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To cite this article: Stellamaris Kembabazi, Florence Muranga , Martin Mutambuka, Ediriisa Mugampoza & Norhasnida Zawawi (2026) Physicochemical drivers of resistant starch and comparative suitability of East African Highland cooking banana cultivars (*Musa acuminata*, AAA) for food industry applications, Cogent Food & Agriculture, 12:1, 2697108, DOI: [10.1080/23311932.2026.2697108](https://doi.org/10.1080/23311932.2026.2697108)

To link to this article: <https://doi.org/10.1080/23311932.2026.2697108>



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Published online: 05 Jul 2026.



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Physicochemical drivers of resistant starch and comparative suitability of East African Highland cooking banana cultivars (*Musa acuminata*, AAA) for food industry applications

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ABSTRACT

East African Highland Cooking Bananas (EAHCB), constituting 70% of Uganda's banana production, represent an abundant and sustainable starch source for the food industry. However, their low amylose content (13–14%) contradicts the high resistant starch (RS) content (57–68%). This study evaluates four cultivars *Mpologoma*, *Bukumu*, *Mbwazirume*, and *Enyeru* for physicochemical and structural properties, and *in vitro* digestibility with respect to industrial suitability. Starch yields varied (10–20%), with *Bukumu* highest and *Mpologoma* lowest, influenced by pulp moisture and A-genome prevalence. Granule sizes ranged 12.9–21.8 µm, exhibiting B-type crystallinity. Despite low amylose, *Enyeru* showed highest RS (68%), low rapidly digestible starch, and optimal pasting temperatures (75–83 °C), revealing crystalline structure, amylopectin chain length distribution, and granule morphology as primary digestibility influencers. These properties position EAHCB starches as potential thickeners, low-GI functional ingredients, and RS sources matching modified corn/cassava starches. *Enyeru* emerges as the best cultivar for functional food applications like food for diabetic patients. These findings call for targeted breeding for enhanced RS/crystallinity and *in vivo* validation.

ARTICLE HISTORY

Received 21 March 2026
Revised 3 June 2026
Accepted 26 June 2026

KEYWORDS

Banana starch; cooking bananas; digestibility; resistant starch; functional foods

SUBJECTS

Food Chemistry; Food Laws & Regulations; Food Additives & Ingredients

1. Introduction

Grains and tubers (cassava, wheat, rice, sweet potato, corn and potato) have been recognised as the conventional starch sources (Kembabazi et al., 2025); however, banana has shown potential as an alternative source of starch due to its abundance in the tropics but also potential health benefits (Marta et al., 2019). Cooking bananas are a major staple food in Uganda, accounting for 70% of banana production, providing up to 30% of daily caloric intake, and serving as a key income source that generates approximately US\$1,244 annually for over 4 million smallholder households across East Africa (Marimo et al., 2020; Kikulwe & Asindu, 2020; Mulugo et al., 2022).

To utilise the physiological properties of banana starch, particularly its high resistant starch (RS) content, the food industry has increasingly developed functional foods incorporating this starch (Marta et al., 2022). East African Highland cooking bananas exhibit high RS content (above 70%), positioning them as a promising starch source for food applications (Chang et al., 2022).

Resistant starch has been shown to offer numerous health benefits, primarily through fermentation in the colon, producing short-chain fatty acids (SCFAs) like acetate, butyrate and propionate, which contribute to improved gut barrier function, immune regulation, and reduced inflammation (Zhang et al., 2022). These effects are significant in managing metabolic disorders such as obesity, type 2 diabetes, and insulin resistance, as SCFAs influence energy metabolism, glucose homeostasis, and lipid metabolism, thereby

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supporting overall metabolic health (Anachad et al., 2023). In the modern era of optimal nutrition, consumers demand high-quality products with health-promoting benefits, such as low glycemic index (GI) foods formulated from starches that resist fast enzymatic hydrolysis (Cammarelle et al., 2025). Starches capable of resisting fast hydrolysis into glucose are particularly promising for such applications. Resistance to enzymatic hydrolysis in other starch sources especially wheat and corn, has been attributed to the arrangement of amylose and amylopectin molecules, which consequently influence other properties like granule size, relative crystallinity, amylopectin chain length distribution, and other functional properties like thermal and pasting properties, solubility and water absorption capacity (Yee et al., 2021)

Despite its relatively low amylose content compared to other starches, banana starch exhibits high resistant starch levels (Yee et al., 2021; Ssonko & Muranga, 2017), highlighting the need to identify the primary structural factors responsible for this resistance. Additionally, studies indicate that the type 2 resistant starch (RS2) native to banana starch lacks thermal stability during any thermal processing, including baking and is not readily fermented into SCFAs, rendering it less suitable for heat-intensive food processing technologies (Lehmann et al., 2002). Thus, for native banana starch to undergo modification into a thermally stable starch, its physicochemical properties in relation to resistance have to be studied. This study analysed four cultivars, *Mpologoma*, *Enyeru*, *Mbwazirume*, and *Bukumu* and how their starch physicochemical properties influence their suitability for the food industry, but most importantly, their physiological functions.

2. Materials and methods

2.1. Materials

Four cultivars of East African Highland Cooking Bananas (EAHCB, *Musa Acuminata*, AAA) were selected from four distinct cooking banana clone sets known for their starch yield. These included *Mpologoma*, *Enyeru*, *Mbwazirume* (soft cooking), and *Bukumu* (hard cooking). The cultivars were obtained from the Banana Industrial Research and Development Centre (BIRDC) in Bushenyi, Southwestern Uganda (Latitude: 0.59°S, Longitude: 30.21°E, Altitude: 1570m). To ensure physiological uniformity, banana stools were tagged at inflorescence emergence. Mature fruits were harvested between 13 and 15 weeks post-inflorescence, corresponding to peak starch accumulation (Kawongolo et al., 2016).

2.2. Starch extraction from East African Highland cooking banana cultivars

Banana starch was extracted using a wet-milling alkaline procedure (Ssonko & Muranga, 2017). Fruits were washed with clean running water, hand-peeled, sliced into pieces (2.5 mm), and kept in a 0.02M sodium hydroxide solution for 10 min to prevent oxidation. The pieces were crushed using an electric blender (Warring commercial blender CB15P, Washington, USA). The crushed slurry was then centrifuged (Rotanta 460RF, 5675 Hettich, Germany) at a speed of 3000 rpm for 10 min. The filtrate (starch) was refrigerated at 4°C and left to stand for 6 hours. The sediment (obtained starch) was washed repeatedly with distilled water and oven-dried at 45°C for 48 hours. The dried starch was then milled using a laboratory miller for about 45 seconds (M20, 82 KIKA-WERKE, Germany), sieved through 200 µm sieves (muslin cloth), and kept in airtight containers for further analysis.

2.3. Starch yield

Starch yield was calculated based on the weight of the freshly peeled pulp (Thanyapanich et al., 2021).

$$\text{Percentage Yield} = \frac{\text{Weight of starch extracted}}{\text{weight of pulp}} \times 100$$

2.4. Proximate analysis of starches from different banana cultivars

Banana starch was analysed for moisture content, fat, and Ash using AOAC standard methods, and the Kjeldahl William's method AACC method 4–19 for protein content (conversion factor 6.25). Moisture

content was determined by AACC method 4–19 (Engel, 1977). Ash content was determined by AACC Method 08- 01 (Method, 2012), samples were incinerated overnight in a muffle furnace (Nabertherm, Germany) at 500°C.

2.5. Morphological and structural analysis

2.5.1. Granular size and shape of the starches

A scanning electron microscope (JOEL, JSM-6400; Tokyo, Japan) was used to analyse the microstructure of the starch samples. Starch samples were attached to the sample holders and sputter-coated with gold. Images were then taken under a high vacuum with an acceleration voltage of 15 kV and a magnification of 1000x

2.5.2. Relative crystallinity of the starches

The relative crystallinity (RC) of the starch samples was determined using an X-ray Diffractometer (Shimadzu XRD 6000, Tokyo, Japan) fitted with Cu-K α radiation ($\lambda K\alpha_1 = 1.5406\text{\AA}$) from $2\theta = 5^\circ$ – 80° with increments of $\Delta 2\theta$: (0.034°) voltage of 40 kV, current of 1.6 KW and counting time of 6°/min. Crystallinity was calculated using the following formula:

$$RC\% = \left(\frac{AC}{(AC + Aa)} \right) \times 100$$

RC is the relative crystalline, Ac is the crystallised area on the X-ray diffractogram, and Aa is the amorphous area on the X-ray diffractogram.

2.6. Thermal and pasting properties of the starches

The thermal properties of the starch were determined using differential scanning calorimetry (Mettler Toledo, DSC 822, Tokyo, Japan). Water (14 μ L) was added with a micro syringe to the starch sample (6 mg dwb) in the DSC pans, which were then sealed, reweighed, and kept at room temperature (approx. 25°C) for 24 hours to ensure equilibration of the starch sample and water.

The samples were scanned from 35°C to 150°C at a heating rate of 10°C/min. An empty pan was used as a reference.

The values of onset (T_o), peak (T_p), and conclusion (T_c) gelatinisation temperatures and enthalpy (ΔH) were obtained from the thermographs of the samples using Universal Analysis 2000 3.9A software.

The pasting properties of the starch samples were determined using a Rapid Vasco Analyzer (Newport Scientific Pty. Ltd, Syarikar, 295514-U, Warriewood NSW, Australia), using a general method STD1 profile. Data were collected directly from the pasting curve using Thermocline for Windows v3.0 (TCW3) software for the RVA.

2.7. Solubility, swelling power and water absorption capacity

Swelling power was determined using a method as per Kusumayanti et al. (2015). A suspension of the starch solution prepared with distilled water (1:50, w/v) was heated in a water bath at 40, 50, 60, 70, 80 & 90°C for 30 min with continuous stirring. The gelatinised starch samples were cooled rapidly to 25°C in an ice water bath and centrifuged at 7000 $\times g$ for 20 min. The supernatant (soluble starch) was dried at 105°C to constant weight.

$$\text{Swelling Power} = \frac{\text{Weight of Starch Precipitate}}{\text{Weight of the Starch Sample}}$$

$$\text{Solubility} = \frac{\text{Solid Content in the Supernatant}}{\text{Sample in dry Weight}} \times 100$$

$$\text{Water Absorption Capacity} = \frac{(\text{Weight of Wet Sediment} - \text{Weight of dry starch})}{\text{Weight of the dry starch}}$$

2.8. Molecular characterisation of the starches

2.8.1. Starch content

The Total Starch (AA/AMG) Assay Kit was used for the determination of total starch using AOAC Method 996.11, AACC Method 76-13.01 following manufacturer's instructions.

2.8.2. Amylose content and resistant starch content

The amylose content of the starch samples was determined using a modified Concanavalin A (Con A) method with the Megazyme Amylose/Amylopectin Kit (Megazyme International, Wicklow, Ireland) following manufacturer's instructions. Resistant starch content was analysed using the Megazyme Resistant Starch Assay Kit. 116 (K-RSTAR, CAT. NO. K-RAPRS) following AACC Method 32-40.01 (Megazyme International, 117 Wicklow, Ireland).

2.8.3. Amylopectin chain length distributions and molecular weight distribution of the starches

The starch sample (5 mg) was dissolved in 0.9 mL ultrapure water and heated for 15 min in a boiling bath with intermittent vortex mixing. NaAc (pH = 3.5) 0.1 mL 0.1 M, 5 mL NaN₃ (40 mg/mL), and 10 µL of iso-amylase (1400 U) were added to the starch dispersion and incubated at 37°C for 3 hours. The debranched starch was precipitated using 5 mL absolute ethanol and centrifuged at 4000 g for 10 min. Finally, DMSO/LiBr solution (1 mL) was added and boiled for 2 hours at 80°C in a thermomixer with shaking at 350 g. Size Exclusion Chromatography with a Refractive Index (RI) detector was used to assess the elution profiles, molecular weight distribution, and homogeneity of various fractions.

The molecular weight distribution of debranched starch was analyzed using a differential refractive index detector (Optilab T-REX, Wyatt Technology Co., Santa Barbara, CA, USA) equipped with two tandem columns (300*7.5 mm, Plael 10 µm MIXED-B and Plgel 5 µm MIXED-D; Agilent Technologies Inc, Santa Clara, USA) which was held at 80°C using a model column heater. The mobile phase for LC separation was 0.5% LiBr-DMSO solution for isocratic elution for 80 min at 0.8 mL/min. Standard dextrans of known molecular weights (342; 3,650; 21,000; 131,400; 610,500; 821,700; 3,755,000) were used for column calibration.

2.9. In vitro digestibility of the starches

Starch samples (0.5 g db.) and water (5 mL) were added to 50 mL polypropylene centrifuge tubes. The tubes were capped, and the contents were vortexed (Stuart Scientific, Great Britain, UK) for 5 min. Each starch sample was left in a boiling-water bath (Julabo, SW22, Seelbach, Germany) for 10 min. The tubes were allowed to cool to room temperature. *In vitro* digestibility values for RDS, SDS, and RS fractions were determined as per Zhang and Hamaker (2012) (McCleary et al., 2019).

Briefly, samples (200 mg), guar gum (20 mg), and distilled water (2 mL) were added to 50 mL polypropylene centrifuge tubes and mixed entirely using a magnetic stirrer. Each sample was left uncooked or cooked in a boiling water bath for 10 min.

The tubes were then placed in a water bath at 37°C with the addition of 4 mL pepsin (250 U/mg; P8160) hydrochloric acid solution (5 mg/mL) and allowed to hydrolyse for 30 min with shaking.

Thereafter, six glass beads (diameter: 3–4 mm) and 2 mL sodium acetate buffer (0.5 M, pH 5.2) were added to the tubes, and the reaction was continued for 30 min. Starch digestion was initiated by adding a 2 mL enzyme mixture (pancreatic extract; P7340, amyloglucosidase (A298984; 300 U/mL), and invertase

(18161; 300 U/mg). The released glucose content at different times (0, 10, 20, 30, 45, 60, 90, and 120 min) was measured using a glucose oxidase-peroxidase kit (Megazyme International Ireland Limited, Wicklow, Ireland).

2.10. Statistical analysis

Analyses were performed in triplicates; results were analysed using one-way Analysis of Variance (ANOVA) and expressed as mean $\pm$ SD. Tukey's multiple comparisons test was used to compare means ($p < 0.05$) using Graph pad Prism 9.01. Principal component Analysis and Multiple linear regression were used to test if the selected independent variables significantly predict RDS, RS, and SDS using XLSTAT (2019.2.2.59614) and thus related the molecular structure and digestibility of the starches.

3. Results and discussion

3.1. Starch yield

Starch yield for the East African Highland Cooking Bananas (EAHCBs) ranged between 10%–20% with significant differences between cultivars (Table 1). Markedly, *Mpologoma* had a low starch yield yet had a high pulp weight, *Bukumu* on the other hand that had a low pulp weight had a higher starch yield. The difference in starch yield could be attributed to differences in moisture content; there is an observed strong inverse linear correlation (Table 4) between moisture content and yield. Moisture causes intramolecular starch associations with non-starch polysaccharides (e.g. crude fiber, proteins), reducing extractability, in addition higher hydration enhances cohesion and limits granule isolation (Sonawane et al., 2021). In banana starch, moisture >12–14% has shown to reduce the flowability and yield, reflecting patterns in Thai (16–20% yield) and Indian cultivars where optimized drying conditions are used to mitigate this (Olawoye & Olaoye, 2025).

Commercial viability of starch requires that it satisfies market demands and maximise economic value (Olawoye et al., 2022). The starch yields of EAHCB yields were markedly lower than Nigerian Cardaba bananas (50%) (Olawoye et al., 2022), It however is similar to Thai cultivars (16–20%) (Thanyapanich et al., 2021), and Indian bananas (27–30%) (Crane & Balerdi, 1998). Genotypic composition dominated by A-genomes in EAHCBs imposes a critical constraint on starch yield compared to B-genome-rich cultivars, which exhibit 20–50% higher yields due to enhanced amylose accumulation and pulp starch biosynthesis (Thanyapanich et al., 2021). Thus, the A-genome prevalence limits EAHCB starch yield potential, highlighting the need for targeted breeding to incorporate B-genome traits, thereby elevating yield and tailoring it for commercial viability.

3.2. Proximate composition of the starches

The Proximate composition of the starch granules is shown in Table 1. The ash content (0.02%–0.08%) and protein content (0.21%–0.24%) showed no significant differences among cultivars. These ash values are notably lower than those reported for Ugandan bananas as well as those reported for Thailand bananas and South African bananas (Jaiturong et al., 2020; Khoza et al., 2021).

Low ash content indicates high starch purity, reflecting effective removal of mineral contaminants during extraction (Gao et al., 2021). Ash levels correlate with soil characteristics and fertiliser practices;

Table 1. Yield and proximate composition of the starches.

Cultivar	Yield	Moisture content (%)	Crude ash (%)	Crude Fat (%)	Crude proteins (%)
<i>Mpologoma</i>	10.53 $\pm$ 1.34 ^c	11.87 $\pm$ 0.03 ^a	0.06 $\pm$ 0.01 ^a	ND	0.21 $\pm$ 0.03 ^a
<i>Enyeru</i>	18.11 $\pm$ 0.41 ^b	10.45 $\pm$ 0.08 ^a	0.06 $\pm$ 0.03 ^a	ND	0.22 $\pm$ 0.01 ^a
<i>Mbwazirume</i>	18.75 $\pm$ 0.59 ^b	10.22 $\pm$ 0.03 ^{ab}	0.07 $\pm$ 0.02 ^a	ND	0.22 $\pm$ 0.01 ^a
<i>Bukumu</i>	24.71 $\pm$ 1.31 ^a	8.85 $\pm$ 0.63 ^b	0.07 $\pm$ 0.05 ^a	ND	0.24 $\pm$ 0.09 ^a

Values are expressed as mean $\pm$ standard deviation ($n=3$). Means with different superscripts within the same the column differs significantly ($p < 0.05$). ND; non-detectable: the detection limit of the method was 0.05% based on petroleum ether extraction.

phosphate-based fertilisers simultaneously enhance crop yield while elevating mineral accumulation (Thatayaone et al., 2022). Additionally, banana ploidy influences ash content, with triploid cultivars (higher B-genome contribution) exhibiting greater mineral retention than diploids (Syukriani et al., 2021).

The low protein values aligned with Ugandan banana starch reports but was lower than values for South African and Indonesian cultivars (Khoza et al., 2021; do Prado Ferreira & Teixeira Tarley, 2020). These low levels confirm that bananas are inherently poor protein sources (Wang et al., 2015). However, the low protein is significant to minimise starch-protein interactions that are known to reduce resistant starch formation (Gao et al., 2021).

The starches from EAHCB had no detectable crude lipids similar to other studies on Ugandan starches but was lower than values for South African and Indonesian cultivars (Khoza et al., 2021; do Prado Ferreira & Teixeira Tarley, 2020). Fat content has technological and nutritional implications due to the amylose-lipid complex formed during the processing, which can produce resistant starch (Li et al., 2018). Generally, bananas are a poor source of fat. To crown it, proximate analysis of the EAHCB starches confirms their high purity, with negligible lipid content (<0.05%) and minimal levels of protein, fiber, and ash. This composition renders EAHCB starches highly suitable for diverse industrial applications, such as food hydrocolloids, extrusion processing, and pharmaceutical excipients, where low impurity profiles enhance functionality, stability, and regulatory compliance.

3.3. Morphological and structural analysis

3.3.1. Granular size and shape of the starches

The granular size of banana starches significantly differed ranging from 12.9 μm to 21.8 μm (Table 2). These values are lower compared to the bananas in Indonesia, China and India (do Prado Ferreira & Teixeira Tarley, 2020; Corgneau et al., 2019). Starch granular size is important in digestibility; Smaller granules provide greater surface area-to-volume ratios, accelerating α -amylase hydrolysis and enhancing digestibility (Rehman et al., 2025), which is critical for food applications requiring rapid gelatinisation (e.g. instant foods). However, EAHCB starches in this study show a weak relationship between resistant starch and granular size (Table 4). This suggests that in these specific cultivars, internal molecular architecture such as crystalline packing or amylose-lipid complexes may play a more dominant role in enzyme resistance than size of the granules. Granule size further influences pasting viscosity, shear thinning, and syneresis (Akuyenze et al., 2025); smaller EAHCB granules suit high-solids formulations but may require stabilisers to prevent retrogradation in gels or coatings (Cornejo-Ramírez et al., 2018). This cultivar-specific variation enables targeted applications corresponding to the functional needs.

The morphological analysis of the EAHCB starches revealed a diverse range of asymmetrical shapes, including oval, elongated, and spherical granules, all of which were notably devoid of surface pores or “dents” (Figure 1). These observations align with previous structural studies of banana starches (Marta et al., 2019; Ssonko & Muranga, 2017; Cornejo-Ramírez et al., 2018), which typically describe a smooth and continuous peripheral surface.

In many botanical starch sources, surface pores serve as micro-channels that originate from the granule’s interior and terminate at the surface as the non-reducing ends of amylose and amylopectin chains (Yang et al., 2023). The presence of such pores is of significant industrial importance, as they act as conduits for the entry of enzymes and chemical reagents into the crystalline matrix. Consequently, the lack of surface pitting in these EAHCB cultivars suggests a highly intact barrier that may limit the rate of enzymatic hydrolysis. Furthermore, this structural characteristic implies that these starches might

Table 2. Granular sizes of the starches.

Cultivar	Granular size (μm)
<i>Mpologoma</i>	12.9 $\pm$ 0.01 ^d
<i>Enyeru</i>	20.7 $\pm$ 0.02 ^b
<i>Mbwazirume</i>	21.8 $\pm$ 0.04 ^a
<i>Bukumu</i>	15.5 $\pm$ 0.01 ^c

Values are expressed as mean $\pm$ standard deviation ($n=3$). Means with different superscripts within the same the column differs significantly ($p < 0.05$).

require more rigorous modification conditions compared to more porous starches like corn or sorghum (Yang et al., 2023).

3.3.2. Relative crystallinity of the starches

The banana starch granules from EAHCB cultivars exhibited crystalline structure with B-type crystallinity, characterised by distinct strong X-ray diffraction peaks at 15° , 17° , and 23° 2θ (Figure 2) consistent with previous reports on banana starches (Cornejo-Ramírez et al., 2018; Cahyana et al., 2024). This polymorph, influenced by cultivar genetics, growth conditions, and isolation methods, confers greater enzymatic resistance compared to A-type (cereal-like) or C-type (root/tuber) starches due to more ordered amylopectin double helices and water molecules within crystalline lattices (Ma et al., 2020). There is indeed a strong positive correlation between resistant starch and relative crystallinity (Table 4). Consequently, the B-type dominance in these EAHCB starches suggests substantial resistant starch potential, beneficial for low-glycemic food formulations despite the observed cultivar variation in granule size and yield.

3.4. Pasting and thermal properties of the starches

The rheological properties of banana starch pastes highlight significant cultivar-specific variations in pasting parameters. Notably, EAHCB starches show low setback viscosity, indicating limited amylose recrystallisation during cooling, provided temperatures remain below their gelatinisation threshold. While this property suggests stability against staling in food applications, it limits their direct suitability as precursors for type 3 resistant starch (RS3), and as thus requires controlled retrogradation for formation of RS3 (Kembabazi et al., 2025). Retrograded form with enhanced thermal stability ideal for functional food applications, such as fortifying products with prebiotic benefits (Mohamed et al., 2024).

Breakdown viscosity further highlights the paste's shear stability, reflecting full granule swelling, hydration capacity, and resistance to shear stress during heating, similar to modified starches (Reyes-Atrizco et al., 2019). High peak viscosity indicates fragile, water-laden swollen granules with substantial water-holding capacity, while elevated pasting temperatures which signify tightly packed crystalline structures resistant to enzymatic digestion (Reyes-Atrizco et al., 2019). Together, these traits affirm banana starch's potential as a native thickener enduring high temperatures and shear, offering stability

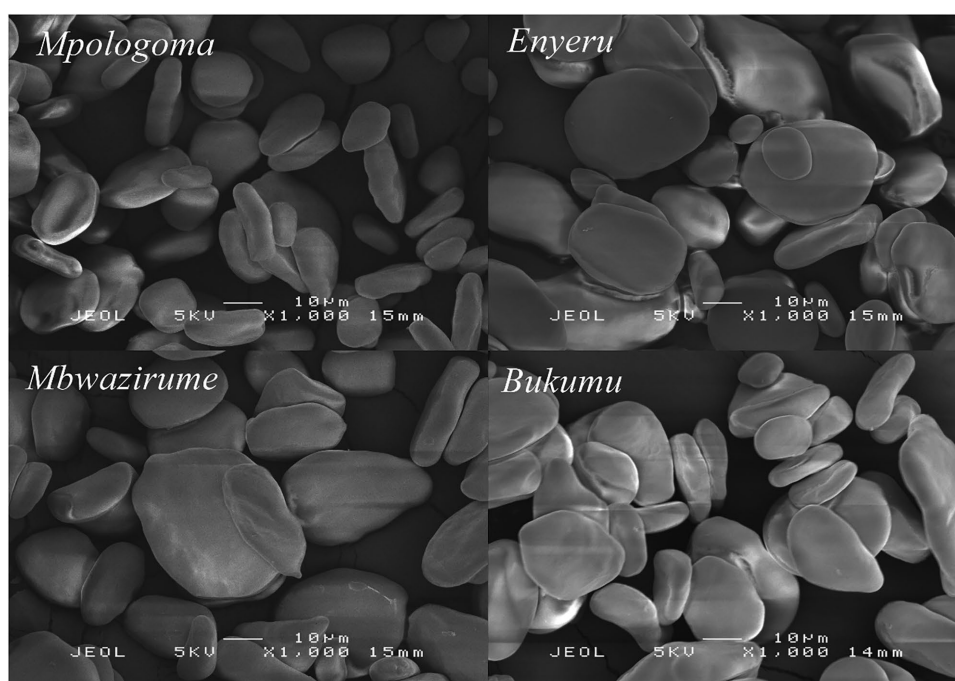


Figure 1. Scanning electron micrographs of starches from different East African Highland cooking banana cultivars. The images were captured at X1000.

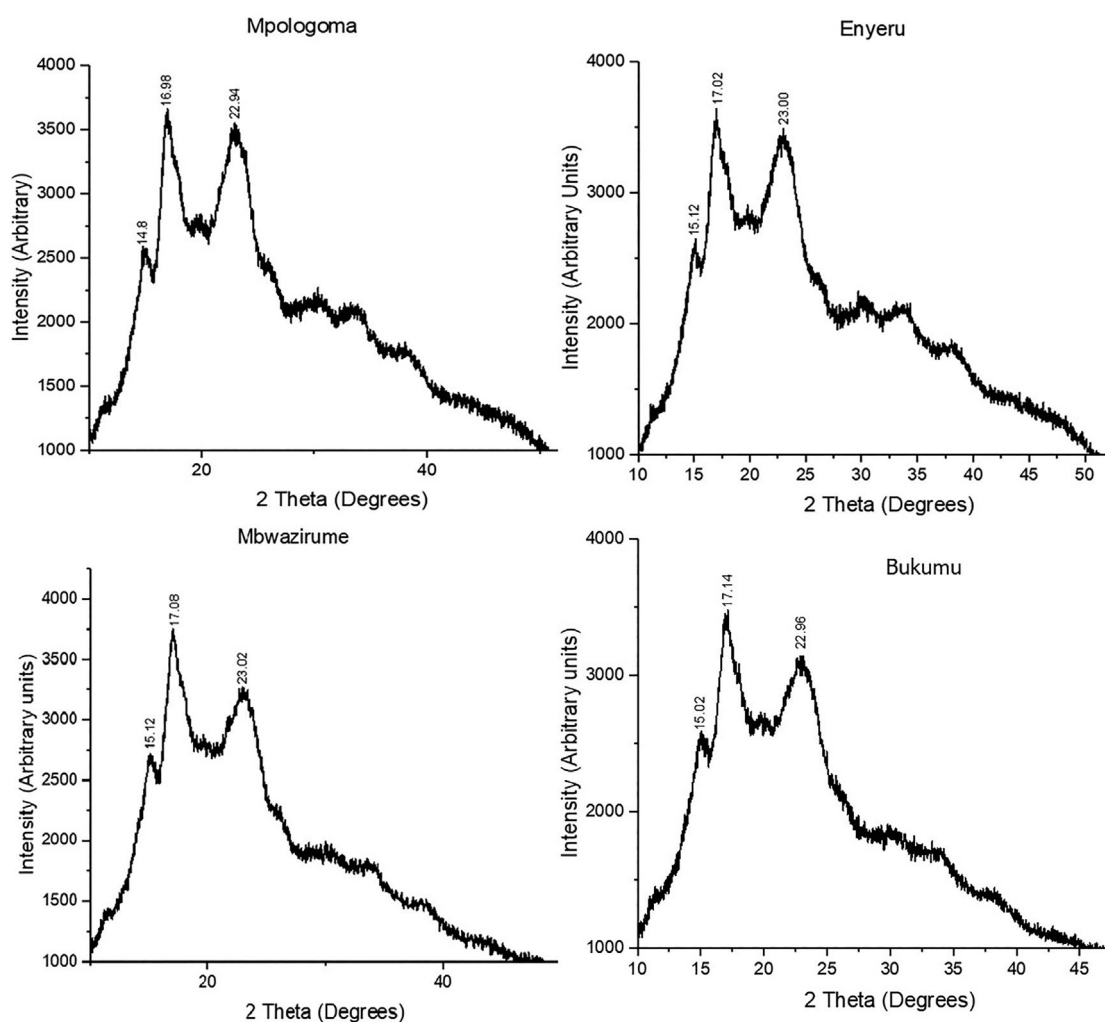


Figure 2. X-ray diffractograms of starches from different East African Highland banana cultivars showing the relative crystallinity of the starches.

comparable to chemical modifications and supporting its use in heat-processed foods like extruded snacks or sauces.

The thermal profile of the starch samples examined in this study is shown in Table 3. The four cultivars exhibited notable variations in onset (T_0), peak gelatinisation temperatures (T_p), and enthalpy (ΔH) similar to previous studies (Ssonko & Muranga, 2017; Cornejo-Ramírez et al., 2018), however, lower than the findings of (Corgneau et al., 2019; Paramasivam et al., 2023; Ul Zaman et al., 2025). These gelatinisation temperatures positively correlate with amylopectin chain length where longer; more branched chains elevate T_p (Sudlapa & Suwannaporn, 2023). The EAHCB starches' unusually low gelatinisation temperatures likely reflect a higher proportion of longer amylopectin chains (50%) over short ones (25%, Figure 4). Narrow R values indicate uniform crystal packing within granules, while elevated ΔH denotes strong intermolecular forces stabilising amylopectin double helices (Sudlapa & Suwannaporn, 2023).

Despite granular thermal instability as shown by low gelatinisation temperatures, EAHCB starches form stable pastes due to elevated pasting temperatures, highlighting a disconnect between granular melting and hot-paste viscosity. This duality is important for their utility in food processing, where low-heat gelatinisation aids energy-efficient cooking, yet high pasting stability withstands shear and heat in applications like thickeners or RS3 ingredients (Samanros & Lin, 2021).

3.4.1. Solubility, swelling power, and water absorption capacity

Figure 3 shows the Solubility, Swelling power, and Water absorption capacity of the EAHCB starches at temperatures from 40–90°C.

Swelling power and solubility ranged from 11–13 g/g and 10–14% respectively with no significant differences between the cultivars at temperatures below 70 °C. The lowest swelling power was seen in the starches at temperatures below 70 °C, which is indicative of starch thermal stability below the gelatinisation temperature. The highest swelling power was observed at 90 °C with significant differences between the cultivar. This temperature-dependent rise in swelling power is in agreement with the studies done by (Khoozani et al., 2020) and (Ssonko & Muranga, 2017). As the temperatures increase, the intermolecular hydrogen bonds in the amorphous region break, consequently the starch granule absorbs water and swells rapidly. Amylose content has been implicated in the low swelling power of EAHCB starches, owing to its ability to lower granule water absorption and expansion (Du et al., 2020). This is contrary to the findings of this study, which show a strong inverse relationship between swelling power and amylose content (Table 4).

Table 3. Thermal and pasting properties of the starches.

Parameter	<i>Mpologoma</i>	<i>Enyeru</i>	<i>Mbwazirume</i>	<i>Bukumu</i>
Pasting Properties				
Pasting temperature/ °C	74.13 ± 0.22 ^a	73.70 ± 0.06 ^a	73.05 ± 0.03 ^{bc}	72.75 ± 0.17 ^c
Peak viscosity/ cP	556.90 ± 6.38 ^b	568.00 ± 1.28 ^a	536.20 ± 1.68 ^c	536.4 ± 12.75 ^c
Breakdown viscosity /cP	252.00 ± 9.38 ^d	261.20 ± 5.50 ^c	311.20 ± 46.25 ^a	275.3 ± 8.09 ^b
Final viscosity/ cP	342.80 ± 12.75 ^a	327.70 ± 15.09 ^b	318.10 ± 2.84 ^c	312.3 ± 4.67 ^d
Set back/ cP	37.92 ± 6.40 ^b	31.69 ± 4.32 ^c	43.09 ± 2.11 ^a	37.67 ± 2.41 ^b
Thermal Properties				
T ₀ /°C	68.08 ± 0.10 ^a	64.84 ± 0.09 ^b	64.46 ± 0.29 ^b	65.21 ± 0.20 ^b
T _p /°C	71.30 ± 0.21 ^a	67.97 ± 0.01 ^b	67.68 ± 0.16 ^b	68.16 ± 0.09 ^b
T _c /°C	75.51 ± 0.29 ^a	72.35 ± 0.20 ^c	72.87 ± 0.09 ^{bc}	73.27 ± 0.14 ^b
ΔH/ Jg ⁻¹	13.23 ± 0.15 ^c	10.27 ± 0.15 ^d	15.20 ± 0.15 ^b	19.50 ± 0.29 ^a
(T _c -T ₀) = R/°C	7.25 ± 0.14 ^d	7.42 ± 0.22 ^c	8.77 ± 0.14 ^a	8.15 ± 0.096 ^b

Values are expressed as mean ± standard deviation (n=3). Means with different superscripts within the same row differs significantly (p < 0.05).

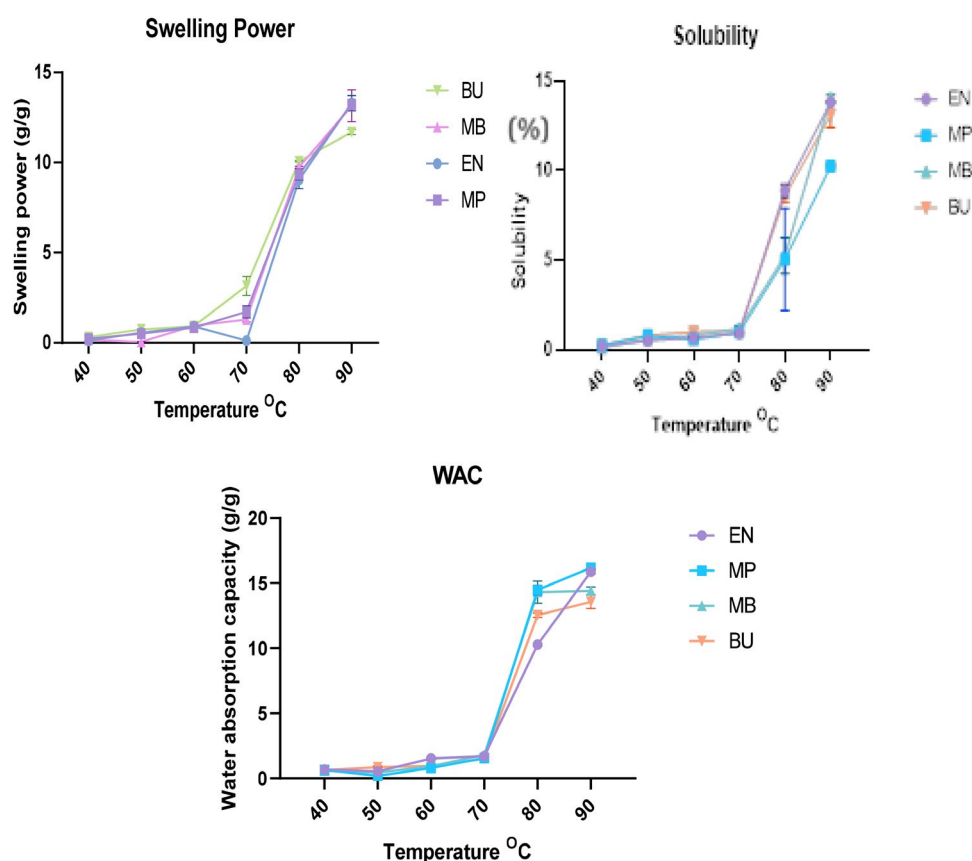


Figure 3. shows the swelling power, solubility and water absorption capacities of the East African Highland Banana starches.

Similarly, Solubility has a weak relationship with amylose content (Table 4). Amylose content could not explain the low solubility and swelling values. Another school of thought suggests that smoothness of the granule surface limits water infiltration compared to when granules have dents (de Barros Mesquita et al., 2016). Banana starch granules as seen under scanning electron microscope have smooth surfaces devoid of dents, which could explain the low solubility and hydration. On the other hand, amylose content has a strong inverse relationship with water absorption capacity (WAC, Table 4), this could account for the WAC trend for the EAHCB starches.

Generally, *Enyeru* has consistently better functional properties as compared to other cultivars. However, as compared to other starches, the EAHCB starches have relatively low swelling power, solubility, and water absorption capacity, this is suggestive that these starches require modification to improve these functional properties for better application in the food industry.

3.5. Molecular characterisation of the starches

The molecular characterisation of the Starches is shown in Table 5

Amylose content ranged from 13%–14%, with a significant difference between cultivars. These values are low compared to cooking bananas in Tanzania (18–25%), Brazil (20–28%), and Thailand (22–30%) (Olawoye et al., 2022; Yang et al., 2022; Sudlapa & Suwannaporn, 2023). Amylose, the linear fraction of starch, greatly shapes key functional properties: it modulates digestibility by forming resistant helices that resist enzymatic breakdown; influences crystallinity via tighter packing in granules; influences

Table 4. Pearson correlation coefficients between properties of the different cultivars.

	AC	RC	GS	SP	S	WAC	PV	RS	MC	SV	Y	FV	BV	PT
AC	1	−0.912	−0.099	−0.943	0.328	−0.962*	−0.816	−0.902	−0.883	0.346	0.846	−0.835	0.404	−0.905
RC		1	0.343	0.995**	−0.098	0.771	0.535	0.985*	0.812	0.007	−0.772	0.649	−0.002	0.701
GS			1	0.335	−0.362	0.005	−0.029	0.469	−0.269	0.054	0.332	−0.459	0.657	−0.330
SP				1	−0.187	0.826	0.614	0.989*	0.814	−0.091	−0.772	0.672	−0.076	0.738
S					1	−0.514	−0.733	−0.241	0.097	0.911	−0.154	−0.025	0.422	−0.208
WAC						1	0.942	0.780	0.804	−0.582	−0.766	0.832	−0.604	0.923
PV							1	0.578	0.590	−0.821	−0.550	0.698	−0.741	0.818
RS								1	0.721	−0.087	−0.671	0.561	0.023	0.644
MC									1	−0.055	−0.997**	0.956*	−0.430	0.933
SV										1	0.021	−0.265	0.752	−0.404
Y											1	−0.960*	0.440	−0.923
FV												1	−0.673	0.981*
BV													1	−0.694
PT														1

*. Correlation is significant at the 0.05 level (2-tailed), **. Correlation is significant at the 0.01 level (2-tailed). AC, amylose content, RC, relative crystallinity, GS, Granular size, SP, swelling power, S, solubility, WAC, water Absorption capacity, PV peak viscosity, RS resistant starch, MC, moisture content, SV, setback viscosity, Y yield, FV final viscosity, BV break down viscosity, PT pasting temperature.

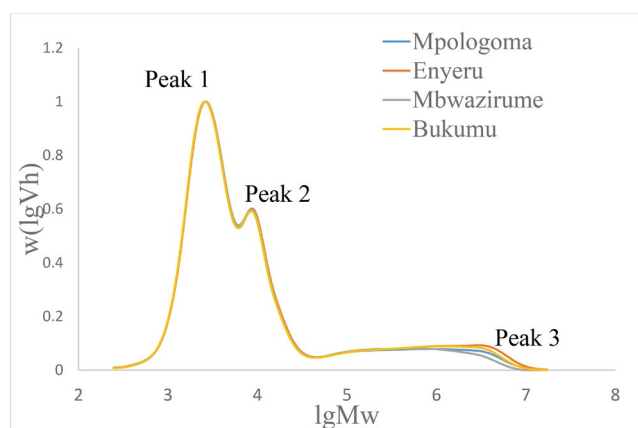


Figure 4. Amylose and amylopectin chain length distribution of starches from different East African Highland Cooking Banana cultivars. Peak 1: Amylose; Peak 2: Short amylopectin chains, Peak 3: long amylopectin chains.

Table 5. Molecular characteristics of the starches.

Cultivar	Starch content DB (%)	Amylose content (%)	Amylopectin content (%)
<i>Mpologoma</i>	96.4 ± 0.07 ^b	12.50 ± 0.05 ^b	87.5 ± 1.57 ^b
<i>Enyeru</i>	99.6 ± 2.45 ^a	14.80 ± 1.00 ^a	85.2 ± 1.78 ^a
<i>Mbwazirume</i>	98.5 ± 0.98 ^{ab}	13.70 ± 1.00 ^{ab}	86.3 ± 0.09 ^{ab}
<i>Bukumu</i>	99.7 ± 2.89 ^a	15.25 ± 0.25 ^a	84.75 ± 1.49 ^a

Values are expressed as mean ± standard deviation (n=3). Means with different superscripts within the same the row differs significantly ($p < 0.05$).

Table 6. Readily digestible starch (RDS), slowly digestible starch (SDS), and resistant starch (RS) of the starches.

Cultivar	RDS (%)	SDS (%)	RS (%)
<i>Mpologoma</i>	8.47 ± 0.67 ^b	28.19 ± 2.31 ^b	63.34 ± 1.67 ^c
<i>Enyeru</i>	6.70 ± 0.30 ^d	24.47 ± 0.74 ^d	68.94 ± 0.58 ^a
<i>Mbwazirume</i>	7.67 ± 0.55 ^c	26.00 ± 1.76 ^c	66.43 ± 1.80 ^b
<i>Bukumu</i>	11.04 ± 2.89 ^a	31.33 ± 1.45 ^a	57.63 ± 1.45 ^d

Values are expressed as mean ± standard deviation (n=3). Means with different superscripts within the same the column differs significantly ($p < 0.05$).

granular size and integrity; and impacts solubility and swelling power during heating, often reducing hydration in high-amylose starches (Samanros & Lin, 2021; Khoozani et al., 2020; Du et al., 2020).

The variation in the amylose content of different cultivars in this study could be attributed to genetic factors like enzyme activity during biosynthesis of the starch and climatic conditions during the growth period (de Barros Mesquita et al., 2016; J et al., 1999; Zhang et al., 2005; Amini Khoozani et al., 2020; Kitara et al., 2018; Wang et al., 2024; Matsue et al., 2002). However, studies have suggested that amylose content is more affected by genetics than by environmental factors (Zhang & Hamaker, 2012). Whereas, high amylose content characteristically reduces digestibility in starches from cereals and tubers, banana cultivars in this study exhibit an inverse pattern: where low amylose levels correspond to enhanced digestibility. This uniqueness could arise from bananas' unique B-type crystalline granules, higher amylopectin branching, or variations in pectin interactions that facilitate rapid α -amylase hydrolysis. These findings highlight banana starch's potential in nutritional applications, like low-glycemic foods, these further warrants genotype-environment studies for breeding, low digestible cultivars.

3.5.1. Amylopectin chain length distribution of starches

Banana starch had a high proportion of long amylopectin chains (Figure 4), consistent with the other findings (Lehmann et al., 2002; Amini Khoozani et al., 2020). These long chains comprise highly branched, low molecular weight amylopectin molecules that intertwine each other with or without the participation of amylose to form swelling-resistant structures during pasting (Lehmann et al., 2002). The long chains confirm the hypothesis that banana amylopectin can retrograde and reassociate faster upon cooling than other starch amylopectins. When the α -1, 6-linked side chains are sufficiently long, banana starch can produce RS type 3 from amylopectin-rich starches, making it a good source for RS3 production (Lehmann et al., 2002).

It is known that retrograded starch is less accessible to amylases and digests slower or less entirely, thus increasing the RS3 content (Mohamed et al., 2024). Banana amylopectin retrogrades substantially faster than corn or potato amylopectin, leading to low digestibility in banana starch (Seung, 2020).

3.6. In vitro digestibility of the starches

The EAHCB starches had high RS content 57%–68% (Table 6), with significant differences between the cultivars. The high RS (RS2) content positioning bananas as a good source of RS, similar to the findings of (Ul Zaman et al., 2025) and (Khoza et al., 2021), who reported 74 and 65% RS, respectively. The RS content in EAHCB starches is higher than 40–50%, as reported by (Chang et al., 2022) for EAHCB in Tanzania. Starch resistance is usually attributed to the amylose and amylopectin chains responsible for forming RS and SDS (63). Banana starch contains a more significant amount of slowly digested and resistant starch than in corn and potatoes, which have a higher amylose level (Marta et al., 2022). This suggests that the slow digestion of banana starch may be due to its amylopectin content.

This study showed that banana starch had a comparatively low amylose percentage of 13–15% (Table 5). This is consistent with the results of (Ssonko & Muranga, 2017) and (13). Differences in banana cultivars could contribute to variations in RS content, consistent with the findings of (Chang et al., 2022). From this study, the *Enyeru* cultivar stood out with the highest RS and *Bukumu* showed lowest RS and highest SDS and RDS likely due to looser amylopectin packing or higher susceptibility to gelatinisation during isolation. These traits make EAHCB starches promising for low-glycemic foods, functional ingredients in gluten-free products, and or therapies targeting metabolic disorders like diabetes, given RS's role in modulating glycemic index and insulin response.

3.7. Relationship between chemical, molecular structure, and digestibility of banana starch

Principal component analysis (PCA) elucidated the possible relationship between digestibility and starch's physicochemical, molecular, and structural characteristics from different banana cultivars (Figure 5). The eigenvalues of the first two principal components explain 83.97% of the total variation. The first principal component (PC1) was mainly contributed by digestibility, pasting viscosity, crystallinity, slowly digestible starch, and amylopectin chain distribution while PC2, explaining 38.80% of the variance, primarily captured distinctions in thermal and pasting temperatures.

Resistant starch clustered closely with crystallinity, linking low digestibility to B-type starch's stable double helices and smooth, compact granules (Figure 2). Despite smaller granule sizes (Table 2) than typical bananas which usually increase digestibility via greater α -amylase surface area, the lack of surface dents preserved resistance in EAHCB. The particle size further influences digestibility with smaller particles and narrower size distribution, providing additional surface areas for α -amylase action (de Barros Mesquita et al., 2016). However, banana starches in this study generally had smaller granular sizes (Table 2) than other banana starches, which could not necessarily contribute to their low digestibility except for their lack of dents on the granular surface, which could explain their low digestibility.

Enyeru and *Mbwazirume* clustered closely with high RS (*Enyeru* highest; Table 6), reflecting shared chemical/granular traits and low digestibility. *Bukumu* and *Mpologoma* dispersed across quadrants, indicating greater variability.

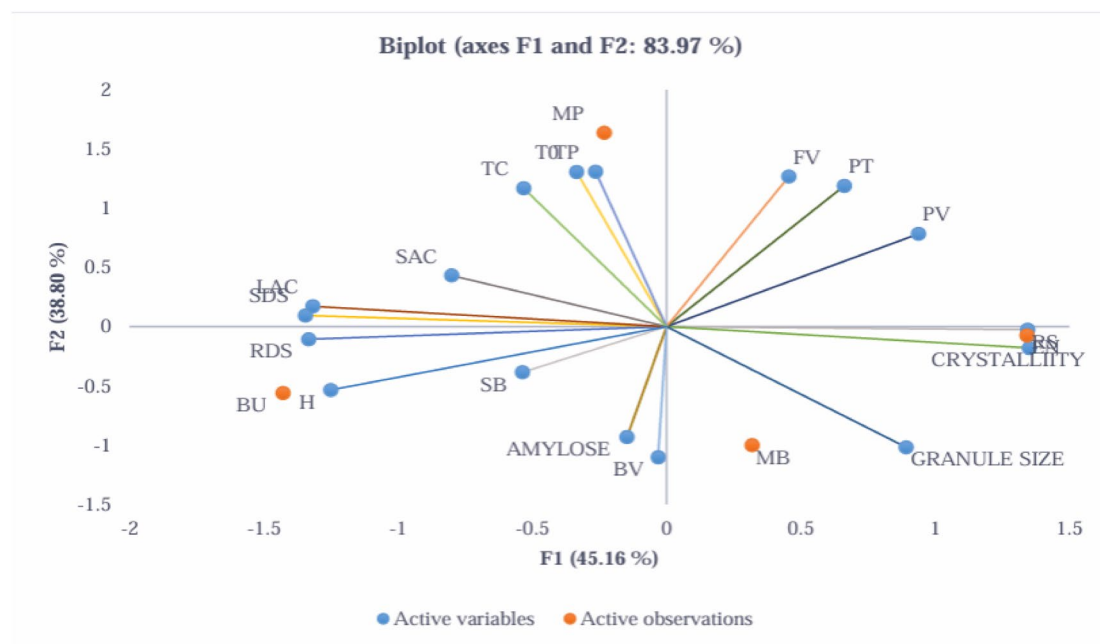


Figure 5. Biplot for structure and digestibility of starches from different East African Highland Cooking Banana cultivars.

MP: Mpologoma, *EN*: Enyeru, *MB*: Mbwazirume, and *BU*: Bukumu. RS: Resistant starch, BV: breaking viscosity, SB: set back viscosity, H: enthalpy change, RDS: readily digestible starch, SDS: slowly digestible starch, SAC: Short amylopectin chains, LAC: Long amylopectin chains, T0: Onset temperature, Tc: Constant temperature Tp: gelatinisation temperature, FV: Final Viscosity, PT: Pasting Temperature, PV: Pasting viscosity.

Table 7. Multiple linear regression model for RS, RDS, and SDS.

Responses	Significant models	R ²
RDS	$Y_1 = 910.67 - 3.83X_1 - 0.22X_2 - 427.79X_3 + 32070.99X_4$	0.75
RS	$Y_2 = -905.60 + 8.40X_1 + 0.09X_2 + 384.01X_3 - 28831.47X_4$	0.84
SDS	$Y_3 = 477.47 - 3.94X_1 - 0.06X_2 - 168.18X_3 + 12522.36X_4$	0.82

X_1 = Relative Crystallinity, X_2 = Granular size, X_3 = Amylose, X_4 = Amylose amylopectin ratio. All the models are significant at $p < 0.05$.

Long-chain amylopectin (LAC) clustered closely with SDS, confirming its role in stable helices/hydrogen bonds that slow digestion. Thermal parameters (T_c , T_0 , T_p) co-clustered with SDS, short-chain amylopectin (SAC), and LAC, as longer chains elevate gelatinisation temperatures via formation complex structures. Amylose aligned with RDS, setback (SB), and enthalpy (H), affirming that amylose influences pasting and thermal properties via leached amylose networks more than it influenced digestibility.

Multiple linear regression (Table 7) revealed RDS/SDS decreasing with crystallinity, granule size, and amylose but rising with amylose: amylopectin ratio and yet RS showed the inverse, emphasizing crystallinity's dominance in influencing digestibility in EAHCB starches.

4. Conclusion

This study answers the question of what causes high resistant starch in low amylose EAHCB starches, it reveals that crystalline structure, amylopectin chain length distribution, and granule morphology predominantly influence the *in vitro* digestibility of EAHCB starches. The *Enyeru* cultivar emerged with superior RS content, highlighting its potential as a high-RS source. While *in vitro* models provide valuable insights, their limitation in mimicking human digestion warrants validation through *in vivo* studies. These findings open doors to targeted breeding to enhance crystallinity and RS in banana cultivars, alongside optimized applications in low-GI functional foods. Future research should explore physiological impacts, processing synergies, and genomic markers for RS enrichment.

Acknowledgments

This work was supported by UNESCO through an OWSD grant awarded to Stellamaris. The authors also thank the Biochemistry Laboratory at Makerere University for their support and facilities during the experimentation.

Author contributions

CRedit: **Stellamaris Kembabazi**: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing; **Florence Muranga**: Methodology, Project administration, Supervision; **Martin Mutambuka**: Conceptualization, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing; **Ediriisa Mugampoza**: Conceptualization, Supervision, Validation, Writing – review & editing; **Norhasnida Zawawi**: Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

Stellamaris Kembabazi's one-year research attachment at Universiti Putra Malaysia, MALAYSIA, was funded by the Organization for Women in Science for the Developing World (OWSD) Sandwich PhD Fellowship, grant number 3240324247.

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Data availability statement

The values behind the means, standard deviations and other measures reported, in addition to the values used to build graphs or other figures, of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.19091584>

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