log (x+1) transformation, numbers in parenthesis are original mean values (non-transformed).

Appendix 3. Mean agronomic performance of backcrossed and parental lines in *Striga* free locations of Raya Azebo & Fedis in 2018/19 cropping season.

Genotypes	Raya Azebo						Fedis					
	DTF	PLHT	PL	DTM	BM	YLD	DTF	PLHT	PL	DTM	BM	YLD
AbaAre-1	106.0	318.7	25.8	161.0	25160.0	4130.0	92.0	243.3	21.0	137.7	17521.3	2336.7
America-1	84.3	272.1	29.7	144.3	18493.3	3840.0	80.0	221.0	30.0	130.7	16781.3	2040.0
BC2F3_ETSC_17001	91.3	312.5	25.1	155.7	20593.3	2623.3	90.0	302.7	30.7	144.0	17524.7	2380.0
BC2F3_ETSC_17002	85.7	300.7	28.8	156.3	16233.3	3463.3	85.0	278.3	29.3	143.3	20238	2096.7
BC2F3_ETSC_17003	97.0	336.0	23.1	159.0	27136.7	3576.7	99.7	309.3	24.3	145.0	16041.3	2456.7
BC2F3_ETSC_17004	92.7	327.7	25.6	147.3	21210.0	3883.3	92.7	288.0	24.3	150.0	32091.3	2263.3
BC2F3_ETSC_17005	103.7	339.7	21.7	145.3	26356.7	3846.7	94.0	288.7	23.3	148.0	19744.7	1903.3
BC2F3_ETSC_17006	96.7	327.4	23.7	149.7	21210.0	3290.0	93.0	304.3	27.7	145.0	22461.3	2920.0
BC2F3_ETSC_17007	93.3	324.3	28.1	154.3	27136.7	5406.7	93.3	297.7	21.7	141.0	21474.7	1710.0
BC2F3_ETSC_17008	89.7	281.0	34.7	153.7	27133.3	3300.0	78.0	221.1	34.3	131.0	18264.7	2963.3
BC2F3_ETSC_17009	85.7	259.6	36.5	148.3	17010.0	4293.3	79.7	210.6	36.3	131.7	21474.7	2580.0
BC2F3_ETSC_17010	88.7	277.4	32.9	152.7	18493.3	5830.0	81.7	223.7	34.7	134.7	17028	2276.7
BC2F3_ETSC_17011	87.3	288.4	35.6	147.3	19236.7	5830.0	78.0	233.0	35.0	131.0	18014.7	2590.0
BC2F3_ETSC_17012	83.7	246.7	32.6	146.7	20713.3	4886.7	77.0	235.0	33.7	131.3	18511.3	2703.3
BC2F3_ETSC_17013	91.0	267.2	37.3	151.3	15776.7	5356.7	79.7	211.7	28.7	134.0	26164.7	2326.7
BC2F3_ETSC_17014	83.7	262.9	35.5	152.0	17256.7	4753.3	82.7	211.7	35.7	132.7	16041.3	2240.0
BC2F3_ETSC_17015	88.3	299.7	30.9	148.0	26643.3	4473.3	77.7	238.0	31.7	132.3	27398	2736.7
BC2F3_ETSC_17016	88.0	293.1	32.9	149.7	31090.0	3863.3	77.3	230.3	35.7	134.0	16284.7	2153.3
BC2F3_ETSC_17017	86.7	314.8	36.9	152.0	29603.3	5173.3	81.7	254.7	31.7	90.3	27644.7	2080.0
BC2F3_ETSC_17018	91.7	322.6	36.8	150.7	25406.7	4503.3	79.0	238.0	34.0	133.0	35054.7	2786.7
BC2F3_ETSC_17019	91.0	307.9	33.5	153.0	23680.0	5320.0	82.7	244.7	33.3	134.0	10361.3	1733.3
BC2F3_ETSC_17020	85.7	261.5	32.7	155.7	13803.3	4533.3	82.7	225.7	33.3	132.7	19251.3	1913.3
BC2F3_ETSC_17021	89.7	322.2	30.7	155.7	22193.3	5283.3	78.0	226.7	33.7	131.3	20731.3	2500.0
BC2F3_ETSC_17022	87.7	324.4	29.3	148.7	19233.3	3396.7	80.7	244.7	25.0	126.0	19994.7	3000.0
BC2F3_ETSC_17023	88.0	337.5	28.6	156.7	18493.3	4660.0	85.7	257.3	24.3	130.7	20978	2380.0
BC2F3_ETSC_17024	85.7	318.7	24.9	155.7	19236.7	2530.0	84.7	267.0	23.0	130.7	19744.7	2163.3

Genotypes	Raya Azebo						Fedis					
	DTF	PLHT	PL	DTM	BM	YLD	DTF	PLHT	PL	DTM	BM	YLD
BC2F3_ETSC_17025	89.7	336.8	30.7	155.0	21950.0	5100.0	84.0	268.3	26.7	127.7	26411.3	3006.7
BC2F3_ETSC_17026	88.0	344.2	29.0	159.7	17753.3	4420.0	84.3	248.7	26.7	128.7	18014.7	2313.3
BC2F3_ETSC_17027	87.7	330.9	29.2	156.0	33803.3	3386.7	79.0	267.0	24.7	139.3	23451.3	2823.3
BC2F3_ETSC_17028	90.0	356.5	29.7	155.0	21456.7	4073.3	81.7	247.7	25.3	129.7	32091.3	2223.3
BC2F3_ETSC_17029	78.0	180.0	25.8	120	20121.0	1880.0	76.6	175.0	22.7	118	17110.0	1580.0
BC2F3_ETSC_17031	93.7	331.8	33.2	156.3	24173.3	3740.0	92.0	272.7	32.0	141.3	18014.7	2193.3
BC2F3_ETSC_17032	92.3	335.9	33.1	151.0	23186.7	4916.7	85.7	270.3	37.0	135.3	28388	2736.7
BC2F3_ETSC_17033	98.7	343.6	34.2	152.0	19976.7	4126.7	86.3	263.7	31.0	137.0	22954.7	2306.7
BC2F3_ETSC_17034	95.0	305.9	36.2	146.3	23186.7	4063.3	84.0	279.7	30.0	129.7	13818	2776.7
BC2F3_ETSC_17035	83.0	350.6	32.6	152.0	18740.0	3960.0	84.7	291.3	32.0	134.0	24684.7	2756.7
BC2F3_ETSC_17036	84.3	321.7	32.4	155.0	19726.7	4190.0	84.3	261.7	30.0	133.3	18508	2256.7
BC2F3_ETSC_17037	90.7	332.6	35.8	150.7	20223.3	3996.7	86.0	263.3	30.0	135.7	19004.7	2620.0
BC2F3_ETSC_17038	94.3	370.3	36.7	150.7	27876.7	4976.7	92.0	286.3	31.0	143.7	24928	2486.7
BC2F3_ETSC_17039	92.7	356.0	32.9	148.3	17753.3	2836.7	91.0	279.7	35.3	135.7	27154.7	2263.3
BC2F3_ETSC_17040	87.3	313.0	30.5	151.3	29110.0	3966.7	89.0	278.3	32.7	137.0	15794.7	2676.7
BC2F3_ETSC_17041	86.0	313.0	31.4	149.7	17996.7	5070.0	87.7	250.3	34.3	135.0	18264.7	1776.7
BC2F3_ETSC_17042	90.0	342.5	33.6	148.7	29356.7	5116.7	87.7	297.3	34.3	136.0	32831.3	2513.3
BC2F3_ETSC_17043	84.0	324.6	32.5	154.0	36766.7	4393.3	84.3	272.3	28.3	134.7	25668	2253.3
BC2F3_ETSC_17044	96.3	324.5	33.6	148.0	12073.3	3796.7	88.7	278.3	31.7	141.0	21968	2060.0
BC2F3_ETSC_17045	93.3	333.6	33.9	153.3	20963.3	5393.3	84.7	264.7	34.7	132.7	27891.3	2686.7
BC2F3_ETSC_17046	86.7	351.1	30.8	151.3	22443.3	3940.0	84.7	270.3	30.7	138.3	21474.7	1810.0
BC2F3_ETSC_17047	94.0	358.7	31.4	151.0	21706.7	3046.7	91.3	287.7	33.7	145.0	21721.3	1760.0
BC2F3_ETSC_17048	100.3	341.3	32.3	151.3	22690.0	2550.0	88.7	291.3	33.3	145.7	23198	2510.0
BC2F3_ETSC_17049	90.3	315.2	33.6	151.0	21456.7	4233.3	88.0	261.7	35.7	136.0	21224.7	2840.0
BC2F3_ETSC_17050	93.7	347.2	31.5	152.3	28123.3	5866.7	89.0	279.3	33.0	143.3	16534.7	2153.3
BC2F3_ETSC_17051	93.3	301.6	21.8	151.3	19726.7	3620.0	79.7	221.0	20.0	128.0	34311.3	1833.3
BC2F3_ETSC_17052	95.7	329.8	25.8	157.0	25163.3	4676.7	84.3	270.0	26.3	128.7	18014.7	1593.3
BC2F3_ETSC_17053	98.3	314.7	27.0	151.7	33803.3	6163.3	82.0	242.0	22.7	130.0	22458	2386.7
BC2F3_ETSC_17054	98.7	310.3	25.5	155.3	19726.7	5446.7	83.7	243.3	20.7	130.0	28388	2396.7

Genotypes	Raya Azebo						Fedis					
	DTF	PLHT	PL	DTM	BM	YLD	DTF	PLHT	PL	DTM	BM	YLD
BC2F3_ETSC_17055	98.0	290.7	28.9	156.3	30100.0	4366.7	83.3	240.7	18.3	127.0	30114.7	2296.7
BC2F3_ETSC_17056	85.0	259.4	32.4	149.0	24666.7	3653.3	78.7	208.7	32.7	128.0	29868	2153.3
BC2F3_ETSC_17057	87.7	279.5	32.7	147.7	15530.0	3756.7	75.3	196.0	29.0	127.3	28881.3	1980.0
BC2F3_ETSC_17058	82.7	290.3	32.4	148.3	26396.7	4353.3	76.0	225.3	29.3	129.3	30114.7	1840.0
BC2F3_ETSC_17059	82.0	262.1	33.4	145.3	20220.0	3943.3	82.0	226.7	35.7	128.3	22711.3	2240.0
BC2F3_ETSC_17060	80.7	271.7	34.5	149.3	20716.7	2886.7	79.3	219.7	35.7	130.7	20734.7	2396.7
BC2F3_ETSC_17061	86.7	257.5	30.9	146.3	26640.0	4193.3	74.7	235.3	27.7	131.7	18014.7	1950.0
BC2F3_ETSC_17062	85.7	299.8	33.8	147.0	28866.7	4953.3	77.3	234.7	32.0	129.7	26658	2130.0
BC2F3_ETSC_17063	83.7	244.0	35.7	149.0	17506.7	5560.0	79.0	143.3	20.7	130.0	36288	2080.0
BC2F3_ETSC_17064	82.3	272.9	34.0	146.0	19976.7	4000.0	78.7	222.0	26.3	129.3	19744.7	2170.0
BC2F3_ETSC_17065	85.0	276.2	35.5	147.7	34543.3	3666.7	83.0	236.0	34.7	131.7	25918	1996.7
BC2F3_ETSC_17066	83.0	279.7	32.3	149.0	27380.0	4683.3	79.3	207.1	32.0	131.7	28388	2440.0
BC2F3_ETSC_17067	83.7	287.9	30.1	152.3	23680.0	4763.3	78.3	231.0	29.7	128.3	25258	3023.3
BC2F3_ETSC_17068	84.3	292.9	28.1	146.7	29603.3	4326.7	81.0	230.0	28.3	131.7	23941.3	2510.0
BC2F3_ETSC_17069	93.7	319.4	32.1	155.3	23186.7	3936.7	80.3	255.7	29.7	132.3	27644.7	2410.0
BC2F3_ETSC_17070	81.7	328.9	32.3	152.7	23433.3	3623.3	79.0	258.3	25.7	134.0	17274.7	2233.3
BC2F3_ETSC_17071	98.0	382.7	30.0	146.7	24910.0	3270.0	93.0	320.0	33.7	136.0	20734.7	1880.0
BC2F3_ETSC_17072	80.7	201.5	33.2	128	14756.7	1686.7	80.7	191.5	29.2	123	12756.7	1406.7
BC2F3_ETSC_17073	79.3	198.7	26.6	124	14756.7	1803.3	75.3	193.7	25.9	119	12756.7	1523.3
BC2F3_ETSC_17074	79.5	199.7	31.8	130.7	15776.7	2176.7	75.3	189.7	30.8	125.7	13776.7	1896.7
BC2F3_ETSC_17075	77	209	28.7	128.7	14490	1706.7	77	204	28.3	123.7	12490	1426.7
BC2F3_ETSC_17076	85	192.8	28	129	16176.7	1820	81	182.8	27.3	124	14176.7	1540
BC2F3_ETSC_17077	78.3	200.9	30	125.7	15200	1916.7	68.3	196.9	28	120.7	13200	1636.7
BC2F3_ETSC_17078	79	186.7	25.7	121.7	14576.7	1916.7	74	176.7	23.7	116.7	12576.7	1636.7
BC2F3_ETSC_17079	80.3	185.9	32.0	122.7	14353.3	1726.7	78.3	175.9	30.3	117.7	12353.3	1446.7
BC2F3_ETSC_17080	85	180.2	29.6	128.3	20110	1703.3	82	170.2	28.5	125.3	16110	1423.3
BC2F3_ETSC_17081	77.3	188.8	32.3	115	14403.3	1883.3	73.3	178.8	30.3	111	12403.3	1603.3
BC2F3_ETSC_17082	80	176.1	29.1	114	14490	1886.7	78	166.1	28.4	109	12490	1606.7
BC2F3_ETSC_17083	81.7	182.9	26.4	127.3	14356.7	1693.3	79.7	172.9	25.2	122.3	12356.7	1413.3

Genotypes	Raya Azebo						Fedis					
	DTF	PLHT	PL	DTM	BM	YLD	DTF	PLHT	PL	DTM	BM	YLD
BC2F3_ETSC_17084	78.7	191.6	27.9	120.7	14313.3	1973.3	77.7	181.6	25.8	115.7	12313.3	1693.3
BC2F3_ETSC_17085	86.7	191.1	24.9	128	19923.3	1790	84.7	181.1	22.5	125	17023.3	1510
BC2F3_ETSC_17086	76	198.8	27.1	118.3	21846.7	2230	79	188.8	26	115.8	20846.7	2050.2
BC2F3_ETSC_17087	88.0	317.4	29.3	149.0	22936.7	5476.7	81.0	249.3	28.3	130.3	26654.7	2216.7
BC2F3_ETSC_17088	89.7	308.2	30.1	149.3	18246.7	4646.7	79.7	241.7	31.0	131.0	34311.3	2653.3
BC2F3_ETSC_17089	86.0	263.0	28.1	145.3	36023.3	5010.0	80.7	243.3	28.0	129.3	27894.7	1783.3
BC2F3_ETSC_17090	90.3	271.3	30.0	147.3	19726.7	5213.3	81.0	230.0	36.0	129.3	23451.3	2113.3
BC2F3_ETSC_17091	92.3	281.2	29.5	154.7	24170.0	4066.7	84.3	254.0	31.3	133.7	20238	1960.0
BC2F3_ETSC_17092	93.7	293.7	31.9	153.3	30100.0	4916.7	82.7	232.3	33.3	133.0	24684.7	2456.7
BC2F3_ETSC_17093	90.7	256.5	32.4	147.0	31826.7	4943.3	76.3	207.0	30.0	87.0	11274.7	2456.7
BC2F3_ETSC_17094	87.0	365.7	31.7	152.7	31580.0	5410.0	82.3	253.7	39.0	133.7	25421.3	2233.3
BC2F3_ETSC_17095	85.7	336.9	33.8	148.0	30593.3	4353.3	74.0	219.0	32.3	129.7	6234.7	1856.7
BC2F3_ETSC_17096	84.7	284.2	32.9	155.0	31826.7	3333.3	75.0	235.0	30.3	129.3	28881.3	2233.3
BC2F3_ETSC_17097	81.3	273.9	32.8	148.0	24423.3	3843.3	76.0	197.3	29.3	128.7	18264.7	1543.3
BC2F3_ETSC_17098	83.7	296.9	33.8	150.0	22446.7	5376.7	74.7	215.7	29.3	126.0	13511.3	2360.0
BC2F3_ETSC_17099	86.3	283.9	29.5	154.3	19726.7	2806.7	76.3	210.7	23.3	134.7	6991.3	2343.3
BC2F3_ETSC_17100	80.7	329.0	29.5	156.7	28370.0	3720.0	78.3	232.0	21.7	127.7	34064.7	1776.7
BC2F3_ETSC_17101	81.3	341.9	30.4	146.3	38000.0	3316.7	77.0	234.7	25.7	129.0	22132.9	1953.3
BC2F3_ETSC_17102	77.3	325.9	26.7	147.3	21456.7	2920.0	78.3	231.3	21.0	128.7	11438.5	2340.0
BC2F3_ETSC_17103	82.7	344.8	29.1	151.3	27630.0	5600.0	80.3	272.7	22.7	127.3	17521.3	2463.3
BC2F3_ETSC_17104	86.3	320.5	28.7	152.0	30100.0	3870.0	79.0	245.7	25.7	129.0	16781.3	2043.3
BC2F3_ETSC_17105	83.3	303.5	28.8	153.0	26970.0	3406.7	74.0	221.0	26.3	124.0	17524.7	2073.3
BC2F3_ETSC_17106	76	219.9	30.8	128.7	19566.7	2710	71	214.2	27.8	118.5	17666	1810
BC2F3_ETSC_17107	80.3	219.1	32.1	127.7	24490	3393.3	76.3	214.1	31.1	122.7	19581	2293.3
BC2F3_ETSC_17108	82.7	221.3	34.7	129.3	22400	2080	77.7	211.3	32.1	125.3	17455	1876.9
BC2F3_ETSC_17109	79	225.3	33.8	128.7	21756.7	2083.3	78	214.3	31.8	120.7	20756.7	2111.3
BC2F3_ETSC_17111	79.3	166.2	26.3	136	19670.6	3260	75.3	146.2	25	126	20684	2149.5
BC2F3_ETSC_17112	94.3	368.7	35.5	153.7	25653.3	5273.3	89.7	279.0	36.7	135.7	20238	2546.7
BC2F3_ETSC_17113	91.0	361.9	31.3	155.3	29356.7	6000.0	92.0	281.0	36.7	135.7	16041.3	2580.0

Genotypes	Raya Azebo						Fedis					
	DTF	PLHT	PL	DTM	BM	YLD	DTF	PLHT	PL	DTM	BM	YLD
BC2F3_ETSC_17114	92.7	369.4	34.9	155.7	18986.7	5706.7	87.3	274.7	35.0	140.3	32091.3	2183.3
BC2F3_ETSC_17115	91.3	356.1	36.4	152.3	22446.7	4063.3	90.3	289.7	37.0	135.3	19744.7	2843.3
BC2F3_ETSC_17116	94.3	361.9	35.1	155.0	28366.7	4276.7	90.7	284.0	35.3	136.3	22461.3	2126.7
BC2F3_ETSC_17117	93.7	349.6	31.5	147.0	36023.3	4350.0	91.3	271.1	33.0	135.7	21474.7	2483.3
BC2F3_ETSC_17119	91.3	351.1	32.8	154.7	29606.7	5480.0	89.7	279.3	31.0	134.0	18264.7	2253.3
BC2F3_ETSC_17120	93.7	356.1	35.0	152.0	25163.3	4660.0	92.0	299.0	22.3	138.0	21474.7	2300.0
BC2F3_ETSC_17121	93.7	360.7	34.9	154.3	21950.0	3380.0	87.3	281.7	35.3	136.3	17028	2426.7
Berjokecoll#1	105.3	349.3	28.0	158.7	26396.7	3886.7	99.7	305.3	25.0	149.0	18014.7	2440.0
Birhan	74.3	120.7	18.3	130.7	12986.7	2850.0	66.0	133.0	23.0	112.0	18511.3	840.0
Debir	77.0	194.7	26.1	129	24223.3	3306.7	71.2	174.7	24	121.0	19721	2145
Dekeba	81.0	151.7	26.2	125.0	24500	4116.7	81.0	131.5	25	119.0	21000	2475
Framida	87.7	223.0	24.8	146.7	27133.3	4680.0	70.7	179.2	17.7	119.0	26164.7	1706.7
Gambella1107	82.7	161.3	23.6	132.0	24756.7	3976.7	78	158	24	124	23120	2244
Gobiye	74.7	145.0	34.8	122.0	17946.7	2740.0	69.0	113.8	17.3	117.0	16041.3	900.0
Jamiyu	91.0	295.1	33.9	153.7	30593.3	6080.0	81.7	223.3	38.0	132.3	27398	2353.3
Jigurti	90.0	365.1	31.3	145.3	19976.7	4533.3	86.3	260.3	27.0	130.3	16284.7	2210.0
Local	91.7	276.5	32.1	115.0	25223.3	2943.3	135.0	281.7	11.3	117.0	27644.7	703.3
SRN39	76.7	152.9	17.7	123.7	24703.3	1653.3	73.3	135.3	17.0	148.7	35054.7	1163.3
Teshale	77.3	199.8	27.1	122.7	24486.7	5150	75	180	25	120	19152	2465
Tseadachimure	78.7	202.7	30.6	128.3	21576.7	3636.7	79	194	26	124	17650	2300
Wediaker	80.0	129.3	23.3	106	20666.7	3520	78.6	125	24	131	15570	1901
Wetetbegunchie	105.0	308.6	28.5	153.7	35776.7	3656.7	93.0	276.0	35.3	137.7	10361.3	1320.0
Mean	87.4	285.2	30.6	145.3	23103.6	3915.0	82.3	234.6	29.0	130.2	20925.5	2151.0
LSD (p<0.05)	5.7	52.5	NS	8.2	13150.5	1858.3	5.6	34.1	7.7	18	20731.3	778.2
CV (%)	3.9	11.3	25.8	3.5	26.6	28.9	4.3	9.3	16.3	8.4	29.3	15.4

DTF = days to 50% flowering, PLHT = plant height (cm), PL = panicle length (cm), DTM = days to maturity, BM = biomass (kg ha^{-1}), YLD= yield (kg ha^{-1}), LSD = Least significant difference, CV = Coefficient of variation, NS = non-significant difference