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BREEDING SORGHUM FOR GRAIN, FORAGE AND BIOENERGY IN BRAZIL

Abstract – Sorghum is a versatile crop used for energy production, human and animal feedings, and raw material for industry. The grain sorghum is the fifth most important cereal worldwide, and Brazil is one of the top 10 sorghum producers. In the last 40 years, the sorghum grain yield in Brazil has increased to 32.70 kg ha^{-1} $year^{-1}$. Although this clear evolution, much remains to be done, and sorghum breeders in Brazil still face several challenges. This review discusses the main characteristics of sorghum genetics and breeding, aiming for sorghum improvement for food, fodder, feed, and fuel uses. Herein will be highlighted essential topics related to the genetic control of the main interest traits; conventional sorghum breeding; the development of sorghum lines and hybrids; the use of male-sterility in sorghum breeding; the implication of genotypes-by-environments interaction in sorghum, the use of genome-wide association studies, and genomic prediction to maximize the efficiency of the sorghum breeding programs.

Keywords: *Sorghum bicolor* (L.) Moench, Male-sterility, Biotic and abiotic stresses, Genomic prediction, Genotypes-by-environments interaction.

MELHORAMENTO DE SORGO PARA PRODUÇÃO DE GRÃOS, FORRAGEM E BIOENERGIA NO BRASIL

Resumo - O sorgo é uma cultura bastante versátil, sendo usada para a produção de energia, alimentação humana e animal, assim como matéria-prima para a indústria. Globalmente, o sorgo granífero é o quinto cereal de maior importância, e o Brasil é um dos dez maiores produtores de sorgo. Nos últimos 40 anos, a produtividade nacional de grãos de sorgo aumentou a uma taxa de 32,70 kg ha^{-1} ano^{-1}. Embora essa clara evolução, ainda se tem muito a ser feito e diversos são os desafios enfrentados pelos melhoristas de sorgo no Brasil. Esta revisão discute os principais pontos da genética e melhoramento do sorgo, visando a produção de alimentos, forragem, ração e combustível. Serão destacados tópicos relacionados ao controle genético das principais características de interesse em sorgo; melhoramento convencional de sorgo; desenvolvimento de linhagens e híbridos em sorgo; o uso da macho-esterilidade no melhoramento de sorgo; implicações da interação genótipos por ambientes; aplicação da associação genômica ampla e predição genômica para maximizar a eficiência dos programas de melhoramento de sorgo.

Palavras-chave: *Sorghum bicolor* (L.) Moench, Macho-esterilidade, Estresses bióticos e abióticos, Predição genômica, Interação genótipos por ambientes.

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Over 10,000 years ago, crop plants were cultivated for the benefit of humankind. Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important and cultivated cereal crops. Sorghum is multipurpose crop used a source of food, fodder, feed, and fuel (Ananda et al., 2020). According to Venkateswaran et al. (2019), the earliest evidence of the use of wild sorghum as food is from 7500 BC (Before Christ) in the Sahara. However, the earliest domesticated sorghum is dated from 4000 BC in Sudan (Winchell et al., 2017), and from there, sorghum was spread across Africa and out of Africa to India, China, the Americas, and Australia.

With a world grain production of 58 million metric tons in 2019/2020, grain sorghum is the fifth most important cereal crop behind wheat, rice, maize, and barley (USDA, 2022). Brazil is one of the top 10 sorghum producers in the world, accounting for 4.3% of global production in 2019/2020 (USDA, 2022). This value corresponds to an amount of 2.08 million tons harvested from an area close to 860 thousand hectares (Acompanhamento da Safra Brasileira de Grãos, 2022). In the last 40 years, Brazil's sorghum grain yield has increased to 32.70 kg ha^{-1} $year^{-1}$ ($r^2 = 0.64$). Since 2000/2001, the agricultural area cultivated with sorghum increased by 72%, while total sorghum grain production increased by 130%.

Despite the evolution of sorghum cultivation in Brazil, much remains to be done. Due to its versatility of use and interesting agronomical characteristics (such as greater drought tolerance than other cereals), sorghum represents a great option to integrate Brazil's agricultural production systems. Wide dissemination of sorghum information, and improving the knowledge about sorghum breeding, may impulse a more significant expansion of the sorghum crop in Brazil. In this context, we aim with this review to gather general information on the subject in question and contribute to the dissemination of knowledge and popularization of sorghum.

A brief history of sorghum breeding in Brazil

The sorghum was first introduced in Brazil during its discovery and was most likely brought from Africa in slave ships (Ribas, 2003). Between 1920 and 1960, sorghum research has been intensified, and sorghum breeding programs at research institutes and universities have initiated. The Instituto Agronômico de Campinas (IAC), Instituto Agronômico de Pernambuco (IPA), Instituto de Pesquisas Agropecuárias do Rio Grande do Sul (IPARGS), as well as agronomy schools, such as Viçosa, Lavras, Piracicaba and Ceará, started to perform sorghum researches and cultivars development.

Ribas (2003) states that, at that time, germplasm collections were introduced from Africa and United States, and the firsts forage commercial sorghum cultivars were developed. During the 1970s, sorghum crop cultivation intensified and became commercially relevant, reaching 80 thousand sorghum-cultivated hectares, concentrated mainly in the Rio Grande do Sul (RS) and São Paulo (SP) (Tabosa et al., 2019). Grain sorghum hybrids from Argentina crossed the frontiers, being introduced in RS and, lately, in SP, from were spread to other states in Brazil. In addition, due to government support and incentives, 50 sweet sorghum genotypes from the United States Department of Agriculture (USDA), Africa, and India were introduced in Brazil. The Embrapa Maize and Sorghum used these germplasms to start developing the Brazilian sorghum cultivars (Carmo, 1977).

In August 1983, Embrapa established a cooperation agreement with INTSORMIL (Internacional Sorghum/Millet Program) in research activities of mutual interest in sorghum and millet. The National Center for Research on Maize and Sorghum would be the coordinator technician for this program and responsible for approving work plans for Brazil. INTSORMIL was created in 1979 in partnership with several American universities, international research centers (CIAT, CIMMYT, ICRISAT, and IRRI), and other organizations (FAO and SAFGRAD).

During the 1990s, there was a significant increase in sorghum-cultivated areas. Menezes et al. (2018) highlight that a group named Grupo Pró-Sorgo, formed by seed companies and public institutes, was greatly responsible for stimulating this increase. The Midwest became the central grain-sorghum crop region, while RS and MG were the top forage sorghum producers.

Currently, the Brazilian top producers' states are Goiás (44%), Minas Gerais (27%), and Bahia (7%) (Acompanhamento da Safra Brasileira de Grãos, 2022). In 2020/2021, the Midwest region accounted for about 55% of sorghum grain production. In regions where agriculture is expanding, such as MATOPIBA (an acronym for the states of Maranhão, Tocantins, Piauí and Bahia), sorghum cultivation proves to be an excellent option. The adoption of the cereal is attractive due to its better adaptation to dry environments, a common situation of the second crop season in the MATOPIBA region. Therefore, grain sorghum cultivars are major cultivated during the second crop season as an alternative to off-season maize. On the other hand, animal feed purpose sorghum takes advantage of the better conditions of the spring/summer season, increasing its biomass production.

The Brazilian grain-sorghum yield was about 2400 kg ha^{-1} in 2020/2021. However, reports presented in Menezes et al. (2018) indicate that the Brazilian sorghum crop may achieve up to 7000 kg ha^{-1} of grain yielding. Furthermore, it is a consensus that only joint efforts of plant breeding, crop science, and crop protection, among others, will change the actual Brazilian sorghum grain yielding scenario, improving the productivity of the sorghum crop.

Types of sorghum and genetic inheritance of main interest traits

Breeding programs must have clear objectives to be successful. In this scenario, sorghum breeders must set breeding objectives based on farmers' needs. As presented by Rakshit and Gomashe (2013), regardless of sorghum types, the primary breeding objectives for sorghum are *i*) high and stable yielding; *ii*) tolerance and resistance to biotic and abiotic stresses. On the other hand, each type of sorghum has its ideotype, which considers the plant size and architecture, length of the production cycle, and sorghum end uses. Ideally, ideotype refers to a set of desired characteristics in a plant genotype to achieve a high yield for a given end-use (Donald, 1968).

In addition, agronomic traits such as uniformity in seed germination, flowering, and grain maturity, and responsivity to better soil fertility and low water demand, are desired traits in any sorghum crop (Rao et al., 2015). However, there are specific must-have traits for each type of sorghum. The sorghum crop is divided into five major commercial types: *i*) Grain sorghum; *ii*) Forage sorghum; *iii*) Biomass sorghum; *iv*) Sweet sorghum; and *v*) Broom sorghum. According to Ribas (2014), these types can be subdivided according to their end uses: *i*) grain production; *ii*) forage for silage purposes; *iii*) forage for animal grazing purposes; *iv*) sweet sorghum for ethanol and *v*) biomass sorghum for energy generation.

In addition to table 1, broom and dual-purpose sorghum types have also their ideotypes. Broom sorghum has value in the panicle, which small producers widely use to produce artisanal brooms. Furthermore, dual-purpose sorghum is an intermediate type with the potential to be exploited in grain and silage production or even forage cultivars with potential use in ethanol and sugar production.

Among the main traits of interest, earliness has become one of the essential sorghum traits for Brazil's growth conditions. Early genotypes optimize agricultural production by allowing crop rotation within the same growing season. In addition, as fast as the plant completes its cycle, the crop will be exposed to unfavorable conditions, such as drought, for a short period. Therefore, earliness is a must-have trait for grain sorghum since this type of sorghum is mainly cultivated during the second crop season as an alternative to maize (Landau & Netto, 2015). However, normal-late genotypes often present great biomass yielding than early genotypes, which is desired in cases of high biomass production needs.

Sorghum plants can be classified as sensitive or not to photoperiod. Although there is variation in response to photoperiod, sorghum is considered a short-day plant, meaning that, originally, the plant would bloom at times of the year with long nights. In cultivars sensitive to photoperiod, the apical bud remains in the vegetative stage until the critical photoperiod of 13 hours; floral induction occurs when the

Table 1. Types of sorghum and their main characteristics and plant ideotypes.

Type of sorghum	Main characteristics and plant ideotypes
Grain	Plant height between 100 and 150 cm Good plant architecture for mechanical harvesting Relatively big grains Hard or chalky endosperm
Forage (Silage)	Plant height between 200 and 300 cm High biomass production High leaves/stalk and panicles/whole plant ratios High digestibility
Forage (Cutting or animal grazing)	*Sorghum bicolor x Sorghum sudanense* hybrids and *Sorghum sudanense* varieties Plants with narrow leaves, thin and succulent stalks, sparse panicles, and low grain yielding Fast growth, easy regrowth, and abundant tillering High nutritional biomass production Up to five cuttings in summer/autumn seasons conditions
Sweet	Phenotypically similar to forage sorghum for silage purposes Succulent and elevated sugar-concentrated stalks High quality for commercial biofuel production
Biomass	Plant height greater than 300 cm Thick and fibrous stalks Plants with small panicles and low grain yielding

Fonte: Adapted from Ribas (2014).

day length becomes shorter than 13 hours (Sanon et al., 2014). Sorghum flowering time and photoperiod sensitivity genetic controls have been elucidated. These traits is controlled by two alleles in six loci: *Ma1*/*ma1*, *Ma2*/*ma2*, *Ma3*/*ma3*, *Ma4*/*ma4, Ma5*/*ma5* and *Ma6*/*ma6* (Rooney & Aydin, 1999). Dominant alleles at each locus contribute to late flowering, with Ma1 being the gene with the greatest effect on the trait (Hao et al., 2021). A dominant Ma1 locus results in photoperiod-sensitive genotypes, regardless of the other loci (Quinby & Schertz, 1970).

In the specific case of biomass sorghum, where the main objective is accumulating as much biomass as possible, it is desirable to prolong the vegetative phase. Therefore, the use of photoperiod-sensitive genotypes and the management of the sowing time of these materials are recommended. Parrella et al. (2010) highlight that the earlier the sowing of biomass sorghum, the longer its vegetative period. The long photoperiod observed for many Brazilian regions in November and December causes a prolongation of the vegetative phase of sorghum plants. On the other hand, photoperiod sensitivity is a disadvantageous characteristic in grain sorghum, in which cycle length must be predetermined regardless of the sowing date.

Grain yield and quality are the main focus of grain sorghum breeding. It is well-known that grain yielding is a complex quantitative trait in sorghum and other plants. Many significant factors influence grain yield in sorghum: grain weight, the number of grains per panicle, and tiller number (Hao et al., 2021). Mace et al. (2019) highlight that about 340 Quantitative Trait Loci (QTL) associated with grain yield in sorghum have already been identified. A list of QTLs associated with many agronomic traits in sorghum can be found in Hao et al. (2021).

In terms of grain quality, the proportion of protein, starch, fat, phenolic compound, and minerals directly influences the nutritional value of sorghum grain (Hao et al., 2021). Kafirin, starch, and tannin are the primary compounds that influence sorghum grain quality. Hao et al. (2021) highlight that kafirin is the major seed protein in sorghum, which can form a tight matrix with starch granules and may reduce the digestion of kafirin and starch. In contrast to usual starch, waxy starch is more digestible because it contains little or no amylose content.

Tannins are polyphenolic substances widely known to be anti-nutritional, reducing nutrient availability and palatability (Hao et al., 2021). However, in animal nutrition, tannins can act differently in monogastric and ruminant animals, even beneficial in some cases. In ruminants, tannins can reduce the amount of protein digested in the rumen and increase the amount of protein available in the small intestine (by-pass protein), have an anthelmintic effect, and decrease frothy bloat (Mueller-Harvey, 2006). It is essential to point out that in high concentrations, beneficial effects are not obtained from tannin. Due to its importance, grain sorghum cultivars are classified according to the presence or absence of tannin (Rodrigues, 2015).

In terms of biomass sorghum, grain yield is less relevant. In this scenario, the breeding programs focus on developing higher plants and more outstanding biomass quality and productive genotypes. Plant biomass is compounded by cellulose, hemicellulose, and lignin. The high content of lignin in biomass enables a high calorific value, a highly desired characteristic for producing heat and energy (Naik et al., 2010). However, lignin becomes a limiting factor for second-generation ethanol production from sorghum biomass. In such a case, obtaining and adopting bmr (brown midrib) sorghum genotypes might be favorable. According to Hao et al. (2021), *bmr2*, *bmr6*, and *bmr19* directly affect lignin content and structure (G-unit and S-unit), while *bmr12* reduces lignin and has positive effect to bioconversion and digestion efficiency. Phenotype characterization can be performed by measuring acid and neutral detergent fibers and lignin.

For sweet sorghum, a sugar-rich stalk is the most important trait. The sugar content can vary between 7 and 15% or present between 13 and 24 ºBrix of soluble solids in the juice (Reddy et al., 2005; Almodares & Hadi, 2009). In addition, sweet sorghum breeding programs may focus on industry-desired traits, such as increasing the period for industrial use (> 30 days), which can be achieved by increasing the sucrose content instead of glucose or fructose (Durães et al., 2012).

Sorghum can serve different purposes in terms of silage production. Forage or dual-purpose cultivars, with high grain yielding, provide higher quality and energy ensilage. Taller cultivars, such as biomass sorghum, can fulfill the demand for greater dry matter volume. Several bromatological parameters can be used to assess silage quality, such as dry matter volume and digestibility (DM and DMD, respectively), crude protein contents (CP), neutral detergent (NDF), and acid detergent (ADF) fiber. The optimal dry matter content should range between 30 and 35%, while DMD above 55% indicates high-quality silage (Tolentino et al., 2016). Furthermore, the good-quality silage should have at least 7% protein content and not exceed 55 and 40% of NDF and ADF, respectively, to maximize animal production (Tolentino et al., 2016; Rodrigues et al., 2021).

In addition, forage sorghum can be used for cutting or animal grazing purposes. Sawazaki (1998) highlights an interspecific crossing between *Sorghum bicolor* x *Sorghum sudanense* to obtain superior genotypes for cutting or grazing. In this scenario, fast growth and easy regrowth are highly desired. However, Simili et al. (2013) highlight the possibility of animal intoxication by dhurrin, a cyanogenic glycoside in sorghum leaves, mainly in the initial vegetative development phase. Therefore, forage sorghum breeding programs may focus on reducing the dhurrin content (HCN below 200 ppm). Furthermore, the *bmr* trait has been studied to increase the digestibility and quality of animal grazing cultivars (Aguilar et al., 2014; Astigarraga et al., 2014).

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Breeding for resistance to biotic and abiotic stresses

Regardless of the type of sorghum, breeding for abiotic and biotic stresses is of utmost importance. Sorghum is considered a drought-tolerant crop due to its root morphology and ability to reduce transpiration and metabolism in general (Schittenhelm & Schroetter, 2014). However, sorghum yielding reduction might be observed under severe drought stress conditions (Albuquerque et al., 2011). Batista et al. (2017) highlight that yield losses depend on the length and intensity of the drought condition, and the plant cycle stage, which is more severe in reproductive stages (Anami et al., 2015).

In Brazil, due to the unstable climatic conditions of the off-season (second crop season), obtaining drought tolerance sorghum cultivars is crucial. In this scenario, selecting stay-green genotypes is an efficient strategy (Oliveira et al., 2020; Souza et al., 2020), and QTLs associated with this trait have been identified in chromosomes 2, 3, and 5 (Sabadin et al., 2012). Furthermore, the ability to keep green leaf area (stay green) under stress allows for better production under these conditions due to the extended time for photosynthesis.

Performing genotype selection based on their root morphology can also be employed. However, root morphology is not easy to evaluate. Therefore, several methodologies of root morphology phenotyping have been developed, such as the PhenoRoots for seeking greater practicality and accuracy in evaluations (Martins et al., 2019), the high throughput phenotyping platform for nodal root angle screening (Joshi et al., 2017), and among other methodologies (Parra-Londono et al., 2018a; Wasaya et al., 2018; Magalhães et al., 2016). In addition, genomic regions associated with root morphology have been identified in sorghum and could help select drought-tolerant genotypes (Li et al., 2014; Mace et al., 2012).

Due to its tropical origin, the sorghum crop is highly susceptible to cold conditions, negatively affecting seedling emergency, plant growth and development, tillering, height, dry matter accumulation, and flowering. Ortiz et al. (2017) also reported a reduction in chlorophyll synthesis in cold conditions, reducing photosynthesis and production. Genetic variance for cold tolerance has been reported in grain, sweet, and biomass sorghum (Patanè et al., 2021; Franks et al., 2006), as well as QTLs, which can be helpful for marker-assisted selection (MAS) (Parra-Londono et al., 2018b; Burow et al., 2011). Furthermore, heterosis for cold tolerance has also been identified, and more tolerant hybrids development can be exploited (Schaffasz et al., 2019; Windpassinger et al., 2017).

To aim for a more sustainable agriculture system, sorghum breeders may focus on developing N and P efficient usage genotypes (Bollam et al., 2021; Bernardino et al., 2019; Hufnagel et al., 2014; Rodrigues et al., 2014). In addition, Al^{3+} tolerant sorghum genotypes are highly desired, considering the existence of this toxic element in most of the country's tropical soils. In this sense, the SbMATE gene plays an important role, conferring tolerance to a plant through its ability to complex the toxic aluminum in the rhizosphere (Carvalho Júnior. et al., 2016). Subsequently, SbWRK1 and SbZNF1 were identified as the SbMATE regulatory genes, improving the plant's tolerance condition (Melo et al., 2019).

Sorghum pests and diseases may cause considerable damage to sorghum crops, reducing crop yielding. Exploiting genetic resistance is an economical and efficient strategy to manage pests and diseases. Sorghum anthracnose, caused by *Colletotrichum sublineolum*, may reduce crop yielding up to 86% (Cota et al., 2017), and due to high pathogen variability, developing genetic resistance is challenging (Xavier et al., 2018). Mehta et al. (2005) and Costa et al. (2011) identified vertical resistance to specific races of *Colletotrichum sublineolum*. Gene pyramiding, sorghum multiline (Costa et al., 2012), and sorghum crop rotation (Silva et al., 2015) have been reported as the most efficient strategies.

Already, sorghum leaf blight (*Exserohilum turcicum*) and rust (*Puccinia purpurea*) may reduce crop yielding potential by up to 50% (Silva et al., 2015). In addition, over the years, works on sorghum genotype evaluation have been performed in Brazil to find new sources of genetic resistance (Lívio et al., 2019; Nunes & Emygdio, 2014; Ramos et al., 2012).

Several genes and QTLs have been identified as necessary for disease resistance in sorghum. Wang et al. (2014) report NBS-LRR genes to rust resistance, while Souza et al. (2016) identified five QTLs associated with the resistance to sorghum leaf blight. Beshir et al. (2016) report eight SSR markers associated with sorghum anthracnose and helminths that could be used for MAS. QTLs in chromosomes 3, 5, and 6 have been proved responsible for resistance to the target leave spot (*Bipolaris sorghicola*) (Kawahigashi et al., 2011; Mohan et al., 2010). In addition, the ARG1 gene was recently identified as responsible for several fungal disease resistances, including several races of *Colletotrichum sublineola* (Lee et al., 2022).

Like diseases, pests have great potential to reduce sorghum production, whether the products are grains, juice or biomass. In addition to quantitative damage, there is also the possibility of qualitative damage to production. In the context of breeding, sources of resistance to the sugarcane aphid (*Melanaphis sacchari*) have been identified by Armstrong et al. (2015) and Boyles et al. (2018). Genomic regions associated with resistance to sorghum midge (*Stenodiplosis sorghicola*) and green aphid (*Schizaphis graminum*) have also been reported (Punnuri et al., 2013; Tao et al., 2003). Mwenda et al. (2019) highlight that genotypes with harder grains and smaller and thinner pericarp present more resistance to storage pests, while Zhai et al. (2016) found QTLs associated with resistance to *Sitophilus oryzae*.

Breeding strategies for sorghum lines development

A good parental selection is crucial for the success of the development of sorghum inbred lines. This step is essential and must consider target traits, the inheritance of these traits, and the genetic divergence between the genotypes. Once selected, parental crosses can be performed.

Since sorghum is an autogamous plant, performing artificial crosses requires self-pollination prevention. Due to its floral morphology, it is necessary to emasculate the sorghum florets. Rakshit and Bellundagi (2019) describe the manual emasculation process in detail. First, a panicle that is near to the anthesis is chosen. Then, the upper and lower florets of the panicle are removed, retaining about 100 to 200 central florets. Optionally, florets close to the rachis can be removed to hold the florets easily. In addition, the non-fertile pedicelled florets must also be removed. Then, the sessile (fertile) florets are opened using sharp forceps, and their anthers are carefully removed without damaging the stigma (Rakshit & Bellundagi, 2019). The emasculated panicles must be protected by covering them with butter or brown paper to avoid unwanted cross-pollination. The emasculation process can be visualized in figure 1, and other sorghum emasculation processes can also be found in Rakshit and Bellundagi (2019).

Two to three days after emasculation, the artificial crosses are performed. For mating, pollen from the male parent is collected in abundance in a paper bag. Then, the pollen is dispersed within the bag of the emasculated panicle. Finally, the bag is tagged with details about the cross. By maturity, the hybrid seeds of each cross are harvested separately and stored (Rakshit & Bellundagi, 2019).

The sorghum hybrids seeds are multiplied, and F_2 seeds are harvested from the F_1 plants. Finally, the F_2 seeds are sown in the field/greenhouse, generating the F_2 population. From the F_2 population, sorghum breeders can apply several selection methods to advance the genotypes and obtain sorghum inbred lines. Pedigree, bulk, and single seed descent (SSD) methods can be applied in this scenario.

In the pedigree method, starting from F_2, the seeds of each selected plant will constitute a row in the next generation until homozygosity. Then, in each generation, progenies tests are performed, and the best ones are selected. After, the selection is accomplished within and between families until the F_5 generation. Finally, single and multi-environment trials must be done. However, since the selection and plant genealogies start in the F_2 generation, the pedigree method requires much effort.

The bulk method is undoubtedly one of the most cost-effective segregating populations. According to Ramalho et al. (2012), the bulk method prioritizes natural selection during the initial generations (F_2 to F_4 or F_5), which means that no artificial selection will be performed until the advanced stages of homozygosity. Briefly, in the bulk method, all the plants of the population

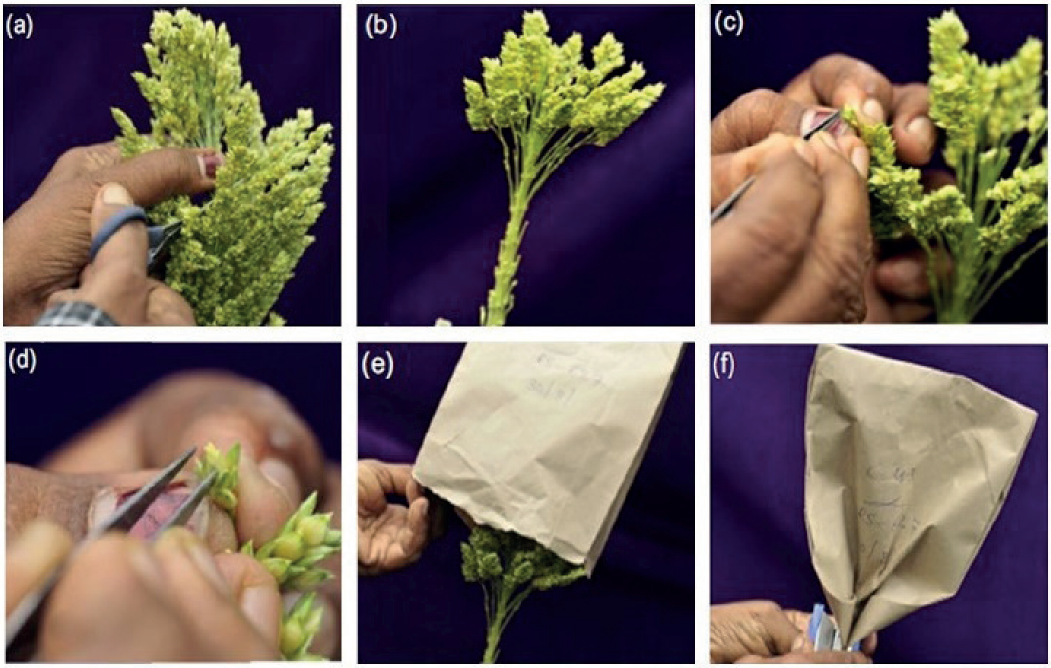

Figure 1. Hand emasculation steps: panicle cleaning (a) and (b); removal of the anthers (c) and (d); emasculated panicle protection using a brown paper bag (e) and (f). Source: Rakshit and Bellundagi (2019).

are harvested, and their seeds are mixed. From this set, a seed sample is taken and will constitute the next population. This process is repeated until to obtain the F_4 population. Then, the desired plants are selected and individually harvested from the F_4 population, and progeny testing is performed. It is essential to highlight that the undesired plants can be eliminated from the initial generations.

In addition, to exploit the heterosis, sorghum breeders may also perform test crosses in F_4 populations to identify and select the best parental for hybrid sorghum. Testcross refers to preliminary crosses of the lines being developed with the program's elite testers, aiming to determine the potential of the lines by evaluating the performance of the hybrids derived from these testcrosses. This process is adopted for R (restorer) and A (sterile male) lines. As a result, the lines that originated best-performance hybrids are advanced in the breeding pipeline (Zhao and Dahlberg, 2019).

Alternatively, the SSD method can be used to obtain sorghum inbred lines. In SSD, a single seed is harvested from each plant, and this process is repeated through F_2 to F_4 or F_5 generations. Finally, the F_4 or F_5 plants are harvested individually, and progenies tests are performed. This method is particularly advantageous in temperate climate regions, where SSD can be performed in greenhouses, speeding up the inbred line development process. In addition, Borém et al. (2017) highlight that the SSD method preserves the F_2 variability through advanced generations. However, it is worth mentioning that non-germinated seed or plant losses reduce the variability (Ramalho et al., 2012). In this scenario, Rakshit and Bellundagi (2019) state that sorghum breeders may select a whole panicle of the plant instead of selecting only seed to preserve the genetic variability of the F_2 generation.

In addition, sorghum breeders may use backcrossing for trait introgression. This method aims to incorporate one or a few traits, such as disease resistance, into an elite line. The F_1 hybrid must be repeatedly backcrossed to the recurrent parent (elite line) to reduce the linkage drag of the donor parent, which often presents poor agronomic performance. Cox and Frey (1984) highlight that backcrossing can be used as a pre-breeding tool, in which exotic germplasm can be improved before being incorporated into the main breeding program. In sorghum, backcrossing has been used to transfer male-sterility genes (Xin et al., 2017; Lawan et al., 2018), pest and disease resistance (Ali et al., 2016; Gorthy et al., 2017), and brown midrib *bmr6* allele (Silva et al., 2020).

Although it is commonly used in maize breeding programs, applying Doubled Haploid (DH) technology to develop sorghum inbred lines is incipient. Teingtham and Borde (2017) highlight that DH technology could reduce the time of line development by 3 to 5 years compared to self-pollination line development. Moreover, haploid induction in a breeding pipeline can be performed in the F_2 generation to exploit the maximum segregation, or DH can be used to develop inbred lines in a hybrid seed production pipeline rapidly.

In general, by using DH, it is possible to obtain 100% homozygous lines in 3 steps: *i*) haploid induction, *ii*) haploid duplication, and *iii*) DH seed multiplication. In this scenario, the primary challenge is to develop efficient haploid induction methods. The study by Teingtham and Borde (2017) presented perspectives about haploid induction methods, such as anther, ovule, and ovary cultures, wide hybridization, chromosome counting, and doubling. In addition, Hussain and Franks (2019) identified two sorghum maternal haploid inducer lines, SMHI01 and SMHI02, that present 1–2 % of induction frequency and the ability to restore the fertility of A1 cytoplasmic-male sterility (CMS) cytoplasm.

These results indicate the possibility of exploiting the double-haploid technology in sorghum. Future DH studies can be performed to improve haploidy induction rates and to develop efficient protocols for chromosome duplication. Developing a double-haploid system in sorghum implies a revolutionary change for sorghum breeding, reducing breeding time, and improving the program's efficiency.

Heterosis and hybrid seeds production in Sorghum

Although sorghum is a self-pollinated crop, some levels of heterosis have been reported in sweet sorghum (Pfeiffer et al., 2010; Bunphan et al., 2015; Lombardi et al., 2018), grain sorghum (Crozier et al., 2020; Gomes et al., 2020; Santos, 2020; Menezes et al., 2017) and biomass sorghum (Packer & Rooney, 2014).

As previously mentioned, preventing self-pollination in sorghum crops is necessary before performing the crosses. However, manual emasculation is not efficient on a commercial scale as it is time-consuming, which means high financial costs. Therefore, to commercially exploit heterosis in sorghum, an alternative approach is required.

Reddy and Reddy (2019) report that the cytoplasmic-male sterility (CMS) and fertility restorers (Rf genes) were discovered in different sorghum varieties of the milo group (grain sorghum) by Stephens and Holland (1954). In general, a sorghum genotype will be male-sterile if it possesses, in homozygoses, the recessive alleles *ms* and *rf* in its cytoplasm and nucleus, respectively (Rakshit & Bellundagi, 2019).

Three distinct lines are used to commercially exploit CMS in Sorghum in this system (House, 1985) (Figure 2): i) “A” male sterile line (*rfrf msms*), ii) “B” maintainer line (*rfrf MsMs*), and iii) “R” fertility restorer line (*RfRf MsMs or msms*).

In general, “A” and “B” are isogenic lines, except that the “B” line is male fertile due to *MsMs* cytoplasm. Due to cytoplasmic maternal inheritance, the “A” line is maintained through the A x B crossing, while the “R” line is used to restore fertility. Therefore, the in-field sorghum hybrid seeds are obtained through ♀A x R crossing.

For hybrid seed production purposes, a ratio of 4:2 rows of female “A” and male “R” lines, respectively, is adopted (Figure 3a). In the case of higher pollination capacity, other ratios such as 6:2 can also be used to reduce costs (Figure 3b).To guarantee flowering synchronism between “A” and “R” lines, the breeder may split male and female rows sowing times. In addition, Rakshit and Bellundagi (2019) highlight that applying 2% of urea or the irrigation suspension of the late flowering line can promote flowering anticipation.

Determining the best Sorghum hybrid combinations is crucial for successfully exploiting heterosis in a sorghum breeding program. In addition, the evaluation of the best combinations aids the sorghum breeders in deciding which ones will be synthesized on a commercial scale. Among several methodologies, the use of diallel crosses to determine general (GCA) and specific (SCA) combining ability is the most applied (Parmar et al., 2019; Chikuta et al., 2017; Menezes et al., 2014).

Using a partial diallel, Rocha et al. (2018) evaluated the combining abilities of four male-sterile “A” lines and five fertility restorer “R” lines of sweet sorghum for ethanol production.

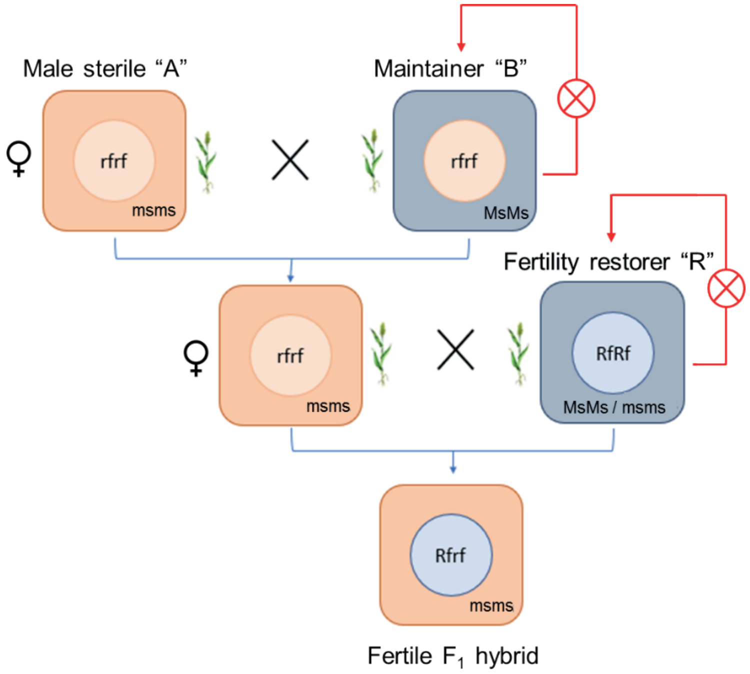

Figure 2. A-B-R system for hybrid seed production. Source: House (1985).

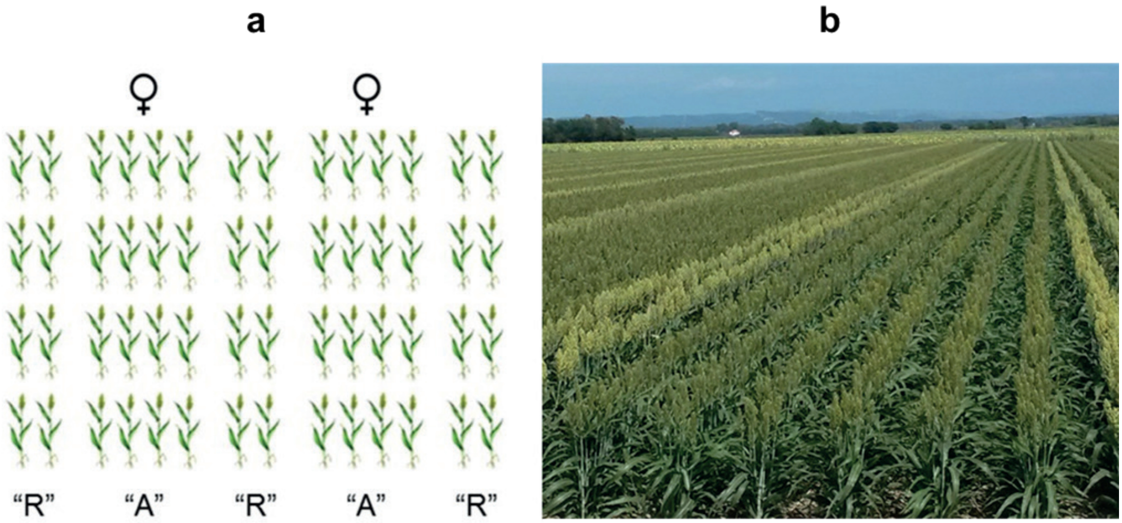

Figure 3. Scheme of 4:2 "A" to "R" lines for hybrid seeds production (a); an in-field 6:2 sorghum hybrid seeds production (b). Picture (b) by Frederic Guedj.

In this work, positive and significant effects of SCA were observed in traits that result in higher ethanol production, which justifies obtaining sweet sorghum hybrids aiming at alcohol production. On the other hand, Gomes et al. (2020) evaluated the GCA and SCA of grain sorghum inbred lines cultivated during the off-season in four municipalities in Brazil, obtaining optimal hybrid combinations for grain production.

It is necessary to highlight that to obtain good quality CGA and SCA information, good quality experiments are crucial. Thus, diallel experiments must be conducted under an appropriate experimental design and in several environments (sites and agricultural years). Once the best hybrid combinations are identified, the hybrids can be synthesized on a larger scale and evaluated in multi-environment advanced trials.

With the reduction in genotyping costs, the use of genomic prediction can also help sorghum breeders to identify the best hybrid combinations. In addition by genotyping the sorghum lines in the breeding pipeline, it is possible to predict the performance of the hybrids using the genomic information of both parents. This powerful genomic tool will be discussed in detail later in this review.

Recurrent selection in sorghum

Population improvement is a two-step approach involving broad genetic-based gene pools followed by recurrent selection methods. In general, recurrent selection is a cyclic process that involves obtaining progenies by crossing, then evaluating, selecting, and recombining the best ones to develop an improved population without exhausting its genetic variability. Ramalho et al. (2012) highlight the benefits of recurrent selection by inreasing the frequency of favorable/desired alleles for traits of interest, which is particularly useful for improving quantitative traits.

Similar to maize, intrapopulation (half-sibs, full-sibs, and inbred progeny) and interpopulation (half and/or full-sibs reciprocal recurrent selection) methods can be applied in sorghum. While intrapopulation recurrent selection aims to extract lines and develop hybrids from a population, interpopulation methods can be applied to maximize the heterosis between two contrasting populations and exploit the hybrid vigor. Furthermore, the reciprocal recurrent selection allows the exploitation of additive x additive and other epistatic gene actions (Aruna et al., 2021). With the development of an efficient male-sterility technique, recurrent selection has become a feasible option for sorghum breeding programs (Leite et al., 2020). Due to their stability, the male-sterility *ms3* and *ms7* alleles have been extensively used (Aruna et al., 2021), being the male-sterility conditioned to homozygous recessive genotypes. In a recent book by Embrapa, the use of genetic male-sterility in sorghum is discussed in detail (Oliveira et al., 2021).

Aruna et al. (2021) mentioned that it is necessary to create a base population before selecting. Menezes et al. (2021) highlight that choosing good parentals is the first and most crucial step to creating a good breeding population. In general, 10 to 20 good agronomic performing parentals are required to obtain a population with high yielding and genetic variability (Menezes et al., 2021).

Once defined, the parental lines need to be crossed with a source of male-sterility genes (*msms*). The F_1 generation is composed of plants in heterozygosity (*Msms*) for male-sterility, that is, male-fertile plants. Therefore, proceeding with a self-fertilization generation is necessary to obtain male-sterile genotypes (*msms*). The F_2 seeds generated from self-fertilization present a 3:1 ratio, originating ¾ fertile plants (¼ *MsMs* and ½ *Msms*) and ¼ male-sterile plants (*msms*). The panicles of male-sterile F_2 plants (*msms*) are identified during flowering and then harvested separately for use in new backcrosses or the first recombination. To obtain the first generation of recombination of the recurrent selection, an equal amount of seeds from male-sterile F_2 panicles is mixed, and the same procedure is performed to obtain the second and third generation of recombination (Oliveira et al., 2021). A detailed scheme of a recurrent intrapopulation selection program for sweet sorghum is presented in Leite et al. (2020).

Leite et al. (2020) obtained about 3.73% (plant height), 8.04% (fresh biomass yield), and 8.65% (tons of Brix per hectare) of genetic progress while applying intrapopulation recurrent selection in sweet sorghum. Furthermore, Aruna et al. (2021) used a population breeding approach to develop high-yielding, grain mold-resistant sorghum genotypes. Rakshit and Bellundagi (2019) highlight that recurrent selection has been performed to improve grain yield, stability, and quality, among other agronomic desired traits such as diseases and pests resistance at the International Crops Research Institute for The SemiArid Tropics (ICRISAT), in India.

Genotype-by-Environment interaction in sorghum

The genotypes-by-environments (GE) interaction is a significant challenge in plant breeding. GE interaction can be defined as the differential genotype responses to types of environments. In severe GE interaction, genotypes re-raking across the environments might be observed, making the selection process more challenging. According to Hunt et al. (2020), plant breeders may adopt one of two strategies to manage GE interaction: *i*) ignore GE interaction by selecting for broad adaptation, or *ii*) exploit GE interaction by performing genotype selection for both broad and specific adaptation. In both scenarios, multi-environment trials (METs) are of utmost importance. Plant breeders may use METs information to understand GE interaction better and select or recommend the best genotypes for a set of target environments or mega-environments.

The implications of GE interaction in sorghum are widely reported in the literature

(Diatta et al., 2021; Ribeiro et al., 2021; Wagaw et al., 2020; Mare et al., 2017; Souza et al., 2013). Many agronomic and nutritional traits in sorghum are harshly affected by GE interaction. For example, Aruna et al. (2020) reported significant GE interaction when evaluating sorghum's total polyphenol content and antioxidant activity. Moreover, Phunke et al. (2017) found significant Genotype-Year-Location interactions for days to flowering, grain yield, plant height, grain iron, and zinc concentration in the recombinant inbred lines (RIL) population of sorghum.

Kaufman et al. (2018) observed expressive GE interaction on grain chemical attributes when evaluating 19 sorghum genotypes in three locations in Kansas/USA. Moreover, the authors decided to perform a selection based on genotype mean values across the three locations. On the other hand, Cysne and Pitombeira (2012) decided to adopt an alternative strategy when evaluating nine genotypes of grain sorghum in seven environments in the state of Ceará/Brazil, choosing a complementary methodology to exploit GE interaction: the study of adaptability and stability of the genotypes.

A similar approach was applied by Delgado et al. (2019) while studying GE interaction in photoperiod-sensitive biomass sorghum hybrids. These authors concluded that the Toler, GGE biplot, and Annicchiarico methods are complementary to describing the relative differential response of genotypes between environments and helpful in studying adaptability and stability.

Many methodologies to study the GE interaction were developed over the years. Most of them aim to estimate the genotype adaptation, adaptability, and stability. For example, Adugna (2007) and Souza et al. (2013) adopted linear regression models (Finlay & Wilkinson, 1963; Eberhart & Russell, 1966) and other methodologies (Wricke, 1962; Shukla, 1972; Francis & Kannenbert, 1978; Lin et al., 1986; Annicchiarico, 1992) to evaluate the adaptability and stability of sorghum genotypes to perform selections and recommendations.

Rakshit et al. (2017) and Aruna et al. (2020) applied Additive Main Effects and Multiplicative Interaction (AMMI) (Gauch, 1992) model to study GE interaction in several traits of sorghum. On the other hand, the GGE biplot methodology was used by Phunke et al. (2017) and Diatta et al. (2021). In addition, a fascinating study was performed by Enyew et al. (2021) using both AMMI and GGE biplot methodology to study 324 sorghum genotypes evaluated across three environments in Ethiopia. These works confirm the above mentioned methods as the most common and effective multivariate models in the study of stability, adaptability, genotype ranking, and selection of suitable mega-environments. A detailed description of the cited methodologies can be found in Ramalho et al. (2012) and Borém et al. (2017).

In tropical conditions of Brazil, the GE interaction is even more challenging. Grain sorghum is one of the best alternatives for soybean crop succession. Therefore, being cultivated during the second crop season (off-season), grain sorghum crops face extreme environmental conditions, such as reduced and non-consistent rainfall. In this scenario, selecting high-stability sorghum hybrids is crucial to mitigate unfavorable conditions impacts.

Applying Wricke's methodology, Almeida Filho et al. (2014) found high stability genotypes when evaluating 25 grain sorghum hybrids during the off-season over seven locations in Brazil. In turn, Silva et al. (2016) found three top-performance grain sorghum genotypes that also present high adaptability and stability over eight locations in five states in Brazil. Furthermore, Alves et al. (2021) and Silva et al. (2022) identified highly stable sweet sorghum genotypes over six and ten environments in several regions of Brazil, respectively. On the other hand, Silva et al. (2021) adopted a different strategy to mitigate GE interaction impacts. By applying the GGE biplot methodology in 22 grain-yield trials, these authors identified three mega-environments for grain sorghum in Brazil.

From a genomic prediction perspective, Hunt et al. (2020) highlight the advantages of using additive and dominance genomic relationships in MET analysis of sorghum breeding trials. In general, prediction accuracies increased by an average of 15% with the addition of dominance effects compared to the additive effect model.

Genomic prediction in sorghum breeding

Although the tremendous genetic gain delivered by sorghum breeding programs over the past years, sorghum breeders face significant challenges in improving breeding program efficiency. The constant reduction in genotyping costs associated with the increasing phenotyping costs drags the attention of sorghum breeders to the opportunity of implementing genomic selection in sorghum breeding programs. First proposed by Meuwissen et al. (2001), sorghum breeders may take advantage of genomic prediction tools to reduce costs and shorten the breeding cycle through early prediction of the phenotypic performance of a set of genotypes, improving genetic gain per unit of time, which makes the breeding program more efficient.

This methodology only predicts individuals' phenotypes based on genomic information (Xu, 2013). However, as described by Heffner et al. (2009), to achieve genomic prediction purposes is necessary to obtain the Genomic Breeding Values (GEBVs) of the individuals: 1- GEBVs are obtained from a training population, in which the individuals have both genotype and phenotype data; 2- the prediction models are trained, and their prediction abilities are measured in a validation population, and 3- the genomic prediction model is applied in a breeding population (only genotyped individuals) to predict their GEBV and perform selections.

Genomic prediction (GP) can be

incorporated into the breeding pipeline in several stages, such as germplasm characterization, genotypes early-stage selection, parental selection, and hybrids prediction, among others. Hao et al. (2021) present several opportunities and challenges in sorghum breeding in the genomic era. In sorghum, GP mainly focused on model training using different training populations (Hao et al., 2021).

Xu et al. (2020) present a standard GP breeding program for open and cross-pollinated crops (Figure 4). It is essential to highlight that the training population must be closely related to or represent the breeding population. Besides genomic prediction, companies may use doubled haploids, which are widely applied in maize breeding but also can be exploited in sorghum (Hussain & Franks, 2019).

In Brazil, some genomic selection works were performed, and most of which were conducted by or in association with Embrapa Maize and Sorghum. For example, Oliveira et al. (2018) applied genomic prediction to high-biomass sorghum for bioenergy production using six prediction models, achieving predictive ability ranging from 0.61 to 0.85 depending on the trait and model. The Bayesian models performed similarly to RRBLUP for traits such as plant height, cellulose, hemicellulose and lignin, acid and neutral detergent fibers, days to flowering, and wet and dry biomass production.

In its turn, significant work was conducted

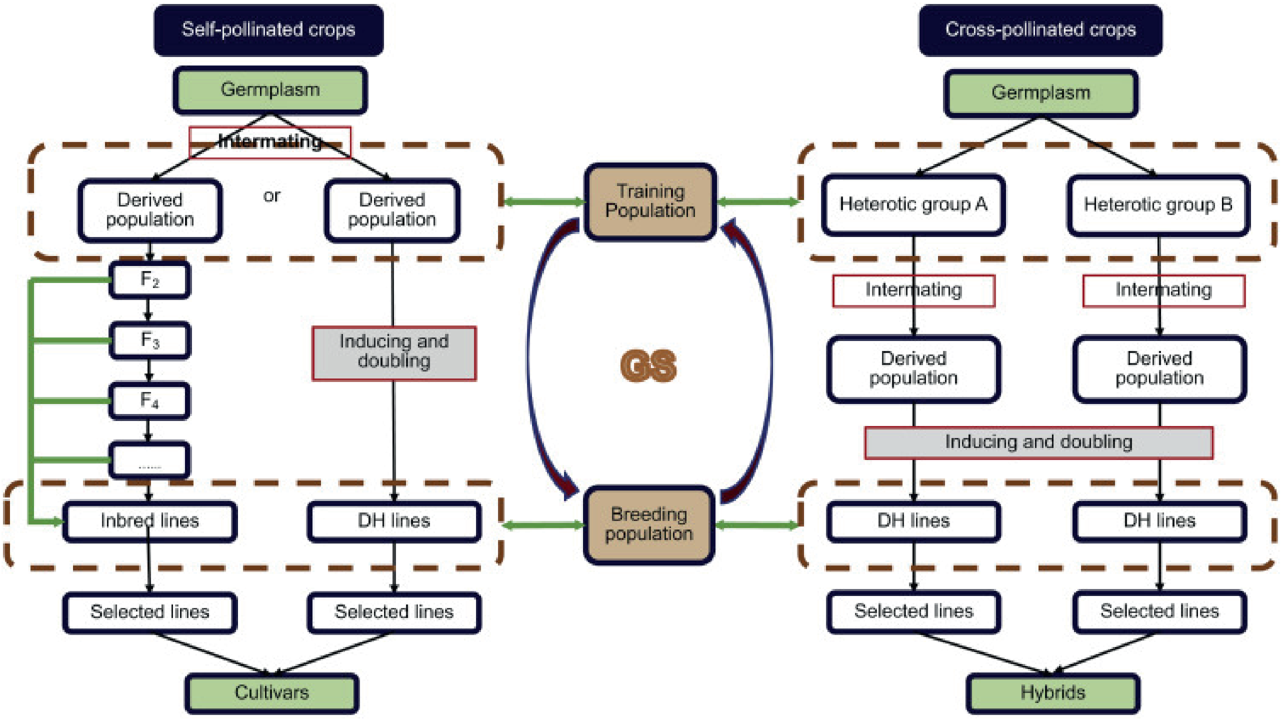

Figure 4. Genomic prediction in self-pollinated and cross-pollinated crops breeding program. GS: Genomic Selection; DH: double-haploid. Source: Xu et al. (2020)

by Bernardino et al. (2021), who applied association mapping and genomic selection for sorghum adaptation to tropical soils of Brazil. The authors mapped two candidate P efficiency genes *ALMT* and *PHO2*, on chromosomes 6 and 9. In addition, they achieve genomic prediction accuracies for grain yield, around 0.22 (absence of dominance effects) and 0.30 (dominance effects plus GWAS-derived fixed cofactors). This work highlighted the importance of combining genome-wide association and genomic prediction.

Fernandes et al. (2018) evaluated the efficiency of multi-trait genomic selection and, in addition, proposed a trait-assisted genomic selection for the improvement of biomass sorghum. The results show that single- and multi-trait strategies performed similarly. However, the so-called trait-assisted genomic selection increased prediction accuracy for yielding by up to 50% when using plant height information in both the training and validation populations.

The genomic prediction approach has been undergoing constant adjustments over the years. Many efforts have been allocated to applying genomic prediction to several crops, such as maize (Dias et al., 2020; Beyene et al., 2019), wheat (Juliana et al., 2020), rice (Labroo et al., 2021b), and sorghum (Oliveira et al., 2018; Bernardino et al., 2021), and to define the best prediction models and approaches (Santos et al., 2015; Dias et al., 2018; Fristche-Neto et al., 2018).

Final considerations

Sorghum is a versatile crop cultivated for several end-uses, such as grain production, forage, alcohol, and biomass. According to the breeding program's goals, the sorghum breeder can define the best strategies to obtain and select superior genotypes.

Most sorghum breeding programs target traits of earliness, high grain yielding, quality, biomass production, resistance, and tolerance to biotic and abiotic factors. For quantitative traits, progeny testing methods (Bulk, pedigree, and SSD) are more efficient than mass selection. However, mass selection benefits high heritable traits, such as male sterility.

Heterosis has been reported for agronomic traits in Sorghum; therefore, breeders may also choose to exploit it through sorghum hybrid seed production. Furthermore, using an efficient male-sterility technique is of utmost importance to exploit heterosis commercially.

Although its exceptional adaptability to a wide range of environments, the genotypes-by-environments interaction is a complicating factor in sorghum breeding, and several methodologies are available. They can be applied to better study and understand this interaction, aiming to minimize or exploit GE interaction. Finally, genomic prediction tools might increase in the next couple of years to reduce costs and improve genetic gain per unit, increasing sorghum breeding program efficiencies.

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