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REVIEW

Bambara groundnut: an exemplar underutilised legume for resilience under climate change

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Abstract

Main conclusion **Bambara groundnut has the potential to be used to contribute more the climate change ready agriculture. The requirement for nitrogen fixing, stress tolerant legumes is clear, particularly in low input agriculture. However, ensuring that existing negative traits are tackled and demand is stimulated through the development of markets and products still represents a challenge to making greater use of this legume.**

Abstract World agriculture is currently based on very limited numbers of crops, representing a significant risk to food supplies, particularly in the face of climate change which is expected to increase the frequency of extreme events. Minor and underutilised crops can help to develop a more resilient and nutritionally dense future agriculture. Bambara groundnut [*Vigna subterranea* (L.) Verdc.[, as a drought resistant, nitrogen-fixing, legume has a role to play. However, as with most underutilised crops, there are significant gaps in knowledge and also negative traits such as 'hard-to-cook' and 'photoperiod sensitivity to pod filling' associated with the crop which future breeding programmes and processing methods need to tackle, to allow it to make a significant contribution to the well-being of future generations. The current review assesses these factors and also considers what are the next steps towards realising the potential of this crop.

Keywords Bambara groundnut · *Vigna subterranea* (L.) Verdc. · Underutilised legume · Marker-assisted breeding · Photoperiod · Hard-to-cook

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Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc.; $2x = 2n = 22$) is an underutilised African legume crop which is grown at low levels very extensively throughout sub-Saharan Africa (Duke 1982; Azam-Ali et al. 2001; Basu et al. 2007b; Okonkwo and Opara 2010; Bamshaiye et al. 2011). It is also grown in Southeast Asia in regions of Indonesia and Thailand. As a legume, it fixes atmospheric nitrogen and contributes to soil fertility (Sprent et al. 2010) in addition to being an agronomically and nutritionally good complement to cereal crops (FAO 1982; Halimi et al. 2019). It is a geocarpic crop, a close relative of cowpea (*Vigna unguiculata*) and morphologically fits into the same niche as groundnut (peanut; *Arachis hypogaea* L.), although compositionally, the seed is closer to chickpea (*Cicer arietinum*) (Halimi et al. 2019). Unlike soybean (*Glycine max*) which has received considerable scientific and financial support since its introduction, bambara groundnut has received limited support from governmental or international agencies and has largely been ignored by the research community (Heller et al. 1997; Oyeyinka et al. 2015). Groundnut was introduced in West Africa from Brazil and may have replaced bambara groundnut, because seeds of groundnut contain significant amounts of oil, so that it can be cultivated as an oil seed crop. Awareness about the potential of Bambara groundnut as a food crop in dry areas has increased in recent years; however, the crop still lacks proper seed systems and best agronomic practices have not been established and shared widely (Hillocks et al. 2012; Feldman et al. 2019).

Beyond cultural value, the main trait which bambara groundnut exhibits is drought resistance with reasonable yield and this is likely to be one of the main reason that it has still been maintained by local populations (Adzawla et al. 2016a, b; Olayide et al. 2018). It is generally grown as landraces, which are mixtures of essentially inbred lines which are likely to have been selected for the agro-ecology in which they have been grown for perhaps thousands of generations, without major directed selection beyond the environment and the farming system itself (Zeven 1998). The effects of climate change which include reduced and erratic rainfall patterns in many parts of the world, will require crops and agricultural systems with more resilience (FAO 2009; IPCC 2014; Padulosi et al. 2011; Mayes et al. 2012). Bambara groundnut and similar crops can be an important part of more resilient and complex systems, which provide additional nutritional and food security.

This paper outlines the values and potential uses of the crop, recent research progress evaluating both beneficial and negative traits and concludes with prospects and requirements for future breeding.

Markets and product value addition

Bambara groundnut production and consumption is predominant among subsistence farmers in West African countries (Goli et al. 1991; Goli 1997). In Ghana, bambara groundnut is sometimes planted on yam mounds, protecting the mound from erosion (Doku and Karikari 1971). A recent study conducted in the driest parts of Zimbabwe (less than 800 mm annual rainfall) has shown preference for this crop over maize, peanut, or cowpea (Mubaiwa et al. 2018). The use and consumer preferences of bambara groundnut are strongly based on the seed testa colour and taste. The testa colours present in bambara groundnut landraces are highly variable with cream or white seeded commanding up to a 10% premium in some countries.

Bambara groundnut seeds are processed and eaten in many ways. They can be boiled and consumed fresh or grilled while immature. Mubaiwa et al. (2018) provide an excellent account of bambara groundnut processing into various products in the semi-arid regions of Zimbabwe. In many West African countries, the fresh pods are boiled with salt and pepper, and eaten as a snack. The seed is used to make flour, which makes it more versatile (Kaptso et al. 2007). The young fresh seeds may be boiled and eaten in a manner-like boiled peanut and are made into a pudding (or steamed-paste) called Moi–Moi or Okpa (bean porridge) in some parts of Nigeria (Okpuzor et al. 2010). It has also been tested as a way to increase protein content in Ojojo made from water Yam (*Dioscorea alata*; Alakali et al. 2016).

In Nigeria, especially in the East, Bambara groundnut is an important food crop and can be used in traditional preparation of various recipes. The seeds are roasted, pulverized, and used in preparing soup (Adu-Dapaah and Sangwan 2004) or roasted and chewed with palm kernel. The fresh immature green seed is produced and consumed raw as a vegetable or cooked, while dry seeds can be processed to flour to prepare diverse forms of Bambara groundnut such as Okpa and cake (Okpuzor et al. 2010). Bambara groundnut seed haulms are also used to feed livestock and poultry (Anchirinah et al. 2001).

According to Linnemann and Azam Ali (1993), bambara groundnut flour can be used to make bread. Milk produced from bambara groundnut is comparable to that produced from soybean with bambara groundnut milk containing 15–16% protein compared with 4% protein in the soy milk (Adu-Dapaah et al. 2016). Bambara groundnut milk is preferred to that from other pulses because of its flavour and colour (Goli 1997). In Indonesia, a deep-fried bambara groundnut snack made from the immature seed is highly sought after. Known as ‘Kacang Bogor’ (‘Bogor nut’), it fetches high prices in supermarkets and even in specialist food shops in Europe. In appearance, it is similar to dry roasted peanut, but is drier (less oil) and more strongly flavoured (Sri Redjeki, pers. comm.). A number of recipes substituting bambara groundnut for other ingredients have also been developed at Crops For the Future (http://www.cropsforthefuture.org; also Fig. 8.3 in Feldman et al. 2019).

Local practices and uses

The production of Bambara groundnut is Africa-wide has been recorded to be approximately 0.3 million tonnes annually (Table 1; Hillocks et al. 2012; Nedumaran et al. 2015) with Nigeria regarded as the largest producer of bambara groundnut in Africa (0.1 million tonnes; Hillocks et al. 2012). Although the yield (t ha^{-1}) of bambara groundnut in Africa varies between landraces and locations (0.5–3 t ha^{-1}) with yield potential of over 3 t ha^{-1} (Begemann 1988), the average yield of 0.85 t ha^{-1} was reported to be comparable

Table 1 Yield and production of legumes in Africa (from Stanton et al. 1966; Hillocks et al. 2012; Nedumaran et al. 2015)

Legumes	Annual production (million tonnes)	Yield (t/ha)
Groundnut (*Arachis hypogaea*)	9.0	0.91
Cowpea (*Vigna unguiculata* L. Walp)	4.9	0.49
Dry bean (*Phaseolus vulgaris*)	3.8	0.66
Soybean (*Glycine max*)	1.4	1.22
Faba bean (*Vicia faba*)	0.6	1.22
Pigeon pea (*Cajanus cajan*)	0.4	0.77
Bambara groundnut (*Vigna subterranea* (L.) Verdc)	0.3	0.85
Chickpea (*Cicer arietinum*)	0.3	0.94
Lentil (*Lens culinaris*)	0.1	1.10

to other legumes (Table 1; Stanton et al. 1966). In spite of the useful characteristics in bambara groundnut, farmers in sub-Saharan Africa obtain low yields and this requires research attention to develop improved varieties and crop management practices.

A critical consideration will be acceptability and local practice, with the need for farmer groups to be closely involved in any future breeding effort to ensure that (farmer) selected lines suit the farmers' immediate needs, with backcrossing in of the new trait into current local lines, if necessary. Hillocks et al. (2012) emphasise the importance of this approach from a socioeconomic perspective.

The diversity in use and preference can be illustrated with country specific examples. For example, phenological studies conducted in southern Ghana, where a bimodal rainfall pattern exists revealed that bambara groundnut can be grown twice in a year (Berchie et al. 2013). The study also revealed that the time of sowing affected the yield of bambara groundnut. Yields were higher in the dry minor rainfall season compared with the major rainy season (Berchie et al. 2013). Berchie et al. (2013) also found that yields were higher in the Transition agro-ecology, where temperatures are higher, and rainfall is lower compared with the forest agro-ecologies. Pod yields of up to 4 t ha^{-1} were obtained in some landraces in the transition agro-ecological zone in Ghana. The study also revealed that when bambara groundnut is cultivated at appropriate time in the forest agro-ecology in Ghana, relatively high yields could be attained.

Bambara groundnut farmers grow the crop for food or for cash or both. In a survey involving 200 bambara groundnut farmers, 33 marketers and 68 consumers in the Brong Ahafo and the Upper East Regions in Ghana, it was revealed that more women (63%) grow the crop compared with men (37%; Berchie et al. 2010b). In the northern part of Ghana, most farmers (78%) grow the crop for food, while in contrast, the vast majority of farmers (73%) in the mid-country (transition zone) grow the crop for cash. Berchie et al. (2010b) also found that most farmers (63–83%) farmed on family lands. In northern parts of Ghana bambara, groundnut production has gone down, while production has gone up in the middle part of the country. Constraints to Bambara groundnut production included erratic rainfall, labour shortage, and lack of credit (Berchie et al. 2010b). The study also revealed that bambara groundnut grain is in high supply in the months of October–December in most parts of the country but scarce in the months of January, July, and August. Most farmers obtain seeds from their own saved seeds and the open markets. The average acreage per farmer under cultivation was 1.1 acres and yield ranges from 0.6 to 1.0 t ha^{-1}. With respect to marketing, most bambara groundnut sellers are women. The major challenge with marketing was the low price particularly in the northern part of Ghana (Berchie et al. 2010b). More recent studies have also addressed these questions further in Ghana (Adzawla et al. 2016a, b) and Nigeria (Olayide et al. 2018).

Evaluation of traits of importance

Bambara groundnut—a drought resilient crop

Drought provokes various above- and below-ground responses in plants. These responses allow drought resistant plants to either avoid (Liu and Stützel 2002; Liu et al. 2005), escape (Ludlow and Muchow 1990) or tolerate (Farooq et al. 2009; Xu et al. 2010; Blum 2011) drought.

1. *Avoidance*: this is most common in plants and occurs mostly in response to intermittent stress. It refers to the capability of plants to maintain fundamentally normal physiological processes under mild, moderate, and intermittent drought stress. Plants enhance soil water capture and minimise water losses through an extensive and prolific root systems (biomass, length, density, and depth as main characteristics), stomatal regulation, reduction in canopy size and duration, leaf rolling, increasing wax accumulation on the leaf surface and heliotropism among other mechanisms. Concomitant downregulation of photosynthesis through reduced radiation capture and a reduced accumulation of antioxidants also accompanies these responses.
2. *Escape*: this is related to phenological plasticity. Plants may hasten their life cycle to allow them to reproduce before water stress becomes terminal. This is commonly the case in annual crops, where flowering and maturity times are hastened. However, this mechanism has trade-offs with reduced biomass accumulation and build-up of harvest index due to reduced growth duration. Breeding

for *earliness* per se could also be a breeding focus of bambara groundnut at agrogeographical regions, where very limited rainfall is observed during the planting cycles and irrigation is not feasible. Some early maturing genotypes of bambara groundnut have been identified, including 'Zebra coloured' which matures in 90 days and 'Mottled cream' which matures in 98–100 days with 12.5–23.6 g pods per plant recorded (Berchie et al. 2010a, c). 'In addition, landraces 'Red' and 'Brown' from Jozini, South Africa, displayed a significantly earlier maturity date [mean: 123 days after planting (DAP)] when bambara groundnut plants were subjected to stress at 30% of crop water use (ET_a) compared to 100% ET_a (mean: 128 DAP; Mabhaudhi et al. 2013) demonstrating developmental plasticity.

3. *Tolerance*: this is perhaps the least common mechanism exhibited by plants under drought stress. It is the ability of plants to sustain a certain level of physiological activity under terminal drought stress through the regulation of thousands of genes and their networks. Plants improve their osmotic adjustment ability and increase the cell-wall elasticity to maintain tissue turgidity. In addition, plants alter a series of metabolic pathways to reduce or repair the resulting stress damage by augmenting osmoregulatory molecules in the cells and adjusting the activities of cell defence enzymes to reduce the accumulation of hazardous by-products.

Bambara groundnut exhibits all three drought tolerance mechanisms—avoidance, escape, and tolerance (Brough and Azam-Ali 1992; Collinson et al. 1995, 1997; Jorgensen et al. 2010; Mabhaudhi and Modi 2013; Mabhaudhi et al. 2013; Muhammad et al. 2015; Chai et al. 2016). This makes bambara groundnut an ideal crop, as it can tolerate a range of environmental conditions and durations of stress (Feldman et al. 2019). Moreover, bambara groundnut has adapted to contrasting environments, from cold temperatures at night and high temperatures during the day in an arid environment in Botswana, through to far milder and more humid environments in Indonesia. This makes it an important crop for promotion in areas that are currently drought prone as well as an important future crop in areas, where climate change projections show an increased frequency and intensity in droughts. For example, Mabhaudhi et al. (2018) projected that yield and water productivity of bambara groundnut will increase by ~37.5% and 33%, respectively, in response to projected climate change in South Africa. Furthermore, Mabhaudhi et al. (2016) also demonstrated that under climate change, the areas suitable for bambara groundnut production would also expand in South Africa, confirming the resilience of the crop under climate change.

Drought-resistance mechanisms in bambara groundnut have been elucidated by several studies in the last 30 years (Collinson et al. 1997, 1999; Jorgensen et al. 2010; Vurayai et al. 2011; Laary et al. 2012; Mabhaudhi and Modi 2013; Al Shareef et al. 2014; Chibarabada et al. 2015; Berchie et al. 2016; Nautiyal et al. 2017). Studies by Collinson et al. (1997) indicated that bambara groundnut can maintain leaf turgor pressure by osmotic adjustment, reduced leaf area, and operational stomatal regulation. The report suggested that bambara groundnut can maintain turgor at water potential of − 2.0 megapascal (MPa), which is much lower than groundnut (− 1.2 to − 1.6 MPa; Bennett et al. 1981). Others have also reported the adjustment of many growth and physiological characteristics of bambara groundnut in response to water deficit stress such as:

- Canopy development, size, and duration (Collinson et al. 1999; Mwale et al. 2007; Jorgensen et al. 2010; Vurayai et al. 2011; Mabhaudhi and Modi 2013; Saglam et al. 2014),
- Biomass accumulation and partitioning (Mabhaudhi and Modi 2013; Mabhaudhi et al. 2013),
- Phenological plasticity (Collinson et al. 1999; Mabhaudhi and Modi 2013; Nautiyal et al. 2017),
- Gas exchange (Mabhaudhi and Modi 2013; Chai et al. 2016; Nautiyal et al. 2017),
- Osmoregulation and regulation of photosynthesis (Collinson et al. 1997, 1999; Mwale et al. 2007; Vurayai et al. 2011; Mabhaudhi and Modi 2013; Chai et al. 2016; Khan et al. 2017; Nautiyal et al. 2017), and
- leaf temperature-transpiration (leaf orientation/paraheliotropism) and epicuticular wax (Collinson et al. 1999; Nautiyal et al. 2017)

In bambara groundnut, it has also been theorised that testa colour could be related to drought tolerance traits, with dark-coloured seeds having better emergence rates compared to light-coloured seed due to the presence of tannins, which are polyphenols that acted as antioxidants under stress conditions (Mwale et al. 2007; Mabhaudhi and Modi 2013), although this may not be a desirable trait for consumption.

However, the degree of drought resistance varies between landraces and their place of origin; the severity and velocity of the drought and phenological stage effected (Collinson et al. 1997, 1999; Jorgensen et al. 2010; Vurayai et al. 2011; Laary et al. 2012; Mabhaudhi and Modi 2013; Al Shareef et al. 2014; Chibarabada et al. 2015; Nautiyal et al. 2017). For example, Berchie et al. (2012) evaluated a number of landraces of bambara groundnuts for their resistance to drought and heat and reported that some landraces could withstand 120 days of drought when irrigation was stopped at 30 DAP. The most drought-resistant landrace identified, Burkina, was a landrace collected from 'Burkina Faso', a Sahelian country, it had the highest leaf and root biomass of the landraces recorded, and few pods were produced, while others failed to produce any pods. There are also other landraces such as ‘NAV 4’, ‘NAV Red’, and ‘Black eye’, which survived prolonged drought under high temperatures of up to 40.2 °C during the growing season (Berchie et al. 2012).

Bambara groundnut has been adapted to contrasting environments, ranging from cool temperatures at night and high temperatures during the day (approximately 10–20 °C difference between day and night, depending on month) in the arid environment of Botswana, to far milder and more humid environments in Indonesia (days around 29 °C and night 23 °C). The observed drought-resistance mechanisms exhibited in bambara groundnut could help this species cope with mild, intermittent, and terminal drought stress. Although drought stress generally decreases the yield of bambara groundnut and most other crops, bambara groundnut was still able to produce a reasonable yield of up to 1.7 t ha^{-1} of dried pods with a range of 1.3–2.1 t ha^{-1} (Mwale et al. 2007). These yields are reported to be higher than chickpea cultivars (0.3–0.5 t ha^{-1}) and are comparable to drought resistant groundnut cultivars under similar drought stress condition (Leport et al. 1999; Collino et al. 2000). In general, high efficiency of resource capture and conversion in bambara groundnut could be key contributors for crop productivity under drought. Despite a reduced radiation conversion coefficient (ε_s) in bambara groundnut from 1.51 to 1.02 g MJ^{-1} due to drought stress, ε_s of bambara groundnut reported in Mwale et al. (2007) was higher than those reported in soybean (*Glycine max*), which ranged from 0.52 to 0.92 g MJ^{-1} (De Costa and Shanmugathasan 2002; Board et al. 1994) and in cowpea ranged from 0.07 ± 0.03 to 0.50 ± 0.01 g MJ^{-1} m^{-2} (Craufurd and Wheeler 1999) under minimal soil moisture conditions. The efficiency of plants converting water into dry matter (ε_w) is essential for high potential yield production. As reported in Mwale et al. (2007), ε_w of bambara groundnut (1.65 g kg^{-1}) under drought stress was shown to be higher than most of the grain legumes grown in low rainfall Mediterranean environments, such as lentil (*Lens culinaris* Medik; 1.37 g kg^{-1}) (Zhang et al. 2000) and chickpea (1.11 g kg^{-1}) (Siddique et al. 2001).

While bambara groundnut has been shown to be comparatively drought resistant, there are still significant gaps that need to be addressed through crop improvement before this trait could be of greater benefit to farmers. A recent assessment of an F_5 segregating population, derived from a cross between single genotype parents Tiga Nicuru and DipC, under progressive mild drought stress in a controlled environment has demonstrated strong genetic variation for many morpho-physiological traits within the population (Chai et al. 2016). This study revealed the potential in selecting individual lines with greater potential drought resistance yet with reasonable yielding characteristics for future breeding programmes in bambara groundnut.

The importance of root studies

Above ground drought adaptations (i.e., increasing water use efficiency) are often associated with yield penalties due to reduced biomass accumulation (Blum 2005). While below-ground adaptations have been associated with enhanced water and nutrient capture and subsequently an ability to maintain higher rates of gas exchange and biomass accumulation under stress (Blum 2011). Roots and their related traits perform an array of fundamental roles including, but not limited to, water and nutrient uptake. Reduction in root growth under drought stress reduces the nutrient acquisition capacity of the root systems, which eventually affects growth, development, yield, and yield quality traits, even if water is later restored. It is essential to have a better understanding of root traits before using these as criteria for selection in breeding programmes. Rooting depth is one of the most commonly assessed traits, because crops with deeper roots can reach water and nutrients located in deeper soil horizons. In cowpea, for example, varieties with well-distributed and deep roots tend to survive longer under drought stress compared to those with shallower roots (Singh and Matsui 2002).

The focus on shoot over root traits is understandable given the technical difficulties involved in setting up and conducting root studies and the complex root–soil interaction. Methods used for phenotyping root traits span from laboratory (paper and gel media) to field and/or greenhouse (soil media) root observation and excavation techniques. Most of these phenotyping approaches are labour intensive, require plot destruction to get to the roots, and most importantly do not mimic or give a true representation of the actual field conditions, i.e., heterogeneity of soil physical properties (Richard et al. 2015). However, emerging technologies and advances in the fields of phenomics are beginning to ease some of the technical difficulties and provide opportunities to analyse root traits. Recent advances have also allowed for high-throughput phenotyping using computational models and software for tracing the root phenotype and its relation to other traits or stresses. These include RootReader3D (Clark et al. 2011), RootScan (Burton et al. 2012), RootNav (Pound et al. 2013), WinRhizo (Himmelbauer et al. 2004; Joshi et al. 2017), X-ray micro-computed tomography (μCT) (Mairhofer et al. 2011), and ImageJ (Ryosuke and Yoichiro 2013). By applying the above tools and algorithms, bambara groundnut root phenotypic studies could be made more efficient and this would further enhance our understanding of how the plants root growth parameters change in response to drought.

Photoperiod response/requirement in bambara groundnut

Bambara groundnut originated around the equator (Begemann 1988; Pasquet and Fotso 1997; Pasquet et al. 1999), where daylength (photoperiod) is reasonably stable. However, the crop is widely grown across various latitudes in Africa with increasing day lengths at higher and lower latitudes during the planting season. The previous investigations have revealed that the crop requires around 12 h photoperiod for maximum pod-set and seed yield (Linnemann et al. 1995), while under long photoperiods more leaves are produced at the expense of pod formation (Linnemann 1993; Azam-Ali 1998; Brink 1999; Oyiga 2010). Linnemann (1993) observed that the onset of flowering, progress of flowering, onset of podding, and progress in pod growth can all be retarded by long daylengths above 14 h. The effect on podding was, however, greater than on flowering and some plants did not produce any pods under photoperiods of 14 h and 16 h. The photoperiod sensitivity of bambara groundnut has limited its cultivation sites further away from the equator. Selecting an appropriate daylength during the season for planting could be an option to allow pod-filling; however, it may not be optimal in terms of water availability.

Photoperiodic responses in plants are reflected in a diverse set of traits, including vegetative growth period extension, bud set, switch to development of flowers, fruit set and seed production, tuberisation, changes in winter hardiness, changes in chemical composition and in enzyme activity (Hamner 1944; Jackson 2009). Among these, the effects on flowering have been extensively studied (Amasino 2010; Izawa et al. 2000) and the timing of the onset of flowering is the basis for the classification of plants that normally flower either in long- or short-day conditions (Garner and Allard 1920, 1927; Summerfield et al. 1998; Craufurd et al. 1999). *Arabidopsis thaliana* and other temperate long-day species such as lentils, pea (*Pisum sativum* L.), chickpea, and barrel medic (*Medicago truncatula*) (Thomas and Vince-Prue 1996; Weller et al. 2012) flower earlier under long daylengths. By contrast, flowering in other species such as rice (*Oryza sativa*), cowpea, soybean, and common bean (*Phaseolus vulgaris*) is promoted by short daylengths (Summerfield et al. 1991; Summerfield et al. 1993; Song et al. 2010). Besides the onset of flowering, several other aspects of reproductive development such as pod and seed yield, and seed filling are influenced by photoperiod, and these are perhaps the most important agronomic traits for agricultural research and policy (Guiamet and Nakayama 1984; Morandi et al. 1988; Bagnall and King 1991a; Harris and Azam-Ali 1993; Linnemann et al. 1995; Brink 1997; Brink 1998; Brink et al. 2000; Kantolic and Slafer 2007; Nico et al. 2015). Therefore, an understanding of the photoperiodic and genetic control of pod set and its relationship with seed production may become potential tools to further raise the yield of bambara groundnut.

Photoperiod regulation has been reported in most grain legumes, e.g., flowering time and seed production in soybean (Summerfield et al. 1993; Kantolic and Slafer 2005; Kantolic et al. 2007, 2013); flowering time in cowpea (Ellis et al. 1994); flowering response in faba bean (*Vicia faba* L.) (Ellis et al. 1990; Imrie and Lawn 1990); flowering in common bean (Wallace et al. 1993; Kornegay et al. 1993); flowering and pod set in bambara groundnut (Linnemann et al. 1995; Brink 1997); and flowering and pod number in groundnut (Flohr et al. 1990; Bell et al. 1991; Bagnall and King 1991b). It is generally assumed that both photoperiod and temperature are important in the phenological development of most annual crops, due to the difficulties in uncoupling photothermal effects in fluctuating field environments (Summerfield et al. 1991). The exposure to long photoperiods in indeterminate soybean, for example, lengthened the reproductive period from flowering to maturity leading to increased pod and seed number, and this was associated with increments in the amount of radiation accumulated during the crop cycle (Kantolic and Slafer 2005, 2007; Nico et al. 2015).

In bambara groundnut, pod formation strongly responds to photoperiodic changes even under prevailing temperatures at the time of growth in tropical countries (Linnemann and Craufurd 1994). Evidently, it is induced by short days (Linnemann 1993; Harris and Azam-Ali 1993; Linnemann et al. 1995; Brink 1997), but the behaviour under long-days is highly variable and it could be either qualitative (obligate) or quantitative (facultative). Time to flowering in bambara groundnut is considered to be photoperiod-insensitive in most genotypes, but in a few landraces, continuous light delayed flowering by 6–11 days (Nishitani et al. 1988). Combined photoperiod and temperature studies showed that photoperiod usually has a stronger effect on pod-filling than on flowering time (Linnemann and Craufurd 1994; Brink 1997; Jorgensen et al. 2009, 2010). Of all the genotypes studied to date, "Tiga Necuru" from Mali has been described as day-neutral for flowering time and photoperiod-sensitive for podding, while "Ankpa 4" genotype from Nigeria appeared to be highly photoperiod sensitive with regard to both time to flowering and pod-set (Linnemann et al. 1995). In another experiment aimed at identifying photoperiod neutral lines for pod set, a collection of 102 landraces from Tanzania (East Africa) was grown in a greenhouse under long photoperiod (16–17 h) (Jorgensen et al. 2009, 2010). This study reported three landraces, namely, Mtwara (TZA-1498), Lindi (TZA-1505), and Shinyanga (TZA-2114) that had reasonable levels of photoperiod-insensitivity, compared to the already widespread landraces such as Tiga Necuru and DipC (from Botswana) (Jorgensen et al. 2009, 2010). Berchie et al. (2013) evaluating performance of 13 bambara groundnut landraces in Ghana under 12 and 14 h photoperiods observed that canopy sizes and leaf area within landraces were greater under a 14 h photoperiod than under a 12 h photoperiod. Under a 14 h photoperiod, five landraces that produced some pods and showed less sensitivity to photoperiod were also early maturing.

Field experiments conducted in Botswana using the Uniswa Red landrace have confirmed that the onset of flowering was photoperiod-insensitive, while the rate of progress from flowering to pod-set was photoperiod sensitive (Harris and Azam-Ali 1993; Sesay et al. 2008). As such, variability in yield is believed to have become more pronounced when grown further from the equator (Linnemann 1993; Linnemann and Azam Ali 1993; Linnemann and Craufurd 1994; Karikari et al. 1996, 1997; Sesay et al. 2008). The photoperiodic control of fruit development is important as pod and/or seed are major components in pulses (Egli 1999; Egli and Bruening 2006; Slafer et al. 2006). Hence, the development of day-neutral lines, defined here as the ability to set pods and seeds at daylength more than 13 h will be highly significant.

It is also well known that pod set is more sensitive to endogenous and environmental signals at the later stages of fruit and seed development (Boyer and McLaughlin 2007) than vegetative growth (Linnemann 1993). For example, in common bean, long photoperiod inhibited the allocation of assimilates to seeds and increased the allocation to vegetative organs. Similarly, in soybean, long photoperiods have been shown to promote vegetative growth (Caffaro et al. 1988; Fleming et al. 1997) by decreasing dry matter partitioning towards pods and seeds (Raper and Thomas 1978; Ellis et al. 2000), seed growth rate were reduced (Morandi et al. 1990) and the reproductive period extended (Summerfield et al. 1998; Kantolic and Slafer 2007). A greater partitioning to peanut pods was reported under short photoperiods (Harris et al. 1988; Witzenberger et al. 1988). Lawn (1989) suggested that in tropical legumes, relative partitioning of assimilates into reproductive or vegetative organs after the start of flowering depends on the degree of determinateness (preference for partitioning to seed) and that photothermal regimes have a direct influence on the expression of determinateness. Long photoperiods, either independently or in conjunction with high temperatures, seem to promote indeterminateness even in the early flowering types through extending the flowering period, reducing synchrony of flowering and pod-set, and delaying pod ripening. In bambara groundnut landrace “Ankpa-4”, fertilisation was observed, and healthy embryos were found to have developed in ovaries up to 32 days after anthesis under a photoperiod of more than 14 h (Linnemann 1993). This evidence suggests that any embryo abortion and the lack of pod-development in bambara groundnut during long photoperiods is primarily caused by the deficiency of or competition for photoassimilates and nutrients among vegetative and reproductive sink organs (Linnemann and Craufurd 1994; Brink 1997; Brink et al. 2000). The quantitative response in terms of pod and seed number to increased duration of the critical period due to photoperiodic effects is not very well understood. A better understanding of photoperiod responses would facilitate the development of cultivars that, in addition to its drought resistance were suitably adapted for a wider geographical range and potentially this would enhance the successful exchange of germplasm between different latitudes.

Hard-to-cook (HTC)

Many pulse legumes can be described as ‘hard-to-cook—HTC’— a term which reflects the amount of energy needed to make a grain legume edible. Mubaiwa et al. (2017) provided a comprehensive review of the cookability of bambara groundnut in comparison with other legumes, and thus, only a few points are highlighted here.

There are a wide range of components involved in cookability, from initial rates of water uptake, through to effects of long-term storage of seed (particularly in humid and hot conditions) before cooking. In practical terms, this HTC phenomenon increases the effort required to prepare seed for meals and in many countries, this means a greater fuel cost. Consequently, this trait has been often identified as one of major bottleneck for the uptake of bambara groundnut (e.g., Adzawla et al. 2016b). While there is clearly both a physical component and a compositional component (and likely genetic underpinning) of this trait, it is important to bear in mind that the limitation is also a reflection of how bambara groundnut is traditionally processed and used. As an example, soybean has a 3.6-h cooking time which is almost identical to that of bambara groundnut (Mubaiwa et al. 2017). However, being an industrial crop and for large-scale production this justifies the investment in appropriate processing methods and machinery which allows the limitation to be minimised. Similar approaches would also be applicable to bambara groundnut and other HTC legumes if demand could be increased and with continuous supply throughout the year (even if from different countries). A number of ways to improve cooking times are cited in Mubaiwa et al. (2017), although some traditional approaches, such as the use of local salts such as *kanwa* in Zimbabwe, appear to have a negative effect on protein quality. However, fermentation to produce *tempe* does appear to produce a good product which was favoured over soybean *tempe* and also reduced the antinutritional factors present in the bean, increasing the bioavailability of the nutritional components in bambara groundnut (Ademiluyi and Oboh 2011). Hard-to-cook also develops with seed storage condition, particularly under humid and hot conditions, and a number of theories have been developed to explain components of this storage trait

(Mubaiwa et al. 2017) and how treatments, such as *kanwa*, may be reducing HTC.

Processing of bambara groundnut into flour (although HTC can affect milling) and its use as a full or partial substitute is one approach to reduce the HTC characteristics. A range of products and lines have been developed and evaluated (Ijarotimi and Esho 2009; Atoyebi et al. 2017; Feldman et al. 2019), as well as the packaging of industrially cooked seed into cans (Zimbabwe and Ghana, now discontinued) or vacuum sealed packets (Ghana), so that seed can be incorporated into food without the limitation imposed by cooking, for middle class consumers, at least. However, for most small-scale farmers, where bambara groundnut is a nutritional food security crop, reducing the components of HTC could be a significant advantage and is associated with traditional uses (e.g., in Zimbabwe; Mubaiwa et al. 2018).

There is considerable genetic variation in bambara groundnut for seed size and also testa colour/patterns. Initial reports have suggested that there could be a relationship between dark testa colour, thicker testa and cooking time. However, most experiments to date have used a limited number of landraces obtained from markets, so that seed history is unknown and genetic variation may be present for this trait in each landrace, as well as between landraces. Analysis within structured populations is needed to investigate such questions. For example, initial data from measuring water imbibition in a controlled cross (Tiga Nicuru × DipC; 65 F_6 lines) identified quantitative trait loci (QTL) on three linkage groups, none of which appear related to testa colour (LCS Licea, unpublished data).

While HTC needs to be investigated within species, there is sufficient information in the literature from other legume species to guide such investigations and the translation of information from model, major and minor crops to underutilised crops may significantly speed up progress.

Nutritional value

Bambara groundnut is largely grown for human consumption, although the remaining biomass can be fed to cattle and other domestic animals (Anchirinah et al. 2001). It is a major source of plant protein in sub-Saharan Africa and constitutes an important part of the local diet, culture and economy (Goli 1997; Adu-Dapaah and Sangwan 2004; Boateng et al. 2013). The seed is regarded as a completely balanced food, because it contains 18–24% protein with high lysine and methionine, 51–70% carbohydrate, 4–12% crude oil, 3–5% ash and 3–12% fibre (see, for example, Halimi et al. 2019). Bambara groundnut is rich in iron 4.9–48 mg/100 g compared to a range of 2.0–10.0 mg/100 g for most food legumes, potassium 11.44–19.35 mg/100 g, sodium 2.9–12.0 mg/100 g, and calcium 95.8–99 mg/100 g (Amarteifio et al. 2006; Fasoyiro et al. 2006). Bambara groundnut has approximately 367–414 kal/100 mg energy (Boateng et al. 2013). The gross energy value of bambara groundnut seed is greater than that of other legumes (Rowland 1993; Anchirinah et al. 2001; and see Table 8.3 in Feldman et al. 2019).

While comparisons appear favourable, with bambara groundnut compositional analysis showing a good combination of components and higher sufficiency of limiting amino acids than most legumes (see Mubaiwa et al. 2017 and Halimi et al. 2019), this does not consider antinutritional factors (Murevanhema and Jideani 2013; Atoyebi et al. 2018) and their effect on the bioavailability of the nutrition in bambara groundnut. Legumes have long been known to contain high levels of antinutritional factors, such as tannin, phytate, phenolics and other compounds which can bind to nutritional components making them completely or partially unavailable for digestion. Anti-herbivory factors can range from relatively simple protease inhibitors through to major toxins, such as the amino acid β-*N*-oxalyl-L-α,β-diaminopropionic acid (ODAP) in grasspea (*Lathyrus sativus*), which can lead to paralysis when consumed as the only major food source during periods of famine (Buta et al. 2019). Simple treatments such as dehulling, soaking, cooking, fermentation, germination and others can potentially reduce antinutritional factors and improve bioavailability (Barimalaa and Anoghalu 1997; Egounlety and Aworh 2003; Ijarotimi and Esho 2009; Nti 2009; Mazahib et al. 2013; Mubaiwa et al. 2017; Atoyebi et al. 2018). Fermentation improved the mineral composition but had little effect on the amino acid content and decreased the antinutritional factors; oxalate, tannic acid, phytic acid and trypsin. (Ijarotimi and Esho 2009). However, bioavailability is an important caveat for any promotion of underutilised crops and needs significant investigation to ensure that the nutritional status of people will genuinely be made better through use of nutrient dense minor crops, given the antinutritional factors present in most.

Germplasm resources of bambara groundnut for future breeding

Germplasm resources for Bambara groundnut

Bambara groundnut probably has a centre of origin in north eastern Nigeria and northern Cameroon. It exists in the wild from central Nigeria eastwards to southern Sudan and is now cultivated throughout tropical Africa. Dalziel (1937) as cited in Doku and Karikari (1971) reported that bambara groundnut was found in its wild state in 1901 in the North Yola province of Nigeria. Linnemann (1987) also found the wild plant near Garoua in northern Cameroon. The wild bambara groundnut is reported to have a distribution from the Jos Plateau and Yola in Nigeria to Garoua in Cameroon (Goli 1997). Cultivated bambara groundnut are landraces that have probably evolved after domestication directly from their wild relatives which have adapted to arid and semi-arid environments and the crop is popular among farmers for its yield stability under different environmental conditions (Doku and Karikari 1971; Hepper 1963; Basu et al. 2007a). Begemann (1988) confirmed that the centre of origin of bambara groundnut is in the region of north-eastern Nigeria and northern Cameroon and extreme spreading types of wild were identified by RS Pasquet (Pasquet and Fotso 1997; Pasquet et al. 1999 and Pasquet 2004). Spreading growth habit in a wild line, VSSP11, has been confirmed as a dominant trait compared with the domesticated bunchy types (Basu et al. 2007a). A recent study of agromorphological diversity of bambara groundnut collected in Benin showed also shows a high degree of morphological variability (Gbaguidi et al. 2018). Thus, accessions from West Africa are expected to have higher genetic variability, assuming a single region of domestication. However, Aliyu et al. (2016) suggested the possibility of the Southern/Eastern African region being a secondary centre of domestication or diversity for the crop based on a detailed analysis of the genetic population structure. This placed the West African and the Southern/Eastern African accessions into two distinct clusters.

According to FAO (2009), 4500 accessions of bambara groundnut are conserved ex-situ globally. The collections are held in 16 countries, and three regional or international genebanks. The Genetic Resources Center (GRC) of the International Institute of Tropical Agriculture (IITA) has 1910 accessions collected from various countries across sub-Saharan Africa (Fig. 1).

Landraces preserve genetic variation which could be of help for genetic improvement of any crop. Bambara groundnut landraces have maintained a significant amount of genetic diversity under low input farming systems (Massawe 2000). Traditional bambara groundnut growing farmers have depended largely on the existing diversity within the landraces that they grow and thus has sustained on-farm genetic diversity conservation with selection on bambara groundnut landraces being agro-ecological, as well as farmer (e.g., practices in Zimbabwe; Mubaiwa et al. 2018).

Ex-situ conservation of bambara groundnut landraces and farmer's on-farm conservation is essential for future genetic improvement programmes of the crop. However, to understand the genetic basis of traits of interest for breeding, landraces are problematic as they are a mix of multiple genotypes which could contribute to a confusion between the effects of environment and those which have a genetic cause. Developing controlled crosses and an association genetics panel could allow molecular breeding, including marker-assisted selection, even if the final "product" needed is a mix of improved lines—an artificial landrace.

A well-characterised germplasm collection with high quality genotype data will be a good resource for plant breeding and crop improvement programmes as the information could be used by scientists and breeders to select

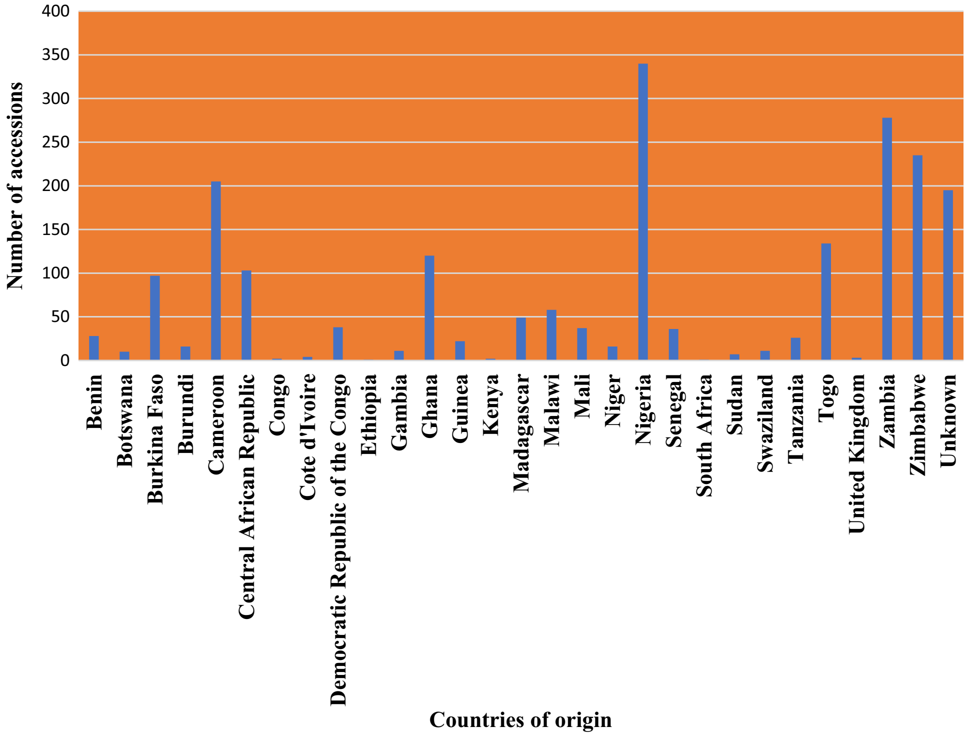

Fig. 1 Origin and distribution of bambara groundnut in the International Institute of Tropical Agriculture (IITA) collection

parental genotypes for breeding programmes (Ntundu et al. 2004; Aliyu et al. 2014, 2016). Accessions collected from different countries or different parts of a country may have a common ancestry or may even be the same genotypes bearing different local names (Massawe et al. 2005). Hence, a genome-wide genotyping-by-sequencing approach is being employed at IITA to characterise bambara groundnut collection with the objective of identifying duplicate accessions (M. Alberton, Pers. Comm.)

Molecular tools and resources

The use of molecular markers and the development of genetic resources will improve the understanding of the genetic control of agricultural traits, leading to quality control, marker-assisted selection, and genomics-enabled breeding for climate change (Mayes et al. 2015b; Kole et al. 2015: Abberton et al. 2015). In bambara groundnut, genetic linkage maps consisting of diversity arrays technology (DArT), simple sequence repeats (SSR) and single nucleotide polymorphisms (SNP) markers have been developed using four populations so far (F_2 generation and above), including wild type and domesticated genotypes (Basu et al. 2007a; Ahmad 2012; Ahmad et al. 2015, 2016; Mayes et al. 2015a; Ho et al. 2017; Chai et al. 2017). The aim is to generate populations segregating for different traits, such as growth habit, drought resistance, and photoperiod sensitivity for genetic studies and development of improved varieties.

The first genome sequence of bambara groundnut has been released recently (Chang et al. 2018). Pipelines for translating genetic resources and information from other species have also been developed to assist breeding programmes with the initial assembly (based purely on high coverage Illumina sequencing) requiring further long-fragment sequencing work to convert this into pseudomolecules (e.g., through Nanopore technology; https://nanoporetech.com/). Examples of translating information and resources from major and model plant species to underutilised and resource-poor crops are reported in bambara groundnut (Mayes et al. 2009; Bonthala et al. 2016; Khan et al. 2017; Ho et al. 2017; Chai et al. 2017). Two individual intraspecific genetic linkage maps developed from two populations (F_2 lines; IITA686 × Ankpa4 and F_3 lines; Tiga Nicuru × DipC), respectively, were successfully mapped onto the physical maps of other well-annotated, closely related legume species in the absence of complete genome sequence in bambara groundnut (Ho et al. 2017). The identification of the conserved synteny between underutilised crops and well-characterised common bean, adzuki bean (*Vigna angularis*) and mung bean (*Vigna radiata*) allows the corresponding flanking positions of QTL defining an agronomic trait in bambara groundnut to be identified in other physical genomes. Ho et al. (2017) demonstrated the importance of a translational framework which permits the likely genes underlying the corresponding positions in the major or model species to be identified as candidate gene orthologues for the traits in the study species. Furthermore, an expression marker-based genetic map containing 218 gene expression markers (GEMs) across 13 linkage groups, spanning 982.7 cM of the bambara groundnut genome, was developed using cross hybridisation of bambara groundnut leaf ribonucleic acid (RNA) onto the Affymetrix Soybean Genome GeneChip to identify QTLs involved in agronomic and drought-related traits in bambara groundnut as well as genome regions potentially harbouring pathway activating genes for response to stress (Chai et al. 2017). The reports of Bonthala et al. (2016) and Khan et al. (2017) the studies demonstrated a technically feasible approach to translate the resources developed from major and model crops to underutilised crops and such approaches could be potentially adopted and replicated in various underutilised crops, such as amaranths (*Amaranthus* spp., winged bean (*Psophocarpus tetragonolobus*) and proso millet (*Panicum miliaceum*).

While understanding the breeding system of this crop is essential for a breeding improvement programme, generating within-species genetic resources has only taken place in the last decade or so due to limited resources. The African Orphan Crop Consortium (AOCC) has included bambara groundnut in their 101 traditional African food crops with nutritional potential in which genomic resources would help to improve their nutrient content. In contrast, common bean which is the most consumed legume (Schmutz et al. 2014) has had molecular-assisted breeding approaches applied for more than two decades; from as early as the 1990s, utilising random amplified polymorphic DNA (RAPD) markers linked to disease-resistance traits (summarised by Kelly and Bornowski 2018). The genetic diversity of a number of bambara groundnut landraces was initially evaluated through RAPD and amplified fragment length polymorphism (AFLP) markers (Amadou et al. 2001; Massawe et al. 2003a, b; Rungnoi et al. 2012; Fatimah et al. 2018). Subsequently, a total of ten SSR markers for bambara groundnut were developed by Basu and colleagues from a microsatellite-enriched genomic library (Basu et al. 2007c). The development of the dominant DArT hybridisation-based array-genotyping system enabled genotyping to be achieved at higher throughput, with four major subpopulations identified among 40 accessions collected from nine countries as revealed by 554 DArT markers (Stadler 2009; Olukolu et al. 2012). While the transferability of SSR markers from closely related species is feasible, only 20 out of 178 amplifiable SSR from *Vigna angularis*, *V. unguiculata* and *V. radiata* were shown to be informative within 240 bambara groundnut accessions (Somta et al. 2011). With the advent of next generation sequencing, a further set of 74 SSR markers were optimised from a leaf transcriptome (Molosiwa et al. 2015; Aliyu and Massawe 2013).

Both Somta et al. (2011) and Molosiwa et al. (2015) studies suggested that individual bambara groundnut plants are highly inbred. However, the farmer landraces are still a mix of (usually related) inbred lines and this was observed to be the case even for released varieties through molecular assessment (Ho et al. 2016). Somta et al. (2011) reported an average of 1.3% heterozygosity, except for three accessions from Guinea and ten accessions from Burkina Faso which had higher heterozygosity (4.99% and 2.99%, respectively), suggesting higher levels of outcrossing in their history. Similarly, 12 SSR markers applied to 123 accessions from Molosiwa (2012) indicated that the inbreeding coefficient ranged from 0.90 to 1.00, with average observed heterozygosity of 0.01. As such, line advancement by means of single seed descent (SSD) would be the first step to develop near homozygous bambara groundnut pre-breeding materials. Given the level of inbreeding observed, seed from a single plant is likely to represent an (unselected) variety—here, we term this approach to produce pure lines 'Single Plant Descent' (SPD).

The DArTseq platform, based on Illumina next generation sequencing, generates both dominant silicoDArT markers and co-dominant SNP markers (SNP variation within the sequence tags of the markers; Alam et al. 2018; Barilli et al. 2018; Kilian et al. 2012). The average level of heterozygous alleles was found to range from 0.8 to 5.0% using 7894 markers after a round of single plant descent (SPD) purification from a subset of genebank accessions ($n=229$), forming a good representation for a 'pure' genotype association genetics panel (S Mayes, unpublished data). While genome-wide association studies (GWAS) in bambara groundnut have yet to be used to unravel predictive and causative variation linked to agronomic traits, genetic resources generated either within species or across species have been exploited. In a pigeon pea (*Cajanus cajan*) heterosis hybrid breeding programme, a number of SSR have been developed not only to distinguish cytoplasmic male sterile maintainer and fertility restorer lines but also to assess the hybrid genetic purity (Bohra et al. 2011). Similarly, artificial crossing in bambara groundnut could be a promising approach to develop new varieties with desirable traits and the approach has subsequently been optimised in UK and Thailand (Massawe et al. 2003c; Suwanprasert et al. 2006; Kendabie 2014). Both cross-breeding attempts have made use of molecular markers (AFLP and then SSR) to evaluate true hybrids before beginning to advance populations to recombinant inbred lines. Bambara groundnut SSR have also been used to evaluate the heterogeneity of commercial cultivars before making selection of candidate individual plant for whole genome sequencing (Ho et al. 2016). In addition to a residual heterozygosity assessment, these SSR markers are useful for line label checking particularly at large-scale multi-locational trials evaluating different line performance within the same growing cycle, e.g., Molosiwa et al. (2015), and also their current use in F_1 hybrid confirmation and in a multilocational field trials supported by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA 2016–2020), Benefit Sharing Funded project involving Nigeria, Ghana, Indonesia and Malaysia.

Towards genetic improvement of bambara groundnut

Domesticated forms of bambara groundnut were derived from their wild relatives through a combination of natural and artificial selection (Massawe et al. 2005). The existence of genetic variation with regards to all drought-resistance mechanisms is encouraging for selection and breeding with an emphasis on harvest index under drought conditions. Bambara groundnut yields range from 0.5 to 3 t ha^{-1} seed in sub-Saharan Africa (Azam-Ali et al. 2001). Given a yield potential of over 3 t ha^{-1}, focus should be on the development of high yielding varieties for own consumption or as a cash crop for use by resource-poor farmers or those farmers in arid conditions. Selection for grain yield under drought conditions has not been easy for many crop species. Significant genotype × environment interactions (GEI) leading to QTL × environment interactions have often resulted in low heritability under drought conditions. Traits that are highly correlated to yield may be less susceptible to GEI and can be targeted for indirect selection (Piepho 2000; Berger et al. 2010). Reliable phenotyping protocols are important in incorporating a targeted trait into molecular breeding programmes and identifying candidate genes underlying traits of interest for forward genetics procedures (Salekdeh et al. 2009). In addition to grain yield, breeding work on bambara groundnut could also focus on traits such as seed nutrient quality, disease resistance, tolerance to heat, high foliage volume, and palatability of the foliage, so it can be utilised as a pasture crop. There is a need to understand better whether there are trade-offs in achieving drought resistance and such desirable traits.

For underutilised crops, the dissection of traits for a subsequent breeding programme is very dependent upon having strong genetic population structures. These allow the trait variation to be partitioned between genetic and other components and the subsequent localisation of the effect to specific genomic regions. Such analysis helps us understand whether a trait gene has pleiotropic effects and, indeed, whether different QTL are genetically linked or independent. To summarise, the development of segregating populations in bambara groundnut and the recent genetic mapping and QTL analyses are really the start of controlled breeding and trait dissection. The combined efforts with an association genetics panel will take this screening to a new height, with the same material being trialled in multiple environments and promising lines made available to farmers and research institutes.

Conclusions

Minor and underutilised legumes will be a critical component of a structured response to climate change. However, there are many factors which complicate their research and deployment to this end. Bambara groundnut is a drought resistant African legume which can be used in complex agricultural systems and companion planting. It is widely grown at low levels in sub-Saharan Africa, but its use is limited by unstable yields and the hard-to-cook phenomenon, which reduces demand, particularly from poor consumers. The development of marker-assisted breeding programmes is a priority, but there is also a need to develop a better understanding of the context and culture-dependent use of bambara groundnut, to ensure that breeding efforts are demand-led and that acceptance in specific agro-ecological contexts is achieved. Alongside such efforts to genetically improve the crop in farmer-defined ways, there is also a need for a parallel track which focuses on the agricultural systems, basic mechanisation and development of new and complex forms of agriculture to deliver improved food and nutritional security in future climates.

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