Handbook of Plant Breeding

Von Mark V. Cruz
David A. Dierig *Editors*

Industrial Crops

Breeding for BioEnergy and Bioproducts

Springer

Industrial Crops - Breeding for BioEnergy and Bioproducts

HANDBOOK OF PLANT BREEDING

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Editors

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Foreword

The last decade of plant breeding truly has been transformational in creating a unified global effort in several key areas, with bio-energy close to the top of that list. Finding alternative energy sources has become a priority for economies facing urgent energy policy decisions. These chapters are very well timed to highlight some of the key breeding challenges. Feedstock development for both fuel and bio-based products is at the forefront of this discussion, which of course comes with the challenge of prioritizing to meet projected needs over the next two decades.

There are numerous political and social discussions surrounding the development of bio-products and bioenergy economies, and whether or not adequate answers emerge for these, the scientific components are important for successful economic progress. Many of the challenges on the plant breeding and crop production side of developing a bio-economy intersects with food production challenges, and it is not the intention of these chapters to make judgments about where those lines intersect, but to focus on a scientific solution. Entering into the discussion also is the need to reduce the carbon footprints, which can be partially solved by developing plants less dependent on energy-intensive fertilizers and fungicides to produce higher outputs of cellulose. Plant breeding strategies will depend on type of feedstock, as well as size of markets, desired availability and strategic placement of processing and distribution facilities for best accessibility. Breeding issues for cellulosic ethanol will be different from biodiesel needs, and smaller local energy demands will bring different breeding challenges to the table. These issues will determine the types of feed stocks to be developed.

I believe a certain level of harmony exists in the food vs. fuel debate, if the discussion leans more towards effective breeding and development of integrated crop production systems. In this regard, research must take into account the critical emerging themes that are now dictating the need for more integrated systems approaches, including environmental friendliness, sustainability and regulatory requirements for specific needs of the production system. There is a real need to reduce agricultural inputs, but this must be done with more sustainable methods; plant breeding is well positioned to lead this charge. The next decade will see the private sector working in better harmony with the public sector to shift more rapidly towards systems approaches to enhance the assisting technologies driving them to higher yields. In concert with advances in breeding, we will see integrated farming systems combined with new biological products from RNAi technology, biotechnology, and novel agricultural chemicals to produce innovative advances and sustainable yield gains.

Government assistance is an important requirement for successful development and implementation of new initiatives. The US Federal government is actively promoting the development of ethanol from cellulosic feedstocks. The US Department of Energy (DOE) supports research to develop better cellulose hydrolysis enzymes and ethanol-fermenting organisms, as well as ethanol production from cellulosic biomass. The 2008 farm bill allowed for the commercialization of advanced biofuels, including cellulosic ethanol. The Food, Conservation, and Energy Act of 2008 provided grants covering up to 30 % of the cost of developing and building demonstration-scale bio-refineries for producing "advanced biofuels," which includes all fuels that are not produced from corn kernel starch. It provided loan guarantees of up to $250 million for building commercial-scale biorefineries to produce advanced biofuels.

The Renewable Fuels Standard, which is a part of the 2007 Energy Independence and Security Act, stipulated an increase in biofuels production to 36 billion US gallons a year by 2022. In January 2011, the USDA approved $405 million in loan guarantees through the 2008 Farm Bill to support the commercialization of cellulosic ethanol at three different facilities to develop a combined 73 million US gallons per year production capacity. The USDA also allocated payments to expand the production of advanced biofuels. In July 2011, DOE granted $105 million in loan guarantees for a commercial-scale plant to be built in Iowa.

Contributions of plant breeding to the renewable energy strategy should be aimed at improving energy efficiency and provide economic growth for as many rural communities as possible. In this discussion, we need to recognize the importance of total cost of production (from developing and growing feed stocks all the way to market costs), reduction of greenhouse emissions, and conservation of natural resources. The crops highlighted here in each of the categories (biodiesel, sugar, starch, cellulosic crops) are sensible targets to develop a national strategy which accommodates many rural communities. For biodiesel, adequate availability of feedstocks is an important issue, as is high sugar, starch, and cellulose production for the "non-oil" crops. Sustainable yield and efficient digestibility are important for the native grasses to maintain consistent biomass conversion. Sugarcane varieties must have high yield and high sugar content, but at the same time need to have cold tolerance and adequate disease packages to maintain stability across wider geographical ranges. Sugar beet has seen its share of challenges with emerging and endemic diseases and, although current breeding programs have saved and earned the industry billions of dollars, must be improved for sugar content and processing quality to sustain both sugar and bioenergy industries.

There are many skeptics regarding the potential success for a bio-energy and bioproduct economy. Many countries, however, currently either have fully operational, or "soon to be on line," biofuels plants. GraalBio in Brazil for example built a facility estimated to produce 82 million liters of cellulosic ethanol per year. Another success story comes from Denmark, where Inbicon's bioethanol plant, with a capacity of 1.4 million gallons annually, has been operating since 2009. An E85 blend of 95 % gasoline and 5 % cellulosic ethanol from wheat straw has been available since 2010 at many filling stations across Denmark.

In the USA, there has been an increasing effort to commercialize cellulosic ethanol during the last 5 years, concentrating on conversion of cellulose into fuel. About a dozen cellulosic ethanol plants in different states are currently either operating or soon to open. Companies, such as Iogen, Poet, and Abengoa, are building, or completed, refineries to process biomass into ethanol. Other companies, such as Diversa, Novozymes, and Dyadic, are producing enzymes to enable cellulosic ethanol conversion. These options will enable shifting from using food crops feedstocks to waste residues, native grasses, and other non-food plants. The first commercial-scale plants to produce cellulosic biofuels began operating in 2013. Among these, multiple pathways for the conversion of different biofuel feedstocks are being used. These refineries are currently expensive to operate, but in the next 5 years the cost of the conversion technologies at commercial scale will predictably become lower.

It is important that the plant breeding research be coordinated and linked with the policy, education and outreach efforts for effective communication with farmers, processors and other renewable energy efforts in the rural community that are involved in feedstock production and value-chain logistics. These efforts must be in sync with feedstock conversion and commercialization strategies. As we go forth in this process, we must acknowledge the role that renewable energy from plant biomass will play in this grand challenge. Integration with other sources in the renewable electricity arena, such as solar, geothermal, wind, and anaerobic digestion will be essential to a sustainable system.

For a plant breeding strategy to be effective, improvement or development of new industrial crops must take into account the challenges of climate change as it relates to the entire agricultural system. Changing temperatures, precipitation and carbon dioxide concentrations generally are thought of as the most major concerns, but equally important are the interactions of new varieties with other inhabitants of the ecosystem, such as insects, weeds, and pathogens that may cause diseases and have significant soil and plant impacts. Breeding crops resilient to these components, while at the same time maintaining the quality components necessary for bioenergy and bioproduct components, though challenging, are essential now and in the future.

It is well known that temperature ranges for optimal biomass production and effects of CO_2 concentrations on crop growth vary with species, especially based on photosynthetic pathways. The greater sensitivity of C3 plants to increased CO_2 levels and effects on water-use efficiency, though not well studied, is not unknown. Effects of ozone fluctuations may impact effects of CO_2 concentrations and must be considered, as breeders develop new selection tools. Field-based phenotyping of new varieties will be essential, and the use of accurate crop models will be important to assist effective genetic manipulations. The well-known strategy of breeding new plant varieties resilient to changing agricultural systems that is evident in these chapters is a sustainable way to adapt the breeding component of production agriculture to climate change. This strategy serves to temper the negative economic implications of displacing a potentially profitable crop from its original production system. In addition, new varieties usually have the advantage of higher productivity.

The bottom line is that breeders of crops for bioenergy and bioproducts must be even more mindful of the entire agricultural system than ever before, and must collaborate with other components, since it takes a strong adaptive capacity at all levels to highlight the plant breeding benefits. If we consider that the entire agricultural system must be made resilient to climate change, it is then evident that breeders will continue to be held responsible for dealing with the eminent evolution of resistance of pests to genetically modified crops and new chemistries used to maintain economic stability. Breeders must be involved in managing the newly created biodiversity at both field and landscape levels through breeding to address environmental, pest and pathogen issues.

Since feedstock development is of major importance in a successful future for bioenergy, and since bioproducts are deeply engrained in this system, all participants of the system are essential partners, including farmers, ranchers, landowners, crushers, fuel producers, etc. Law-makers and policy makers worldwide are key to successful implementation. Providers of energy and consumers at various levels must engage and communicate effectively to develop and maintain a successful bioenergy and bioproduct future. The top players at all levels should not forget the huge role that plant breeding has in maintaining a viable bio-economy.

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Preface

The scope of the definition of industrial crops undoubtedly has changed. The traditional distinction between food crops and industrial crops have blurred with the emerging opportunities and additional uses of food crop species. Among these uses include being as source of raw materials for non-food products such as fibers, energy, industrial lubricants and starches, resins, plastics, cosmetics, and many other important compounds that are used for manufacturing. This handbook presents advancements in research and breeding for non-food applications and associated commercialization efforts in a selected set of crop species.

The idea of this book volume was initially brought to us by Hannah Smith of Springer Media, and it is a timely suggestion due to rapid advancements in plant science technologies that are important in accelerating developments in crop improvement and the changing pace of agricultural materials being tapped as source of industrial raw materials. Among these technologies also include advances in screening methodologies to look at genotypic and phenotypic variation and the greater inclusion of molecular markers and biotechnology applications in industrial crop breeding programs. Some crops presented in this volume may also have additional information in other handbook volumes in this Springer series and we encourage the readers to consult them.

As part of *The Handbook of Plant Breeding* series, we hope that the collection of papers in this volume will be useful to plant breeders, biologists, students, and other stakeholders of these important species and promising new crops. We attempted to gather developments in these species globally and we have organized this volume by categorizing crops according to their primary non-food use, whether for biodiesel, bioenergy, or bioproduct. A separate section was also assembled to present current issues and emerging technologies in bioenergy and biofuels, providing a situation overview of advances in biofuel technologies, economic feasibility, and the perceived effects of public policy mechanisms at the time this volume was written.

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Fort Collins, CO, USA

David A. Dierig
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Chapter 1
Sweet Sorghum: Breeding and Bioproducts

P. Srinivasa Rao, C. Ganesh Kumar, R.S. Prakasham, A. Uma Rao, and Belum V.S. Reddy

Abstract Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important cereal crop and is the dietary staple of more than 500 million people in over 90 countries, primarily in the developing world. However, sweet sorghum which is similar to grain sorghum except for accumulation of stalk sugars, is considered as a potential energy crop without impacting the food security of millions. Further, the sorghum stover is considered to be a potential lignocellulosic biofuel feedstock. Being a C4 plant, it has high photosynthetic rate, and several mechanisms are known to confer resilience that help produce higher yield in varied environmental conditions. This chapter not only discusses different breeding methodologies for improving candidate sugar and biomass traits but also the possible utilization of this smart feedstock for diverse biochemicals (lactic acid, xylitol, glycerol, etc.) and bioproducts (nanomaterials, anticancer and microbial compounds, adhesives, polymers, antidiabetic compounds, etc.) development.

Keywords Sweet sorghum • Biofuel • Stalk sugar • Genetic variability • Biochemicals • Bioproducts

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Introduction

The current scenario of declining fossil fuel reserves along with increased concerns on environment pollution and climate change is fundamentally responsible for greater interest in renewable energy sources globally. Sustainable availability of raw material for any economic and constant product production is one of the essential requirements. This has become more appropriate for the constant consumption products like biofuels, as the entire world economy is dependent on the availability of fuel resources. Interest in sweet sorghum (*Sorghum bicolor* (L.) Moench) in semiarid and rain-fed environments is increasing because of the multiple uses of this novel feedstock either for production of biofuels from stalk juice or for power generation from bagasse or for utilization in dairy industry as nutrient rich and easily digestible fodder [1, 2]. Additionally, sweet sorghum biomass is used for fiber, paper, syrup, and biopolymers. Sweet sorghum being a C4 crop has wide environmental adaptation, rapid growth, high grain and biomass productivity, suitability for marginal soils, and high concentrations of the easily fermentable sugars like sucrose, glucose, and fructose [3]. Drought and salinity are widely prevalent abiotic stresses that significantly lower the yields of various crops, and their frequency of occurrence is expected to increase due to climate change. Sweet sorghum grows in marginal areas because of its high tolerance to saline and drought conditions. Sweet sorghum has higher water-use efficiency than other summer crops under both well-watered and water-stressed conditions [4–6]. From the agronomic point of view, sweet sorghum is more environmentally friendly than maize because of its relatively low nitrogen needs and water requirements. It was reported that sorghum requires 310 kg of water to produce 1 kg of biomass, while maize consumes 23 % more water, i.e., 370 kg to produce same quantity of biomass [7]. Besides biofuel production from sweet sorghum, a plethora of food products such as beverage, cookies, syrup, sweets, chocolates [8], and bioproducts like biopolymer resin can be produced [9]. However, the commercialization of this smart feedstock primarily hinges on the national biofuel policy of respective countries besides identification of productive cultivars adapted to the targeted region owing to significant genotype $\times$ environment interaction [10].

This chapter will focus on genetic enhancement of sweet sorghum through conventional plant breeding and the production of various bioproducts based on this novel feedstock.

Food: Fuel Trade Off

It is often stated that sweet sorghum cultivars do not produce grain yield or the grain yield is very less vis-a-vis that of grain sorghum. Studies at the International Crops Research Institute for the Semiarid Tropics (ICRISAT) showed that sweet sorghum hybrids had higher stem sugar yield (11 %) and higher grain yield (5 %) compared to grain sorghum types, while sweet sorghum varieties had 54 % higher sugar yield and 9 % lower grain yield compared to non-sweet stalk varieties in the rainy season. On the other hand, both sweet sorghum hybrids and varieties had higher stalk sugar yields (50 and 89 %) and lower grain yields (25 and 2 %) in the post-rainy season. Thus, there is little trade-off between grain and stalk sugar yields in the sweet sorghum hybrids in the rainy season, while the trade-off is less in varieties in the post-rainy season [2, 3].

This is further corroborated by other published work [11] showing that there is significant soluble sugar content in the stems (79–94 %) during post-anthesis period, with the hybrids exhibiting significantly high soluble sugar content over varieties with same maturity period and effects of year, harvest time, and genotype on calculated ethanol yield (CEY) are highly significant. The experimental data on the relationship between stalk sugar traits and grain yield shows that the regression coefficient of stalk sugar yield on grain yield is not significant, thereby indicating that the grain yield is not affected when selection is done for stalk sugar yield. Hence, selection programs can aim to improve both the traits simultaneously.

Climate Change

Global warming due to climate change will affect grain and stover yields in crops, more so in tropical Africa and Asia where sorghum is a major food crop. Most climate change models predict rise in air and soil temperatures and sea levels and increased frequencies of extreme weather events leading to unprecedented changes in agricultural production in the years to come. In the Intergovernmental Panel on Climate Change (IPCC), climate models predict an increase in global average surface temperature of between 1.4 and 5.8 °C from 2001 to 2100, the range depending largely on the scale of fossil fuel burning between now and then and on the different models used. At the lower range of temperature rise (1–3 °C), global food production might actually increase, but above this range, it would probably decrease [12]. However, broad trends will be overshadowed by local differences, as the impacts of climate change are likely to be highly spatially variable. In general, the sorghum maturity period of current varieties decreases with increased temperatures. Climate change effects in terms of high temperatures and erratic rainfall may drastically reduce sorghum yields in South Asia, Southern Africa, and West Africa [13]. Climate change will cause changes in the length of the growing period (LGP) in some regions. Cooper et al. [13] showed that the extent of global semiarid tropical (SAT) areas will be changed through (1) SAT areas being "lost" from their driest margins and become arid zones due to LGPs becoming too short or (2) SAT areas being "gained" on their wetter margins from subhumid regions through the reduction in the current LGPs in those zones. It means sorghum could be grown in new areas of the currently humid tropics where sorghum is not grown at present. Therefore, development of crop cultivars with a maturity duration that suits the prevailing LGP will be one of the best options to cope with changes in LGP. ICRISAT and Indian National Agricultural Research System (NARS) have developed a wide variety of sweet sorghum female parental lines and restorers besides varieties with altered LGP that can play pivotal role in achieving the above said option.

Taxonomy

Sorghum was first described by Linnaeus in 1753 under the name *Holcus*. In 1974, Moench distinguished the genus *Sorghum* from genus *Holcus* [14, 15]. Subsequently, several authors have discussed the systematics, origin, and evolution of sorghum since Linnaeus [16–19]. Sorghum is classified under the family *Poaceae*, tribe *Andropogoneae*, subtribe *Sorghinae*, and genus *Sorghum.* The genus was further divided [20] into five subgenera: *Sorghum*, *Chaetosorghum, Heterosorghum, Parasorghum*, and *Stiposorghum*. Variation within these five subgenera except the subgenera *Sorghum* has been described [14]. *Sorghum bicolor* subsp. *bicolor* contains all of the cultivated sorghums. Harlan and deWet [20] have developed a simplified classification of cultivated sorghum which proved to be of real practical utility for sorghum researchers. They classified *Sorghum bicolor* (L.) Moench, subsp. *bicolor* into five basic and ten hybrid races as depicted in Table 1.1. The 15 races of cultivated sorghum can be identified by mature spikelets alone, although head type is sometimes helpful. The Biodiversity International [formerly International Plant Genetic Resources Institute (IPGRI)] advisory committee on sorghum and millet germplasm has accepted and recommended this classification to be used in describing sorghum accessions.

Table 1.1 Classification of *Sorghum bicolor* (L.) Moench. subsp. *bicolor*

Basic races	Intermediate/hybrid races
(1) Race bicolor (B)	(6) Race *guinea-bicolor* (GB)
(2) Race guinea (G)	(7) Race *caudatum-bicolor* (CB)
(3) Race caudatum (C)	(8) Race *kafir-bicolor* (KB)
(4) Race kafir (K)	(9) Race *durra-bicolor* (DB)
(5) Race durra (D)	(10) Race *guinea-caudatum* (GC)
	(11) Race *guinea-kafir* (GK)
	(12) Race *guinea-durra* (GD)
	(13) Race *kafir-caudatum* (KC)
	(14) Race *durra-caudatum* (DC)
	(15) Race *kafir-durra* (KD)

Sweet Sorghum Distribution and Climatic Conditions

In simple terms, wherever sorghum is currently grown, sweet sorghum can also be cultivated commercially. Thousands of hectares are grown with sweet sorghum for biofuels production in Brazil, China, and the USA, while in the Philippines, it is grown for vinegar synthesis, and considerable areas in India, the USA, Indonesia, West Asia, and North Africa go for fodder production. In Western and Southern Africa, it is widely used for chewing purposes and local beverage production. This feedstock is well adapted to the SAT and is one of the most efficient dryland crops in converting atmospheric CO_2 into sugar [3]. The crop can be grown in a wide range of climatic conditions as given below.

Latitude

Sweet sorghum can be grown between 40°N and 40°S latitude on either side of the equator.

Altitude

Sorghum can be found at elevations between sea level and 1,500 m asl. Most East African sorghum is grown between the altitudes of 900–1,500 m, and cold-tolerant varieties are grown between 1,600 and 2,500 m in Mexico.

Environmental Conditions

Sweet sorghum can be grown in the temperature range of 12–37 °C. The optimum temperatures for growth and photosynthesis are 32–34 °C, day length is 10–14 h, optimum rainfall 550–800 mm, and relative humidity between 15 and 50 %. However, the lower the diurnal and nocturnal temperature differential, the less stalk sugar accumulation observed is in tropical sweet sorghums.

Soil Conditions

Alfisols (red) or vertisols (black clay loamy) with pH 6.5–7.5, organic matter >0.6 %, soil depth >80 cm, soil bulk density <1.4 gcc, water holding capacity

>50 % field capacity, N $\geq$ 260 kg ha^{-1} (available), P $\geq$ 12 kg ha^{-1} (available), and K $\geq$ 120 kg ha^{-1} (available) are optimal soil conditions for sorghum growth.

Water

While sorghum will survive with a supply of less than 300 mm over the season of 100 days, sweet sorghum responds favorably with additional rainfall or irrigation water. Typically, sweet sorghum needs between 500 and 1,000 mm of water (rain and/or irrigation) to achieve good yields, i.e., 50–100 t ha^{-1} total aboveground biomass (fresh weight). The great advantage of this feedstock is that it can become dormant, especially in the vegetative phase, under adverse conditions and can resume growth after relatively severe drought. Early drought stops growth before panicle initiation and the plant remains vegetative; it will resume leaf production and flowering when conditions become favorable for growth again. Mid-season drought stops leaf development. Although this crop is susceptible to sustained flooding particularly at early vegetative phase, it tolerates water logging better than maize and sugarbeet [2].

Radiation

Being a C4 plant, sweet sorghum has high radiation use efficiency (RUE) (about 1.3–1.7 g MJ^{-1}). It has been shown that taller sorghum types possess higher RUE, because of a better light penetration in the leaf canopy.

Photoperiodism

Most hybrids of sweet sorghum are relatively less photoperiod-sensitive vis-a-vis purelines. Traditional farmers, particularly in West Africa, use photoperiod-sensitive varieties. With photoperiod-sensitive types, flowering and grain maturity occurs almost during the same calendar days regardless of planting date, so that even with delayed sowing, plants mature before soil moisture is depleted at the end of rainy season.

Reproductive Biology

Breeding procedures that are used with a particular crop species are determined by its mode of reproduction. Understanding the details of phenology, i.e., floral biology, pollination, fertilization, and seed development in a crop, makes it possible to develop orderly and efficient breeding procedures.

Panicle Initiation

Sorghum blooming is hastened by short days and long nights. However, varieties differ in their photoperiod sensitivity [21]. Tropical sweet sorghum varieties initiate the reproductive stage when day lengths return to 12 h. Usually, the floral initial is 15–30 cm above the ground when the plants are about 50–75 cm tall [22]. Floral initiation marks the end of the vegetative growth due to meristematic activity. The time required for transformation from the vegetative apex to reproductive apex is largely influenced by genetic characteristics and the environment (photoperiod and temperature). The grand period of growth in sorghum follows the formation of a floral bud and consists largely of cell enlargement. Hybrids take less time to reach panicle initiation and are relatively less influenced by photoperiod and temperature [2, 3].

Panicle Emergence

During the period of rapid cell elongation, floral initials develop into an inflorescence. About 6–10 days before flowering, the boot will form as a bulge in the sheath of the flag leaf. This will occur, in a variety that flowers in 60–65 days, about 55 days from germination. Sorghum usually flowers in 55 to more than 70 days in warm climates, but flowering may range from 30 to more than 100 days. These observations are valid for tropical sweet sorghums, while temperate sorghums that mature in 5 months take 20–30 days longer for panicle emergence [2, 3].

Panicle Structure

The inflorescence is a raceme, which consists of one or several spikelets. It may be short, compact, loose, or open and composed of a central axis that bears whorls of primary branches on every node. The spikelet usually occurs in pairs, one being sessile and the second borne on a short pedicel, except the terminal sessile spikelet, which is accompanied by two pediceled spikelets. The first and second glumes of every spikelet enclose two florets: the lower one is sterile and is represented by a lemma and the upper fertile floret has a lemma and palea. Two lodicules are placed on either side of the ovary at its base. Androecium consists of one whorl of three stamens. The anthers are attached at the base of the ovule by a very fine filament and are versatile and yellowish. Gynoecium is centrally placed and consists of two pistils with one ovule from which two feathery stigmas protrude. The sessile spikelet contains a perfect flower. It varies in shape from lanceolate to almost rotund and ovate and is sometimes depressed in the middle. The pediceled spikelets, usually lanceolate in shape and possess only anthers, occasionally have a rudimentary ovary and empty glumes [9].

Anthesis and Pollination

Anthesis starts after panicle emergence from the boot leaf. Flowers begin to open 2 days after full emergence of the panicle. Floret opening or anthesis is achieved by swelling of the lodicules and is followed by the exertion of anthers on long filaments and of stigmas between the lemma and palea. Sorghum head begins to flower at its tip and flowers successively downward over a 4- or 5-day period. Flowering takes place first in the sessile spikelets from top to bottom of the inflorescence. It takes about 6 days for completion of anthesis in the panicle with maximum flowering at 3 or 4 days after anthesis begins. Flowering proceeds downwards to the base in a horizontal plane on the panicle. When flowering of the sessile spikelets is halfway down the panicle, pedicellate spikelets start to open at the top of the panicle and proceed downwards [22]. Anthesis takes place during the morning hours and frequently occurs just before or just after sunrise, but may be delayed on cloudy damp mornings. It normally starts around midnight and proceeds up to 10:00 AM depending on the cultivar, location, and weather. Maximum flowering is observed between 6:00 and 8:00 AM. The anthers dehisce when they are dry and pollen is blown into air. The pollen remains viable several hours after shedding. The flowers remain open for 30–90 min. Dehiscence of the anthers for pollen diffusion takes place through the apical pore. The pollen drifts to the stigma, where it germinates; the pollen tube, with two nuclei, grows down the style, to fertilize the egg and form a *2n* nucleus [2, 3, 19].

Cytoplasmic male sterility has been found in sorghum (A_1-A_4 systems) and has made possible the development of a hybrid seed industry. A good male-sterile plant will not develop anthers, but in some instances dark-colored shriveled anthers with no viable pollen will appear. Partially fertile heads are also observed, and although the anthers frequently have viable pollen, the quantity is less than in normal plants. There are two types of male sterility, viz., (a) genetic male sterility (GMS) and (b) cytoplasmic nuclear male sterility (CMS), both widely used in sorghum improvement programs [4].

Table 1.2 Genetic male sterility genes, their designated symbols, and mechanism of sterility

Gene symbol	Mechanism	Reference
ms_1	Normal pollen is dominant over aborted or empty pollen cells	[25]
ms_2	-do-	[26]
ms_3	-do-	[27]
ms_4	Empty pollen cells	[28]
ms_5	Aborted pollen	[29]
ms_6	Micro anthers without pollen	[29]
ms_7	Empty pollen cells	[30]
al	Antherless stamens	[31]

Genetic Male Sterility

Genetic male sterility is expressed in sorghum in many ways. Several sources of male sterility are identified. In all the cases, it was shown that a recessive allele in homozygous condition designated with a series of alleles, ms_1, ms_2, ms_3, ms_4, ms_5, ms_6, ms_7, and *al*, confers male sterility [19, 23, 24]. The genetic male sterility genes are represented in Table 1.2.

Cytoplasmic Nuclear Male sterility

The discovery of the male sterility resulting from the interaction of cytoplasmic and nuclear genes [32] laid the foundation and revolutionized the development of hybrid cultivar and hybrid seed production technology. The milo cytoplasm was from *durra* race, which induced male sterility in the nuclear background of *kafir* race, and this is designated as A_1 cytoplasm. Since then, several sources and types of male-sterile-inducing cytoplasms have been discovered and reported. In all these cytoplasms, recessive genes in the nucleus and sterile cytoplasm induce male sterility. These male-sterile cytoplasms have been differentiated based on the inheritance patterns of their fertility restoration. The inheritance of fertility restoration is not clear, as it is dependent on the specific cytoplasm and nuclear combinations. Fertility restoration is controlled by single gene in some combinations (e.g., A_1) but is controlled by two or more genes when the same nuclear genotype interacts with a different cytoplasm [33]. Although diverse male-sterile cytoplasms have been identified, by far, only the milo cytoplasmic male sterility system is widely used because the hybrids based on this cytoplasm produce sufficient heterosis (20–30 %) over the best available pure lines in sweet sorghum. In spite of A_2 cytoplasm being as good as A_1 cytoplasm for mean performance as well as heterosis for economic traits such as stalk yield, juice yield, grain yield, days to 50 % flowering, and plant height, it is not popular as the anthers in A_2 male steriles, unlike the A_1 male steriles, mimic the fertile or maintainer lines and lead to difficulties in monitoring the purity of hybrid seed production, and also the restoration frequency is low. ICSSH 58 (ICSA 738 × ICSV 93046) is the first A_2-based sweet sorghum hybrid in the world bred at ICRISAT and reached the farmers' fields. Other alternate sources like A_3, A_4, A_{4M}, A_{4VZM}, A_{4G1}, A_5, A_6, 9E, and KS are not useful primarily because (1) restorer frequencies are low (restorer frequency: $A_1 > A_2 > A_4 > A_3$) and (2) male steriles cannot be readily distinguished from male fertiles. There is a need to search for more useful form of male sterility yet different from milo (A_1). Milo restorers need to be diversified in guinea background to further enhance the yield advantage in hybrid development. Restorer frequency is very low on non-milo cytoplasms. So, there is a need to identify and breed for high-yielding non-milo cytoplasm restorers [2, 34]. The high Brix% possessing (>14 %) female hybrid parents are not available in plenty on sweet sorghum breeding programs across the globe to exploit the potential heterosis for stalk yield and juice yield [2].

Breeding Sweet Sorghum

Breeding Behavior

Sorghum is basically a self-pollinating crop, but natural cross-pollination varies from 0.6 to 6 % depending on the cultivar. Sorghum has the advantage of possessing complete self-pollination due to its floral biology, cleistogamy, and genetic and cytoplasmic genetic male sterility. Breeding methods relevant to self as well as cross-pollinated crops are, therefore, applied to breed pure line varieties, hybrids, and populations in sorghum. Hand pollination should begin around 9:30 or 10:00 AM and can be extended up to 11:30 AM to 12:30 PM on a foggy morning [22].

Candidate Traits and Variability

The major characteristics which a sweet sorghum cultivar should possess are:

1. High biomass productivity (75–100 t ha^{-1})
2. High Brix% (20–23 %)
3. Thick stems and juicy internodes
4. Photo- and thermo-insensitivity aids to fit into diversified cropping systems
5. Tolerance to shoot pests and diseases
6. Good digestibility of residues when used as forage
7. Tolerance to mid-season and terminal drought
8. Salinity and heat tolerance
9. High water, nitrogen, and radiation use efficiencies
10. Juice quality and quantity sustenance during post-harvesting
11. Grain yield (4.0–7.0 t ha^{-1})

Ayyangar [35] suggested that a single dominant gene confers the non-sweet character. Later, it was reported that stalk sugar is under the control of recessive genes with additive and dominance effects [36]. On the contrary, subsequent studies provided support for the existence of multiple genes with additive effects. Continuous variation in the amount of extractable juice was observed in juicy genotypes and inbred progeny of juicy × dry lines, suggesting multiple genes may be involved in controlling the trait [8, 37, 38]. There was also a report suggesting the involvement of several genes affecting the biofuel traits in sweet sorghum background. The evaluation of four promising sweet sorghum lines [Keller, BJ 248, Wray, and NSSH 104 (CSH 22SS) along with the check SSV 84] indicated substantial genotypic differences for extractable juice, total sugar content, fermentation efficiency, and alcohol production [39]. An analysis of 53 ICRISAT-bred elite hybrids in both the rainy and post-rainy seasons showed that the correlation and regression coefficients are significantly high for all the component traits of sugar yield (Brix%, stalk yield, juice weight, and juice volume) [2]. Knowing general (GCA) and specific (SCA) combining ability effects of genetic materials is of practical value in breeding programs. GCA effects represent the fixable component of genetic variance and are important to develop superior genotypes. SCA represents the non-fixable component of genetic variation, and it is important to provide information on hybrid performance. The line × tester analysis of 171 hybrids along with their parents in both rainy and post-rainy seasons showed that the magnitude of SCA variance was higher suggesting the importance of nonadditive gene action in inheritance of sugar yield-related traits though both additive and dominant genes controlled overall sugar yield during both rainy and post-rainy seasons in tropical sweet sorghums. Hence, selection in early generations would be ineffective and recurrent selection with periodic intercrossing is advocated. However, breeding for good combining restorer parents can produce high sugar yields in post-rainy season. There is an indication of existence of transgressive segregation for sugar yield that can be exploited [39]. The heritability for traits such as stem juice content, stem sugar concentration, total stem sugars, juice glucose, juice fructose, and juice sucrose was low [40, 41]. The predominant role of nonadditive gene action for plant height, stem girth, total soluble solids, millable stalk yield, and extractable juice yield and substantial magnitude of standard heterosis for candidate sugar traits (stem girth: up to 5.3 %, total soluble solids%: up to 7.4 %, millable stalk yield: up to 1.5 %, and extractable juice yield: up to 122.6 %) indicate the importance of heterosis breeding for improving ethanol productivity of cultivars [42]. The significant positive correlation of general combining ability (GCA) effects with per se performance of parents in sweet sorghum facilitates quicker identification and development of sugar rich, high biomass yielding hybrid parents [2, 43]. The generation mean analysis of two crosses has shown predominantly additive gene action for traits like sucrose% and Brix% of juice. However, for cane and juice yield, dominance gene action and dominance × dominance gene interaction were of higher magnitude in both the crosses. Since the traits important for high sugar content have dominance and overdominance inheritance, utilization of hybrid vigor by developing sweet sorghum hybrids is an attractive option. Also one of the parents with high sucrose content will suffice in getting good hybrids with high sugar and juice yield [44].

From these studies, it is quite evident that significant diversity exists in traits important for biofuel production and this opens up excellent opportunities for sweet sorghum improvement. Biofuel traits are governed by multiple genes and both additive and dominant components of gene action have to be exploited while breeding for high stalk sugar and juice-yielding genotypes. It was demonstrated that the improved hybrids top ranking for grain and sugar yields in rainy season are not top ranking in the post-rainy season and vice versa. It is important to breed for rainy and post-rainy seasons separately [2–4]. The selections for post-rainy season adaptation should be made in post-rainy season only, and for rainy season adaptation, selections can be made in both rainy and post-rainy seasons.

Breeding Objectives

In general, the sweet sorghum breeding programs aim to develop parents and hybrids which can address both first and second generation (lignocellulosic feedstock development) biofuel production issues. The breeding objectives are:

1. To develop sweet sorghum female parents with high stalk sugar and grain yield
2. To develop restorer lines/varieties with high sugar content and resistance to stem borer and shoot fly
3. To develop and identify sorghum hybrids (amenable for mechanical harvesting) with high biomass suitable for use in bioethanol and bioenergy production

Breeding Methods

The most commonly used programs in sweet sorghum improvement are short-term programs (pedigree method and backcross) and long-term programs (population improvement methods). The most common approach in sweet sorghum breeding has been elite × elite crosses followed by pedigree selection. Breeding new female lines, B and R lines have increasingly become dependent on crossing elite by elite lines, B × B and in some cases such as improving for resistance B × R lines. In case of male lines (R lines) improvement, it is R × R crosses. This process progressively narrows the genetic base of breeding programs and requires new traits, especially resistances, to be brought in by pre-breeding and often backcrossing. The success of a backcrossing program depends on the precision with which the desired trait can be identified and thus introgressed into the recurrent parent through backcrossing.

Fig. 1.1 Comparison of grain sorghum (front) and sweet sorghum crop (rear) at flowering

Pedigree Method

Pedigree breeding method is the most commonly used method of breeding in sorghum where the selection begins in the F_2 generation targeting superior plants which are expected to produce the best progenies. Hybrids between diverse parents segregate for a large number of genes, and every F_2 individual is genetically different from other individuals. The population size becomes crucial for the success of recovering desirable genotypes, when several genes are involved. In this method (Fig. 1.1), superior individual plants are selected in successive segregating generations from the selected families, and a complete record of parent progeny relationship is maintained. Identifying a potentially good cross is essential since the best F_1 plants produce better yielding F_4 progenies. The selection in segregating generations should be based on (1) performance of the families of the selected cross on the whole and (2) the individual plants performance within the selected family. Selection for many of the per se selection criteria encompassing various traits like tallness, stem thickness, and juice yield can be rapidly applied in the first two or three segregating generations since crosses between elite lines produce a high proportion of progeny with desirable per se values. Once the promising lines have been identified, they can be test crossed onto male-sterile lines for checking fertility restoration and may be classified as B or R lines. Lines with high biomass yield and other desirable agronomic characters can be released as varieties. The pedigree method has been utilized to create new recombinants, transfer of few to many genes governing resistances to various insects, diseases, cold tolerance, etc. in sorghum. In India, the important sweet sorghum genotypes released through pedigree method of selection are SSV 74, SSV 84, CSV 19 SS, and CSV 24SS [45].