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Research Article

Changes in Seed Quality during Seed Development and Maturation of Bambara Nut (*Vigna subterranea* (L.) Verdc.) Landraces

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This study aimed at determining changes in the seed quality of bambara nut (BN) landraces during seed development and maturation so as to more precisely time seed harvest for better seed quality. Three bambara nut landraces, AbiBam001, LocalBam, and TVSU544, were sown in two field experimental sites in northern Uganda in October 2020 and 2021. Seeds were harvested at 83, 93, 103, 113, and 123 days after sowing (DAS) in the first experiment and at 123, 130, and 138 DAS in the second. Seeds were subjected to quality tests of seed dry weight, final germination percentage (FGP), germination velocity index (GVI), and seedling dry weight (SDW). All landraces showed significant differences ($P < 0.05$) in seed weight and seedling dry weight at progressive developmental stages in the first experiment. All parameters showed no differences ($P > 0.05$) in the second experiment except for the seed weight of AbiBam001 and the FGP of TVSU544. Both TVSU544 and LocalBam attained mass maturity (highest seed weight) at approximately 113 DAS, while AbiBam001 reached mass maturity at about 130 DAS. Seeds of the highest quality were obtained at 103 DAS for TVSU544 and at 113 DAS for both LocalBam and AbiBam001. For both AbiBam001 and TVSU544, the highest quality seeds occur before mass maturity, while for LocalBam, at about mass maturity. Seed harvest should be timed at 103–113, 113–123, and 120–130 DAS for TVSU544, LocalBam, and AbiBam001, respectively. The assessment of seed development before 83 DAS and maturation after 138 DAS in the main growing season will synchronize growing conditions with farmers' practices and crucially provide a complete picture of the developmental patterns of the landraces.

1. Introduction

Bambara nut (BN) (*Vigna subterranea* (L.) Verdc.) is an important grain legume grown mostly by subsistence farmers in the dry land regions of sub-Saharan Africa (SSA) [1]. In many countries where BN is cultivated including Uganda, it is considered a "minor" crop and as a result often neglected and underutilised, despite its huge potential for food and nutrition security [2–4]. Consequently, the majority of the resource-constrained BN farmers rely on traditional knowledge to carry out crop production and seed management ([2, 5];) and use their own seeds saved from previous harvests, seeds obtained from neighbors, or in the local market to sustain production [4–6]. An important aspect of seed management is the timing of harvest. It is critical to the seed quality of most species including BN, with too early or delayed harvest seriously compromising seed quality [7–9]. For most BN farmers in Uganda, timing of seed harvest is tied to such physical indicators as yellowing and browning of leaves, drying of leaves and stems, and characteristic colour development ([5, 10]). While this can be a good guide for timing of harvest, soil and environmental conditions can potentially alter these indicators

[11, 12], thereby compromising their reliability. A robust method based on physiological developmental indicators during seed development and maturation would provide a more stable and reliable method of timing seed harvest. The process of seed development and maturation of seeds such as BN begins with ovule fertilisation and typically follows three stages. Histodifferentiation is a process in which ordered cell division and differentiation results in formation of the embryo, seed filling involving cell expansion and storage reserves accumulation, and maturation drying marked by seed moisture loss and reduced metabolism occurs [13–15]. Seed filling ceases at physiological maturity, with subsequent maturation drying [14]. The length of each of the phases usually varies from several days to many months depending on the species and prevailing environmental conditions [14]. The whole process is under genetic control of quite complex and distinct biosynthetic pathways and physiological processes ([13, 14, 16]). Seed development and maturation in relation to seed quality of BN has only previously been partially described for any landrace. Embryo development in a bambara nut landrace was observed to proceed up to at least 41 days after anthesis and was photoperiod sensitive whereby ≥14 hours photoperiod terminated growth altogether [17]. Likewise, grain filling was delayed and reduced at this photoperiod [17]. A report by Linnemann [18] had determined the mass maturity of a BN landrace named "Tiga Nicuru" from Mali to be approximately 103 days after sowing (DAS) under a 12 hr photoperiod regime. More recently, Mandizvo and Odindo [19] estimated that BN landraces from a field experiment in South Africa reached physiological maturity at about 65 days after flowering (approximately 100 DAS). In Uganda, however, the seed developmental processes of the country's landraces and their physiological and harvest maturity remain to be understood. A better understanding of the seed development and maturation process at critical stages could provide a scientific basis for the timing of harvest for landraces and therefore "fine tune" the harvest stages of BN landraces in Uganda. This will result in better quality seeds and higher yields for farmers, hence is the focus of this study.

2. Materials and Methods

2.1. Field Experimental Sites. The field experiments were set up at two on-farm sites in Ocettoke, Kitgum district (2020/2021), and Koro, Omoro district (2021/2022), both in the northern region of Uganda. Both Ocettoke (03°22′33.071″N/032°51′55.69″E, 1020 masl) and Koro (02°39′22.92N/032°18′44.27E, 1085 masl) are found within the warm subhumid zone of the northern moist farmlands agroecological zone (AEZ) [20]. This AEZ has a unimodal rainfall pattern stretching from April to October (average annual temperature is >20°C and annual rainfall >1200 mm) and a long dry season from November to March [20, 21]. The landscape is mostly of gentle rolling plains punctuated with narrow valleys, while the soils are generally sandy and sandy clay, having low organic matter and low nutrient availability [20]. Dryland food crops such as pigeon pea, cowpea, millet, sorghum, and cash crops such as cotton, sesame, and tobacco are the most predominantly cultivated in this AEZ [20]. The zone also covers one of the regions in Uganda where bambara nut is commonly grown [5].

2.2. Plant Material. Bambara nut seeds of two landraces (LocalBam and TVSU544) were obtained from the market in Arua (north western region), while a third landrace (AbiBam001) was bought in Lira market (northern region) (Figure 1). Seeds for subsequent plantings were obtained from the previous experiments. Landraces were selected on the basis of their seed coat colour (dark, intermediate, and light), seed size (small, medium, and large), and frequency of occurrence ("preference") among the BN farming communities. TVSU544 has medium-sized cream seeds with "black eyes" and is of light colour (Figure 1). AbiBam001 has small round seeds that are cream with black stripes and of intermediate or dark colour. LocalBam has large oblong mottled seeds with brown or purplish specs and of dark colour (Figure 1). Both AbiBam001 and LocalBam were encountered at several locations during a baseline survey, while TVSU544 was only found at a single location [10].

2.3. Field Experimental Setup and Sampling. The three bambara nut landraces were planted in randomised complete blocks and replicated three times at each site. The Kitgum experiment was established on 25th October, 2020, while the Omoro experiment was achieved on 19th October, 2021. Standard crop management practices were applied at all stages of the crop growth. The crop was irrigated twice a week during periods of extended dry spells, especially in December and January. Pods were harvested from randomly selected rows in each plot on 16th and 26th January and 5th, 15th, and 25th February, 2021, (at the Ocettoke site) and on 19th and 26th February and 6th March, 2022 (at the Koro site). These predetermined days corresponded to 83, 93, 103, 113, and 123 days after sowing (DAS) for Ocettoke and 123, 130, and 138 DAS for Koro. Pods were sun-dried and temporarily kept at room temperature and then later transferred to a −20°C freezer until use. Pods were hand threshed and used for seed quality analyses. Daily weather data (temperature, RH) were recorded with a Tinytag® data logger (Gemini Data Loggers, UK) suitably located in the field. Soil samples were collected from each experimental site and analysed for pH, organic carbon, total N, exchangeable K, available P, Ca, Mg, Na, and S.

2.4. Seed Size Measurements. Seeds from each replicate were visually size graded as small, medium, and large and a proportionate number of each size grade was included in subsequent measurements. The seed length and width were measured with a digital Vernier calliper. Ten seeds were representatively selected from each replicate and measured. Seed dry weight was measured with a weighing balance. Twenty separately drawn seeds from each replicate (40 per replicate) were weighed, and an average of the 2 measurements was recorded as 20 seeds weight. The result of which was expressed as 100 seed weight by multiplying by 100.

2.5. Germination Tests. A germination test was performed with 15 seeds and 20 seeds, respectively, for the Ocettoke and Koro experiments, in three replications. As with the size

(a) (b) (c)

Figure 1: Seeds of bambara nut landraces that were sown at the experimental sites. (a) TVSU544, (b) AbiBam001, and (c) LocalBam.

measurements, a proportionate number of each seed size grade from every replicate was included in the germination test. The seeds were sterilized with 1% sodium hypochlorite solution for 1-2 minutes and rinsed with distilled water. The sand medium was sterilised, moistened with distilled water, and placed in plastic trays, into which the sterilised seeds were sown. Seeds were incubated in a growth chamber at alternating conditions of 30°C 8 hr light and 20°C 16 hr darkness. In the first experiment, the WTB Binder® (Binder GmbH, Tuttlingen, Germany) growth chamber was used, while the Biobase-B400II® (Biobase Biodustry, Shandong, China) was used for the second experiment. Light in both cases was provided by fluorescent bulbs inside the incubation chambers. The sand medium was monitored daily and hydrated accordingly to keep it moist. The number of seeds germinated was recorded on a daily basis for 16 days. A seed was considered germinated when the plumule had emerged from the sand surface. At 16 days, seedlings were evaluated and the percentage of normal and abnormal seedlings was determined. Five normal seedlings from each tray (each replication) were air-oven dried at 95°C for 24 hr and weighed to determine seedling dry weight (SDW). The final germination percentage (FGP) and germination velocity index (GVI) were calculated as follows. The final germination percentage (FGP) was calculated using the following formula:

$$\mathrm{FGP} = \left(\frac{N_g}{N_T}\right)100, \tag{1}$$

where N_g is the number of germinated seeds and N_T is the total number of seeds sown [22].

The germination velocity index (GVI) was calculated as proposed by Maguire [23] as follows:

$$\mathrm{GVI} = \left(\frac{G_1}{N_1}\right) + \left(\frac{G_2}{N_2}\right) + \cdots + \left(\frac{G_n}{N_n}\right), \tag{2}$$

where $G_1, G_2, \cdots .G_n$ are the number of seeds germinated on first, second, and last count. $N_1, N_2, \cdots, N_n$ are the number of days at first, second, and last count from the day of sowing.

2.6. Data Processing and Analysis. Data were entered in Excel from where germination parameters were calculated, and germination and seed size-related graphs were generated. A seven-day fixed average of both temperature and relative humidity were calculated in Excel and used to generate a time series profile at the two experimental sites, while descriptive statistics were used to identify similarities and differences between the two environments. Non-normal percentage data (FGP) were arcsine transformed, and analysis of variance (ANOVA) was performed on germination and seed size data in GenStat® 14$^{\text{th}}$ Edition (VSN International Ltd, Hemel Hempstead, UK). Means were compared using Tukey's procedure at the 0.05 level. To describe relationships between the different germination and seed size variables, Kendall's rank correlation coefficient (τ) (Kendall's tau-b) was calculated in IBM® SPSS® Statistics (Version 20) statistical software (IBM Corporation, Armonk, New York, USA) for paired variables and subjected to significance tests at both the 0.05 and 0.01 levels. For both LocalBam and TVSU544 at Ocettoke, however, τ values were calculated excluding the developmental stage of 123 days after sowing to ensure linearity of the data points.

3. Results

3.1. Temperature, Relative Humidity (RH), and Soil Conditions at the Field Experimental Sites. Temperatures at both the Ocettoke (Kitgum) and Koro (Omoro) field experimental sites were quite similar in terms of average daily/weekly values during the respective periods they were measured (Figure 2). Average temperature at Ocettoke for the entire period of 13 weeks was 28.16°C with a range of 10.43°C. That for Koro for the 12 weeks period was 26.8°C with a range of 9.103°C. Ocettoke was therefore slightly hotter than Koro by an average temperature of 1.36°C. Essentially, the overall temperature fluctuations during the measurement periods for both sites were similar (Figure 2). There was, however, a slight difference in the average RH between the sites (Figure 2), with Ocettoke having a higher average RH of 54.59% compared to 47.74% at Koro. This made Ocettoke more humid than Koro by an average of

9.51% RH. Notably, for both sites, towards the end of the experiment, temperature was consistently rising, while RH was declining in the same time period (Figure 2). Nevertheless, the within site variation in relative humidity was similar for both sites. Generally, during the growing seasons at both sites (April to June for the first season and July to October for the second season), temperatures were comparatively low in most months with the corresponding higher RH, except in June, July, and October [24]. Soil conditions at the two sites were generally similar in characteristics, though with slight variations for certain essential macro and micronutrients (Table 1).

3.2. Seed Size Characteristics. All landraces showed consistent increase in the seed length, width, and weight from the early to the latter stages of sampling/development in the first experiment (Table 2). Each landrace differed significantly in terms of its seed length, width, and weight ($P < 0.01$) at every stage of development except between 113 and 123 DAS, where the increases in all three parameters were not significant for LocalBam and TVSU544 and for both seed length and width in AbiBam001 (Table 2). Interestingly, however, AbiBam001 showed a significant increase in seed weight beyond 113 DAS ($P < 0.01$) compared to the other two landraces (Table 2). Also, as expected, there were significant differences in the seed length, width, and weight among landraces at all stages of development ($P < 0.01$). LocalBam was consistently the largest seed for all three parameters followed by TVSU544, while AbiBam001 was the smallest seed (Table 2), thereby conforming to the size categorisation of large, medium, and small seeds of LocalBam, TVSU544, and AbiBam001, respectively. Sampling in the second experiment at 123, 130, and 138 DAS was able to validate the trend of nonsignificant increase in the seed size between 113 and 123.

DAS exhibited by LocalBam and TVSU544 in the first experiment. Both LocalBam and TVSU544 showed no difference in seed length, width, and weight between 123 and 138 DAS (Table 2). Equally, AbiBam001 did not differ in seed length and width between 123 and 138 DAS ($P > 0.05$). However, it showed a clear difference in seed weight between 123 and 130 DAS but not between 130 and 138 DAS (Table 2). This therefore establishes a point of diminished increase in seed weight for AbiBam001. Collectively, these patterns strongly suggest that the stage of mass maturity (highest seed mass) for the landraces is approximately 113 DAS for both LocalBam and TVSU544 and 130 DAS for Abibam001. This also means that both LocalBam and TVSU544 mature earlier than AbiBam001.

3.3. Seed Germination. Both AbiBam001 and LocalBam exhibited relatively high germination percentage (FGP) at the early developmental stage of 83 (71% and 82%, respectively), while TVSU544 had comparatively lower germination (58%) at this stage in the first experiment (Figure 3). The final germination percentage of the landraces steadily increased from 83 DAS onwards, with the highest FGP occurring at 103, 113, and 123 DAS for TVSU544, LocalBam, and AbiBam001, respectively (Figure 3). This is similarly depicted by the cumulative germination curves of the landraces (Figure 4). Beyond these peaks, the FGP begin to decline for both LocalBam and TVSU544, but for AbiBam001, there was still a steady increase between 103 and 123 DAS (Figure 3). At Koro, seed germinability remained relatively uniform at all sampling stages, albeit with a general declining trend for all landraces (Figure 3). There were no differences among the germination speed of seeds at different developmental stages for all landraces at both sites ($P > 0.05$). Nevertheless, the fastest germinating seeds (highest GVI) were at 113 DAS for both AbiBam001 and LocalBam and 103 DAS for TVSU544 at the Ocettoke site, while at Koro, they were at 123 for both AbiBam001 and TVSU544 and 130 DAS for LocalBam. For both AbiBam001 and TVSU544, the seedling dry weight increased from 83 to the highest recorded value at 103 DAS and then declined or steadied afterwards (Figure 5). For LocalBam, however, the seedling dry weight steadily increased throughout the seed developmental period at Ocettoke (Figure 5). At the Koro site, the seedling dry weight remained relatively uniform for all landraces (Figure 5). Accordingly, cumulative germination curves suggest that by speed (GVI) and extent of germination (FGP), seeds of the highest quality from Ocettoke are obtained at 103, 113, and 123 DAS for TVSU544, LocalBam, and AbiBam001, respectively (Figure 4; Table 3). At Koro, the FGP was highest at 123 DAS for both AbiBam001 and TVSU544 and then declined from 123 to 138 DAS for both landraces (Figure 3). For LocalBam, however, it was marginally highest at 130 DAS, although this did not seem to differ much from that at 123 DAS (Figures 3 and 4). This trend is confirmed by a combined ranking of sampling days (DASs) for the seed quality parameters of FGP, GVI, and SDW, which shows that the best ranked DAS for each landrace (i.e., the developmental stage when the seed quality is highest) is 103 for TVSU544 and 113 DAS for both LocalBam and AbiBam001 (ranking data not shown). Conversely, the poorest quality seeds from Ocettoke were obtained at 93 DAS for both AbiBam001 and TVSU544 and at 123 DAS for LocalBam (Figure 4). For Koro, the poorest quality seeds were at 138 DAS for all landraces (Figure 4). However, the ranking of DAS shows that the poorest quality seeds from Occetooke occur at 83 DAS for both AbiBam001 and TVSU554, while for LocalBam, it is maintained at 123 DAS. Similarly, at Koro, the poorest quality seeds for ranked DAS were obtained at 138 DAS for all landraces. This means that for both AbiBam001 and TVSU544, seeds with the highest quality are obtained before mass maturity, while for LocalBam, they are obtained at approximately mass maturity. Differences between the two experiments for the first day of germination, last day of germination, time spread of germination, and speed of germination (Figure 5) were largely attributed to differences in incubators' conditions.

3.4. Relationships among Seed Germination and Seed Size Parameters. All germination parameters had positive relationships with all the seed size characteristics of seed weight, seed length, and seed width at Ocettoke with both

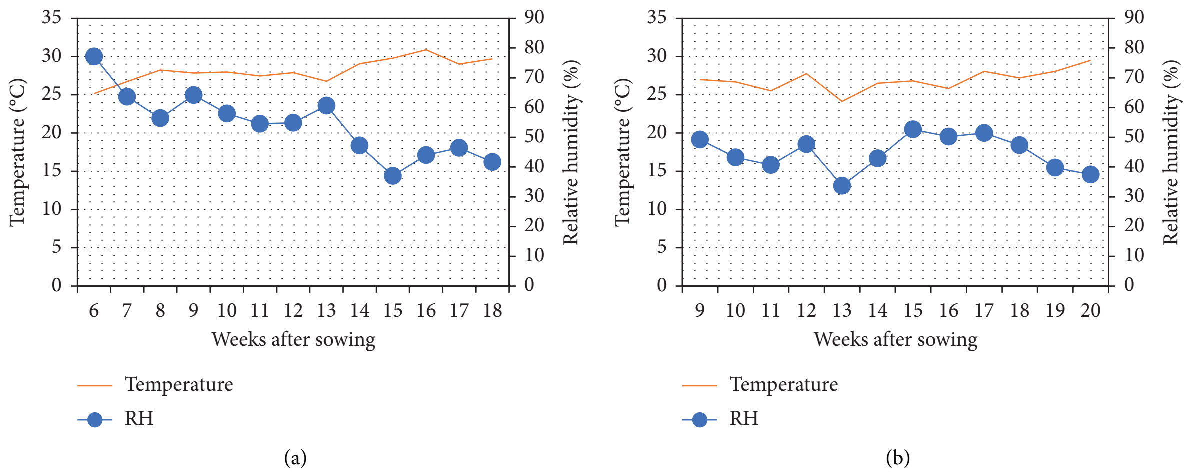

FIGURE 2: Temperature and relative humidity (RH) at the experimental sites during the crop growth and sampling periods. (a) Ocettoke (Kitgum) and (b) Koro (Omoro) readings.

TABLE 1: Soil characteristics of the two fields' experimental sites.

Parameters	Ocettoke		Koro	
	Value	Rating[a]	Value	Rating
pH	6.48	Slightly acidic	5.65	Moderately acidic
Organic carbon (%)	1.60	Low	1.44	Low
Total nitrogen (%)	0.09	Low	0.06	Low
Available phosphorus (mgkg^{-1})	21.29	High	8.23	Moderate
Exchangeable potassium (ppm)	158.00	Moderate	283	High
Calcium (ppm)	989.00	High	72	Low
Magnesium (ppm)	—	—	262	Low
Sulphur (ppm)	56.00	Moderate	—	
Sodium (ppm)	—	—	106	Moderate

[a]Rating according to Okalebo et al. [25].

FGP and GVI having quite strong relationships with the seed size characteristics (Table 4). At Koro, FGP and GVI had negative relationships with the seed size characteristics for all landraces, with those for AbiBam001 being very strong (Table 5). Conversely, at Koro, SDW had positive relationships with all the seed size characteristics for all landraces, except for TVSU544, which were all negative relationships (Table 5). A positive relationship was observed between the FGP and GVI for all landraces at both sites with that of both AbiBam001 and TVSU544 being very strong at Koro (Tables 4 and 5). As would be expected, Kendall's τ values were strongly positive for seed weight and seed length, seed weight and seed width, and seed length and seed width for all landraces at both sites (Tables 4 and 5).

4. Discussion

4.1. Seed Size Characteristics. Landraces showed clear differences in the seed size (weight, length, and width) at different stages of development, attaining mass maturity at approximately 113–123 DAS for both LocalBam and TVSU544 and between 130–138 DAS for AbiBam001. These trends are well aligned with the result of a survey preceding and linked to the current study, which showed that farmers harvest their BN crops 4-5 months after sowing (roughly 120–150 DAS) [10]. Typically, farmers harvest the crop at harvest maturity, usually some days to a few weeks after mass maturity and the survey was able to highlight the fact that harvesting lasts nearly a whole month [10]. A recent study by Mandizvo and Odindo [19] estimated that BN landraces from a field experiment in South Africa reached physiological maturity at about 65 days after flowering (approximately 100 DAS). Earlier, Linnemann [18] had determined the mass maturity of a BN landrace named "Tiga Nicuru" from Mali to be approximately 103 DAS under a 12 hr photoperiod regime. Further reports from other parts of SSA indicate that the maturity period for most landraces is about 4-5 months [2, 26, 27]. The maturity periods of landraces reported elsewhere closely relate to the findings of the present study. Differences in the maturation of landraces are basically determined by the genotypic characteristics of a given landrace and the environmental conditions under which the landrace is cultivated [28–30]. In general, after ovule fertilization, orthodox seeds such as BN undergo histodifferentiation, in which ordered cell division and differentiation result in formation of the embryo, seed filling involving cell expansion and storage reserves accumulation, and maturation drying marked by seed moisture loss and reduced metabolism [13–15]. Seed filling ceases at physiological maturity, with subsequent maturation drying

Table 2: Size characteristics of seeds of landraces harvested at different stages of maturation from the Ocettoke and Koro sites.

Locations	Seed developmental stage (DAS)	Landrace								
		AbiBam001			LocalBam			TVSU544		
		100 seed weight (g)	Seed length (mm)	Seed width (mm)	100 seed weight (g)	Seed length (mm)	Seed width (mm)	100 seed weight (g)	Seed length (mm)	Seedwidth (mm)
	83	17.83a	7.51a	5.75a	39.50a	10.82a	7.18a	33.00a	8.80a	7.35a
	93	33.50b	9.41b	7.42b	75.83b	13.59b	9.25b	46.00b	10.48b	8.22b
Ocettoke	103	42.33bc	9.96bc	8.07bc	94.17bc	14.43bc	10.00bc	60.50bc	11.26b	9.19c
	113	51.83cd	10.75c	8.80cd	109.50c	15.22bc	10.77c	67.83c	11.36b	9.52c
	123	58.33d	10.95c	9.11d	111.83c	15.28c	10.72c	68.50c	11.54b	9.57c
	P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	<0.001
	s.e.d.	2.936	0.922	0.231	6.900	0.474	0.374	5.00	0.450	0.237
	l.s.d.	6.77	0.673	0.532	15.91	1.094	0.863	11.54	1.038	0.546
	123	59.50a	10.99a	9.14a	110.67a	14.56a	10.55a	74.50a	11.63a	9.93a
Koro	130	68.17ab	11.16a	9.41ab	115.00a	14.71a	11.22a	84.33a	12.27b	10.40b
	138	72.50b	11.39a	9.65b	123.75a	15.51a	11.39a	79.25a	11.98ab	10.32b
	P value	0.03	0.326	0.019	0.194	0.088	0.371	0.074	0.019	0.021
	s.e.d.	3.04	0.232	0.102	5.44	0.290	0.535	2.66	0.103	0.084
	l.s.d.	8.45	0.643	0.284	17.31	0.924	1.702	8.46	0.327	0.267

Means followed by the same letter within a column are not significantly different at the 5% level.

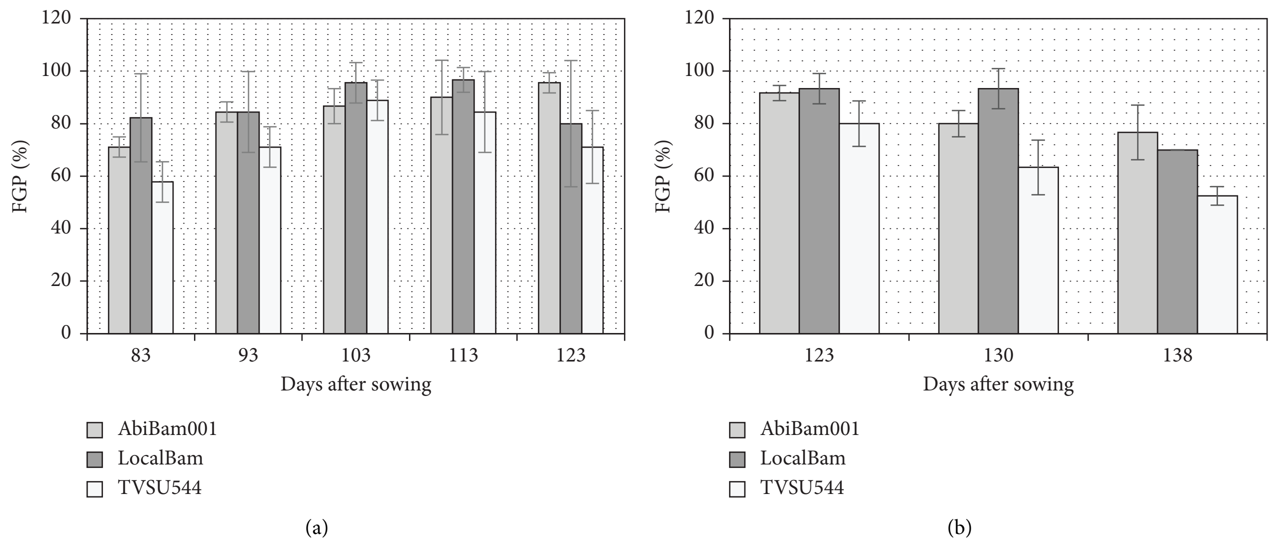

Figure 3: Final germination percentage (FGP) of seeds of the landraces at different stages of maturity: (a) at Ocettoke and (b) at Koro. Error bars are the means ± standard deviation.

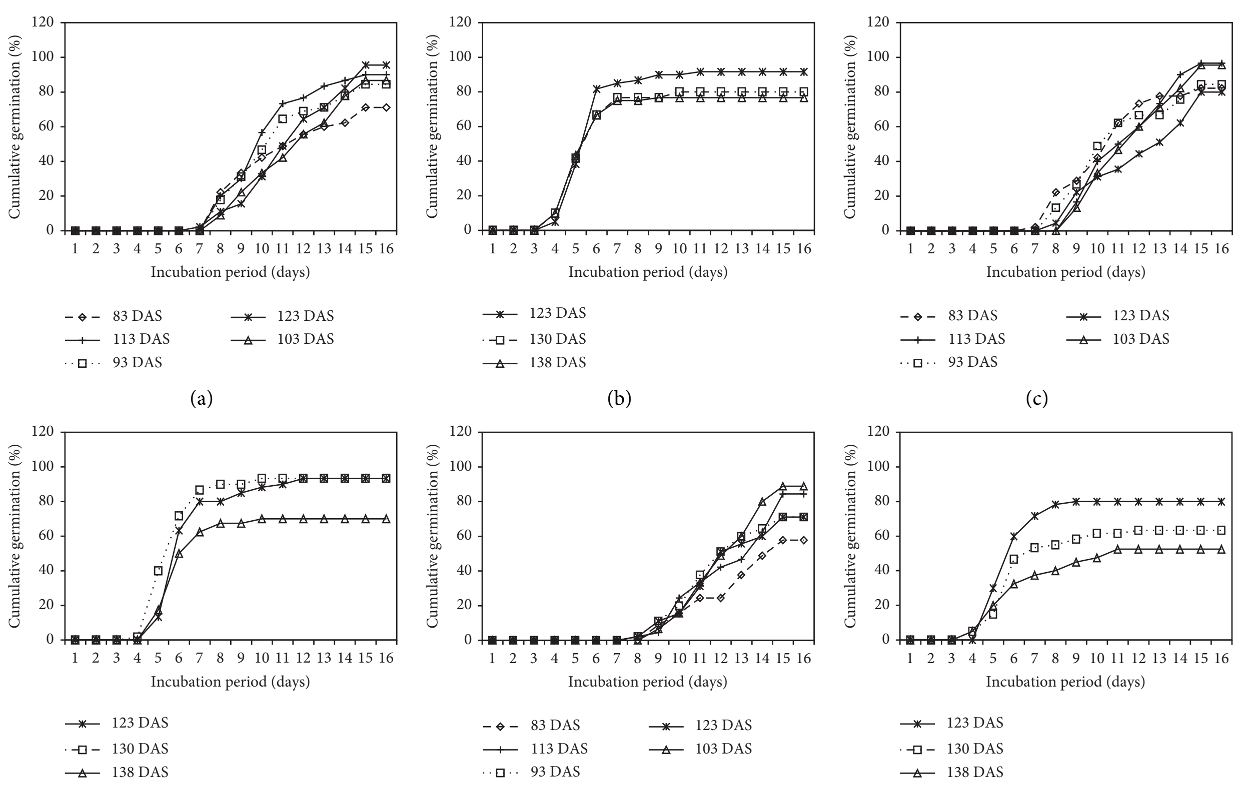

Figure 4: Cumulative germination (CG) of seeds of the different landraces from the two sites of Ocettoke (a, c, e) and Koro (b, d, f): (a, b) AbiBam001, (c, d) LocalBam, and (e, f) TVSU544. DAS = days after sowing.

[14, 15]. In the present investigation, from the start of sampling at 83 DAS–113 DAS at Ocettoke, there was a steady and steep rise in seed weight, suggesting that these developmental stages fall within the seed filling stage. It is also very likely that the seed filling stage for all landraces start 10 or more days earlier than the first date of sampling. Beyond 113 DAS, the slowed increase in the seed dry weight suggests the drawing to an end of the seed filling period and the onset of maturation drying for both LocalBam and TVSU544. For AbiBam001, however, seed filling continued

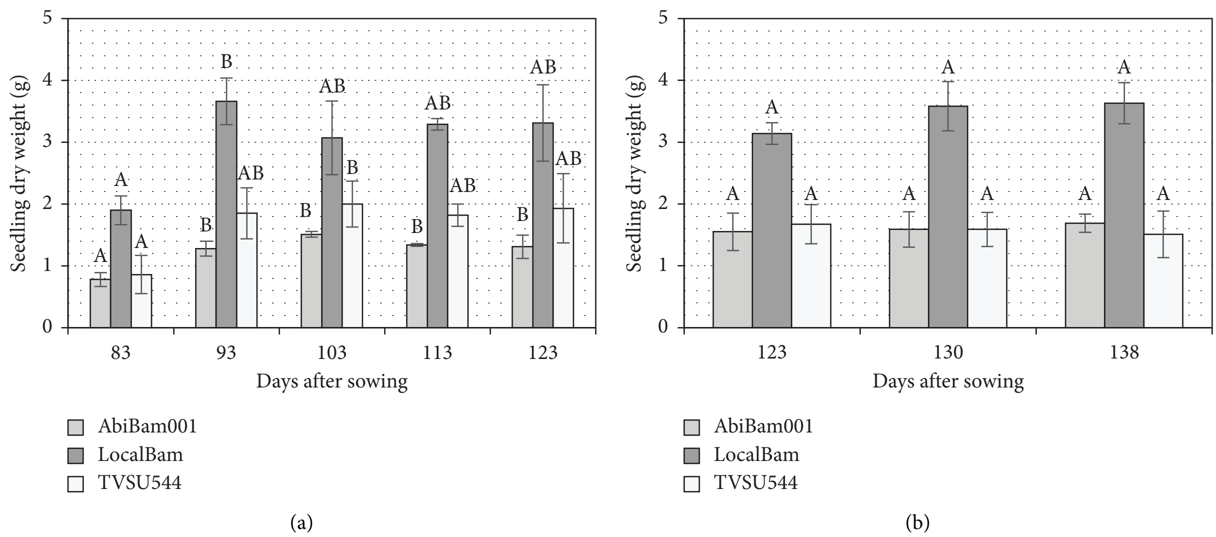

Figure 5: Seedling dry weight of seeds of the landraces harvested at different stages of maturity: (a) at Ocettoke and (b) at Koro. Means followed by the same letter are not significantly different at the 5% level. Error bars are the means ± standard deviation.

Table 3: Stages at which seeds of the different landraces attain key indicators of maturity.

Landraces	Highest FGP		Highest GVI		Highest seedling dry weight		Mass maturity (approx.)
	Ocettoke	Koro	Ocettoke	Koro	Ocettoke	Koro	Both sites
AbiBam001	123	123	123	123	103	138	130
LocalBam	113	123	113	130	93	138	113
TVSU544	103	123	103	123	103	123	113

Table 4: Values of Kendall's rank correlation coefficient (τ) among the various seed and germination parameters for the landraces at Ocettoke.

Landraces	Parameters	FGP	GVI	SDW	Seed weight	Seed length	Seed width
AbiBam001	FGP (%)	1.0					
	GVI	0.6	1.0				
	SDW (g)	0.4	0.4	1.0			
	Seed weight (g)	1.0**	0.6	0.4	1.0		
	Seed length (mm)	1.0**	0.6	0.4	1.0**	1.0	
	Seed width (mm)	1.0*	0.6	0.4	1.0**	1.0**	1.0
LocalBam	FGP (%)	1.0					
	GVI	0.7	1.0				
	SDW (g)	0.3	0.0	1.0			
	Seed weight (g)	1.0**	0.7	0.3	1.0		
	Seed length (mm)	1.0**	0.7	0.3	1.0**	1.0	
	Seed width (mm)	1.0**	0.7	0.3	1.0**	1.0**	1.0
TVSU544	FGP (%)	1.0					
	GVI	1.0*	1.0				
	SDW (g)	0.7	0.7	1.0			
	Seed weight (g)	0.7	0.7	0.3	1.0		
	Seed length (mm)	0.7	0.7	0.3	1.0**	1.0	
	Seed width (mm)	0.7	0.7	0.3	1.0**	1.0**	1.0

*Correlation is significant at the 0.05 level; **correlation is significant at the 0.01 level.

beyond 113 DAS which was strongly alluded to by the trend at the Koro site where there was a diminished increase in the seed weight between 130 and 138 DAS. Variation in the length of each of the phases is known to be dependent on the species and prevailing environmental conditions [14]. An earlier study of seed development in a BN landrace ("Ankpa") from Nigeria indicated that embryo development proceeds up to at least 41 days after anthesis (roughly 70–75

Table 5: Values of Kendall's rank correlation coefficient (τ) among the various seed and germination parameters for the landraces at Koro.

Landraces	Parameters	FGP	GVI	SDW	Seed weight	Seed length	Seed width
AbiBam001	FGP (%)	1.0					
	GVI	1.0**	1.0				
	SDW (g)	−1.0**	−1.0**	1.0			
	Seed weight (g)	−1.0**	−1.0**	1.0**	1.0		
	Seed length (mm)	−1.0**	−1.0**	1.0**	1.0**	1.0	
	Seed width (mm)	−1.0**	−1.0**	1.0**	1.0**	1.0**	1.0
LocalBam	FGP (%)	1.0					
	GVI	0.8	1.0				
	SDW (g)	−0.8	−0.3	1.0			
	Seed weight (g)	−0.8	−0.3	1.0**	1.0		
	Seed length (mm)	−0.8	−0.3	1.0**	1.0**	1.0	
	Seed width (mm)	−0.8	−0.3	1.0**	1.0**	1.0**	1.0
TVSU544	FGP (%)	1.0					
	GVI	1.0**	1.0				
	SDW (g)	1.0**	1.0**	1.0			
	Seed weight (g)	−0.3	−0.3	−0.3	1.0		
	Seed length (mm)	−0.3	−0.3	−0.3	1.0**	1.0	
	Seed width (mm)	−0.3	−0.3	−0.3	1.0**	1.0**	1.0

**Correlation is significant at the 0.01 level.

DAS) and that longer photoperiod of 16 hr delayed flowering by as much as 7 days compared to 10 hr photoperiod. [17]. While the precise effect of environmental conditions (temperature, RH, and day length) during the experiments was difficult to ascertain, it is very likely that the relatively high temperatures, low RH, and more or less constant photoperiod of about 12 hr shortened each of the development stages for a landrace [30, 31]. High temperatures and low RH are known to influence photoheterotrophic metabolism, which in turn provide cues for auxins, cytokinins, abscisic acid (ABA), and gibberellic acid (GA)-mediated seed growth, development, and maturation [13, 14, 16, 32, 33]. Given that the landraces in the present study were cultivated in a relatively uniform environment, it is plausible that differences in maturity periods are almost entirely due to their genotypic variations. One likely effect of the environment could arise from the soil factors of Ca levels and associated acidity of the two sites, with a much higher Ca value for Ocettoke than Koro and lower acidity at Ocettoke than Koro. This is due to the fact that Ca is perhaps the most limiting nutrient element in BN seed development [34].

4.2. Seed Germination. Seeds of landraces exhibited relatively high germinability when harvested at 83 DAS which strongly suggests that a proportionate number of seeds of all landraces acquire germination capacity earlier than this developmental stage. However, seeds at a developmental stage before physiological (mass) maturity have low physiological potential [35, 36], which is demonstrated in this study by the relatively low seedling dry weight and germination capacity. While the moisture content of the seeds was not determined at the different stages of development, it is expected to be relatively high before and at physiological maturity [14, 15, 37], thus further impacting negatively on the seed quality at this stage. The more mature seeds at latter stages of development showed higher germination capacity, faster speed of germination, and higher seedling dry weight until a point when all these parameters steadied or began to decline except for AbiBam001. The increase in seed germinability at latter stages of development can be attributed to temporal changes in seed maturation, whereby the lapse in time in the maturation process results in more seeds acquiring germination capacity [15, 38, 39]. In a normal process of ageing, seeds begin to lose their vigour and germination capacity soon after physiological maturity, a phenomenon best explained by the seed survival curve [40, 41]. The seed ageing process is accelerated by unfavorable environmental conditions during and after maturation while the seeds are still attached to the mother plant, during harvest, and in storage [40, 42, 43]. This is a plausible explanation for the decline in most of the seed germination characteristics after physiological maturity. It is also possible that the lowering of seed quality is the effect of hard-seededness [44–47]. Many seeds including dry legumes develop hard-seededness as a dormancy mechanism to defer germination until favourable conditions exist after maturation drying and as a means of seed survival during seed dispersal and prior to seed germination [44, 46, 47]. Hard-seedeness in many seeds is proposed to start almost around the same time seeds attain physiological maturity and that it is enhanced by dry and hot conditions during the seed ripening process [45]. The major regulators of dormancy and germination are ABA and GA and their interaction, with high levels of ABA relative to GA towards physiological maturity and during maturation drying, ensuring that seeds go into a quiescent state [13–16, 32, 33]. It is likely therefore that the timing of harvest of seeds for this study (in the dry and hot months of January–March) could have to some extent contributed to the seeds becoming harder than usual. Bambara nut seeds have been reported to show extended period to emergence under field conditions (up to 35 DAS) and hard-seedednees has been suggested as a likely cause of this phenomenon [29]. Nevertheless, a combined assessment of three seed quality parameters (FGP, GVI, and seedling dry weight) revealed that seeds of the highest quality were obtained at 103, 113, and 123 DAS for TVSU544, LocalBam, and AbiBam001, respectively. Accordingly, for both TVSU544 and AbiBam001, the best quality seeds are obtained before mass maturity, while for LocalBam, they are obtained at approximately mass maturity.

4.3. Relationships among Seed Germination and Seed Size Parameters. For the Koro site with mostly mature seeds of all the landraces, seed germinability (FGP) and the GVI exhibited negative relationships with all the seed size characteristics, while SDW had positive relationships with all seed size characteristics for two landraces. It is likely that for all landraces, the smaller the seed, the higher the extent of and the faster the germination and vice versa. This trend has been observed for soybeans, whereby medium sized seeds had better physiological potential (germinability and vigour) than larger or smaller seeds [36]. It would therefore seem that medium-sized seeds for all the landraces are the best for sowing. The positive relationships between germination parameters and seed size characteristics at Ocettoke is attributed to temporal changes in the process of seed maturation, whereby as time passes, seeds become larger in sizes (weight, length, and width) with more and more of them acquiring germination capacity as they pass through stages of maturation [14, 15, 38, 39]. The weak relationship between seed germination and seedling dry weight observed in this study seems to suggest that BN seed lots with high germination capacity do not proportionately produce the most vigorous seedlings or even at worst produce seedlings with the least vigour as was the case for AbiBam001 and LocalBam at Koro. This trend was alluded to by Mandizvo and Odondo [48], who observed that BN seed lots with higher viability did not necessarily produce seedlings of higher vigour. Strong positive relationships among the seed size characteristics of weight, length, and width is expected since they normally tend to have a pattern of concomitant increase as a result of cell expansion, especially during seed filling, thus proportionately maintained at all stages of development and maturation [14, 15].

5. Conclusion

Landraces exhibited typical patterns in seed development and maturation with both AbiBam001 and TVSU attaining highest seed quality before mass maturity, while LocalBam seeds had the highest quality at approximately mass maturity. There was reduced germinability and generally lower seed quality beyond mass maturity for all landraces, suggestive of the influence of physiological and physical factors that reduce germinability such as normal seed deterioration and hardseededness. For better quality seeds, harvest should be timed at 103–113, 113–123, and 120–130 DAS for TVSU544, LocalBam, and AbiBam001, respectively. This would result in medium-sized seeds of relatively high seed quality. A germination test involving properly size graded seeds from the respective stages of highest seed quality, i.e., 103, 113, and 123 for TVSU544, LocalBam, and AbiBam001, could also be performed to validate the size vs. extent vs. speed of germination relationship to ensure more precise criteria for future seed selection for the landraces. A broader spectrum and higher frequency of sampling including maturity stages outside what was possible in the present study, i.e., before 83 and beyond 138 DAS will provide a more complete picture of the developmental patterns of the landraces. This should target the main growing season, i.e., April–August/September to synchronise growing conditions with farmers' practices and ensure better seed yield. [49].

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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