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REVIEW

Sweet sorghum ideotypes: genetic improvement of stress tolerance

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Abstract

Stress tolerance is a prerequisite for the success of biofuel production, which normally requires the use of marginal lands and nonfood biofuel feedstocks. Sorghum is known for its ability to withstand stress conditions, however, terminal stresses threaten its growth and development negatively impacting yield and sugar accumulation. It is crucial, therefore, that research aimed at developing sorghum resistance to stress factors should be pursued to expand the range of its growth to marginal and barren soils to meet the needs of a growing population, changing diets, and biofuel production. In this context, the leaf architectural trait of stay-green drought tolerance, in addition to salinity, cold, and aluminium toxicity and biotic stress tolerance and their genetic basis discussed in this review are expected to be available in future sweet sorghum ideotypes. Also highlighted is the key role of efficient management of farming systems, in particular the use of herbicides to control weeds, to ensure the sustainability of the sweet sorghum biomass productions.

Introduction

Abiotic and biotic stress limits plant growth, crop productivity, and biofuel production. Changes in precipitation patterns due to climate change and meteo-climatic variability have become a critical issue and a limiting factor for the crops under rain-fed systems and for the water resource when irrigation is applied. In arid and semiarid areas where water is limiting, the cultivation of irrigated energy crops could exacerbate the problem of competitiveness with food crops for the water use. Therefore, drought-tolerant energy crops should be the preferred choice in terms of both adaptation and environmental sustainability.

Sorghum originated from Africa and is currently the fifth most important cereal crop in the world and a staple crop for humans and other animals for food, feed, fodder, fiber, and fuel. Cultivation of sweet sorghum for the production of bioenergy is an attractive option to cope with the challenges of climate change to which adaptation is necessary in order to maintain good levels of productions (Berndes et al. 2003; Sims et al. 2006; Orlandini et al. 2007; Dalla Marta et al. 2014).

Sweet sorghum accumulate soluble sugars in the stalk at the expense of panicle production, these sugars could be mechanically extracted and directly fermented to obtain first generation bioethanol. Abiotic stress is a serious environmental obstacle for sugar production in sweet sorghum and strongly threatens biomass production and biofuel yields (Zegada-Lizarazu and Monti 2013). For instance, the structural carbohydrates (cellulose, hemicelluloses, and lignin) and biomass yields in sweet sorghum are significantly affected by drought stress (Zegada-Lizarazu and Monti 2013). In addition, during the 2010–2011 La Niña period in East Africa, drought led to sharp declines in the production of sorghum, a staple food in this semiarid region. For Somalia, the total sorghum production in 2011 was 25 kilotons, more than 80% below normal and the lowest for the last decade (Anyamba et al. 2014). However,

sweet sorghum is considered water stress-resistant and suitable for arid and semiarid marginal areas (Staggenborg et al. 2008), due to morphophysiological characteristics which confer the drought tolerance (Zegada-Lizarazu and Monti 2013), and to the C_4 photosynthetic system which allows efficient CO_2 fixation and an outstanding dry matter accumulation (Mastrorilli et al. 1999).

The high sugar content, and therefore the sweetness in sweet sorghum attracts about 150 insect pests throughout its life cycle, which negatively impacts on biomass production (Guo et al. 2011). Common examples of pests that can severely damage a sorghum crop include the Miridae and Lygaeidae (Kruger et al. 2008), sorghum midge, Greenbug, fall armyworm, corn borers (Munson et al. 1993; Wu and Huang 2008; Damte et al. 2009), grasshoppers, sorghum shoot fly, corn rootworm, and sorghum aphid. Sorghum may also be affected by a number of diseases including anthracnose, down mildew, and Fusarium.

Climate change is associated with an increase in the frequency of heat stress, droughts, and floods (Kim et al. 2014) that negatively affect crop yields and biomass production and the ability of the climate smart sorghum to adapt and yield under such harsh environment. Resistance to abiotic and biotic stress is crucial in determining the sustainability of food and biofuel production in future (http://dialogues.cgiar.org/blog/millets-sorghum-climate-smart-grains-warmer-world/).

Here, we review the abiotic and biotic stress resistance, key traits expected to become available in new sweet sorghum ideotypes dedicated for biofuel production in the future and the control of these traits at the genetic level. We highlight the key role of a proper management of the farming systems, in particular, the use of herbicides to control weeds, to ensure the sustainability of the sweet sorghum biomass and biofuel productions.

QTLs related to abiotic and biotic stress tolerance in sorghum

Traditional breeding and QTL analysis have been applied for the identification of genes responsible for biotic and abiotic stress tolerance in crops plants (Collins et al. 2008; Takeda and Matsuoka 2008). Thus, 350 QTLs related to abiotic and biotic stress tolerance in sorghum (Table 1) were identified. These genetic loci have the potential to be utilized in developing superior sorghum ideotypes for various agroecological climates through marker-assisted breeding and genetic engineering once candidate genes have been fine mapped. In total, 51 and 182 loci were found to have known physical and genetic map positions, respectively. To have an idea of their chromosomal distribution in relation to biotic and abiotic stress traits they control, an atlas map (Fig. 1) was generated. The outer rectangular marks indicate QTLs with known genetic position and the inner circular marks shows QTLs with known physical map positions on sorghum chromosomes. The next-generation sequencing and advanced metabolic profiling might impact the field of QTL analysis and facilitate the cloning of more genes responsible for tolerance to abiotic and biotic stresses. The ability to resequence a large number of F2 or recombinant inbred lines coupled with statistical linkage analysis could open the way for a very rapid and new type of marker-assisted mapping at the genome or metabolome level (Zheng et al. 2011).

Leaf stay-green drought resistance trait in sorghum

Sorghum is a drought-tolerant crop due to its ability to display morphological changes such as dense and deep root system, reduction in transpiration through leaf rolling and stomatal closure, and lowering of metabolic processes to near dormancy in response to terminal stress (Schittenhelm and Schroetter 2014). In fact, sorghum can survive prolonged dry periods, then 'resurrect' and resume growth once the soil moisture becomes available. However, depending on the severity, sorghum still suffers yield and biomass losses of up to 90% (House 1985). Recently, drought led to a sharp decline in agricultural production of sorghum up to 80% below the normal in Somalia during the 2010–2011 La Nina period (Anyamba et al. 2014). The impact of drought stress is greater during the grain-filling stage and causes premature leaf death, plant senescence, stalk lodging, and charcoal rot with poor yield of seed and stover. Cultivars tolerant to drought stress at postflowering stage are referred to as stay-green cultivars.

Stay-green is an integrated heritable drought adaptation trait characterized by a distinct green leaf phenotype during grain filling or postflowering under drought (Borrell et al. 2014a), Indeed, genetic studies show that QTLs for temperature and drought responses coincide with loci for leaf senescence, and in numerous examples of improvements in stress tolerance achieved by simultaneous selection for stay-green (Ougham et al. 2008; Vijayalakshmi et al. 2010; Jordan et al. 2012; Emebiri 2013). Stay-green trait is characterized either as cosmetic in which a lesion interferes with an early step in chlorophyll catabolism or functional in which the transition from the carbon capture period to the nitrogen mobilization (senescence) phase of canopy development is delayed, and/or the senescence syndrome proceeds slowly. Alteration in hormone metabolism and signaling, particularly affecting the networks involving cytokinins and ethylene, could contribute to the stay-green phenotype.

Table 1. The biofuel-associated traits of stay-green drought resistance trait, resistance to abiotic and biotic stresses, and their genetic determinants.

Traits	Trait category	No. of QTLs	*QTL names*	References
Abiotic stress tolerance	Stay-green/leaf senescence	1	*Stg1 (green leaf area retention)*	Subudhi et al. (2000), Xu et al. (2000), Kebede et al. (2001), Sanchez et al. (2002), Harris et al. (2007), Sabadin et al. (2012)
		1	*Stg2 (green leaf area retention)*	
		1	*Stg3 (green leaf area retention)*	
		1	*Stg4 (green leaf area retention)*	
		1	*St2-1 (Stay green 2-1)*	Sabadin et al. (2012)
		1	*St2-2(Stay green 2-2)*	
		1	*St3 (Stay green 3)*	
		1	*St4 (Stay green 4)*	
		1	*St6 (Stay green 6)*	
		1	*St8 (Stay green 8)*	
		1	*St9 (Stay green 9)*	
		1	*St10 (Stay green 10)*	
		1	*Stg C.2 (Stay green C.2)*	Kebede et al. (2001)
		1	*Stg C.1 (Stay green C.1)*	
		1	*Stg B (Stay green B)*	
		1	*Stg E (Stay green E)*	
		1	*Stg D (Stay green D)*	
		1	*Stg A (Stay green A)*	
		3	*Ldg G (Lodging G)*, *Ldg F (Lodging F)*, *Ldg J (Lodging J)*	
		4	*Prf C(Preflowering drought tolerance C)*, *Prf F(Preflowering drought tolerance F)*, *Prf E(Preflowering drought tolerance E)*, *Prf G(Preflowering drought tolerance G)*	
		1	*Stg F(Stay green F)*	
		9	*(% GL15) (green leaf area percentages)*	Haussmann et al. (2002)
		14	*(% GL30)green leaf area percentages)*	
		13	*(% GL45)green leaf area percentages)*	
		6	*t-E8/102, th19/50, tD9/103, t329/132, bB20/205, umc84*	Tuinstra et al. (1997)
		1	*SGA (Stay-green A)*	Crasta et al. (1999)
		1	*SGD (Stay-green D)*	
		1	*SGG (Stay-green G)*	
		1	*SGB (Stay-green B)*	
		1	*SG1.1 (Stay-green 1.1)*	
		1	*SG1.2 (Stay-green 1.2)*	
		1	*SGJ (Stay-green J)*	
		1	*MB6-84-TS136*	Tao et al. (2000)
		1	*TXS654-TXS943*	
		1	*ST1668-TXS558*	
		1	*CDO460-SSCIR165*	
		2	*QLsn.txs-B, QLsn.txs-Ea/Eb (Leaf senescence)*	Feltus et al. (2006)
	SPAD at booting	3	*QSpadb-dsr09-1, QSpadb-dsr06-1, QSpadb-dsr03*	Reddy et al. (2014)
	SPAD values at maturity	1	*QSpadm-dsr09-1*	
	Green leaves at booting	4	*QGlb-dsr01-1a, QGlb-dsr04-1, QGlb-dsr02-1, QGlb-dsr04-3*	
	Green leaves at maturity	2	*QGlm-dsr04-1, QGlm-dsr09-2*	
	Per cent green leaves retained at maturity	2	*QPglm-dsr04-2, QPglm-dsr09-2*	
	Green leaf area at booting	2	*QGlab-dsr10-1, QGlab-dsr02-1,*	
	Green leaf area at maturity	1	*QGlab-dsr02-2*	

(*Continued*)

Table 1. Continued.

Traits	Trait category	No. of QTLs	*QTL names*	References
	Rate of leaf senescence	1	*QRls-dsr10-1*	
	Cold germinability/field emergency and early seedling vigor	16	*Germ30-1.1, Germ30-1.2, Germ30-2.1, Germ12-2.1, Germ12-9.2; Fearlygerm-1.2, Fearlygerm-7.1, Fearlygerm-9.2, Fearlygerm-9.3, Fearlygerm-1.1, Fearlygerm-4.1, Fearlygerm-9.1, Fearlygerm-9.3; Xtxp43, Xtxp51, Xtxp211*	Burow et al. (2011a,b),
	Aluminium tolerance	1	*Alt(SB)*	Magalhaes et al. (2007)
	Salinity stress (germination vigor, germination percentage, shoot height, root length, shoot fresh weight, root fresh weight, total fresh weight, shoot dry weight, root dry weight, total dry weight)	38	*qGV2-1, qGV2-2, qGV3; qGV1-1, qGV1-2, qGV4; qGP1, qGP2,qGP7-1, qGP7-2; qSH8, qSH1,qSH2, qSH4, qSH10;qRL1, qRL8, qRL3, qRL10-1, qRL10-2; qSFW8, qSFW9-1, qSFW4,qSFW9-2; qRFW6-1, qRFW2, qRFW6-2; qTFW6, qTFW9-1, qTFW1, qTFW4, qTFW9-2; qSDW4, qSDW9, qSDW6;qRDW3, qRDW6;qTDW6, qTDW8*	Wang et al. (2014a,b)
	Number of rhizomes/ subterranean rhizomes/ number of rhizome-derived shoots/ Overwintering	7	*pSB300a-pSBO88, pSB195-SH068, pSBJ02-pSB158; Overwintering2011A, Overwintering2011B; Ln2010RDS, Ln2010Dist*	Paterson et al. (1995), Washburn et al. (2013)
Subtotal		159		
Biotic stress tolerance	Midge disease egg count	2	*Flanking markers (ST698- RZ543, ST1017 -SG14)*	Tao et al. (2003)
	Midge disease pupal infestation	3	*Flanking markers (ST698- RZ543, ST1017 -SG14, TXS1931-SG37)*	
	Target leaf spot	1	*tls (*Target leaf spot)	Mohan et al. (2009)
	Zonate leaf spot	1	*Zls (*Zonate leaf spot)	
	Drechstera leaf plight	1	*Dls (*Drechstera leaf plight)	
	Rust resistance	8	*BNL5.09, TXS1625, RZ323, ISU102, ISU102, TXS2042, PSB47, TXS422*	Tao et al. (2003)
	Anthracnose resistance	14	*7 QTLs not named, Cg1, Locus 1-8, QAnt1, QAnt4,* SC326-6, SCA 12, OPJ 0_{11437}	Boora et al. (1998), Klein et al. (2001), Singh et al. (2006), Singh et al. (2006), Perumal et al. (2009), Mohan et al. (2010), Upadhyaya et al. (2013)
	Percentage ergot infection	9	*Not named*	Parh et al. (2008)
	Pollen quantity	5	*Not named*	
	Pollen viability	4	*Not named*	
	Greenbug resistance to biotype I and K, C, and K/ greenbug feeding	34	*B18-885, OPC01-880, Sb5-214, Sb1-10, SbAGB03, Sb6-84, SbAGA01, OPA08-1150, OPB12-795; Ssg1, Ssg2, Ssg3, Ssg4, Ssg5, Ssg6,Ssg7, Ssg8, Ssg9; (8 unnamed QTLs);QSsgr-09-01, QSsgr-09-02;Qstsgr-sbi09ii, Qstsgrsbi09iii, Qstsgr-sbi09i, Qstsgr-sbi09iv;Xtxp16–Starssbem162, Starssbem162–Starssbem265*	Agrama et al. (2002), Katsar et al. (2002), Nagaraj et al. (2005), Wu and Huang (2008), Punnuri et al. (2013)
	Head bug resistance/ damage	10	*SbRPG943-RZ630, RZ476-SbRPG872, SbRPG667-CDO580, BNL5.37-SbRPG749, BNL5.37-SbRPG749, BNL5.37-SbRPG749, CDO20-C223, RZ630-SbRPG826, RZ244b-SbRPG852, mAGB03-UMC139*	Deu et al. (2005)
	Leaf scotch	1	*QLsc.txs-B (Leaf scotch)*	Feltus et al. (2006)

(*Continued*)

Table 1. Continued.

Traits	Trait category	No. of QTLs	*QTL names*	References
	Stalk rot resistance(No of internode, length of infection, percent lodging)	8	*xtxp297, xtxp213, AC13, xtxp343, xtxp176, (3 unnamed QTL for lodging resitance*	Reddy et al. (2008), Felderhoff et al. (2012)
	Shoot fly leaf glossiness	8	*QGs.dsr-3, QGs.dsr-5, QGs.dsr-6, QGs.dsr-10; QGs.dsr-1, QGs.dsr-4.1, QGs.dsr-2, QGs. dsr-4.2*	Satish et al. (2009), Aruna et al. (2011)
	Shoot fly seedling vigor	8	*QSv.dsr-3, QSv.dsr-6.1, QSv.dsr-6.2, QSv. dsr-10; QSv.dsr-1.1, QSv.dsr-1.2, QSv.dsr-2, QSv.dsr-9*	Satish et al. (2009), Aruna et al. (2011)
	Shoot fly oviposition	7	*QEg21.dsr-1, QEg21.dsr-7, QEg21.dsr-9, QEg21.dsr-10, QEg28.dsr-5, QEg28.dsr-7, QEg28.dsr-10*	Satish et al. (2009)
	Shoot fly deadheart	13	*QDh.dsr-5, QDh.dsr-10.3, QDh.dsr-10.4; QDh. dsr-1.1, QDh.dsr-1.2, QDh.dsr-2, QDh.dsr-6.1, QDh.dsr-6.2, QDh.dsr-7.1, QDh.dsr-7.2, QDh. dsr-9, QDh.dsr-10.1, QDh.dsr-10.2*	Satish et al. (2009), Aruna et al. (2011)
	Shoot fly adaxial trichome density	4	*QTdu.dsr-10.1, QTdu.dsr-10.2; QTdu.dsr-7, QTdu.dsr-10*	Satish et al. (2009), Aruna et al. (2011)
	Shoot fly abaxial trichome density	7	*QTdl.dsr-1.1, QTdl.dsr-1.2, QTdl.dsr-4, QTdl. dsr-6, QTdl.dsr-10.1, QTdl.dsr-10.2; QTdl.dsr-3*	Satish et al. (2009), Aruna et al. (2011)
	Root and crown rot resistance (*Pc* locus)	1	*PC*	Nagy et al. (2007)
	Striga resistance	39	*38 QTLs Not named; lgs*	Haussmann et al. (2004), Satish et al. (2012)
	Resistance to down mildew	3	*bin 2.04/05, bin 3.04/05, bin 6.05*	Nair et al. (2005)
Subtotal		191		
Total QTLs		350		

Cytokinin production increases growth and yield by improving foliar stay-green indices under drought conditions and improving processes that impact grain filling and grain number (Wilkinson et al. 2012). This suggests that the stay-green phenotype could be achieved by the biotechnological expression of isopentenyltransferase (*IPT*) gene whose protein catalyzes the rate-limiting step in cytokinin biosynthesis. Indeed, transgenic tobacco plants overexpressing *IPT* gene produced more trans-zeatin, did not senesce, had water content of 86%, maintained photosynthetic activity, and resurrected upon rewatering (Rivero et al. 2010). In addition, members of the WRKY and NAC families, and an ever-expanding cast of additional senescence-associated transcription factors, are identified by mutations that result in stay-green phenotype (Thomas and Ougham 2014).

Retention of chlorophyll in leaves of stay-green genotypes is associated with enhanced capacity to continue normal grain fill and maintenance of the ability to undergo photosynthesis for longer periods under drought conditions, reduced lodging, high stem carbohydrate content and grain weight, and resistance to charcoal stem rot (McBee et al. 1983; Borrell et al. 2000b; Burgess et al. 2002; Jordan et al. 2012). Hybrids involving stay-green sources produced close to 47% more biomass between anthesis and maturity in comparison with senescent checks (Borrell et al. 2000a). Moreover, the stay-green cultivar Sorcoll-141/07 had high plant height and green leaf number that contribute to its high biomass (Yemata et al., 2014). Leaves of stay-green cultivars have higher nutritional quality (Jordan et al. 2012). The high leaf nitrogen content and the simultaneous prolonged photosynthesis associated with stay-green trait (Borrell et al. 2000b) are correlated with higher sugar production in sorghum (Serrão et al. 2012) suggesting that leaf nitrogen concentrations and increased photosynthetic capacity are indicators for predicting sugar production in sweet sorghum. Therefore, breeding for stay-green trait specifically associated with high stem carbohydrates and leaf nitrogen will undoubtedly boost biofuel production in sweet sorghum cultivars.

The sources of stay-green trait used in most of the genetic studies and associated breeding programmes are lines BTx642, formally (B35), SC 56, E36-1, and KS19 (Haussmann et al. 2002; Mahalakshmi and Bidinger 2002; Hash et al. 2003) and have been reported to have greater

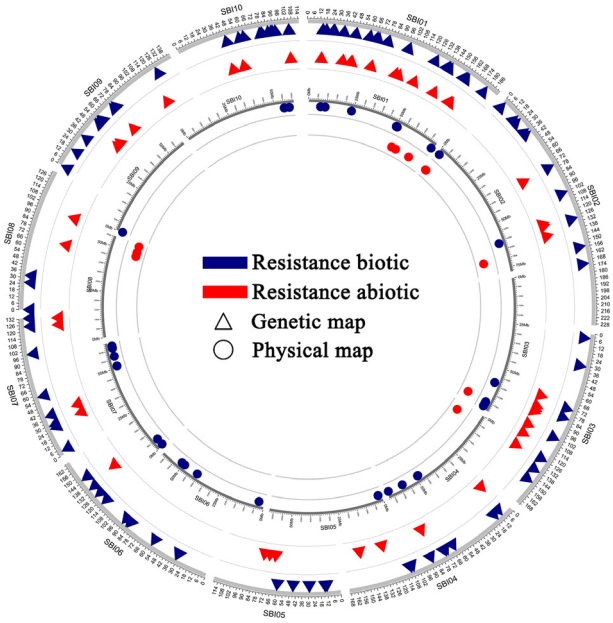

Figure 1. QTLs atlas map for biofuel-associated abiotic and biotic resistance traits in sorghum.

adaptation to drought stress through osmotic adjustment (Zhou et al. 2013). Indeed, the leaf relative water content of stay-green lines is much higher than those in nonstay-green lines, indicating that the stay-green lines keep the stalk transportation system functioning under severe drought conditions (Xu et al. 2000). Four loci *Stg1, Stg2*, *Stg3*, and *Stg4* (Table 1) controlling the stay-green trait in sorghum have consistently been identified across several environments in different mapping populations derived from crosses with BTx642, SC 56, E36-1, and KS19 lines, though each study reported varying phenotypic variation contributed by each QTL (Crasta et al. 1999; Subudhi et al. 2000; Tao et al. 2000; Xu et al. 2000; Kebede et al. 2001; Sanchez et al. 2002; Feltus et al. 2006; Harris et al. 2007; Sabadin et al. 2012). This suggests that although the ability of leaves to delay senescence has a genetic basis in sorghum, the expression of the character is strongly influenced by environmental cues (van Oosterom et al. 1996). QTLs controlling chlorophyll content colocated with the *Stg1, Stg2*, *Stg3*, and *Stg4* loci controlling stay-green (Subudhi et al. 2000) and (Xu et al. 2000). Therefore, chlorophyll content or loss of chlorophyll is a marker for the stay-green trait in sorghum during grain filling under drought.

The consistency of the four QTLs in various mapping populations across various environments and their combined phenotypic variation contribution of 54% to the stay-green drought trait suggest that they are stable and major QTLs for stay-green drought trait in sorghum (Tanksley 1993; Xu et al. 2000; Sanchez et al. 2002). Fifteen (15) novel QTLs (Table 1) for various measures of stay-green trait have been identified using a genetic linkage map based on 245 F_9 Recombinant Inbred Lines (RILs) derived from a cross between M35-1 (more senescent) and B35 (less senescent) (Reddy et al. 2014). The phenotypic variation explained by each QTL ranged from 3.8 to 18.7%. Several other stay-green loci have also been reported (Table 1) but are generally unstable across environments (Crasta et al. 1999) with the potential to spontaneously reverts back to their parental phenotypes. The sorghum line E36-1, for instance, displays stay-green phenotype when grown under drought conditions in the field (van Oosterom et al. 1996), but not under well-watered conditions. (Tuinstra et al. 1997; Kebede et al. 2001; Thomas and Ougham 2014) identified six genetic loci controlling preflowering drought stress tolerance in sorghum from RILs derived from the crosses, SC 56 × Tx7000 and Tx7078 × B35, respectively with phenotypic variation contributed ranging between 15 to 40% under different environments, suggesting a strong genotype × environment (G × E) interaction at these loci.

Under water limited conditions, the stay-green alleles have been implicated to individually enhance grain and biomass yields in sorghum by modifying canopy development and water uptake patterns (Borrell et al. 2014b), indicating that stay-green phenotype and biomass yield could be achieved via the modification of root architecture (Mace et al. 2012), canopy development through reduction in tillering via increased size of lower leaves (Borrell et al. 2000a), or both. Thus far, breeders have transferred through marker-assisted backcrossing the stay-green trait into elite cultivars (Hash et al. 2003). The approach has been compromised because stress-related QTLs are dependent on the environmental conditions to which they were characterized (high G × E interaction) (Collins et al. 2008). In addition, different QTLs associated with stress-related traits can explain only a low percentage of the variation in the phenotype and that the effects of a favorable allele could not be transferred due to epistatic interactions (Peleg et al. 2009). Therefore, identifying QTLs of major effect that are independent of the particular genetic background and cloning the genes in the QTL could enhance breeding through biotechnology.

Functional analysis of the genes can be significantly aided through the application of reverse genetics approaches such as RNA interference (RNAi) and the type II CRISPR/Cas system (Jiang et al. 2013) in order to characterize the individual gene function(s). Emphasis should be given to forward genetics studies where the identified genes can be expressed in genotypes that have been already selected for their adaptation to stressful environmental conditions. The availability of the sorghum genome may aid in fine

mapping of the candidate genes responsible for the stay-green trait through increasing marker density within the target chromosomal region in addition to increasing the number of segregating population for which phenotypic information linked to the QTL can be obtained.

Proline accumulates to high levels in many plant species in response to environmental stresses and its role has been extensively investigated under stress conditions (Verbruggen and Hermans 2008). Recently, the Arabidopsis proline dehydrogenase (*AtProDH2*) was found to be strongly expressed in senescent leaves and in roots (Funck et al. 2010), suggesting that proline could have a new role during plant developmental processes. Similar findings in oilseed rape (*Brassica napus*), demonstrated that the *BnaProDH2* genes are specifically expressed in vasculature in an age-dependent manner in roots and senescent leaves (Faës et al. 2014). Thus, indicating that such expression could be related to the provision of reducing power for cell degradation mechanisms when chloroplasts become dysfunctional, an early process in autophagy (Avila-Ospina et al. 2014). The catabolism of proline could also contribute to recycling of metabolites in senescent leaves and provides glutamate then glutamine, principal forms of nitrogen compounds transported in the phloem from senescing leaves to sink organs (Tilsner et al. 2005). Similar studies could be carried out in sorghum in order to link the role of proline in abiotic stress conditions and in the developmental process of leaf senescence and biomass production.

Molecular mechanisms involved in the response of sorghum to abiotic stress

MiRNA expression

MicroRNAs (miRNAs) are a recently discovered class of gene expression regulators that have also been linked to several plant stress responses (Sunkar et al. 2007; Rajwanshi et al. 2014; Zhai et al. 2014) and in the biosynthesis pathways of carbon, glucose, starch, fatty acid, and lignin and in xylem formation, which could aid in designing next-generation sweet sorghum for biomass and biofuel. Differentially expressed miRNAs involved in the regulation of transcription (*bZIPs*, *MYBs*, *HOXs*), signal transduction (phosphoesterases, kinases, phosphatases), carbon metabolism (*NADP-ME*), detoxification (*CYPs*, *GST*, *AKRs*), osmoprotection mechanisms (*P5CS*), and stability of protein membranes (*DHN1*, *LEA*, *HSPs*) were upregulated upon imposition of drought stress in a four-leaf-old sorghum genotype IS1945 (Pasini et al. 2014), indicating that these drought-related genes could be used to screen for potential drought tolerance in other sorghum genotypes including sweet sorghum. Indeed, rice miRNA 169 g, upregulated during drought stress (Zhao et al. 2007), has five sorghum homologs (*sbi-MIR169c*, *sbi-MIR169d*, *sbi-MIR169.p2*, *sbi-MIR169.p6*, and *sbi-MIR169.p7*), suggesting that the miRNA may be involved in many different processes related to drought stress resistance. The computationally predicted targets of the sbi-MIR169 subfamily comprise members of the plant nuclear factor Y (*NF-Y*) B transcription factor family, linked to improved performance in Arabidopsis, and maize under drought stress (Nelson et al. 2007). *GmNFYA3* gene, a target of miR169, is a positive regulator of plant tolerance to drought stress and has potential applications in molecular breeding to enhance drought tolerance in crops (Ni et al. 2013).

Using a deep sequencing approach to generate a genome-wide transcriptome of foxtail millet after exposure to simulated drought stress, one long noncoding RNAs (lncRNAs) was found to share sequence conservation and colinearity with its counterpart in sorghum suggesting that the lncRNAs in sorghum have the potential to have an impact on drought-regulated gene expression (Qi et al. 2013). The analysis of *cis*-elements of miRNA targets including transcription factors, genes for chaperonins, and metabolic enzymes and other genes necessary for proper plant development provides molecular evidence for the possible involvement of miRNAs in the process of abiotic stress tolerance in sorghum, indicating that miRNAs could play an important role in water stress tolerance in future sorghum studies (Ram and Sharma 2013). Therefore, miRNA 169 could be an excellent target for the generation of drought-resistant sweet sorghum genotypes through genetic engineering.

Auxin-related genes

Auxin-related gene families in *Sorghum bicolor* have also been implicated in abiotic stress response. The Gretchen Hagen3 (GH3) *SbGH3* and lateral organ boundaries (LBD) (*SbLBD*) genes, expressed at low levels under natural condition, were highly induced by salt and drought stress consistent with their products being involved in both abiotic stresses. Three genes, *SbIAA1*, *SbGH3-13*, and *SbLBD32*, were highly induced under all the four treatments, Indole-3-Acetic Acid, brassinosteroids, salt, and drought. The analysis provided new evidence for role of auxin in stress response, implying there are cross talk between auxin, brassinosteroids, and abiotic stresses (Wang et al. 2010).

Moisture stress triggered the upregulation of more transcription factor genes of MADS-box, Auxin Responsive Factors, Heme Activator Protein 2, Multiprotein Bridging Factors, and Homeobox families in root tissues compared to shoot tissues in sorghum (Aglawe et al. 2012). Under ABA, salt and drought treatments, sorghum auxin transporters *SbPIN4*, *-5*, *-8*, *-9*, and *-11* were highly increased,

whereas *SbPIN1-3*, *-6*, *-7*, and *-10* were almost inhibited by all three treatments (Shen et al. 2010). The expression levels of *SbLAX1*, *-2*, *-4*, and *-5* compared with *SbLAX3* in leaves were lower than those in roots when treated with ABA. However, the response of *SbLAX* genes to salt and drought stresses was irregular, with *SbLAX4* expression downregulated dramatically under the stresses. Interestingly, transcription of the *SbPGP* gene family was almost inhibited in roots under salt treatment. *SbPGP1*, *-2*, *-5*, *-13*, *-14*, and *-15* were induced in roots under ABA treatment, whereas *SbPGP2*, *-3*, *-4*, *-7*, *-12*, and *-23* were induced in leaves under salt or drought stress. Under salt and drought treatment, *SbPGP13*, *-15*, *-17*, *-18*, *-20*, *-21*, and *-24* were all downregulated in both leaves and roots. Exploiting RNA-Seq technology in combination with the sorghum genome sequence (Paterson et al. 2009) and the SorghumCyc metabolic pathways database, (Dugas et al. 2011) characterized the sorghum transcriptome and reexamined the differential expression of sorghum genes in response to exogenous ABA and osmotic stress (Buchanan et al. 2005). Fifty differentially expressed drought-responsive gene orthologs specific to sorghum were identified for which no function had been previously assigned either in maize, rice, or Arabidopsis and were enriched for ABREs and CGTCA-motifs, or motifs that are involved in responses to ABA.

Transcription factors

The ethylene response factor family, members of the APETALA2 (AP2)/ERF transcription factor superfamily, is known to play an important role in plant adaptation to biotic and abiotic stress (Lata et al. 2014) and 105 sorghum ERF (*SbERF*) genes, categorized into 12 groups (A-1 to A-6 and B-1 to B-6) based on their sequence similarity have been identified in sorghum (Yan et al. 2013) Glutathione reductases (GRs) are important components of the antioxidant machinery that plants use to respond against abiotic stresses. Phylogenetic analysis identified two chloroplast GRs in sorghum that could possibly have a role in the modulation of abiotic stress. Since chloroplasts GR are also targeted to mitochondria suggest a combined antioxidant mechanism in both chloroplasts and mitochondria (Wu et al. 2013). In addition, phylogenetic analysis of the rice heterotrimeric G-protein complexes Gα subunit revealed high homology with sorghum. The promoter sequence analysis of RGA1(I) confirms the presence of stress-related *cis*-regulatory elements viz. ABA, MeJAE, ARE, GT-1 boxes, and LTR suggesting its active and possible independent roles in abiotic stress signaling. Furthermore, transcript profiling of RGA1(I) showed upregulation following NaCl, cold and drought stress, but under an elevated temperature, its transcript was downregulated. Heavy metal(loid)s stress showed rhythmic response in ABA stress and strong upregulation. These findings provide critical evidence for the active role of G-protein complexes in regulation of abiotic stresses in rice and possibly in sorghum and suggest that the Gα subunit of the heterotrimeric G-protein complexes could be exploited in the development of abiotic stress tolerance in sorghum. Genes coding for drought response element-binding (*DREB*) proteins regulate transcription of a large number of downstream genes involved in the plant response to abiotic stresses. An integration of abscisic acid, ethylene, auxin, and methyl jasmonate signaling was probably involved in regulating expression of the drought response through *DREB* transcription factors. The *SbEST8* gene was implicated to have a role in abiotic stress tolerance since imposition of drought resulted in rapid accumulation *SbEST8* mRNA in the germinating seeds of drought susceptible cultivar ICSV-272 (Dev Sharma et al. 2006).

Compatible solutes

The introduction of compatible solute synthesis pathway has emerged as a potential strategy for enhancing abiotic stress tolerance in crop plants (Rathinasabapathi 2000). The ability to synthesize and accumulate glycine betaine is widespread among angiosperms and is thought to contribute to salt and drought tolerance. Betaine aldehyde dehydrogenase *BADH1* and *BADH15* mRNA in sorghum were both induced by water deficit and their expression coincided with glycine betaine accumulation. The leaf water potential in stressed sorghum plants reached −2.3 MPa in the course of 17 days of water stress. Water deficit induced a 26-fold increase in glycine betaine levels and proline levels increased 108-fold (Wood et al. 1996). The upregulation of *Sorghum bicolor* glycine-rich RNA-binding protein designated as sbGR-RNP was induced by salinity and ABA and regulated by blue and red light, suggesting that there exists a cross talk between abiotic stress and light signaling in sorghum (Aneeta et al. 2002).

The mannitol biosynthetic pathway was engineered into *Sorghum bicolor* L. Moench cv. SPV462 with the *mtlD* gene encoding for mannitol-1-phosphate dehydrogenase from *E. coli*. The transgenic leaf segments were found to retain higher leaf water content when exposed to polyethylene glycol 8000 (−2.0 MPa) and maintained a 1.7- to 2.8-fold higher shoot and root growth, respectively, under NaCl stress (200 mmol/L) when compared to untransformed controls (Maheswari et al. 2010). These studies establish a role for a number of genes in modulating drought stress tolerance in sorghum. Therefore, functional characterization of these genes in sorghum including their overexpression or down regulation using

genetic engineering could provide additional information as to their roles in broad abiotic stress tolerance.

Expression analysis of key stress inducible regulatory genes that play crucial roles in proline biosynthesis, *SbP5CS1* and *SbP5CS2*, revealed that the transcripts were upregulated after treatment of 10-day-old seedlings of sweet sorghum with drought, salt (250 mmol/L NaCl) and MeJA (10 μmol/L) indicating that the two genes could have the potential to be used in improving stress tolerance of sweet sorghum and other bioenergy feedstocks (Su et al. 2011).

Cold tolerance in sorghum

Soil temperatures below 15°C limit germination and seedling establishment for sorghum during early-season planting in temperate areas. Developing fast-growing sorghum seedlings is an important breeding goal for temperate climates since low spring time temperatures result in a prolonged juvenile development. In addition, this would allow expansion of sorghum to temperate region and for earlier planting in areas where it is being grown (Singh, 1985). In China, sorghum landrace, *kaoliang*, has poor agronomic characteristics though it exhibits higher seedling emergence and greater seedling vigor under cold conditions. The genetic basis of early-season cold tolerance in sorghum associated with germination, emergence, and vigor has been investigated and 15 QTLs have been identified (Table 1, (Burow et al. 2011a; Knoll and Ejeta 2008; Knoll et al. 2008). Using marker-assisted selection these desirable genomic regions can be introgressed into elite lines to improve early-season performance in sorghum. The quality of the messenger RNAs stored during embryo maturation on the mother plant, proteostasis, and DNA integrity play a major role in the germination phenotype. In addition, the sulfur amino acid metabolism pathway represents a key biochemical determinant of the commitment of the seed to initiate its development toward germination (Rajjou et al. 2012). Therefore, the characterization of molecular variables for germination and seed vigor under cold stress is expected to deliver new markers of seed quality that can be used in breeding programs and/or in biotechnological approaches to improve biomass yield in sweet sorghum. Further, a higher respiration rate is positively correlated with a higher germination rate and cultivars with higher respiration rate are likely to be resistant to early-season cold (Balota et al. 2010). Therefore, selection for a higher respiration rate can improve early-season vigor (germination, elongation, and growth rate in sorghum).

Rhizome formation trait is correlated and genetically linked to overwinter survival in sorghum (Washburn et al. 2013). The understanding of the genetic mechanisms controlling overwintering has the potential to create perennial sorghums that can overwinter in climates where they previously could not. These overwintering sorghum types could be used for improvements in biofuel sorghum production by extending the period of biomass production and reducing production costs. In sorghum, rhizomatousness and overwintering are controlled by seven QTLs (Paterson et al. 1995; Washburn et al. 2013) Table 1). The QTLs were identified from a mapping population of a cross between BTx623 and *S. propinquum* and that regrowth after overwintering was associated with both rhizomatousness and tillering.

Salinity tolerance in sorghum

Salinity stress affects plant growth and productivity in many parts of the world and plants have developed adaptive responses to this external stress at the genetic level. For example, under sodium stress, *SbHKT1;4*, a member of the high-affinity potassium transporter gene family from *Sorghum bicolor*, functions to maintain optimal Na^+/K^+ balance (Wang et al. 2014b). Upon Na^+ stress *SbHKT1;4* expression was more strongly upregulated in salt-tolerant sorghum accessions, correlating with better balanced Na^+/K^+ ratio and enhanced plant growth. To gain insight into the genetic mechanism of salt tolerance at germination and seedling stage as a basis for improving salt tolerance in sorghum, (Wang et al. 2014a) identified 38 QTLs underlying salt tolerance (Table 1) from a 181 recombinant inbred lines derived from Shihong 137 and L-Tian. Six major QTLs with more than 10% phenotypic variation were detected at seedling stage under salt stress. These data indicate that the genetic mechanism for salt tolerance at germination and seedling stage in sorghum is different and that further research need to be done to identify genetic loci determining salt tolerance at different growth stages of sorghum during development.

Sorghum tolerance to Aluminium toxicity

Aluminum (Al) toxicity is an important limitation to food security in tropical and subtropical regions. In acidic soils, aluminum is solubilized into ionic forms (Al^{3+}), especially when the soil pH falls to lower than 5. This ionic form of Al is very toxic to plants, limiting the growth of roots either by inhibition of cell division, cell elongation, or by both. In this way, water and nutrient uptake by the roots is affected and as a consequence, plant growth and development is seriously hindered (Foy et al. 1993). Aluminum toxicity is, therefore, a major constraints for sorghum production in tropical and subtropical regions of the world (Doumbia et al. 1993, 1998). In addition

to naturally occurring acid soils, agricultural practices may decrease soil pH, leading to yield losses due to Al toxicity. Elucidating the genetic and molecular mechanisms underlying sorghum Al tolerance is expected to accelerate the development of Al-tolerant cultivars. Using positional cloning, a gene encoding a member of the multidrug and toxic compound extrusion (MATE) family, an aluminum-activated citrate transporter, was identified as responsible for the major sorghum aluminum tolerance locus, Alt(Sb), on sorghum chromosome 3 (Magalhaes et al. 2007). These markers have been used by breeders to introgress rapidly the most favorable *SbMATE* alleles into sorghum germplasm, which is currently being field-tested in acid soils. Similar results have recently been demonstrated in maize where *ZmMATE1* expression, controlled either by three copies of the target gene or by an unknown molecular mechanism, is responsible for Al tolerance mediated by QTL mapped on chromosome 6 (*qALT6*) (Guimaraes et al. 2014). Polymorphisms in regulatory regions of Alt(Sb) are likely to contribute to large allelic effects, acting to increase Alt(Sb) expression in the root apex of tolerant genotypes. Furthermore, aluminum-inducible Alt(Sb) expression is associated with induction of aluminum tolerance via enhanced root citrate exudation (Magalhaes et al. 2007). These information could allow scientist to identify superior Alt(Sb) haplotypes that can be incorporated via molecular breeding and biotechnology into acid soil breeding programs, thus helping to increase crop yields in developing countries where acidic soils predominate.

Resistance to biotic stresses

Insect pests

Sorghum biomass and sugar yield are severely affected by biotic stresses including about 150 insect pests with more than 100 of them occurring in Africa (Guo et al. 2011), and new parental lines having genes for various biotic stress tolerances have the potential to mitigate this negative effect. The most destructive pests are the lepidopteran stem borer (*Chilo partellus*) and the dipterans, midge (*Stenodiplosis sorghicola*) and shoot fly (*Atherigona soccata*). Given the wide host range of some of the insect pests, and low level of resistance in the cultivated germplasm against major sorghum pests such as stem borers, head bugs, and armyworms, it will be highly desirable to invoke molecular plant breeding approaches combining conventional plant resistance with novel genes from other sources such as *Bacillus thuringiensis* (*Bt*) toxic protein. Insecticidal crystal proteins (*CRY*) from *Bacillus thuringiensis* are very effective against the lepidopterans and dipterans. *Bt* and other genes including protease inhibitors, enzymes, secondary plant metabolites, and plant lectins with insecticidal activities are being evaluated for eventual use in transforming cotton, maize, rice, sorghum, grain legumes, tobacco, potato, sugarcane, groundnuts and tomatoes and reducing losses due to these pests(Sharma et al. 2004; Visarada and Kishore 2007). A transgenic sorghum plant was generated carrying a synthetic gene, *Bt cry*1Ac, under the control of a wound-inducible promoter from a maize protease inhibitor gene (*mpi*) (Girijashankar et al. 2005). The transgenic sorghum had low levels of *Bt* protein of 1–8 ng/g of fresh leaf tissue. A moderate level of tolerance was reported, which in turn conferred partial protection against neonate larvae of the spotted stem borer (*Chilo partellus*). Transgenic sorghum plants expressing *Bt cry1Ab* gene displayed insect-resistance to pink rice borer (*Sesamina inferens*) (Zhang et al. 2009).

Sorghum midge is the most damaging pest of grain sorghum worldwide (Young and Teetes 1977). Though sweet sorghum accumulates sugar at the expense of grain, the damage caused on the grain of sweet sorghum by sorghum midge could impact biomass and sugar accumulations. At flowering, female midges oviposit into spikelets, and the larvae feed on the ovary during the following 2 weeks, resulting in the failure of kernel development. Using classical approach, over 40 sorghum cultivars resistant to midge have been identified (Sharma et al. 1999) and could be useful for use in resistance breeding programs and to mitigate against biomass and sugar lose in sweet sorghum. Two genetic mechanisms of midge resistance, antixenosis and antibiosis, have been resolved in a recombinant inbred population from the cross of sorghum lines ICSV745 × 90,562 (Tao et al. 2003). Two genetic regions (between loci *ST698* and *RZ543* of linkage group A and loci *ST1017* and *SG14* of linkage group G, respectively, were significantly associated with egg counts (antixenosis) and the degree of phenotypic variation explained by each region was 12% and 15%, respectively. Three genetic regions located on linkage group A, linkage group G, and linkage group J, respectively, were found to be associated with pupal infestation. The levels of phenotypic variations explained by each region are 8.8% and 15%, respectively. The other region associated with pupal counts is the interval between loci *TXS1931* and *SG37* on linkage group J. explained 33.9% of total variation in pupal counts (antibiosis). The identification of genes for different mechanisms of midge resistance will be particularly useful for exploring new sources of midge resistance and for gene pyramiding of different mechanisms for increased security in sorghum breeding through marker-assisted selection and for the development of agronomically superior sorghum hybrids (Tao et al. 2003). Indeed, a putative candidate gene (*gm3*) for the recessive gall midge resistance gene (*gm3*) in rice was

identified using a mapping population consisting of 302 F_{10} recombinant inbred lines derived from the cross TN1 (susceptible)/RP2068-18-3-5 (Sama et al. 2014). Comparative genomics could, therefore, identify similar syntenic genomic regions in sorghum for incorporation into midge sorghum resistance breeding programmes.

Greenbug, *Schizaphis graminum* (Rondani) is one of the major insect pests of sorghum and can cause serious damage to sorghum plants, particularly in the US Great Plains. Identification of chromosomal regions responsible for greenbug resistance will facilitate both map-based cloning and marker-assisted breeding. A total of 36 QTLs have been identified affecting both resistance and tolerance to greenbug insect pest (Agrama et al. 2002; Katsar et al. 2002; Nagaraj et al. 2005; Wu and Huang 2008; Punnuri et al. 2013).

Mirid panicle-feeding bugs (head bugs), particularly *Eurystylus oldi* Poppius, are major pests of sorghum in sub-Saharan Africa (Ajayi et al. 2001) and could also affect biomass and sugar accumulation upon infecting sweet sorghum panicles. Three significant QTLs on linkage group C accounted for 13% of the phenotypic variation for reduction in thousands kernel weight trait. Nine additional genomic regions in sorghum were identified to have a role in controlling head bug resistance in sorghum (Deu et al. 2005) and one leaf scorch QTL, *QLsc.txs-B*, explained 8.5% of the genetic variance (Feltus et al. 2006).

The shoot fly is a pest of sorghum, especially in America and Australia, and the larvae of this insect cut the growing point of the growing apical shoot resulting in a deadheart symptom. Genetic variations in sorghum resistance to shoot fly have been detected and this polymorphism has been used to identify genetic loci-controlling resistance to shoot fly. Nine QTLs associated with the resistance to leaf glossiness with phenotypic variation explained by individual QTL ranging from 7.6 to 14.0% were identified (Satish et al. 2009; Aruna et al. 2011). Seven QTLs distributed on five chromosomes, two each on SBI-07 and SBI-10, one each on SBI-01, SBI-05, and SBI-09, controlling oviposition were identified and the phenotypic variation explained by individual QTL ranged from 5.0 to 19.0%. A major QTL for this trait was detected on chromosome SBI-10 near the marker Xnhsbm 1044, explaining 19.0 and 16.1% of the phenotypic variation for mean eggs on 21 days after seedling emergence and mean eggs on 28 days after seedling emergence. Six QTLs for deadheart trait, which is a direct measure of resistance, were distributed on three chromosomes with one each on SBI-05 and SBI-09, and four on SBI-10 were identified in (Satish et al. 2009) study. The phenotypic variation explained by the individual trait ranged from 5.5 to 15.0%. Two major QTLs, *QDh.dsr-10.2* (explaining 11.4% of the phenotypic variation) and *QDh.dsr-10.3,* explaining 15.0% of the phenotypic variation, were located on chromosome SBI-10. However, (Aruna et al. 2011) identified 10 QTLs on six chromosomes, SBI-02, SBI-09, SBI-01, SBI-06, SBI-07, and SBI-10) controlling deadheart trait with individual QTL explaining 4.5 to 12.8% phenotypic variation. Two major QTLs, *QTdu.dsr-10.1* and *QTdu.dsr-10.2*, were detected for adaxial trichome density on chromosome SBI-10, explaining 15.7 and 33.0% of the phenotypic variation, while six QTLs (*QTdl.dsr-1.1*, *QTdl.dsr-1.2*, *QTdl.dsr-4*, *QTdl.dsr-6*, *QTdl.dsr-10.1*, *QTdl.dsr-10.2*) were detected for abaxial trichome density distributed on four chromosomes with two on SBI-01, one each on SBI-04 and SBI-06, and two on SBI-10. The phenotypic variation explained by individual QTL ranged from 5.2 to 22.7% (Satish et al. 2009). In (Aruna et al. 2011) study, two QTLs (*QTdu.dsr-7*, *QTdu.dsr-10*) distributed on two chromosomes (one each on SBI-07 and SBI-10) were identified for adaxial trichome density, explaining 4.3-44.1% of the phenotypic variation with a QTL on chromosome SBI-10 being a major QTL contributing for 44.1% of phenotypic variation. In addition, three QTLs controlling abaxial trichome density were identified on chromosomes SBI-03 and SBI-10 accounting for 5.0 to 24.1% of the phenotypic variation. Cloning of genetic these genomic loci underlying resistance to sorghum diseases and the understanding of the mechanisms of how pathogens circumvent the genetic resistance will contribute toward sustainable intensification of biomass production.

Foliar diseases

Sorghum is also negatively affected by foliar diseases, viz. anthracnose, target leaf spot, zonate leaf spot, Drechstera leaf blight, and rust. Sorghum anthracnose is caused by *Colletotrichum sublineolum* and is characterized by weakening the plant, severely reducing grain yield, and quality and biomass production. The disease is more prevalent and severe in warm and humid environments, where it causes substantial economic losses. The pathogen causes seedling blight, leaf blight, stalk rot, head blight, and grain molding, and thus limits both forage and grain production. Among these, foliar anthracnose is the most pronounced and devastating, especially on sweet sorghum cultivars directly impacting sugar production (Dalianis 1997). The *Cg1* anthracnose resistance dominant gene located at the distal region of linkage group SBI-05 has been mapped in sorghum cultivar SC748-5 using four AFLP markers (Perumal et al. 2009; Ramasamy et al. 2009). In planta and ex planta *C. sublineolum*, infection assays were carried out using 1-week-old seedlings and it was observed that transgenic line, KOSA-1, was found to be significantly more tolerant to anthracnose than the parent wild-type, KAT 412 (Akosambo-Ayoo et al. 2013).

Association analysis of a sorghum mini-core collection consisting of 242 diverse accessions identified eight loci (loci 1-8) linked to anthracnose resistance in sorghum (Upadhyaya et al. 2013) and found genes associated with anthracnose resistance. They include NB-ARC class of R genes (*Sb10 g021850*, *Sb10 g021860*) in locus 7 that share 20% homology to *Pib* (accession number BAA76281) which confers resistance to rice blast disease (Wang et al. 1999). Autophagy-related protein 3 (*Sb01 g029070*) in locus 6 coding for *SbATG3* gene is 77% identical and 85% similar to the tobacco homolog *ATG3* (*AAW80629*). Silencing *ATG3* in tobacco resulted in unrestricted TMV-induced hypersensitive cell death due to increased pathogen propagation (Liu et al. 2005). The sorghum loci *Sb08 g003690*, *Sb08 g003705*, *Sb08 g003710*, and *Sb08 g003720* on locus 4 code for harpin-induced *Hin 1* and is a well-known hypertensive response marker gene (Pontier et al. 1999). Overexpression of the Arabidopsis *Hin 1* homolog, *AtNHL3,* enhances resistance to infection by *Pseudomonas syringae* pv.tomato DC3000 in Arabidopsis (Varet et al. 2003). RAV transcription factor (*Sb01 g049150*) in locus 3 is also associated with anthracnose resistance. Silencing RAV homolog in tomato abolished the resistance to bacterial wilt caused by *Ralstonia solanacearum* (Li et al. 2011). In addition, overexpression in Arabidopsis enhanced resistance to infection by *Pseudomonas syringae* pv.tomato DC3000 and to osmotic stresses by high salinity and dehydration (Sohn et al. 2006). The oxysterol-binding protein *Sb01 g010720* in locus 5 was also found to have a role in the disease resistance pathway. It is homolog in tomato (*StOBP1*) was found to be induced rapidly by *Phytophthora infestans* (Avrova et al. 2004). In addition, four homologs of menthone:neomenthol reductase 1 (*MNR*) in locus 1 potentially were found and silencing the *MNR* in pepper (*Capsicum annuum*) significantly increased its susceptibility to *Xanthomonas campestris* pv *vesicatoria* and *Colletotrichum coccodes* infection (Choi et al. 2008). Overexpressing rice PR-5 enhances resistance to *Rhizoctonia solani*, the causal agent of sheath blight (Datta et al. 1999). In sorghum, protein expression level of one TLP, sormatin, correlates with resistance to grain mold (Bueso et al. 2000). Taken together it suggests that modulation of genes with a role in resistance pathway has the potential to provide simultaneous resistance to multiple biotic and abiotic stresses in sorghum. These genes potentially play a role in countering pathogen attack in sorghum through the hypersensitive response, the rapid death of plant cells at the site of pathogen infection. Therefore, these genes and markers may be developed into molecular tools for the genetic improvement of anthracnose resistance in sorghum. (Mohan et al. 2010) mapped four (*QAnt1 QAnt2, QAnt3, and QAnt4)* anthracnose resistance loci. *QAnt3* was also mapped by (Klein et al. 2001) and locus 8 from the (Upadhyaya et al. 2013) study was most likely *QAnt3* and locus 1 was close to *QAnt2* (Upadhyaya et al. 2013). A recessive anthracnose resistance gene in SC326-6 sorghum cultivar was mapped with a RAPD marker (Boora et al. 1998). Another recessive anthracnose resistance gene was mapped in G 73 sorghum cultivar with RAPD markers OPJ 0_{11437} at the same loci with SCAR marker SCJ 01 at 3.26 cM (Singh et al. 2006) and a RAPD-based SCAR marker SCA 12 at 6.03 cM (Singh et al. 2006). Anthracnose can be avoided by growing the sorghum in arid and semiarid environment. Additional genetic loci responsible for resistance to folia diseases in sorghum have been identified. Using 168 F7 recombinant inbred lines derived from a cross between 296 B (resistant) and IS18551 (susceptible) parents one major QTL with significant effects for each disease that colocated on SBI-06 was identified (Mohan et al. 2009). The variance explained by each QTL ranged from 12% to 50% with the QTL (*tls*) for target leaf spot explaining 50% of the total phenotypic variance. Similarly, one QTL each for zonate leaf spot (*zls*) and Drechstera leaf blight (*dls*) was identified as colocating with the QTL for target leaf spot disease. The QTL for Drechstera leaf blight explained 12%, while QTL for zonate leaf spot explained 16% of the phenotypic variance. The draft genome sequence of *Colletotrichum sublineola* has been presented and represents a new resource that will be useful for further research into the biology, ecology, and evolution of this key pathogen to find ways to mitigate its destructive ability on cultivated sorghum (Baroncelli et al. 2014).

Sorghum rust disease caused by *Puccinia purpurea* is important because its presence predisposes sorghum to other major disease problems like stalk rot and charcoal rot. Eight loci with significant effect on rust resistance have been identified (Tao et al. 1998) (Table 1). The percentage of the total phenotypic variation explained by each of these genomic regions varied from 6.8% to 42.6%.

Disease of the panicle

Sorghum ergot, caused predominantly by *Claviceps africana* is a significant threat to the sorghum industry worldwide and impacts juice and brix content in sweet sorghum (http://fenalce.org/archivos/SorFee.pdf). Ergot resistance in sorghum is controlled by many genes and that the pollen traits, pollen quantity, and pollen viability have moderate genetic correlation with percentage ergot infection. Nine genetic loci (Table 1) control percentage ergot infection in sorghum (Parh et al. 2008).

Stalk rot

Stalk rot caused by *Macrophomina phaseolina*, is also an economically important, soil-borne disease in major

sorghum-growing areas across the world. It is associated with premature stem lodging and pith disintegration leading to inferior grain and fodder quality. Five QTLs were identified at Dharwad location and four QTLs at Bijapur locations for the component traits of stalk rot disease resistance (Reddy et al. 2008). Two QTLs associated with marker *xtxp297*, *xtxp213* for number of internodes crossed on linkage group B, one QTL associated with marker *AC13* for length of infection on linkage group D, and two QTLs associated with markers *xtxp343*, *xtxp176* for per cent lodging on linkage group I accounted for 31.83, 10.76, and 18.90 per cent at Dharwad location and 14.87%, 10.47%, and 26.44% phenotypic variability at Bijapur location, respectively. The root and crown rot of sorghum known as milo disease is caused by the peritoxin produced by the saprophytic fungus *Periconia circinata* (Leukel 1948). The *PC* locus of sorghum (*Sorghum bicolor*) determines dominant sensitivity to a host-selective peritoxin. The *Pc* region was cloned by a map-based approach and found to contain three tandemly repeated genes with the structures of nucleotide-binding site-leucine-rich repeat (NBS-LRR) disease resistance genes (Nagy et al. 2007). The agronomically important gene *chi II*, encoding rice chitinase under the constitutive CaMV 35S promoter, has been transferred to sorghum for resistance to stalk rot (*Fusarium thapsinum*) (Krishnaveni et al. 2001). In addition, particle bombardment was used to genetically transform a sorghum genotype, KAT 412, with chitinase (harchit) and chitosanase (harcho) genes isolated from *Trichoderma harzianum*.

Resistance to *Striga* parasitism

Witchweed (*Striga* spp.) infestations are the greatest obstacle to sorghum [*Sorghum bicolor* (L.) Moench] grain and biomass production in many areas in Africa and Asia where they have a 20-100% yield reduction in any given season (Ejeta and Gressel 2007; Parker 2009). Sorghum coevolved with *Striga* in Africa and thus possesses intrinsic modicums of resistance that could be combined. Seeds of an acetolactate synthase (ALS) herbicide-tolerant sorghum hybrid mutant were treated with ALS-inhibiting herbicides before planting and the results showed that seeds treated with the highest herbicide rates had the fewest *Striga* attachments and the greatest delay in attachment (Tuinstra et al. 2009). Once the necessary sorghum genes are isolated and cloned, they could be transformed in a single, dominantly inherited construct containing a group of clustered genes, which would be a very effective strategy (Gressel 2010). Such resistance could easily be backcrossed into local varieties and land races preserving crop biodiversity, because it is inherited as a single dominant gene and not four separate recessive genes. Perhaps the resistance genes from sorghum, once isolated, could be stacked with those responsible for Desmodium allelochemical production, along with resistance genes being found in cowpea and rice (Tuinstra et al. 2009), all into mini-chromosomes or into the genome at one locus. It would be very hard for the parasitic weeds to overcome such resistance and many crop species could be engineered with the same gene cluster. RNAi constructs encoding genes that suppress parasite-only metabolic pathways have been engineered into tomatoes (Aly et al. 2009) and the same strategy could be attempted in sorghum. In the field, drought stress and Striga infestation are rarely presented individually and sorghum plants are often subjected to a combination of stress types limiting its productivity. Identification of pathways and genetic loci directing specificity and crosstalk of sorghum responses combined with functional characterization of theses genetic signatures could lead to new targets for the enhancement of sorghum stress tolerance and identification of sorghum ideotypes specific to Africa.

Nevertheless, major QTLs for resistance of sorghum to the hemi-parasitic weed *Striga hermonthica* have been mapped in two recombinant inbred populations of $F_{3:5}$ lines developed from the crosses IS9830 × E36-1 and N13 × E36-1 (Haussmann et al. 2004) (Table 1). Sorghum cultivars resistant to Striga are known to produce low levels of strigolactone, a Striga germination stimulant. An in vitro assay for germination stimulant activity toward *Striga asiatica* in 354 recombinant inbred lines derived from SRN39 (low stimulant) × Shanqui Red (high stimulant), a single recessive gene *lgs* was precisely tagged and mapped (Satish et al. 2012) explaining about 40% of the phenotypic variance for area under the *Striga* number progress curve (Haussmann et al. 2004). So far, no QTL has been found to direct multiple disease resistance in sorghum. Given the selection pressure that many pathogens exert directly on natural plant populations and indirectly via variety improvement programs on crop plants, it is proposed that research should be focused on finding genetic loci responsible for multiple disease resistance as this has important implications for plant fitness. In maize, evidence of a locus conditioning resistance to multiple pathogens was found in bin 1.06 of the maize genome with the allele from inbred line 'Tx303' conditioning quantitative resistance to northern leaf blight (NLB) and qualitative resistance to Stewart's wilt and that *pan1* a gene conditioning susceptibility for NLB and Stewart's wilt was cloned (Jamann et al. 2014). Therefore, to reduce the risk of resistance breakdown and increase the levels of disease resistance in sorghum, new sources of disease resistance need to be explored to isolate and incorporate alternative mechanisms of resistance and to pyramid different resistance genes into commercial hybrids.

Weed control

Weeds cause a host of problems in agriculture, competing with crops for light, water, and nutrients, providing a reservoir for insects and diseases, and contaminating seedlots. Vegetative dispersal by rhizomes (underground stems) and seed dispersal by disarticulation of the mature inflorescence ("shattering") cause perennial monocots such as "johnsongrass" to rank among the world's most noxious weeds. Improvements in agricultural production have correlated well with the use of herbicides in controlling weeds. Transgenic glyphosate-resistant crops overexpressing 5-en olpyruvylshikimate-3-phosphate synthase (*cp4 epsps)* gene accelerated widespread use of glyphosate becoming the most widely used herbicide in world agriculture (Duke and Powles 2008) for its effectiveness in controlling recalcitrant weeds such as Johnsongrass. However, the increased utilization of these herbicides over a long period of time exerts selective pressure leading to widespread evolution of resistance in several weed species (Busi et al. 2013). For instance, metabolic resistance (enhanced metabolic capacity to detoxify herbicides) can be endowed by the increased activity of the endogenous cytochrome P450 mono-oxygenases, glucosyl transferases (GTs), glutathione S-transferases (GSTs), and/or other enzyme systems such as aryl acylamidase (Carey et al. 1995) that can metabolize herbicides (Yu and Powles 2014). Combined with lack of novel herbicides being brought to the market over the last 30 years and tougher registration and environmental regulations on herbicides have resulted in a loss of some herbicides, particularly in Europe, threatening crop production worldwide (Heap 1997).

Integrated weed management approach to control weed populations has been hailed as an effective tool in addition, reduce the environmental impact of individual weed management practices, increase cropping system sustainability, and reduce selection pressure for weed resistance to herbicides (Harker and O'Donovan 2013). Maize plants transformed with an aryloxyalkanoate dioxygenase (*AAD-1*) gene showed robust crop resistance to aryloxyphenoxypropionate herbicides over four generations and were also not injured by 2,4-dichlorophenoxyacetic acid (2,4-D) applications at any growth stage. Arabidopsis plants expressing *AAD-12* were resistant to 2,4-D as well as triclopyr and fluroxypyr, and transgenic soybean plants expressing *AAD-12* maintained field resistance to 2,4-D over five generations indicating that single *AAD* transgenes can provide simultaneous resistance to a broad repertoire of agronomically important classes of herbicides, including 2,4-D, with utility in both monocot and dicot crops which can help transgenes preserve the productivity and environmental benefits of herbicide-resistant crops (Wright et al. 2010). Recently, the use of multicopy transposons bearing unfitness genes has been proposed in the management of weeds. Multicopy transposons rapidly disseminate through populations, appearing in ~100% of progeny unlike nuclear transgenes, which appear in a proportion of segregating populations (Gressel and Levy 2014). Here, weed populations could be generated that contain the unfitness gene under chemically or environmentally inducible promoters, activated after gene dissemination, or under constitutive promoters where the gene function is utilized only at special times (e.g., sensitivity to a herbicide), and thus are easily controllable. Efforts need to be accelerated to understand the genetic basis of weed resistance for employment of an RNAi approach to interfere with the expression of herbicide resistance genes in weeds (Sammons et al. 2012) and restore sensitivity of weeds to glyphosate (Green 2014). Enhancing crop competitiveness, for example, by genetic engineering with genes encoding phosphates, and the application of fertilizers with phosphites as the main source of phosphates is a key strategy for crops to outcompete weeds for essential nutrients (López-Arredondo and Herrera-Estrella 2012).

Perspectives: Sweet sorghum ideotypes with enhanced resistance to abiotic and biotic stresses

In the field, multiple abiotic stresses (drought, salinity, heat, cold, chilling, freezing, nutrient, high light intensity, ozone, and anaerobic stresses) and biotic stresses (insect pests and diseases) are presented. The performance of the plant, therefore, is affected by the degree of heterogeneity between stress levels, simultaneous occurrence of different stresses, the timing of the stress event with respect to the developmental stage of the plant and the intensity and duration of the stress (Mittler and Blumwald 2010). Plants respond differently to combined stresses as compared to their response to individual stress as it happens under laboratory conditions. The later response activates a specific program of gene expression relating to the exact environmental condition encountered. The responses are complex and could involve changes at transcriptomic, cellular, and physiological level. Genetic and genomic resources for sorghum breeding are available (Carpita and McCann 2008), and they offer an opportunity to employ multidisciplinary approaches involving traditional breeding and biotechnology to contribute to future improvements of sweet sorghum to adapt to both biotic and abiotic stresses. For instance, in tropical climate, drought stress is ranked most important followed by striga parasitism, and fungal and bacterial diseases in terms of limiting sorghum potential for growth and reproduction. Therefore, breeding for sorghum ideotypes tolerant to combined drought and Striga parasitism will be ideal for this region.

As discussed previously, resistance to abiotic and biotic stresses has been demonstrated through genetic engineering and classical breeding. Tolerance to both abiotic and biotic stresses has also been achieved. In maize, breeding programs have developed plants tolerant to drought and have additional resistance to the parasitic weed *Striga hermonthica* (Bänziger et al. 2006; Badu-Apraku and Yallou 2009). In Sudan, sorghum cultivars resistant to drought and striga infectivity have been developed through classical breeding (Nair Suliman personal communication), this suggests that hormone signaling pathways orchestrating the interaction between abiotic and biotic stresses are altered and in particular abscisic acid. This alteration could be interesting to breeders to further design sorghum ideotypes that can withstand a combination of stresses as presented in the field. In addition, research programs need to focus on developing tolerance to multiple stresses in order for the improved varieties to respond predictably under field condition.

In temperate environment, cool temperatures below 15°C during the early growing season limits optimal growth of sorghum, it is a key agronomic trait for warm season cereal crops such as sorghum. Breeding for sorghum ideotypes with improved early-season cold tolerance would be appropriate for temperate environments (Yu and Tuinstra 2001). So far, Chinese sorghum kaoliang, Shanqui Red (Knoll et al. 2008) and and F7 RIL population of RTx403xPI567946 (Burow et al. 2011b) have been found to exhibit higher emergence and greater seedling vigor under cool temperature than most breeding lines currently available. However, they lack desirable agronomic characteristics. Sorghum ideotypes' resistance to cold could be developed by introgression of desirable genes from Chinese landraces into elite lines through marker-assisted selection (Knoll et al. 2008; Burow et al. 2011a).

The use of herbicides is increasing in global crop production. Improved weed control with herbicides promotes fertilizer use and has the potential to improve crop yields in many developing countries in the near future (Gianessi 2013). Shattercane and *Sorghum halepense* (johnsongrass) are natural weeds for sorghum and resistant to most other herbicides used for their control (Heap 2014). In addition, they outcross with cultivated sorghum (Morrell et al. 2005; Muraya et al. 2011). This suggests that transgenes introduced to sorghum would readily introgress and be retained in these wild species, which often occur sympatrically with cultivated sorghum in Africa (Mutegi et al. 2010). Compared to other weed control strategies including manual hand weeding, herbicides are the key to sustainable crop production throughout the world, and, will remain the mainstay for weed control in the foreseeable future. Therefore, when developing sweet sorghum ideotypes for different ecological regions, the use of herbicides to control weeds should be considered. The rhizome formation trait is correlated and genetically linked to overwinter survival in sorghum. Genetic mechanisms controlling overwintering have the potential to minimize the risk of weediness and create perennial sorghums that can overwinter in climates where they previously could not (Paterson et al. 1995; Washburn et al. 2013). These perennial overwintering sorghum ideotypes could be used for improvements in biofuel production in sweet sorghum by extending the period of biomass production and reducing production costs.

Conflict of Interest

None declared.

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