



# Profiling Cultivars Development in Kersting's Groundnut [*Macrotyloma geocarpum* (Harms) Maréchal and Baudet] for Improved Yield, Higher Nutrient Content, and Adaptation to Current and Future Climates

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Kersting's groundnut [*Macrotyloma geocarpum* (Harms.) Maréchal and Baudet], Fabaceae, is an important source of protein and essential amino acids. As a grain legume species, it also contributes to improving soil fertility through symbiotic nitrogen fixation. However, the crop is characterized by a relatively low yield ( $\leq 500$  kg/ha), and limited progress has been made so far, toward the development of high-yielding cultivars that can enhance and sustain its productivity. Recently, there was an increased interest in alleviating the burdens related to Kersting's groundnut (KG) cultivation through the development of improved varieties. Preliminary investigations assembled germplasms from various producing countries. In-depth ethnobotanical studies and insightful investigation on the reproductive biology of the species were undertaken alongside morphological, biochemical, and molecular characterizations. Those studies revealed a narrow genetic base for KG. In addition, the self-pollinating nature of its flowers prevents cross-hybridization and represents a major barrier limiting the broadening of the genetic basis. Therefore, the development of a research pipeline to address the bottlenecks specific to KG is a prerequisite for the successful expansion of the crop. In this paper, we offer an overview of the current state of research on KG and pinpoint the knowledge gaps; we defined and discussed the main steps of breeding for KG' cultivars development; this included (i) developing an integrated genebank, inclusive germplasm, and seed system management; (ii) assessing end-users preferences and possibility for industrial exploitation of the crop; (iii) identifying biotic and abiotic stressors and the genetic control of responsive traits to those factors; (iv) overcoming the cross-pollination challenges in KG to propel the development of hybrids; (v) developing new

approaches to create variability and setting adequate cultivars and breeding approaches; (vi) karyotyping and draft genome analysis to accelerate cultivars development and increase genetic gains; and (vii) evaluating the adaptability and stability of cultivars across various ecological regions.

**Keywords:** adaptability, biotic and abiotic stresses, climate change, cultivars development, Fabaceae, genomics, karyotyping, Kersting's groundnut

## INTRODUCTION

Agriculture is a major economic, social, and cultural activity that is highly weather and climate-dependent (Yohannes, 2015). Climate change is the worldwide environmental threat that would seriously cause shifts in crop production and affect mankind in several ways, due to more unpredictable and hostile weather patterns (Enete and Amusa, 2010; Cheng et al., 2017) including changes in average temperatures (heat and cold stress), distribution of rainfall (drought and floods) with an important impact on soils erosion and fertility, and increased occurrence of biotic stresses (pests and diseases) (Padi and Ehlers, 2008; Sileshi et al., 2010; Tirado and Cotter, 2010). The shifts in agricultural production also affect the food systems of consumers and the nutritional quality of many crops around the world (Gobu et al., 2020).

To cope with varying weather conditions, farmers adopted new cultivation practices including changes in the cropping calendar, weeding and fertilization regimes, crops varieties, and species (Snapp et al., 2018). To ensure ecosystem resilience, future agriculture systems should necessarily focus on species that can ensure both agriculture sustainability and food' nutritional quality (Mabhaudhi et al., 2019). Orphan species can contribute to developing a more resilient and nutritionally dense future agriculture in arid and semi-arid regions. Resilient alternative crops such as underutilized legumes are examples of such species that have the potential to contribute more to agriculture fitness. Among those orphan legumes, key species produced in sub-Saharan Africa included Bambara groundnut [*Vigna subterranea* L. (Verdc.)], Yam bean [*Sphenostylis stenocarpa* (Hoechst ex. A. Rich.) Harms.], Faba bean (*Vicia faba* L.), and Kersting's groundnut [*Macrotyloma geocarpum* (Harms.) Marechal and Baudet].

Kersting's groundnut (KG) is a diploid with  $2x = 2n = 22$  (Miège, 1954) or  $2x = 2n = 20$  (Odo and Akaneme, 2021). It is a geocarpic crop like Bambara groundnut, grown by smallholder farmers throughout West Africa. Kersting's groundnut is well-adapted to natural and agricultural conditions, making it a suitable surrogate to the major crops (Achigan-Dako and Vodouhè, 2006). Kersting's groundnut is a high value source of protein for many people in West Africa (Ajayi and Oyetao, 2009). It is also a rich source of minerals and crude fiber and low crude fat content (Obasi and Agbatse, 2003; Aremu et al., 2011). In Benin, the grains are sold in rural, semi-urban, and urban markets and provide substantial incomes to many smallholder farmers of its cultivated areas, where scarcity periods can cause prices to rise by as much as 10 dollars per

kg (Assogba et al., 2015; Akohoué et al., 2018). In addition to being an agronomically and nutritionally beneficial supplement to cereal crops (Tamini, 1995), it fixes atmospheric nitrogen and contributes to soil fertility (Mohammed et al., 2018, 2019). Unlike other legumes like groundnut (*Arachis hypogea* L.), soybean [*Glycine max* (L.) Merr.], cowpea [*Vigna unguiculata* (L.) Walp.] that have received considerable scientific and financial supports, less attention has been devoted to this crop by mainstream research and development institutions, perhaps due to a lack of awareness about its values. It is grown as landraces, which are mixtures of lines that have been naturally selected across agroecologies where they have been grown for perhaps thousands of years and are likely to have low yields and are/become less suitable to climate variations. Furthermore, the crop still lacks adequate germplasm management strategy, suitable seed systems, and optimal agronomic practices. Therefore, the absence of high yielding cultivars with tolerance/resistance to biotic and abiotic stresses is causing a progressive decline in areas where it is cultivated (Akohoué et al., 2018; Coulibaly et al., 2020). Other production challenges include the lack of marketing channels that limit crop promotion. Fortunately, researchers' increasing interest in underutilized crops to ensure food security has breathed new life into this long-forgotten crop.

Because climate change is expected to induce extreme weather conditions, particularly with negative consequences for agriculture in tropical areas (Lane and Jarvis, 2007; Burke et al., 2009; Bellon and Van Etten, 2014), there is a clear need to select crop genotypes that can tolerate severe environmental conditions. For KG, farmers in Benin, Burkina Faso, and Ghana, for instance, modified their cropping calendars to accommodate the weather issues by planting earlier (in June) or later (in August) (Adu-Gyamfi et al., 2011; Assogba et al., 2015; Akohoué et al., 2018; Coulibaly et al., 2020). However, given the rapid deterioration of climate conditions, cultural practices alone will likely not be enough to ensure the endurance of the crop landraces. Hence, high yielding and stress-tolerant cultivars development are required for the promotion and sustainable production of KG (Akohoué et al., 2018; Coulibaly et al., 2020).

Initial researches on KG included ethnobotanical studies, analysis of genetic diversity to assist breeding programs in selecting diverse parental material based on morphological (Bayorbor et al., 2010; Assogba et al., 2015; Akohoué et al., 2019) and biochemical markers (Pasquet et al., 2002). More recently, molecular markers including SSRs and SNPs were used to harness the genetic diversity among and within KG landraces (Mohammed et al., 2018; Kafoutchoni et al., 2021a), and analyze the marker-trait association and genomic

prediction accuracy (Akohoue et al., 2020). However, basic and accurate knowledge about physiology, resistance/tolerance to biotic and abiotic stresses, and the genetic basis underpinning traits of interest is still lacking for this species. In addition, the crop lacks an appropriate breeding pathway, genetic and genomic resources [i.e., breeding populations, inbred lines (ILs), and reference genome] that could be exploited to accelerate cultivars development and make its production profitable to smallholder farmers.

This review provides an overview of the background and the recent research progress into the West-African grain legume, KG; it highlights the existing gaps that need to be addressed and gives a pathway for future breeding and promotion. The main objectives of this paper are (i) to provide an overview of the background on the current research on KG; (ii) to pinpoint knowledge gaps hindering the crop improvement; and finally, (iii) to suggest and discuss future research and breeding programs on KG. The following questions are addressed throughout this review: where do we stand in the research on KG? What are the research gaps hindering the production and promotion of KG? What should be the key components of a successful breeding program for KG to overcome the identified limits?

## BASIC KNOWLEDGE ABOUT KERSTING'S GROUNDNUT

### Origin, Distribution, and Production

Kersting's groundnut is an underutilized legume species that thrives in West Africa, cultivated across the savannah zone from Senegal to Nigeria and Cameroon and probably, in Tanzania and Mauritius. Although its origin is still uncertain, northern Togo and central Benin were suggested as the source of the crop (Achigan-Dako and Vodouhè, 2006). The crop is grown in contrasting environments, ranging from arid and milder environments of Sudanian zones to more humid environments of Guinean agroecological zones (Baudoin and Mergeai, 2001). Recent investigations and wide germplasm collection by Akohoué et al. (2018) and Coulibaly et al. (2020) revealed the Southern Sudanian zones of West Africa as the centre of diversity for the crop. Kersting's groundnut was found by Hepper (1963) in its wild form *M. geocarpum* var. *tisserantii*, in Cameroon and the Republic of Central Africa. However, Pasquet et al. (2002) found a high genetic distance between the var. *geocarpum* and var. *tisserantii* suggesting that they should be assigned to two different species.

Six different landraces were identified in KG based on the seed coat colour are grown across West Africa and include the White/Cream, White mottled with black eye, White mottled with greyed orange eye, Black, Brown, and Red landraces (Adu-Gyamfi et al., 2011; Assogba et al., 2015; Akohoué et al., 2018; Coulibaly et al., 2020).

Kersting's groundnut is grown annually during the cropping season, as sole crop, in rotation, intercropped with cereals, with generally low yields (500 kg ha<sup>-1</sup>) (Amujoyegbe et al., 2007; Adu-Gyamfi et al., 2011; Assogba et al., 2015; Akohoué et al., 2018; Coulibaly et al., 2020), which is far less than the yields reported

for other legume crops like Bambara groundnut (Nedumaran et al., 2015) and groundnut (Abady et al., 2019; Konate et al., 2020). The low yield levels observed in KG are attributed to various stresses such as biotic (pests such as pulses beetles and rodents, and diseases including fungi and viruses) (Badii et al., 2013; Assogba et al., 2015; Agoyi et al., 2019) and abiotic (drought, high humidity, and low soil quality). Furthermore, farmers are cultivating unimproved varieties, at a small scale (cultivated areas <1 ha), using poor agronomic practices. The crop can grow and fix nitrogen in drought-prone environments where many other crops can hardly survive (Dakora and Keya, 1997). Prolonged water stresses (droughts and excess water) may result in changes in crop growth, development, and grain yield losses (Akohoué et al., 2018; Coulibaly et al., 2020). Improving KG farming systems through integrated approaches could help to enhance crop productivity. However, improving the cropping system alone would not be sufficient to face the evolving climate. Hence, research investigations in KG should focus on both, development of high yielding cultivars, and establishment and promotion of best agronomic practices.

### Nutritional, and Market Benefits

Kersting's groundnut is cultivated for its palatable seeds, an important source of nutrients including protein (12.9–21.3%), fiber (2.01–10.9%), minerals (zinc, calcium, and magnesium), and essential amino acids (Ajayi and Oyetayo, 2009; Aremu et al., 2011; Abiola and Oyetayo, 2015). The comparative analysis between KG and some legume crops grown in Sub-Saharan Africa (**Supplementary Table 1**) revealed a higher level of arginine content (4.1–15.9% of crude protein) in KG than in the other legumes. Arginine is the main amino acid recommended for pediatric growth (Ajayi and Oyetayo, 2009) and pregnant women. Kersting's groundnut seeds are low in crude fat content compared to many other legumes such as African yam bean, chickpeas (*Cicer arietinum* L.), and soybean. The seeds of KG can be used as a complementary food to other crops like maize (*Zea mays* L.), rice (*Oryza sativa* L.), and cassava (*Manihot esculenta* Crantz) (Aremu et al., 2011; Awolu et al., 2015, 2020; Awolu and Osigwe, 2019). Kersting's groundnut haulms are also used to feed livestock. Moreover, KG's protein can be used in juice industries to improve juice quality and storage properties (Osungbade et al., 2021). Seeds of KG are reported to exhibit relatively high content in tannins and polyphenols compared to other legumes and have antioxidant properties (Akpavi et al., 2008). However, the anti-nutritional properties of these compounds can bind to nutritional components making them completely or partially unavailable for digestion (Obasi and Agbatse, 2003). Fortunately, treatments such as dehulling, soaking, cooking, and fermentation can potentially reduce antinutritional factors and improve the bioavailability of nutrients (Obasi, 1996; Ijarotimi and Esho, 2009). In addition, KG exhibits several medicinal and therapeutic benefits according to local communities; the decoction of its seeds (mainly the Black and Brown landraces) or leaves is used to treat stomach aches (Tamini, 1995; Amujoyegbe et al., 2007; Akohoué et al., 2018). The economic importance of the crop for local populations was reported in Benin where its price can rise from 2 to USD 7–10 per kg in a scarcity period (Assogba et al., 2015).



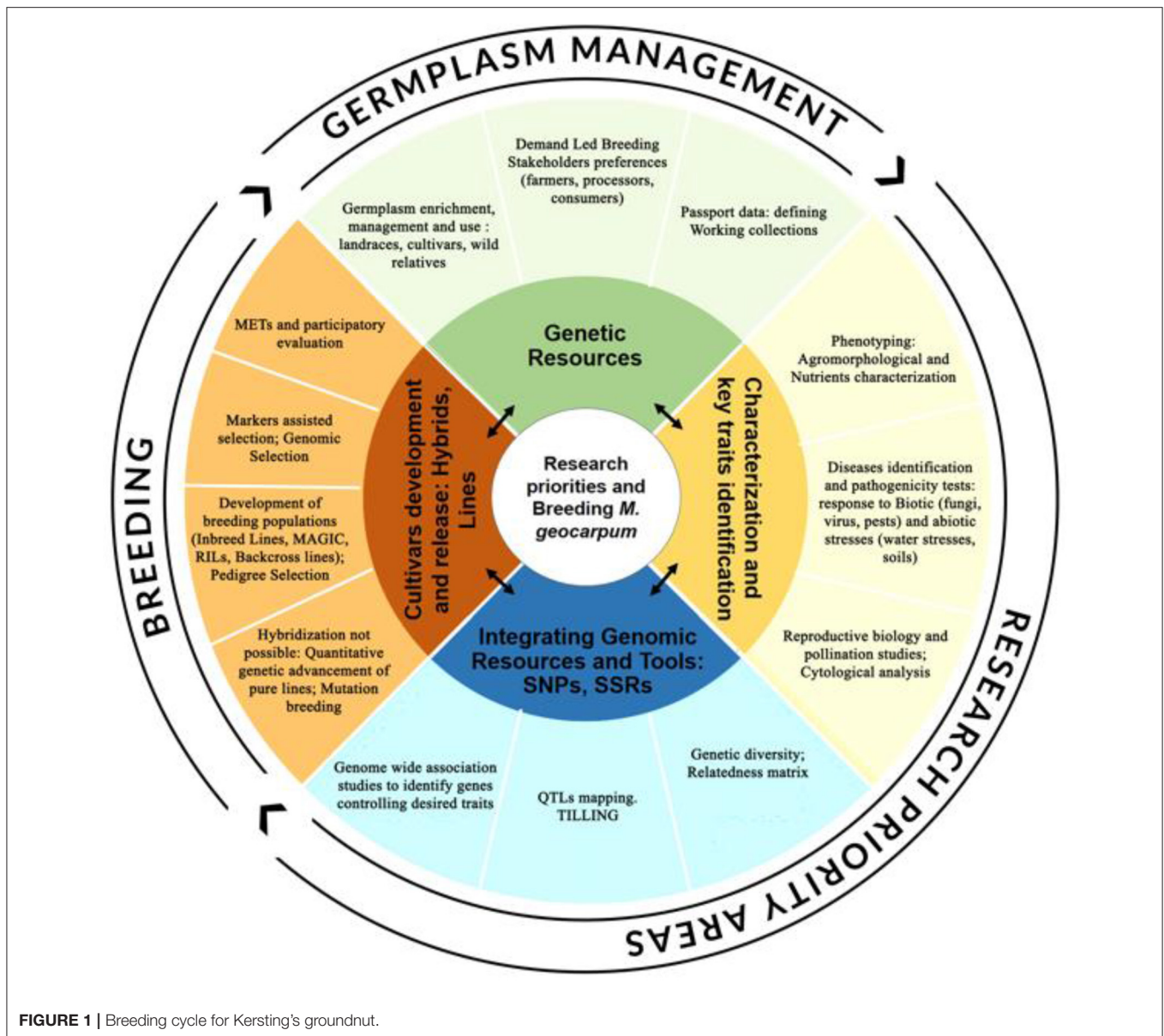


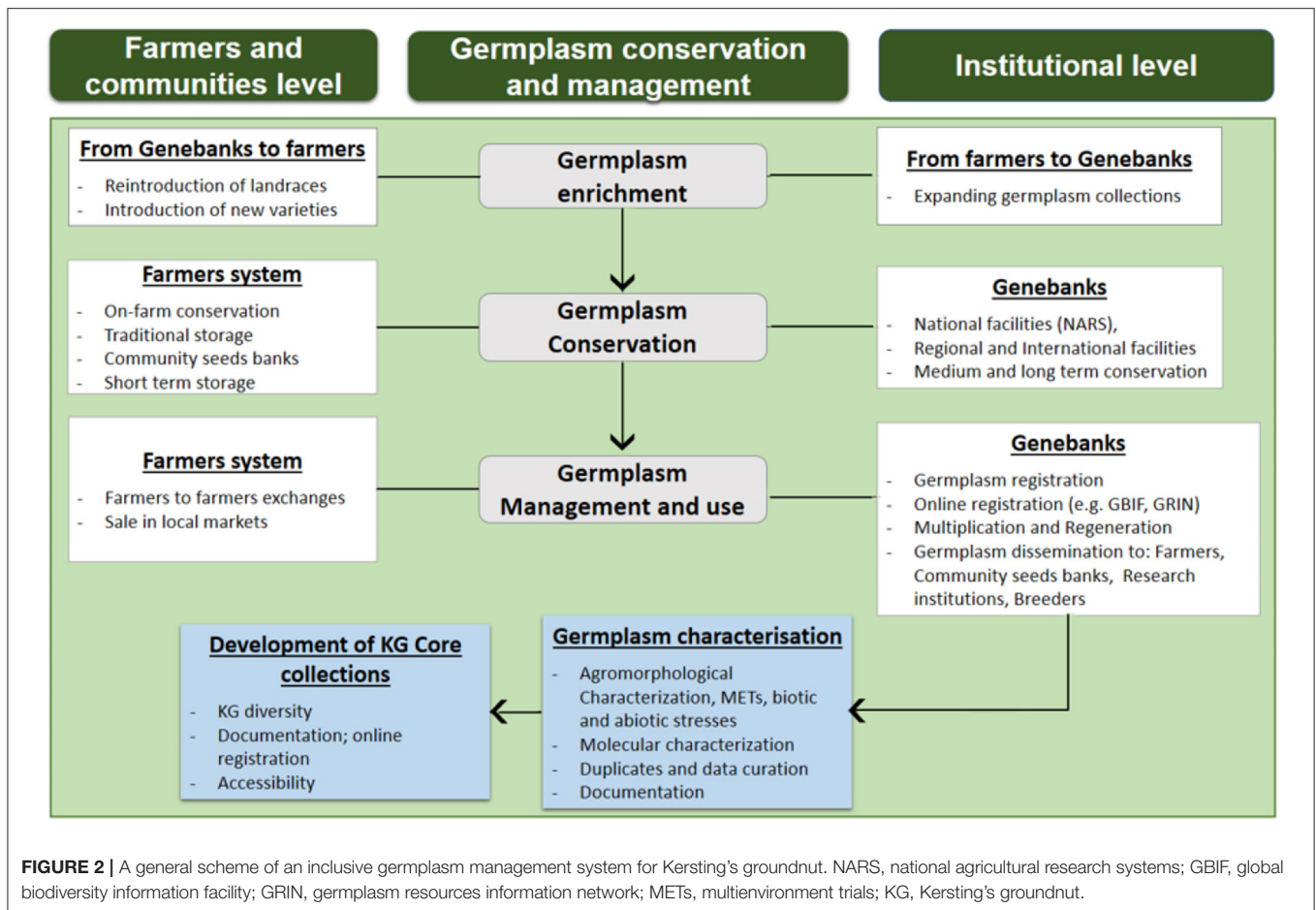
FIGURE 1 | Breeding cycle for Kersting's groundnut.

In other countries such as Burkina Faso, Ghana, and Nigeria, the changes in cropping patterns and the introduction of new cash crops such as groundnut, cowpea, cotton (*Gossypium hirsutum* L.), have negatively impacted the market value of KG's seeds (Tamini, 1995; Amujoyegbe et al., 2007). Therefore, promotion actions would be necessary for those countries to encourage stakeholders and policymakers toward sustainable production of the crop.

### DEVELOPING A BREEDING PROGRAM FOR KERSTING'S GROUNDNUT

The development of improved cultivars in KG that meet farmers' and end-users' preferred traits requires the design of a comprehensive approach. Such an approach should

integrate (i) germplasm assembly, characterization, evaluation, and definition of breeding objectives, (ii) parental lines and hybrids selection, and (iii) participatory breeding through multi-location evaluation trials (METs) of lines and on-farm participatory evaluations (Figure 1). Successful germplasm screening and selection of best KG genotypes requires accurate and high throughput phenotyping across contrasting environments. The target characteristics are measured over multiple growing cycles throughout different environments and stress conditions. Field evaluations of genotypes require the use of appropriate experimental designs, data collection techniques, and interpretation to make accurate decisions. The cultivars development pathway can also integrate tools such as marker-assisted breeding (MAB) and genome-wide selection.



**FIGURE 2** | A general scheme of an inclusive germplasm management system for Kersting's groundnut. NARS, national agricultural research systems; GBIF, global biodiversity information facility; GRIN, germplasm resources information network; METs, multienvironment trials; KG, Kersting's groundnut.

## Genetic Resources Management for Kersting's Groundnut Breeding and Utilization

### Germplasm Conservation and Management

The availability of various genetic resources is the prerequisite for initiating genetic improvement in any crop. The adequate and sustainable conservation and use of KG resources might be categorized into three main steps including the additional collections, conservation, and proper germplasm management and use (Figure 2).

In recent decades, the conservation of the genetic resources of orphan crops, including *M. geocarpum*, has attracted more attention because of their role in facing the climate change scenario (Kamenya et al., 2021) and food security. Efforts were made in the collection of KG germplasm and assessment of its on-farm diversity in West Africa (Adu-Gyamfi et al., 2011; Akohoué et al., 2018; Coulibaly et al., 2020). These collections have been further utilized in KG research programs, are sources of useful genes for the development of improved varieties. Overall, about 700 accessions including six landraces based on seed coat color were collected across Benin, Burkina Faso, Ghana, Togo, Nigeria, and Ivory Coast. These accessions are safeguarded and maintained, *ex-situ* at seven national genebanks located in

four countries (Table 1). In Benin, the University of Abomey-Calavi holds the largest KG germplasm, with more than 600 accessions representing six countries of origin. In Burkina Faso, 32 accessions were collected from two countries and conserved at the INERA. The SARI in Ghana holds 16 accessions, collected in Ghana. However, efforts are still required when compared to the genetic resources accessible *ex-situ* for most of the other legume crops like Bambara groundnut (Massawe et al., 2005, 2007; Aliyu et al., 2016; Mayes et al., 2019), chickpea (Raina et al., 2019; Jha et al., 2020; Kushwah et al., 2020), horse gram (Singh et al., 2014; Chahota et al., 2020), mungbean [*Vigna radiata* (L.) Wilczek] (Ha and Lee, 2019; Mogali and Hegde, 2020; Shanthala et al., 2020), pigeon pea [*Cajanus cajan* (L.) Millsp.] (Foyer et al., 2016; Sharma et al., 2020). Moreover, in Nigeria and Ivory Coast, there is no clear information about the crop genetic resources collection and conservation in genebanks. Although KG production was mentioned in other countries outside West Africa, in Cameroon, Tchad, Mauritius, Tanzania, and Fiji (Achigan-Dako and Vodouhè, 2006), no proper germplasm collection has been undertaken in those countries. Considering the threats to KG, the first and urgent action is to expand germplasm collection mainly across countries and locations not yet explored. This is essential for preserving germplasm and for the setup of a formal seed system for KG. *In-situ* and *ex-situ*

**TABLE 1** | Kersting's groundnut germplasm collection available in national genebanks in West Africa.

Country	Institution	Num of accessions	Num of landraces*	References
Benin	Laboratory of Genetics, Biotechnology, and Seed Sciences (GBioS)—UAC	409	6	Akohoué et al., 2018; Coulibaly et al., 2020
Benin	Laboratory of Applied Ecology (LEA)—UAC	217	5	Kafoutchoni et al., 2021a
Benin	Laboratory of Biotechnology, Genetic Resources, and Plant and Animal Breeding (BIORAVE)—UAC	32	3	Assogba et al., 2015
Burkina Faso	Institute of Environment and Agriculture Research-Farako-Ba (INERA-FBa)	32	3	Coulibaly et al., 2020
Ghana	Savanna Agricultural Research Institute (SARI)	16	3	Adu-Gyamfi et al., 2011
Nigeria	University of Agriculture, Makurdi, Nigeria	No data	No data	Obasi and Agbatse, 2003
<b>Total</b>		<b>706</b>	<b>6</b>	

\*: Landraces are based on seed coat color; UAC: University of Abomey-Calavi.

conservations are the most efficient methods to conserve the genetic diversity of KG resources and minimize losses through time. Although the resources of KG are more abundant in Benin, apparently there is no National plan for *in-situ* conservation of the crop genetic diversity, nor in other countries of production. Unfortunately, many cultivation areas of KG are threatened with the loss of invaluable genetic resources. This is more critical for the wild relatives of the species for which the genetic diversity collection and conservation are not well-documented. To restore lost or reduced crop resources in these areas, the re-introduction or restoration of the species would be essential. This approach can be effective through farmers' fields school, participatory on-field characterization, and evaluation of accessions, and promotion of KG's products with added values.

Farming communities have been preserving or conserving their local crop and varieties in small stores (e.g., clay pots, gourds, underground pits) that represent a "de facto" *ex-situ* conservation system that is likely more dynamic than the conventional one. Moreover, farmers consistently maintain seeds as a security net to provide a backup in case of crop failures to thrive, as well as for sowing the next season. This traditional seed system, mainly based on the farmers' varieties, is an important backup to agricultural crop production in a country (Halewood, 2016). However, both public and private sectors are reluctant to invest in underutilized crops such as KG. In this context, a possibility for an establishment of a community-based seed system, as a complementary measure (Stolton et al., 2006) would be explored toward integrated and inclusive genetic resources management of KG. An example of this system is the community seeds banks (CSB) (Vernooy et al., 2015). Depending on how they are organized, CSB serves functions including conservation and reintroduction of germplasm, access to quality seeds, and enhancing seed and food sovereignty (Vernooy et al., 2015). Moreover, These institutions may facilitate linkages between genebanks and local seed banks considering biodiversity use policies. Genebanks or scientists can also interact, distribute, and organize KG datasets and resources through biodiversity research-data portals, which have proliferated in recent decades. Several specialized portals (PROTA: Plant Resources of Tropical Africa, GBIF: Global Biodiversity Information Facility; GRIN: Germplasm Resources

Information Network, POWO: Plants of theWorld Online, etc.) and platform (NARS: National Agricultural Research Systems), collect, disseminate, and promote particular data types for a large number of species, including legumes (Legumes of the World Online, LOWO). However, the use of such platforms in KG germplasm management and use still lacks or is very limited. Indeed, KG remains absent and not documented in the Legumes dataset portals. The recent characterization including agromorphological and molecular information (Assogba et al., 2015; Akohoue et al., 2019, 2020; Kafoutchoni et al., 2021a), can also be incorporated into these online platforms and continuously updated for use by breeders and genetic resources managers. Moving forward, the development of core collections (Paredes et al., 2010; Upahyaya, 2015) using characterization, evaluation, and further collections datasets is the importance of paramount for the effective future management of KG genetic resources, to make germplasm more accessible for interested scientists for breeding purposes or scientific studies. Moreover, these collections could be used for association mapping and genes discovery for targetting material into the original germplasms collected (Gupta et al., 2019). The accessions that have been highly characterized within the collections can be used to inform decisions in breeding programs (Zhang et al., 2019; Abdi et al., 2020).

### Assessing Farmers and End-Users' Preferences for New Cultivars Development

Agronomic and processing qualities are important criteria for breeding crops, which must meet specific quality parameters. Kersting's groundnut resources are being managed and maintained by farmers over centuries for their own needs. They have been the growers, germplasm managers, and main users of the species. Thus, to ensure the efficiency of KG new cultivars development, adoption, and sustainable use, access farmers' preferences sought in new varieties is fundamental in defining breeding objectives and priorities, and implementing a successful breeding program. In this context, Coulibaly et al. (2020) investigated farmers' desired traits and found that high yield, resistance/tolerance to pests and diseases, and abiotic stresses were major traits sought in KG new varieties. Among the abiotic stresses, heat, drought, and moisture, are most prevalent

**TABLE 2** | Genetic characterization in KG using morphological and molecular markers.

References	Number of accessions	Landraces used	Origin	Markers involved	Genetic variability
Pasquet et al., 2002	20 (2 wild and 18 cultivated)	White (White with black eye), Black, and Gray seeds (White)	Cameroon; Togo, Burkina Faso	19 allozymes encoding 32 putative loci	No variation among domesticated accessions, within and between the two wild accessions. Very high genetic distance between wild and domesticated accessions
Bayorbor et al., 2010	12	Black, White (White with black eye), mottled (Brown)	Ghana	Morphological traits: PHT, CDM, LAI, FSW, DSW, FRW, DRW, NDN, DFF, YLD, HSW	Two clusters
Adu-Gyamfi et al., 2012	16	Black, White (White with black eye), mottled (Brown)	Ghana	Morphological traits: LAI, FSW, DSW, NDN, NPD, YLD, HSW	Variation between landraces and genotypes for LAI, HSW, YLD
Assogba et al., 2015	32	Black, White, Red	Benin	Morphological traits: PHT, DIP, LEL, LEW, PEL, DFF, DTM, NPP, YPP, YLD, HSW, SEL, SEW, PTC, FPC, SCC	Three different clusters for LEW, DFF, YLD
Mohammed et al., 2018	5	Black, White with black eye, mottled (Brown)	Ghana	12 single sequence repeats markers (SSRs) derived from cowpea	Eight monomorphic bands in KG; high genetic variation among landraces
Akohoue et al., 2019	297	White, Black, White with black eye, Red	Benin, Togo	Morphological traits: PHT, DIP, LEL, LEW, PEL, DFF, DTM, NPP, YPP, YLD, HSW, SEL, SEW, PTC, FPC, SCC	Four different clusters for all traits except for SEW
Akohoue et al., 2020	281	White, Black, White with black eye, Red	Benin, Togo	- 493 Single nucleotide polymorphisms (SNPs) - 15 quantitative traits	- Four different clusters defined based on seed coat color and; - Two genetic populations; - 10 significant SNPs related traits, with six SNPs consistent across environments; - Moderate to high prediction accuracies
Kafoutchoni et al., 2021a	227	Cream (White), Cream seed with black eye (White with black eye), Black, Brown mottled, Brown	Benin, Burkina Faso, Ghana, Togo, and Nigeria	886 Single nucleotide polymorphisms (SNPs)	Eight different clusters based on collection sources

PHT, plant height; CDM/DIP, canopy diameter or diameter of plant; LEL, leaflets length; LEW, leaflets width; PEL, petiole length; LAI, leaf area index; FSW, fresh shoot weight; DSW, dry shoot weight; FRW, fresh root weight; DRW, dry root weight; NDN, nodulation; DFF, number of days to 50% flowering; DTM, days to maturity; NPD, number of pods; NPP, number of seeds per plant; YPP, yield per plant; YLD, grain yield; HSW, hundred seed weight; SEL, seeds length; SEW, seeds width; PTC, petiole color; FPC, fresh pod color; SCC, seed coat color.

in KG production. They found that farmers' preferences varied with social factors such as sociolinguistic membership. This suggests that the genetic improvement of the crop should consider not only agroecologies conditions but also socio-economic factors during the cultivars development process. Moreover, integrating end-users' (processors and customers) preferences is also important to better direct plant breeding objectives (Brouwer et al., 2015; Ragot et al., 2018; Dufour et al., 2021; Tchokponhoue et al., 2021). Hence, further investigations must be carried out across the cultivated areas, involving all stakeholders toward its efficient genetic improvement and end products dissemination. Once desired traits are defined, breeders can then collect genotypes that have the attributes required through characterization and screening of the available germplasm collections.

## Research Priority Areas for KG Cultivars Development

### Genetic Resources Characterization and Evaluation

#### *Genetic Diversity Analysis and Evaluation*

Kersting's groundnut is a small legume species with a maximum spread of 50 cm and a height of up to 40 cm. Unlike other geocarpic legumes such as peanuts, KG branches are coiled and interspersed in a spiral form lying above the ground. On the other hand, the leaves are erected on the branches, giving the plant a bushy growth habit. Kersting's groundnut accessions were characterized and evaluated for various agromorphological traits (Bayorbor et al., 2010; Assogba et al., 2015; AVRDC, 2015; Akohoue et al., 2019) (Table 2). Major descriptors included growth habit, flowering and maturity times, plant height, spread diameter, grain yield, and yield components.



All morphological markers were reported to be significantly affected by environmental factors, except growth habit traits (Adu-Gyamfi et al., 2012; Assogba et al., 2015; Akohoue et al., 2019). Adu-Gyamfi et al. (2012) reported significant variation among the White mottled with black eye (White), Black, and Brown (Mottled) landraces of Ghana, based on their agro-morphological performance. Similarly, in Benin, the agromorphological evaluation showed that the White, Black, and Red landraces were significantly different for agronomic performance (Assogba et al., 2015). Still, in Benin, Akohoue et al. (2019) analyzed the diversity in four landraces of KG (White, Black, White mottled with black eye, and Red) using morphological markers and found four clusters based on genotypes performance. The first three clusters were mainly composed of the White landrace while the fourth cluster included the other coloured-coat ones. In terms of performance, individuals in clusters 2 and 4 exhibited higher performance and were intermediate and early maturing genotypes, respectively. Although there is a relatively increasing genetic and phenotypic data on traits, in-depth phenotypic characterization through multi-trait and multi-environmental trials should be conducted using the available germplasm, as a whole, to shed light on the trait variations in the characterized germplasm as well as the performance of landraces grown by farmers. In addition, investigating the response of these landraces under biotic and abiotic stress conditions could be relevant for the improvement of KG. Low yields were obtained in KG by farmers, as well as by researchers, hence, breeding activities must focus on improving yield and tolerance to biotic and abiotic stress factors. However, genotype by environment interactions (GEI) affects yield, making it challenging to select genotypes with wide adaptation, resulting in delayed cultivar release (Abady et al., 2019). Crop breeding strategies for higher yield and disease tolerance can be accelerated through the use of high throughput phenotyping (Shakoor et al., 2017). This technique was successfully used in phenotyping groundnut for the total oil and high oleic acid contents (Sundaram et al., 2010; Awada et al., 2018). Although the high-throughput phenotyping technique is an emerging approach, and its application in crop breeding is still very limited, its utilization in KG breeding could be explored. In 2002, Pasquet used isoenzymes to assess the diversity within and between cultivated KG and its wild form. He found a low variability within each group and high genetic divergence between the cultivated and the wild types. Mohammed et al. (2018) assessed the transferability of cowpea-derived Simple Sequence Repeat markers (SSRs) to KG and revealed genetic variability among the landraces studied. More recently, Akohoue et al. (2020) and Kafoutchoni et al. (2021a) applied SNP markers to assess KG genetic diversity and population structure and found low variation within landraces and relatively high genetic distance between landraces. Furthermore, Akohoue et al. (2020) analyzed marker-trait association and genomic prediction accuracy for main agronomic traits of KG. They found markers related to plant morphological traits, flowering time, maturity, yield, yield components, and seed characteristics. Their results also showed low prediction accuracies for yield and related traits and high prediction accuracies for flowering time, maturity, and 100 seeds

weight traits. The findings of these different researches showed the existence of genetic variability in KG and provided the first insight into the relationships of phenotype-to-genotype in KG.

### *Proximate and Anti-nutrient Contents in Kersting's Groundnut*

Quantifying the biochemical properties in KG can serve as a guide to exploit its potential and benefits for human and animal nutrition. Proximate compositions of KG (**Supplementary Table 1**) showed that crude protein content varied from 12.90 to 22.95%, while total fiber ranged between 2.01 and 10.90%, and crude carbohydrate of 57.87–81.00%. Results also indicated a low crude fat in KG with a proportion of 1.00–5.29%. The proteins of KG exhibit interesting essential amino-acid profiles (32.7–44.1%) that make the crop attractive for smallholder farmers. It has a higher arginine proportion compared to many other legumes such as Bambara groundnut (0.064–5.48%, Aremu et al., 2017; Oyeyinka et al., 2017), cowpea (3.5–8.52%, Khattab et al., 2009; Eashwarage et al., 2017), common bean (*Phaseolus vulgaris* L.) (1.17–7.59%, Junkanti et al., 2012; Bouchenak et al., 2013). These findings showed high variability in the levels of nutrients and anti-nutrients in KG, which is potentially due to the biochemical analysis techniques, seed quality, environments, as well as landraces used. Akpavi et al. (2008) compared the proteins and antinutrient contents of two landraces of KG (White and Black) and found a difference between the landraces. Moreover, Badii et al. (2011) suggested that the higher tannins content in the Black and Brown landraces compared to the White ones conferred them more resistance to pulse beetles. Based on these results, we can hypothesize that the varying content of these compounds among landraces is genetically determined. Such genetic variations in KG seed composition offer possibilities for the improvement of related traits through intraspecific crosses. Therefore, accurate information about the proximate and antinutrient compositions of each landrace has become essential for the development of cultivars with high-quality nutrient content.

### **Analysis of Biotic and Abiotic Stresses in Kersting's Groundnut**

Abiotic stresses affecting KG production include drought, high relative humidity, heat, and low soil quality. Although the crop is known to be drought-tolerant (Baudoin and Mergeai, 2001), its yield can be reduced significantly when exposed to long and extreme water stresses. Thus, more resilient varieties and agricultural systems are required for the promotion of KG in the era of global climatic change.

The biotic stresses associated with KG's production include insect pests, rodents, and diseases (Agoyi et al., 2019). In the fields, leaves and pods are destroyed by grasshopper (*Locustra* spp.) and Millipede (*Myriapoda* spp). In storage, bruchid weevils (*Callosobruchus maculatus* F.) cause serious damage to the grains. Badii et al. (2011) analyzed the susceptibility of KG seeds to this insect and found the proportion of weight loss in seeds ranged from 8.0 to 14.4% and susceptibility index varying between 4.3 and 12.5. They also found that the effects of these pests on KG seeds differed among landraces; the White landrace



showed higher susceptibility to *C. maculatus* than the Black and Brown ones. To minimize grain losses in storage, farmers stored KG as pods or used chemical products or extracts of plants (Assogba et al., 2015; Akohoué et al., 2018; Coulibaly et al., 2020). Badii and Nyarko (2013) and Badii et al. (2013) proposed the extracts from *Hyptis spicigera* (Lam.) and diatomaceous earth for protecting KG against *C. maculatus* infestation. Although the application of biopesticides and insecticides can help farmers in controlling those pests, the development of pest and disease-resistant cultivars remains non-explored and is needed. Drought followed by heavy rain can raise the risk of floods, thereby creating conditions suitable for fungal infestations (Tandzi and Mutengwa, 2020). Agoyi et al. (2019) observed the wilting of the aerial parts, mold, rust, and viruses diseases in KG. A clear knowledge of the pathogenicity of these diseases and the response of KG to the pathogens still lacks and needs to be thoroughly investigated for the development of integrated pests and diseases management, and breeding strategies. In general, legume crops, are attacked in the field by more than one disease and pest at a time (Reddy, 2009), therefore the development of multiple disease resistant varieties is needed and should be explored in KG.

### Integrating Molecular Tools and Resources in Breeding Kersting's Groundnut

The availability of genomic information and modern technologies offers a unique opportunity for efficiently improving crops species (Xu and Crouch, 2008; Varshney et al., 2013; Pandey et al., 2016). Many crops' genes and gene activities are constantly being studied and characterized to maximize agricultural production and feed the world's rising population (Ibrahim Bio Yerima and Achigan-Dako, 2021). These studies added value to plant breeding scheme by opening the door to Marker-assisted breeding (MAB). MAB has been successfully used in several legumes' selection programs such as cowpea and soybean; it has accelerated the selection process, and improved genetic gains (Boukar et al., 2016; Omoigui et al., 2017; Ojiewo et al., 2018). Developing and applying genomic tools in legume breeding is therefore of particular relevance to facilitate their promotion and improvement for sustainable production. In KG, Akohoué et al. (2020), Kafoutchoni et al. (2021a) provided the first insights into population structure and the existence of genetic diversity among landraces or morphotypes using SNP markers. In addition, the application of genomic tools such as genome-wide association study (GWAS) and genomic selection (GS) lead to high prediction accuracies (~0.79) and the identification of 10 significant SNP-traits associations (Akohoué et al., 2020). These studies revealed the high potential and perceived impact of the application of genomics tools for the improvement of KG. Unfortunately, the absence of the reference genome of KG represents a major challenge for proper and precise association and prediction studies, and the application of marker-assisted selection (MAS) within the species (Akohoué et al., 2020). Moreover, low alignment of SNP markers with sister species such as Adzuki bean [*Vigna angularis* (Willd.) Ohwi and H. Ohashi], Bambara groundnut, the common bean was reported in previous studies (Akohoué et al., 2020; Kafoutchoni et al., 2021a). Thankfully, the whole-genome sequence of

horsegram (*Macrotyloma uniflorum*), a closely related species, was recently released for the first time by Shirasawa et al. (2021) and offers a unique opportunity for phylogenetic and comparative genomic analyses in KG. Comparative genomic analysis between the two species will enable the identification of genes coding for quantitative and complex traits of interest in KG. Furthermore, transcriptomic analysis can also be performed to identify stress-responsive expressed sequence tags to develop KG cultivars with multiple resistances to abiotic and biotic stresses. Therefore, future efforts for in-depth studies for KG include: (i) the whole genome sequence assembling, (ii) QTLs identification and validation for farmers and end-users preferred traits, (iii) integration of validated QTLs into MAB programs, and (iv) validation of GS and prediction for accelerated cultivar development. Once the KG complete genome is sequenced, backcrossed inbred lines (BIL), recombinant inbred lines (RILs), and multiparent advanced generations inter-cross (MAGIC) breeding populations can be developed to refine the construction of genetic linkage maps (QTLs mapping) and the discovery of genes associated with desired traits (Pandey et al., 2012; Priyadarshan, 2019). Likewise, by developing an F2 population, the bulk segregant analysis (BSA) can be also a useful tool for detecting significant SNPs and identifying candidate genes in plants (Quarrie et al., 1999; Magwene et al., 2011). This is particularly useful for species like KG for which association panels are not readily available. However, the development of such populations in the crop can only be possible if hybridization barriers are unlocked.

### Overcoming the Cross-Pollination Challenges in KG Surveying the Pollination System

The development of breeding populations through intraspecific hybridization is required to efficiently address the absence of improved cultivars in KG (Ayanan and Ezin, 2016; Akohoué et al., 2018; Coulibaly et al., 2020; Kafoutchoni et al., 2021a). For a successful hybridization in the crop, the flower biology and structure, as well as the pollination patterns have to be well-understood. Hence, floral anatomy and physiology, floral and fruiting phenology, and reproductive biology were at the heart of the rising research interest in KG. This is timely, as limited knowledge of reproductive biology is a hindrance to the improvement of most orphan crops (Cullis et al., 2019). Such knowledge has represented breakthroughs in the improvement of many plants, thus contributing to the Green Revolution (Singh et al., 2010; Whitford et al., 2013; Jaiswal et al., 2016). For instance, the proper knowledge of the flowering stage at which emasculation should be performed and the adequate time to pollinate is the basis in achieving a high rate of successful hybridization in peanut (Chu et al., 2016), *Capsicum annum* L. (Kivadasannavar et al., 2013; García-Tierrablanca et al., 2015).

In the efforts to improve grain yield in KG, plant breeders and geneticists encounter several challenges including the high rate of flower abscission, which represents a major source of continuous failure in attempts to cross KG and low productivity of the crop (Obasi, 1989). As a response to that, three main studies investigated the reproduction systems in KG. Amuti (1980) gave the first description of KG floral biology and

deduced from their observations that the crop is a self-pollinated plant with white or purple flowers. Obasi and Ezedinma (1994) focused on floral biology while Kafoutchoni et al. (2021b) went further to study the floral and fruiting phenology, stigma receptivity, pollen viability, and germinability, to devise insights to designing hybridization protocol that guarantees maximum success in the development of breeding lines. Similar research efforts in pigeon pea, which previously had a low success of artificial hybridization (Kalve and Tadege, 2017), has led to the development of hybrid varieties with 25–69% yield superiority over the local cultivars in India (Saxena, 2015).

Allen and Allen (1981) reported that KG has a cleistogamous flower type while Pasquet et al. (2002) classified the crop as chasmogamous. Lord (1981) described the “pre-anthesis cleistogamous” phenomenon as when bud pollination occurs before anthesis, which contributes to increasing the selfing rate. Such a floral structure is known to promote spontaneous selfing (Freitas and Sazima, 2009; Kumari and Sharma, 2017). On the other hand, bud pollination occurs after anthesis in chasmogamous species, which may allow a relatively low rate of allogamy. Based on the changes observed in flower color and size, Kafoutchoni et al. (2021b) described six floral phenological stages followed by six fruiting stages for KG, viz initiated flower (S1), young bud (S2), developed bud (S3), mature bud (S4), opened flower (S5), and wilted flower (S6) for flower development and beginning peg (F1), beginning pod (F2), full pod (F3), beginning seed (F4), full seed (F5), and mature seed (F6) for pod development. Although studies of reproductive biology on KG have provided useful insights into flower and reproductive description and physiology, further investigations are needed to deepen the understanding of cross-pollination processes. Particularly, the information about the species flower category, whether KG is chasmogamous or cleistogamous must be established. A clear knowledge of the pollination of KG would be very useful in determining the handling procedures and the possible strategy for artificial hybridization to increase hybrids' production efficiency.

### ***Reducing Genetic and Environmental Barriers for the Development of a Hybridization Protocol***

The small size of flowers, and climate conditions are potential barriers to successful hybridization in KG. These barriers make it necessary to proper timing, skilfully and delicately operating while emasculating and pollinating flowers of KG. Kumar and Singh (2005), reported also the relatively low efficiency of hand emasculation in species with smaller flowers such as sorghum and rice compared to species with larger flowers such as cotton and okra. Moreover, Tamini (1997) showed that variations in weather conditions influence KG flowering cycle, by delaying or accelerating the flowering time. In Bambara groundnut, for instance, temperatures of 33–36°C, adversely affect pollen viability and germination Dhanaraj (2018). The evaluation of thermo-tolerance of pollen is hence recommended before any hybridization activity. However, the physiological effects of environmental parameters

on pollen viability and stigma receptivity in KG are not yet known.

In self-pollinating crops, various crossing methodologies such as mechanical emasculation, genetic male sterility, the use of chemical hybridizing agents (CHAs), and genetic transformation have been used for the development of breeding lines and hybrid seeds (Veerappan et al., 2014). However, hand emasculation combined with hand pollination which remains the most widely used technique is tedious, time-consuming, labour-intensive, and costly (Fu, 2014). Moreover, it requires proper skills and delicate operations, especially when flowers are of small size or present several physical and physiological barriers. Therefore, emasculation techniques such as hot-water treatment, anther aspiration (McDonald, 1994), plastic-bag method (Schertz and Clark, 1967), alcohol emasculation, and cold treatment using CHAs, genetic emasculation (Salgare, 2004; Sleper and Poehlman, 2006; Mohammed et al., 2019) need to be potentially explored to cope with pollination issues in KG.

### ***Analyzing the Chromosomes Number in KG***

Understanding the appropriate karyotype is important for characterizing genomes of a species and for identifying closely related species (Saensouk and Saensouk, 2018; Senavongse et al., 2018). Kersting's groundnut is a diploid species for which, different numbers of chromosomes were reported for the wild and cultivated types (Pasquet et al., 2002). Miège (1954) evaluated the karyotype of the cultivated KG and found a chromosome number of  $2n = 22$ . However, According to Hepper, (1963), the chromosome number of KG wild type was  $2n = 20$ . More recently, Odo and Akaneme (2021) used six accessions and found a chromosome number of  $2n = 20$  in the cultivated KG. The clarification in the chromosomal number will certainly be fueling for further investigations particularly relevant to understand the compatibility phenomenon of reproductive organs in intraspecific cross-pollination toward accelerating KG breeding.

## **Cultivars Development**

### **Defining Breeding Objectives for Kersting's Groundnut**

The non-existence of improved varieties for KG despite its economic and nutritional importance is a wake-up call for an improvement program. Identifying plants with desirable traits among existing plant resources, or developing new phenotypes is the initial and most important step in plant breeding. Because the preferences of both growers and consumers are essential in setting up breeding objectives and product targets, they should be investigated at an early stage of the breeding program to guide germplasm collection and characterization strategies. Ethnobotanical studies have been conducted by Tamini (1995), Amujoyegbe et al. (2007), Akohoue et al. (2019), and Coulibaly et al. (2020), and reported on factors constraining the production of KG. In addition, farmers' preferred traits for KG new cultivars were also reported by Coulibaly et al. (2020). Thus, defining and prioritizing breeding objectives for *M. geocarpum* must take into account the identified constraints and stakeholders' desired traits. **Table 3** provides an overview of some of the

**TABLE 3** | Breeding objectives for Kersting's groundnut according to farmers, processors, and consumers' preferences.

End-user	Constraints	Traits of interest	Performance desired compared to current variety	Name of landraces to be improved
Farmer	Low yields	Economic yield and related traits	Dry grain yield 1,500–2,000 kg.ha <sup>-1</sup>	White, White with black eye
	Small seed size	Big seed size	>Current landraces	White, White with black eye
	Biotic stresses	Diseases resistance: fungi (crop wilting) and viruses	<3 (CIAT scale, degree of infestation)	All
	Abiotic stresses	Abiotic stress tolerance: drought, heat, high humidity	Medium tolerance—at reproductive and maturation stages	All
	Post-harvest loss	Tolerance to storage pests: pulses beetles	Medium tolerance—whether stored in pods or shelled in grain	White, White with black eye
	Long crop cycle duration	Early maturation	<90–105 days after planting (dap)	White, White with black eye
Processor/Consumer	Taste: less sweet	Organoleptic properties (Palatability and good taste)	Sweet taste	Black, Brown
	Appearance	Seed coat color	Uniformity of seeds: White and White mottled with black eye	White, White with black eye
	Food preparation	Facility to cook seeds	Short cooking time (90–120 min)	All

breeding objectives; improved cultivars are expected to possess five major traits: (1) early maturing attribute, (2) high yield (>500 kg/ha), (3) resistance to pathogen attacks (viruses, and fungi), (4) resistance to pulse beetles infestations (5) tolerance to abiotic stress especially to drought and high humidity. Yield in KG can be improved indirectly through genetic resistance/ tolerance to biotic and abiotic stressors. Important yield components in KG that could be improved include: number of seeds per plant, days to 50% flowering, and 100 seeds weight (Akohe et al., 2019). Moreover, according to farmers, water stresses during the reproductive stage in KG are critical as they directly affect pod yield and quality by causing pods rots (Coulibaly et al., 2020). To cope with this situation, farmers modified the planting periods of the crop (Akohe et al., 2018; Coulibaly et al., 2020). However, changes in rainfall patterns are unpredictable and random. Hence, developing water use efficient cultivars should be an important target trait. In addition, breeding for early maturing varieties for KG, as an escape mechanism to avoid water stress should be explored. Moreover, KG breeding objectives should also include value-adding traits such as higher nutrient-rich seeds, fast cooking time, and market class/seed colour. For the successful breeding purpose, short-term, medium-term, and long-term improvement goals should be set according to the urgency of the impact and traits to be improved. Also important is the participatory definition of breeding objectives with all stakeholders and the establishing the future KG breeding products profile.

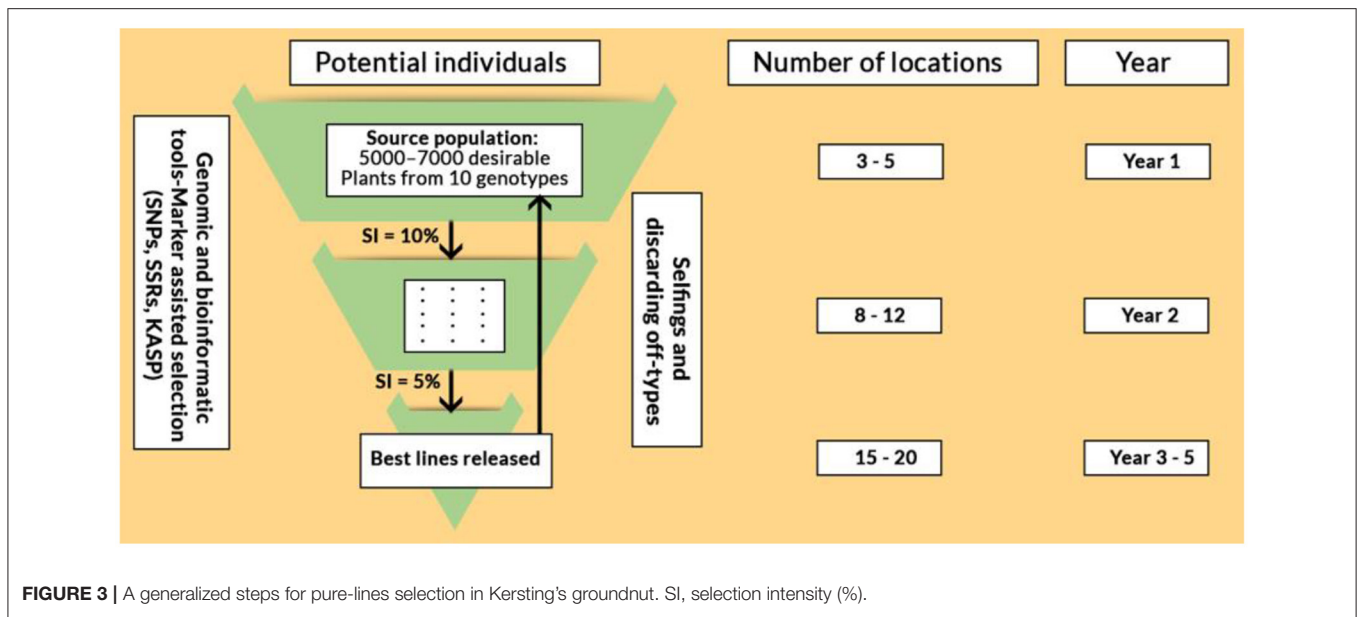
### Breeding Approaches for Cultivars Development

The objective of KG breeding programs is to develop improved lines with high yield potential, tolerance to abiotic factors, resistance to biotic stresses, adaptation to major agroclimatic conditions, taking into account consumers' and producers'

desired traits. The germplasm available in different genebanks must be characterized and screened for the identification of the source of genes for those traits. Improved cultivars can be pure lines, ILs, hybrids, or mutant lines. Several techniques are used to increase or create genetic variability within species (Bhandari et al., 2017) and could be applied to KG. The hybridization technique (e.g., interspecific or intraspecific) is the most and widely used in breeding to increase genetic variability in a plant. Genetic variability is also created through mutation breeding (Reha-Krantz, 2013).

### Selection of Pure Lines

Kersting's groundnut is naturally a highly self-pollinated crop (Allen and Allen, 1981) with a narrow genetic basis (Pasquet et al., 2002), suitable for pure-line cultivars development (Figure 3). Improved varieties can be developed mainly through mass selection, pedigree breeding, and backcross methods, using the available landraces. Landraces are a valuable source of genetic diversity and possess useful traits for breeding (Lopes et al., 2015). For instance, the average yield in the research stations ranged from 77 to 1,548 kg.ha<sup>-1</sup> (Assogba et al., 2015) and from 126.89 to 1444.29 kg.ha<sup>-1</sup> (Akohe et al., 2019). Hence, there is evidence that crop landraces can potentially produce high yields. Moreover, the genetic differentiation among KG landraces was found to be moderately high, suggesting a possible low rate of outcrossing. In that case, for the development of pure lines, landraces should be purified through subsequent selfings and selections for a minimum of five generations (Acquaah, 2007; Singh et al., 2015) to reduce unwanted alleles (Ahmar et al., 2020). The evaluation of selected genotypes in different environments/agroecologies is required to fix the homogeneity, stability, and adaptability of new lines. However, pure line cultivars may not respond effectively to producers and consumers



desires for many reasons: (1) pure lines have very low adaptability due to their narrow genetic base, the selection is powerless to bring changes in hereditary factors i.e., to develop new genotype (Acquaah, 2015); (2) pure lines are poor candidates for multiple trait selection because of the difficulty of finding all the desired traits in a single genotype (Priyadarshan, 2019), (3) Pureline selection requires more time, space, and expensive yield trials (Acquaah, 2015). These lines can often be used as parents in the production of other types of cultivars or breeding populations such as BILs, ILs, RILs, MAGIC, or mutants. Developing such populations in KG would create an avenue to unravel the genetic potential in the crop.

**Mutation Breeding**

Mutation breeding is an alternate method to conventional plant breeding for increasing genetic variability and conferring specific improvement without influencing the crop phenotype expression (Kulthe and Kotheekar, 2011). Whether chemical or physical, the use of mutagenic agents in the creation of genetic variability is becoming increasingly important in plant breeding (Reharkrantz, 2013). This technique was very successful in the genetic improvement of several leguminous species such as common bean, groundnut, pigeon pea, soybean, pea (*Pisum sativum* L.), cowpea, mungbean, Bambara groundnut, for which the improved traits were different and consist in: disease and pest resistance, earlier or later flowering, higher yield, higher protein content, or less toxic compounds (Adu-Dapaah and Sangwan, 2004). Given the success of this technique in the legumes listed above, the application of mutation breeding may be an alternative to improve the traits of interest in KG. However, mutation induction is a random process and does not always guarantee an ideotype variety ready for commercialization; it just provides a large population of mutants each with specific characteristics (Micke, 1993). It is often difficult and rare to obtain after mutation induction, a mutant possessing all the

characteristics of interest. Thankfully, the possibility to combine the chemical mutagenesis with the Targeted Induced Local Lesions in Genomes (TILLING) tools is important progress for accelerating the mutation breeding and enhancing selection accuracy of mutant desired products. In addition, hybridization can be used as a complementary method to mutation breeding insofar as it can support the transfer of the genes in a traditional way between the mutants or lines used as parents (Solanki et al., 2011).

**Intraspecific and Interspecific Hybridization**

The genetic characterization of KG revealed that there exists a moderate genetic distance between the White landrace and the other landraces which exhibited higher performances. However, landraces with White and White with black eye seed coat color are the most preferred and widely grown by farmers for consumption (Coulibaly et al., 2020). The opportunity for intraspecific hybridization can be exploited to transfer genes between KG landraces, particularly from coloured landraces to the White landrace. Moreover, the interspecific crosses for enhancing genetic variability and introgressing useful genes into KG from closely related species could be explored. Interspecific hybridization involves two different species and is widely used in breeding programs (Da Motta et al., 2020; Pratap et al., 2021). Although this technique is widely used, it remains challenging in the case of KG for several reasons. It seems that the wild form of KG is still unknown and is not found in any genebank (Ayanan and Ezin, 2016). However, Pasquet et al. (2002) had reported using two wild accessions from Cameroon in genetic diversity study. No studies on the agronomic potential and reproductive biology of any wild species have been published to date. Furthermore, possibilities of hybridization of KG with Horsegram can be considered to create early maturing hybrids resistant to drought and pest attacks (Chahota et al., 2013; Amal et al., 2020). In this case, a study of crossability barriers must be



carried out to understand the factors of success or failure of a crossing between the two species (Akkerman and Bakker, 2011; Martins et al., 2019; Ferreira et al., 2021).

## Testing the Adaptability and Stability in KG Cultivars Across Various Agroclimatic Zones

Stability and adaptability have always been considered as important topics in plant breeding but will be more crucial due to the continuous variations in climatic conditions. Conducting multi-environment trials would help to ensure accurate evaluation of new cultivars' performance to respond to climate change, as well as KG market demand. Thus, multi-location evaluations should be carried out throughout the breeding process by prioritizing end-users preferences for the newly developed varieties. High-yielding, stable, and well-adapted cultivars are much desired in the KG breeding program to ensure sustainable agriculture of the crop. The choice of locations for cultivars' performance evaluation should be based on the range of agroclimatic conditions under which the species is cultivated. Kersting's groundnut is grown during the rainy season (rain-fed cultivation system only), and its production shifts into three main agroclimatic zones of West Africa including Northern and Southern Sudanian zones and the Northern Guinean zone. Through these evaluations, KG cultivars would be successfully and reliably selected to respond to target growth areas. The GEI study is used to optimize the selection of cultivars across testing environments and can be used in breeding KG. Several approaches (METs and statistics) (Resende and Thompson, 2004; Gauch, 2006; Meyer, 2009) and tools (Coe, 2002; Aparicio et al., 2019) were developed in breeding crops, to examine the GEI for specific traits such as yield.

Furthermore, recent, studies showed the importance of the applications of genomics and bioinformatics tools in improving the understanding of GEI and the effects of climate change in species (Heslot et al., 2014; Gotelli and Stanton-Geddes, 2015; Monteverde et al., 2019). These methods allowed the analysis of the phenotypic plasticity of crops by incorporating the environment covariables to understand the relationship between environmental parameters and genes expression, at the specific developmental stage of the plant. Phenotypic plasticity refers to the ability of a single genotype to exhibit different phenotypic expressions across environments and ecological settings (Oostru et al., 2018; Klingenberg, 2019). Virtually, biotic stresses and any variation of environmental factors can induce the plastic response of genotypes, resulting in different phenotypic performances across environments. The extend of phenotypic plasticity in a crop relates to its capacity to active physiological mechanisms to adapt to external biotic and abiotic stimuli. In KG, several abiotic stresses such as drought, high soil moisture, temperature, and biotic stresses including fungal pathogens and insects are major factors contributing to the high yield gap within the crop (Assogba et al., 2015; Akohoué et al., 2018; Coulibaly et al., 2020). Understanding the magnitude of phenotypic plasticity in KG is therefore required to inform breeding options and strategies with regards to disease resistance

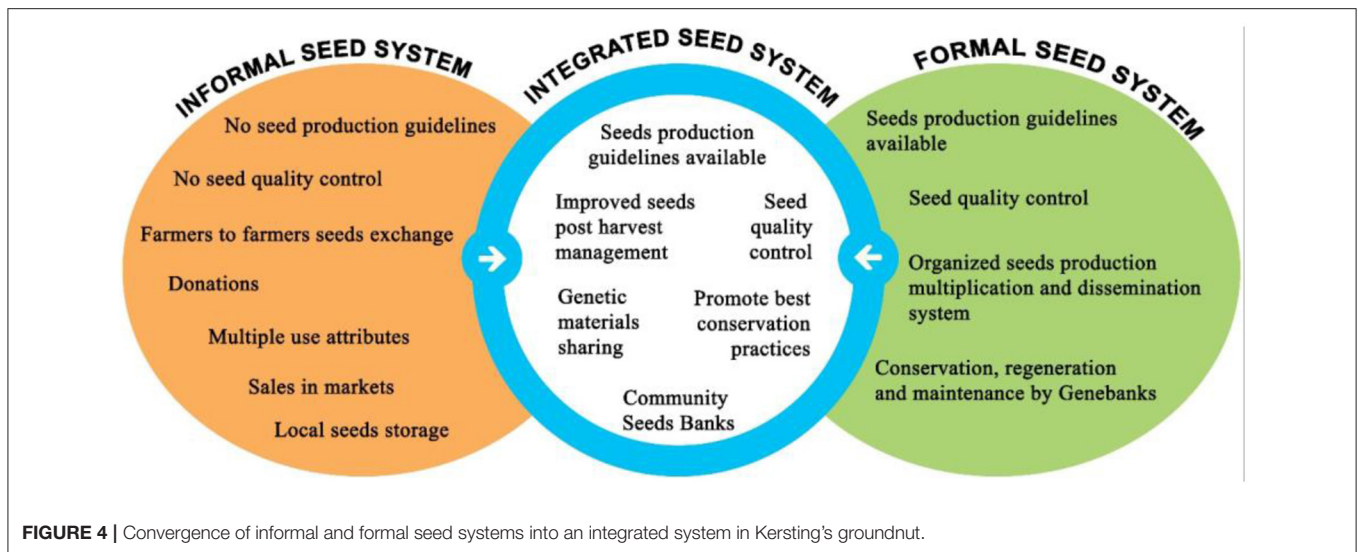
and abiotic stresses tolerance of genotypes. The use of METs combined with modeling approaches in breeding KG will enable a better analysis of GEI for the selection of potential parental lines and superior cultivars (lines or hybrids) that meet end-users' requirements.

## DEVELOPING AN INTEGRATED SEED SYSTEMS MANAGEMENT

Kersting's groundnut is traditionally produced and managed by local communities without an established formal seed system. Farmers grow seeds they purchase from markets, sometimes for high prices but low quality. This is mainly leading to the low yields of currently cultivated landraces, combined with their susceptibility to pulses beetles in storage which decrease the quality and quantity of stored products (Badii et al., 2011; Assogba et al., 2015; Akohoué et al., 2018). Moreover, farmers use their previous harvests as seeds or get from other farmers (Akohoué et al., 2018; Coulibaly et al., 2020). On the other hand, for the sake of increasing the crop yields, farmers increase plant density, raising, therefore, the production costs (Akohoué et al., 2018). Thus, farmers identified the non-availability of seeds as an important constraint limiting KG production. In fact, in most of the growing areas where the crop production was declining or disappeared, farmers lost their seeds and could not renew their seeds stock (Coulibaly et al., 2020). Without a formal seed supply system, management, and distribution, farmers' seeds demand remains unsatisfied. To ensure the availability of genetic resources for farmers and breeding programs, it is critical to creating an integrated seed system for KG resource management and use (Figure 4). The development of an organized and formal seed supply system appears as one of the biggest challenges for sustainable and improved KG production (Assogba et al., 2015; Akohoué et al., 2019). Improving KG productivity calls for research and institutional efforts concerning the development and release of new varieties in close partnerships with national and/or private seed companies.

## CONCLUSION

The last few years witnessed in West Africa an increasing interest in Kersting's groundnut which represents an excellent source of income for many households in marginal areas. The crop is disappearing in many countries because of the lack of knowledge about best cultivation practices, the lack of improved varieties, climate hazards, and biotic constraints. Despite this increased interest, many bottlenecks still hamper the wider dissemination and exploitation of the crop. Major drawbacks include the lack of improved cultivars that are high-yielding, drought-tolerant, pests and disease-resistant, and compliant with farmers' and consumers' needs. The development of such varieties still requires extensive investigations such as increase and maintenance of genetic resources, evaluation against biotic and abiotic factors, pollination and hybridization studies, development of molecular markers. Furthermore, breeding activities should include conventional and modern approaches.



A limiting factor is low skill and weak knowledge about the pollination system for successful hybridization that will unlock the opportunities to create genetic variability. Current studies are also focusing on mutagenesis that can allow the creation of more diversity and mutant lines. Meanwhile, breeders can develop open-pollinated varieties but also select high-yielding parents as pure lines. The growth of KG' market in Africa leans on the acceleration of the genetic gains in the crop as well as defining a suitable environment for increased production. Furthermore, access to research funds and technology (genomic and phenomic technologies), will aid in the mapping of KG genetic resources for rapid selection and breeding in West Africa. The development of research collaboration and partnerships with potential institutes working on legumes improvement is needed for successful breeding programs.

## AUTHOR CONTRIBUTIONS

MC and EA-D: conceptualization and writing—review & editing. GB, FA, EA, FM, and CA: writing—review & editing. MS: review & editing. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

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