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RESEARCH ARTICLE

Genetic diversity and morphological variation of aibika [*Abelmoschus manihot* (L.) Medik.] in Melanesia

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Abstract Aibika [*Abelmoschus manihot* (L.) Medik.], also known as island cabbage, is a highly nutritious leafy vegetable crop which is traditionally cultivated in Southwest Pacific countries. The study presents the results of genetic analyses of 227 aibika accessions conserved in the genebanks of three Melanesian countries (New Caledonia, Papua New Guinea, and Vanuatu), and French Polynesia. Genotyping with 21 novel microsatellite markers revealed that 216 accessions had a diploid genome, while eleven exhibited a third allele at one locus or more. Among the diploid accessions, we observed a total of 196 unique multilocus genotypes. Using K-means clustering method, we identified six genetic groups, including one specific to Papua New Guinea. Discriminant analysis of principal components revealed the relations between these groups, the probability of membership, and the level of admixture of the accessions. Genetic analyses by country also shown that Papua New Guinea accessions exhibited the highest genetic diversity, allelic richness, and number of private alleles, which is consistent with the history of the introductions of the crop in the Pacific. The genetic diversity observed is likely the result of a cultivation process combining selection of seedlings issued from natural sexual reproduction and clonal propagation. Morphological analyses of 76 accessions conserved in Vanuatu national ex situ germplasm collection were also conducted using a set of four quantitative and five qualitative morphological descriptors. We further discussed future challenges for the conservation and breeding of this neglected crop that contributes to the diversification and quality of the diets of Pacific Islands communities.

Keywords Genotyping · Leafy vegetable · Malvaceae · Microsatellite markers · Pacific · Vanuatu

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Introduction

Aibika [*Abelmoschus manihot* (L.) Medik.], also called island cabbage or slippery cabbage, belongs to the Malvaceae family. Other common names are *bele* or *pele* (Fiji, Polynesia), *chou kanak* (New Caledonia), and *aelan kabis* in Bislama (bis), the English-based creole of Vanuatu. It is a tropical shrub well appreciated for its highly nutritious leaves and shoot tips throughout Melanesia (Papua New Guinea, Solomon Islands, Vanuatu, New Caledonia, and Fiji) (Preston 1998). The centre of diversification of the genus *Abelmoschus* is South and Southeast Asia (Borssum Waalkes 1966). Wild and cultivated species are found in Burma, Thailand, Indonesia, Malaysia, and Papua New Guinea (Charrier 1984). This geographical distribution includes *A. moschatus* (L.) Medik., *A. manihot* (L.) Medik., *A. esculentus* (L.) Moench., *A. ficulneus* (L.) Wight & Arn., *A. crinitus* Wall., and *A. angulosus* Wall. ex Wight & Arn. It has been suggested that *A. manihot* most likely originated in Malesia, a biogeographical region encompassing Sulawesi, the Moluccas, New Guinea and the Bismarck Archipelago (Johns 1995). Given its dehiscent capsules and large and smooth seeds, *A. manihot* is unlikely to disperse through long distances via natural means like wind, water, or animal carriers. Stem cuttings were probably distributed eastwards to the Pacific Islands with the Lapita peoples during their migrations which began 3500 years ago from the Bismarck archipelago and reached Vanuatu about 3000 years ago (Lebot 1999; Bedford and Spriggs 2008). The great diversity of uses and vernacular names for *A. manihot* in Melanesia is seen as evidence for its long history in this region (Preston 1998). In contrast with aibika, okra (*A. esculentus*) is probably the most studied *Abelmoschus* species from pioneering works in genetics (Charrier 1984) to recent diversity research using various molecular markers (Schafleitner et al. 2013; Fougat et al. 2015; Werner et al. 2016; Kumar et al. 2017; Nieuwenhuis et al. 2024).

Although it is considered a neglected crop globally, aibika makes a significant contribution to food supply and to a nutritionally well-balanced diet at national and regional levels (Preston 1998). It is also an important cash crop in local markets in Melanesia, as well as in the export market for Pacific Island communities in New Zealand, Australia, and the United States (Fa'anunu 2009). The leaves are rich in essential nutrients such as proteins, fibres, calcium, iron, zinc, magnesium, potassium, vitamin A, vitamin C, and vitamin B6, providing a substantial portion of recommended daily intakes (Preston 1998; Rubiang-Yalambing 2014; Rubiang-Yalambing et al. 2016). However, the nutritional composition varies according to the variety and how it is prepared, whether raw, boiled, fried, baked, or steamed (Preston 1998).

Generally, consumers prefer young soft rounded green leaves with either light to dark green or pink petiole colour, associated to good taste and soft texture when cooked in traditional recipes or simply steamed. In Melanesia, the leaves are mainly consumed as a complement of starchy foods. In Vanuatu, aibika leaves are added into the *laplap* (bis), a paste made of grated bananas, taro, yam, or cassava and cooked in the traditional oven of hot stones (Walter and Lebot 2007, p. 41). *Simboro* (bis) is a small roll made of the same paste, wrapped in aibika leaves and cooked in fresh coconut milk (Fig. 1). Deeply lobed leaves, which are tougher and more fibrous than entire leaves, are mainly chopped and used in soups or fried.

Throughout Melanesia, aibika is also used for medicinal purposes. The boiled leaf juice is consumed to treat digestive disorders, asthma, stomach aches, diarrhoea, dysentery, and to alleviate childbirth and menstrual pains (Bourdy and Walter 1992; Preston 1998). In Asia, *A. manihot* flowers have been extensively analysed for their medicinal properties. They present flavonoids which are valuable to treat various ailments like inflammatory chronic kidney diseases, liver damage, and gastrointestinal ulcers and burns (Sudewi et al. 2017; Yang et al. 2018; Luan et al. 2020).

Abelmoschus manihot stems can reach a height of four meters when cultivated under optimal conditions. Its leaves vary greatly in shape, size, and lamina colour (Qian et al. 2023). The flowers are usually sulphur yellow, sometimes light rose, with a dark purple centre (Fig. 2). Although the seeds are fertile and capable of producing seedlings, the plant is predominantly propagated asexually using stem cuttings. However, despite this clonal propagation, significant polymorphism exists for *A. manihot* across Papua New Guinea, Solomon Islands, New Caledonia and Vanuatu, exceeding that observed elsewhere in the Pacific (Preston 1998).



Fig. 1 Preparation of *simboro* (bis), a popular delicacy of Vanuatu. Pieces of paste made of pounded cassava are wrapped in aibika leaves and cooked in fresh coconut milk. Photos F. Lawac

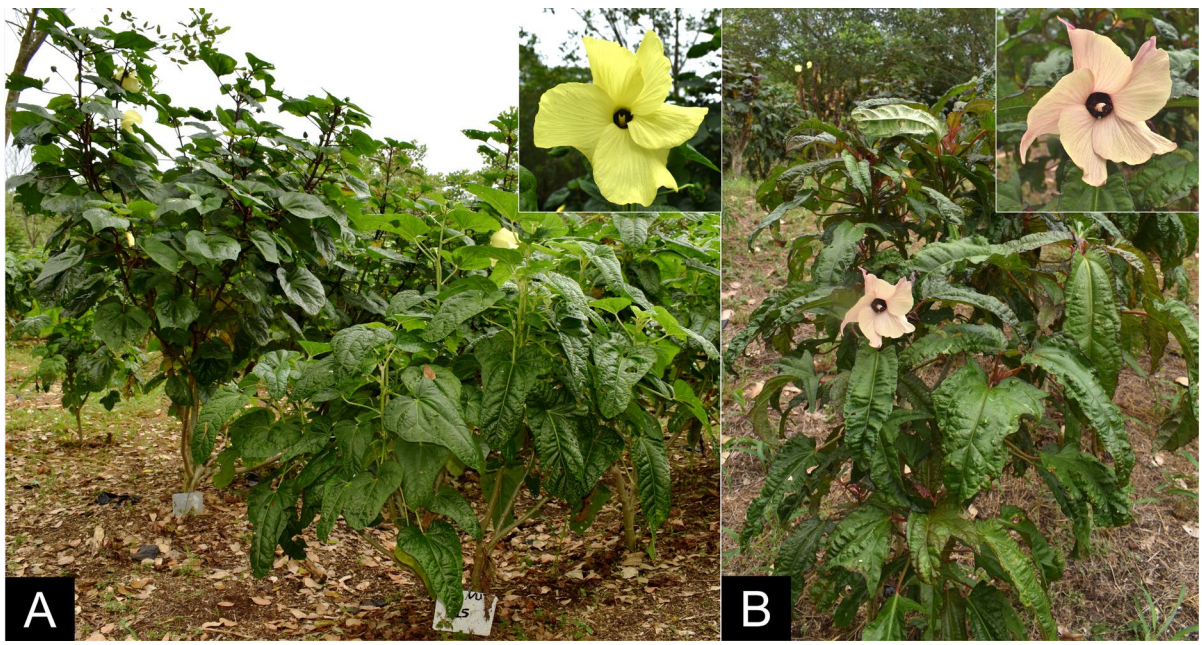


Fig. 2 Three aibika accessions in the Vanuatu Agricultural Research and Technical Centre (VARTC) genebank. **A**. From left to right, accessions 123 and 115 with yellow sulfur flowers. **B**. Accession 076 with light rose flowers. Photos F. Lawac

To date, the genetic diversity of *A. manihot* is poorly documented. Rubiang-Yalambing et al. (2016) used RAPD (random amplified polymorphic DNA) and DAMD (directed amplification of minisatellite-region DNA) for genotyping 23 cultivars of aibika collected from six provinces in Papua New

Guinea. They identified five genetic groups; however, they found that these genetic groups did not correlate with leaf morphology or micronutrient content, suggesting that environmental factors may influence the plant's micronutrient composition more than its genetics.

Given its cultural aspects and nutritional importance, it is crucial to assess morphological and genetic diversity of aibika, especially with regard to breeding and adaptation to on-going economic and climatic changes. A key step towards this goal was the collection of cultivars across the Vanuatu archipelago during three campaigns conducted in 2010, 2020 and 2021. The sampling strategy was to collect cultivars that exhibited distinct morphological traits and had distinct vernacular names. In 2010, Bruerre compiled a catalogue (unpublished) of 225 cultivars collected from 23 villages on seven islands, and a first field genebank was established in the Vanuatu Agricultural Research and Technical Centre (VARTC). However, by 2024, only 76 accessions remained in the VARTC genebank where they are at risk of loss due to poor adaptation and environmental factors, such as cyclones, pests and diseases. In New Caledonia, surveys have been carried out across the country since 2005 and 108 different morphotypes have been identified (Robert et al. 2024). Around 40 accessions are currently conserved ex situ by the Institut Agronomique néo-Calédonien (IAC) at the stations of Atha (Maré) et Port-Laguerre (Païta). In Papua New Guinea, the National Agricultural Research Institute (NARI) conserves 63 accessions in its research centers in Bubia (Morobe Province), Laloki (Central Province), and Keravat (East New Britain Province) (NARI 2024).

In the present study, we provided the first integrated and comparative analysis of the genetic diversity existing in three Melanesian countries (New Caledonia, Papua New Guinea, and Vanuatu) and in French Polynesia by genotyping 227 samples using 21 single sequence repeat (SSR) markers. We also characterized the morphological traits of the 76 accessions currently conserved in the VARTC genebank. Finally, we discussed the results and future challenges for conservation and use of *A. manihot* germplasm at regional level.

Materials and methods

Plant material

In Vanuatu, the national aibika genebank is located in the VARTC station on the island of Espiritu Santo (latitude 15° 27.1′ S, longitude 167° 11.4′ E, 80 m a.s.l.). The soil is deep, ferrallitic, weakly desatured, rich in clay and fine silts (Quantin 1982). In 2024, the genebank was composed of 76 accessions, consisting of 63 cultivars collected in the villages and 13 spontaneous seedlings collected in VARTC experimental plots. The 63 cultivars originated from eleven islands, from the island of Vanua Lava in the north of the archipelago to Aneityum in the south. Within these islands, 38 villages were surveyed. The planting materials were cuttings, 50–70 cm long, collected six to eight internodes below the terminal bud. All accessions were planted in rows of five plants each, with 1 m × 1 + m spacing.

A total of 141 accessions from Vanuatu were genotyped, consisting of 76 accessions collected from the VARTC genebank as well as a further 65 leaf samples that were collected from farmers' fields specifically for this purpose. Additionally, 47 accessions were provided by the National Agricultural Research Institute (NARI) of Papua New Guinea, 37 accessions by the Institut Agronomique Néo-Calédonien (IAC), and two by the Direction of Agriculture (DAG) of French Polynesia. Overall, 227 accessions were genotyped. We also characterized the 76 accessions of the VARTC genebank with morphological descriptors. Table 1 presents a summary of the number of accessions characterized morphologically and/or genotyped, with their collection locations. More detailed information can be found in Tables S1a, S1b, S1c, and S1d in Supplementary Information 1 (Supp. Inf. 1).

DNA extraction

For each accession, a healthy green mature leaf, preferably the third or fourth leaf counting from the terminal meristem, was collected from the field genebank. A piece of about 20 cm^2 was taken from the leaf and dried in a ventilated oven at 40 °C for 48 h. The dried leaf samples were sent to CIRAD (Centre de

Table 1 List of accessions used in the study with their origin

Country and main areas*	Islands	Phenotyped accessions	Genotyped accessions
Vanuatu		**76**	**141**
Northern islands:	Vanua Lava	3	15
	Malo	3	3
	Santo	17	19
	Ambae	4	6
	Maewo	3	7
	Pentecost	10	17
Central islands:	Malekula	4	4
	Efate	2	2
	Epi	7	36
Southern islands:	Tanna	6	12
	Aneityum	4	8
Seedlings from Vanuatu Agricultural Research and Technical Centre (VARTC)		13	12
New Caledonia			**37**
Grande Terre			24
Loyalty Islands			13
Papua New Guinea			**47**
Main Land			44
Bismarck Archipelago			3
French Polynesia			**2**
Total		**76**	**227**

*Countries (in bold), main areas (in italics) and islands are represented in Fig. 4 and Fig. 5

Coopération Internationale en Recherche Agronomique pour le Développement), Montpellier, France for genotyping. For each sample, 50 mg of dry leaves were ground twice at 1400rpm during 1 min 30 s with 2 steel beads of 3 mm on Genogrinder 2010 (Cole-Palmer®, Antylia Scientific, Vernon Hills, IL, USA), incubated at 56 °C for 45 min with 600 µL of Lysis Buffer CF (Macherey–Nagel, #740,946, Düren, Germany) and 200 ng of Proteinase K (Macherey–Nagel, #740,506). DNA was then purified on Thermo Scientific KingFisher™ Duo Prime System (Thermo Fisher Scientific, Watham, MA, USA) with NucleoMag® C-Beads (Macherey–Nagel, #744,401). Genomic DNA was checked for quality by 1% agarose gel electrophoresis and quantified with a Fluoroskan Ascent FL fluorometer (Thermo Fisher Scientific).

Development of microsatellite markers specific to *A. manihot*

In the absence of SSR markers specific to *A. manihot*, an initial test was carried out using 16 SSR markers already developed for okra *A. esculentus* (Kumar et al. 2017). Seven of these markers revealed polymorphism but no significant differences were observed between the Vanuatu accessions. It was therefore decided to search for markers specific to *A. manihot*. The DNA library was prepared by pooling DNA extracts from four accessions of *A. manihot* from Vanuatu (084, 290, 301, 313) exhibiting different morphological characteristics and geographical origins. After sequencing on an Illumina MiSeq system, the identification of microsatellites motifs was obtained by a bioinformatic analysis. The full protocol of *A. manihot* SSR development is detailed in a separate data paper by Rivallan et al. (2026). Finally, a set of 21 polymorphic markers (Supp. Inf. 2, Table S2) with no ambiguity in allele size determination was selected for genotyping the 227 accessions of the study.

Genotyping

Due to the presence of mucilaginous and sticky compounds, the DNA solution had to be diluted 50-fold. Before the PCR reaction, we also had to purify a few recalcitrant samples with AMPure XP magnetic beads (Beckman Coulter, A63881) with a 0.8X bead/DNA ratio. PCR was performed separately for each primer pair in 10 µL final solution, containing 5–10 ng template DNA, 0.5 mM MgCl2, 200 µM dNTPs, 0.2 µM reverse primer, 0.16 µM M13-tailed forward primer, 0.2 µM M13 primer fluorescently labelled with FAM, VIC, PET, or NED (Applied Biosystems, Foster City, California, USA), 0.04 ng bovine serum albumin, 0.75X Q-Product (Qiagen, Hilden, Germany) and 0.06 U Taq DNA polymerase with 1X ThermoPol® reaction buffer (New England Biolabs, Ipswich, MA, USA). PCR was performed on a thermocycler Mastercycler® nexus, Eppendorf AG (Hamburg, Germany) with the following settings: initial denaturation at 95 °C for 5 min; 10 cycles of touchdown, starting at 95 °C for 30 s, then annealing temperature (Ta) plus 5 °C (0.5 °C decrease at each cycle) for 1 min, and 68 °C

for 1 min; 23 cycles at 95 °C for 30 s, Ta for 1 min, and 68 °C for 1 min; and a final elongation step at 68 °C for 10 min. Allele size was determined after separation on an ABI 3500 xL Genetic Analyzer (Applied Biosystems, Foster City, California, USA). Genemapper v.6.0 software (Applied Biosystems, Thermo Fisher Scientific) was used for data collection, calculation of allele size and visualization of alleles.

Flow cytometric analysis

For the accessions that exhibited more than two alleles at one or more loci, a flow cytometric analysis was performed using a Partec PA-II flow cytometer (Partec, Münster, Germany) equipped with a UV mercury short-arc lamp for excitation (420 nm). Samples were prepared according to Doležel et al. (2007). Approximately 0.5 cm piece of young root was chopped with a razor blade in a petri dish with 1 ml ice-cold Otto I buffer, then left to incubate for a few minutes. The homogenate was filtered through a 20-µm nylon mesh to remove large particles. DAPI (4′,6-diamidino-2-phenylindole) is a blue-emitting fluorescent dye that binds strongly to adenine–thymine-rich regions in DNA. Prepared with Otto II solution, it was added to the sample tube at 4 µg/ml and left to incubate for a few minutes to stain the nuclear DNA. The preparations were run on the flow cytometer using the FloMax software, ensuring between 1000 and 3000 nuclei counts were obtained per sample. The flow cytometric data are displayed as histograms. From the positions of the nuclei's peaks, we calculated the DNA content ratio of the diploid accessions used as controls and of the samples bearing three alleles.

Morphological characterization

Morphological descriptions of the 76 accessions from Vanuatu were conducted in VARTC from 2023 to 2024 using nine descriptors related to the size, the shape and the colour of the leaf, petiole and stem (Table 2). These were chosen specifically for their utility to farmers in differentiating local cultivars.

Data analyses

Genotypic data analyses

We used the discriminant analysis of principal components (DAPC), a multivariate method designed to identify the number of clusters (genetic groups) and describe the relationships between these clusters (Jombart et al. 2010; Thia 2023). We determined the number of genetic groups using the K-means non-hierarchical partitioning algorithm with the function *find_cluster* of the R *adegenet* package (Jombart 2008). Different clustering solutions were compared

Table 2 Morphological traits used to characterize 76 accessions of *Abelmoschus manihot* from Vanuatu Agricultural Research and Technical Centre (VARTC) genebank

Traits	Phenotypic classes
Quantitative traits:	
Number of lobes	Lobes of an individual leaf
Petiole length (cm)	Petiole length (cm) of the 3rd leaf counting from the proximal end to the distal end
Leaf length (cm)	Lamina length (cm) of the 3rd leaf counting from the proximal to the distal end
Leaf width (cm)	Lamina width (cm) of the 3rd leaf counting from the proximal to the distal end
Qualitative traits:	
Leaf lobe	1 Aciculate, 2 Linear, 3 Lanceolate, 4 Oblanceolate, 5 Elliptical
Leaf dissection	1 Entire, 2 Dissected slightly on upper half, 3 Moderately dissected on upper half (less than 50% of the lobe vein), 4 Moderately deeply dissected (50–75% of the lobe vein), 5 Deeply dissected (over 75% of the lobe vein), 6 Leaf deeply dissected till the petiole insertion point
Leaf colour	1 Light green, 2 Dark green, 3 Green with red/purple spots, 4 Other
Petiole colour	1 Light green, 2 Dark green, 3 Pink, 4 Red, 5 Purple, 6 Green with of pink/red splashes, 7 Pink/red with green splashes, 8 Other
Stem colour	1 Light green, 2 Dark green, 3 Pink, 4 Red, 5 Purple, 6 Green with pink/red splashes, 7 Other

using Bayesian Information Criterion (BIC). Then, DAPC was performed, using the function *dapc*. Scatterplots were drawn from the first principal components of DA. The DAPC results were also be used to derive the probability of membership to genetic groups and identify admixed accessions.

The following genetic parameters were calculated: the number of multilocus genotypes (*MLG*), the ratio *MLG:N* which is the number of MLGs found at the 21 loci studied divided by the sample size (*N*) (Halkett et al. 2005), the number of observed alleles per locus (*A*), and the allelic richness (*Ar*) which is the number of alleles corrected from sample size by using the rarefaction method proposed by El Mousadik and Petit (1996). The number of private alleles was determined by counting the number of alleles that are specific to each genetic group or country (Kalinowski 2004). The observed heterozygosity *Ho,* the expected heterozygosity *Hexp* under Hardy–Weinberg equilibrium (Nei 1978), and the inbreeding coefficient *Fis* were estimated at each locus. When calculated across all loci, *Hexp* is the projected percentage of the population that would be heterozygous for each randomly selected locus. As *Hexp* is less susceptible to sample size than observed heterozygosity *Ho*, it is typically estimated for characterizing genetic diversity (Kanaka et al. 2023). The inbreeding coefficient *Fis* is equal to [1—(*Ho/Hexp*)] and represents the deviation from Hardy–Weinberg equilibrium. The number of MLGs, the number of observed alleles per locus, and the number of private alleles were calculated using the R package *poppr* (Kamvar et al. 2014). Allelic richness, *Ho, Hexp,* and *Fis* were estimated using the R package *hierfstat* (Goudet 2005).

Phenotypic traits analyses

The statistical analyses were conducted on a set of 76 accessions from Vanuatu. For quantitative data, the basic statistical parameters (minimum, maximum, mean, median, standard deviation, and coefficient of variation) and the Spearman correlation coefficients between pairs of traits were calculated using XLSTAT software (Lumivero 2024). The histograms and the bar graphs of frequency distribution were generated using R packages *ggplot2* (Wickham 2016) and Microsoft Excel. After converting the four quantitative data into qualitative data, we carried out a multiple correspondence analysis (MCA) with the R packages *FactoMineR* (Lê et al. 2008) and *Factoshiny* (Vaissié et al. 2025) to investigate whether morphological characters could be linked to the geographical origin. From the results of the MCA, a hierarchical clustering was also performed using the Ward's method, and a dendrogram was generated.

Results

Flow cytometry

Among the 227 genotyped accessions, eleven exhibited a third allele at one locus at least: three accessions from Vanuatu (057, 253, and 317), six from Papua New Guinea (LAL035, LAL082, LAL084, LAL241, LAL242, and LAL248), and two from New Caledonia (NCL008 and NCL027).

We found that accessions 057, 253, and 317 had the same third allele at the AmCir2957 locus. Accession 253 also had a third allele at the locus AmCir9548a. These three accessions of Vanuatu were analysed by flow cytometry and compared to three other accessions that exhibited diploid profiles. An example of the histograms of DNA content obtained with the accessions 317 and 300 (diploid control) is presented in Supp. Inf. 2, Fig. S1.

On the DAPI-stained nuclei scale (x-axis of the histograms), the average peak positions for accessions 057, 253, and 317 were 110.9 (CV = 4.45%), 113.3 (CV = 3.86%), and 114.7 (CV = 3.94%), respectively. For the three diploid accessions used as controls, the average peak position was 92.3 (CV = 5.75%). This suggests that accessions exhibiting a third allele had approximately 21% more DNA than diploids. Hence, we assumed that the remaining 216 accessions were diploid and the genetic analyses detailed below were performed with these 216 accessions.

Determination of genetic groups and DAPC

The optimal number of genetic groups was determined from the genotyping data using the K-means algorithm. The value of k corresponding to the lower point of the curve of BIC values (here, k = 6) was

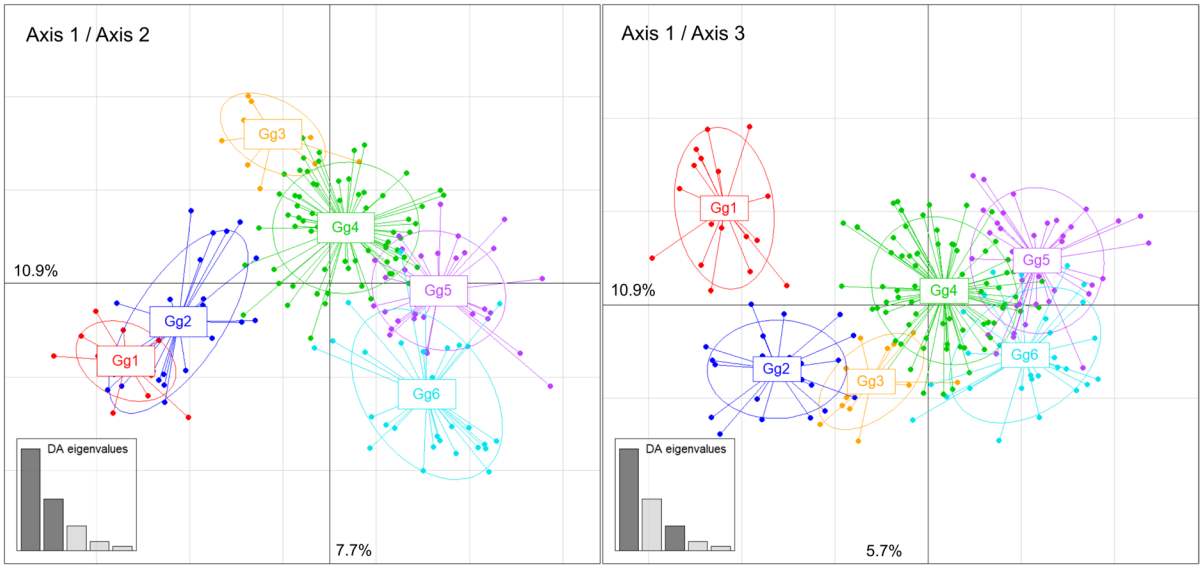


Fig. 3 Scatterplots of discrimnant analysis of principal components (DAPC) generated from genotyping data of 216 diploid accessions assigned to the six genetic groups defined by the K-means procedure

retained (Supp. Inf. 2, Fig. S2). The 216 accessions were classified into six genetic groups (Gg1 to Gg6) (Supp. Inf. 2, Table S3). The two scatterplots in Fig. 3 were generated from DAPC. They allow for a graphical assessment of the genetic structures between clusters. Axis 1 explained 10.9% of the variation and distinctly separated the accessions assigned to Gg1 and Gg2 from the accessions of the other groups. Axis 2 (7.7% of the variation) separated Gg3 from Gg1, Gg2, Gg5, and Gg6. Axis 3 (5.7% of the variation) separated Gg1 from Gg2.

Determination of multilocus genotypes and distribution across the countries

The number of unique multilocus genotypes (*MLG*) was found to be 196. One hundred and sixty accessions had a unique SSR pattern and the 36 remaining ones were distributed into 16 clone-mate groups (Supp. Inf. 2, Table S4). The distribution of the number of MLGs according to the genetic group and country of origin is presented in Table 3 and on the map of the Southwest Pacific (Fig. 4).

From the DAPC results, we also retrieved the membership probability to genetic groups and determined the number of admixed accessions (see stacked bar plots in Supp. Inf. 2, Fig. S3a, b). We

Table 3 Distribution of the number of diploid accessions (*N*) and of the number of multilocus genotype (*MLG*) into the six genetic groups, according to their origin

PNG = Papua New Guinea, NCL = New Caledonia, VUT = Vanuatu, PYF = French Polynesia

Genetic	PNG		NCL		VUT		PYF		Total	
group	N	MLG	N	MLG	N	MLG	N	MLG	N	MLG
Gg1	19	17							19	17
Gg2	21	18	1	1	5	4	1	1	28	24
Gg3			12	9	3	3			15	12
Gg4	1	1	18	14	60	58	1	1	80	74
Gg5			2	2	37	36			39	38
Gg6			2	2	33	29			35	31
Total	41	36	35	28	138	130	2	2	216	196

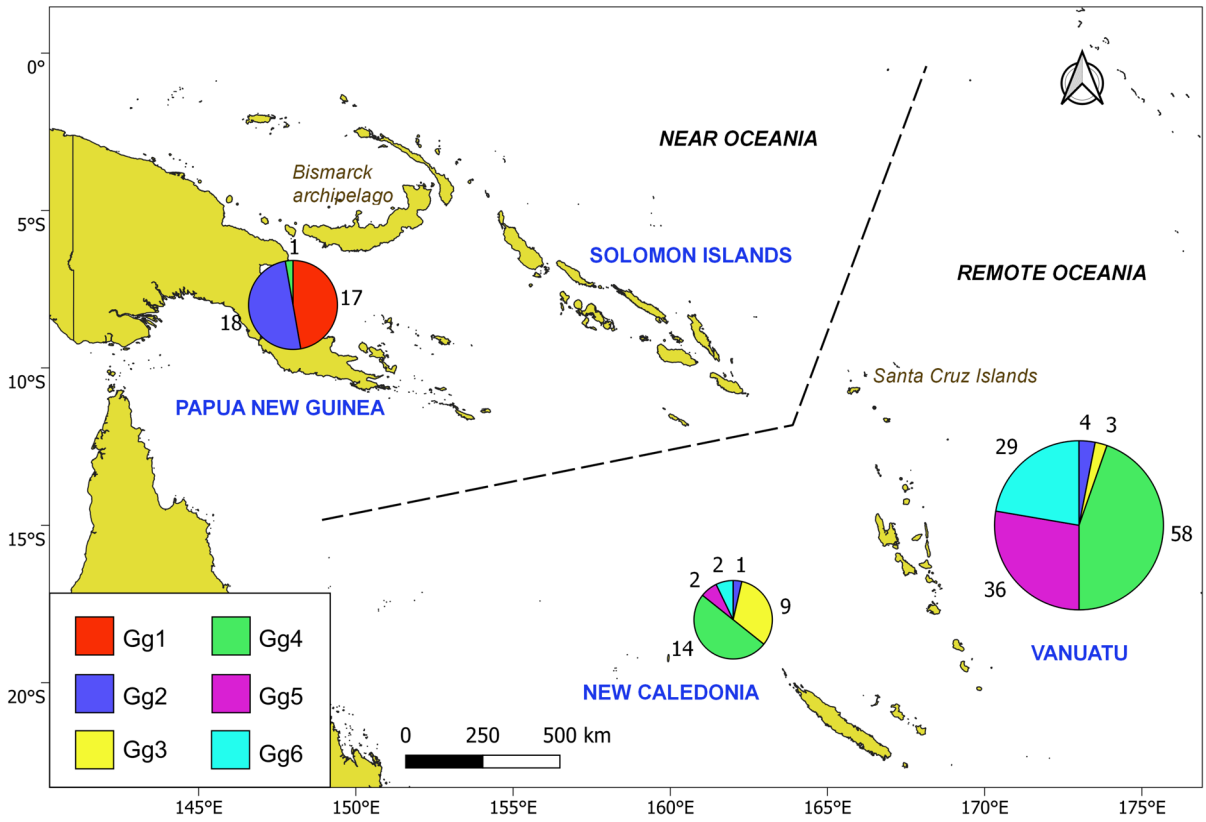


Fig. 4 Map of Southwest Pacific. Distribution of multilocus genotypes (MLGs) by genetic group and country of collection. The two MLGs of French Polynesia are not shown. The dash line marks the limit between Near Oceania and Remote Oceania, as defined by Green (1991)

arbitrarily defined admixed individuals as those with no more than a 90% probability of belonging to a single group. Most MLGs from Papua New Guinea belonged to a single group: Gg1 or Gg2. Group Gg1 appeared to be specific to this country. We found only four admixed MLGs, all of them between the groups Gg1 and Gg2, except the accession LAL207 (74% Gg4, 17% Gg2, and 1% Gg1). Among the 28 MLGs from New Caledonia, 13 (46%) were admixed (mainly between groups Gg3 and Gg4). One accession NCL007 was assigned to group Gg2 (93%). Among the 130 MLGs from Vanuatu, 45 (35%) were admixed (mainly between groups Gg4, Gg5, and Gg6). The accession PYF-AM2 from French Polynesia was assigned to group Gg3 (93%), while PYF-AM1 was admixed (83% Gg2 and 16% Gg4).

Allelic diversity per genetic group and per country

The number of observed alleles per locus and other diversity parameters were calculated per genetic group (Table 4) and per country (Table 5), the two accessions from French Polynesia being excluded due to insufficient sample size (see data per locus in Supp. Inf. 2, Tables S5 and S6a). The average number of observed alleles (*A*), calculated across the 214 samples and the 21 loci, was 8.86. Despite its small sample size, Papua New Guinea exhibited the greatest genetic diversity, as indicated by higher values for the average number of observed alleles *A*, allelic richness *Ar*, expected heterozygosity *Hexp* and the number of private alleles. There were no significant differences in *Ar* and *Hexp* between New Caledonia and Vanuatu, despite the different sample sizes (35 accessions against 138 accessions, respectively) (see comparison tests in Supp. Inf. 2, Table S6b,c).

Table 4 Allelic diversity parameters per genetic group calculated across 214 accessions and the 21 loci, French Polynesia accessions excluded

	Genetic groups						
	Gg1	Gg2	Gg3	Gg4	Gg5	Gg6	Overall
Number of diploid accessions (*N*)	19	27	15	79	39	35	214
Number of multilocus genotypes (*MLG*)	17	23	12	73	38	31	194
MLG:N	0.89	0.85	0.80	0.92	0.97	0.89	0.91
Average number of observed alleles (*A*)	5.43	4.95	3.19	5.67	4.43	3.76	8.86
Average allelic richness (*Ar*)	5.00	4.19	3.13	3.67	3.45	3.14	
Average *Hexp*	0.63	0.52	0.42	0.46	0.42	0.45	0.53
Number of private alleles	28	9	5	9	1	3	

Table 5 Allelic diversity parameters per country, calculated across the 214 accessions and the 21 loci, French Polynesia accessions excluded

Values with the same superscript letter are not significantly different ($\alpha = 0.05$)

	Country			
	PNG	NCL	VUT	Overall
Number of diploid accessions (*N*)	41	35	138	214
Number of multilocus genotypes (*MLG*)	36	28	130	194
MLG:N	0.88	0.80	0.94	0.91
Average number of observed alleles (*A*)	6.90	4.71	5.57	8.86
Average allelic richness (*Ar*)	6.584^{A}	4.686^{B}	4.349^{B}	
Average *Hexp*	0.613^{a}	0.507^{b}	0.464^{b}	
Number of private alleles	47	12	21	

Heterozygosity observed (*Ho*), heterozygosity expected (*Hexp*) and inbreeding coefficients (*Fis*) were calculated per locus and per country (see Supp. Inf. 2, Table S7). Significant differences were observed between countries for the same locus and between the 21 loci within each country. In Vanuatu, *Fis* values ranged from close to zero ($Fis = -0.049$ for AmCir5534) to 0.475 for AmCir1965. Most loci had positive *Fis* values, which are consistent with a deficit in heterozygotes relative to the Hardy Weinberg equilibrium. Conversely, a majority of loci in New Caledonia accessions exhibited negative *Fis* values, revealing an excess of heterozygotes.

Diversity within Vanuatu

Using the same methods, we analysed the genotyping data from Vanuatu by distinguishing between the main geographical areas of collection (North, Centre and South). The geographical distribution of 130 MLGs from Vanuatu is presented on the map of the country (Fig. 5).

In the north, 66.1% of the MLGs belonged to the group Gg4, 30.7% to Gg5, and 3.2% to Gg6; the groups Gg2 and Gg3 were not represented. Gg6 was predominant in central Vanuatu (59.4%) followed by Gg5 (21.6%) and Gg4 (16.2%). In the south, the distribution of the MLGs was the most balanced with all the groups represented, including Gg2 which is also found in Papua New Guinea. The 12 seedlings found in VARTC fields, whose parental origins are unknown, were classified into the groups Gg4 (the most represented with 41.6% of the MLGs), Gg2, Gg5, and Gg6. Membership probability to genetic groups and admixed accessions obtained from DAPC are presented in Supp. Inf. 2, Fig. S4b. The proportion of admixed MLGs is higher in the South (52.6%) compared to the North (33.8%) and the Centre (27.0%).

Allelic diversity parameters per geographical area of Vanuatu are presented in Table 6 (see data per locus in Supp. Inf. 2, Table S8a). The 12 seedlings collected in VARTC fields were not included. There were no significant differences in average allelic richness and *Hexp* between the geographical

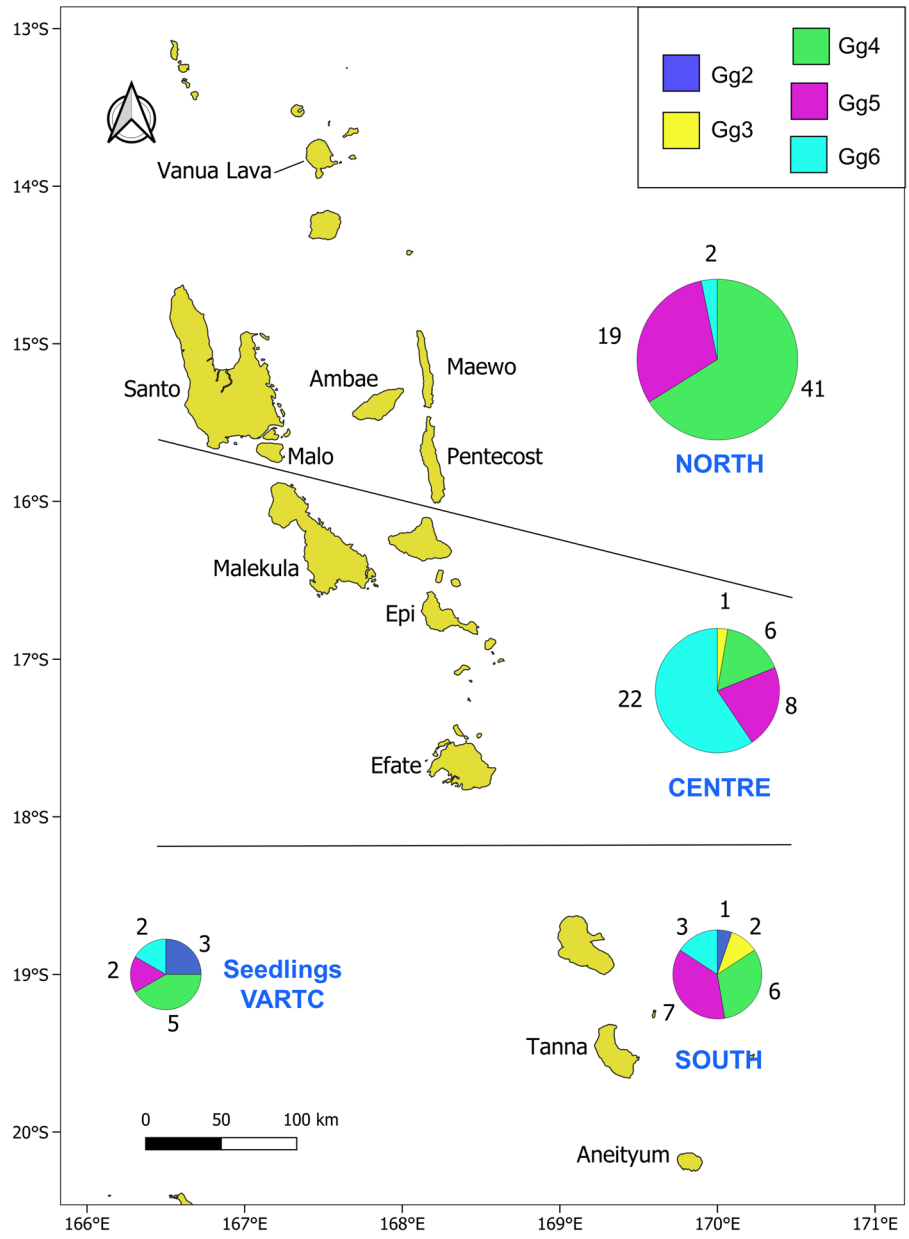


Fig. 5 Map of Vanuatu. Distribution of MLGs by genetic group and main geographical area. The names of geographical areas are in blue and of the islands of collection in black. The seedlings collected in Vanuatu Agricultural Research and Technical Centre (VARTC) fields have unknown parental origins

areas of Vanuatu (see comparison tests in Supp. Inf. 2, Table S8b, c). However, we found that the Central region hosted the highest number of private alleles.

Morphological traits

Descriptive statistics

The morphological traits of the 76 accessions of VARTC genebank were characterized three months after planting. The basic statistical results for the four quantitative descriptors are presented in Table 7. Only one significant and positive correlation ($r_s = 0.438$) was observed between petiole length and leaf width. The frequency distributions are illustrated by histograms for quantitative traits (Fig. 6) and by bar graphs for qualitative traits (Fig. 7).

Most of the accessions in the collection exhibited dark green (42%) or light green leaves (37%). However, nine other colours or combinations of two

Table 6 Allelic diversity parameters per main geographical area of Vanuatu, calculated across the 21 loci on 126 accessions from Vanuatu, 12 seedlings collected in Vanuatu Agricultural Research and Technical Centre (VARTC) fields not included

	Vanuatu		
	North	Centre	South
Number of diploid accessions (*N*)	65	41	20
Number of MLGs (*MLG*)	62	37	19
MLG:N	0.95	0.90	0.95
Average number of observed alleles (*A*)	4.57	4.76	3.62
Average allelic richness (*Ar*)	3.373[A]	3.739[A]	3.497[A]
Average *Hexp*	0.425[a]	0.464[a]	0.476[a]
Number of private alleles	9	13	3

Values with the same superscript letter are not significantly different ($\alpha = 0.05$)

colours were also observed. Leaf dissection ranged from entire (28% of the accessions) to deeply dissected (25%). Accessions with elliptical leaf lobe shape are predominant (55%). The most common stem and petiole colours were light green or dark green with red or pink splashes, though other colours were also observed.

Multiple correspondence analysis and hierarchical clustering

To perform MCA, we retained seven variables: 'Leaf length', 'Leaf width' and 'Petiole length', which were discretised into three intervals per variable; 'Number of lobes' with four modalities (1 Lobe, 3 Lobes, 5 Lobes, and 7 Lobes); and three qualitative traits that farmers use to select and classify their cultivars: 'Leaf colour', 'Petiole colour', and 'Leaf dissection', which were simplified with three or four modalities per trait (see Supp. Inf. 3, Table S9). The seven variables, which characterize the morphological traits, were complemented by the geographical origin as illustrative variable. The 12 accessions collected as seedlings in the VARTC fields were not included in the MCA.

The results of the MCA are presented in Supp. Inf. 3, Figs. S4–S6. No particular characteristic was associated with a geographical origin (Fig. S4). Axis 1, which represented 15.18% of the global variability, was mainly determined by the dimensions of the leaf and the petiole, and axis 2 (12.57% of the variability) by the number of lobes and the level of leaf dissection (Figs. S5 and S6). Similar MCA was conducted with the genetic groups as illustrative variable (data not shown). No discriminant characteristic was associated with a genetic group.

From the MCA results, a dendrogram was generated and five clusters were selected (Fig. 8). The characteristics that had the greatest discriminatory power in classifying accessions into clusters were, in order: 'Number of lobes', 'Leaf dissection', 'Leaf colour', 'Leaf length', 'Petiole colour', and 'Leaf width' (Supp. Inf. 3, Table S10). Table 8 provides a description of the main traits of each cluster, with a picture of a typical leaf.

Discussion

Regional study

We started the study with the assessment of genetic diversity of *A. manihot* germplasm collected from the genebanks of three Western Pacific countries. Two additional samples from French Polynesia were also included. The 21 microsatellite markers developed by Rivallan et al. (2026) proved to be sufficiently polymorphic to distinguish between a large number of accessions, regardless of their origin. Using the

Table 7 Descriptive statistics for four quantitative morphological traits in 76 *Abelmoschus manihot* accessions from Vanuatu (measurements made three months after planting)

Statistic parameters	Petiole length (cm)	Number of lobes	Leaf length (cm)	Leaf width (cm)
Minimum	3.67	1.00	5.62	3.33
Maximum	26.17	7.00	36.33	23.33
Median	14.00	5.00	20.00	13.83
Mean	14.63	4.21	20.35	13.65
Standard deviation	4.34	2.17	5.67	4.24

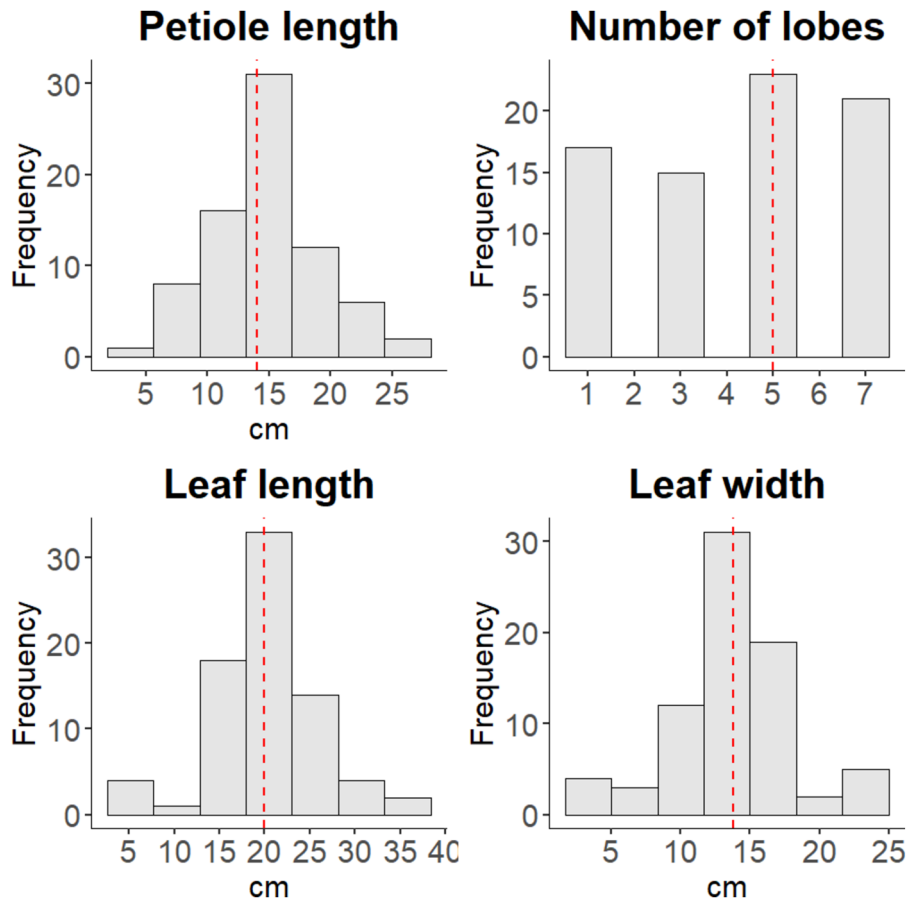


Fig. 6 Frequency distribution of four quantitative traits of 76 accessions from Vanuatu. The median is represented by the red broken line

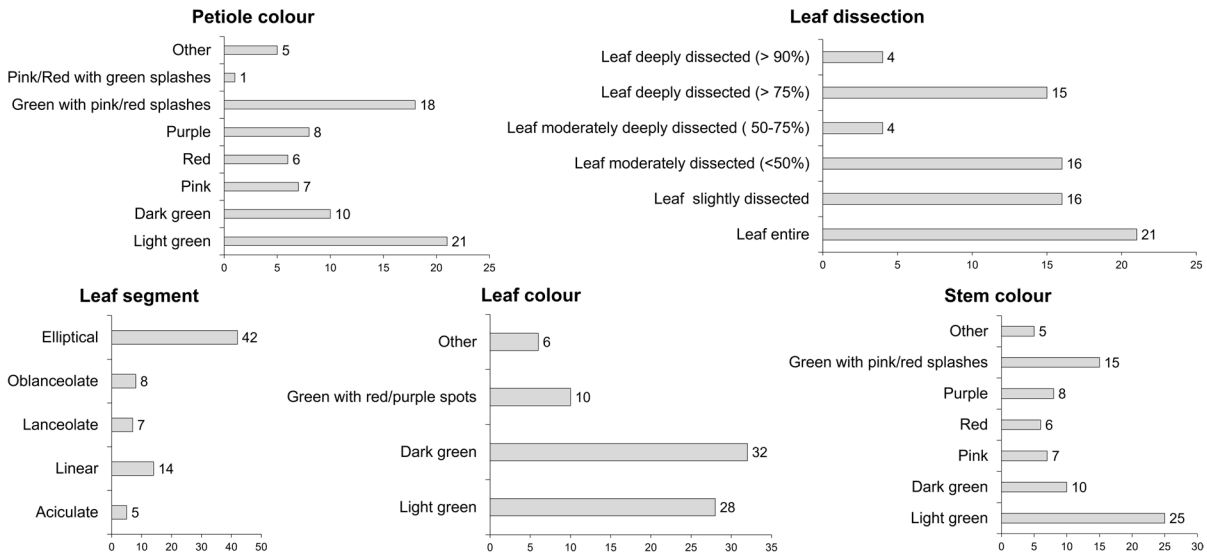


Fig. 7 Frequency distribution of five major qualitative traits observed on the 76 accessions of Vanuatu

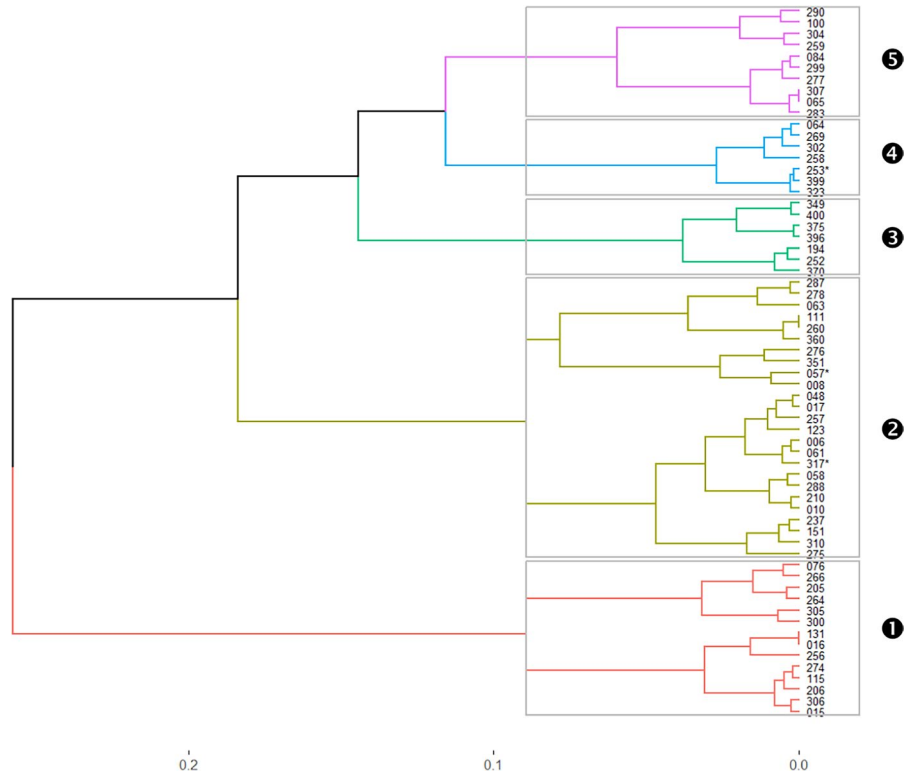


Fig. 8 Dendrogram of hierarchical clustering generated from the results of multiple correspondence analysis of morphological traits. The branches of the five clusters are identified by different colours

Table 8 Description of the main morphological traits of the accessions according to the cluster they belong



Traits	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Number of lobes	1 Lobe***	3–5 Lobes*	n.d	5 Lobes*	7 Lobes***
Leaf dissection	Entire***	Slightly to moderately dissected***	n.d	n.d	Deeply dissected***
Leaf colour	n.d	Two colours*	Red***	Light green*	n.d
Leaf length	n.d	Medium**	Long*	Short**	n.d
Petiole colour	n.d	Two colours*	Red***	Red*	n.d
Leaf width	n.d	Medium*	n.d	Short**	n.d

The modalities that characterize each group are rated according to their discriminant power: *** = highly discriminant; ** = fairly discriminant; * = poorly discriminant; n.d. = not discriminant. For the scale: white bar = 10 cm

K-means clustering method, we classified the accessions into six genetic groups. DAPC method showed that the groups Gg1 and Gg2 were clearly separated from the other ones (Fig. 3). All the accessions from Papua New Guinea were mainly distributed into those two genetic groups, Gg1 being specific to this

country. The accessions from New Caledonia and Vanuatu were mainly distributed within the groups Gg3, Gg4, Gg5, and Gg6.

Of the two accessions collected in French Polynesia, PYF-AM1 (locally called *bélé vert*) exhibited the following probabilities of membership: 83% to Gg2 and 16% to Gg3. The accession PYF-AM2 (called *bélé rouge*) was classified into the Gg3 group, a group which is much more prevalent in New Caledonia than in Vanuatu (Fig. 4). Both accessions are likely to have been imported from Southwest Pacific countries, as *A. manihot* is not commonly cultivated in French Polynesia, where it is known as *chou kanak*, as it is in New Caledonia, or *bele*, as in Fiji.

Despite a small sample size, the accessions from Papua New Guinea exhibited the highest genetic diversity compared to the ones from New Caledonia and Vanuatu. Such difference can be explained by genetic bottlenecks occurring during the dispersion of the species across the Pacific (Lebot 2002). It is now well established that the occurrence and diversity of crops in the Pacific are closely linked to the ancient migrations of small populations travelling eastward from Near Oceania (New Guinea and northern Solomon Islands) (Fig. 4). These Austronesian seafarers reached Remote Oceania via the Santa Cruz Islands, an archipelago north of Vanuatu, about 3200 years ago (Kirch 1997). They brought with them a number of staple crops under the form of propagules (suckers, corms, rhizomes, tubers) that had been domesticated in Southeast Asia and Near Oceania (Gosden 1992; Yen 1993; Lebot 1999). They established the Lapita civilisation during which there were active exchanges between the islands of the Southwest Pacific, from the Bismarck Archipelago to New Caledonia in the south and to Tonga and Samoa further east. Successive waves of Papuan populations followed about 2300 years ago, settling in the islands of Vanuatu, New Caledonia and Fiji (Skoglund et al. 2016). The consequence is that genetic variability across the Pacific decreases from west to east. This has been demonstrated for several cultivated species that exhibit a narrow genetic base in Remote Oceania. Examples include taro *Colocasia esculenta* (L.) Schott (Lebot and Aradhya 1991; Kreike et al. 2004), bananas and plantains *Musa spp*. (Kagy et al. 2016; Thomson et al. 2022), and breadfruit (Ragone 1997; Zerega et al. 2004).

Aibika is typically propagated by farmers using stem fragments stuck into the ground, a simple method that has proven effective in achieving high recovery rates and facilitating rapid leaf harvesting. If clonal propagation were the only method employed, one would expect a small number of distinct MLGs. However, in the three Melanesian countries that were sampled, high *MLG:N* ratios were observed with an average of 0.91 (Table 5). In general, farmers do not allow their aibika plants to grow until flowering and fruit setting, but this can occur in neglected plots and sometimes in cultivated fields. Similar to okra, *A. manihot* is primarily self-pollinating, but cross-pollination by insects can also occur, resulting in the production of fertile seeds (Tyagi 2002). Such high *MLG:N* ratios, as well as a high percentage of admixed accessions (particularly in New Caledonia and Vanuatu), support the assumption that farmers commonly gather cuttings from aibika seedlings. Another reason for farmers to use seedlings is that they tend to be more vigorous than their clones, which may have accumulated viruses and fungal diseases over many generations of cloning.

In addition to sexual recombination, somatic mutation is another source of morphological variation. In branching plants, bud sports differing in foliage shape or colour, or branch structure may appear from apical or axillary meristems (Schoen and Schultz 2019). Whether the plants are grown from seed or sports, if they exhibit novel morphological or organoleptic characteristics, they can be selected by farmers and propagated by cuttings. The advantages of a mixed clonal/sexual reproductive system were presented by McKey et al. (2012). Such process combining sexual reproduction and clonal propagation has been already observed in Vanuatu for taro *Colocasia esculenta* (L.) Schott (Caillon et al. 2006; Sardos et al. 2012; Vandenbroucke et al. 2016), breadfruit *Artocarpus altilis* (Parkinson) Fosberg (Walter 1989; Kaoh et al. 2026), Pacific yam *Dioscorea nummularia* Lam. (Lebot et al. 2017), and cassava *Manihot esculenta* Cranz (Sardos et al. 2008).

Estimations of inbreeding coefficient (*Fis*) per country and per locus (Supp. Inf. 2, Table S7) revealed significant differences between countries, with Vanuatu showing a deficit in heterozygotes and New Caledonia showing an excess. This difference might be a response to photoperiod, as it was observed on okra *A. esculentus* (Tenga and Ormrod

1985; Yao et al. 2025). The variation in periods of light and darkness is more pronounced in New Caledonia (average latitude of 21° S) than in Vanuatu (17° S), which could lead to more frequent flowering in fallow fields when aibika plants are not rejuvenated by frequent harvesting and to a higher rate of outcrossing. In each country, significant differences in the value of *Fis* were also found between loci. This heterogeneity may be due to different human or environmental selection pressures acting on traits determined by distinct loci.

Vanuatu germplasm

The sampling strategy used to compose the VARTC germplasm collection aimed at capturing *A. manihot* diversity across the Vanuatu archipelago, spanning from Vanua Lava in the north to Aneityum in the south. However, it is important to note that the survey was not exhaustive, as only 38 villages, on eleven of the 65 inhabited islands, were included. Another limitation of the study is the unbalanced sampling within the country. For example, in the north, Santo, the Vanuatu's largest island with an area of around 4000 km^2, is represented by only 19 genotyped samples. In contrast, in the centre, Malekula (2000 km^2) is represented by four samples, while Epi (444 km^2) is represented by 36 samples (Table 1). Consequently, one should be careful when making conclusions from the examination of morphological and genetic information based on the geographical origin of the cultivars.

The results of genotyping with 21 microsatellites on 138 diploid accessions from Vanuatu showed that there was an average of 5.57 alleles per locus (Table 5). Allelic richness and expected heterozygosity were lower than in Papua New Guinea, but not significantly different from those in New Caledonia. No significant differences were observed for these parameters between the three main geographical areas of the Vanuatu archipelago.

However, the distribution of genetic groups varies greatly within the country. The group Gg6 was predominant in the Centre (59.4%) but represented only 2.7% of the MLGs in the North. The group Gg3 was absent in the North and rare in the Centre (2.7%), but it represented 10.5% of the MLGs in the South Vanuatu and 32.1% in New Caledonia. This situation could be explained by the geographical proximity of New Caledonia to southern Vanuatu (only 250 km away), which may have facilitated ancient or recent introductions and exchanges between the two areas. The high proportion of admixed accessions in South Vanuatu (52.6% of MLGs) compared to other areas could be a consequence of photoperiodism being more significant in southern latitudes.

Three accessions from Vanuatu had a third allele at one or two loci. Flow cytometric analysis revealed an excess of DNA (+21% on average) compared to diploid controls. True polyploidy (tri- or tetra- ploidy) seems to be ruled out for these three accessions. As a literature review by Charrier (1984) points out, variation in chromosome number is quite common in the *Abelmoschus* genus. Regarding *A. manihot*, Charrier cited chromosome numbers ranging from 60 to 68 according to various authors, but questioned whether this was due to the difficulty of counting a large number of small chromosomes or 'the existence of chromosome races through loss of chromosomes during mitotic divisions'. Tyagi (2002) counted the chromosomes of seven aibika cultivars from Fiji and Papua New Guinea. He found a number between 62 and 66 and stated that 'it is therefore safe to conclude that the 2n (diploid) chromosome numbers in the cultivars was 66'. Further investigations are needed to confirm the genome structure of these atypical cultivars that could be due to aneuploidy (chromosome number that deviates from a multiple of the haploid set), chromosome rearrangement (duplication or translocation of chromosome segments) or even hybridization with another *Abelmoschus* species.

Morphological characterization of 76 accessions from Vanuatu using nine major descriptors revealed significant polymorphism. The shape of the leaves varied from entire to highly dissected. The leaves, petioles and stems displayed a remarkable palette of colours, ranging from white to various shades and tones of green and red (Fig. 7). In a number of cultivars, these organs were bicoloured, in the form of dots or patches, which suggests a chimeric or a genetic mosaic structure (Frank and Chitwood 2016). Such rare cultivars (for example, those of clusters 2 and 5) have always attracted the attention of horticulturalists, who have selected them primarily for their novelty value rather than for their practical use, as it has been observed on other crops, such as taro, by Caillon and Lanouguère-Bruneau (2004, 2005). These authors analysed why rare taro cultivars, which

Vanuatu farmers say are not always high-yielding or particularly tasty, are preserved. In fact, these cultivars enable farmers to differentiate themselves from their peers. They can be given as gifts or exchanged within farmers' social networks (e.g., their family and in-laws). If a cultivar is highly valued, its distribution network may extent throughout the village community, or even across the whole island and beyond.

The farmers give specific names to their aibika cultivars, which correspond to different morphotypes. Of the accessions collected from farmers' fields (Supp. Inf. 1, Table S1a), accessions from VARTC fields excluded, 36.8% have been given a local name that was recorded during the collection process. For that purpose, the farmers use their local languages or Bislama. With 138 vernacular languages spoken by only about 350,000 inhabitants in 2025, Vanuatu has the highest language density in the world (François et al. 2015). One consequence is that when a cultivar is moved from one place to another, it may be given a different name, meaning that the name is not a reliable indicator of a cultivar's identity. A morphological description combined with genotyping analysis is therefore required to better understand the diversity of aibika, distinguish between cultivars and eventually identify true clones and somatic mutants.

Future challenges for conservation and breeding

Climatic and environmental changes are expected to cause considerable damage to the agriculture sector in the Pacific Islands countries, due to an increasing frequency of extreme events such as droughts and cyclones (Lebot 2013; Taylor et al. 2016). Drought reduces the stem growth and the size of the leaves of aibika, and drier weather generally increases attacks from the insect pests. Aibika is also susceptible to a number of diseases, the most significant of which is collar rot, caused by a fungal complex. The main component of this complex is *Phytophthora nicotianae* var. *nicotianae* (McGregor et al. 2016). The incidence and severity of the disease increases in areas with high rainfall and poorly drained soil. Although Pett (1995) observed varietal differences in susceptibility to collar rot, the disease can still cause serious losses in farmers' fields. Germplasm conserved in field genebanks is also at risk of being lost.

Given these climatic and environmental risks, as well as the erosion of traditional farming systems, efforts should be made to conserve and exchange *A. manihot* germplasm, and increase the diversity available for breeding purposes in the Pacific countries. The collection of cultivars should resume and be extended to areas that are still not surveyed. Due to its higher genetic diversity, aibika germplasm from Papua New Guinea has a greater potential for adaptation than that from countries further east, and this country could be a valuable source of genetic material. The germplasm of the Solomon Islands, which lie between Papua New Guinea and Vanuatu, would also be worth studying and could provide additional insight on the diversity within the Southwest Pacific. Since quarantine measures prevent the movement of plant material in vegetative form between countries, the exchange of seeds or in vitro plants should be encouraged (Shandil et al. 2025).

According to the Genesys platform (https://www.genesys-pgr.org), 492 *A. manihot* accessions are currently conserved in genebanks around the world, most of them by the United States Department of Agriculture (USDA, USA). However, this figure does not include accessions conserved in the Pacific Islands field genebanks. In 2012, the Pacific Community organized a regional network on *A. manihot* including Fiji, New Caledonia, Papua New Guinea, the Solomon Islands, and Vanuatu (Tuia et al. 2015). The objectives were to catalog the diversity of the crop in these countries and to establish a core collection of 41 accessions conserved in the first regional in vitro aibika collection at the Centre for Pacific Crops and Trees (CePaCT, Suva, Fiji; https://lrd.spc.int/work-areas/genetic-resources/cepact). According to Genesys, only 23 accessions (nine from New Caledonia, seven from Papua New Guinea, and seven from Vanuatu) are currently conserved in vitro at the CePaCT genebank. Other initiatives are underway to strengthen and expand this collection.

However, the germplasm currently conserved in the field genebanks of the three countries is sufficiently diversified to set up breeding programmes based on controlled pollinations. There are very few publications on intraspecific crossing in *A. manihot*. Tyagi (2002) crossed seven accessions of aibika from Fiji and Papua New Guinea. He found them fully self-compatible, but observed differences in cross compatibility between Fijian and Papuan accessions. Future research should focus on the pollination mechanisms of *A. manihot* to understand its reproductive strategies, including the potential for asynchronous

development of reproductive organs within a single flower that might favour cross-pollination, as well as the degree of autogamy between flowers on the same plant or between clones planted in close proximity. Observations of parents and their offspring obtained through controlled pollination are also likely to provide information on the determinism of some morphological traits.

Furthermore, research should also concentrate on performing genetic analysis with a larger number of markers such as SNPs developed by sequencing. This will enhance our understanding of aibika evolution, genome structure (especially for accessions with non-diploid profiles), and help to detect association with traits of interest (genome-wide association studies GWAS) or with environmental data (genome-environment association analyses).

Conclusion

The current study has revealed a wealth of information about the morphological and genetic diversity of aibika cultivars that are being conserved in the national genebanks of Papua New Guinea, New Caledonia, and Vanuatu. These cultivars should also be evaluated for their productivity, organoleptic and nutritional qualities, and susceptibility to pests and diseases. Strengthening the regional strategy for the conservation and breeding of aibika would be very beneficial to improve this crop, which is neglected at the global level but is vital for maintaining nutritional diversity, improving the diet and livelihood status of Pacific Islands communities.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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