Cytogenetics of Sorghum

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Abstract

Sorghum is an interesting genus having a large number of well-recognized species taxonomically classified into five subgenera. Cytogenetic analysis led to the understanding of the nature of chromosomal variations, origins, and probable relationships based on chromosome morphology. Progress in the science of conventional and molecular cytogenetics, and genomic research provide a detailed insight into the genome organization of an individual or species, leading to enhanced utilization of genetic and physical information towards improvement of the crop. The integration of genetic, physical, and cytomolecular maps of the *Sorghum* genus is useful to scientists working on genomics of grass species. Large-scale molecular karyotyping of grass genomes would facilitate alignment of related chromosomal regions among different grass species and also facilitate genetic and cytogenetic studies of chromosome organization and evolution. As compared to other crop species little is known about the karyomorphology in sorghum mainly due to the small size of its chromosomes. In this chapter efforts have been made to collate the scattered information on karyotype studies, cytotaxonomy, phylogenic relation, numerical and structural variations, genome architecture, and wide introgression in sorghum. Implications of the information on sorghum improvement are discussed.

1 Introduction

Cytogenetic analysis of a crop and its wild relatives yields a wealth of information about their homology and genome compositions, which forms the basis of understanding for the breeders and researchers about the ways and means of genetic manipulations in crop plants. Sorghum is an interesting genus having 25 well-recognized

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species, which are taxonomically classified into five subgenera: Eusorghum, Chaetosorghum, Heterosorghum, Parasorghum, and Stipossorghum. Sorghum is grouped under the family Poaceae, tribe Andropogoneae, subtribe Sorghastrae, and genus *Sorghum*. The genus has diploid chromosome numbers of 10, 20, 30, or 40 (Garber 1950; Lazarides et al. 1991).

Cytogenetic analysis in sorghum by various workers led to the understanding of the nature of chromosomal variations, origins, and probable relationships based on chromosome morphology. Extensive studies on cytological and breeding behavior involving different sorghum species have been carried out by various workers. Huskins and Smith (1932) were the first to report on chromosome morphology in sorghum. With the advent of the science of conventional and molecular cytogenetics, and genomic research, it is now possible not only to organize and integrate the genetic, molecular, and cytological information of the genomic resources, but also to have a detailed insight into the genome organization of an individual or species giving the sequence and chromosomal view of the genome. Cytogenetic analysis of chromosomes also complements and enhances the utilization of genetic and physical information developed from large-scale genotyping and sequencing projects. The integration of genetic, physical, and cytomolecular maps of genus *Sorghum* is useful to scientists working in various disciplines particularly for those involved in genomic investigation of grass species. Large-scale molecular karyotyping of grass genomes would facilitate alignment of related chromosomal regions among different grass species and also facilitate genetic and cytogenetic studies of chromosome organization and evolution.

2 Basic Chromosome Number and Cytogenetic Structure

2.1 Basic Chromosome Number

Researchers proposed different basic chromosome numbers to the members of the tribe Andropogoneae. Huskins and Smith (1934) proposed basic chromosome number, $x = 7$, whereas Sharma and Bhattacharjee (1957) proposed $x = 4$. Garber (1950) and Celarier (1956) considered the base chromosome number of this tribe to be either five or ten. Doggett (1976) concluded that the basic chromosome number of Sorghastrae is $x = 5$. This supports the suggestion of Garber (1950) who observed predominance of genera with chromosome numbers of five and ten. However, Garber (1950) raised the question whether five indicated the endpoint of base chromosome numbers in the order of descending series or whether it is the starting point of a polyploid series. Morakinyo and Olorode (1988) reported that evidence supporting the basic number to be five was not available. Spangler et al. (1999) attempted to resolve the base chromosome number of Andropogoneae using chromosome number information with the phylogenetic tree derived from *ndhF* gene sequence analysis. A wide variety of taxa with $n = 10$ at the base of the tree led them to the understanding that $n = 10$ and not 5 for the tribe. However, the occurrence of $n = 5$ and $n = 10$ species raises questions regarding the base number of this genus and the widely accepted basic chromosome number of sorghum is $x = 5$.

In sorghum, the reported occurrence of bivalents during meiosis of haploids (Brown 1943; Kidd 1952; Endrizzi and Morgan 1955) further supports the idea of its tetraploid origin. Endrizzi

and Morgan (1955) observed translocations in the progeny of haploids and proposed that these originated from recombination between homologous duplicated regions (resulting from polyploidy) in the haploid genome. However, no strong evidence supporting tetraploid origin is observed from meiotic pairing of diploid sorghum (Brown 1943; Endrizzi and Morgan 1955). Celarier (1959) opined that polyploidy was of widespread occurrence in Sorgheae, as he assumed the basic chromosome number to be five. He observed that most of the tetraploid sorghums cytologically behave as diploids except those representing Parasorghum and Stiposorghum, which behave as autotetraploids. But, use of single-copy probes in fluorescent in situ hybridization (FISH) consistently identified two loci on two different chromosomes, which provided evidence that sorghum is not of tetraploid origin (Gomez et al. 1997). However, the basic chromosome number of subtribe Sorghastrae is assumed to be five and therefore it is often believed that sorghum is of tetraploid origin. A large number of complementary genes between them also indicate their tetraploid origin (Rooney 2000).

2.2 Karyotype Analysis

Karyotype analysis is very useful for understanding the origin, chromosomal variation, and genetic relationships at species or genus level. Very little is known about the karyomorphology in sorghum mainly due to the small size of its chromosomes. Huskins and Smith (1932) analyzed the chromosomal structure in various sorghum species and observed that the somatic chromosome length ranged from 1.2 to 3.3 μm, half the length of chromosomes observed from root tips of maize. They reported a chromosome with one long portion having a prominent subterminal attachment constriction and the shorter portion connected with the longer portion by only a fine thread of chromatin. The differences observed in the morphology of chromosomes seem to be small but definite enough to be considered as appropriate for systematic classification. Most of the chromosomes have median or submedian constrictions and often some of them have secondary subterminal constriction attachment. In *S. halepense* they observed the somatic chromosome number of 40, whereas in other species and varieties studied it was 20. The study also gave indication that *S. halepense* is an allotetraploid originated from chromosome doubling of a hybrid.

Huskins and Smith (1934) further studied the cytological structure of the meiotic chromosomes of the genus *Sorghum*. They observed 10 bivalents in all the diploid sorghums. However, quadrivalent and hexavalents were also noticed by them. In *S. halepense* they commonly observed 10–14 bivalents, and the rest of the chromosomes were in quadrivalent or higher associations. In sorghum the chromosome pairing of the normal 10 chromosomes is similar to that of pairing in hexaploid wheat and oats where the 42 chromosomes form 21 bivalents and multivalents are rarely observed. However, asynaptic pairing in sorghum leads to formation of multivalents and is known to occur very commonly (Huskins and Smith 1934). Endrizzi (1957) reported cytological investigations involving sorghum parents and hybrids with $2n = 20$ and $2n = 40$ chromosomes. He reported that the parental and hybrid combinations showed similar chromosome pairing with only 10 bivalents. Hybrids formed with $2n = 20$ and $2n = 40$ generated trivalents in meiosis with either allotetraploids or segmental allopolyploids (Raman and Sankaran 1979). The total chromosome length of the karyotype complement in their study varied from 19.28 μm ($2n = 20$) to 61.69 μm (*S. Purpureo-sericeum*, $2n = 40$).

Sharma and Bhattacharjee (1957) and Celarier (1958) studied karyotypes of 18 species of the genus *Sorghum* in detail. The studies of Sharma and Bhattacharjee (1957) showed the number of chromosomes with secondary constrictions to vary between species, which indicates their role in evolution. They also reported 23 idiograms based on the position of primary and secondary constrictions and the relative size of the

chromosomes made for all species. They reported five pairs of chromosomes in *S. vulgare* to have satellites with one pair of chromosomes at both ends. The chromosome length in *S. halepense* and *S. nitidum* were in the range of 2.31–4.41 and 1.63–3.33 μm, respectively. *S. versicolor* and *S. purpureo-sericeum* possessed chromosomes with longer length. All chromosomes of *S. purpureo-sericeum* had lengths longer than 6.90 μm, whereas those of *versicolor* were in lengths of 5.99–7.42 μm. The chromosome lengths of *S. stipoideum* and *S. intrans* were in the range of 3.72–4.89 and 5.41–6.52 μm, respectively. They grouped sorghum chromosomes as large, medium, and small. The species *S. purpureo-sericeum* and *S. versicolor* were reported to have larger chromosomes, whereas *S. subglabrescens* and *S. durra* recorded both the medium and small category. They observed clear karyotypic differences between different strains or genotypes in the idiograms in terms of number and position of constriction regions. However, the karyotype similarities observed in the study led to inclusion of strains under a common bigger taxonomic unit. From the observation made on chromosome structure they also labeled 10 major chromosomes from A to J. Further based on minor differences of these they were again subclassified as B, B1, B2, and B3. Sharma and Bhattacharjee (1957) reported six species with chromosomal fragments in their somatic cells. In most cases there were no more than two fragments per cell and none were observed during the meiotic division.

Gu et al. (1984) analyzed the karyomorphology of seven sorghum species, namely *S. bicolor*, *S. halepense*, *S. nitidum*, *S. versicolor*, *S. purpureo-sericeum*, *S. stipoideum*, and *S. intrans*. All the species studied differed in chromosome number, size, position of centromere, secondary and tertiary constrictions, and staining ability of chromosomes. In the cultivated species *S. bicolor*, the chromosome size ranged from 2.7 to 5.6 μm with the most of the chromosomes in the range between 2.5 and 4.0 μm. From staining it was observed that the heterochromatin regions adjacent to the centromere were more stainable than other regions. Other than the longest chromosome, all had a median centromere, and the longest chromosome showed submedian constriction with a tertiary constriction on its long arm. Gu et al. (1984) observed greater variation among chromosomes of the complement of *S. bicolor*. In their study *S. halepense* recorded similarities to *S. bicolor* for arm ratio and relative lengths especially for longer chromosomes. A similar trend was observed between *S. purpureo-sericeum* and *S. versicolor*. Likewise, *S. stipoideum* and *S. intrans* showed resemblances. However, in the mentioned study of Gu et al. (1984) karyographs of Parasorghum and Stiposorghum showed a clear-cut difference from Eusorghum. *S. purpureo-sericeum* recorded the largest somatic chromosome among the seven species studied. In *S. versicolor*, the SAT chromosome is the longest, which supports earlier reports (Schlarbaum and Tsuchiya 1981; Singh and Tsuchiya 1982). A similar phenomenon is reported in *S. nitidum*. Chromosomes of the species in Eusorghum tend to stain differentially in prophase with deep stain only in the regions adjacent to centromeres. Wu (1982) reported the terminal or subterminal position of the nucleolus organizer region (NOR) in meiotic configurations of *S. versicolor*, *S. nitidum*, and *S. purpureo-sericeum*.

Kim et al. (2005a, b) developed a FISH-based karyotype of the sorghum inbred line Btx623. The ordering and nomenclature of the chromosomes were based on chromosome length at metaphase as SBI-01 (longest) to SBI-10 (shortest). The SBI-01 chromosome of BTx623 is exceptionally long. It has eight pairs of metacentric chromosomes from SBI-02, SBI-03, SBI-04, SBI-05, SBI-07, SBI-08, SBI-09, and SBI-10 and one pair of medium-sized submetacentric chromosomes SBI-06. In addition to its long length (5.11 μm), the SBI-01 chromosome is one among the only two submetacentric chromosomes and is the only satellite chromosome. Lengths of chromosomes SBI-02, SBI-03, SBI-04, and SBI-05 were in the size range of 3.87–3.44 μm, and those of SBI-06, SBI-07, SBI-08, and SBI-10 were in the size range between 3.15 and 2.97 μm. The only secondary constriction and NOR observed in BTx623 was

near the centromere in the short arm of the SBI-01 chromosome. NOR in type Combine-kafir60 is located in the center of the fifth longest chromosome (Yu et al. 1991), and NOR of *S. propinquum* is located in the short arm of the smallest chromosome (Magoon and Shambulingappa 1961). Such variation in structure can complicate linkage analysis beyond a particular parental combination. The procedure of unique nomenclature followed in designating BTx623 could be the basis for genetic, breeding, and genomic applications.

2.3 Cytotaxonomy

The first taxonomic report of sorghum and related materials in the name of *Holcus* was given by Linnaeus (1753). Linnaeus added several other species such as *H. lanatus* and *H. laxus*, which were later included in another tribe, *Aveneae*, and have retained the generic name *Holcus*. Use of sorghum as a generic name was first given by Adanson (1763) as a substitute for Linnaeus' *Holcus*. This remained as a base for Moench (1794) to differentiate sorghum from *Holcus* in the materials originally considered by Linnaeus. Taxonomic studies by Stapf (1919), Snowden (1935, 1936, 1955) and Garber (1950) led to the understanding that sorghum is a genus of wide variability. Garber (1944, 1948, 1950) made a detailed cytological investigation in a number of species of this genus and established a large number of facts governing the distribution and taxonomy of the genus. His findings are the most detailed among various research conducted in cytogenetic analysis in sorghum.

Haeckel (1885) grouped sorghum into a broader group *Andropogon sorghum*, which he subdivided into *A. sorghum halepensis* and *A. sorghum sativus*. *A. sorghum halepensis* included wild perennial and annual types whose spikelet is deciduous at maturity, and *A. sorghum sativus*, annual forms having persistent spikelets. Hackel (1889) considered all the subtribe of *Sorgheae* under subgenus *Andropogon*. In contrast, Stapf (1919) considered it distinct from *Andropogon* and grouped them together as *Sorghastrae* under subtribe *Andropogonineae*. Piper (1916) stressed the need for distinction between Johnsongrass (*S. halepense*) and cultivated forms indicating that they are confined to Mediterranean regions and absent in tropical parts of Africa and also the probable center of origin for *A. sorghum sativus*, the cultivated types. Huskins and Smith (1932) indicated that the sorghum genus includes a wide range of forms. The classification in the section *Sorgastrum* is well understood, but within section *Eusorghum*, it includes all the numerous cultivated and wild forms. Keng (1939) proposed a separate subtribe under the name Sorgheae. The genera *Sorghum* Moench, *Sorghastrum* Nash, *Astenochloa* Buse, *Lasiorrhacis* Stapf, *Cleistachne* Benth, *Rhaphis* Lour, *Vetiveria* Bory, and *Chrysopogon* Trin were included in the subtribe Sorgheae. Keng (1939) placed the genus *Pseudosorghum* in the subtribe Sorgheae and shifted the *Chrysopogon*, *Rhaphis*, and *Vetiveria* to the subtribe *Rottboelliinae*. Celarier (1959) later considered *Pseudosorghum, Chrysopogon*, and *Vetiveria* as members of the Sorgheae due to their close resemblance. He opinioned that sorgheae was derived from both riochloeae and also believed that the pseudosorghum occupies an intermediate position.

Celarier (1958) made an extensive review of the cytotaxonomy of the *Andropogoneae* subtribe *sorgheae*, genus *Sorghum*. They used the subdivision of the genus into subgenera as given by Garber (1950).

2.3.1 Various Subgenera Within Sorghum

Eusorghum

Eusorghum is also referred to as true sorghum. Snowden (1955) classified the section into two subsections, Arundinacea and Halepensia, and further into series and subseries. The subsection Arundinacea has series Spontanea and Sativa. Sativa was further subclassified into six subseries: Drummondii, Guineense, Nervosa, Bicoloria, Caffra, and Durra. Hybridization among different species and subseries are feasible and there are no barriers for gene exchange

between any of these species (Karper and Chisholm 1936). The detailed studies on taxa in series Sativa was studied by Laubscher (1945). The cross between *S. drummondii* and *S. caffrorum*, two partners within Eusorghum, was cytologically analyzed by Endrizzi (1957) and the F_1s were regular. Under the subsection Arundinacea in series Spontanea Snowden (1955) identified 17 species, which are grasses in nature. Of these, 16 are African and two are Indian species. The African species were found on the eastern half of the continent and three in West Africa. Two species, *S. verticilliflorum* Stapf and *S. sudanense* Stapf, have been introduced extensively and become naturalized in many tropical countries. Endrizzi (1957) analyzed the chromosome behavior in the F_1 of *S. verticelliflorum* × *S. sudanense*, *S. arundinacea* × *S. caffrorum*, and *S. verticelliflorum* × *S. dochna* var. *technicum*. All the crosses studied had 10 bivalents in the F_1s; however, in some instances the chiasma frequency observed was lower than the parents.

Under subsection Halepensia six species were included by Snowden (1955): *S. halepense* (L.) Pers, *S. miliaceum* (Roxb.) Snowden, *S. controversum* (Steud.) Snowden, *S. almum* Parodi, *S. randolphianum* Parodi, and *S. propinquum* (Kunth) Hitchc. Several species of this subsection were crossed with various species of subsection Arundinancea and hybrids were cytologically studied. Crosses with $2n = 20$ species with the Arundinancea subsection have proven fertile with regular meiotic divisions (Celarier 1958). From crosses with the $2n = 40$ species two types of F_1s are produced. A normal F_1 with $2n = 30$ is infrequent and many of the F_1s that have been studied are $2n = 40$.

Parasorghum

This subgenus was first proposed by Snowden (1935), which includes all sorghum species having bearded nodes and simple panicle primary branches. Both cytological and morphological differences observed in this subgenus were observed in subgenera *parasorghum* and *stiposorghum* as well but these were isolated geographically (Celarier 1958). Five species were included in *Parasorghum*: *S. purpureo-sericeum* Aschers. and Schweinf., *S. versicolor* JN Anderss, *S. nitidum* Pers., *S. leiocladum* CE Hubb, *S. australiense* Garber and Snyder. *S. purpureo-sericeum* is an extremely variable species with several varieties and distributed in East Africa and West India. Most accessions were reported to have 10 somatic chromosomes and completely regular meiotic divisions. *S. versicolor* is in many respects similar to *S. purpureo-sericeum*. The natural distribution of the species is spread towards Southeast Africa. *S. nitidum* has the largest geographical distribution among *parasorghums* and is spread mostly in Southeast Asia, Indonesia, and Australia. Ayyanger and Ponnaiya (1941) first reported this species as $2n = 10$ from a collection in western India. *S. leiocladum* is an Australian species and was studied cytologically by Garber (1950, 1954). It is a tetraploid with $2n = 20$. At diakinesis and metaphase I it showed univalents, bivalents, trivalents, and quadrivalents. *S. australiense* is an annual species from Australia. It is similar to *S. trichocladurn* with $2n = 20$ (Garber and Snyder 1951). Detailed studies by Garber (1954) showed that it is similar to *S. leiocladum* in meiotic chromosome behavior and is also considered to be an autotetraploid.

Stiposorghum

This subgenus is mainly found in Northern Australia and includes six species: *S. intrans* F. Muell, *S. stipoideum* Gardner and Hubbard, *S. brevicallosum* Garber, *S. matarankense* Garber and Snyder, *S. plumosum* Beauv, and *S. timorense* Buese. *S. intrans* was previously studied by Garber (1948, 1950) who observed $2n = 10$ with regular meiosis. Attempts were made to cross this species with *S. stipoideum* and *S. brevicallosum* but no seeds could be obtained (Garber 1950). *S. stipoideum* was studied by Garber (1950) from collections from the Northern Territory of Australia. All accessions studied were diploid with regular meiotic behavior. Attempts made to cross this species with *S. intrans* and *S. brevicallosum* resulted in no seed formation (Garber 1950). All the accessions of *S. brevicallosum* as studied by Garber (1950) were found to be diploid with regular meiotic behavior. He

also attempted to cross this species with *S. intrans* and *S. brevicallosum* but no seeds were produced. *S. matarankense* represents diploid species in the *S. intrans–S. stipoideum–S. brevicallosum* complex (Garber and Snyder 1951). *S. plumosum* has widest distribution in the subgenus and is the only perennial in this subgenus. Both tetraploid and hexaploid types are known (Garber 1954) and both have high frequency of multivalents. He analyzed two tetraploid accessions and found that they were similar to the *Parasorghum* species, *S. leiocladum*, and *S. australiense* in meiotic behavior. *S. timorense* is morphologically very similar to *S. plumosum* and possibly should only be considered as a variety of that species.

Chaetosorghum

The species *S. macrospermum* Garber was accommodated in this subgenus by Garber (1950). Though they are glabrous noded, they would not fit in either Eusorghum or Sorghastrum. Garber (1950) analyzed the meiotic behavior of the species and found that it had 20 bivalents at metaphase I. However, he observed one plant that had a high frequency of univalents which he explained as partial desynapsis.

Heterosorghum

This is another subgenus that was mentioned by Garber (1950) to include one species that will not fit easily into other subgenera. The species, *S. laxiflorum* FM Bailey, had very extensive distribution and is found in Australia, New Guinea, and the Philippine Islands. Garber (1950) analyzed one accession from northern and another from southern Queensland. In both the cases the $2n$ number was 40, and meiosis observed was regular with 20 bivalents at the diakinesis state and metaphase I stage.

2.3.2 Phylogenetic Relationship Within Sorghum Subgenera

Celarier (1958) detailed the phylogenetic relationship within sorghum subgenera (Fig. 1). In *Parasorghum*, *Stiposorghum*, and *Eusorghum*, the pedicellate spikelets are staminate type, whereas in *Chaetosorghum* and *Heterosorghum* only glumes are seen. The entire pedicellate spikelet is lost in the genus *Sorghastrum*. Likewise, panicle branching is significant in phylogenetic relationships. The open divided type is observed in *Eusorghum* and *Heterosorghum*, which are primitive type. Simple branching is observed in *Parasorghum*, *Stiposorghum*, and *Chaetosorghum*, which are the advanced types. Cytologically, the chromosome number and size vary among the subgenus. Chromosomes of *Parasorghum* and *Stiposorghum* are quite large whereas *Eusorghum* and *Heterosorghum* are much smaller. In *Parasorghum* and *Stiposorghum* five is the lowest basic chromosome number and examples of polyploidy suggest autopolyploidy of building units by 10 (i.e., $2n = 10, 20, 30$). In *Eusorghum*, the lowest number is 10, and allopolyploids are built by units of $2n = 20$ and 40. *Chaetosorghum* and *Heterosorghum* are allopolyploids with $2n = 40$. Celarier (1958) opined that *Parasorghum* and *Stiposorghum* are closely related and are to be considered in one subgenus and these genus can be clearly differentiated from *Eusorghum*. Relationships of *Chaetosorghum* and *Heterosorghum* are not clearly understood.

2.3.3 Cytological Relationship Among Various Species of Sorghum

The wild species of sorghum represent a potential diverse source of germplasm for sorghum breeding. Parvatham and Rangaswamy (2004) made a detailed study of the karyomorphological and phylogenetic studies in six cultivated and wild sorghum species, *S. intrans*, *S. Propinquum*, *S. purpureo-sericeum*, *S. halopense, S. sudanense*, and *S. bicolor*. They used relative chromosome length, arm ratio, chromosome index, and nucleolar organizers for characterizing the chromosomes of different species. All the species possessed basic chromosome number, $x = 5$. *S. intrans* possessed one pair of long median and four pairs of submedian chromosomes, whereas the tetraploid species *S. propinquum* ($2n = 20$), *S. purpureo-sericeum* ($2n = 20$), and *S. bicolor*

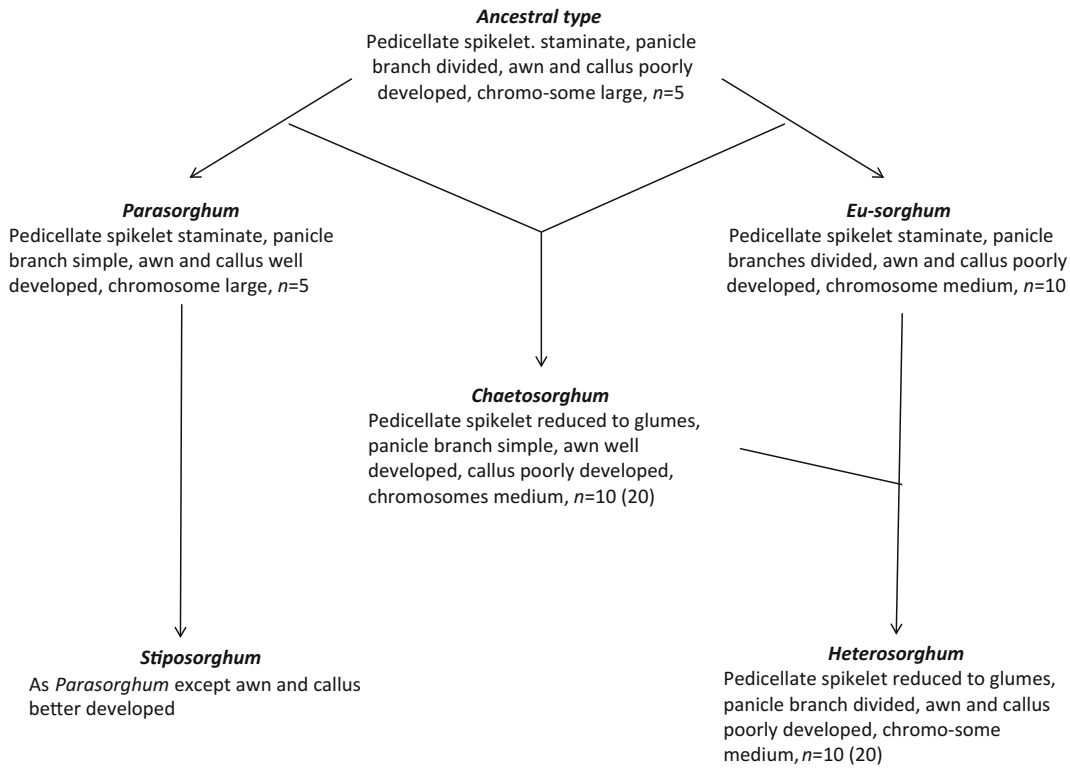

Fig. 1 Phylogenetic relationship between different subgenus in sorghum (adapted from Celarier 1958)

($2n = 20$) were reported to possess median, submedian, and smaller chromosomes. *S. propinquum* and *S. purpureo-sericeum* showed similarity in having seven and three pairs of median and submedian chromosomes, respectively. The hexaploid species, *S. halepense* and *S. sudanense*, possessed comparable chromosome architecture but differed in sizes. One pair of satellites (SAT) each was observed in all the species revealing their role in nucleolar organization. Their study revealed the uniqueness of the SAT regions, occupying only the longest chromosomes except hexaploid species *S. sudanense* where it was observed in the second longest chromosome. Variation in chromosome number of species is attributed to the duplication of the chromosome complements (Stebbins 1950). Those species with lower chromosome number are believed to be primitive as also evidenced from the taxonomic characteristics (Parvatham and Rangaswamy 2004). Vinall (1926) revealed that the wild annual sorghums cross readily with large annual grain sorghum but crosses between Johnsongrass and annual forms is possible only with great difficulty and the hybrids are mostly sterile. He attempted crosses between sorghum and Johnsongrass and could obtain only two successful crosses. The study further revealed that the successful cross could be obtained only when sorghum variety, Black amber sorgo, was used as the pistillate parent. No successful cross was obtained when Johnsongrass was fertilized with the sorghum pollen. However, chromosomal studies did not reveal any major differences from those of other cultivated sorghums. Allopolyploidy could have played a major role in the evolution of species in sorghum (Parvatham and Rangaswamy 2004).

Hadley (1953a, b) attempted crosses between *S. vulgare* ($2n = 20$) and *S. halepense* ($2n = 40$) and they obtained two hybrids with 30 and one with 40 chromosomes. One hybrid having 30

chromosomes set seed when backcrossed with *S. vulgare*, however, the other was sterile. In the backcross progeny the chromosome numbers varied from 20 to 22. Plants having 20 chromosomes appeared regular with some plants sterile. On the other hand, the 40-chromosome hybrid was fertile and set a large number of seeds and in their F_2s the chromosome numbers ranged from 38 to 40.

Hybrids formed using *S. propinquum* and *S. bicolor* are reported to be meiotically regular with 10 bivalents (Doggett 1988). Analysis of meiosis of *S. bicolor* × *S. halepense* hybrids proved that *S. halepense* possesses one genome similar to *S. bicolor*, and another divergent or a rearranged genome. This leads to the understanding that *S. halepense* is an allopolyploid or segmental allopolyploid (Duarra and Stebbins 1952; Tang and Liang 1988).

2.3.4 Molecular Phylogenic Relation Among Sorghum Species

It is evident that *Sorghum* genera are highly heterogeneous. Efforts have been made to decipher the phylogenetic relationship among them at the molecular level. DNA markers have been deployed in establishing the relationship of sorghum to other grasses such as maize (Whitkus et al. 1992). Allozymes (Morden et al. 1990), nuclear genes, for example, *ITS1* (Sun et al. 1994; Dillon et al. 2004; Ng'uni et al. 2010), *ndhF* (Spangler et al. 1999; Dillon et al. 2004, 2007a), *Adh1*(Dillon et al. 2007a), *chitinase-b* (Qin et al. 2008), and chloroplast genes, such as *psb*Z-*trn*G, *trn*Y-*trn*D, *trn*Y-*psb*M, and *trn*T-*trn*L (Ng'uni et al. 2010) have helped in better understanding the phylogenetic relationship within the *Sorghum* genus. Spangler (2003) suggested the existence of three distinct lineages—*Sarga*, *Sorghum*, and *Vacoparis*—representing sorghum. He included the set of species that formerly represented the bulk of the subgenera, *Parasorghum* and *Stiphosorghum*, and placed Australian taxa, *S. macrospermum* and *S. laxiflorum* in a new genus *Vcoparis*. *S. bicolor*, *S. halepense*, and *S. nitidum* were retained in *Sorghum*. However, sequence comparison of *ITS1* and *ndh*F genes showed Australian species *S. laxiflorum* and *S. macrospermum* most closely related to cultivated sorghum (Dillon et al. 2004). The study suggested reduction of subgeneric sections from five to three: *Eusorghum* (unchanged), a combined *Chaetosorghum*/*Heterosorghum* to reflect the very close relationship between these two species, and a combined *Parasorghum*/*Stiphosorghum* section. Findings of Dillon et al. (2007a) further supported this conclusion and contradicted the result of Spangler (2003). Using *ITS* and chloroplast *ndh*F sequences Price et al. (2005a) put *Sorghum* into two lineages, one comprising the $2n = 10$ species with large genomes and their polyploid relatives, and the other with the $2n = 20$ and 40 species with relatively small genomes. Qin et al. (2008) used the *Chi-b* gene to establish molecular phylogeny among 10 sorghum species. Their study placed the 10 species into three sections: the first with *S. halepense*, *S. almum*, and *S. silk*; the second with *S. bicolor*, *S. propinquum*, and *S. arundinaceum*; and the third with *S. nitidum*. A combined sequence analysis with four regions of chloroplast DNA and *ITS* of nuclear DNA by Ng'uni et al. (2010) clearly demonstrated that classifying Australian species *S. macrospermum* and *S. laxiflorum* as a separate section was not well supported. They further found that *S. almum* was closely associated with *S. bicolor*, suggesting the latter to be the maternal parent of the former.

All the reports on molecular phylogeny of sorghum are in agreement that there are two well-supported major clades within sorghum (Kellogg 2013). *S. bicolor* and its close relatives, *S. halepense*, *S. propinquum*, *S. arundinaceum*, *S. almum*, and *S. drummondii* are represented in clade 1. Except *S. propinquum*, which is Asian, all are of African origin. Australian species *S. macrospermum* and *S. laxiflorum* are also in this clade (Dillon et al. 2004; Price et al. 2005b). Seventeen species are included in clade 2. These are Australian species representing subgenera *Stiposorghum* and *Parasorghum*, which are cross-compatible with cultivated sorghum (Price et al. 2006).

3 Ploidy Variations

The number of complete sets of chromosomes in a cell of an organism is referred to as ploidy. Hence ploidy variation deals with differences in terms of chromosome numbers. Ploidy variation is considered to be an important adaptive mechanism leading to evolution and speciation. The preceding discussion has shown that different species within the subtribe Sorghae have considerable ploidy variations. However, such variation has also been reported within cultivated species of a crop and has much cytogenetic significance with anticipated agronomic significance as well. Two types of ploidy variations in crop plants have been reported, namely, euploidy and aneuploidy. Euploids of a species vary in terms of complete chromosome set, whereas aneuploids differ in terms of one or more chromosomes from the normal set.

3.1 Euploidy

Since the 1930s sorghum scientists observed abnormal plants within the experimental materials of sorghum. However, it was Brown (1943) from Texas Agricultural Experiment Station who first recognized them as ploidy variants of cultivated sorghum. Since his report, haploids, triploids, autotetraploids, and higher ploidy variants in sorghum have been published by various authors (reviewed by Murty and Rao 1974).

3.1.1 Haploids

Brown (1943) reported the occurrence of abnormal plants over 10–12 years among grain and forage sorghums grown at Chillocothe, Texas. Observing the characteristics of these abnormal plants he surmised them to be haploid plants and characterized two such plants: one was obtained from the F_3 progeny of a Blackhull kafir × Feterita cross in 1940, and the other was found in a genetic stock in 1941. Haploid plants had relatively slender stalks, narrow leaves with smaller stomatal guard cells, small and highly sterile panicles, and particularly small glumes. Pollen grains of haploids are in general smaller, empty, and collapsed. Brown (1943) observed 4–6 and 3–7 anaphase separation to be most common, whereas the separation ranged from 5–5 to 0–10 in a number of cases. Out of 150 metaphase nuclei he studied in one case, he reported 3 II + 4 I, two cases of 2 II + 6 I, and 13 cases of 1 II + 8I. In addition, in nearly 8 % of the cases he reported anaphase bridge formation among other abnormal disjunctions. Observed bivalents in sorghum haploids supported earlier suggestions that five is the basic chromosome number in sorghums (Karper 1930; Longley 1932; Karper and Chisholm 1936).

Since the report of Brown (1943), haploids in sorghum have been reported by various authors (Kidd 1952; Endrizzi and Morgan 1955; Schertz 1963). Kidd (1952) obtained the haploid as a "twin seedling" from variety Resistant Wheatland (GC 38288). Out of the 55 haploid cells Kidd studied, eight recorded 1 II + 8 I, four 2 II + 6 I, seven had 1 III + 7 I, and the rest had 10 I. Gaines and Aase (1926) and Levan (1941) observed di- and poly-ploid cells in haploid plants of wheat and *Phleum*, respectively, in which univalents remained the rule. Similarly, Kidd (1952) also observed diploid cells in nearly 30 % of the cases. However, in these cases he noticed "stickiness" among the chromatids, whereas Gaines and Aase (1926) and Levan (1941) reported "syncytes". Endrizzi and Morgan (1955) obtained haploids from a cross of *S. vulgare* Pers. cv. "Texas Blackhull kafir" × *S. arundinaceum* (Willd.) Stapf. They recorded 1 II + 8 I in four out of 26 diakinesis or metaphase I cells studied. In the remaining 22 cases, 10 irregularly distributed univalents were observed. Although the haploids were predominantly sterile in nature, they could obtain seeds by pollinating haploid plants with Texas Blackhull kafir pollen.

Schertz (1963) reported 19 haploids from a population of 41,300 plants at Chillicothe, Texas, a ratio of 1 in 2174 plants. The haploids reported by all authors recorded smaller stature, glumes, anthers, and panicles with sparse seed set. Schertz (1963) further added that the pollen stainability varied from 0 to 1.5 %, and seed set

on selfing ranged from 0 to 2 %. They could obtain 394 progeny of haploids by cross-pollination. Cytology of the haploids recorded around 3 % of metaphase cells with 8 Is and an association of two chromosomes. He also recorded unequal chromosome distribution during anaphase I leading to a large nucleus in one secondary sporocyte and no or small nucleus in the other sporocyte. He also observed multinucleate secondary sporocytes, many micronuclei and nuclei of varied sizes. He recorded varied distribution of chromosomes to poles at anaphase.

Murty and Rao (1974) have concluded that the occurrence of bivalents in the haploids indicates the duplicate nature of the genome of grain sorghum. Almost all authors have observed the occasional production of diploid plants from haploids. This suggests that diploid nuclei with full haploid complement as occasionally observed by Brown (1943), Kidd (1952), and others are formed during disjunction leading to normal ovule development.

3.1.2 Triploids

Kidd (1952) obtained a triploid plant from the F_1 of a cross between *ms*#2Dwarf Tan Kafir and Redlan F_1, which was sterile. Because male sterility is a recessive trait, the sterile plant in the F_1 generation itself was diagnosed and investigated. Out of 24 cells investigated eight cells showed 10 III, five had 9 III + 1 II + 1 I, six recorded 8 III + 2 II + 2 I, three had 7 III + 3 II + 3 I, and one each was detected with 6 III + 4 II + 4 I and 4 III + 5 II + 8 I cytological configurations. Subsequently triploids in sorghum have been reported by Price and Ross (1957), Erichsen and Ross (1957), Quinby et al. (1958), Munoz et al. (1963), and Schertz and Stephens (1965). These were obtained from both natural populations and from controlled crosses. Schertz and Stephens (1965) obtained triploids in progeny from plants that had been emasculated with hot water and pollinated subsequently. It is suggested that when hot water is used for emasculation, subsequent pollinations were often delayed or incomplete, which may lead to self-pollination from pedicelled spikelets. This delayed pollination enhances the probability of triploid formation (Schurtz 1966). Hybrid plants with 30 chromosomes from interspecific crosses of *S. vulgare* (2 N = 20) and *S. halepense* ($2n = 40$) have also been reported (Hadley 1953a, b, 1958; Hadley and Mahan 1956; Endrizzi 1957). Triploids can be distinguished from diploids of the same cultivar in terms of fertility and morphology and cytologically (Murty and Rao 1974). However, in most cases, triploids were not morphologically different from tetraploids, except for high levels of sterility (Roony 2000). Triploids are highly sterile and consistently have large stomatal guard cells. Meiotic pairing of chromosomes is irregular with most common meiotic configuration of 9 IIIs (Murty and Rao 1974). Upon backcrossing triploid plants to diploids in general produce diploid and aneuploid stocks (Price and Ross 1957; Schertz and Stephens 1965). Sengupta and Weibel (1971) reported the occurrence of male sterile triploids to the extent of 0–22 % upon crossing diploid sorghum cultivars to tetraploid *S. halepense*.

3.1.3 Tetraploids

Autotetraploids and other polyploids in sorghum have been reported by Salomon (1940), Dusseau (1945), Chin (1946), Casady and Anderson (1952), Butany (1955), Atkinson et al. (1957), Doggett (1957), Krishnaswamy et al. (1958), Narayan (1961), Ross and Chen (1962), Doggett (1962), Magoon and Tayyab (1968), Sengupta and Weibel (1971), and others. Crosses between cultivated sorghum and other *Sorghum* species, particularly *S. halepense* are reported to produce F_1 hybrids with 40 chromosomes along with triploids (Hadley 1953a, b; Endrizzi 1957; Hadley 1958). Schertz and Stephens (1965) suggested that the tetraploids in such interspecific crosses were derived from abnormal eggs with 20 chromosomes. Tetraploids are reported to produce dark foliage with wavy margins, shorter but stouter straw, larger pollen grains and grain

size, higher protein content, longer stomata with a general tendency to flower late and varying degrees of male and female fertility (Murty and Rao 1974; Roony 2000). Chiasmata percentage in the tetraploids is similar to the diploids (Chin 1946). Quadrivalent formation in sorghum tetraploids, particularly of an apomictic culture R 473, is much lower compared to maize (Murty and Rao 1974). Mean quadrivalent frequency per cell in tetraploid sorghum ranges from 0.13 (Krishnaswamy et al. 1958) to 6.22 (Doggett 1964).

Ross and Chen (1962) made a cross between an autotetraploid derived from grain sorghum variety, Experimental 3, and a colchicine-induced mutant *M15* derived from Experimental 3. They observed an increase in fertility from 0.5 % in the autotetraploid to 56.9 % in the hybrid. Among the hybrids a reduced number of quadrivalents and univalents, and a higher number of bivalents were observed at diakinesis. From this they concluded that a mutation that might have occurred in diploid *M15* aided in reduction of univalent formation.

Tetraploids recorded increased seed size, thus there was a renewed interest in the 1960s to develop autotetraploid grain sorghum cultivars for cultivation (Doggett 1962). A lower level of fertility among tetraploids was the main hindrance towards this direction. However, selection for improved fertility led to identification of tetraploids with nearly the fertility level of diploids (Doggett 1962; Luo et al. 1992). Doggett (1962) suggested that certain neutral genes present in the diploid level influence seed set of the autotetraploid. However, with the initial excitement no substantial progress in this direction has been made over subsequent decades.

3.1.4 Higher Polyploids

Octaploids along with tetraploids in sorghum were first reported by Chin (1946) after treatment of grain sorghum with colchicine. Longley (1946, see Murty and Rao 1974) also found octaploid forms of grain sorghum with the use of colchicine. Octaploids are stouter and shorter than diploids, slower in growth, and lower in fertility.

3.1.5 Hypoploidy

Schertz (1962) reported the occurrence of hypoploids with chromosome number of 38–39 from a colchicine-treated population of cultivar SA403. Hypoploids in general had less fertile pollen; lower spikelet number, seed number, and total seed weight; but higher grain weight. They observed more univalents, and fewer secondary sporocytes and microspore quartets free of micronuclei as compared to tetraploids.

3.2 Aneuploidy

Vigor and fertility level are relatively better among aneuploids as compared to euploids, and often play an important role in gene mapping across plant species. Price and Ross (1955, 1957) were the first to report aneuploids in grain sorghum. They made a triploid × diploid cross and obtained nine normal diploids, nine single trisomics, one probable tetratrisomic, one triple trisomic, one tetrasomic quadruple trisomic complex, and one with undetermined chromosome number from a total of 25 plants. They did not find any noticeable increase or decrease in vigor due to extra chromosomes.

3.2.1 Trisomics

Price and Ross (1955, 1957) reported isolation of trisomics in sorghum. Their studies indicated likelihood of failure to identify trisomic plants. This was probably due to possible heterozygosity of their sources leading to segregating population. Although karyotype analysis enabled the successful identification of trisomics in other species, in sorghum this yielded limited success. While handling haploids derived from a wide cross Endrizzi and Morgan (1955) encountered a trisomic and they suggested that it might have originated during irregular meiosis of the haploid. Hadley and Mahan (1956) obtained a male sterile triploid by crossing male sterile (*ms2*) Texas Blackhull Kafir to Johnsongrass.

This sterile line was backcrossed to sweet sudangrass. In the progeny they obtained plants with 21 chromosomes along with normal diploids and other aberrants. They observed the occurrence of 10 II + 1 I as well as 9 II + 1 III. Schertz (1963) recovered five trisomics upon crossing haploids to normal diploids. Pi and Tsai (1965) reported trisomics in Shallu-type sorghum. Poon and Wu later in 1967 studied pachytene chromosomes of seven of them. Heterozygous segregation and associated heterosis often masked the distinguishable phenotypic effect of the extra chromosome (Lin and Ross 1969). To circumvent this Schertz (1966) used a homozygous background of Tx403, an early four-gene dwarf cultivar. They obtained trisomics by crossing triploid Tx403, obtained as a result of hot water emasculation, to diploids of the same cultivar. Based on characteristic features of the derived trisomics, Schertz (1966) grouped them into "Small-glume trisomic", "Stiff-branch trisomic", "Cone trisomic", "Large-glume trisomic", and "Bottle-brush trisomic". These trisomics were distinguishable only after panicle emergence, and became distinct near seed maturity. Using these cytological stocks Venkateswarulu and Reddi (1968) through karyotype analyses linked the bottle brush trisome to chromosome number 9 and large-glume to number 10. Lin and Ross (1969) obtained ten different types of trisomics by selfing a homozygous triploid from the sorghum cultivar, *SD100*, which was derived by selfing a haploid (Erichsen and Ross 1963). Based on the frequency of trivalent types and total number of trivalents all obtained trisomics were grouped into tens, and arranged in order of decreasing vigor compared to the normal diploid. These ten types were all primary trisomics as there was no association of more than three chromosomes or no ring configuration was observed. The Type 9 involved the nucleolar chromosome. The probable relationship between trisomic frequency and chromosome length was postulated by them. They postulated that Types 4 and 5 identified by them were the same as that of bottle brush and large-glume described by Venkateswarulu and Reddi (1968).

Hanna and Schertz (1971) succeeded in uncovering the identity of these trisomics by crossing to translocation stocks. They succeeded in identifying all 10 primary trisomics described by Schertz (1966) and Lin and Ross (1969). They identified these as A—bottle brush, B—sparse branch, C—compact, D—stiff branch, E—large glume, F—asymmetric, G—cone, H—light green, I—small glume, and J—spear. Schertz (1974) further characterized 5 (B, C, F, H, and J) of the 10 primary trisomics discussed above.

The first effort to localize genes using trisomics was made by Hanna and Schertz (1970). Using trisomic stocks they made an effort to localize 24 seedling lethal mutations. F_2 segregation ratios of trisomic × genetic stocks showed that the gene w_{18} was associated with the bottle-brush trisome, and the genes w_{10} and w_{20} with the cone trisome. Coleoptile color-controlling genes (Rs_1 and Rs_2) were associated with the small-glume and stiff-branch trisomes, respectively.

3.2.2 Other Aneuploids

Reports on other aneuploids in sorghum are scanty. Hadley and Mahan (1956) while backcrossing male sterile triploids to sweet sudangrass obtained a series of aneuploids with 22, 30, 33, 41, and 43 chromosomes along with predominant normal diploids and occasional trisomics. All these plants showed reduced fertility and loss of vigor upon selfing. Schertz (1962) suspected the occurrence of hypotetraploidy in his colchicine-induced tetraploid progeny. In the mentioned work of Lin and Ross (1969) they most frequently obtained single trisomics. Among 111 offspring obtained upon selfing of the triploid cultivar, *SD100*, they obtained 40 normal diploids, 58 primary trisomics, 11 double trisomics, one triple trisomic, and one plant with unknown configuration as it did not reach heading. They grouped the double trisomics on morphological bases as Types 1–4, 2–8, 3–6, 4–6, 5–3, 5–6, and 8–9. Similarly the triple trisomic was typed as 4–5–6.

Since the 1970s not many reports on aneuploidic variations in sorghum have been available in the published literature.

4 Structural Variations

Occurrence of structural variants is a common phenomenon among plant species. Such variants are distinguished only in heterozygous conditions. Garber (1948) first reported the occurrence of reciprocal translocation in *S. versicolor*. While handling haploids derived from a cross of *S. vulgare* cv. Texas Blackhull kafir × *S. arundinaceum*, Endrizzi and Morgan (1955) encountered structural variants in sorghum. Like Brown (1943) and Kidd (1952) they also observed occasional bivalents in the haploid. Upon crossing the haploid as female with pollen from Texas Blackhull kafir they obtained three out of 29 F_1s with atypical cytological behavior. In one case they observed a ring or chain of four, typically exemplifying a case of reciprocal translocation. They attributed this occurrence of reciprocal translocation to "crossing over in interstitial duplicate regions of two partially homologous chromosomes during megasporogenesis of the haploid." A second cytologically atypical F_1 indicated occurrence of the "loss of a major portion of the long arm of a heterobrachial chromosomes by crossing over in the duplicate segments of two otherwise non-homologous chromosomes of the hybrids." The third derivative was a trisomic case. Similarly, Schurtz (1963) also reported the occurrence of a translocation derivative in a haploid × diploid cross. Haensel (1960) obtained reciprocal translocations upon gamma irradiation of "colchicin reactive" grain sorghum variety Experimental 3. Huang et al. (1963) studied three such reciprocal translocation stocks, T165, T231, and T396, during meiosis. They recorded approximately 50 % viable pollens, which indicated occurrence of duplications and deficiencies. T396 involved the nucleolar chromosome and a common chromosome pair was found to be involved in T165 and T231. Lessman (1965) used two of these translocation stocks, T231 and T396, for the first time towards gene mapping. He could associate seed color with T396 and midrib color with T231. He concluded that the gene for midrib color is located either distal to the centromere near the breakpoint of one of the interchanged segments, or on one of the opposite arms of the chromosomes involving the centromere. Papathanasiou and Lessman (1969) proposed male sterile CK60 as a standard for chromosome analyses in sorghum and further associated midrib color (*Dd*) and seed coat color (*Yy*) to T231 and T396, respectively. Schertz (1970a, b) developed a set of 11 homozygous translocation stocks through gamma irradiation of cv. Combine 7078. These 11 stocks represent at least two translocations involving each of the 10 chromosomes. Using these translocation stocks Hanna and Schertz (1971) identified all 10 trisomes and associated them with their respective phenotypes (discussed in Sect. 4.2.1). Reciprocal translocations in wild and cultivated sorghum accessions have been reported by Morakinya and Olorode (1988). They observed a ring of up to nine chromosomes with the tenth sticking out of the ring at each pole in a cross, TH2 × IB12. This suggests the occurrence of terminal reciprocal translocations involving all the chromosomes except one in which it is restricted to only one arm. The study suggested the possible origin of sorghum and its wild relatives through segmental allotetraploidy.

5 *B*-Chromosomes

B-chromosomes are extra chromosomes that are dispensable for the cell, either in certain cells within the organism or in certain individuals within the population. The first report on occurrence of the *B*-chromosome in sorghum was made by Janaki-Ammal (1939, 1940). Among 100 plants of wild diploid grass, *S. purpureosericeum*, the author reported 40 extra chromosomes, which varied from one to six in number. They found that such extra chromosomes were confined to the shoot system alone and were never in the roots. Garber (1944) observed *B*-chromosomes in 38 % of the plants they studied.

Darlington and Thomas (1941) studied the mechanism of the loss of *B*-chromosomes (subsequently referred to as *B*s) in roots in the same material of Janaki-Ammal (1940). They recorded three types of *B*s. The first types are of similar

length to those of *A*-chromosomes, the second were shorter than the *A*-chromosomes, and the third were very long isochromosomes. They found that the young roots lose *B*s during seed development itself, whereas among shoot cells there is rare loss of *B*s. Furthermore, in growing inflorescence the *B*s are eliminated from those floral parts not involved in germ cell production. Pollen mother cells (PMC) are free from micronuclei and found to contain an invariable number of *B*s, yet other walls rarely contain mucronuclei. It is found that *B*s are always delayed in metaphase orientation and sometimes may fail to congregate on the plate altogether. *B*s may sometimes fail to disjoin, leading to the formation of the micronucleus. Sometimes misdivision of the centromere may lead to formation of telocentric chromosomes. All these anomalies often lead to the loss of *B*s in cell lineages. However, in PMCs *B*-chromosomes occur in regular numbers in all first methaphase cells. They congregate perfectly but pass on to one pole only without division. At second mitosis they divide without any delay. Primary division in the pollen grains is regular irrespective of whether *B*s are present or not, which occurs roughly one week after meiosis. During this division some structural changes may occur. However, it is observed that the vacuole, which generally separates the vegetative and generative nuclei, disappears and the nuclei remain close together. This is followed by certain abnormalities including nonpolarization, subequal division of cytoplasm, and rapid divisions of the vegetative nucleus. The supernumerary division of the vegetative nucleus is quite uncommon in other species. During these rapid supernumerary divisions *B*-chromosomes show somatic defects by lagging on the anaphase spindle. However, they do not get lost from the cell, and mostly pass undivided towards the generative pole. At this point the germ-track nucleus doubles its set of *B*s. The supernumerary divisions during stated polymitosis are believed to be stimulated by the presence of *B*-chromosomes. During sperm formation polymitosis leads to three developments: no sperm, two sperm, and two pairs of sperm of unequal size. Janaki-Ammal (1940) observed much increase in empty grains in *B*-chromosome "plus" plants, and this happens due to increased occurrence of polymitosis during middle pollen grain growth. Both Janaki-Ammal (1940) and Darlington and Thomas (1941) observed that *B*-dosage effect on polymitosis is geometric rather arithmetic. This is a typical disjunction of the *B*-chromosome, which is referred to as "sorghum type disjunction" (Schulz-Schaeffer 1980). Garber (1950) observed that the *B*-chromosome did not influence pollen fertility or seed set until four *B*s are present.

B-chromosomes are heterochromatic with variable behavior in different cells. A varied degree of condensation depending on the activity of the cell and the size of the nucleus may be behind this variable behavior. Variation in the sizes of nucleoli and persistence to anaphase are the characteristic features of polymitotic pollen grains.

Darlington and Thomas (1941) suggested that differential behavior of *B*-chromosomes in sorghum is a special adaptive behavior. They opined that polymitosis is a suicidal action (they also referred to it as "malignant mitosis") and there needs a powerful compensation for this to survive. They found that this is achieved by doubling of the *B*s in the second generative nucleus. Such doubling leads to an increase in the content of *B*s in every generation; opposite physiological selection reduces their frequency to an equal extent. Bosemark (1957) summarized that *B*-chromosomes in *S. purpureo-sericeum* are of various size classes, heterochromatic, observed in anthers and never in root tissues, do not pair with ordinary chromosomes but among themselves and show nondisjunction on the male side. Basic microscopic organizational differences between the centromeres of *A*- and *B*-chromosomes have been observed (Reddy 1958). This structural difference is considered to be the causal factor underlying the abnormal behavior of *B*s at mitosis.

Magoon et al. (1961) observed a different degree of sterility in *S. purpureo-sericeum*, which was dependent on the numbers of *B*-chromosomes. They observed one stunted plant with fewer tillers showing 95–98 % sterility.

Cytologically they found it to contain 10 A + 3 fairly large *B*-chromosomes. In this cytological stock they observed partial pairing at pachytene but pronounced desynapsis to follow during diakinesis, leading to less than 2 bivalents at metaphase I in the majority of cells. Fragmentation predominantly of B^{II} type was also observed in nearly 50 % of the cells in metaphase I. In addition, they reported other meiotic abnormalities as well. This further supports the observation of Janaki-Ammal (1940) and Darlington and Thomas (1941) that *B*-chromosome numbers have a geometric effect on pollen viability. The work of Reddy (1958) suggested that the marked heterochromatic nature of *B*s' rather inadequate centromeres likely causes nondisjunction of *B*s at the second pollen mitosis.

B-chromosomes have not been reported from any other species of Parasorghum or Eusorghum (Murty and Rao 1974). Wu reported the occurrence of *B*-chromosomes in three other species of sorghum: *S. nitidum* (Wu 1980), *S. purpureosericeum* (Wu 1984), and *S. stipoideum* (Wu 1992). The findings in these reports are in unison with earlier observations. At meiosis a more stable and regular fashion of behavior by *B*-bivalents was reported than the *B*-univalents, particularly in male mitosis. These reports suggested mosaicism of *B*-chromosomes in microsporocytes and tapetal cells, and total elimination from stems and leaves.

6 Molecular Cytogenetic Maps and Genome Architecture

6.1 Molecular Cytogenetic Map

Advances in molecular tools have aided in understanding the genome of plant species more precisely, often making conventional cytological tools obsolete. Draye et al. (2001) discussed a technique for generating synaptonemal complex (SC) spreads from sorghum cv. BTx623, in which all 10 bivalents could be differentiated based on relative lengths and arm ratio. They observed distinct kinetochores in some SC sets, which are otherwise not common in sorghum. SC sets are six to seven times longer than mitotic metaphase chromosome sets. The longest SC is often found to be associated with remnants of nucleolus. It was further observed that the sixth longest SC often was closely associated with an amorphous structure of unknown identity. They suggested the possibility of use of linkage group specific bacterial artificial chromosomes (BAC) in fluorescence in situ hybridization (FISH)-based "chromosome paint," which is also referred to as "cytomolecular mapping." Efforts towards construction of a robust physical map of sorghum were initiated towards the end of the last millennium. The BAC library of cultivated sorghum and wild species *S. propinquum* was created (Woo et al. 1994; Lin et al. 1999; Klein et al. 2000).

Perhaps the first deployment of FISH in sorghum genome analysis was made by Gomez et al. (1997) who showed that a sequence complementary to maize *sh2* cDNA is located at one end of a midsize metacentric sorghum chromosome. For this purpose they used a marker-selected 205-kb sorghum BAC clone and a sorghum plant containing an extra copy of one arm of the sorghum chromosome arbitrarily designated with the letter D. The results suggested an homology between one arm of chromosome D in sorghum and the long arm of chromosome 3 in maize. Zwick et al. (1998) analyzed the liguleless (*lg-1*) linkage group in sorghum and compared it with rice and maize taking advantage of the available sorghum BAC library of Woo et al. (1994). Using six liguleless-associated rice RLFP markers they selected 16 homologous sorghum BACs to map an *lg-1* linkage group to chromosome I physically. This was confirmed using sorghum cytogenetic stock, trisomic for chromosome I. Using FISH Sang and Liang (2000) reported that 18S-5.8S-26S rDNA sequences were located at two sites on the chromosomes in *S. bicolor* and *S. versicolor* ($2n = 10$), but at

four sites on the chromosomes of *S. halepense* ($2n = 40$) and the tetraploid *S. versicolor* ($2n = 20$). The rDNA sequence is found on the sorghum chromosome 1. With this study they excluded *S. versicolor* as the possible progenitor of *S. bicolor*.

Multiple molecular cytogenetic probes using BAC clones containing molecular markers mapped across sorghum linkage groups were developed by Kim et al. (2002). Using 17 such BAC clones they could successfully identify all 10 chromosomes. Islam-Faridi et al. (2002) further using 19 BAC clones harboring markers for linkage group (LG) 1 could physically map different markers to the short and long arm of chromosome 1. Following a similar strategy Kim et al. (2005b) painted LG-02 and LG-08 using 21 and 19 BAC clones, respectively. They successfully localized *Rf1* gene to the ~0.4 Mbp euchromatic region of LG-08. FISH painting of all 10 SB chromosomes was completed by Kim et al. (2005a). They found that euchromatic DNA spans ~50 % of the sorghum genome, with the maximum (~60 %) in chromosome 1 (SB-01) and the minimum in chromosome 7 (SB-07). Heterochromatic regions (~411 Mbp) are characterized by a ~34-fold lower rate of recombination and ~3-fold lower gene density. Their study also revealed macrocolinearity between sorghum and rice chromosomes even though the sorghum genome is ~2-fold bigger than that of rice.

6.2 Integrated Physical and Genetic Map

Towards development of an integrated physical and genetic map in sorghum, Klein et al. (2000) adopted a strategy to use arbitrary primer PCR-based amplified fragment length polymorphism (AFLP) fingerprinting of complex DNA populations resulting from pooling of low-coverage BAC libraries. The robustness of physical maps was further improved by merging probe-to-BAC hybridization data with DNA fingerprint data and using the restriction fragment matching method using pools of BAC DNA (Lin et al. 2000). This aided in resolving the chromosomal origin of BAC clones (Draye et al. 2001). Bowers et al. (2005) integrated genetic markers, BAC fingerprints, and BAC hybridization data to develop an integrated physical map of sorghum. It largely represented a genomic component containing 80 % of the single-copy genes. It showed conserved microsynteny with rice. Combining this integrated physical map, detailed genetic map (Chittenden et al. 1994; Bowers et al. 2003), and a whole-genome shotgun sequence (Gardner et al. 1981) approach, Paterson et al. (2009) released the genome sequence of sorghum cv BTx623. It was found that ~75 % of DNA in the sorghum genome was mostly heterochromatic. Euchromatic regions that represent gene-rich regions are nearly 252 Mb in size. One third of the sorghum genome is recombination rich and the rest is assumed to be recombination poor.

6.3 Molecular Architecture of the Centromere

The centromere plays the most important role in the functioning of chromosomes. Centromeres remain highly heterochromatic throughout the cell cycle and are found to possess very intriguing features. The presence of a repetitive sequence is one of the most characteristic features of the centromere across species (Melters et al. 2013). Jiang et al. (1996a, b) isolated a 745-bp repetitive DNA clone, *pSau3A9* from the sorghum BAC clone 13I16 (renamed from 52A4). Through FISH they demonstrated that this element is located in the centromeric regions of all sorghum chromosomes. Such an element could be obtained from other cereal species, including rice, maize, wheat, barley, rye, and oats. The *pSau3A9* family is associated with the centromere function of cereal chromosomes, and its absence in dicot suggests a faster divergence

of centromere-related sequences compared to the telomere-related sequences in plants. Miller et al. (1998) isolated another 823-bp repetitive DNA element from the sorghum BAC clone, 13I16, which was named *pSau3A10*. Sequence analysis showed that *pSau3A10* consists of six copies of an approximately 137-bp monomer. This six monomers are organized into three dimers. They further found that the monomers within the dimers shared 62–72 % homology and the dimers were 79–82 % homologous with each other. Long stretches of *Sau3A10* sequences are interrupted by other centromeric DNA elements. The *Sau3A10* sequence is one of the most abundant families located in sorghum centromeres. It is conserved in closely related sorghum species but not in other grass species, including rice, sugarcane, bamboo, rye, and wheat. The study suggested that the *Sau3A10* family is probably an important part of sorghum centromeres.

Gomez et al. (1998) discovered a 45-kb sorghum BAC (22B2) that differentially hybridizes to centromere regions of 10 of the 20 chromosomes of sorghum. Furthermore, hybridization of this BAC to trisomics for chromosomes E, H, and I displayed 11 signals, which provided strong evidence for the tetraploid origin of sorghum and existence of two subgenomes of five chromosomes each in the *S. bicolor*. A subclone, *pCEN38*, which is a 1047-bp insert was soon isolated from the reported BAC 22B2 (Zwick et al. 2000). This sequence produced the strongest signal near the centromeres of half of the chromosome sets as reported by Gomez et al. (1998). *pCEN38* showed narrow taxonomic distribution across 21 crop plants tested. DNA sequence analysis revealed that the *pCEN38* fragment contained three tandem dimer (280 bp) repeats of the same sequence family found in sorghum clone *pSau3A10*. Furthermore, each dimer consisted of two divergent monomers (140 bp). Sequence homology between the *pCEN38* monomers and the *SCEN* 140-bp tandem repeat family of sugarcane was striking. With these findings Zwick et al. (2000) suggested that sugarcane and sorghum share at least one ancestor harboring elements similar to *pCEN38* and *SCEN* and that each species had an ancestor in which the repetitive element was weakly present or lacking. In a recent study of candidate centromere tandem repeat sequence comparison of 282 animal and plant species did not display readily apparent conserved characteristics (Melters et al. 2013). This study showed that the closely related *Sorghum* and *Miscanthus* species have similar 137-bp repeats, but interestingly, no sequence similarity was found between the closely related *Zea* and *Sorghum* species or between *Oryza* species and *Brachypodium*, *Aegilops*, or *Hordeum*. Organization of the centromere and its significance in plant phylogeny is still an active area of research.

7 Wide Introgression Program

7.1 Wild Relatives of Sorghum: A Treasure-Trove of Valuable Traits

Wild sorghum species have greater adaptability due to continuous exposure to harsh climates, and have resistance to many biotic and abiotic stresses that affect sorghum grain production. Introgression of genes from undomesticated *Sorghum* species into cultivated sorghum is the first step towards accessing these unique unexploited genes for both biotic and abiotic stresses and agronomic traits. However, genes from wild sorghums are underutilized in crop improvement programs. Based on the extent of crossability of the wild species with a cultivated gene pool, wild species are classified into three gene pools: (i) cross-compatible wild species that produce fertile F_1 plants categorized into the *primary gene pool*; (ii) the *secondary gene pool* consisting of distant wild species that produce partially sterile hybrids; and (iii) the *tertiary gene pool* consisting of far distant wild species that have

difficulty producing F_1 hybrids (Harlan and de Wet 1972). The primary gene pool contains all three subspecies of *S. bicolor*: subsp. *arundicum*, *bicolor*, and *drumondii* (Cox 1983; de Wet et al. 1976). The two species in *Eusorghum*, *S. propinquum* and *S. halepense*, constitute the secondary gene pool. *Sorghum bicolor* and *S. propinquum* crosses are easily made, in which the meiosis is normal and progeny are fertile. However, there has been negligible use of this germplasm in applied sorghum improvement (Wooten 2001). Sorghum and *S. halepense* hybrids are possible with difficulty. Major efforts to utilize *S. halepense* are directed towards developing perennial grain crops (Piper and Kulakow 1994; Cox et al. 2002; Dweikat 2005). The tertiary gene pool contains the remaining 17 species within the four other sections. Most of the desirable traits for cultivated sorghum are contained in the tertiary gene pool (Harlan 1965), but this gene pool has remained more or less inaccessible as successful hybrids could not be recovered despite numerous efforts (Kuhlman et al. 2010). Regarding genetic improvements of sorghum, most common genetic variations from within the primary gene pool have been used.

As early as 1967, Magoon et al. observed irregular chromosome pairing in the two interspecific hybrids between the nonrhizomatous subsect, Arundinacea, the *S. propinquum* and rhizomatous subsect, Halepensia species, based on which they suggested alienating *S. propinquum* from the subsect Arundnacea. Other taxa of sorghum were crossable with cultivated types leading to formation of different races. Introgression of genes from *arundinaceum* into the early cultivated types produced the *guinea* phenotype and permitted extension of grain sorghum cultivation into forest areas (de Wet et al. 1976). Race *virgatum* crosses with *durra* sorghums; race *verticilliflorum* is widespread and crosses with cultivated types; and race *aethiopicum* crosses with cultivated races *caudatum* and *durra*. *S. halepense* or Johnsongrass, is one among 10 worst weeds of the world but it has tremendous vigor and adaptation. Several desirable traits from Johnsongrass, including resistance to greenbug and chinch bug, and adaptability to cold temperatures, can be transferred to the hybrid progeny.

Sorghum downy mildew (SDM) caused by *Peronosclerospora sorghi* Weston and Uppal (Shaw) is a serious disease of sorghum. Out of 16,000 world sorghum collections screened at ICRISAT only about 130 accessions were resistant against the SDM pathogen (Pande et al. 1997). Kamala et al. (2002) reported 36 potential sources of resistance against this fungus from wild species of sorghum. Members of the tertiary genepool, representing Chaeto-, Hetero-, Stipo-sorghum, and the Australian Parasorghum, are reported to be immune to the disease. Although in the study they found *S. versicolor*, *S. purpureo-sericeum*, and *S. nitidum* to be highly resistant, these accessions showed susceptibility in other reports (Bonde and Freytag 1979; Bonman et al. 1983). It has been found that the majority of wild Eusorghum are highly susceptible to SDM with the exception of two accessions (IS 18821 and IS 18882) and a weedy accession of *S. halepense* (IS 33712).

Striga is an important parasitic weed of sorghum, with much economic significance in Africa. *S. versicolor* was reported to be highly resistant to *striga* (Deodikar 1951). Rich et al. (2004), while screening 55 wild accessions and 20 sorghum cultivars, reported the presence of various mechanisms towards *Striga* resistance among wild species. These include low germination stimulant production, germination inhibition, and low haustorial initiation activity among others. PQ-434 and IS18803 and others were found to be potential sources of *Striga* resistance. Wild species harbor sources of resistance against insects as well. Kamala et al. (2009) identified 32 accessions from Para-, Stipo- and Hetero-sorghum with near immune response to shoot-fly (*Atherigona soccata* Rond.) under field conditions. They further identified one accession each from Heterosorghum (*S. laxiflorum*) and Chaetosorghum (*S. macrospermum*) with very low shoot-fly damage. Wild species, *S. versicolor* and *S. purpureo-sericeum,* were reported to be immune to shoot-fly infestation in

India (Bapat and Mote 1983). Sources of resistance against spotted stem borer (*Chilo partellus*) were also identified in wild species of Heterosorghum, Parasorghum, and Stiposorghum (Kamala et al. 2012). The stem borers were reported to develop on Sudan grass (Khan et al. 2000) and *S. arundinaceum* (Muyekho et al. 2005). Sources of resistance against sorghum midge (*Stenodiplosis sorghicola*) have been reported from Australian sorghum species (Harris 1976; Sharma and Franzmann 2001). *S. macrospermum* ($2n = 40$), the only member of the section Chaetosorghum, does not possess any agronomically desirable traits, but was reported to have significant resistance against sorghum midge (Franzmann and Hardy 1996; Sharma and Franzmann 2001). It is also resistant to sorghum downy mildew (Kamala et al. 2002) and has high tolerance to shoot-fly (Sharma et al. 2005). Resistance against green bug [*Schizaphis graminum* (Rondani)] biotype C and E is found in the race *virgatum* of *S. bicolor* ssp. *verticilliflorum* and in *S. halepense*, respectively (Duncan et al. 1991). Johnson- and sudangrass possess allelopathic properties by reducing the growth of weeds (Kamala et al. 2015). However, this is likely to affect growth of subsequent plants as well (Weston et al. 2013).

Australian native *Sorghum* species are reported to possess good grain starch and nutrition properties (Dillon et al. 2007b). Increased protein in the starchy endosperm of the wild species has been reported that influences the digestibility of sorghum.

7.2 Utilization of Wild Species in Sorghum Improvement and Application of *Iap* Allele

Wild species of sorghum are rich sources for various traits, however, there has been only limited exploitation of wild species in secondary and tertiary gene pools due to cross incompatibility (Rao et al. 2003). Using three-generation backcross (BC_3) lines and hybrids with *S. propinquum* Wooten (2001) attempted to improve cultivated grain sorghum with limited success. Dweikat (2005) succeeded in obtaining an interspecific hybrid with $2n = 20$ chromosomes between a nuclear male sterile sorghum and *S. halepense*. The hybrid plant was fertile and segregated normally in the F_2 generation. Hadley and Mahan (1956) derived F_1 progeny from kafir Johnsongrass, *S. halepense*, which were triploids. However, backcross progeny resulted in 20 chromosome plants with large morphological variation.

Huelgas et al. (1996) pollinated *S. bicolor* with four wild species from the tertiary gene pool —*S. macrospermum*, *S. timorense, S. matarankense*. and *S. stipoideum*—without success. Hybridization with an Australian species, *S. macrospermum* and *S. bicolor*, demonstrated partial compatibility among themselves (Kuhlman 2007). Hodnett et al. (2005) determined that pollen–pistil incompatibilities are the main cause of reproductive isolation between sorghum and the tertiary gene pool. Incompatible reaction leading to no pollen tube growth of wild species in the stigma and style leads to unsuccessful fertilization (Dhillon et al. 2007a, b).

Laurie and Bennett (1989) screened *S. bicolor* accessions using maize pollens. They discovered a sorghum accession (Nr481) from China in which the maize pollen germinated and pollen tubes grew into the styles of some sorghum plants. It was found that a recessive allele, *iap* (*inhibitor of alien pollen*), when present in the pistillate sorghum plant in the homozygous state, allows the maize pollen tubes to grow through the sorghum pistils, whereas the dominant allele *Iap* did not. The authors demonstrated that the recessive *iap* allele circumvents pollen–pistil incompatibilities and permits hybrids to be made between *S. bicolor* and species of the tertiary gene pool. Using this allele, hybrids were obtained between *S. bicolor* and *S. macrospermum* (Price et al. 2005a). The hybrids were phenotypically intermediate between the parents. These hybrids revealed moderate levels of allosyndetic recombination (2.6 II per PMC), indicating that introgression through genetic recombination is possible. The interspecific hybrids obtained by Price et al. (2005a) were derived by crossing CMS sorghum lines with

pollens from *S. macrospermum*. The efficiency of hybrid production was improved dramatically with the use of a sorghum genotype homozygous for the *iap* allele. Using a similar strategy Price et al. (2006) recovered hybrids between sorghum and *S. macrospermum*, *S. nitidum*, and *S. angustum*, though only hybrids with *S. macrospermum* survived till maturity. Promising sorghum lines with fodder attributes were developed through interspecific hybridization between cultivated sorghum CO 27 ($2n = 20$) and *S. halepense* ($2n = 40$) (Raveendran et al. 2000).

Discovery of the *iap* mutant and its transfer in homozygous condition to an improved parental line has opened up the introduction of variation from incompatible sources into cultivated sorghum. Identification of the *iap* allele in germplasm and transfer of the allele to a cultivated background was carried out by Mullet et al. (2010). Kuhlman and Rooney (2011) transferred the *iap* allele and *ms3* into an agronomically superior germplasm line, Tx3361. This new line was released by the Texas Agrilife Research sorghum breeding program in January 2010 (Reg. No. GP-661, PI 659454). Bartek (2010) and Bartek et al. (2012) recorded high levels of pollen tube growth into the ovaries of this line even when pollens from *Pennisetum ciliare* and four accessions of maize were used. This germplasm is unique because it lacks a key factor that represses alien pollen growth on the stigma. This line is restricted for use in breeding programs through patents (Publication No. EP2312935 A1). Lower humidity was reported to maximize maize pollen adhesion and germination on the stigmas of Tx3361 (Gill et al. 2014). At 45 % humidity multiple maize pollen tubes were observed in the sorghum style and ovary. Thus, intergeneric crosses with *iap* sorghum should be performed at low humidity levels. Using this genetic stock as a female parent, interspecific crosses with wild species of sorghum and intergeneric crosses with sugarcane were obtained (Hodnett et al. 2005, 2010; Price et al. 2006; Kuhlman et al. 2008, 2010). The intergeneric hybrid between sorghum and sugarcane was called Sorcane. Introgression of wild genes from an Australian species *S. macrospermum* was successful after repeated backcrosses of the progeny (Kuhlman et al. 2010). In BC_2F_1 relatively stable lines with alien addition and substitution were obtained. Interspecific hybrids between cultivated sorghum (*iap/iap*) and three *S. halepense* accessions were successfully made by Whitmire (2011). The *Iap* gene is localized to a 48-kb region on the short arm of chromosome 2 (Gill et al. 2014). This has opened up the possibility of transfer of this allele to other germplasm.

7.3 Sorghum × Sugarcane Crosses

Crosses between sorghum and sugarcane were taken up to introduce resistance to shoot-fly in sorghum. Intergeneric hybrids between the sorghum male sterile line, ICSA56, and *Saccharum officinarum* (IJ76-316) were obtained and the hybridity was demonstrated through cytological evidence (Nair 1999). Four out of five hybrid seedlings obtained from 3670 sorghum florets could survive. The number of hybrids obtained was higher when sugarcane was used as the female parent and lower when sorghum was the female parent. These hybrids more resembled *S. officinarum* in gross morphology with a few sorghum characters such as soft, narrow, and drooping leaves. The somatic chromosome number of the hybrids ranged from 62 to 66. Sorghum × sugarcane hybrids in general lacked vigor and were slow in growth and establishment. Though the hybrids were phenotypically close to the sugarcane parent, random amplified polymorphic DNA (RAPD) markers could precisely identify the true hybridity (Nair et al. 2006). These hybrids did not set seeds at Coimbatore, India (where sugarcane sets seed) or at Hyderabad, India. At the ICAR-Indian Institute of Millets Research, Hyderabad, India, these are maintained vegetatively. They flower during the winter season in November and December. The panicles resemble sugarcane. Pollen fertility in these florets was 10–15 %.

8 Male and Female Sterility

8.1 Male Sterility

Cytoplasmic-genic male sterility, a potential system for hybrid seed production, results from the interaction between the cytoplasm and nuclear genetic factors. Commercial hybrid development and cultivation in sorghum became possible with the discovery of cytoplasmic-nuclear male sterility (CMS) designated as A1 (milo) developed from the progeny of a cross between cultivars, dwarf yellow sooner milo (female) and Texas blackhull kafir (male; Stephens and Holland 1954). From then onwards, CMS-based hybrids have been developed and commercialized worldwide. However, these are principally A1 CMS system-based (Reddy et al. 2007) with infrequent establishment of A2-based hybrids (Qing Shan et al. 2000). Subsequently several non-milo CMS systems, namely A2, A3, A4, IndianA4 (A4 M, A4VZM, A4G), A5, A6, 9E, and KS were reported in sorghum (Webster and Singh 1964; Ross and Hackerott 1972; Schertz and Ritchey 1978; Quinby 1981; Worstell et al. 1984; Schertz 1994).

Several genes have been reported for male sterility in sorghum resulting in failure of pollen production or pollen abortion. Three independent genes *ms1*, *ms2*, and *ms3* were identified and described by Ayyangar and Ponniaya (1937), Stephens (1937), and Webster (1965). The pollens are nonfunctional but anthers are normal in these male sterile plants. Ayyangar (1942) reported male sterility with the absence of pollen. A male sterility source with the absence of anthers was reported by Karper and Stephens (1936). Barabas (1962) in his study used mutagenic treatment to induce male sterility and the resultant plant showed very small anthers without pollen inside. Singh and Hadley (1961) attempted to study the reason for pollen abortion in sorghum. They revealed that the meiosis towards development of anthers is normal in both fertile and sterile plants. However, the post-meiotic abnormal tapetum behavior in the MS plant caused pollen abortion. The tapetum of sterile plants was thicker especially at later stages and varied greatly from the fertile plants. Damon (1961) and Warmke and Overman (1972a, b) attributed this to the destruction and regeneration of the callose walls of the microsporocytes in cytoplasmic male sterile plants. Erichsen and Ross (1963) also observed similar irregularities in colchicine-induced male sterile mutants. They further described abnormal chromosome numbers in male sterile plants at microsporogenesis resulting from failure of breakdown of the cell walls of microsporocytes during meiosis prophase I, followed by fusion of their cytoplasm.

8.2 Female Sterility

Female sterility in sorghum was first reported by Casady et al. (1960) resulting in the development of rudimentary stigma, ovary, and style. The sterility was reported to be governed by two genes (*Fs1* and *Fs2*) with dominant complementary interaction. However, male fertility was not affected in the presence of these genes. The sterility was governed by the dosage of alleles. Heterozygous plants at two loci (*Fs1fs1Fs2fs2*) resulted in female sterility, whereas plants with three heterozygous loci resulted in dwarf plants with no heading. A third locus, *Fs3* was reported by Malm (1967) also governing female sterility.

8.3 Fertility Restoration

The inheritance of fertility restoration is dependent on the type of cytoplasm and nuclear genes. A single gene is responsible for fertility restoration in A1 cytoplasm but is controlled by two or more genes when the same nuclear genotype interacts with a different cytoplasm (Schertz

1994). Ashok Kumar et al. (2008) reviewed different genes restoring fertility in different CMS backgrounds. Progeny segregating with A1 cytoplasm in the F_2 generation showed that a single gene was responsible for fertility restoration in A1 cytoplasm (Murty 1986; Murthy and Gangadhar 1990). Other results on A1 cytoplasm have described that one or two genes (Qian 1990) or even up to three genes (Lonkar and Borikar 1994) are involved in controlling fertility restoration. Murthy (1986) described at least three genes controlling the fertility restoration of A_2 cytoplasm. Lonkar and Borikar (1994) described that two to four genes are required, but three genes were optimal for the fertility restoration in backcross generations in A2 cytoplasm. In another study, Murthy and Gangadhar (1990) concluded that two complementary genes are required for fertility restoration in A2 cytoplasm. ICRISAT studies showed that the recovery of fertile plants' frequency were less on A3 than A4, A2, and A1 indicating a higher number of genes are involved in governing fertility restoration on A3 than the other CMS systems (Reddy and Prasad Rao 1992).

9 Future Prospects

Undomesticated wild species of sorghum are found to be the repository for resistance to biotic and abiotic stresses and these are underexploited in sorghum breeding programs. Breaking the pre-fertilization barriers and introducing the wild traits through backcrossing can open a new avenue to increasing sorghum production. With the genome sequence available in sorghum, and a large number of genotypes being resequenced, it is high time that promising wild species with proven traits of importance are to be sequenced so that genes or alleles can be discovered and deployed in breeding programs. With the advent of molecular genomics, conventional cytogenetic tools might have become redundant but are needed to bring together the plethora of cytological information generated over this period with the genomic information being generated at a rapid pace.

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