

Chemotype Profiling To Guide Breeders and Explore Traditional Selection of Tropical Root Crops in Vanuatu, South Pacific

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The objectives of the present study were to characterize good-quality cultivars, identify relationships between local eating preferences and primary compound content, and reveal biofortification potential in tropical root crop species aroids, yams, cassava, and sweet potato. A core sample of about 500 cultivars was assembled to represent the widest agro-morphological diversity. Very high coefficients of variation were found within species for proteins, sugars, cellulose, and mineral contents, whereas starch exhibited the lowest variation. Starch content was negatively correlated with other primary compound contents. For the national dish in Vanuatu, consumers prefer cultivars with high starch content. In contrast, preferences for daily consumption of boiled or roasted tubers are linked to average starch content, indicating great potential for improving primary compounds. Interestingly, relationships between flesh color and requirements for the traditional dish were revealed, suggesting opportunities for biofortification. The data produced will assist breeders in adopting appropriate biofortification strategies.

KEYWORDS: Aroids; biofortification; cassava; primary compounds; flesh color; sweet potato; yam

INTRODUCTION

In Vanuatu, Melanesia, tropical root crops (aroids, cassava, sweet potato, and yams) are staple foods. Traditional agroforestry systems host other starchy crops such as bananas, plantains (*Musa* sp. L.), and breadfruit (*Artocarpus altilis* L.). Several methods are used to process and cook these foods, including boiling, roasting, and baking on hot stones. In Vanuatu, unlike in other Melanesian and Pacific countries, these starchy foods are processed into traditional *laplap*, which is a pudding-like dish prepared from hand-grated fruits, corms, roots, or tubers. The raw paste is wrapped in *Heliconia indica* leaves (commonly named *lif laplap* in local Pidgin English) and slowly steamed in a ground oven. Although *laplap* is by far the most common preparation, there are variants such as *bougna*, for which rough pieces are cooked in a ground oven, and *nalot*, for which cooked pieces are pounded to form a sticky paste similar to West African *fufu*. Each of these food preparation methods requires the raw plant material to exhibit specific physicochemical properties, and this is possible thanks to the extraordinary diversity in species and varieties. Producers and consumers alike are unanimous in their appreciation of the potential of specific cultivars for *laplap* or other traditional dishes. However, the chemical bases for such appreciations are unknown, as are traditional means of chemotype selection. This lack of basic knowledge hinders the launching of biofortification programs with appropriate parental clones.

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Most root crop species have been cultivated since ancient times, and their early domestication was followed by constant selection to improve nutritional quality and to subtract some of the wild genetic load often associated with antinutritional factors, such as alkaloids and polyphenols in yams, calcium oxalate and acidity in aroids, and cyanide in cassava. Because these species share common biological traits and are cultivated together in traditional agrosystems, their traditional selection process followed the same steps. We can therefore propose the hypothesis that if all of these species are currently processed into *laplap*, their selection processes were probably biased toward retaining only chemotypes suitable for *laplap*. Because genotypic diversity is regarded as too broad for vegetatively propagated crops, it is assumed that sexual propagation took place during the traditional selection process. Evidence that local farmers sometimes practice unconscious selection on volunteer seedlings has already been reported (1, 2). This kind of traditional practice was most likely used in selecting cultivars for suitable preparation of *laplap*.

With the population doubling every 25 years in Vanuatu, population growth and urban drift are responsible for significant urban development, which also raises food security issues. Improving the nutritional value of the staples through breeding is thus a priority. There is also a need to speed the preparation process of *laplap* so that the demand of urban populations can be satisfied with modern quality products. An excellent *laplap* can be directly prepared from easy-to-store and ready-to-use finely ground complete flours, which, when mixed with water, are used to prepare a paste wrapped in *lif laplap* (*H. indica* leaves) and

cooked in a casserole dish (3). Flours made from root crops have a longer shelf life, and their transport is cheaper than that of fresh products.

Crop improvement and breeding strategies depend on the existence of genetic variation for the targeted traits. Molecular markers have been developed to estimate the genetic diversity of some germplasm collections of sweet potato (*Ipomoea batatas* L.) and cassava (*Manihot esculenta* Crantz) (4, 5). However, no genetic marker is known to be linked to crop quality and, in Vanuatu, taro (*Colocasia esculenta* Schott) and the greater yam (*Dioscorea alata* L.) are the most widely consumed crops. Another relevant experimental approach is to characterize variations in chemotypes as they are the most important traits that parents should present, especially for breeding programs aimed at improving quality. As parents and hybrids are selected on their per se value, characterization of chemical content plays a key role in breeding programs. To increase the occurrence of outstanding hybrids, choosing parents with the most valuable traits is crucial. The most comprehensive study that provided an overview of chemical composition of tropical root crop species was conducted in the Pacific (6). A similar work on yam species was carried out (7) in Africa. However, these studies dealt with cultivars from different geographic origins grown in very different places, making comparisons somewhat difficult.

The aims of the present study were to (i) characterize chemotype variations between and within root crop species, (ii) identify relationships among primary compounds and between primary compound content and flesh color, (iii) define consumer preferences for a good quality *laplap*, and (iv) produce relevant data to assist breeders during the selection of parents and progenies.

MATERIALS AND METHODS

Germplasm and Growing Conditions. All accessions were grown in the same field at VARTC (the Vanuatu Agricultural Research and Technical Centre, Espiritu Santo, 15° 23' S and 166° 51' E) to minimize variations due to environmental factors. They were grown at the same time (one season), and their storage organs were harvested when fully mature to limit differences due to ontogeny. Except for this special care, no particular experimental design was used to grow the accessions, and this was possibly a slight source of error. Germplasm mainly originated from Vanuatu but also included cultivars from various Southeast Asian countries and hybrids produced for breeding purposes.

Cultivars. Traditional knowledge of local accessions was recorded during interviews with farmers. Blind panel tests were conducted in a previous study to assess eating quality according to traditional preferences and knowledge (3). The results were recorded in the germplasm database. To reinforce this assessment, accessions have been evaluated in VARTC every year since 1998, and taste ratings have also been recorded.

Sampling Strategy and Preparation. Throughout this paper, "cultivars" refers to varieties that are commonly grown and consumed, whereas "hybrids" are new varieties still under evaluation. A core sample was assembled to cover the broadest range of agro-morphological variation and geographical origins. The core sample contained 11 different species, including *C. esculenta* (111 accessions, including 66 cultivars and 45 hybrids obtained by polycross), *Xanthosoma sagittifolium* (9 accessions), *D. alata* (93 accessions), *Dioscorea cayenensis-rotundata* (7 accessions), *Dioscorea esculenta* (13 accessions), *Dioscorea nummularia* (4 accessions), *Dioscorea transversa* (9 accessions), *Dioscorea pentaphylla* (3 accessions), *Dioscorea bulbifera* (6 accessions), unidentified *Dioscorea* (3 accessions), *M. esculenta* (63 accessions), and *I. batatas* (183 accessions, including 37 cultivars and 146 hybrids obtained by polycross). The complete edible part of underground storage organs (one or two depending on accession availability and yield) from a single plant of 505 accessions was peeled, washed, dried with a clean towel, hand-grated, and dried in a ventilated oven at 60 °C until constant weight. The dried powders were then placed in paper bags and stored in a dry place until analysis.

Table 1. Number of Local Cultivars Rated for *Laplap* Preparation

species	cultivars	good	average	poor
<i>Colocasia esculenta</i>	45	27	2	0
<i>Xanthosoma sagittifolium</i>	9	9	0	0
<i>Dioscorea alata</i>	77	5	3	3
<i>D. cayenensis-rotundata</i>	7	7	0	0
<i>D. bulbifera</i>	6	0	0	6
<i>D. esculenta</i>	14	0	0	14
<i>D. nummularia</i>	4	4	0	0
<i>D. pentaphylla</i>	3	0	0	1
<i>D. transversa</i>	9	9	0	0
<i>Dioscorea</i> spp.	3	3	0	0
<i>Ipomoea batatas</i>	37	0	0	37
<i>Manihot esculenta</i>	63	63	0	0
total	277	127	5	61

Chemical Analysis. Analyses of primary compounds were performed according to AFNOR (French standards association) and/or CEE protocols (8). Samples of about 150 g of dry matter prepared in VARTC (Vanuatu) were sent to France, where residual moisture, starch, sugars, proteins, minerals and cellulose were quantified. Following NF (Norme Française) V 18-109 for dry matter determination (8), samples of powder were dried again in an air oven to remove residual moisture and then analyzed on a dry matter basis. Mineral contents (8) were estimated from ash produced at 550 °C (NF V 18-101). Crude cellulose (8) was measured using Weende's method (NF V 03-040) of quantification of non-water-soluble organic residue after sulfuric acid and alkaline treatments. Protein content (8) was measured using the Kjeldahl method (NF V 18-100) of quantification of total nitrogen ($N \times 6.25$). After starch extraction, reducing sugars were estimated using the standard iodometric method of Luff Schoorl (CEE 98/54/CE). Starch (8) was quantified using the Ewers protocol (NF ISO 10-520) based on the hydrolysis in HCl, filtration, and polarimetric measurement. All measurements are expressed in percentages of dry matter (DM).

Color Assessment. A color code ranging from 1 to 7 was attributed to each storage organ at harvest. Colors were assessed visually. The flesh color observed at the central portion of the organ (corm, cormels, roots, and/or tubers) was coded as follows: 1 = white, 2 = yellow, 3 = orange, 4 = pink, 5 = red, 6 = reddish, 7 = purple, and 8 = multicolored (e.g., yellow-purple two-colored).

Data Analyses. A database was created containing the primary compound contents, morphological description, traditional uses, and eating quality indices for each cultivar. To increase the reliability of the results, data on similar species were pooled. Consequently, aroids include *C. esculenta* and *Xanthosoma sagittifolium* accessions, and yams include all *Dioscorea* species. For statistical analyses, coefficients of variation (CV) of the mean were calculated to provide a normalized estimate of the dispersion of a probability distribution (expressed as a percentage). Principal component analysis (PCA) and linear correlations were performed with the free open source software environment for data analysis and graphics, R version v2.9.0 (9) and the "RcmdrPlugin.FactoMineR" and "ade4TkGUI" packages with mean-centered data scaled to unit variance. Relationships between primary compounds, visually determined flesh color codes, and quality were estimated by calculating Pearson's product-moment correlations. Significance was determined using Student's *t* test.

RESULTS AND DISCUSSION

Traditional Knowledge. According to farmers and consumers, some traditional cultivars are suitable for *laplap* preparation, whereas others are not. **Table 1** lists the local cultivars (excluding introduced varieties and hybrids) that are considered to be good, average, or poor for *laplap*. The statements are based on hedonic tests related to food organoleptic properties (3). All cultivars of *D. bulbifera*, *D. esculenta*, and *I. batatas* are considered to be "poor" sources for *laplap*. As a result, these species are never used to prepare the Vanuatu national dish. Although farmers and

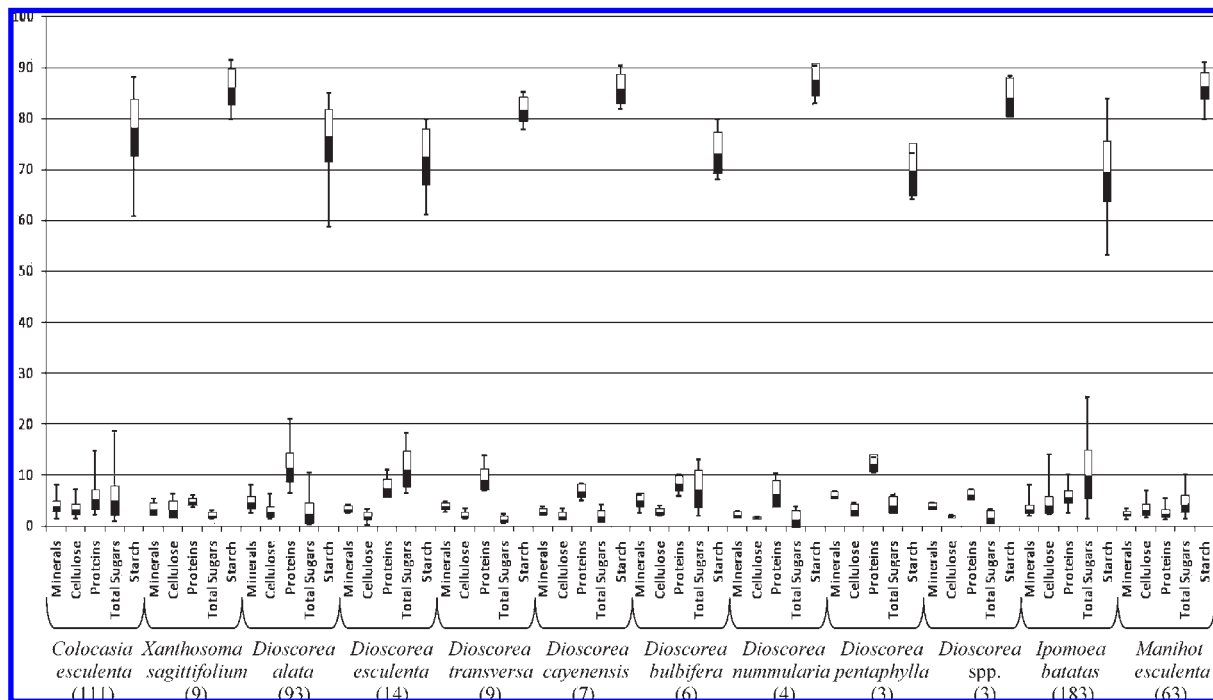


Figure 1. Variation in primary compounds represented by the minimum–maximum intervals and expressed as percentages of dry matter (vertical lines). The box represents the standard deviation around the mean, the upper limit (white area), and the lower limit (black). Below the species names is the core sample size.

consumers unanimously agree the species are not suitable, they cannot explain why.

The two species with the most ancient cultivation history in Vanuatu are *C. esculenta* and *D. alata*. They were introduced by the first settlers ca. 3000 BP and are also the two most prestigious species with the greatest number of different cultivars. Significant genetic variation has been documented (1, 10–13), and variation exists for quality. Previous studies already reported local organoleptic preferences for *laplap* and showed how they differ from species used for other cooking methods (3). This kind of home-made pudding requires firmness and elasticity to produce a texture that is considered by every consumer to be excellent.

Interspecific Variation of Primary Compounds. Starch. The highest starch contents were found in *M. esculenta* and *X. sagittifolium*, with 91.2 and 91.5% of DM, respectively (Figure 1), and the lowest maxima were found in the yam species, *D. esculenta*, *D. bulbifera*, and *D. pentaphylla*. Among yam species, *D. nummularia* and *D. cayenensis-rotundata* showed the highest values, which were far above the others. *I. batatas* displayed the lowest minimum starch content with only 53.3% of DM, whereas *D. cayenensis-rotundata* and *D. nummularia* showed the highest minimum. Regarding the minimum–maximum (min–max) intervals for starch (Figure 1), a wide range was observed among *I. batatas*, taro, and *D. alata*, with correspondingly high standard deviations (SD) of 5.9, 5.6, and 5.2, respectively. The lowest min–max intervals were observed in *D. nummularia* and *D. transversa*. This is probably linked to the small sample size and limited genetic diversity of these two species. These values are similar to those found in 98 accessions from Cameroon (representing 8 yam species), except for *D. cayenensis-rotundata* and *D. esculenta* (14), the starch contents of which were lower than ours. Lower starch contents were found in 65 *Dioscorea* spp. accessions from southern Ethiopia (15). Nigerian *D. alata* accessions from the IITA (International Institute for Tropical Agriculture) yam breeding program were also reported to display lower maximum DM (74.4%) (16).

Sugars. The highest amounts of total reducing sugars were found in *I. batatas*, with 25.3% of DM, whereas the lowest maximum contents were found in *Dioscorea* spp. and *D. transversa*. As expected, *D. esculenta*, also called “sweet yam”, had the highest maximum sugar content among yam species. The lowest minimum contents were observed in *D. alata* and *D. nummularia* and the highest in *D. bulbifera*, *D. pentaphylla*, and, not surprisingly, *D. esculenta*. Thus, *D. bulbifera* and *D. esculenta* accessions differed greatly with respective standard deviations of 3.7 and 3.6. In *D. transversa* and *X. sagittifolium*, sugars varied only slightly, perhaps due to sampling size. In taro accessions from Vanuatu, variations were extremely high, with values ranging from 0.9 to 18.6% of DM; however, the SD was only 2.9. Some African accessions (7) exhibited maximum contents that were almost half of ours. Our *D. alata* accessions showed a remarkable maximum sugar content, twice as high as that observed previously (11), but equivalent to values observed in Nigerian accessions (16). However, the 48 accessions in the core sample previously studied (11) were selected to represent the range of variation for eating quality, among other traits. Previous surveys (14) also reported maximum sugar contents in *D. bulbifera* and *D. esculenta* that were clearly lower than those observed in the present study. Previously reported maximum sugar contents (17) were almost twice as high as those observed in Vanuatu.

Proteins. The highest total protein content (21.0% of DM) was found in a *D. alata* accession and was about 3 times higher than any other *Dioscoreaceae*. The lowest contents were also found in an accession of this species with 6.5% of DM. Taro had a high maximum (14.8% of DM), whereas *M. esculenta* and *X. sagittifolium* had the lowest protein maximum contents, 5.6 and 6.2% of DM, respectively. These findings agree with observed SD. Indeed, *D. alata* showed a relatively high SD of 2.9, whereas *M. esculenta* and *X. sagittifolium* showed the lowest SD values of 0.8 and 0.7. The highest minimum contents were found in yam species, especially in *D. pentaphylla*, *D. transversa*, and *D. alata*, and the lowest were found in *M. esculenta* and taro

(Figure 1). In terms of variation illustrated by the min–max interval (Figure 1), extensive ranges were observed for the two most widely consumed species in Vanuatu, *D. alata* and *C. esculenta*. Previously reported protein contents of seven *D. alata* accessions in Ivory Coast (18) showed maximum contents well below ours. Similarly, in 131 *D. alata* accessions from New Caledonia (19), maximum contents were twice lower than ours. However, these authors sun-dried their samples, which could explain their low values. Also, low maximum contents (8.7%) were previously reported in Nigerian *D. alata* accessions (16). In comparison, 65 *Dioscorea* spp. accessions from southern Ethiopia showed lower protein contents (15). Maximum contents observed in *D. bulbifera* and *D. esculenta* were higher than those previously reported for our accessions (14). Our data indicate that Samoan taro (20) contains less protein than Vanuatu's. Previous study on several hundred accessions of *I. batatas* (21) found maximum protein contents similar to ours (10.1% of DM). Work on *M. esculenta* previously suggested the existence of significant genetic variation in protein content (17). Variation in crude protein content reached the highest level ever recorded in a cultivar from Colombia, with 6.42% of DM, and the lowest level in an accession from Thailand, with 0.95% of DM (22). The min–max range of 1.3–5.6% of DM observed in our cultivars from the VARTC collection was equivalent.

Minerals. Highest maximum total mineral contents were found in *I. batatas*, taro, and *D. alata*, with about 8.2% of DM. The highest variation (min–max interval) paralleled these high maxima. *M. esculenta* and *D. nummularia* showed the lowest maximum contents, 1.2 and 1.6% of DM, respectively, and these two species also showed the lowest minimum contents. The highest SD was found in *D. alata* and the lowest in *M. esculenta*. Our 111 taro accessions (Figure 1) showed a maximum mineral content of 8.1% versus 6.0% (10) or 4.4% (20) in previous studies. *D. alata* accession maximum contents were reported as almost half below ours (16). Varieties studied in Ivory Coast were found to have maximum contents well below ours (18). Similarly, in 131 *D. alata* from New Caledonia (19) were described maximum contents twice as low as ours. Differences in cultivars may explain these differences.

Cellulose. Maximum cellulose contents were found for *I. batatas* (14.0% of DM), far above those of species such as *C. esculenta* (7.3% of DM). The lowest maximum contents were found in yam *D. nummularia*, *Dioscorea* spp., and *D. esculenta*, with 1.4, 1.8, and 0.1% of DM, respectively. Similar trends were observed for minimum cellulose contents, the highest minimum contents being recorded in *I. batatas* and the lowest in *D. nummularia* and *D. esculenta*. Again, *D. alata* had the highest cellulose fiber contents, up to 3 times higher than those of other *Dioscorea* species.

Dry Matter. Dry matter in *I. batatas* was in the upper range of previously reported values (21). A survey conducted on 2500 *M. esculenta* accessions from the CIAT international collection (17) reported an average dry matter content (34.3%) that is slightly higher than ours (33.2% of fresh matter).

Intraspecific Variation of Primary Compounds. **Yams.** Average starch content was the highest in *D. nummularia* (87.7% of DM). Other yam species, *D. cayenensis-rotundata*, *Dioscorea* spp., and *D. transversa*, had high-range means and *D. bulbifera*, *D. esculenta*, and *D. pentaphylla* had low-range means. *D. alata* displayed a midrange mean value of 76.7% of DM for starch content. An extensive range of variation was found in *D. nummularia* and *D. alata* reducing sugar contents, with exceptional CVs of 115.5 and 76.1%, respectively. Moreover, species with low starch content appeared to have high sugar contents. With regard to proteins, *D. pentaphylla* and *D. alata*

exhibited the highest means. The highest CVs were found in *D. nummularia* and *D. alata*, most likely reflecting their genetic diversity.

Aroids. Significant differences in starch contents were observed in *C. esculenta*, the CV of which was among the highest of all genera studied. This suggests major genetic variation in the genetic control of synthesis of primary compounds in our sample. Protein contents varied considerably from 0.9 to 18.6% of DM with a CV of 57.9%. *X. sagittifolium* is another aroid crop that is widely used for the preparation of *laplap*. It exhibited relatively low CVs for most primary compounds we measured, thus indicating a narrow genetic base in Vanuatu. Low CVs were obtained for starch, total sugar, and protein contents, and high CVs were obtained for minerals and cellulose. Major opportunities thus exist for biofortification of mineral content.

Manihot esculenta. Although the mean starch content was high (86.5% of DM), the corresponding CV was very low. For total sugar content, midrange values with high CVs were observed. Mean protein content was low, with high CV (31.5%). In terms of variation in mineral contents, both the mean and the CV were low, thus indicating a limitation for biofortification of *M. esculenta* in Vanuatu. Inversely, cellulose content displayed a high mean and a high CV.

Ipomoea batatas. Average starch content was the lowest among the genera we studied even though its corresponding CV was the highest, in agreement with the great morphological and genetic variability of this accessions in our collection. Total sugar contents had a very high mean and a high CV, 10.2% and 46.7% of DM, respectively. Protein content was among the lowest, and its corresponding CV was in the lower range.

Interspecific and intraspecific variations in Vanuatu are comparable to those observed in previous studies. This is particularly true for the two most widely consumed species (*C. esculenta* and *D. alata*), which show high CVs for most compounds (10, 11, 19). Broad genetic bases are reflected in the chemical expression of genotypes. There is thus potential for biofortification.

Relationships between Chemotype and Quality. All species known to be a good source of cultivars for *laplap* (*M. esculenta*, *X. sagittifolium*, *D. cayenensis-rotundata*, *D. nummularia*, and *D. transversa*) had high starch and low sugar contents. However, in Vanuatu, these four species are not represented by many cultivars. The African Guinea yam (*D. cayenensis-rotundata*) and the American cocoyam (*X. sagittifolium*) were introduced at the beginning of the 20th century, and only a few cultivars are grown, but they are all known to produce good *laplap*. Likewise, the two Melanesian yam species (*D. nummularia* and *D. transversa*) are considered to be the most suitable for the production of *laplap* and, as a matter of fact, this is the only way these species can be prepared. Starch contents of *C. esculenta* and *Dioscorea* spp. were shown to be negatively correlated with total sugar, protein, mineral, and cellulose contents (data not shown). Thus, a good *laplap* should be made with varieties with high dry matter and starch contents and low protein, mineral, and total sugar contents. This was confirmed by the analysis of species chemotypes (Table 2). Sorting species by increasing starch content confirmed their evaluation as “good” or “poor” species. *C. esculenta* and *D. alata* accessions were grouped at the borderline between the two classes, in agreement with local uses. On the other hand, species that are unsuitable for *laplap* (*D. bulbifera*, *D. esculenta*, *I. batatas*) showed low starch and high sugar contents. These results provide a rational, chemical-based definition of what is a “good” species chemotype for *laplap*.

PCA was performed on a data set obtained on 293 accessions using their 5 primary compound contents and their ratings for *laplap* preparation as variables (Figure 2). It distinguished

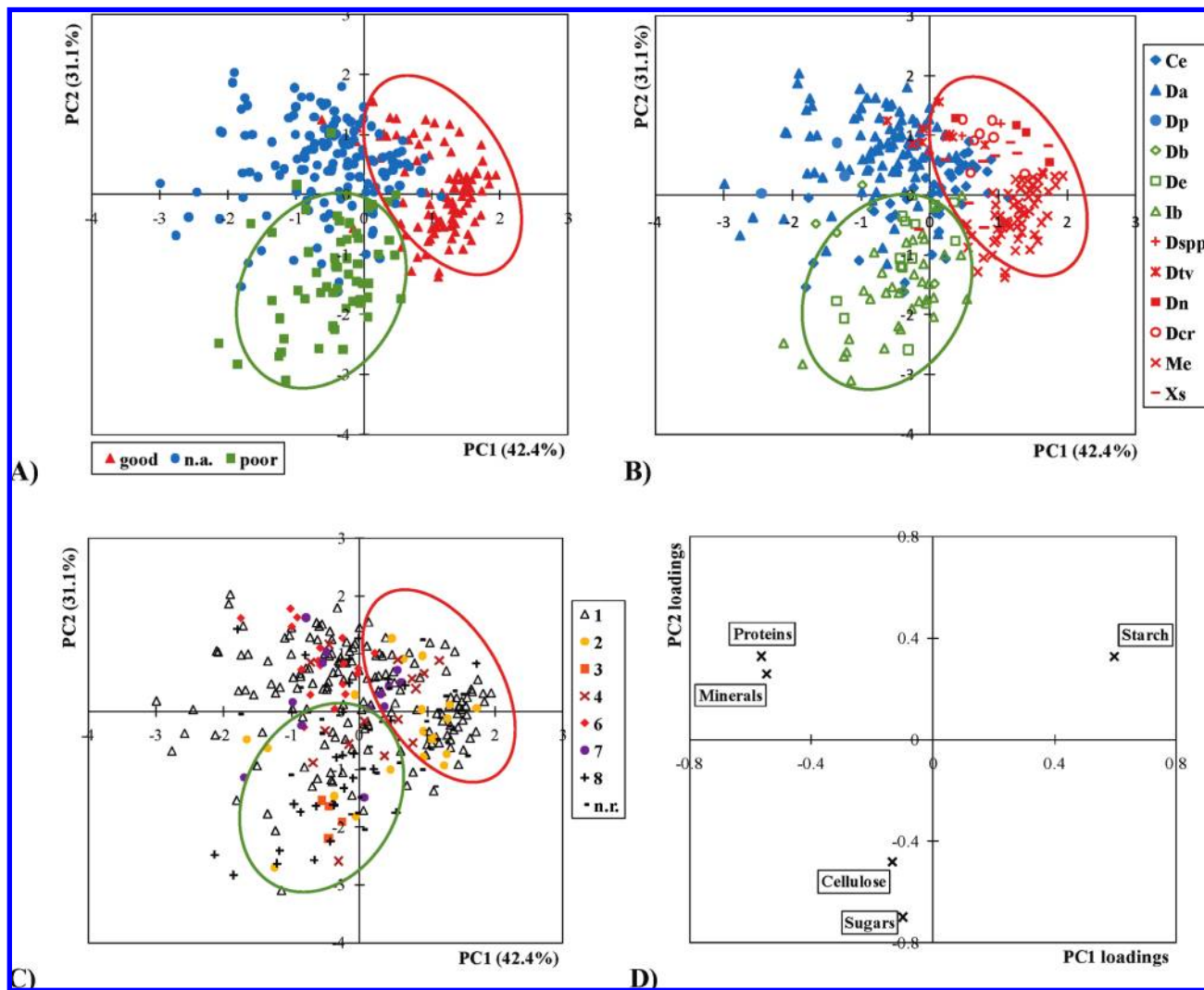


Figure 2. Principal component analysis of 5 primary compounds from 293 local accessions rated for preferences according to local consumers: score plot featured with quality for *laplap* preparation (A), score plot featured by species (B), score plot featured by color assessment (C) and loadings plot (D). Mean-centered data scaled to unit variance were used for PCA. n.a., not available. Species: *C. esculenta* (Ce), *D. alata* (Da), *D. pentaphylla* (Dp), *D. bulbifera* (Db), *D. esculenta* (De), *I. batatas* (Ib), *D. spp.* (Dspp), *D. transversa* (Dtv), *D. nummularia* (Dn), *D. cayenensis-rotundata* (Dcr), *M. esculenta* (Me), and *X. sagittifolium* (Xs). Colors: white (1), yellow (2), orange (3), pink (4), reddish (6), purple (7), two-colored (8), not registered (n.r.).

Table 2. Variation in Primary Compounds within Each Species (in Percent of Dry Matter)

species	accessions (n)	starch		sugars		proteins		minerals		cellulose	
		mean	CV%	mean	CV%	mean	CV%	mean	CV%	mean	CV%
<i>D. nummularia</i>	4	87.7	3.7	1.4	115.5	6.5	40.2	2.3	25.1	1.6	10.9
<i>M. esculenta</i>	63	86.5	3.1	4.4	35.8	3.4	31.5	2.5	18.1	3.4	32.1
<i>X. sagittifolium</i>	9	86.2	4.1	2.2	25.6	4.8	13.7	3.4	34.5	3.3	48.9
<i>D. cayenensis-rotundata</i>	6	85.9	3.4	1.9	64.3	7.1	18.0	3.0	22.2	2.1	34.9
<i>Dioscorea spp.</i>	3	84.1	4.5	1.9	70.7	6.2	16.1	4.0	15.2	1.9	12.0
<i>D. transversa</i>	9	81.9	2.9	1.4	45.9	9.2	21.3	3.9	16.0	2.2	24.7
<i>C. esculenta</i>	111	78.2	7.2	5.1	57.9	5.3	35.7	4.0	25.3	3.4	31.0
<i>D. alata</i>	93	76.7	6.8	2.6	76.1	11.6	24.5	4.7	24.7	2.9	34.8
<i>D. bulbifera</i>	6	73.4	5.5	7.4	50.0	8.5	17.4	5.2	24.7	2.9	22.7
<i>D. esculenta</i>	14	72.5	7.5	11.3	31.7	7.5	22.9	3.4	17.3	2.1	33.5
<i>D. pentaphylla</i>	3	70.1	7.4	4.3	37.8	12.4	13.1	6.1	11.0	3.2	37.5
<i>I. batatas</i>	183	69.6	8.5	10.2	46.7	5.9	21.5	3.5	24.0	4.2	40.8

accessions rated as good and poor (Table 1) on the basis of their suitability for the preparation of an excellent *laplap* (Figure 2A). Despite the fact that the physicochemical characteristics of

I. batatas and *D. esculenta* were usually very different, a few accessions of each species grouped in a similar area of the biplot. This suggests that a slight genetic improvement could lead to their

acceptance by consumers. The two emblematic species, *C. esculenta* and *D. alata*, showed high CVs, corresponding to greater genetic variation, and are known to host good and poor cultivars for *laplap*. This is congruent with the results presented in **Figure 2B**, where some of their accessions are distributed in the two groups.

It is now possible to define a good accession according to these representations. For example, some accessions of *D. alata* and *C. esculenta* were not rated for their culinary quality but were plotted in a given group, suggesting that their rating would have been similar to the average rating of the group concerned. By observing distribution patterns and the position of the mean within its interval of variation (**Figure 1**), additional information can be obtained. With regard to starch, means were located in the upper range of intervals for *C. esculenta*, *M. esculenta*, and *D. alata*, indicating that selection was conducted for high starch contents. However, the mean value of *I. batatas* was in the midrange of the interval. These observations are consistent with traditional uses. On the other hand, mean sugar and protein contents were located in the lower range of their variation intervals for species rated as “good” for *laplap* preparation (*X. sagittifolium*, *M. esculenta*, *D. transversa*, *D. nummularia*, *D. alata*, *C. esculenta*), indicating that selection was mostly conducted for lower sugar and protein contents. Moreover, the two most widely used species, *C. esculenta* and *D. alata*, had the lowest minimum sugar contents of all species studied (**Figure 1**). Because mean values for cellulose appeared in the lower range of the interval of variation for each species, high cellulose content is thought to be a rebuttal factor. These findings agree with the analyses of traditional selection processes and local preferences.

In Vanuatu, local consumers consider that an excellent traditional *laplap* made of yam or *C. esculenta* must be white. Flesh color is determined by the presence of pigments such as anthocyanins, flavonols, and isoprenoids. This visual aspect of the dish can play a crucial role in consumer acceptance. However, the color of the *laplap* is less important when other species, such as *M. esculenta* or *X. sagittifolium*, are used. In **Figure 2C**, the relationships between the color of the raw flesh and the suitability of the cultivar for *laplap* preparation reveal an interesting pattern: every white-fleshed *C. esculenta* was regarded as “good” (except accession CeVU1934). The same was true for pink, reddish, and purple accessions, which were all rated as “good”. All yellow-fleshed *C. esculenta* were plotted at the boundary between the two groups, indicating midrange accessions. Among the white-fleshed *D. alata* accessions, a few were plotted next to “good” or “poor” cultivars, although most were plotted in a separate area of the biplot, thus constituting a separate group. Exactly the same was true of pink, reddish, and purple accessions.

Relationships among Primary Compounds. Linear correlations among physicochemical characteristics of 505 selected cultivars were tested. There were significant negative correlations between starch content and cellulose, mineral, protein, and total sugar contents with 0.01% of significance (**Table 3**). This supports the statement that difficulties will be encountered when attempts are made to improve starch and other components at the same time. However, like total sugar and cellulose contents, mineral and protein contents could be improved together. These findings are based on the whole core sample, plus on *I. batatas* and yam specific data (**Table 3**). The same correlations were obtained for aroids and *M. esculenta*, except that protein and cellulose contents did not correlate with starch content.

With regard to the 183 *I. batatas* accessions, data presented in **Table 3** show an unexpected positive correlation between sugar and protein contents. Because children generally like sweet foods, this correlation is of particular interest. *M. esculenta* exhibits a

Table 3. Simple Linear Correlation Coefficients for Five Major Compounds in Four Root and Tuber Crop Species

species	compounds	starch	sugars	proteins	minerals
aroids 120 accessions ^a	sugars	-0.7388*			
	proteins	-0.1788	-0.0206		
	minerals	-0.6361*	0.2062	0.1490	
	cellulose	-0.5340*	0.2707*	0.0663	0.5483*
yams 139 accessions ^b	sugars	-0.4929*			
	proteins	-0.5781*	-0.2891*		
	minerals	-0.2397*	-0.2365*	0.4221*	
	cellulose	-0.4743*	-0.0420	0.4488*	0.1874
sweet potato 183 accessions ^c	sugars	-0.7559*			
	proteins	-0.5106*	0.2001*		
	minerals	-0.4380*	-0.2615*	0.3453*	
	cellulose	-0.2011*	-0.0225	0.0406	0.1243
cassava 63 accessions ^d	sugars	-0.6945*			
	proteins	-0.3821*	0.1842		
	minerals	-0.5823*	0.4041*	-0.0764	
	cellulose	0.0377	-0.0521	-0.0267	0.0428
overall 505 accessions ^e	sugars	-0.7292*			
	proteins	-0.3096*	-0.1925*		
	minerals	-0.3290*	-0.0684	0.5298*	
	cellulose	-0.3907*	0.2622*	-0.1093	0.0404

^a Value of *r* at 1% = 0.235 (*). ^b Value of *r* at 1% = 0.218 (*). ^c Value of *r* at 1% = 0.190 (*). ^d Value of *r* at 1% = 0.323 (*). ^e Value of *r* at 0.01% = 0.173 (*).

different pattern. Protein content did not correlate with sugar content, and the same was true for cellulose and sugar contents. A characteristic of *M. esculenta* was the positive correlation between total sugar and mineral contents, indicating that selection for increased sweetness could simultaneously improve mineral content.

Focusing on our 120 aroid accessions, and including accessions from various Southeast Asian countries and hybrids (**Table 3**), major differences appeared between protein and mineral contents. A similar conclusion was drawn when protein and mineral contents were analyzed separately in our 111 *C. esculenta* accessions (excluding *X. sagittifolium* accessions) and our *M. esculenta* accessions.

Of particular interest is the fact that in aroids, there was a positive correlation between cellulose and mineral contents, whereas in yams, there was a correlation between cellulose and protein contents. Both were positive and species-specific, suggesting that selecting for enhanced cellulose content may have different consequences for *C. esculenta* and *D. alata*, that is, the enhancement of mineral content in taro and of protein content in *D. alata*.

Understanding the traditional selection process conducted by local farmers is crucial in assisting breeders select the best cultivars and thus increase health and food security. We have shown that some accessions studied are essential to the improvement process because of their outstanding values. This integrative approach provides added value to previous genetic diversity studies (1, 10–13). Thus, combined with studies using molecular markers, the choice of the right parents for breeding purposes will now be more efficient if it is based on the right genotype. Daily and traditional uses related to consumer preferences are also in accordance with potential biofortification, but different breeding programs should be initiated to satisfy local requirements.

Traditional Chemotype Selection. On the basis of the findings of the present study, opportunities for biofortification do exist. For example, in aroids, it appears to be feasible to enhance protein

contents without negatively affecting starch content. Negative correlations will probably slow progress because high starch content is under intense selection in most breeding programs. It would thus not be recommendable to increase protein, total sugar, cellulose, or mineral contents as a new breeding objective in the first cycles of ongoing programs. It has been reported that *laplap* made with good taro accessions is based on high dry matter, amylose, and starch contents and concomitantly low mineral and fructose contents (10). *Laplap* made from *D. alata* tubers must have high dry matter, low protein and mineral, and very low total sugar contents (11). These statements are consistent with correlations found in the present study and consumers' opinions concerning the traditional use of selected cultivars.

However, the fact that numerous *D. alata* accessions are considered to be suitable for preparing an excellent *laplap* suggests that more chemical traits than those assayed in this study may play a role. Starch composition is known to play an important role in texture. Yam mucilage (a glycoprotein complex abundantly present in *Dioscoreaceae*) might also play a key role in this process. Of particular interest is the observation that the presence of flesh pigments (isoprenoids, flavonols, and anthocyanins) in the two most widely consumed species is not associated with poor quality, revealing potential scope for biofortification of secondary metabolites. Contrary to a paradigm distributed throughout the Pacific area, nowadays it is important for nutritionists to explain to consumers that varieties with colored flesh are also suitable for preparing a good traditional dish. Isoprenoids (including provitamin A) and anthocyanins exhibit antioxidant activity associated with potential health benefits (23).

Biofortification Opportunities. Fortunately, other cooking methods such as boiling or roasting are not known to be as demanding of tuber quality as the preparation of *laplap*. High starch content yields dry and floury foods, which do not meet local taste preferences. In Vanuatu, where no starch industry exists, a commercial variety is mainly grown for sale at the market. Taking into account the correlations among primary compound contents found in this study and the fact that cooking does not significantly influence major nutrient contents (24), it appears feasible to increase mineral, protein, and cellulose as well as total sugar contents in commercial varieties.

With the aim of improving staple foods by plant breeding, some *I. batatas* and *D. alata* accessions appear to be excellent starting materials, whereas some *M. esculenta* accessions should be considered as somewhat poor. Proteins and reducing sugars are of great concern in the biofortification of staple foods. Except in *D. nummularia*, their contents are highly variable. Unidentified *Dioscorea* species displayed low coefficients of variation for minerals, proteins, and cellulose, very much like *D. cayenensis-rotundata* accessions, and may therefore also belong to the *Enantiophyllum* section.

Our findings support local consumers' and farmers' appreciations of the organoleptic properties of tuber crops. For all of the compounds analyzed except reducing sugars, the distribution ranges of our estimated content values appear to be slightly higher than those previously reported (11). The same conclusion was reached for all of the primary compound content values previously reported in *D. bulbifera*, a wild yam species (25), because they were clearly lower than ours. This supports the hypothesized narrow differences among yam chemotypes. Indeed, similar coefficients of variation were calculated for Ethiopian yam cultivars (15). A comprehensive survey of *D. alata* in Africa (7) also showed maximum contents and means that were markedly lower than ours. Of particular concern for traditional selection in Vanuatu is total sugar content, which was low in this species. The

African study (7) showed that sugars were mainly composed of sucrose.

With regard to *C. esculenta*, the original core sample was built to characterize the diversity in organoleptic properties (10). As a consequence, several accessions with poor eating quality were discarded. In addition, five years of selection process could reasonably have led to a decrease in the coefficient of variation. Except for starch, the results obtained in taro are consistent with previous reports (10). Our *X. sagittifolium* collection comprised only 9 accessions exhibiting relatively little agro-morphological variation compared to our collection of more than 500 *C. esculenta* accessions. Thus, the chemotypic variation observed in *X. sagittifolium* was somewhat unexpected.

In *M. esculenta*, our maximum and means of major primary compound contents (except proteins) are much lower than those previously estimated in the CIAT germplasm (17, 22), in agreement with the fact that *M. esculenta* is an introduced species in the Pacific.

Relationships between primary compounds, flesh color, and quality have been widely studied, and starch is often shown to be negatively correlated with other primary compounds. Flesh color is not a constraint to biofortification processes. Genetic improvement is possible. To prepare a "good" traditional pudding-like dish (*laplap*), high starch and dry matter are required, whereas middle-range contents are more convenient for classical processing for daily consumption (boiling, roasting, etc.). Our results revealed useful correlations suggesting associations that could be exploited to facilitate genetic improvement and biofortification of tropical root crops.

Even if consumer preferences vary considerably around the world, particular organoleptic traits are needed to prepare similarly processed dishes. For example, for the pounded yam dish called *futu* or *fufu* in Nigeria and Ivory Coast (West Africa), cultivars should be selected for their suitability for *fufu*. According to a previous survey (7), the corresponding properties are similar to those required for *laplap* in Vanuatu. Texture is considered to be more important than taste in hedonic evaluation by consumers. Consistency and springiness were reported to be positively correlated with Nigerian preferences, whereas lumpiness was negatively correlated (26, 27). Another study conducted in Nigeria showed a strong correlation between consumer preferences and consistency, stickiness, and color (28). Similarly, consistency is demonstrated as the main trait of interest in defining excellent traditional *fufu* (29). Primary compounds are major characteristics that determine food texture and starch properties, also related to sugar composition. In *C. esculenta*, the negative correlations observed between starch and mineral contents (Table 3) are in agreement with previous studies (10). On the basis of correlations established among *Dioscorea* spp. accessions (Table 3), the selection of an accession suitable for a good *laplap* is more complex. Despite negative correlations, breeders should take into consideration the fact that high starch and mineral contents are required together. To characterize diversity, *D. alata* chemotypic variation was studied in 131 New Caledonia and 48 Vanuatu cultivars, and organoleptic properties were linked to genetically controlled chemotypes (11, 19).

The present study highlights the importance of understanding the chemotypes of tropical root and tuber crops for clonal selection of elite cultivars. Because breeders have often observed the rebuttal of improved varieties based on poor quality (30), it is crucial to include local consumer preferences in the biofortification approach. Loss of biodiversity is a topic of increasing concern, and in developing countries, the cost of maintaining and screening germplasm remains too high. Participatory conservation involving the distribution of suitable cultivars is an

attractive alternative. However, to assist breeders, novel low-cost and high-throughput tools to strengthen the selection of the right parents as well as efficient screening of large progenies are needed.

ACKNOWLEDGMENT

We thank the staff of the Root Crops Section of VARTC at Espiritu Santo, in particular Roger Malapa, Tari Molisale, and Sylvano Malres, for their helpful collaboration. Special thanks are due to Elodie Tariot from Laboratoires d'Analyses Agricoles Teyssier for assistance in analyzing our samples. We also thank the reviewers for giving us the opportunity to improve our manuscript.

Supporting Information Available: Details of accessions. This material is available free of charge via the Internet at <http://pubs.acs.org>.

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Received for review July 21, 2009. Revised manuscript received September 29, 2009. Accepted September 30, 2009. This research was financially supported by the Fonds Français pour l'Environnement Mondial (FFEM) and represents a part of the Root Crops Agrobiodiversity Project in Vanuatu.