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Location of major effect genes in sorghum (*Sorghum bicolor* (L.) Moench)

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Abstract Major effect genes are often used for germplasm identification, for diversity analyses and as selection targets in breeding. To date, only a few morphological characters have been mapped as major effect genes across a range of genetic linkage maps based on different types of molecular markers in sorghum (*Sorghum bicolor* (L.) Moench). This study aims to integrate all available previously mapped major effect genes onto a complete genome map, linked to the whole genome sequence, allowing sorghum breeders and researchers to link this information to QTL studies and to be aware of the consequences of selection for major genes. This provides new opportunities for breeders to take advantage of readily scorable morphological traits and to develop more effective breeding strategies. We also provide examples of the impact of selection for major effect genes on quantitative traits in sorghum. The concepts described in this paper have particular application to breeding programmes in developing countries where molecular markers are expensive or impossible to access.

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Introduction

Major effect genes are often used for germplasm identification by sorghum breeders and for diversity analysis in germplasm collections, e.g. Upadhyaya et al. (2009); Grenier et al. (2004); Abdi et al. (2002). Major effect genes can also be important as targets for selection in their own right. To date, approximately 35 major effect genes have been mapped in sorghum (*Sorghum bicolor* (L.) Moench) as simply-inherited markers across a range of genetic linkage maps based on different types of molecular markers. This represents less than 20% of the more than 200 named morphological loci (Doggett 1970). Until recently, the integration of this information has been complicated by the lack of common markers across populations; for example Bennetzen et al. (2001) attempted to place a selection of major effect genes onto a framework map for sorghum, but due to the lack of common markers across the populations available at that time, they were able to map only nine genes and even then with only approximate locations. In the last 5 years, there has been a massive expansion in the range of markers, genetic maps, consensus maps and other genomic resources developed for sorghum, culminating in the recent sequencing of the genome (Paterson et al. 2009). These resources now permit the effective integration of major effect genes.

The pedigree breeding method and various modifications of this method (Newman 1912) are the dominant breeding methods used by sorghum breeders (House 1985; Rooney and Smith 2000; Jordan et al. 2004) and breeders of most crops that tolerate inbreeding. This breeding method typically involves the development of inbred lines which are either tested in hybrid combination or as inbred varieties. Inbred parents that carry genes that the breeder wants to combine are intercrossed. Selection for simply-inherited

traits is often applied to early generations, with selection for quantitative traits being practised in later generations in replicated trials. During these early generations, segregating major effect genes may either be under positive selection or present as neutral markers until fixed. In recent years, marker aided selection (MAS) has begun to be used on a large scale in breeding programmes in some crops (e.g. Gupta et al. 2009; Ottoman et al. 2009; William et al. 2007). MAS is often used in conjunction with elements of conventional pedigree breeding. In most sorghum breeding programmes, the implementation of MAS is limited (e.g. Hash et al. 2003; Rooney and Klein 2000) and pedigree breeding based on phenotype remains the most widely used breeding method. While MAS will undoubtedly become important in sorghum breeding programmes, it is likely that some component of early generation, phenotypic selection will continue for the foreseeable future.

The first association of a simply-inherited major effect gene with a quantitative trait in plants was observed more than 80 years ago (Sax 1923) and the phenomenon has since been observed for a range of traits in a range of crops, e.g. the linkage between the quantitative trait flowering time and the simply-inherited flower colour trait in pea (Rasmusson 1935). Strong selection for simple traits with high heritability in early generations can rapidly drive fixation of these genes and the associated genomic regions. In the absence of knowledge about the location and linkage relationships of the major effect gene, linkage drag may have unintended favourable or unfavourable consequences. For example, if these regions contain favourable QTL alleles linked in repulsion to the major effect genes, then strong selection for the major effect genes can dramatically reduce the frequency of favourable QTL alleles in the population and reduce the potential for genetic progress for the quantitative traits. Alternatively if the major effect genes are linked in coupling phase with favourable QTL alleles, then selection for the simple trait will potentially increase genetic gain. A number of studies have estimated the extent of linkage drag, which is dependent on the number of chromosomes and number of cross-over events per bilvalent, i.e. on the number of independently inherited chromosome segments (Hillel et al. 1990). Stam and Zeven (1981) calculated the theoretical length of the donor chromosome segment on a 100-cM chromosome after six backcross generations without background selection to be 32 cM. Young and Tanksley (1989) confirmed these results and reported donor segmental lengths of up to 51 cM linked to the target resistance gene after six backcross generations in tomato. These studies indicate that linkage drag is likely to be quite extensive and Klein et al. (2008) recently detailed the extensive introgression of the donor haplotype flanking the ma_1/dw_2 genomic region on SBI-06 in sorghum, suggesting that genetic hitchhiking persists during directional selection.

The last 20 years has seen a wealth of information produced on the location of quantitative trait loci (QTL) in sorghum for a range of important traits such as plant height (Lin et al. 1995; Pereira and Lee, 1995; Brown et al. 2008), maturity (Crasta et al. 1999; Chantereau et al. 2001; Hart et al. 2001; Feltus et al. 2006), stay-green drought tolerance (Tuinstra et al. 1996; Crasta et al. 1999; Subudhi et al. 2000; Tao et al. 2000; Xu et al. 2000; Kebede et al. 2001; Hausmann et al. 2002; Harris et al. 2007), fertility restoration (Klein et al. 2001a; Jordan et al. 2010), aluminium tolerance (Magalhaes et al. 2004) and insect resistance (Tao et al. 2003). Integrating all available previously mapped major effect genes onto a complete genome map would supply sorghum breeders with a number of advantages. In particular, as our knowledge of the location of QTL controlling important traits increases it becomes possible for breeders to be aware of the consequences of selection for major effect genes. This information could be used to enhance genetic gain by managing unfavourable linkages or to exploit favourable linkages. In this paper, we locate many of the major effect genes selected or commonly observed in segregating populations by sorghum breeders to a recently published consensus map (Mace et al. 2009) which is anchored to the sorghum genome sequence. We also provide examples of the impact of selection for major effect genes on quantitative traits in sorghum.

Materials and methods

Major effect genes mapped

In total, 35 major effect genes were integrated into the sorghum DArT consensus map (Table 1). Where possible, these genes have been associated with the classical genes and the gene symbols originally described (Doggett 1970). The 35 genes consisted of two genes relating to seedling traits controlling coleoptile colour Rs_1 and Rs_2; four genes relating to leaf traits (bmr_6, bmr_{12}, *Lg* and *Trit*); one gene relating to leaf sheath traits (*bm*); one gene relating to plant colour (*P* or *Q*); five genes relating to stem traits (Tb_1, *d*, dw_2, dw_3 and *Sb.Ht9.1*); four genes relating to maturity (Ma_1, Ma_3, Ma_4 and Ma_5); one gene relating to glume traits (*gc*); one gene relating to awn traits (*A*); three genes relating to male fertility (ms_3, Rf_1 and Rf_2); six genes relating to grain traits (B_2, *I*, *R*, Sh_1, *Y* and *Z*); one gene relating to endosperm traits (*wx*); four genes relating to disease resistance traits (Pl_a, *Pu*, *rlf* and Shs_1); one gene relating to resistances to insecticide (*opr*) and one gene relating to abiotic stress tolerance (Alt_{SB}).

Table 1 Details of the 35 genes mapped onto the sorghum consensus map (Mace et al. 2009)

Gene symbol	Plant trait[a]	Dominant:recessive character	Original citation	Chromosome	Location (cM)	Mapping study	Methodology
Tb_1	Stem	Tillering (phase unknown)	Webster (1965)	SBI-01	25.2	Kebrom et al. (2006)	Sequence mapping (Sb01g010690)
Sh_1	Grain shattering	Shattering:persistent	Karper and Quinby (1947)	SBI-01	30.2–33.3	Wise et al. (2002)	Projection
Y	Grain	Yellow colour:white (rrY-:-yy)	Graham (1916)	SBI-01	121.9–123.8	Knoll et al. (2008), Mace and Jordan, unpublished	Projection
Ma_3	Maturity	Lateness:earliness	Quinby and Karper (1945)	SBI-01	115.5–125.7	Childs et al. (1997)	Sequence mapping (Sb01g037340)
Rf_2	Anthers	Partial fertile:sterile	Miller and Pickett (1964)	SBI-02	20.5–24.1	Jordan et al. (2010)	Projection
B_2	Grain	Presence of testa:no testa	Vinall and Cron (1921)	SBI-02	32.3–36	Dufour et al. (1997), Rami et al. (1998)	Projection
Z	Grain	Pearly (thin mesocarp):chalky (thick mesocarp)	Ayyangar et al. (1934)	SBI-02	89.9–104.4	Tao et al. (2000), Boivin et al. (1999)	Projection
Ma_5	Maturity	Photoperiod sensitivity:insensitive	Rooney and Aydin (1999)	SBI-02	152.5–166	Kim (2003)	Projection
Pl_a	Disease resistance	Resistance to downy mildew:susceptibility	Reddy et al. (1992)	SBI-03	24.6–38.4	Bennetzen et al. (2001)	Projection
R	Grain	Pericarp colour red (with Y present)	Graham (1916)	SBI-03	87.9	Xu et al. (2000)	Projection
Alt_{SB}	Abiotic stress tolerance	Aluminium sensitivity:Aluminium tolerance	Duncan (1988)	SBI-03	152	Magalhaes et al. (2007)	Sequence mapping (Sb03g43890)
ms_3	Anthers	Normal pollen:aborted	Webster (1965)	SBI-03	155.3	Jordan, unpublished	Projection
A	Awns	Awnless:Awned	Sieglinger et al. (1934)	SBI-03	157.9–161.6	Boivin et al. (1999), Tao et al. (2000), Bennetzen et al. (2001), Hart et al. (2001)	Projection
bmr6	Leaf	Normal:brown midrib	Porter et al. (1978)	SBI-04	25.1–44.2	Saballos et al. (2009)	Sequence mapping (Sb04g005950)
opr	Resistances to insecticides	Susceptibility to organophosphate insectide:resistant	Schertz and Stephens (1966)	SBI-05	61.7–63	Tao et al. (1998a), Tao et al. (2000), Xu et al. (2000)	Projection
dw_2	Stem	Height, tall:short	Quinby and Karper (1945)	SBI-06	43.6–48	Klein et al. (2008), Lin et al. (1995)	Projection
Ma_1	Maturity	Lateness:earliness	Quinby and Karper (1945)	SBI-06	42.1–54	Klein et al. (2008), Lin et al. (1995)	Projection
gc	Glumes	Seed glume cover opened:closed	–	SBI-06	78.5–82.2	Srinivas et al. (2009)	Projection

Table 1 continued

Gene symbol	Plant trait[a]	Dominant:recessive character	Original citation	Chromosome	Location (cM)	Mapping study	Methodology
d	Stem	Pithy:juicy (white:green mid-rib)	Hilson (1916), Swanson and Parker (1931)	SBI-06	84.2–93.2	Xu et al. (2000), Hart et al. (2001), Srinivas et al. (2009)	Projection
Rs_1	Seedling	Coleoptile, seedling stem red:green	Reed (1930)	SBI-06	108.1–109.5	Xu et al. (2000), Knoll et al. (2008), Mace et al. (2008)	Projection
Lg	Leaf	Junction normal:ligueless and without auricles	Ayyangar et al. (1935)	SBI-06	134.8–136.9	Bennetzen et al. (2001)	Projection
P or Q	Plant colour	Purple:brown (tan)	Ayyangar et al. (1933a)	SBI-06	144.2–146.5	Rami et al. (1998), Klein et al. (2001b), Srinivas et al. (2009)	Projection
bmr_{12}	Leaf	Normal:brown midrib	Porter et al. (1978)	SBI-07	56.5–59.5	Bout and Vermerris (2003)	Sequence mapping (Sb07g003860)
I	Grain	Pericarp colour intensified:normal	Ayyangar et al. (1933b)	SBI-07	91.1–103.3	Tao et al. (2000)	Projection
dw_3	Stem	Height, tall:short	Karper (1932)	SBI-07	105	Multani et al. (2003)	Sequence mapping (Sb07g023730)
Pu	Disease resistance	Resistance to rust (*Puccinia purpurea*):susceptibility	Coleman and Dean (1961)	SBI-08	28.7–30.8	McIntyre et al. (2004)	Projection and sequence mapping
Rf_1	Anthers	Normal:cytoplasmic sterile	Brengman (1995)	SBI-08	88.5	Klein et al. (2005)	Sequence mapping (Sb08g019750)
Shs1	Disease resistance	Resistance to head smut:susceptibility	Frederiksen (1986)	SBI-08	94.1	Bennetzen et al. (2001)	Projection
Sb.Ht9.1	Stem	Height, tall:short	Quinby and Karper (1954)	SBI-09	146.6–150	Brown et al. (2008), Lin et al. (1995), Pereira and Lee (1995)	Projection
bm	Leaf sheath	Waxy bloom present:absent	Ayyangar and Ponnaiya (1941)	SBI-10	0–4.4	Burow et al. (2009)	Projection
rlf	Disease resistance	Virus reaction:red leaf reaction to SCMV	Henzell (1977)	SBI-10	4.4	Parh (2005), Mace et al. (2008)	Projection
wx	Endosperm	Endosperm starch normal:waxy	Karper (1933)	SBI-10	25.7–32.4	McIntyre et al. (2008)	Sequence mapping (Sb10g002140)
Rs_2	Seedling	Coleoptile and leaf axil purple:green	Woodworth (1936)	SBI-10	32.1–35.3	Boivin et al. (1999), Tao et al. (2000)	Projection
Ma_4	Maturity	Lateness:earliness	Quinby (1966)	SBI-10	22.2–39.1	Hart et al. (2001)	Projection
Trit	Leaf	Bicellular blunted:unicellular pointed	–	SBI-10	85.9	Satish et al. (2009)	Projection

[a] Plant trait as defined in Doggett (1970) and Rooney (2000)

Table 2 Comparison of genetic linkage mapping studies used to map the targeted major effect genes

Reference	Pedigree of mapping population	Cross type	Population type	Population size	# Loci mapped	# Linkage groups	Total map length (cM)
Boivin et al. (1999)	IS2807/379	Cultivated/cultivated	RI	110	298	11	1,352
Boivin et al. (1999)	IS2807/249	Cultivated/cultivated	RI	91	131	12	849
Burow et al. (2009)	KSF2021/BTx623	Mutant/elite	F_2	120	30	1	118
Dufour et al. (1997)	IS2807/379	Cultivated/cultivated	RI	110	155	13	977
Dufour et al. (1997)	IS2807/249	Cultivated/cultivated	RI	91	129	12	878
Hart et al. (2001)	BTx623/IS3620C	Cultivated/cultivated	RI	137	145	10	1,278.8
Jordan et al. (2010)	R939145-2-2/IS8525	Cultivated/cultivated	RI	146	596	10	1,431.6
Jordan et al. (2010)	B923296/SC170-6-8	Cultivated/cultivated	RI	88	10	1	23.3
Klein et al. (2001b)	RTx430/Sureno	Cultivated/cultivated	RI	125	130	10	970
Knoll et al. (2008)	Shan Qui Red/SRN39	Cultivated/cultivated	RI	153	132	14	2,128
Lin et al. (1995)	*S. bicolor*/*S. propinquum*	Cultivated/wild	F_2	370	78	11	935
Tao et al. (1998b)	QL39/QL41	Cultivated/cultivated	RI	160	166	21	1,400
Rami et al. (1998)	IS2807/379	Cultivated/cultivated	RI	110	128	11	878
Rami et al. (1998)	IS2807/249	Cultivated/cultivated	RI	90	151	11	977
Srinivas et al. (2009)	296B/IS18551	Cultivated/cultivated	RI	168	152	15	1,098.7
Tao et al. (2000)	QL39/QL41	Cultivated/cultivated	RI	160	311	10	~2,750
Tao et al. (1998a)	QL39/QL41	Cultivated/cultivated	RI	120	194	21	1,400
Xu et al. (2000)	B35/Tx7000	Cultivated/cultivated	RI	98	145	10	837
Mace et al. (2008)	R939145-2-2/IS8525	Cultivated/cultivated	RI	146	596	10	1,431.6
Mace and Jordan, unpublished	R890562/ICSV745	Cultivated/cultivated	RI	119	488	12	1,405.8
Mace and Jordan, unpublished	B923296/SC170-6-8	Cultivated/cultivated	RI	88	10	1	23.3
Parh (2005)	R939145-2-2/IS8525	Cultivated/cultivated	RI	146	286	15	1,599.1
Satish et al. (2009)	296B/IS18551	Cultivated/cultivated	RI	168	162	16	1,143

Mapping methodology

The recently published high-density sorghum consensus map (Mace et al. 2009), consisting of 2,029 unique loci (1,190 DArT loci and 839 other loci) spanning 1,603.5 cM and with an average marker density of 1 marker/0.79 cM, was used as the framework map. The consensus map then served as a backbone onto which the genes, mapped across studies with different base genetic linkage maps (as detailed in Tables 1, 2), were either projected, in a "neighbours" map approach as described by Cone et al. (2002), or sequence-mapped using an in silico mapping strategy analogous to e-PCR (Schuler 1998). The projection strategy involved identifying the two nearest flanking bridge markers shared by the consensus map and by the maps in the individual studies for each target gene, and then calculating the coordinate of this locus relative to the ratio of the intervals defined by the flanking bridge markers on the two maps. For placing genes at group extremities, projection was based on the relative genetic distance of common markers nearest to the end of the linkage group (LG) between the framework map and the base map in the original mapping study. For instances with very limited numbers of markers in common flanking the target gene, the physical (bp) location of the markers flanking the target loci on the original base genetic linkage map were determined via BLAST similarity search against the sorghum WGS sequence, using either PCR primer sequences or RFLP probe sequences and then aligned to the consensus map. When the gene was mapped in more than one study, the mapping information from the multiple papers was used to determine a location range on the consensus map. For sequence mapping, BLAST similarity (Altschul et al. 1990) between targeted genes and the sorghum WGS sequence was conducted via Phytozome (http://www.phytozome.net), requiring hits with $E \leq$ 1e-10 based on BLASTn.

Simulation

QuLine is an integrated genetic and breeding simulation tool based on the QU-GENE platform (Podlich and Cooper 1998) which is capable of simulating most breeding methodologies for developing inbred lines (Wang et al. 2001, 2004). For the purpose of this study, QuLine was used to simulate a pedigree-based inbred line development programme typical of methods used by many sorghum breeders. A genetic region based on a ~100-cM region of

Table 3 Genetic characteristics of the two parental genotypes in the simulation study

	Pericarp colour (*R*)	Stg2	Stg1	Awns (*A*)
Parent 1	Rr (lemon-yellow)	Stay-green	Stay-green	aa (awned)
Parent 2	RR (red)	Senescent	Senescent	AA (awnless)

chromosome SBI-03 was simulated using gene locations identified by the mapping methodology previously described. The genetic region included the locations of two mapped genes, awns (*A*) and pericarp colour (*R*) (Table 1) and two of the major effect QTL for the stay-green drought resistance trait, stg1 and stg2 (Crasta et al. 1999; Xu et al. 2000; Subudhi et al. 2000; Harris et al. 2007), explaining ~20 and ~30% of the phenotypic variability, respectively. Hypothetical molecular markers were located across this region at 1-cM intervals.

To illustrate the impact of strong selection for the two genes on the surrounding genome, we simulated five hypothetical selection strategies for crosses between two inbred parent lines, parent 1 and parent 2. Parent 1 had the recessive alleles for the morphological genes awns (*A*) and pericarp colour (*R*) (Table 3) and the favourable alleles for the two stay-green QTL. This is the same genetic makeup as the line BTx642 (also known as B35) which is the source of the favourable allele of stg1 and stg2 in a number of QTL studies (Crasta et al. 1999; Xu et al. 2000; Subudhi et al. 2000; Harris et al. 2007). Parent 2 was awn-less and had a red pericarp (i.e. homozygous dominant for both genes) and had the unfavourable alleles for the stay-green QTLs. For these characteristics, parent 2 is typical of many of the inbred lines used in the developed world as hybrid parents.

Five selection scenarios are described in Table 4. In each of the five selection scenarios, a large F_2 population was produced by crossing the two inbred parents. The size of the population was such that it was possible to select at least 1,000 individual F2 plants ($F_{2:3}$ families) that met the phenotypic selection criteria in Table 4. A typical sorghum plant produces 500–1,000 seeds per plant and a typical single row nursery plot contains 30 plants. It was assumed that 30 plants from each of the 1,000 $F_{2:3}$ families were grown as single row nursery plot. A single plant from each row was selected that met the selection criteria and was used as the seed source for the next generation (i.e. $F_{2:4}$) again of 30 plants. This selection procedure was continued until $F_{2:5}$ where the genetic makeup of a single representative individual of each the 1,000 $F_{2:5}$ families was investigated. The $F_{2:5}$ stage is typically the generation when evaluation for yield and other quantitative traits, such as stay-green and grain yield, commences (either as $F_{2:5}$ inbred lines or $F_{2:5}$ testcross hybrids). For each scenario, frequency of genes, marker and QTL alleles were plotted against the map location at 1-cM intervals. A similar plot was produced for the number of recombination events in a 10-cM window and for frequency of heterozygous loci at each 1-cM interval. The frequencies of genotypes with different combinations of the alleles of the two stay-green QTL were also calculated for each scenario.

Results

In total, 35 genes were placed on the recently published sorghum consensus map; 26 using the projection strategy, 8 using a sequence mapping strategy, and 1 using a combined projection/sequence mapping strategy. These genes and their locations are detailed in Fig. 1, Table 1 and ESM.

Four of the targeted genes were located on SBI-01. A major gene controlling tillering, *Tb_1* (Teosinte Branched1), was originally cloned in maize (Doebley et al. 1997) and was found to suppress bud outgrowth. The orthologous genes in rice (Takeda et al. 2003), Arabidopsis (Finlayson 2007) and sorghum (Kebrom et al. 2006) have been identified. The sorghum orthologue, termed *SbTB1* by Kebrom et al. (2006), exists as a single copy in the sorghum genome with 93.9% nucleotide identify with the maize TB1 gene. Sequence mapping located *Tb_1* in

Table 4 Five different selection strategies adopted in the simulation study

Scenario	Selection pressure	Phenotype selected
1	No selection	Random
2	Selection for the dominant phenotype (RR and Rr) of the pericarp colour gene (R)	Red grain
3	Selection for the recessive phenotype (rr) of the pericarp colour gene (R)	White grain
4	Selection for the dominant phenotype (RR and Rr) of the pericarp colour gene (R) and the dominant phenotype (AA or Aa) of the awns gene (A)	Red grain and awnless
5	Selection for the recessive phenotype (rr) of the pericarp colour gene (R) and the recessive phenotype (aa) of the awns gene (A)	White grain and awned

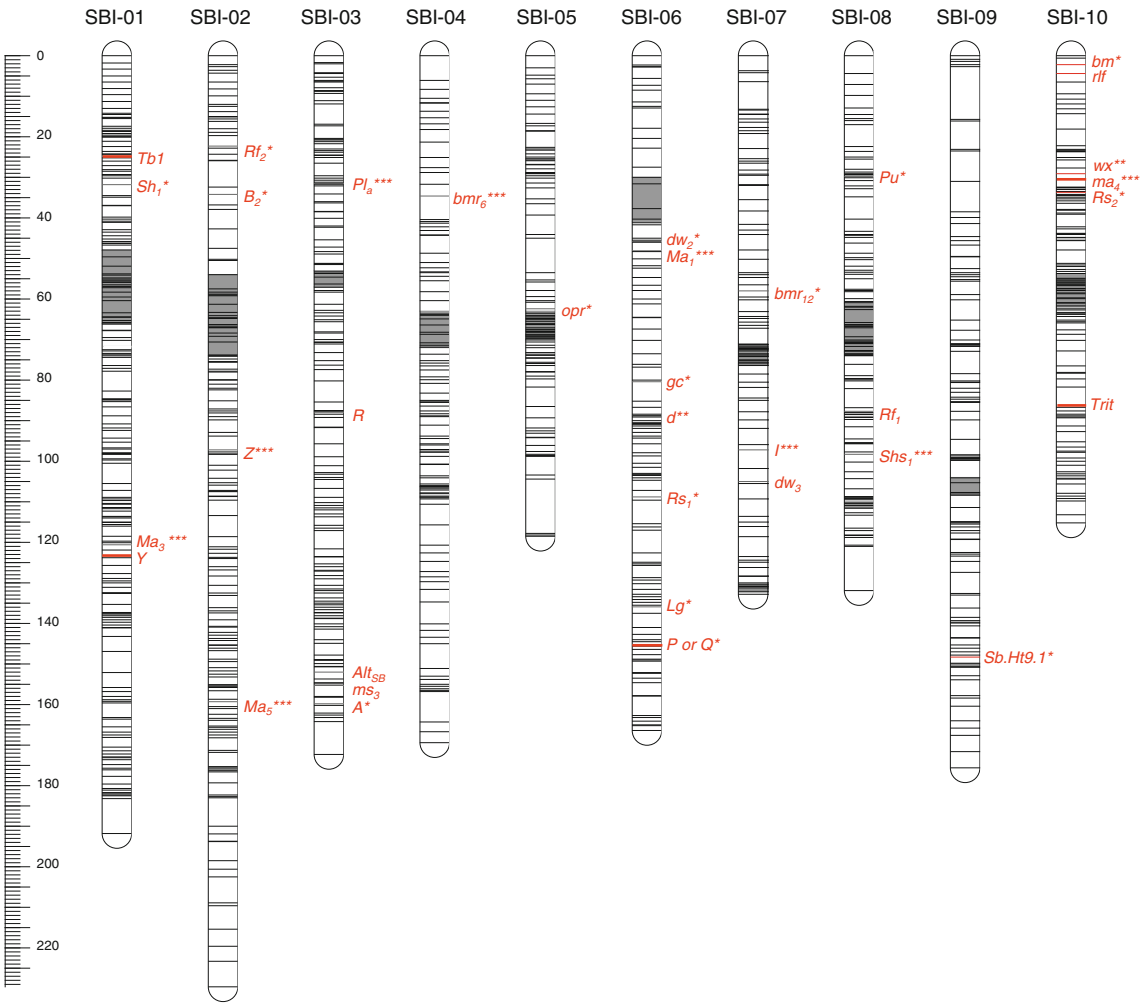

Fig. 1 Schematic view of the sorghum consensus map. The 2,049 loci of the consensus map are displayed schematically by *horizontal lines* across the *bars* representing the ten chromosomes. The left-most bar indicates the length of each chromosome in cM. The *grey shaded regions* on each chromosome represent the heterochromatin. The map locations of the 35 targeted major effect genes are included in italics; the degree of confidence of the location is indicated by the suffix; no asterisk equates to a precise location, * equates to less than a 5 cM location range, ** equates to between 5 and 10 cM location range and *** equates to greater than a 10 cM location range

sorghum from 9,506,057 to 9,507,199 bp, corresponding to gene Sb01g010690 with the annotation "similar to Teosinte branched1" (Phytozome Sbi1.4 gene set). This corresponds to a genetic linkage map location of 25.2 cM, closely linked to the flanking SSR markers txp302 and txp482. This location also corresponds to major effect tillering QTL identified in three studies (Paterson et al. 1995a; Hart et al. 2001; Feltus et al. 2006). The grain shattering gene (*Sh1*) was originally located using QTL mapping by Paterson et al. (1995a, b) in an F_2 generation of a *S. bicolor* × *S. propinquum* cross. Paterson et al. (1995b) mapped *Sh1* between the flanking RFLP markers pSB766 and pSB195. Wise et al. (2002) subsequently fine-mapped the locus between the flanking markers umc140a and umc27; both of these RFLP markers are present on the consensus map and were used in a projection strategy to determine the location range of *Sh1* on the consensus map (30.2–33.7 cM), closely linked to the SSR marker sbAGFO8. The gene controlling grain colour has been mapped in three studies. Knoll et al. (2008) mapped a gene for pericarp colour (red/white) on a recombinant inbred (RI) population of a cross between Shan Qui Red and SRN39. The pericarp locus was weakly linked to the SSR marker txp32 (36-cM interval) and the RAPD marker OPK18 (30 cM). However, Mace and Jordan (unpublished) also mapped a gene controlling grain colour (red/white) in two independent populations (R890562 × ICSV745; B923296 × SC170-6-8), mapping to a concordant location of between 121.9 and 128.8 cM on the consensus map, closely linked to the flanking SSR marker txp279. Due to the weak linkage in the genetic map described by Knoll et al. (2008), the location determined by Mace and Jordan

(unpublished) has been presented here. We postulate that this gene corresponds to the classical gene *Y*, which interacts with the second epicarp colour gene, *R*, to produce a red (RRYY), yellow (rrYY), or colourless or white (RRyy or rryy) pericarp (Rooney 2000). A putative candidate gene for *Y*, Sb01g037670, was identified that is orthologous to the maize *p1* gene (pericarp colour), described by Sidorenko and Chandler (2008). The gene ma_3, one of the six known classical genes that control maturity in sorghum, maps to the distal end of the long arm of SBI-01. Childs et al. (1997) determined that the ma_3^R mutation of this gene causes a phenotype similar to plants known to lack phytochrome B and concluded that the ma_3 locus is a PHYB gene that encodes a 123-kD phytochrome. Sequence mapping of the PHYB gene located the ma_3 locus at between 60,910,479 and 60,917,763 bp, corresponding to gene Sb01g037340. This corresponds to a genetic linkage map location of between 115.5 and 125.7 cM, closely linked to the flanking SSR markers txp229 and txp279.

Four of the targeted genes were located on SBI-02, all using the projection strategy. The fertility restorer gene, Rf_2, was recently mapped by Jordan et al. (2010) in two RI populations of the crosses R931945-2-2 × IS 8525 and B923296 × SC170-6-8, flanked by the SSR markers txp50 and txp304; these SSRs were used to determine that the location range of *Rf2* on the consensus map was between 20.5 and 24.1 cM. The gene B_2, which controls the presence of testa in the grain in the presence of B_1, was mapped in RI populations of the crosses IS 2807 × 379 and IS 2807 × 249 by Dufour et al. (1997) and subsequently by Rami et al. (1998), both studies calling this locus B_2. Both studies mapped the gene to the distal end of the long arm of SBI-02, and the location range of B_2 on the consensus map was determined to be between 32.3 and 36 cM, closely linked to the SSR marker txp304. The gene for mesocarp thickness (*Z*), also referred to as the pearly trait, was initially mapped by Tao et al. (1998a), and further refined in Tao et al. (2000), on an RI population of the cross QL39 × QL41 and found to be adjacent to the SSR marker txp13. Based on the RFLP map generated by Boivin et al. (1999), *Z* mapped between umc88 and umc22. Its location on the consensus map was determined to be between 89.9 and 104.4 cM, closely linked to the SSR markers txp298 and SbAGAB03. The fourth gene mapped to SBI-02 is the maturity locus, ma_5, which, when present in the dominant form together with ma_6, very strongly inhibits floral initiation regardless of day length (Chantereau et al. 2001; Kim 2003). The physical location of molecular markers flanking ma_5 was determined by Kim (2003) by applying fluorescence in situ hybridisation (FISH) together with genetic linkage mapping, and found ma_5 to map between the AFLP txa3424 and the SSR txp100. Using the genetic linkage map generated for BTx623 × IS 3620C by Menz et al. (2002) which includes AFLPs, RFLPs and SSRs, as a bridging map, the location of ma_5 on the consensus map was determined to be between 152.5 and 166 cM, closely linked to the SSR markers txp429 and txp431.

SBI-03 contained five of the targeted genes, four mapped onto SBI-03 using a projection strategy and one via sequence mapping. A downy mildew resistance gene conferring resistance to pathotype 1 of *Peronosclerospora sorghi* was identified by Gowda et al. (1995) in the F_2 population of the cross BTx623 × IS3620C, between the RFLP markers txs1053 and txs1092, and subsequently placed on a sorghum framework map by Bennetzen et al. (2001). The projection strategy determined the location range of this locus, which we postulate could be Pl_a, to be between 24.6 and 38.4 cM, closely linked to the SSR markers txp451, txp452, txp215 and txp488. The gene controlling the red pericarp colour was mapped by Xu et al. (2000) and identified as *R* on an RI population of the cross B35 × RTx7000 and was found to map between the RFLP markers txs584 and wg889. Both RFLP markers are present on the consensus map and were used in a projection strategy to determine the location range of *R* on the consensus map of 87.9 cM, flanked by the RFLP marker umc63 and the SSR marker txp120. The major gene conferring aluminium tolerance in sorghum, Alt_{SB} was recently mapped and cloned by Magalhaes et al. (2004, 2007). Using a sequence mapping strategy, the Alt_{SB} gene was determined to be Sb03g43890, located at 71,142,280–71,144,686 bp, which is equivalent to 152 cM on the consensus map, co-locating with the DArT markers M188347, M342305, M342567 and M188920. The male sterility gene, ms_3, conferring non-functional pollen was mapped by Jordan (unpublished) on an ms_3 introgression population based on the line R931945-2-2 and found to be adjacent to the SSR txp427. The projected location of ms_3 on the consensus map was determined to be 155.3 cM, between the RFLP marker txs1075 and the DArT marker sPb-6770. The gene determining the presence or absence of awns (*A*) was mapped independently by three groups (Boivin et al. 1999; Tao et al. 2000; Hart et al. 2001) and subsequently included on Bennetzen's (2001) framework map. Using a projection strategy, *A* was determined to be located between 157.9 and 161.6 cM on the consensus map, closely linked to the SSR markers txp427, txp69 and txp425.

SBI-04 only contains one of the targeted genes, bmr_6. The brown midrib (*bmr*) mutants of sorghum have brown vascular tissue in the leaves and stem as a result of changes in lignin composition. Bmr_6, resulting in altered lignin composition, affects cinnamyl alcohol dehydrogenase (CAD) activity (Saballos et al. 2009). Using a sequence mapping strategy, the bmr_6 gene was determined to be

Sb04g005950, located at 5,776,540–5,780,582 bp, which is equivalent to between 25.1 and 44.2 cM on the consensus map, linked to the SSR marker gpsb050.

SBI-05 also contains only one of the genes targeted, *opr*, which confers resistance to organophosphate insectide. The gene *opr* was mapped by Tao et al. (1998a; 2000) flanked by RFLP markers txs713 and isu140, and by Xu et al. (2000) as *rcb* (chemical burning resistance). Using a projection strategy, *opr* was determined to have a location range on the consensus map of between 61.7 and 63.15 cM, closely linked to the RFLP marker isu120.

SBI-06 contains the highest number of the targeted genes; seven, in total, all of which were mapped using the projection strategy. Two genes, closely linked, controlling maturity (Ma_1) and height (dw_2) were originally mapped by Lin et al. 1995, and subsequently placed on the BTx623 × IS3620C map of Menz et al. (2002) by Klein et al. (2008). Ma_1, which has the largest impact on flowering date of all the maturity genes, was determined to be flanked by the AFLP marker txa4001 and the indel marker txi20 by Klein et al. (2008), and RFLP markers pSB0189 and pSB0580 by Lin et al. (1995). The projected location on the consensus map was determined to be between 42.1 and 43.7 cM based on Klein et al. (2008), but based on the mapping information of Lin et al. (1995), the projected location was determined to be between 48 and 54 cM. Consequently, the projected location of Ma_1 on the consensus map was widened to between 42.1 and 54 cM, closely linked to the SSR markers gap7 and gap72. dw_2 was mapped adjacent to Ma_1 by Klein et al. (2008) and also by Lin et al. (1995). In contrast to Ma_1, the projected location of dw_2 was in agreement between Klein et al. (2008) and Lin et al. (1995) and was determined to be between 43.6 and 48 cM, closely linked to the DArT markers sPb-7169 and sPb-1395. The gene conferring seed glume cover (*gc*) was mapped by Srinivas et al. (2009) in an RI population of the cross 296B × IS 18551 to the distal end of their SBI-06b adjacent to the gene conferring stem mid-rib type (pithy: juicy or *d*), which they refer to as Mrco. Using a projection strategy, the gc locus mapped to between 78.5 and 82.2 cM on the consensus map, closely linked to the DArT markers sPb-2463 and sPb-1543. The *d* locus has also been mapped by Xu et al. (2000), to between RFLP markers umc34 and txs1030, and Hart et al. (2001), co-locating with the SSR txp97. Using a projection strategy, *d* was determined to map between 84.2 and 93.2 cM, closely linked to the SSR marker txp145. A gene conferring seedling colour was mapped to SBI-06 by three independent groups. Xu et al. 2000 identified the gene as *Rs* (red coleoptile) and mapped it between umc44 and txs1139. Subsequently, Knoll et al. (2008) remapped it as seedling plant colour (red/green) between txp95 and txp145. Mace et al. (2008) also mapped the same gene as CC (coleoptile colour) in the R931945-2-2 × IS 8525 population, which was included as a component map in the development of the sorghum consensus map. The projected map location of this gene, renamed as Rs_1, was determined to be between 108.1 and 109.5 cM, closely linked to the DArT marker sPb-5802. The *Lg* (liguleless) locus is the sixth gene mapped to SBI-06, as determined by Bennetzen et al. (2001), drawing on the classical genetic studies of Webster (1965) who mapped *Lg* approximately 7 cM from *P* and 20 cM from *Rs*. On the consensus map, *Lg* was determined to map between 134.8 and 136.9 cM, closely linked to the SSR marker txp176. The gene determining adult plant colour (*P* or *Q*) was mapped initially by Rami et al. (1998) as *P*, flanked by two RFLP markers umc53 and umc5. Klein et al. (2001b) then mapped this gene as plcolour using an RI population of the cross RTx430 × Sureno flanked by the SSR txp57 and the AFLP marker txa10077. Srinivas et al. (2009) mapped this gene as Plcor flanked by SSRs txp57 and txp17. Bennetzen et al. (2001) included *P* on the sorghum framework map flanked by txp57 and isu147. Based on details of the plant colour segregating in Klein et al. (2001b) and Srinivas et al. (2009), purple (*P_Q_*)/tan (*ppqq*), it is not possible to determine whether the gene is *P* or *Q*, and we have therefore called it *P* or *Q*. Using a projection strategy, the location range of *P* or *Q* on the consensus map was determined to be between 144.2 and 146.5 cM, closely linked to the RFLP marker isu47.

Three of the targeted genes mapped to SBI-07. The intensifier gene, *I*, controlling the intensity of the pericarp colour, was mapped by Tao et al. (2000) adjacent to the RFLP marker isu38. Using a projection strategy, *I* was determined to map between 91.1 and 103.3 cM, closely linked to the SSR marker msbcir300. The other two genes on SBI-07, bmr_{12} and dw_3, were mapped via sequence mapping. The new bmr allelic group nomenclature proposed by Saballos et al. (2008) has been followed, which adopts the most widely recognised allele for each allelic group as the reference allele for the group. The bmr_{12} allelic group contains six known alleles (bmr12-ref, bmr12-7, bmr12-15, bmr12-18, bmr12-25 and bmr12-26). Bout and Vermerris (2003) determined that bmr12-ref, bmr12-18 and bmr12-26 are all allelic mutants of the gene encoding the lignin biosynthetic enzyme caffeic acid O-methyltransferase (COMT). Using a sequence mapping strategy, the bmr_{12} gene was determined to be Sb07g003860, located at 4,756,272–4,759,637 bp, which is equivalent to 58 cM on the consensus map, and co-locates with the SSR marker txp312 and the DArT marker sPb-6942. The major height gene, dw_3, was cloned and sequenced by Multani et al. (2003). Using a sequence mapping strategy, the dw_3 gene was determined to be Sb07g023730, located at 58,610,896–58,618,660 bp, which is equivalent to 105 cM on the

consensus map, and is flanked by the co-locating SSR msbcir300 and DArT marker M340509 and the RFLP marker SSCIR57.

SBI-08 also contains three of the targeted genes. A major gene for rust resistance was identified by McIntyre et al. (2004) as homologous to the maize Rp1-D rust resistance gene in addition to co-locating with a major rust resistance QTL with a LOD of 9.41 explaining 42.6% of the phenotypic variation (Tao et al. 1998b). In addition to using a projection strategy to determine the location of the rust resistance gene, which we postulate could be *Pu*, on the consensus map based on the flanking RFLP markers psb47 and txs422, a sequence mapping strategy was also used based on the Rp1-SO sequence information detailed by McIntyre et al. (2004). The location of *Pu* was determined to be between 28.7 and 30.8 cM, closely linked to the RFLP marker RG8167 and the DArT marker sPb-5054. There is a cluster of six putative rust resistance gene candidates in this genomic region (Sb08g002340, Sb08g002345, Sb08g002350, Sb08g002380, Sb08g002390 and Sb08g002410) from 2,487,742–2,514,226 bp. The consensus map location of a major gene for fertility restoration, Rf_1, was determined through sequence mapping based on Klein et al. (2005), building on their initial work in mapping Rf_1 based on the F_2 population of the cross ATx623 × RTx432 (Klein et al. 2001a). On the consensus map, Rf_1 co-located with the RFLP marker txs560 at 88.5 cM and is flanked by the SSR marker txp250. A second resistance gene to head smut (Shs_1) was also mapped to SBI-08, as detailed in Bennetzen et al. (2001), and based on a projection strategy using the flanking RFLP markers txs1220 and txs1294, the location range of Shs_1 on the consensus map was determined to be between 89.7 and 106.8 cM, closely linked to the SSR markers txp105 and gpsb123.

SBI-09 contains only one of the targeted genes, Sb.Ht9.1, controlling height. Major effect QTL for height co-locate in this region, as identified by Lin et al. (1995), Pereira and Lee (1995) and Brown et al. (2008). Using an association mapping approach, Brown et al. (2008) fine-mapped the likely interval for major effect QTL, which they termed Sb-HT9.1, to approximately 100 kb, with the most highly significant marker located at 57.21 Mb. This corresponds to a genetic linkage map location on the consensus map of between 146.6 and 150.5 cM, and is closely linked to the RFLP marker txs307b. Based on knowledge of pleiotropic effects of the *Dw* loci, Pereira and Lee (1995) attempted to correspond the major effect QTL with the *dw* loci. Pleiotropic effects were not observed for either dw_1 and dw_4. Due to the lack of co-locating QTL around the major effect height locus on SBI-09, in contrast to dw_2 and dw_3, it is likely that locus represents either dw_1 or dw_4, most probably dw_1 (Brown, pers. comm.).

SBI-10 contains five of the targeted genes. The first locus, *bm*, confers the production of profuse amounts of epicuticular wax or bloom. Burow et al. (2009) mapped this locus, which they termed blmc, using an F_2 population of the cross BTx623 × KFS2021 and delimited *bm* to a 0.7-cM region. The locus was flanked by newly identified SSRs, which were sequence-mapped onto the consensus map using the primer sequences. The location range of the *bm* locus on the consensus map was determined to be between 0 and 4.4 cM, closely linked with the SSRs, detailed in Burow et al. (2009), Xsbarslbk10.48 and Xsbarslbk10.57. The gene conferring the red leaf response to plants infected with Johnson Grass Mosaic Virus, *rlf*, was mapped in the R931945-2-2 × IS 8525 population by Parh 2005 and Mace et al. (2008), as RL. This population was included as a component map in the development of the sorghum consensus map and consequently this gene was projected onto the consensus map at 4.4 cM, closely linked with five DArT markers (sPb-2041, sPb-5079, sPb-4129, sPb-6833, sPb-0600) and one RFLP marker PSB305 (Mace et al. 2009). The gene conferring waxy endosperm, *wx*, encodes granule-bound ADP-glucose-gluosyl transferase (McIntyre et al. 2008). Using a sequence mapping strategy, the *wx* gene was determined to be Sb10g002140, located at 1,827,074–1,831,279 bp, which is equivalent to 29.1 cM on the consensus map, and is flanked by two co-locating SSR markers msbcir331 and msbcir324 and a DArT marker M189136. The maturity gene, ma_4, has been reported to map near to txs1163 in Hart et al. (2001), however, no detailed genetic linkage mapping data has been reported in the literature for this locus. The projected location of this gene onto the consensus map was therefore based on the location of the RFLP marker, txs1163, together with the location of a closely linked major effect QTL for photoperiod sensitivity described by Chantereau et al. (2001). The ma_4 gene was thus determined to be located between 22.2 and 39.1 cM, closely linked to both *wx* and Rs_2. This latter gene, conferring coleoptile colour, has been mapped by Boivin et al. (1999) as Rs_2 flanked by RFLP markers rz123 and umc113 and Tao et al. (2000) as SDCR (seedling colour) between RFLP markers umc156 and psb107. Using a projection strategy, Rs_2 was placed on the consensus map between 32.1 and 35.3 cM closely linked to the SSR marker gpsb027. Satish et al. (2009) mapped a gene controlling trichome morphology, which they termed *Trit*, using the RI population of the cross 296B × IS 18551, between their new SSR markers Xnhsbm1044 and Xnhsbm1013. Using a sequence mapping strategy, the physical location of these new SSRs was identified and their corresponding location in cM on the consensus map determined. Using a projection strategy, the location of *Trit* on the consensus map was determined to be 85.9 cM, adjacent to the RFLP marker umc150.

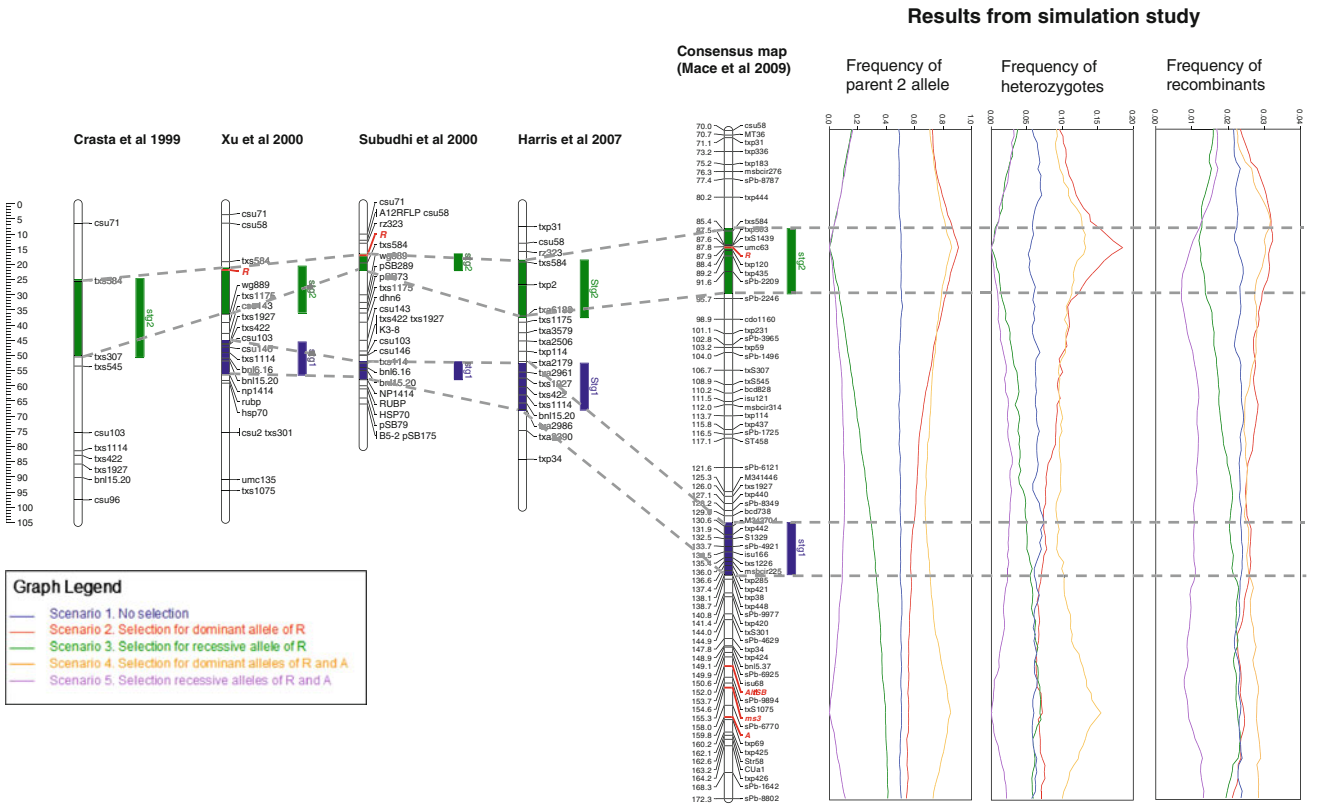

Fig. 2 Sections of SBI-03 with stay-green QTL compared across four previous publications and aligned to the consensus map, in addition to the results from the simulation study

Simulation studies

To illustrate the impact of selection for major effect genes on the surrounding genomic region, a 100-cM region on the long arm of SBI-03 was selected containing the genes controlling the morphological traits awns (*A*) and grain colour (*R*) and two major effect QTL for stay-green (Crasta et al. 1999; Xu et al. 2000; Subudhi et al. 2000; Harris et al. 2007). Figure 2 details the location of the QTL as determined in the original studies and the projected location on the consensus map.

Five different selection strategies based on the genes *A* and *R* were simulated using Qu-Line and allele frequency, number of recombination events and heterozygosity calculated (Fig. 2). Scenario 1 can be considered as a control scenario with no selection on either major effect gene, and the frequency of parental alleles across all loci in the 100-cM region is equal and constant. Similarly, both the recombination and heterozygosity frequencies remain constant across all loci.

For scenario 2, with selection for the dominant allele of *R*, the frequency of the parent 2 allele remains higher than in scenario 1 across all loci, and above 60% for the 60-cM region surrounding *R*. The heterozygosity and recombination frequencies peak in the genomic region containing *R* and remain higher than in scenario 1 across over 90% of the 100-cM region.

For scenario 3, with selection for the recessive allele of *R*, the frequency of the parent 2 allele is below 10% in a 20-cM window around *R* and remains lower for the parent 2 allele frequency compared to scenario 1 across all loci. The heterozygosity and recombination frequencies drop in the genomic region containing *R* and remain lower than in scenario 1 across over 90% of the 100-cM region.

For scenario 4, with selection for the dominant alleles of both *R* and *A*, the frequency of the parent 2 allele remains above 67% across all loci in the 100-cM region. Both heterozygosity and recombination frequencies remain high across all loci; higher than 100% of loci with scenario 1 and higher than approximately 50% of loci with scenario 2.

For scenario 5, with selection for the recessive alleles of both *R* and *A*, the frequency of the parent 2 allele is below 10% across 80% of all loci and both heterozygosity and recombination frequencies remain low across all loci; lower than 100% of loci with scenario 1 and lower than approximately 90% of loci with scenario 3.

By selecting for the recessive alleles of both the *A* and *R* loci (scenario 5), the frequency of recombinant individuals

Table 5 Frequency of favourable (parent 2) alleles at two stay-green QTL loci (stg2 and stg1) across the five simulated selection scenarios

	Scenario 1 No selection	Scenario 2 Dominant R	Scenario 3 Recessive R	Scenario 4 Dominant R and A	Scenario 5 Recessive R and A
Stg2	0.495	0.199	0.975	0.164	0.984
Stg1	0.499	0.424	0.688	0.306	0.906

between the stg1 and stg2 QTL loci is reduced to 4.5%; with selection for the recessive allele of *R* only (scenario 3), the frequency of recombinant individuals between the stg1 and stg2 remains low at 8.5%. In contrast, by selecting for the dominant alleles of both *A* and *R* (scenario 4), the frequency of recombinant individuals between the stg1 and stg2 QTL loci is 16.5%, compared to 13.5% with no selection (scenario 1).

Table 5 details the frequency of the favourable stay-green alleles at the peak location of the QTL for stg1 and stg2, across all five selection scenarios. The highest frequencies of the stay-green alleles for both stay-green QTL were produced with scenario 5, with over 90% of 1,000 simulated progeny containing the favourable stay-green alleles at both QTL loci. Even with selection for the recessive allele of only one gene (scenario 3), almost 70% of 1,000 simulated progeny contained the favourable (parent 1) stay-green alleles at both QTL loci. In contrast with scenarios 2 and 4, selecting for the dominant allele of *R* or both *R* and *A*, the frequency of individuals containing the favourable (parent 1) stay-green alleles at both QTL loci remains lower than with scenario 1 (no selection) and falls to just under 20% for the stg2 loci with scenario 2.

Discussion

Thirty-five major effect genes commonly observed in segregating sorghum populations have been successfully placed on a single consensus map (Mace et al. 2009). While these genes have been mapped in a range of studies, until recently it has been difficult to integrate them into a single map due to the lack of common markers across populations. The recent sequencing of the sorghum genome (Paterson et al. 2009) and the construction of dense molecular marker maps (Bowers et al. 2003; Menz et al. 2002; Mace et al. 2009) has made this possible. Where possible, these genes have been associated with the classical genes and their gene symbols, which had been identified prior to the development of molecular markers. In many cases, the link between the classical gene and the mapped gene is tenuous as the genotypes used in the mapping studies vary from those used in the original classical genetics study.

The locations of 9 of the 35 genes were determined through sequence mapping of cloned genes or tightly linked markers; Tb_1 (Kebrom et al. 2006), ma_3 (Childs et al. 1997), Alt_{SB} (Magalhaes et al. 2007), bmr_6 (Saballos et al. 2008), bmr_{12} (Bout and Vermerris 2003), dw_3 (Multani et al. 2003), *Pu* (McIntyre et al. 2004), Rf_1 (Klein et al. 2005) and *wx* (McIntyre et al. 2008). The determination of the equivalent genetic linkage map location in cM from the physical location was dependent on the marker's location along the chromosome, whether it was located in a heterochromatic or euchromatic region, in addition to the density of sequenced markers on the consensus map. This resulted in five genes (bmr_{12}, *Pu*, *wx*, ma_3 and bmr_6) being placed at an approximate position with a location range; the latter two markers had a range greater than 10 cM. The location of the other 26 genes was determined using a projection strategy, based on markers in common between the maps detailed in the original reference and the consensus map. Two of the major effect genes mapped using the projection strategy (Sh_1 and ma_5) were based on the results of physical mapping (Wise et al. 2002; Kim 2003). The projection of the remaining 24 genes was based on the results of genetic linkage mapping (Tables 1, 2). The determination of the projected locations on the consensus map for these genes was dependent upon the parameters of the original genetic linkage mapping studies; in particular the population size, the morphological trait phenotyping methodology, the density of the original genetic linkage map and the number of markers in common with the consensus map. The latter issue, however, is becoming increasingly redundant with the availability of SSR primer sequence information in addition to RFLP sequence information, allowing previously excluded markers to be sequence-mapped onto the consensus map. Of the 24 genes projected onto the consensus map based on data from original genetic linkage mapping studies, 11 were mapped in more than one study. The projected locations based on multiple studies mapped within a 5-cM region on the consensus map for the majority of the genes. The projected locations of three genes (*Z*, ma_1 and *d*) were less consistent, based on multiple mapping studies, resulting in a location range of 10 cM up to 14.5 cM. The maturity gene, ma_4, had the largest location range on the consensus map, due to the lack of detailed genetic linkage mapping data.

However, despite the lack of detailed information on the precise location of ma_4, its inclusion in this study was considered important as this gene will likely be under strong selection pressure when using tropical germplasm in temperate environments or temperate germplasm in tropical environments. Hence, knowledge of its genomic location provides breeders with critical information.

Many major effect genes, such as those controlling seed colour (*R*, *Y*, B_2 and *Z*), plant height (dw_3), lignin content (bmr_6 and bmr_{12}) and endosperm type (*wx*), are important targets for selection particularly in the early generations of sorghum pedigree breeding programmes. Other genes such as those controlling plant colour (*P* or *Q*) or awns (*A*) and epicuticular wax (*bm*) are relatively neutral as far as breeders are concerned and are often not subjected to selection. Regardless of the inherent value of the traits that they control, these genes can usually be scored quickly and cheaply on a single plant basis in the early generations of pedigree breeding programmes. The integration of these genes into this map permits them to be used as easily recognised landmarks for specific chromosomal segments providing a bridge between conventional breeding and the increasing volume of QTL data that is becoming available, providing a unique opportunity to use the mapped major effect genes as an easily recognised landmark for a specific chromosomal segment, with opportunities for sorghum breeders to be aware of both the dangers and opportunities of early generation phenotypic selection for these traits. The use of morphological markers for indirect selection with associated traits is not new; for example Nagaraja Reddy et al. (2008) recently reported that among the many traits, brown and pithy leaf midrib, presence of awn, types of glumes in the panicles and plant colour, have been found to be useful as markers since they are often associated with economically important traits such as increased fodder quality (brown midrib) (Porter et al. 1978) and resistance to bird damage (presence of awns; Kullaiswamy and Goud 1983). Closed glume type panicles have been observed to confer an advantage over open type panicles in offering resistance to grain mold infection (Murty 2000) and tan-coloured plants are reported to exhibit immunity to various fungal diseases (Melake-Berhan et al. 1996). Additionally, a recent report on the effects of plant colour on agronomic characters of sorghum showed lower grain yields from a group of tan hybrids compared to pigmented hybrids (Williams-Alanis et al. 1995). These associations are frequently directly linked to the effects of the major gene, e.g. the chromosomal segment containing the B_2 gene controlling the presence of the high-tannin testa layer in the sorghum grain has been associated with grain quality (Rami et al. 1998) and it is possible that the high tannin content in the sorghum contributes to grain mold resistance. Similarly, the association between tan plant colour and foliar disease resistance is suggestive of a relationship between plant pigmentation and the hypersensitive response in sorghum (Klein et al. 2001b). Such pleiotropic effects of major genes have been observed in other crop species too, e.g. Millar et al. (1999) determined that CUT1, an Arabidopsis gene required for cuticular wax biosynthesis, has a pleiotropic effect and results in conditional male sterility, caused by the absence of waxes in the trypine layer of the pollen grain disrupting pollen–pistil interactions. However, in addition to providing further insights into pleiotropic effects, the placement of 35 major effect genes onto a single consensus map, providing a convenient framework to link QTL information across historical studies, offers the opportunity to identify whether a morphological marker is linked, either favourably or unfavourably, to other agronomic traits of importance. To illustrate this, we have detailed examples of additional QTL linked to the major effect genes in Table 6 which indicates the potential for unforeseen consequences, due to linkage drag, of selection decisions based on major genes. It is very likely that a proportion of linked QTL are due to pleiotropic effects of the major gene, however, there are other examples of QTL for independent traits linked to major genes. It is beyond the scope of the current paper to detail all the linked QTL; instead to illustrate the potential risks and opportunities of selection for major effect genes, a simulation study was conducted using a scenario based on two genes that can be the target of early generation selection. The two genes flank a region of $\sim$100 cM of the long arm of SBI-03. The simulated study revealed the impact of five different selection strategies on allelic, heterozygosity and recombination frequencies across all loci in the targeted region. When the recessive alleles of *A* and *R* were under selection, either singly (scenario 3) or in combination (scenario 5), recombination and heterozygosity were limited across the entire region and the frequency of favourable QTL alleles at both stg1 and stg2 QTL loci was on average 80% higher than with no selection (scenario 1) or with selection for the dominant alleles of the genes (scenarios 2 and 4). By selecting for progeny with awns and lemon-yellow grain, breeders therefore significantly increase the probability of selecting individuals with both stg1 and stg2 QTL. In contrast, when the dominant alleles of *A* and *R* were under selection, recombination and heterozygosity were increased across the entire region and the frequency of favourable QTL alleles at both stg1 and stg2 was lower compared to the alternative selection strategies.

One of the simulated parents (parent 1) has the same genetic constitution as the line BTx642 (also known as B35) which is the primary source of valuable alleles for stg1 and stg2 and has been used in the DEEDI sorghum breeding programme to improve drought adaptation. Parent

Table 6 Examples of QTL linked to 17 major effect genes

Gene	QTL trait	Publication
Tb_1	Shoot fly resistance	Satish et al. (2009)
Sh_1	Endosperm colour	Salas Fernandez et al. (2008)
Ma_3	Rhizome number	Paterson et al. (1995b)
Y	Grain mold resistance	Rami et al. (1998)
Rf_2	Cold tolerance	Knoll et al. (2008)
B_2	Grain mold resistance	Rami et al. (1998)
B_2	Ergot resistance	Parh et al. (2008)
Z	Stay-green (stg3)	Harris et al. (2007)
Ma_5	Rust resistance	McIntyre et al. (2005), Tao et al. (1998b)
Pla	Stay-green (stgA)	Tao et al. (2000)
opr	Stay-green (stg4)	Harris et al. (2007)
gc	Ergot resistance	Parh et al. (2008)
d	Shoot fly resistance	Satish et al. (2009)
d	Ergot resistance	Parh et al. (2008)
Rs_1	Ergot resistance	Parh et al. 2008)
P	Grain mold resistance	Klein et al. (2001b)
bmr_{12}	Stay-green (stgE)	Kebede et al. (2001)
I	Ergot resistance	Parh et al. (2008)
Rs_2	Stay-green (stgI)	Tao et al. (2000), Kebede et al. (2001)

2 is typical of the red-grained senescent germplasm widely used in Australia and other developed countries. Consequently in the late 1980s and 1990s, the DEEDI sorghum breeding programme carried out early generation selection for the dominant R allele (scenario 2), while conducting late generation selection for the quantitative stay-green trait using the BTx642 source, prior to the knowledge of the association between stg1 and stg2 and grain colour. The consequence of the early generation selection for R was that stg2 was entirely absent from elite breeding populations developed during this period (unpublished data). Key lines with moderate levels of stay-green that emerged from this initial cycle of selection all carried the favourable stg1 allele and the recessive A allele (unpublished data). Not surprisingly, the frequency of individuals with high levels of stay-green was low and none of the derived lines had stay-green levels equivalent to BTx642. In the light of our knowledge of the association between these major effect genes and stg1 and stg2 (that the favourable, dominant allele of the R gene is linked in repulsion with the favourable stg1 and stg2 alleles), much more effective strategies can be deployed. For example, a strategy that involves selecting for red-grained individuals from families that segregate for grain colour (heterozygous R) and that also had awns (recessive A) would result in a very much higher frequency of individuals carrying the favourable stg1 allele and a much improved chance of carrying the favourable stg2 allele (i.e. a high frequency of recombinant individuals. Alternatively, since commercial cultivars in Australia are exclusively F_1 hybrids, and the preferred red-grain colour (R) is dominant, and the stay-green trait partially dominant (Tao et al. 2000), an even more effective strategy of increasing the frequency of individuals containing the favourable stg2 allele would be to select for the lemon-yellow (recessive) allele of the R gene together with awns, and ensure that the other parent of the F_1 hybrid had red grain.

The *D* gene, controlling dry (dominant, unfavourable allele) versus juicy (recessive, favourable allele) stems, is a further example of a major effect gene used as a target of selection in its own right that is also linked to a QTL. The gene is characterised by a highly heritable white midrib phenotype that can be easily selected on a single plant basis. The *D* gene is located within the region of a sorghum ergot resistance QTL, which was found to control 14% of the variation in ergot resistance by Parh et al. (2008). Ergot resistance is a quantitative trait with low to moderate heritability on a single plant basis. Resistance to the disease is valuable in dual purpose sorghum as the alkaloids produced by the fungus have negative effects on cattle growth rates and lactation and can even cause death (Blaney et al. 2000). The source of resistance used in the study by Parh et al. (2008), IS8525, is linked in repulsion with the favourable, recessive allele of d and hence if this source of resistance is used in a forage breeding programme, strong selection in early generations for juicy stems would eliminate this QTL from the resulting progeny. Assuming no pleiotropy, then a more effective strategy may be to select for the dominant, unfavourable allele of *D* (dry, pithy stems) for a number of generations to maintain heterozygosity and enhance

recombination, then identify juicy segregants from the later generations.

Another favourable linkage identified in this study is that between the aluminium tolerance gene (Alt_{SB}), the awn gene (A) and the genetic male sterility gene ms_3. Alt_{SB} is linked to ms_3 at 3 cM and to awns at 8 cM; the cluster of genes being located on the end of the long arm of SBI-03 (Fig. 2). Aluminium tolerance in a plant, conferred by Alt_{SB}, can only be determined using a specific phenotypic screening method or molecular markers. In contrast, both genetic male sterility and the presence of awns can be readily scored on a single plant basis. The genetic male sterility gene ms_3 is widely used by sorghum breeders to facilitate crossing, particularly in recurrent selection programmes (Doggett and Eberhart 1968). The linkage between ms_3 and awns is already used by some breeders to identify sterile plants prior to flowering (Jordan DR unpublished data). If an Alt_{SB} donor line is used to introgress aluminium tolerance into a line with a contrasting allele for the awns gene, then selection for the awn allele present in the Alt_{SB} donor would greatly enrich the resulting progeny lines for Alt_{SB}. If ms_3 is segregating in an elite line or population, then making use of the linkage between ms_3 and Alt_{SB} offers an attractive scenario for very efficient single gene backcrossing without the need for molecular markers or specific selection environments for aluminium tolerance. A cross between the Alt_{SB} donor and a sterile plant from a suitable recurrent parent will result in an F_1 plant that can be back-crossed to another sterile plant from the recurrent parent and so on until the recurrent parent phenotype is recovered. At any backcross F_1 generation, the progeny can be selfed and the resulting BC_nF_2 population selected for fertility. In the absence of recombination between the Alt_{SB} and ms_3, homozygous fertile lines will be homozygous for the favourable allele of Alt_{SB}. The close linkage between the genes is such that relatively few unique lineages would be needed to ensure a plant carrying Alt_{SB} was obtained.

The recent development of a sorghum consensus genetic linkage map and the inclusion of major effect genes on this map, now makes it possible for sorghum researchers and breeders to link information on the location of genes controlling simple traits to QTL studies. This, in turn, provides new opportunities for breeders to take advantage of readily scorable major effect genes and to develop more effective breeding strategies. These include indirect selection using genes controlling simply-inherited morphological traits, and using these genes to enrich populations for favourable alleles or recombination events or mitigating the consequences of unfavourable linkages. The concepts described in this paper and the particular case studies illustrated have particular application to breeding programmes in developing countries where the application of molecular markers is expensive or not possible.

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