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Genetics and genomics of sorghum perennity, resistance to Striga, and efficient mycorrhizal symbiosis in Ugandan germplasm.

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ABSTRACT

Sorghum [*Sorghum bicolor* (L.) Moench] is a critical cereal crop for food security in sub-Saharan Africa, especially in Uganda, where it is a staple food. This review synthesizes current research on the genetics and genomics underlying sorghum perennity, resistance to the parasitic weed Striga, and its symbiotic efficiency with mycorrhizal fungi in Ugandan germplasm. Sorghum's perennial traits offer the potential for sustainable agricultural systems by reducing the need for annual replanting and improving soil health. The resistance to Striga, a significant biotic stress factor, is crucial for enhancing sorghum yield stability and food security. Additionally, effective mycorrhizal associations can enhance nutrient uptake, particularly phosphorus, thereby improving sorghum's growth and resilience in nutrient-poor soils. Advancements in genomic tools and breeding techniques have facilitated the identification of key genetic loci associated with these traits. Quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have identified several candidate genes and molecular markers linked to sorghum's perenniality and Striga resistance. For instance, the discovery of specific resistance genes and associated signaling pathways has provided deeper insights into the genetic mechanisms of Striga resistance. Concurrently, studies on the genetic diversity of arbuscular mycorrhizal fungi (AMF) symbiosis highlight the potential for selecting sorghum varieties with enhanced mycorrhizal efficiency. Integrating these genetic insights into sorghum breeding programs can accelerate the development of resilient and high-yielding varieties suited to Ugandan agro-ecosystems. This review underscores the importance of multi-disciplinary approaches combining genetics, breeding, and agronomy to address key challenges in sorghum production. Future research directions include the application of advanced genomic editing tools such as CRISPR/Cas9 to further refine trait integration and the exploration of genomic selection for rapid breeding cycles. These efforts are pivotal for ensuring sorghum's contribution to food security and sustainable agriculture in Uganda.

Key words: Sorghum, Striga, AMF, perennity, genetics

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RESUME

Le sorgho [*Sorghum bicolor*] est une culture céréalière essentielle pour la sécurité alimentaire en Afrique subsaharienne, en particulier en Ouganda. Cette revue synthétise les recherches actuelles sur la génétique et la génomique qui sous-tendent la pérennité du sorgho, sa résistance au Striga et son efficacité symbiotique avec les champignons mycorhiziens dans le germoplasme ougandais. Les caractéristiques pérennes du sorgho offrent la possibilité de mettre en place des systèmes agricoles durables en réduisant la nécessité de replanter chaque année et en améliorant la santé des sols. La résistance au Striga, un facteur de stress biotique important, est cruciale pour améliorer la stabilité du rendement du sorgho. En outre, des associations mycorhiziennes efficaces peuvent améliorer l'absorption des éléments nutritifs, en particulier le phosphore, améliorant ainsi la croissance et la résistance du sorgho dans les sols pauvres en éléments nutritifs. Les progrès des outils génomiques et des techniques de sélection ont facilité l'identification de loci génétiques clés associés à ces caractéristiques. La cartographie des loci de caractères quantitatifs (QTL) et les études d'association à l'échelle du génome (GWAS) ont permis d'identifier plusieurs gènes candidats et marqueurs moléculaires liés à la pérennité du sorgho et à sa résistance au Striga. Parallèlement, des études sur la diversité génétique de la symbiose avec les champignons mycorhiziens à arbuscules (AMF) mettent en évidence le potentiel de sélection de variétés de sorgho ayant une meilleure efficacité mycorhizienne. L'intégration de ces connaissances génétiques dans les programmes de sélection du sorgho peut accélérer le développement de variétés résistantes et à haut rendement adaptées aux agro-écosystèmes ougandais. Les orientations futures de la recherche comprennent l'application d'outils avancés d'édition génomique tels que CRISPR/Cas9. Cette étude souligne l'importance des approches multidisciplinaires combinant la génétique, la sélection et l'agronomie pour relever les principaux défis de la production de sorgho.

Mots clés : Sorgho, striga, pérennité, mycorhize, génétiques

INTRODUCTION

Sorghum (*Sorghum bicolor*) is Africa's second most important cereal in terms of tonnage. The continent produces approximately 20 million tonnes of sorghum annually, accounting for about one-third of the world's crop (FAO, 2017). Sorghum is a vital cereal crop in Sub-Saharan Africa (SSA), playing a crucial role in food security, economic stability, and cultural practices. It is the fifth most important cereal crop globally and a staple food for millions in SSA (FAO, 2017). However, these figures don't fully capture its significance. It is a vital food grain for many of the world's most food-insecure

populations. In term of climate adaptation, sorghum originated in Africa and is uniquely suited to the continent's semi-arid and sub-tropical climates. It is both drought-resistant and capable of withstanding water-logged conditions. In Africa, sorghum is processed into a wide variety of traditional foods, including semi-leavened bread, couscous, dumplings, and fermented/non-fermented porridges. It's also the grain of choice for brewing traditional African beers Taylor (2003). However, the new products like instant soft porridge and malt extracts have been successful. Sorghum competes favorably with barley for lager beer brewing in multinational enterprises, highlighting his economic potential Taylor (2003). Sorghum has the potential to drive economic development in Africa and be a cornerstone of food security African Farming (2023). Sorghum's resilience to harsh climatic conditions, including drought and high temperatures, makes it particularly suited to the semi-arid regions of SSA, where other crops often fail (Doggett, 1988). Nutritionally, sorghum is a significant source of calories, protein, and essential micronutrients for many communities (Taylor, 2003). It can be processed into various food products, including porridge, bread, and beverages, contributing to dietary diversity. Beyond its nutritional value, sorghum is integral to numerous traditional and cultural practices in SSA, ranging from its use in rituals to its role in brewing traditional beverages (Deu *et al.*, 2006).

Economically, sorghum supports the livelihoods of smallholder farmers who dominate agricultural production in SSA. It is not only grown for subsistence but also for sale in local and regional markets, providing a source of income and economic resilience (ICRISAT, 2012). Furthermore, sorghum's versatility extends to its use as animal feed and raw material for industrial products, including biofuels, thus contributing to diverse economic activities (Ratnavathi *et al.*, 2016). Adaptability of the sorghum to adverse environmental conditions, its nutritional and economic importance, and its cultural significance underscore its critical role in the agricultural landscape of SSA. Continued research and development efforts are essential to enhance sorghum productivity and sustainability in the region (Yohannes *et al.*, 2019).

Sorghum plays a crucial role in food security across Uganda's diverse regions. Occupying substantial arable land, it serves as a staple cereal crop, with traditional preparations Andiku *et al.* (2020). Notably, sorghum's adaptability to dry and hot conditions ensures consistent yields, even in challenging climates. Beyond food, its market potential is growing, driven by diversification away from maize. East African Breweries and Nile Breweries utilize sorghum for alcoholic beverages, contributing to the economy Andiku *et al.* (2020). Additionally, sorghum's bioenergy potential is multifaceted: sweet sorghum produces first-generation ethanol sustainably, while biomass sorghum offers second-generation biofuel possibilities (Regassa and Wortmann, 2016; Upadhyaya *et al.*, 2011). Genetic insights from population genomics using molecular approaches and breeding strategies, aid in selecting bioenergy-focused cultivars (Regassa and Wortmann, 2016; Upadhyaya *et al.*, 2011; Kpoviessi *et al.*, 2024). By analysing the relevant scientific literature, this review aims to highlight the key strategies for enhancing sorghum production in Uganda through striga management and efficient mycorrhizal symbiosis.

Genetic Resources and Breeding

Sorghum research has entered an exciting and fruitful era, thanks to the availability of robust genetic, genomic, and breeding resources. As the world grapples with population growth and climate change, sorghum emerges as a resilient C4 plant, well-suited for semi-arid and arid regions. Its adaptability, stress tolerance, and versatility make it a valuable crop species with multifaceted applications. Genetic resources, encompassing the diverse sorghum germplasm collected either from local landraces or global repositories, are pivotal in breeding programs aimed at developing improved cultivars. Uganda's unique geographical and climatic conditions have fostered the evolution of diverse sorghum varieties, possessing inherent traits valuable for breeding, such as drought tolerance, resistance to pests and diseases, and adaptability to low-fertility soils (Paterson *et al.*, 2009). Striga, a parasitic weed, poses a significant threat to sorghum productivity. The genetic basis for striga resistance includes diverse mechanisms such as low striga germination stimulant production, mechanical barriers to parasite penetration, and post-attachment resistance (Ejeta and Gressel, 2007). Breeding for striga resistance requires the identification of quantitative trait loci (QTLs) associated with these resistance mechanisms. Marker-assisted selection (MAS) has been effectively employed to introgress striga resistance genes from resistant genotypes into susceptible but high-yielding varieties. Resistance genes have been mapped to specific chromosomes, enabling breeders to develop striga-resistant sorghum cultivars more efficiently (Satish *et al.*, 2012).

The aspect of perennity, or perennial growth habit, is equally crucial for sorghum cultivation in Uganda. Perennial sorghum can reduce the need for replanting, thereby conserving soil and labor. Recent advances in genomic studies have identified key genes and regulatory pathways that control the perennial trait in sorghum (Paterson *et al.,* 2009). These findings have significant implications for breeding programs focused on developing perennial sorghum varieties by either direct selection from perennial species or incorporating perennial traits into annual cultivars through hybridization and genomic-assisted breeding techniques. Furthermore, mycorrhizal symbiosis significantly enhances sorghum's nutrient uptake, particularly phosphorus, and contributes to better growth and yield under low-input conditions prevalent in Uganda. Genetically, the capacity for efficient mycorrhizal association varies among sorghum genotypes. Identifying and breeding for genetic traits that foster efficient mycorrhizal symbiosis is essential. Genes associated with root architecture and exudation of mycorrhizal signaling molecules have been targets for enhancing this beneficial symbiosis (Smith and Read, 2008). Genomic tools such as genome-wide association studies (GWAS) have been instrumental in pinpointing alleles that confer superior mycorrhizal symbiosis, facilitating their incorporation into breeding programs (Bender *et al.,* 2015). Leveraging genetic resources through advanced breeding strategies and genomic tools holds significant promise for improving sorghum's perennity, in Ugandan germplasm. The integration of traditional breeding methods with modern genomic technologies enables the development of resilient and high-yielding sorghum cultivars tailored to the specific agricultural challenges and ecological conditions of Uganda. As we harness the potential of Uganda germplasm and leverage genomics, we contribute to sustainable agriculture, food security, and bioenergy production.

Striga Resistance

Striga, commonly known as witchweed, is a severe parasitic weed that significantly impacts the productivity of sorghum in many regions, including Uganda. Developing striga-resistant sorghum varieties is a critical focus for both researchers and farmers in combating the yield losses inflicted by this pest. Striga causes damage by attaching to the host plant's roots, siphoning off essential nutrients and water, which results in stunted growth, wilting, and ultimately reduced crop yields. The genetic and genomic approaches to enhancing striga resistance in sorghum involve understanding the mechanisms that allow certain sorghum varieties to withstand striga infestation and identifying the specific genes associated with resistance. Several strategies have been employed to develop striga-resistant sorghum varieties. Traditional breeding techniques have had some success, primarily through identifying and crossbreeding naturally resistant varieties. For instance, Ejeta (2007) identified sorghum cultivars with natural resistance to *Striga hermonthica* by examining varieties that displayed resistance traits and integrating them into breeding programs. These traditional approaches, however, are often time-consuming and labor-intensive, requiring extensive field trials and phenotypic evaluations.

With the advent of modern genomics, there has been a significant shift towards understanding the genetic basis of resistance. Quantitative trait loci (QTL) mapping is one common method used to identify genomic regions associated with striga resistance. Research by Mohamed *et al.* (2014) utilized QTL mapping to locate specific regions in the sorghum genome that contribute to resistance against striga. By employing molecular markers, the researchers could more efficiently link phenotypic resistance traits to specific genetic loci, thereby speeding up the breeding process. Another significant advancement in this area is the use of marker-assisted selection (MAS). This technique allows for the identification of resistant genotypes at the seedling stage, well before they are exposed to striga in field conditions. For example, Haussmann *et al.* (2004) demonstrated the effectiveness of MAS in selecting striga-resistant sorghum plants by combining phenotypic selection with molecular markers associated with resistance traits. This not only improves the efficiency of breeding programs but also ensures the development of more robust and reliable resistant varieties.

Recent genomic studies have also highlighted the potential role of specific resistance genes, such as those encoding for proteins involved in the plant's defense mechanisms. For instance, genes related to the production of phytoalexins, which are antimicrobial substances produced in response to pathogen attack, have been investigated for their role in conferring resistance to striga. A study by Swarbrick *et al.* (2008) found that certain sorghum lines with elevated levels of phytoalexin production exhibited enhanced resistance to striga parasitism. Moreover, integrating genotypic data with advanced biotechnological approaches, such as CRISPR/Cas9 gene editing, offers promising potential. This technology allows for precise modifications of the sorghum genome to enhance resistance traits. Studies like those conducted by Sander and Joung (2014) illustrate the feasibility of editing resistance-related genes to develop crops with improved resistance profiles. Tackling striga infestation in sorghum through genetic and genomic approaches holds significant promise. By implementing advanced breeding techniques, QTL mapping, marker-assisted selection, and biotechnological innovations, researchers can develop sorghum varieties that are resilient against striga, thereby ensuring improved food security and agricultural sustainability in Uganda and other affected regions. The continuous integration of these methods will likely lead to more effective and durable resistance, benefiting farmers and the agricultural industry as a whole.

Mycorrhizal Symbiosis

Mycorrhizal symbiosis represents a critical aspect of sorghum's ability to thrive in nutrient-poor soils, a common challenge in Ugandan agriculture. This symbiotic relationship involves the association of sorghum roots with mycorrhizal fungi, primarily arbuscular mycorrhizal fungi (AMF), which enhances nutrient uptake, particularly phosphorus, an otherwise immobile nutrient in the soil. According to Smith and Read (2008), mycorrhizal associations significantly improve the host plant's phosphorus uptake by effectively increasing the root surface area, allowing the absorption of nutrients from a larger volume of soil. Ugandan sorghum germplasm shows varying degrees of mycorrhizal dependency, largely influenced by genetic factors and soil conditions. Studies by Odeny *et al.* (2011) demonstrated that certain sorghum varieties inherently possess a higher propensity for forming effective mycorrhizal associations, which can be attributed to the genetic makeup of these varieties. This variation offers an avenue for the selection and breeding of sorghum cultivars with enhanced mycorrhizal symbiosis, potentially translating into improved crop performance under limited nutrient conditions.

The benefits of mycorrhizal symbiosis extend beyond nutrient acquisition; they also encompass improved water uptake and stress tolerance. A report by Augé (2001) highlighted that mycorrhizal sorghum plants exhibited higher drought resistance. This is particularly pertinent for the Ugandan context, where erratic rainfall patterns and prolonged dry seasons can adversely affect sorghum yields. Mycorrhizal fungi improve soil structure by binding soil particles into aggregates, which enhances water infiltration and retention, thereby mitigating the impact of drought (Rillig and Mummey, 2006). Furthermore, mycorrhizal symbiosis plays an integral role in the biological control of soil-borne pathogens, including *Striga hermonthica*, a notorious parasitic weed afflicting sorghum in Uganda. Inoculation with AMF has been shown to reduce striga infestation by improving the host plant's vigor and altering root exudation patterns that may otherwise favor striga germination and attachment (Douds *et al.,* 2000). Consequently, the integration of AMF inoculation in sorghum cultivation can serve as a sustainable approach to managing striga infestation, thereby safeguarding yield and reducing reliance on chemical control measures.

Research efforts have also delved into the mechanisms underpinning efficient mycorrhizal symbiosis. Key genes involved in the AMF signaling pathway, such as DMI1 (Doesn't Make Infections 1) and PT4 (Phosphate Transporter 4), have been identified and characterized in sorghum (Gutjahr and Parniske, 2013). Understanding these genetic determinants is crucial for developing sorghum varieties with enhanced mycorrhizal responsiveness. Marker-assisted selection and genetic engineering may facilitate the breeding of sorghum cultivars optimized for mycorrhizal symbiosis, thus harnessing its full potential for sustainable agriculture in Uganda. Mycorrhizal symbiosis is pivotal for the growth and resilience of sorghum in Uganda. By enhancing nutrient and water uptake, and providing biocontrol against pathogens like striga, mycorrhizal associations significantly contribute to the productivity and sustainability of sorghum cultivation. Continued research and breeding efforts to exploit this symbiosis will likely prove beneficial in addressing the agricultural challenges faced by Ugandan farmers.

Future Prospects

Harnessing the Genetic Potential for trait improvement of Ugandan Sorghum Germplasm. The genetic diversity of Ugandan sorghum germplasm holds immense potential for improving sorghum production and addressing key challenges faced by farmers in the region. For example, the Genetic diversity, population structure, and a genome-wide association study of sorghum lines assembled for breeding have been studied for a collection of 543 sorghum accessions. This study highlighted that sorghum breeding in Uganda stands to benefit significantly from harnessing SNP markers for genetic diversity assessment and trait association studies, thereby contributing to enhanced food security and livelihoods in the region (Kasule *et al.*, 2024). Future research and breeding efforts should focus on harnessing this diversity to develop sorghum varieties with enhanced perennity, resistance to Striga, and efficient mycorrhizal symbiosis. Moreover, genome-wide association studies (GWAS) and other genetic mapping approaches can identify specific genetic regions and candidate genes associated with desirable traits. This knowledge can guide breeding programs to develop sorghum lines with improved perennity, Striga resistance, and mycorrhizal symbiosis. Marker-assisted selection (MAS) can further accelerate the introgression of these traits into elite sorghum varieties.

Developing Climate-Resilient Sorghum Varieties. Perennial sorghum varieties offer significant advantages in terms of climate resilience and sustainable agriculture. They can withstand prolonged drought and establish new tillers after grazing or harvesting, reducing the need for replanting and conserving soil moisture. By identifying and incorporating perennity traits into improved sorghum varieties, farmers can reduce production costs and increase yields, even in challenging environmental conditions.

Enhancing Striga Resistance. Striga is a parasitic weed that causes significant yield losses in sorghum crops. Ugandan sorghum germplasm harbors natural resistance to striga, and understanding the genetic basis of this resistance can lead to the development of striga-resistant sorghum varieties. This would greatly benefit farmers in striga-infested areas, reducing crop losses and improving food security.

Promoting Efficient Mycorrhizal Symbiosis. Mycorrhizal fungi form symbiotic associations with sorghum roots, enhancing nutrient uptake and drought tolerance. Identifying sorghum genotypes with efficient mycorrhizal symbiosis can guide breeding programs to develop varieties that can better utilize soil nutrients and withstand water stress. This will reduce the need for chemical fertilizers and improve sorghum productivity in low-input farming systems.

Capacity Building and Knowledge Sharing. Investing in capacity building and knowledge sharing is crucial to harness the full potential of Ugandan sorghum germplasm. Training programs for researchers, extension workers, and farmers can empower them with the skills and knowledge to utilize genetic resources effectively. Establishing collaborative research networks and knowledge exchange platforms, especially collaborations between Universities, research centers, national research organizations, NGOs and local communities, will facilitate the dissemination of research findings and best practices, ensuring that innovations reach those who need them most.

By harnessing the genetic diversity of Ugandan sorghum germplasm and integrating advanced breeding technologies, we can develop sorghum varieties that are better adapted to local conditions, more resilient to climate change, and more productive. This will contribute to food security, improve livelihoods, and promote sustainable agriculture in Uganda and beyond.

Current Research Efforts. In Uganda, a collection of 543 sorghum accessions actively used, has been evaluated in breeding program according to the Genetic diversity, population structure, and a genome-wide association study of sorghum lines assembled for breeding. It has been concluded that sorghum breeding in Uganda stands to benefit significantly from harnessing SNP markers for genetic diversity assessment and trait association studies, thereby contributing to enhanced food security and livelihoods in the region (Kasule *et al.*, 2024). In addition, current research efforts into the genetics and genomics of sorghum focusing on perennity, resistance to Striga, and efficient mycorrhizal symbiosis in Ugandan germplasm represent a critical intersection of agricultural science and genetic engineering aimed at both alleviating food insecurity and promoting sustainable agriculture in the region. As such, these research efforts are multifaceted, involving various advanced molecular, genetic, and agronomic approaches. Below is the overview of the state of these ongoing researches.

(i) Genetic Analysis and Breeding for Perennity and strategies against Striga hermonthica

Perennity in sorghum is its ability to regrow after harvest without needing to be replanted conferring numerous agronomic benefits, including reduced need for ploughing and planting, which can conserve soil structure and reduce labor costs. Current research is leveraging high-throughput genotyping and phenotyping techniques to identify genetic loci associated with perennial growth habits of sorghum (Ferguson *et al.*, 2021). By employing next-generation sequencing (NGS) technologies, we are constructing high-resolution genetic maps to pinpoint quantitative trait loci (QTL) directly linked to perennial characteristics of sorghum (Guden *et al.*, 2023; Sahu *et al.*, 2020). Marker-assisted selection (MAS) is then used to breed sorghum varieties that can sustain multiple growing cycles, enhancing yield stability (Mwamahonje *et al.*, 2021). Striga, commonly known as the witch weed, is a parasitic plant that poses a significant threat to sorghum yields, particularly in sub-Saharan Africa (Ahmed *et al.*, 2024). We are focusing on uncovering and mapping resistance genes through genome-wide association studies (GWAS).

(ii) Molecular Consequences of Drought Stress on Sorghum-Soil Microbiome Interaction

Drought stress is a significant environmental constraint that impacts plant growth and productivity, particularly in crops like sorghum, which is a drought-tolerant cereal vital for food security in arid regions. Understanding the molecular consequences of drought stress on the sorghum-soil microbiome interaction is critical for developing strategies to enhance crop resilience and productivity. Sorghum has evolved several mechanisms to cope with drought stress, including morphological, physiological, and molecular adaptations. One of the key molecular responses is the alteration in gene expression patterns that govern various physiological processes such as water uptake, osmotic adjustment, and root architecture modifications (Muhammad *et al.*, 2022; Kang *et al.*, 2022). These changes help the plant to optimize water use efficiency and maintain growth under limited water conditions (Hatfield and Dold 2019).

At the molecular level, drought stress triggers the activation of stress-associated genes, including those coding for dehydrins, aquaporins, and various transcription factors like DREB (Dehydration-Responsive Element Binding) and NAC (NAM, ATAF, and CUC) family proteins (Hu *et al.*, 2022; Liu *et al.*, 2023) . These genes play crucial roles in mediating drought responses byregulatingprotectiveproteins, osmoprotectants, and antioxidative enzymes, thereby mitigating cellular damage caused by water deficit (Haghpanah *et al.*, 2024). The soil microbiome, comprising bacteria, fungi, archaea, and other microorganisms, significantly influences plant health and stress resilience (Wang *et al.*, 2024; Vincze *et al.*, 2024). Under drought conditions, the composition and function of the soil microbiome can be altered, impacting its interaction with sorghum roots.

CONCLUSION

This review highlights the remarkable genetic diversity and untapped potential of Ugandan sorghum germplasm for improving perennity, resistance to striga, and efficient mycorrhizal symbiosis. Despite the challenges faced by sorghum production in Uganda, the analysis of genetic variations and molecular markers has shed light on the genetic bases of these traits. With further research, the insights gained can be harnessed to develop sorghum varieties that are resilient to environmental stresses and more productive, ultimately contributing to food security and sustainable agriculture in Uganda.

Future research efforts should focus on exploring the specific genetic regions responsible for perennity, striga resistance, and mycorrhizal associations, including the identification of candidate genes and conducting genome-wide association studies. Additionally, field trials evaluating the performance of improved sorghum varieties are crucial to validate their effectiveness in Ugandan agro-ecological conditions. By harnessing the genetic diversity of Ugandan sorghum germplasm, we can unlock the potential to transform sorghum production systems, enhancing resilience and productivity for the benefit of farmers and communities. Continued research and collaboration among breeders, geneticists, and agronomists are crucial for the sustainable advancement of sorghum cultivation in the region.

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STATEMENT OF NO-CONFLICT OF INTEREST

The Authors declare no conflict of interest in the paper.

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