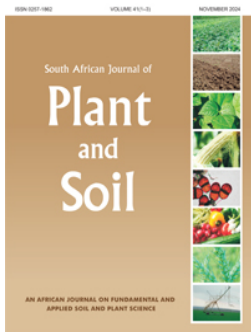


Stability and performance of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes in different South African environments

Sithembile Kunene, Abe Shegro Gerrano & Alfred Oduor Odindo

Accessibility Disclaimer:

For a more accessible version of this document, please submit an accessibility request form through the Montana State University Library website.



Stability and performance of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes in different South African environments

Sithembile Kunene, Abe Shegro Gerrano & Alfred Oduor Odindo

To cite this article: Sithembile Kunene, Abe Shegro Gerrano & Alfred Oduor Odindo (08 Jan 2025): Stability and performance of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes in different South African environments, South African Journal of Plant and Soil, DOI: [10.1080/02571862.2024.2420109](https://doi.org/10.1080/02571862.2024.2420109)

To link to this article: <https://doi.org/10.1080/02571862.2024.2420109>



© 2025 The Author(s). Co-published by NISC Pty (Ltd) and Informa UK Limited, trading as Taylor & Francis Group



Published online: 08 Jan 2025.



[Submit your article to this journal](#)



Article views: 568



[View related articles](#)



[View Crossmark data](#)

Stability and performance of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes in different South African environments

Sithembile Kunene ^{1*}, Abe Sheguro Gerrano ^{2,3,4} and Alfred Oduor Odindo ¹

¹University of KwaZulu-Natal, Pietermaritzburg campus, College of Agriculture, Engineering and Science, School of Agricultural Earth, and Environmental Sciences, Pietermaritzburg, South Africa

²Agricultural Research Council, Vegetable, Industrial and Medicinal Plants, Pretoria, South Africa

³Montana State University, Department of Plant Sciences and Plant Pathology, Bozeman, USA

⁴Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho, South Africa

* Corresponding author: kunenesithembile50@gmail.com

Global food security faces challenges arising from population growth, climate change, and the prevalence of monoculture agriculture. In addressing these concerns, Bambara groundnut (*Vigna subterranea* (L.) Verdc.) emerges as a promising crop due to its nutritional richness and resilience in marginal environments. Despite its potential, research gaps persist, particularly in the context of South Africa. The study aimed to evaluate the performance and stability of Bambara groundnut genotypes in two South African agroecological environments. Field trials were conducted at Brits and Ukulinga, with data collected on grain yield, hundred-seed weight, and other agronomic traits. Genotypes Acc 179, 184, and 82 demonstrated significant stability and high yields across both locations, showing promise for future breeding programs. The results suggest that these genotypes can adapt to diverse agroecological areas, enhancing Bambara groundnut production in South Africa. Future research should focus on breeding efforts to further improve crop resilience.

Keywords: agroecology, agronomic traits, breeding programs, environmental effects, environmental stability, phenotypic variation

Introduction

There are many challenges threatening global food and agriculture systems, including rapid population growth, climate change, and intensive monoculture farming (Tan et al. 2020). Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is considered a promising crop for several reasons, including its nutritional value, ability to generate income, and ability to maintain food security (Khan et al. 2020; Majola et al., 2021). Increasing crop efficiency and finding suitable environmental sites to meet the demands of an ever-growing population are challenges faced by farmers and researchers (Mubaiwa et al. 2018). Legume crops have long been neglected in breeding programs (Mayes et al. 2019). Bambara groundnut is indigenous to Africa and is cultivated throughout the semi-arid regions of sub-Saharan Africa. It is necessary to explore some value-added processing methods to provide a further boost to the utilisation of Bambara groundnut beyond its traditional use (Oyeyinka et al. 2018). The Bambara groundnut is mostly grown by smallholder and subsistence farmers in Africa (Mubaiwa et al. 2018). By preserving the seed on farms and in conventional storage facilities for the following growing season, smallholder and subsistence farmers who

cultivate these landraces preserve the genetic variety and resources of the species (Sidibé et al. 2020). Most farmers cultivate Bambara using landraces (Nafula et al. 2021).

Research has been conducted on Bambara groundnut landraces from a variety of locations; however, these valuable plant genetic resources have not been fully exploited (Massawe et al. 2005; Uba et al. 2021). Bambara groundnuts are grown mainly in the KwaZulu-Natal, Limpopo, Mpumalanga, and Northwest provinces in South Africa under a variety of climatic conditions (air temperature, rainfall, and day length) (Mabhaudhi and Modi 2013). Although little research has been conducted on Bambara groundnut, it is an important legume in many parts of Africa, regardless of its lack of intensive study (Akinola et al. 2020). In addition to improving soil fertility and enhancing microbial diversity, Bambara groundnut fixes atmospheric nitrogen. Unlike other crops, it can tolerate adverse air temperatures and provides yields in acidic and degraded soils (Tan et al. 2020).

For Bambara groundnut production, the production environment may be a constraint (Unigwe et al. 2016). Inconsistent yields is one of the characteristics of Bambara groundnut that has evolved under harsh conditions (Khan

et al. 2020). Breeders can improve yields and select genotypes for different agroecological regions by identifying genotypes adapted to different growing conditions for Bambara groundnut production (Massawe et al. 2005; Olanrewaju et al. 2022). Bambara groundnut landraces have been grown continuously in recent years owing to their high productivity under adverse conditions (Obidiebube et al. 2020). Growing without fertilisers, irrigation, or pest and disease control, these landraces have shown a remarkable ability to survive in the poorest environments (Khan et al. 2020). Bambara groundnut is adapted to marginal areas characterised by hot and dry conditions (Chimonyo et al. 2020; Majola et al. 2021). Bambara plants can grow up to 2 000 m above sea level on marginal soils (Salazar-Licea et al. 2022). Climate conditions necessary to grow Bambara plants include air temperature ranges between 20 and 34°C, average annual rainfall ranging between 600 and 750 mm, and pH values between 5.0 and 6.5 (Ayerdi and Marraccini 2022). The species can also thrive under wetter conditions with an annual rainfall of more than 2 000 mm and in most soils with good drainage (Khan et al. 2021). Bambara groundnut is also adapted to marginal areas characterised by hot and dry conditions (Chimonyo et al. 2020).

As global food shortages worsen, plant breeders are researching crop improvement, which involves diversifying crops, improving crop adaptation to climate change, and upgrading underutilised crops to better meet global food demands (Shahzad et al. 2021). To diversify the food supply, underutilised crops, including Bambara groundnut, must be bred to overcome environmental, health, and climate challenges (Sarkar et al. 2019). Owing to the unknown

morphological characteristics of most varieties of Bambara groundnut, despite its benefits, it needs to be characterised in terms of its agro-morphological characteristics (Mubaiwa et al. 2018). Significantly, women grow this crop in cultures without modern technology and produce high yields with low input. The rest of their harvest is consumed by them and between 10 and 40% is sold in the local market and the women and their families consume the rest of the harvest (Adzawla et al. 2016).

To the best of our knowledge, South Africa has never had a comprehensive breeding program for Bambara groundnut species. The aim of this study was to characterise agronomic traits, examine trait relationships, and identify promising genotypes in two South African production environments.

Materials and methods

Plant material

A total of 24 genotypes (Figure 1) of Bambara groundnut were used in this study. The genotypes were obtained from the Agricultural Research Council (ARC) GenBank in Pretoria, South Africa. The 24 genotypes were comprised of 16 seed coat colours: ochre brown, graphite black, red-brown, sepia brown, brown beige, mahogany brown, golden yellow, red-brown, clay brown, jet black, fawn brown, signal brown, ochre brown, steel blue, terra brown, and brown olive.

Production environments

The genotypes were planted at the Brits (Northwest Province) and Ukulinga (KwaZulu-Natal Province) research farms of the ARC and University of KwaZulu-Natal (UKZN), respectively during the 2018/2019 summer cropping



Figure 1: Images of 24 different Bambara groundnut genotypes evaluated at Brits and Ukulinga sites

seasons. Table 1 shows the monthly rainfall in Brits and Ukulinga during the summer cropping season (2018/2019). The Brits site lies at 25°36'S latitude, 27°48'E longitude at an altitude of 1 119.1 m a.s.l., with a mean air temperature of 22.4°C. The maximum and minimum air temperatures recorded during the cropping period ranged from 14.5 to 30.3°C. The soil type is a clay loam with a pH of 7.08 (ARC-VOPI 2019). Ukulinga lies at 29°24' E latitude and 30°24' S longitudes at an altitude of 840 m a.s.l. The location receives an average annual rainfall of 750 mm over 113 rainy days, with 23% of the mean annual precipitation (MAP) falling during the winter months (Mabhaudhi et al. 2018). The maximum and minimum recorded air temperatures at Ukulinga ranged from 14.7 to 26.8°C during the cropping season, with a mean air temperature of 22.8°C (Mabhaudhi et al. 2018). The soil type was clay loam.

Experimental design, layout, and treatment structure

At each production environment (site), the experiment was laid out as randomised complete block design (RCBD) with 24 genotypes as the main factor and replicated three times, giving a total of 72 experimental units (plots). Each plot measured 2.5 m × 2.0 m, with in-row and inter-row spacing of 30 mm × 45 mm. A smaller plot size was chosen due to the limitations of land and material availability. Three rows 4 m in length were planted at each site. The plant spacing was 0.4 m between the plants and 1 m between rows. Two seeds were hand-sown per hole, and the plants were thinned to one after full seedling emergence. A central row of five randomly selected plants was used for data collection and analysis.

Data collection

Data collection began during the vegetative growth stages of the crop. Data collected included leaf length, leaf width, leaf area, petiole length, plant height, number of pods per plant, plant canopy, days to maturity, number of seeds per plant, hundred seed weight, and grain yield (Table 2). The average daily rainfall data (Table 1) were obtained from the Agricultural Research Council – Soil, Climate, and Water Institute, Pretoria, South Africa.

Table 1: Monthly daily rainfall at Brits and Ukulinga during the summer cropping seasons 2018 and 2019

Month	Brits Research Farm Rainfall (mm)		Ukulinga Research Farm Rainfall (mm)	
	2018	2019	2018	2019
October	49.8	11.9	67.6	67.6
November	19.3	14.7	138.4	138.4
December	5.1	0.5	269.6	269.6
January	67.6	14.1	36.0	113.0
February	12.2	8.4	87.4	145.4
March	0.0	0.5	113.0	100.8
April	0.5	6.9	77.8	345.4
May	0.0	0.0	34.6	3.6
June	9.1	0.0	1.8	12.0
July	11.2	0.5	9.2	4.4

Parameters measured and data analysis

Twelve quantitative morphological characteristics (Table 2) were measured among the 24 Bambara groundnut genotypes using the Bambara groundnut descriptor.

Data analysis

The data were analysed using ANOVA. Least significant difference (LSD) tests were used to compare means at a significance level of 0.05. To determine the degree of association between each phenotypic trait and its correlation coefficient, phenotypic correlation coefficients were computed. R Version 4.4.1. R Foundation for Statistical Computing, Vienna, Austria was used for correlations and heatmap analysis. XLSTAT for Microsoft Excel, Version 2020.6 (Addinsoft, Paris, France) was used to perform principal component analysis (PCA), and non-linear regression. The variability between these two environmental sites was analysed only using common data for both sites.

Results and discussion

Plant growth and development in response to the production environment

Plant growth and development in the two production environments were compared by measuring petiole length, leaf width, and plant height. A highly significant ($p < 0.001$) difference between these two environments was observed in the petiole length (Figure 2a) and leaf width (Figure 2b) of the plants. These differences in morphology suggest a genotype-specific response to environmental effects, reinforcing the notion that plant genotypes respond differently to differing growth conditions (Sultan 2017). The genotype-environment interactions are crucial for understanding plant adaptation and can have implications for agricultural practices, crop management, and breeding programs (de Leon et al. 2016). The height of the plants (Figure 3) ranged from 193.3 (Ukulinga) to 307.4 mm (Brits). Mabhaudhi et al. (2018) reported that plants do not use water because of reduced soil water accessibility, therefore height and leaf length decreased. A number of factors affect plant growth, including solar radiation, air temperature, soil water, rainfall, soil texture, and nutrition (Mabhaudhi and Modi 2013). These factors have an impact on the plant growth hormones, which might cause the plant to grow rapidly or slowly (Waadt et al. 2022).

There was a significant ($p < 0.05$) difference in plant height between the genotypes. Acc 100 (307.4 mm) was the tallest plant in Brits, whereas Acc 61, with a height of 286.7 mm, was the tallest in Ukulinga. Reduced leaf canopy size allows more water to evaporate, although this often results in a reduced yield potential (Chimonyo et al. 2020). The plant may experience stress from changes to any of these factors, which could alter, stunt, or promote growth (Msimbira and Smith 2020). Oyeyinka et al. (2018) also reported that air temperature, altitude, soil type, and rainfall are among the factors that affect the growth of Bambara groundnuts. Acc 100 from Brits had the longest leaf (844 mm), followed by Acc 55 (773 mm) from Ukulinga. Unigwe et al. (2016) also reported similar results. They

Table 2: List of quantitative morphological characters recorded from 24 Bambara groundnut accessions

Quantitative characters	Code	Description	Measurement type
Days to maturity (count)	DM	Number of days from emergence to maturity in each plot	Counting
Grain yield (g plot ⁻¹)	GY	Total weight of seed per plot	Weighing balance
Hundred seed weight (g)	HSW	Weight of hundred seed counts at 12% moisture content	Weighing balance
Leaf area (mm ²)	LA	Area of leaf	Leaf area meter
Leaf length (mm)	LL	Length of leaf from base to tip	Tape measure
Leaf width (mm)	LW	Width of leaf at widest point	Tape measure
Number of pods plot ⁻¹ (count)	NPP	Number of pods plant ⁻¹	Counting
Number of seeds plot ⁻¹ (count)	NSP	Total count of seeds per five plants	Counting
Petiole length (mm)	PL	Length of panicle from base to tip	Tape measure
Plant canopy area (mm ²)	PC	Measuring canopy area, at a height where the canopy was the widest	Tape measure
Plant height (mm)	PH	Height of main stalk from ground to tip of main pannicle	Tape measure
Yield plant ⁻¹ (g)	YPP	Weight of seed per plant (average of five plants)	Weighing balance

emphasised that Bambara groundnut accessions should be characterised agronomically, physiologically, biochemically, and molecularly to determine their true genetic diversity. At Ukulinga, the plant canopy area varied from 266.7 to 363.3 mm². At the Brits site, the plant canopy area varied from 82 to 336 mm². Furthermore, Acc 25 had the widest canopy area at Ukulinga (363.3 mm²), and Acc 175 had the widest canopy area (82.1 mm²) at Brits.

Yield performance in response to the production environment

Yield performance was determined in terms of grain yield per plot and converted to grain yield per hectare and hundred seed weight. There was a highly significant difference ($p < 0.001$) between genotypes with respect to grain yield (Figure 4a), and hundred-seed weight (Figure 4b). In Brits, Acc 179 yielded the highest grain yield (54.2 kg ha⁻¹), followed by Acc 184 (43.3 kg ha⁻¹) and Acc 150 (35.3 kg ha⁻¹). Breeding programs can use these genotypes to produce high-quality Bambara groundnut. In Ukulinga, grain yield ranged between 34.0 and 68.7 kg ha⁻¹, with Acc 190

having the lowest yield and Acc 177 having the highest. The grain yield of the 24 genotypes tested ranged from 18.9 to 68.7 kg ha⁻¹. Bambara groundnut production at Ukulinga showed greater yields than in Brits (≤ 34.0 kg ha⁻¹), implying that environmental conditions were more favourable at Ukulinga. Obura et al. (2021) highlighted the fact that seed quality determines seed yield. They emphasised that proper drying and unshelled storage are just two examples of effective seed management techniques that contribute to comparatively high seed quality for high yield.

A hundred-seed weight of 77.5 g for Acc 97 was the highest recorded at Brits, followed by 72.2 g for Acc 179 and 71.1 g for Acc 150. It has been suggested that hundred-seed weight plays an important role in enhancing yield in morphological trait evaluations (Unigwe et al. 2016). In this study, hundred seed weight ranged from 21.7 to 83.7 g. Seed size may be a good indicator of seed quality in terms of vigour (Mandizvo and Odindo 2019). In addition to being a valuable measure of yield, it is an excellent indicator of how the genotype and environment influence quantitative traits (Rogé et al. 2016).

A significant level of phenotypic variation was observed among the genotypes in this study, leading to the conclusion that breeding programs can benefit from traits that are genetically diverse within the genotypes. Previous studies on South African Bambara populations have reported similar results. Albertazzi (2020) highlighted that the genetics, environment, and management triangle ($G \times E \times M$) connection governs how plants behave phenomenally. Numerous genes are known to play a role in regulating each physical trait of a plant during the course of its life cycle (Ali et al. 2022).

In this study there was a wide range in grain yield per hectare, from 34.0 to 68.73 kg ha⁻¹ for both sites. A maximum yield of 68.73 kg ha⁻¹ was recorded at the Ukulinga site, this being a significant increase over that reported by Unigwe et al. (2016), who found a yield variation between 9.9 and 12.6 kg ha⁻¹. According to this study, the Bambara groundnut genotypes examined had adapted to the farming conditions in Brits and Ukulinga. Pesticides are commonly applied to Bambara groundnut

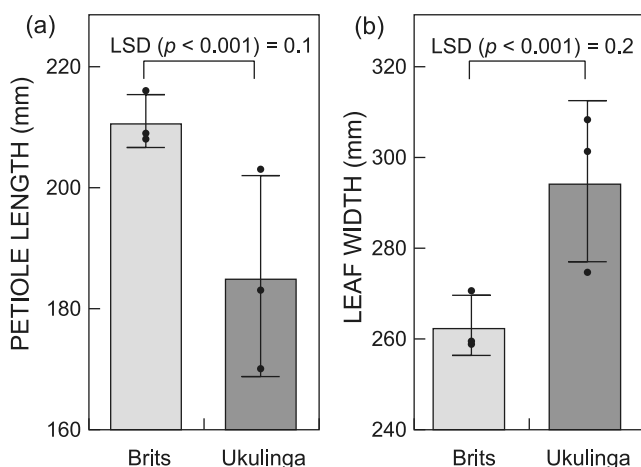


Figure 2: The variation in petiole length (a) and leaf width (b) between genotypes observed at the Brits and Ukulinga research farms. LSD: least significant difference

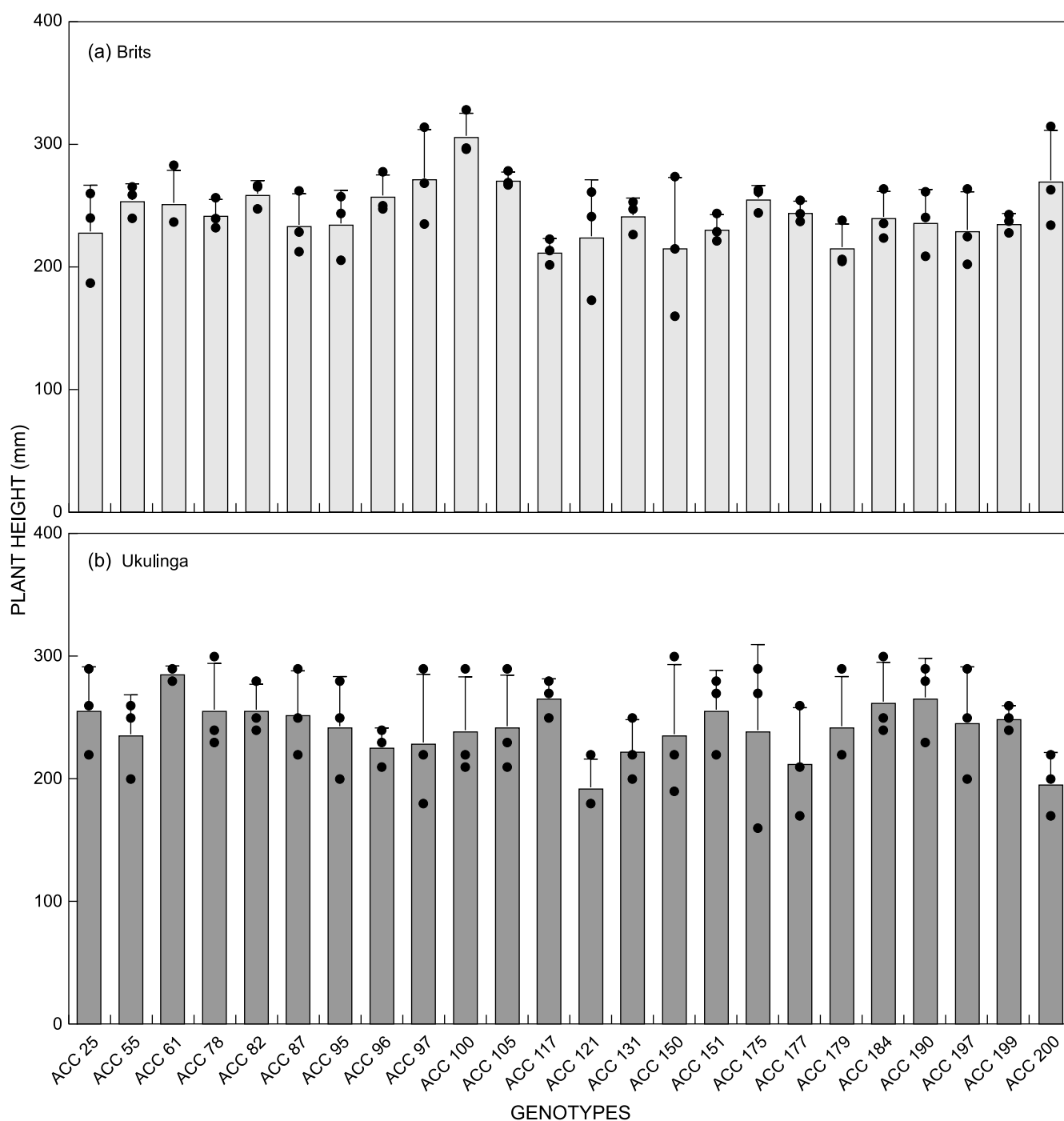


Figure 3: The variation in plant height between genotypes observed at (a) Brits and (b) Ukulinga research stations

because of its susceptibility to diseases and insects (Shahzad et al. 2021). Muhammad et al. (2021) reported an average yield of 650–850 kg ha⁻¹ for Bambara groundnuts, which varied significantly with location, season, and genotype. This is consistent with other researchers, who have reported that grain yield and other traits vary widely among landraces (Marone et al. 2021). Pod and seed yields were reported by Berchie et al. (2010) as 4 173.1 and 3 084.4 kg ha⁻¹, respectively. Like many plants,

Bambara groundnut grows differently in different environments (Mabhaudhi et al. 2018), and subsistence farmers typically experience low yields and encounter frequent crop failures (Sidibé et al. 2020).

Performance of 24 Bambara groundnut genotypes for agronomic traits at Brits and Ukulinga sites

It is important to select agronomic traits as key components of genetic improvement to enhance Bambara groundnut

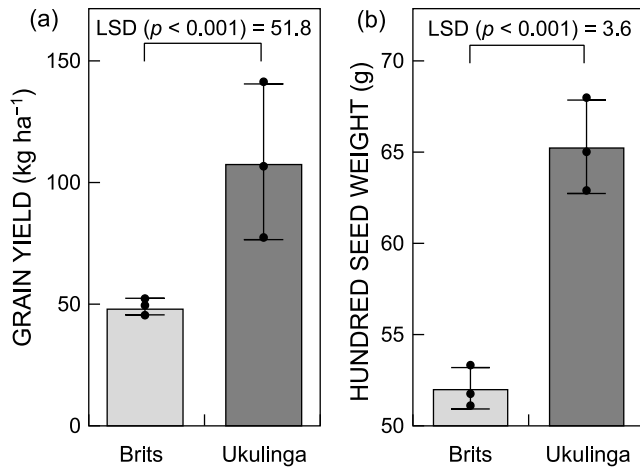


Figure 4: Assessing environmental effects on Bambara groundnut growth: (a) comparative analysis of grain yield and (b) hundred seed weight at Brits and Ukulinga study sites. LSD: least significant difference

yields (Khan et al. 2016). Table 3 shows the mean values of the studied agronomic traits among Bambara genotypes across the two environments. There was a high level of significance between the genotypes in HSW (Table 3). Grain yield, hundred seed weight, leaf width, petiole length, and plant canopy were highly significant among locations. Heilmeier (2019) highlighted the fact that the performance of plants, and thus how they may react to environmental effects, can be influenced by characteristics such as leaf size and rooting depth. Plant characteristics, such as how well they use water, can be integrated into or connected to a specific functional plant response (Grossiord et al. 2020). In terms of the interaction between genotypes and locations, highly significant differences were observed among the genotypes for GY, HSW, and PH (Figure 5). Plant height and leaf length of the genotypes were not significant in terms of the interaction between genotype and location (Figure 5). Plants can also differ in a number of traits (Mathakutha et al. 2019). This may be related to the fact that phenotypic variation is more likely to be expressed in the environment than genotypic variation because of its greater influence on expression (Ralls et al. 2020).

The hierarchical clustering analysis

The hierarchical clustering analysis grouped the genotypes based on their performance across measured traits, as shown in the two heatmaps (Figure 6). Genotypes were classified into three clusters (C1, C2, and C3), with red indicating C1, green for C2, and blue for C3.

At Brits (Figure 6a), genotypes in Cluster 1 showed predominantly negative values for most traits, such as plant height (PH), plant canopy (PC), and leaf width (LW). For example, Acc 55, Acc 78 and Acc 131 exhibited negative values across several traits, with Acc 78 showing particularly low scores for LW (−2.5). In contrast, C2 displayed some genotypes with more positive values across traits including leaf length (LL), leaf width (LW), plant canopy (PC), grain yield (GY), hundred seed weight (HSW), and petiole length (PL), as demonstrated by Acc 97, Acc 105, Acc 150, and Acc 179 which performed well in these traits. Cluster 3 included genotypes with moderate trait values, such as Acc 100 and Acc 200, with neutral or slightly positive scores for most traits.

At Ukulinga (Figure 6b), the clustering pattern remained consistent with some variation in the trait performance within each cluster. Cluster 1 continued to display some negative values across traits, while C2 genotypes, such as Acc 55 which showed strong positive values for LL, and LW and Acc 177, showed strong positive associations with LL, and GY, where values exceeded +1.3. Acc 200 showed a strong association with LW. Meanwhile, Cluster 3 contained only one genotype, Acc 199, which had positive associations for all the traits (LL, LW, GY, HSW, PL, PH, and PC) with PC, PL, HSW, and LW showing strong positive associations. Consistently grouped genotypes with lower performance across key traits, as evidenced by negative values in both heatmaps, suggests that these genotypes may be less desirable for improving yield-related traits (Linus et al. 2023). The comparison of the two heatmaps reveals that the clustering of genotypes is relatively stable, with consistent groupings across different conditions. Genotypes that excelled in most of the traits hold potential as high performers in breeding programs aiming to enhance crop yield. Cluster 3 comprises genotypes with moderate or mixed performance across traits; while these genotypes may not be top performers, they can still offer valuable traits under targeted breeding or specific environmental conditions. The trait contributions within clusters, particularly for PH,

Table 3: Analysis of variance showing mean squares and significant tests for physiological traits of 24 Bambara groundnut genotypes evaluated at Brits and Ukulinga study sites

Source of variation	df	GYPlot	HSW	LL	LW	PL	PC	PH
Genotype	23.0	29 107.0	324.6**	7.9	4.3	1.4	174.5	114.7
Location	1.0	3 083 472.0**	6 458.9**	0.8	36.4**	23.6**	4 663.6**	19.8
Genotype × location	23.0	44 763.0*	234.5*	9.1	2.8	1.5	130.4	166.8*
Residual	94.0	24 525.0	120.1	7.8	2.7	0.9	151.2	101.3

df = degrees of freedom
GYPlot = grain yield per plot
HSW = hundred seed weight

LL = leaf length
LW = leaf width
PC = plant canopy

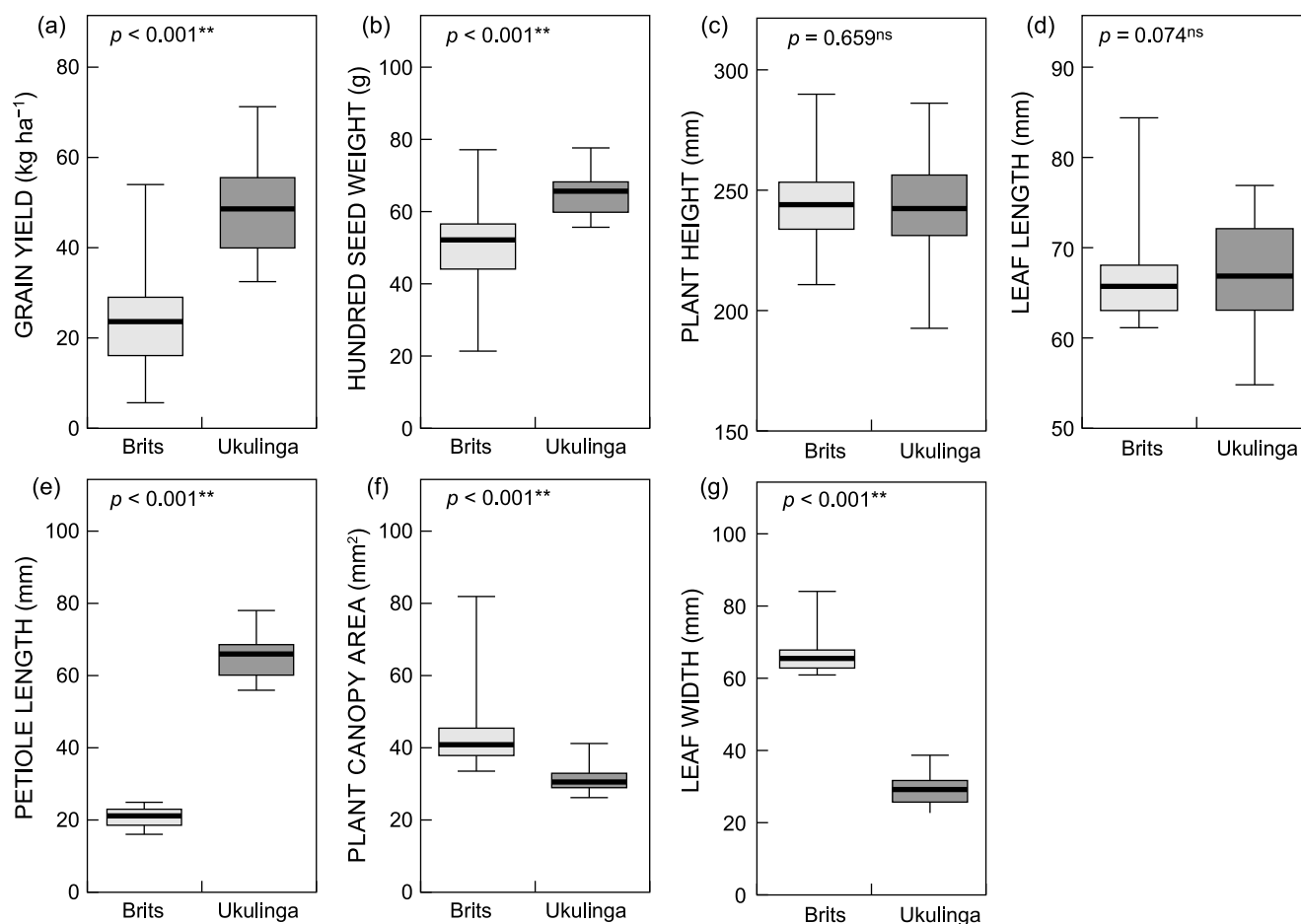


Figure 5: Response of Bambara groundnut for agronomic traits under Brits and Ukulinga conditions: (a) grain yield, (b) hundred seed weight, (c) plant height, (d) leaf length, (e) petiole length, (f) plant canopy, (g) leaf width. * = $p < 0.05$, ** = $p < 0.01$, ns = non-significant

PC, LW, and LL, shifted slightly between the environments. These changes could be due to genotype-by-environment interactions or varying experimental conditions influencing the expression of these traits (Olanrewaju et al. 2021; Linus et al. 2023).

Understanding the adaptive strategies of these cultivars could therefore be beneficial in developing resilient cultivars for agricultural use (Lin 2011).

Principal component analysis

This study examined the associations and comparisons between Bambara groundnut genotypes based on the traits measured. We used principal component analysis (PCA) in order to determine whether trait variation observed between genotypes was affected by their production environments (Brits and Ukulinga). Using linear independent composite traits, the maximum variation of a set of characters can be separated into linear independent composite traits. The PCA results with eigenvalues, factor loadings, and percent variances between 24 Bambara groundnut genotypes under Brits and Ukulinga conditions are shown in Table 4. PC 1 accounted for 28.4% of the total variation and was positively correlated with GY, HSW, LL, LW, PL, PC, and PH and highly significant with GY,

HSW, LL, and PC. PC 2 also correlated positively with GY, HSW, LL, LW, PL, PC, PH and contributed 21.1% of the total variation. PCA has been demonstrated to be useful in predicting trait relationships in Bambara groundnut accessions (Khan et al. 2021).

Principal component biplots (Figure 7) were used to analyse the relationship between Bambara groundnut genotypes and agronomic traits. Traits represented by parallel vectors or near one another showed a strong positive association, whereas those adjacent to each other (at 180°) showed a strong negative association, and vectors toward the sides showed a weak relationship. At Brits, Acc 200, Acc 105, and Acc 82 were grouped together based on high LL and PL, while Acc 184, Acc 87, Acc 197, Acc 150, Acc 199, Acc 121, Acc 179, and Acc 150 were grouped based on high HSW, LW, and GY. Acc 175, Acc 96, Acc 61, and Acc 151 were not associated with any of the agronomic traits measured. At Ukulinga Acc 177, Acc 117, Acc 61, Acc 96, Acc 97, and Acc 199 were grouped based on high GY, HSW, PC and PH, while Acc 184, Acc 190, Acc 105, Acc 197, Acc 78, Acc 95, Acc 179, Acc 25, and Acc 151 were grouped based on high PL. Acc 100, Acc 150, Acc 200, Acc 131, and Acc 121 were not associated with any of the traits measured. Further

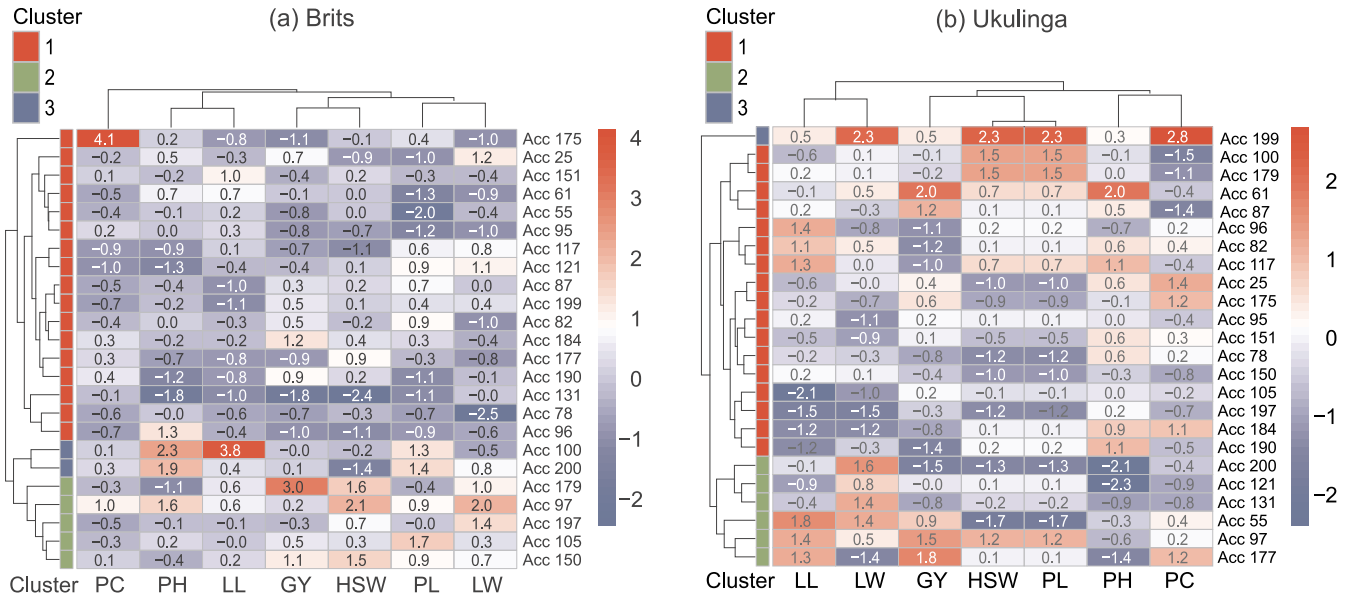


Figure 6: Heatmap illustrating hierarchical clustering of genotypes and traits at (a) Brits and (b) Ukulinga. Genotypes are grouped into three distinct clusters, indicated as C1, C2, and C3. Traits include plant canopy (PC), plant height (PH), leaf length (LL), grain yield (GY), hundred seed weight (HSW), petiole length (PL), and leaf width (LW)

research is needed to understand the underlying genetic mechanisms responsible for the observed traits. The genotypes identified as being related could be tested genetically to understand their relationships better. In addition, the genotypes could be crossed to produce hybrid plants that could be used to identify genes responsible for the observed traits (Huang et al. 2015).

Bambara groundnut genotypes were associated across environmental conditions, showing a pairing orientation, that is, sharing most of the measured traits. Comparing the PC analyses and PCA biplots, certain growth and yield characteristics were found to be shared among genotypes.

Table 4: Principal component analysis showing eigenvectors, eigenvalues, and percent variability of physiological traits measures at Brits and Ukulinga study sites

Agronomic traits	PC1	PC2	PC3	PC4	PC5
GY	0.7	0.0	0.0	0.1	0.0
HSW	0.7	0.0	0.1	0.1	0.0
PH	0.1	0.2	0.4	0.0	0.2
LL	0.3	0.1	0.2	0.2	0.0
PL	0.2	0.2	0.4	0.0	0.2
PC	2.1	0.5	0.0	0.2	0.2
LW	0.0	0.4	0.2	0.2	0.0
Eigenvalue	1.5	1.4	1.2	0.8	0.7
Variability (%)	28.4	21.1	17.2	11.6	9.5
Cumulative (%)	59.5	49.5	66.7	78.3	87.9

GY = grain yield ha⁻¹ PC = plant canopy
 HSW = hundred seed weight PH = plant height
 LL = leaf length PL = petiole length
 LW = leaf width

Bold type = vector loadings greater than or equal to 0.3

Similar findings were reported by Unigwe et al. (2016). They emphasised that the South African development initiative will be more effective with knowledge of the genetic diversity among the local Bambara groundnut accessions. Molecular markers have been suggested by Uba et al. (2021) to strengthen these relationships. Their research has further extended the knowledge base for the genetic makeup of the African Bambara groundnut, which will be useful for planning crop management and conservation efforts. Ntundu et al. (2006) also reported a strong association between landraces. They recommended doing a thorough comparison between the large collections of Bambara groundnut and the new collections in order to evaluate the genetic diversity of conserved germplasm for preservation and use in crop improvement.

Non-linear regression

Using non-linear regression, one can simulate a non-linear relationship between a dependent variable and a number of independent variables, and plots between measured agronomic traits reveal a clear nonlinear pattern (Figure 8). The association between agronomic traits at the Brits and Ukulinga locations appears to be very strong, however, it is non-linear. This is shown in Figure 8, where the PH series exhibited a general downward trend as the GY declined over time, based on the relationship between GY and PH. The GY appears to improve as leaf length increases. However, the agronomic traits seem to be strongly associated with each other. One reason for the decline in yield and its variability is climatic variation (Guntukula and Goyari 2020). Climatic variation is one of the fundamental causes of yield variability in several crops, including Bambara groundnut (Olanrewaju et al. 2022). Maqueira-López et al. (2019) emphasised that in order to maximise productivity, modern agriculture has a tendency to place

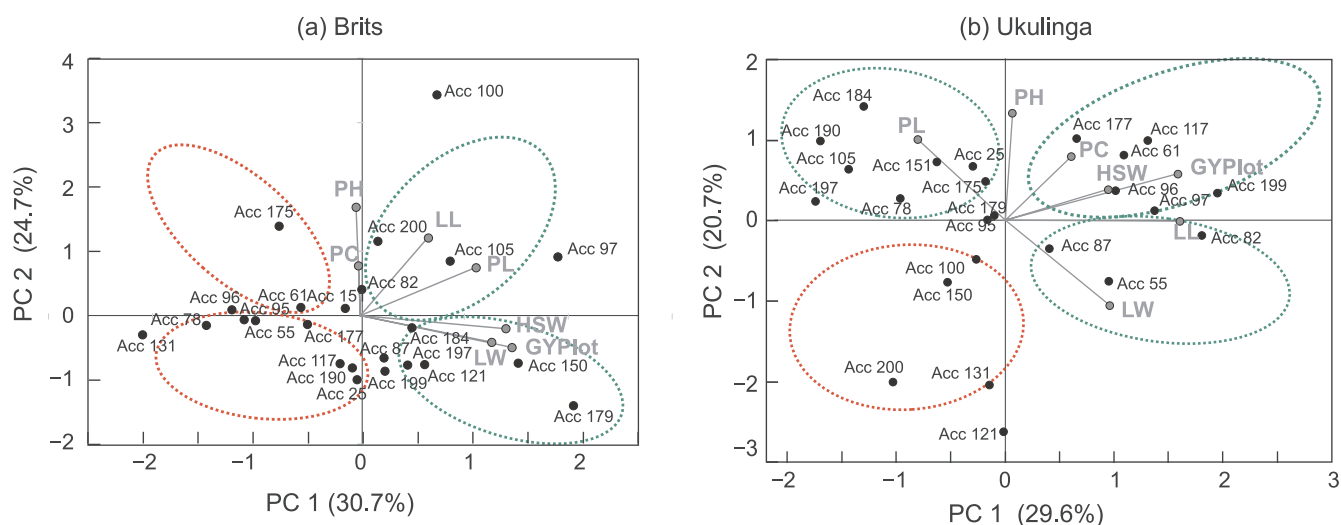


Figure 7: Rotated principal component score and percentage explaining the variance of PC 1 versus PC 2 and showing similarities between 24 Bambara groundnut genotypes at (a) Brits and (b) Ukulinga

more emphasis on genotype behaviour in local contexts. In this sense, it is essential to understand the mechanisms and processes that control growth and, as a result, biological and agricultural yield, as well as how weather affects these factors. All of these aspects can be used to

provide guidance to breeders on how to use inputs more effectively to create cultivars that are more suited to and have greater yield potential for particular agro-economic conditions (Jacquet et al. 2022). Breeders may concentrate on growth traits during vegetative stages, such as plant

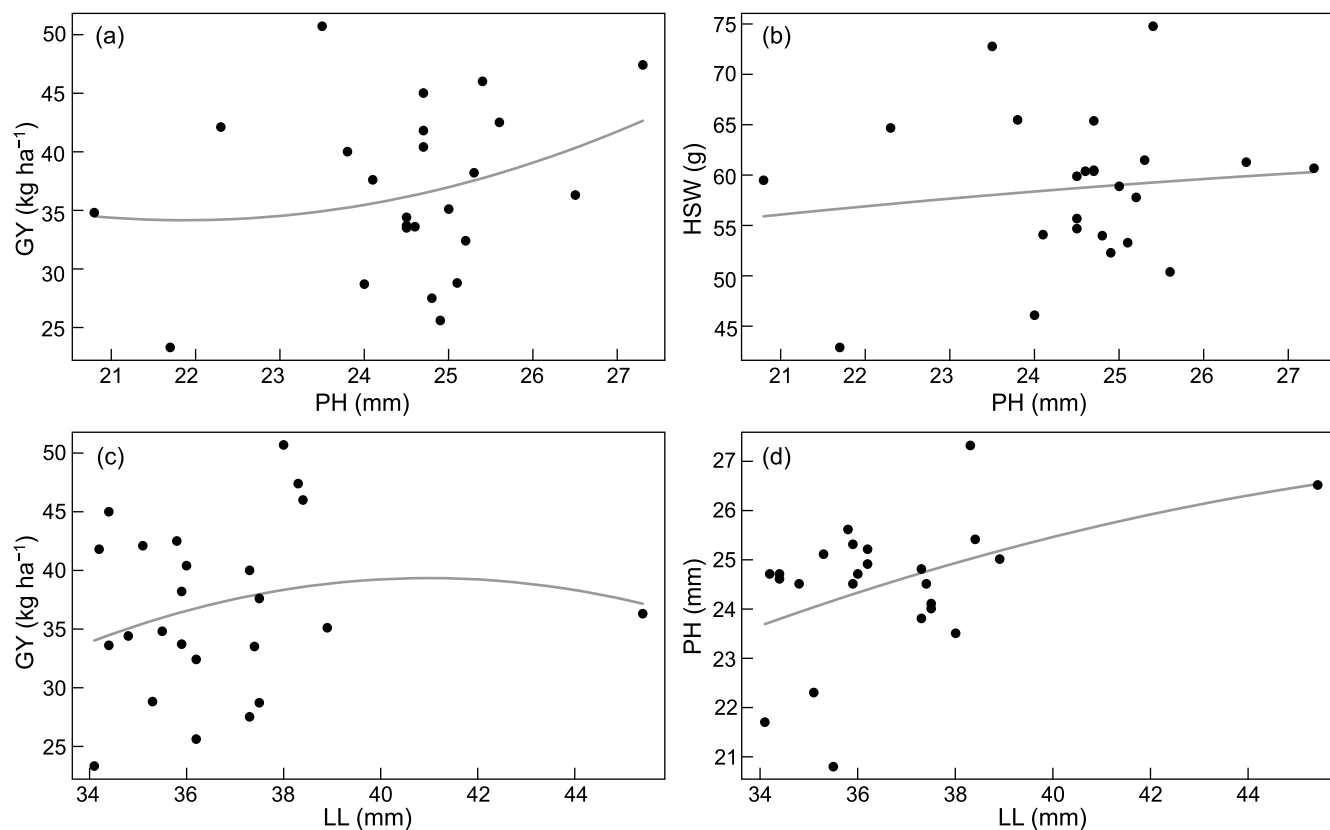


Figure 8: Non-linear regression diagrams showing the relationship between agronomic traits: (a) grain yield to plant height; (b) hundred seed weight to plant height; (c) grain yield to leaf length; and (d) plant height to leaf length

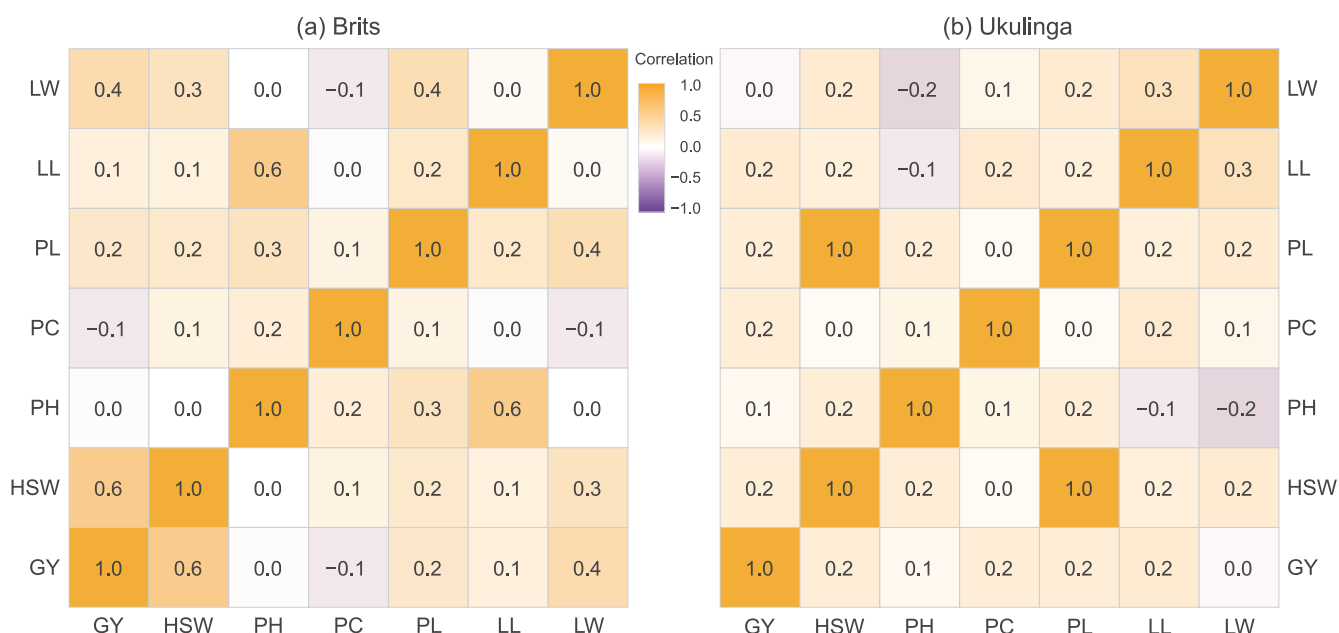


Figure 9: Pearson correlation coefficient among seven traits in Bambara groundnut genotypes for (a) Brits and (b) Ukulinga

foliar surface and dry matter of the third internode, to increase potential yields (Murchie et al. 2023). Combining these traits into one cultivar for high yielding capacity has proven to be a difficult task up to this point (Maqueira-López et al. 2019).

Pearson correlations for assessed traits under Brits and Ukulinga conditions

A Pearson correlation coefficient is shown (Figure 9) for agronomic traits evaluated on Bambara groundnut genotypes under Brits and Ukulinga conditions. At Brits, positive correlations were observed between GY and HSW, GY and PL, GY and LL, GY and LW, HSW and PL, HSW and LL, HSW and LW, PH and PC, PH and PL, PH and LL, PC and PL, PL and LL, PL and LW. Negative correlations were observed between GY and PC, GY and LW, LW and PC.

At Ukulinga, positive correlations were observed between GY and HSW, GY and PH, GY and PC, GY and LL, GY and PL, HSW and PH, HSW and PL, HSW and LL, HSW and LW, PH and PC, PH and PL, PC and LL, PC and LW, PL and LL, PL and PW, LL and LW. Negative correlations were observed between PH and LL, PH and LW.

It is possible that the weak correlations are due to the changing rainfall conditions in the production environments (Mabhaudhi et al. 2018). According to Unigwe et al. (2016), unequal accessions may have different seed sizes and colours. It is generally believed by farmers that seeds of large sizes and apartment shapes germinate faster and grow larger plants than those of small sizes (Mueller 2017). Atoyebi et al. (2017) highlighted the many potentials of Bambara groundnut, while they also stated that there is a need to increase its use and market potentials, particularly in emerging African countries.

Conclusion

Significant genetic variation among Bambara groundnut genotypes was demonstrated in response to environmental conditions at Brits and Ukulinga. Genotypes Acc 179, 184, and 82 showed stable performance and high yields across both agroecological areas, making them strong candidates for breeding programs aimed at improving Bambara groundnut production in South Africa. There is a need for continued efforts in breeding to enhance crop resilience and yield.

Geolocation

Pietermaritzburg: 30°24'S, 29°24'E; Brits: 25°36' S, 27°48' E

Data availability

The data that supports the findings of this study are available from the corresponding author upon reasonable request.

Conflict of interest — The authors declare no conflict of interest.

Author contributions — S. Kunene: Conceptualisation, methodology, performed the experiments, validation, investigation, analysed and interpreted the data, data curation, wrote the original paper. A.S. Gerrano: Conceptualisation, methodology, validation, investigation, contributed materials, and provided feedback on the manuscript. A.O. Odindo: Conceptualisation, methodology, validation, investigation, analysed and interpreted the data, and provided feedback on the manuscript.

Extent of use of artificial intelligence tools — The authors confirm that they have not used any artificial intelligence tools to improve the manuscript.

Acknowledgments — The first author acknowledges the University of KwaZulu-Natal, South Africa, South African National Seed Organisation (SANSOR), and Agricultural Research Council, South Africa for supporting this study.

ORCID iDS

Sithembile Kunene — <http://orcid.org/0000-0002-8151-0883>

Abe Shegro Gerrano — <http://orcid.org/0000-0001-7472-8246>

Alfred Oduor Odindo — <http://orcid.org/0000-0003-1743-4406>

References

- Adzawla W, Donkoh SA, Nyarko G, O'Reilly P, Mayes S. 2016. Use patterns and perceptions about the attributes of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Northern Ghana. *Ghana Journal of Science, Technology and Development* 4: 56–71.
- Akinola R, Laura MP, Mabhaudhi T, De Bruin F, Loubie Rusch. 2020. A review of indigenous food crops in Africa and the implications for more sustainable and healthy food systems. *Sustainability* 12: 3493.
- Albertazzi L. 2020. Styled morphogeometry. *Axiomathes* 30: 227–50.
- Ali F, Ghulam Q, Fuguang L, Wang Z. 2022. Updated role of ABA in seed maturation, dormancy, and germination. *Journal of Advanced Research* 35: 199–214.
- ARC-VOPI (Agricultural Research Council-Vegetable and Ornamental Plants Institute). 2019. *Annual Report 2019*. Pretoria: Agricultural Research Council.
- Atoyebi JO, Olaniyi O, Odutola O, Olugbenga A, Abberton M. 2017. Morphological characterisation of selected African accessions of Bambara groundnut (*Vigna subterranea* (L.) Verdc.). *International Journal of Plant Research* 7: 29–35.
- Ayerdi G, Marraccini E. 2022. Innovative pulses for western european temperate regions: a review. *Agronomy* 12: 170. <https://doi.org/10.3390/agronomy12010170>
- Berchie JN, Sarkodie-Addo J, Adu-Dapaah H, Agyemang A, Addy S, E A, Donkor J. 2010. Yield evaluation of three early maturing Bambara groundnut (*Vigna subterranea* (L.) Verdc.) landraces at the CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. *Journal of Agronomy* 2010: 175–179.
- Chimonyo VGP, Wimalasiri EM, Kunz R, Modi AT, Mabhaudhi T. 2020. Optimizing traditional cropping systems under climate change: a case of maize landraces and Bambara groundnut. *Frontiers in Sustainable Food Systems* 4: 562568.
- de Leon N, Jannink J-L, Edwards JW, Kaeppler SM. 2016. Introduction to a special issue on genotype by environment interaction. *Crop Science* 56: 2081–89.
- Grossiord C, Thomas NB, Cernusak LA, Kimberly AN, Benjamin P, Rolf TWS, John SS, McDowell NG. 2020. Plant responses to rising vapor pressure deficit. *New Phytologist* 226: 1550–66.
- Guntukula R, Goyari P. 2020. Climate change effects on the crop yield and its variability in Telangana, India. *Studies in Microeconomics* 8: 119–48.
- Heilmeyer H. 2019. Functional traits explaining plant responses to past and future climate changes. *Flora* 254: 1–11.
- Huang X, Shihua Y, Junyi G, Zhao Y, Feng Q, Gong H, Wenjun L, Zhan Q, Benyi C, Junhui X. 2015. Genomic analysis of hybrid rice varieties reveals numerous superior alleles that contribute to heterosis. *Nature Communications* 6: 6258.
- Jacquet F, Jeuffroy M, Jouan J, Cadre EL, Litrico I, Malausa T, Reboud X, Huyghe C. 2022. Pesticide-free agriculture as a new paradigm for research. *Agronomy for Sustainable Development* 42: 8.
- Khan F, Azman R, Chai HH, Mayes S, Lu C. 2016. Genomic and transcriptomic approaches towards the genetic improvement of an underutilised crops: the case of Bambara groundnut. *African Crop Science Journal* 24: 429–58.
- Khan M, Mahmudul H, Rafii MY, Shairul IR, Mashitah J, Mamun AI. 2020. Genetic variability, heritability, and clustering pattern exploration of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) accessions for the perfection of yield and yield-related traits. *BioMed Research International* 2020: 2195797.
- Khan MMH, Mohd YR, Shairul IR, Mashitah J, Al-Mamun M. 2021. Bambara groundnut (*Vigna subterranea* (L.) Verdc.): A crop for the new millennium, its genetic diversity, and improvements to mitigate future food and nutritional challenges. *Sustainability* 13: 5530.
- Lin BB. 2011. Resilience in agriculture through crop diversification: adaptive management for environmental change. *BioScience* 61: 183–93.
- Linus RA, Olanrewaju OS, Oyatomi O, Idehen EO, Abberton M. 2023. Assessment of yield stability of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) using genotype and genotype–environment interaction biplot analysis. *Agronomy* 13: 2558.
- Mabhaudhi T, Chibarabada TP, Vimbayi GPC, Modi AT. 2018. Modelling climate change impact: a case of Bambara groundnut (*Vigna subterranea*). *Physics and Chemistry of the Earth* 105: 25–31.
- Mabhaudhi T, Modi AT. 2013. Growth, phenological and yield responses of a Bambara groundnut (*Vigna subterranea* (L.) Verdc.) landrace to imposed water stress under field conditions. *South African Journal of Plant and Soil* 30: 69–79.
- Majola NG, Gerrano AS, Shimelis H. 2021. Bambara groundnut (*Vigna subterranea* (L.) Verdc.) production, utilisation and genetic improvement in Sub-Saharan Africa. *Agronomy* 11: 1345.
- Mandizvo T, Odindo AO. 2019. Seed coat structural and imbibitional characteristics of dark and light coloured Bambara groundnut (*Vigna subterranea* (L.) Verdc.) landraces. *Heliyon* 5: e01249.
- Maqueira-López LA, Morejón-Rivera R, Roján-Herrera O, Torres-de-la-Noval W. 2019. Relationship between growth traits and yield formation in indica-type rice crop. *Agronomía Mesoamericana* 30: 79–100.
- Marone D, Maria AR, Mores A, Donatella BMF, Giovanni L, Anna MM, Grazia MB. 2021. Importance of landraces in cereal breeding for stress tolerance. *Plants* 10: 1267.
- Massawe FJ, Mwale SS, Azam-Ali SN, Roberts JA. 2005. Breeding in Bambara groundnut (*Vigna subterranea* (L.) Verdc.): strategic considerations. *African Journal of Biotechnology* 4: 463–71.
- Mathakutha R, Christien S, Peter CR, Blom IJ, Steven LC, Barnabas HD, Brad SR, Anche L, Greve M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30: 994–1006.
- Mayes S, Wai KH, Chai HH, Gao X, Aloyce CK, Kumbirai IM, Zahrlakmal M, Hahiree MKIM, Kendabie P, Luis L. 2019. Bambara groundnut: an exemplar underutilised legume for resilience under climate change. *Planta* 250: 803–20.
- Msimbira LA, Smith DL. 2020. The roles of plant growth promoting microbes in enhancing plant tolerance to acidity and alkalinity stresses. *Frontiers in Sustainable Food Systems* 4: 106.
- Mubaiwa J, Fogliano V, Cathrine C, Bakker EJ, Linnemann AR. 2018. Utilization of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) for sustainable food and nutrition security in semi-arid regions of Zimbabwe. *PLoS one* 13: e0204817.
- Mueller NG. 2017. Documenting domestication in a lost crop (*Polygonum erectum* L.): evolutionary bet-hedgers under cultivation. *Vegetation History and Archaeobotany* 26: 313–27.
- Muhammad I, Mohd YR, Muhamad HN, Ramlee SI, Harun AR, Oladosu Y. 2021. Determination of lethal (LD) and growth reduction (GR) doses on acute and chronic gamma-irradiated Bambara groundnut [*Vigna subterranea* (L.) Verdc.] varieties. *Journal of Radiation Research and Applied Sciences* 14: 133–45.
- Murchie EH, Reynolds M, Slafer GA, Foulkes MJ, Acevedo-Siaca L, McAusland L, Sharwood R, Griffiths S, Richard BF,

- Gwyn J. 2023. A wiring diagram for source strength traits impacting wheat yield potential. *Journal of Experimental Botany* 74: 72–90.
- Nafula WC, Masinde IT, Otaye DO, Wafula WV. 2021. Incidence and severity of *Fusarium* wilt on Bambara nut (*Vigna subterranea* (L.) Verdc.) landraces in Western Kenya. *African Journal of Biological Sciences* 3: 67–75.
- Ntundu WH, Shillah SA, Marandu WYF, Christiansen JL. 2006. Morphological diversity of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) landraces in Tanzania. *Genetic Resources and Crop Evolution* 53: 367–78.
- Obidiebube EA, Eruotor PG, Akparobi SO, Okolie H, Obasi CC. 2020. Assessment of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) varieties for adaptation to rainforest agroecological zone of Anambra state of Nigeria. *Crops* 5: 1–6.
- Obura M, Oballim G, Ochuodho JO, Maina FNW, Anjichi VE. 2021. Seed management and quality of farmer saved seeds of Bambara groundnut from North Western, Northern and Eastern Uganda. *Ghana Journal of Agricultural Science* 56: 1–15.
- Olanrewaju OS, Oyatomi O, Babalola OO, Abberton M. 2021. Genetic diversity and environmental influence on growth and yield parameters of Bambara groundnut. *Frontiers in Plant Science* 12: 796352.
- Olanrewaju OS, Oyatomi O, Olubukola OB, Abberton M. 2022. Breeding Potentials of Bambara groundnut for food and nutrition security in the face of climate change. *Frontiers in Plant Science* 12: 3186.
- Oyeyinka SA, Taiwo ST, Oyeyinka AT, Abimbola KA, Mutiat AB, Fausat LK, Muinat AO, Kolade JJ. 2018. Value added snacks produced from Bambara groundnut (*Vigna subterranea*) paste or flour. *LWT—Food Science and Technology* 88: 126–31.
- Oyiga BC, Uguru MI. 2011. Interrelationships among pod and seed yield traits in Bambara groundnut (*Vigna subterranea* (L.) Verdc.) in the derived savanna agroecology of south-eastern Nigeria under two planting dates. *International Journal of Plant Breeding* 5: 106–11.
- Ralls K, Sunnucks P, Lacy RC, Frankham R. 2020. Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biological Conservation* 251: 108784.
- Rogé P, Sieglinde S, Mayamiko NK, Leah M, Jambo I, Brad P. 2016. Ratooning and perennial staple crops in Malawi. A review. *Agronomy for Sustainable Development* 36: 1–18.
- Salazar-Licea L, Kumbirai LM, Xiuqing G, Razlin AH, Liliana AH, Chai HH, Wai KH, Graham JK, Massawe F, Mayes S. 2022. The Bambara groundnut genome: from the crop to the genome – the progress and constraints of genome-related studies in Bambara groundnut. *Underutilised Crop Genomes* pp: 189–215.
- Sarkar A, Sensarma RS, vanLoon GW. 2019. *Sustainable solutions for food security: combating climate change by adaptation*. Cham: Springer.
- Shahzad A, Sana U, Afzal AD, Muhammad FS, Tariq M, Muhammad AT, Awais S, Muhammad H. 2021. Nexus on climate change: agriculture and possible solution to cope future climate change stresses. *Environmental Science and Pollution Research* 28: 14211–32.
- Sidibé A, Gennifer M, Harouna C, Stefano P, Issa T, Gaoussou D, Adja RS, Charlie M. 2020. Revitalizing cultivation and strengthening the seed systems of fonio and Bambara groundnut in Mali through a community biodiversity management approach. *Plant Genetic Resources* 18: 31–48.
- Sultan SE. 2017. Developmental plasticity: re-conceiving the genotype. *Interface Focus* 7: 20170009.
- Tan XL, S Azam-Ali, Von Goh EE, Mustafa M, Chai HH, et al. 2020. Bambara groundnut: an underutilized leguminous crop for global food security and nutrition. *Frontiers in Nutrition* 7: 601496.
- Uba CU, Oselebe HO, Abush AT, Wosene GA. 2021. Genetic diversity and population structure analysis of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) landraces using darts markers. *PloS one* 16: e0253600.
- Unigwe AE, Gerrano AS, Adebola P, Pillay M, Monrovia L. 2016. Morphological variation in selected accessions of Bambara groundnut (*Vigna subterranea* (L.) Verdc) in South Africa. *Journal of Agricultural Science* 8: 69–80.
- Waadts R, Charles AS, Po-Kai H, Takahashi Y, Munemasa S, Schroeder JI. 2022. Plant hormone regulation of abiotic stress responses. *Nature Reviews Molecular Cell Biology* 23: 680–94.