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Variation of mineral composition in different parts of taro (*Colocasia esculenta*) corms

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ABSTRACT

Taro (*Colocasia esculenta*) is an important root crop in the humid tropics and a valuable source of essential mineral nutrients. In the presented study, we compared the mineral compositions of four main parts of taro corm: the upper, marginal, central and lower (basal) parts. The freeze-dried taro samples were analysed for eleven minerals (K, P, Mg, Ca, Zn, Fe, Mn, Cu, Cd, Pb and Cr). The upper part, which plays a critical role in vegetative propagation based on headsets, contained high levels of P, Mg, Zn, Fe, Mn, Cu and Cd. The central part, which is essential for human nutrition, was characterised by higher concentrations of K, P, Mg, Zn, Fe, Cu and Cd. Ca was concentrated in the lower and marginal parts. The effect of the genotype was significant for more than half of the analysed minerals (i.e., Mg, Ca, Zn, Fe, Mn).

1. Introduction

Taro (*Colocasia esculenta* (L.) Schott) is an important food crop of the humid tropical rain forest areas of the world, growing best where annual rainfall is well distributed, with 2500 mm average annual precipitation or more (Weightman, 1989). The term “taro” is frequently used for four aroid species: *Alocasia macrorrhiza* (L.) G. Don (giant taro), *C. esculenta* (taro, true or ordinary taro), *Cyrtosperma merkusii* (Hassk.) Schott (giant swamp taro) and *Xanthosoma sagittifolium* (L.) Schott (cocoyam, tania, taro Fiji). For agriculture and human consumption, the more important aroid species is *C. esculenta*. This species is polymorphic and involves two botanical varieties: *C. esculenta* var. *esculenta* or dasheen (characterised by a large main or central corm and several smaller side cormels) and *C. esculenta* var. *antiquorum* or eddoe (characterised by a relatively small central corm and well-developed side cormels) (Ivancic & Lebot, 2000).

Taro corm represents a large underground stem that stores starch and other nutrients. Corms can vary in size, shape and colour, depending on the genetic structure, age, and interactions between the genotype and the environment. Taro cultivars are frequently divided in two groups: cultivars adapted to upland conditions and cultivars adapted to permanent irrigation (paddy cultivars). Corms of typical upland varieties are usually round or slightly elongated, whereas extremely elongated corms are more characteristic for paddy genotypes (Lebot, 2009).

The corm consists of three main parts: the skin, the cortex and the core (the central part). The skin is covered by a thick periderm that consists mainly of phellem (cork cells) that are flattened radially and are arranged in compact radial rows. Three regions of phellem can be distinguished: an outer region of 2–3 cell layers, which are brown in colour; a middle region of 5–10 cell layers; and an inner region of 10–15 cell layers. The phellogen is one to two cells in width, and no clear demarcation is evident between the phelloderm and the underlying outer cortex. The cortex consists of parenchymatic tissue characterised by intercellular spaces. The cells of the core are larger, with thinner cell walls than those of the cortex and smaller intercellular spaces (Harris, Ferguson, Robertson, Mckenzie, & White, 1992).

Essential minerals, as inorganic substances, are present in all body fluids and tissues and play important roles in metabolic and physicochemical processes like maintenance of pH and osmotic pressure, muscle contraction, transport of gases. These minerals are important components of enzymes and hormones, crucial for bones’ formation and the synthesis of vitamins (Biziuk & Kuczynska, 2007). Humans require sufficient intakes of many mineral elements which are, on the basis of their requirements, usually

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divided into macro- (g or mg day^{-1}) and microelements (few mg or μg day^{-1}) (Barroso et al., 2009). The availabilities of minerals from agricultural products to humans are affected by the presence of promoter substances and anti-nutrients that can reduce the nutrient utilisation. Mineral malnutrition affects over two-thirds of the world's population and is considered as one of the main global challenges. Micronutrient deficiencies are a major public health problem in many developing countries. Iron, zinc and magnesium deficiencies may cause health problems in pregnant women and infants. The excessive intakes of some minerals, however, can upset homeostatic balance and cause toxic side effects (Rivera, Hotz, González-Cossío, Neufeld, & García-Guerra, 2003; Soetan, Olaiya, & Oyewole, 2010). Food is also the main source of consumers' exposures to some toxic elements like lead, cadmium, arsenic, and mercury. Cadmium and lead affect several tissues and organs including the kidneys, lung, heart and brain, and cause a variety of diseases (Goyer & Clarsksom, 2001). Infants and children up to the age seven are particularly threatened since Pb and Cd intestinal absorption at these ages is significantly higher than in adults (González-Muñoz, Peña, & Meseguer, 2008). The levels of minerals and their accumulation in plants depend on numerous factors, like the type and chemical composition of the soil, soil fertility, the root-soil interface, the absorption mechanism and translocation in the plant (Welch & Graham, 2004).

Studies of taro nutritional composition suggest that it contains a range of important macronutrients and micronutrients. Some studies of the mineral compositions of taro corms suggest that potassium is the more abundant mineral. Other abundant minerals include magnesium, phosphorus, and calcium (Bradbury & Holloway, 1988; Huang, Chen, & Wang, 2007; Lewu, Adebola, & Afolayan, 2010a; Mwenye, Labuschagne, Herselman, & Benesi, 2011). Data from the literature reveal that appreciable amounts of zinc are also present. From a nutritional standpoint, taro is rather low in iron and manganese (Lewu et al., 2010a; Mwenye et al., 2011). The nutritional composition of taro corms can vary widely and depends on the genotype, the growing conditions, and the interaction between the genotype and the environment (Mwenye et al., 2011). Another factor is the age of a plant (Wills, Lim, Greenfield, & Bayliss-Smith, 1983).

Although the literature contains numerous reports on the mineral contents in taro corms, little research attention has been devoted to the mineral distribution within different parts of corms. However, the mineral distribution does not appear to be uniform; calcium oxalate, for example, is more concentrated in the distal part (Bradbury & Holloway, 1988). To our knowledge, only one study in which corms were divided into separate sections has been reported, and the distribution of the studied minerals was not uniform (Sefa-Dedeh & Agyir-Sackey, 2004). This previous study (Sefa-Dedeh & Agyir-Sackey, 2004), however, did not include the marginal part, which is usually removed by peeling. Peeling, especially deep peeling, can significantly influence the concentrations of minerals accumulated in the upper, lower and marginal parts of corm. The material used in the previous study (Sefa-Dedeh & Agyir-Sackey, 2004) did not originate from uniform growing conditions; it was harvested at different local farms, and the authors did not take into account accumulation amongst different varieties.

Several questions related to the quality of the different parts of the corm deserve more data. The pattern of taro partitioning during its growth and development is somewhat different from other root crops. Unlike other species that present phasic partitioning, taro partitioning occurs when the storage organ growth begins and continues throughout the vegetative period. Taro exhibits continuous partitioning with an almost linear increase in fresh and dry weights. Cassava, sweet potato and yams develop through phasic partitioning. The continuous partitioning of aroids appears to be similar to sugar beet. The taro corm includes tissues developed over two consecutive seasons: (1) the tissue from the previous season (the corm base) and (2) the tissue from the current season (the rest of the corm). It is thought that the distributions of different minerals within corm differ from mineral to mineral. A comprehensive analysis could reveal the distribution of essential and potentially toxic elements inside the corm flesh (i.e., inside tissues which are used in human nutrition), which is currently little understood. Hence, it would be possible to predict sections with higher and lower concentrations. Data about chemical composition of the marginal part is also needed because of the adjustment when peeling. If some essential minerals dominate in the marginal part, peeling should be limited to a very thin layer, however, it should be deeper if there are harmful or undesired substances in this part. The central part will always be the more important part but, in order to increase corm yield, it is necessary to reduce waste due to removal of the marginal part. Data about chemical composition of four main parts of corms could also be useful for corm processing, especially for the taro chips industry which is becoming very popular. If there are significant differences amongst the basal and the upper part, horizontal slicing should be avoided, or the part with undesired chemical composition should be removed. The youngest tissue is in the upper part (close to the shoot). This part is characterised by low eating quality (watery tissue, low dry matter content) and farmers could increase the thickness of the slice attached to the head-set in order to improve the qualities of the propagules used for establishing the new crop. Data related to mineral composition could also aid in design programs for micronutrient biofortification through breeding.

2. Materials and methods

2.1. Plant material and sample preparation

Our study involved eight accessions from various Vanuatu Islands that were maintained in the Vanuatu National Taro Germplasm Collection at the Vanuatu Agricultural Research and Training Centre (VARTC) on the Island of Espiritu Santo (15° 23′ S and 166° 51′ E, c. 80 m a.s.l.). The studied accessions corresponded to the following cultivar names: (1) VU 105 ('Peta ni Bankis' from Banks Islands), (2) Vu 360 ('Maewo' from the island of Maewo), (3) Vu 372 ('Noholihopoe' from Espiritu Santo), (4) Vu 384 ('Analick' from Ambrym), (5) Vu 468 ('Pentsecost' from Tanna), (6) Vu 1654 ('Akale' from Ambrym), (7) Vu 1765 ('Bwel Tememe' from Pentecost) and (8) Vu 1822 ('Vouvou' from Ambae). The trial was planted in one of the experimental fields of the VARTC and was based on a complete randomized block design planted in 7 replications. The concentrations of the extractable nutrients in the soil of the experimental field determined by Melteras (2007) were: 4.3 mg kg^{-1} ($NH_4 - N$), 20.0 mg kg^{-1} (Colwell P), 38.0 mg kg^{-1} (BSES P), 14.8 cmol kg^{-1} (Ext Ca), 0.54 cmol kg^{-1} (Ext K), 5.68 cmol kg^{-1} (Ext Mg), 0.18 cmol kg^{-1} (Ext Na), 16.0 mg kg^{-1} (Ext S) and 2.40 wt% (total C). Calibrated headsets (having total weight 290–300 g) were planted on the same day: 15 December 2011. The distances between rows and between plants within rows were 1 m. The corms were harvested when they were fully mature in order to minimise ontogenic differences. For the chemical analyses, three randomly selected and equally developed plants of each cultivar were collected. No mineral fertilizers were used during the trial, and no fertilizers had been used in previous years.

Immediately after the harvest, the corms were washed, placed on a clean wooden table and left until their surfaces were dry. They were subsequently peeled using a ceramic knife. Peeling removed the skin and the cortex. As previously mentioned, the remaining part was divided into 4 sections (parts): upper, lower (basal), marginal (outer) and central sections (Fig. 1). The plant tissues of each

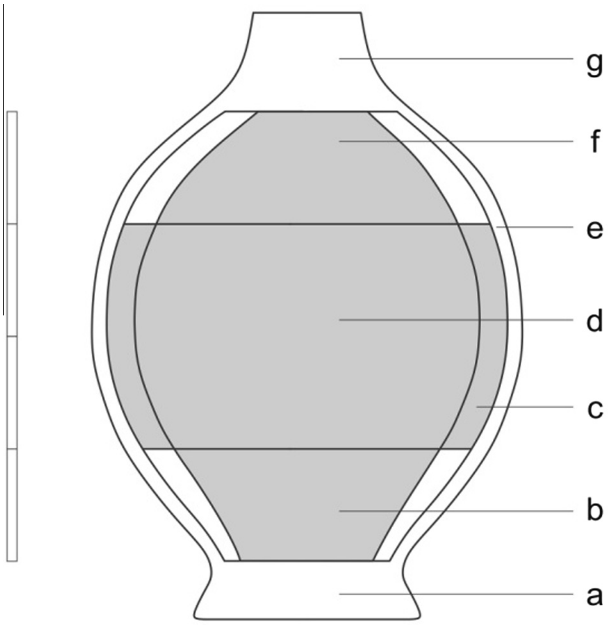

Fig. 1. The principal parts of a taro corm: a – corm base, b – lower part, c – marginal part, d – central part, e – skin (periderm), f – upper part, and g – corm head. The analysis involved b, c, d, and f. The heights of portions b and f are ¼ each, and the height of portion d is ½ of the total part used for the analysis (after the removal of portions a and g). The thickness of the marginal part (e) was 1 cm.

section were sliced into thin chips. The sample aliquots were taken from each section for moisture determination. They were weighed before and after drying in an oven at 102 °C to a constant weight. The remaining slices were freeze-dried for two days using a Telstar Cryodos-50 (Terrassa, Spain) freeze drier. The freeze-dried samples were vacuum packed and stored at −75 °C until analysed.

2.2. Chemical analysis

The analysis involved three corms of each cultivar and the tissues of four sections for each corm (Fig. 1). The freeze-dried corm samples were crushed into a fine flour using a mortar and pestle. The samples were digested in a microwave oven according to the previous published procedure (Kristl, Veber, & Slekovec, 2002). The prepared solutions were then diluted to 25 mL with Milli-Q water. The blank solutions were prepared in the same manner as the samples. The concentrations of Ca, Mg, and Zn were determined by flame atomic absorption spectrometry (AAS), whereas the contents of K were determined by flame atomic emission spectrometry (AES). For the determination of Fe, Mn, Cu, Cr, Pb and Cd, electrothermal atomic absorption (ETAAS) was used. P was determined by a vanadate–molybdate method. The colour developed was measured at 406 nm. Four commercial reference materials (NIST 1515, NIST 1547, NIST 1575 and NIST 8433) were used as quality-control samples. The accuracies were adequate for all of the studied mineral elements (data not presented). Each sample was analysed in duplicate, and the results were expressed as mg kg^{-1} of dry weight (DW).

2.3. Statistical analysis

The statistical analysis was performed using the statistical program package R. Means, standard deviations, minimums, maximums and coefficients of variation were computed for each corm part and for the concentrations of the investigated minerals. For the analysis of differences between the mineral contents of the different corm parts, we applied a linear mixed effects models using the function *lmer* from the library *lme4*. The "corm part" was defined as a fixed factor, whereas the nested factor, "plant within cultivar," was considered as a random factor to account for the non-independence of the corm parts of the same plant and for the non-independence of the plants of the same cultivar. The eight cultivars included in the study were assumed to be a representative random sample of the majority of cultivars grown on Vanuatu Islands; the cultivar was therefore considered a random factor. Visual inspections of residual plots for models did not reveal any obvious deviations from homoscedasticity or normality. *Post hoc* analysis of Tukey contrasts was performed using the function *glht* from the library *multcomp* (Hothorn, Bretz, & Westfall, 2008).

3. Results and discussion

3.1. Moisture content

The averages and variations in moisture contents of the studied cultivars are presented in Table 1. The cultivar Vu 360 had the lowest mean moisture content (64.2%), whereas the highest (79.5%) was determined for Vu 1654. The average moisture content was different in all corm sections. The cultivars Vu 105, Vu 360, Vu 372, Vu 384, Vu 1765 and Vu 1822 exhibited the highest values in the central and upper parts, Vu 468 in the central part and Vu 1654 in the lower part (Table 1). The differences, however, were not high and could be caused by differences in the lengths of growth periods and the corm sizes. The differences in moisture content amongst cultivars in earlier research (Lebot et al., 2004) (the samples were taken from the central part of corms) revealed that they were closely associated with the eating quality of corms. The cultivars with low moisture content and thus higher dry matter were more desirable than those with high moisture and low dry matter (Lebot et al., 2004).

3.2. Minerals in taro corms

The mean values of the mineral contents of taro corms are presented in Table 2. The results for K and P are expressed in percentages (%), whereas the contents for all other minerals are stated in mg kg^{-1} on a dry weight basis (DW). The main minerals found in the taro corms in relatively high concentrations were K, P, Mg and Ca, with mean values of 2.240%, 0.139%, 1000 mg kg^{-1} and 867 mg kg^{-1}, respectively. The root crops are valuable sources of carbohydrates and therefore have an especially high requirement for K. As expected, the most abundant nutrient was K, with values ranging from 1.595% to 2.901%. These results were similar to those reported for taro samples from Taiwan (Huang et al., 2007) and Malawi (Mwenye et al., 2011). The contents of P (0.115–0.210%) and Mg (766–1332 mg kg^{-1}) were comparable to those reported in samples from Malawi (Mwenye et al., 2011), but were higher than the values reported in samples from Ghana (Sefa-Dedeh & Agyir-Sackey, 2004). The lowest contents were determined for Fe (7.1–18.5 mg kg^{-1}), Mn (7.4–13.9 mg kg^{-1}) and Cu (5.4–8.5 mg kg^{-1}). The concentrations of Fe were rather low compared with those reported in other studies (Huang et al., 2007; Mwenye et al., 2011).

The concentrations of Cr and Pb were observed to be below the limit of quantification (LOQ). With respect to the estimation of the LOQ, ten calibration blanks were prepared by microwave digestion. The LOQ was calculated as 10 times the standard deviation of the blank divided by the slope of the calibration curve. The LOQ for Pb and Cr were 2.15 and 2.79 ng mL^{-1}, respectively. The greatest variations in mineral concentrations amongst the studied cultivars were observed for Zn, Cd and Fe and were most likely due to

Table 1
Mean and variation of corm moisture contents amongst cultivars and amongst four different corm sections.

Cultivar	*N*	Lower		Marginal		Central		Upper	
		Mean (%)	St. Dev.	Mean (%)	St. Dev.	Mean (%)	St. Dev.	Mean (%)	St. Dev.
Vu 105	3	68.1	1.4	70.4	1.2	73.8	0.6	74.9	0.2
Vu 360	3	64.2	0.5	61.7	1.0	65.3	0.5	65.7	0.5
Vu 372	3	71.2	1.8	72.7	0.9	72.2	1.0	74.9	1.2
Vu 384	3	71.3	1.4	71.0	2.3	75.4	0.9	75.5	0.9
Vu 468	3	74.7	1.3	75.0	0.7	77.3	0.43	74.9	1.8
Vu 1654	3	80.5	1.2	78.3	1.8	79.8	0.6	78.7	0.3
Vu 1765	3	71.0	0.3	71.9	0.4	73.9	0.4	72.7	0.4
Vu 1822	3	69.6	1.6	67.8	2.1	70.4	1.4	70.8	1.9

Section	N	Mean (%)	St. Dev. (%)	Min. (%)	Max. (%)	CV (%)
Lower	24	71.3	4.7	63.6	81.2	6.6
Marginal	24	71.2	4.9	61.0	80.0	6.9
Central	24	73.6	4.3	64.8	80.6	5.8
Upper	24	73.5	3.8	65.3	79.6	5.2

Table 2
Mean and standard deviation (St. Dev.), minimum (Min), maximum (Max) and coefficient of variation (CV) of corm minerals content of studied taro minerals. The results are given on dry weight basis.

Mineral	*N*	Mean	St. Dev.	Min.	Max.	CV (%)
K (%)	96	2.24	0.480	1.595	2.901	21.5
P (%)	96	0.139	0.040	0.115	0.210	28.8
Mg (mg kg^{-1})	96	1000	230	766	1332	22.9
Ca (mg kg^{-1})	96	867	226	581	1159	26.1
Zn (mg kg^{-1})	96	51.4	26.1	29	93	49.5
Fe (mg kg^{-1})	96	11.6	4.4	7.1	18.5	37.7
Mn (mg kg^{-1})	96	11.2	3.2	7.4	13.9	29.1
Cu (mg kg^{-1})	96	6.7	2.8	5.4	8.5	32.7
Cd (mg kg^{-1})	96	0.084	0.038	0.038	0.137	45.4
Pb (mg kg^{-1})	96	nq	nq	nq	nq	nq
Cr (mg kg^{-1})	96	nq	nq	nq	nq	nq

nq – not quantified.

genetic differences because the growing conditions (i.e., the same plot, the same planting distance, and the same planting date) were identical. A high level of variability not only for the total mineral contents but also for other nutrients in the South East Asian and Pacific taro germplasm have also been documented (Lebot et al., 2004).

3.3. Distribution of macro- and micro-elements in the four analysed parts of taro corms

Plant development and growth depend on the adequate availabilities of minerals in soil and their uptake through the rhizosphere. Plant uptake of minerals is a complex process depending on numerous factors like mineral concentrations in the soil, rate of mass flow in the soil, rate of root elongation and the surface area of the root (Marschner, 1995). From the rhizosphere minerals enter the apoplasm of the root cells and once they are absorbed by the root cells, the nutrients must be translocated to other tissues. Subramanian, White, Broadley, and Ramsay (2011) found out that patterns of accumulation in potato tubers for each mineral depended on numerous factors like developmental anatomy of tuber, phloem and xylem loading and unloading, movement across the periderm and mechanisms for transport and sequestration within the tuber. Low-transpiring tubers like the potato primarily receive minerals through redistribution from above-ground tissues through the phloem (Baker & Moorby, 1969). Taro growth and development, however, is more similar to sugar beet although there are also many similarities with the potato. The formation and rapid growth of taro roots begins immediately after planting. The intensity of roots' growth starts declining approximately 6 months after planting. At this time, the main corm and side cormels become the main sink and their growth intensifies, whilst the number of active leaves decreases and their petioles become shorter. It is also necessary to consider that underground organs (e.g., tubers and corms) and above ground parts are both botanically parts of the shoot system. The aerial portion of the shoot is exposed to a markedly different environment than the underground organs (Busse & Palta, 2006).

In our study, the distribution of P, Mg, Fe, Cu, and Cd followed a similar pattern and showed the highest, but not significantly different, mean values of their contents within the central and upper parts of corms, and the lowest in the marginal and lower parts (Fig. 2). Calcium, however, had a completely different distribution, exhibiting the highest values in the lower and marginal parts. The distribution of Zn was similar to the distributions of P, Mg, Fe, Cu, and Cd with the exception of the marginal part which was not significantly different in comparison to the upper and central parts. Potassium showed the highest content in the central part but its concentration in the upper part was lower and not significantly different when compared to the lower and marginal parts. Similarly to P, Mg, Fe, Cu, and Cd, Mn showed the highest concentration in the upper part, although its distribution in the central and the marginal parts was different.

3.3.1. Potassium

Potassium is one of the most important intracellular ions and is essential for the homeostatic balance of body fluids. It is involved in the transfer of phosphate from ATP to pyruvic acid, and probably plays a role in other enzymatic reactions. It controls muscle contraction particularly the cardiac muscle (Haas, 2000). In all of the studied cultivars, the highest levels of K were observed in the central part, with a mean value of 2.521%, ranging from 1.655% to 3.585% (Fig. 2). No significant differences ($P < 0.05$) were observed in K contents when comparing the lower, marginal and upper parts (Fig. 2). However, substantial differences were observed amongst the cultivars. The percentage of variance which could not be explained by the variation amongst different corm sections and was related to differences amongst cultivars was 39.1% (Table 3). The cultivar Vu 360 exhibited the lowest K contents in all of the analysed parts, and the cultivar Vu 1654 exhibited the highest contents, with the exception of the K content in the upper part, which was lower in the cultivars Vu 468 and Vu 384 (Fig. 3). Our findings differed from those previously reported by Sefa-Dedeh and Agyir-Sackey (2004), who observed higher K contents in the distal part and lower K contents in the apical and central parts.

In the plants, K is involved in many vital processes like osmoregulation, ribosome mediated protein synthesis and proper func-

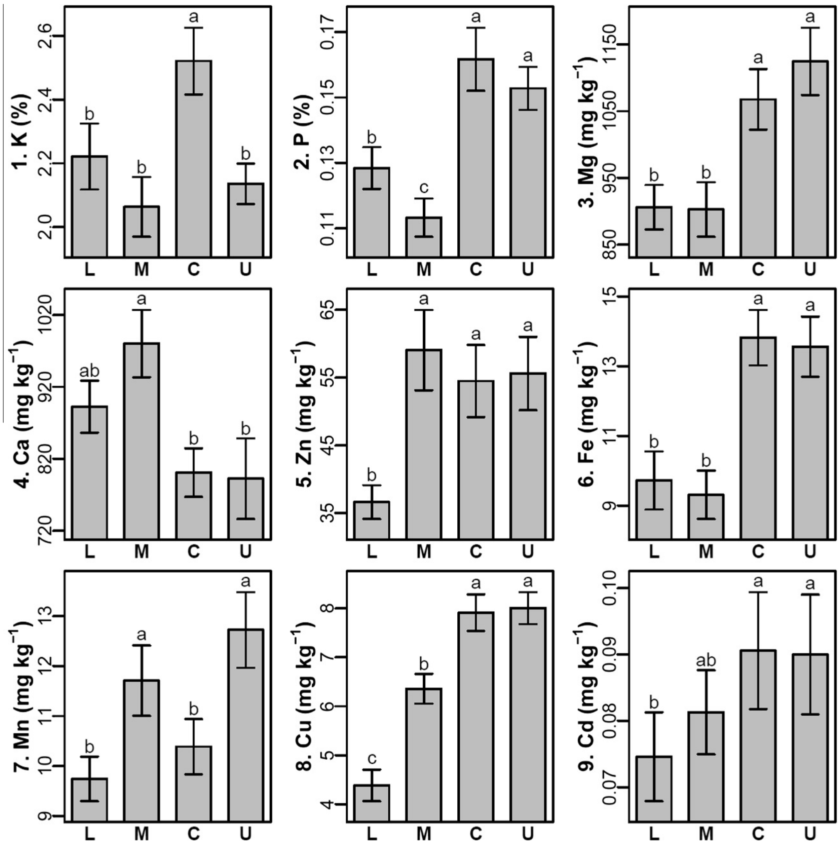

Fig. 2. Means and standard errors of minerals determined in four different parts of taro corm: lower (L), marginal (M), central (C) and upper (U). The results for K and P are expressed in %; those for the other elements are expressed in mg·kg^{-1} DW. Means labelled with the same letter are not significantly different (Tukey, $p < 0.05$).

Table 3
Variances and their percentages that could not be explained by the variation associated with the studied corm sections.

Mineral	Variance				Percentage (%)			
	Within cultivars	Cultivars	Residual	Total	Within cultivars	Cultivars	Residual	Total
K (%)	0.017	0.154	0.222	0.394	4.4	39.1	56.5	100
P (%)	0.000	0.001	0.018	0.019	1.0	4.5	94.5	100
Mg (mg kg^{-1})	1488	39,955	80	41,523	3.6	96.2	0.2	100
Ca (mg kg^{-1})	0	29,095	141	29,236	0.0	99.5	0.5	100
Zn (mg kg^{-1})	0	428	14	442	0.0	96.8	3.2	100
Fe (mg kg^{-1})	0.0	10.1	2.4	12.5	0.0	80.2	19.8	100
Mn (mg·kg^{-1})	0.5	7.1	1.6	9.2	5.5	77.2	17.3	100
Cu (mg kg^{-1})	0.122	1.156	1.215	2.493	4.9	46.4	48.8	100
Cd (mg kg^{-1})	0.000	0.001	0.016	0.018	0.8	6.5	92.7	100

tioning of the numerous enzymes that are involved in C-metabolism, like pyruvate kinase, phosphofructokinase, starch synthase, and vacuolar PPase isoforms that accumulate protons within the vacuolar lumen (Marschner, 1995). It is the principal cation in establishing cell turgor and maintaining cell electroneutrality (Taiz & Zeiger, 2010). K also plays an important role in the translocation and storage of assimilates. It ensures an abundant supply of photosynthates from the source during the early and middle growth stages and promotes the translocation of photosynthates to storage roots, mainly during the late growth stage (Liu, Shi, Zhang, & Chai, 2013). In plants, K is characterised by high mobility. The vacuoles represent the metabolic pool of K. K is deposited in vacuoles of the parenchyma cells temporally and is successively transported and utilised in metabolic processes (Marschner, 1995). The parenchymatic cells of the central part are characterised by large vacuoles (Harris et al., 1992), which could explain why the highest concentration of K was observed in the central part of the corm. K is known to influence the metabolism of sugars, their polymerisation, and the synthesis of starch (Marschner, 1995). The concentration of starch was observed to be higher in the central and upper parts compared with the lower part (Sefa-Dedeh & Agyir-Sackey, 2004). Therefore, the involvement of K in sugar metabolism may explain the highest K values observed in the central part; however, it cannot explain its lower values in the upper part. We may conclude that the distribution of K within taro corm is probably not directly related to starch accumulation.

3.3.2. Phosphorous

Phosphorus is one of the crucial elements for all living beings. P is an important element in plant metabolism, carbohydrate biosynthesis and energy transfer reactions. It is involved in the synthesis of adenosine triphosphate (ATP), phospholipids, phosphoproteins, phosphorylated metabolic intermediates and nucleic acids like DNA and RNA (Mayes, 1996). Formation and disruption of the

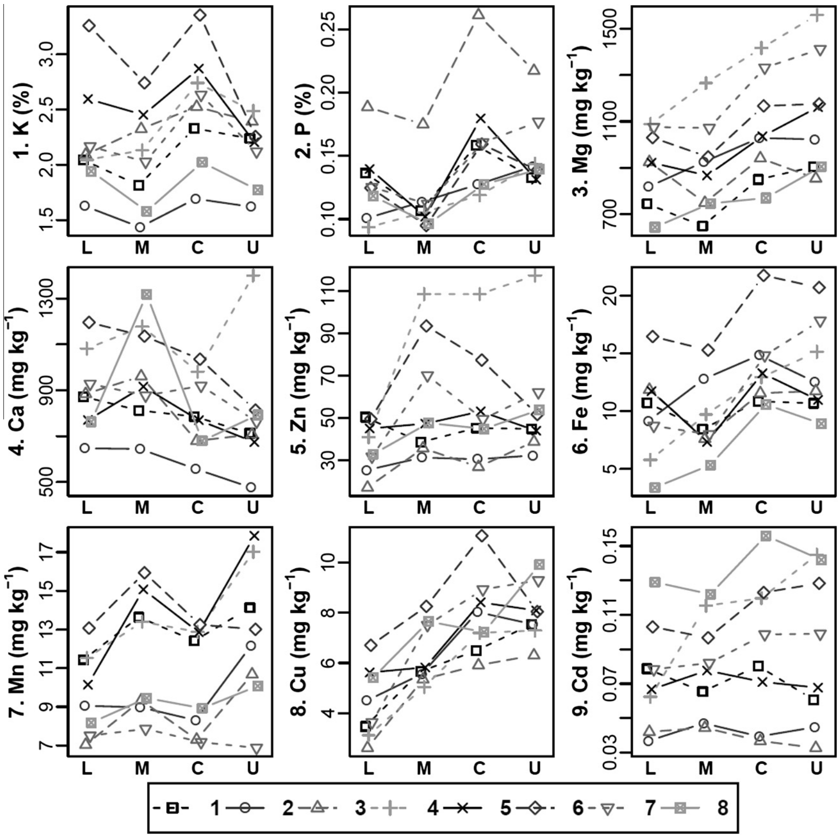

Fig. 3. Minerals distribution in different parts of corm (lower – L, marginal – M, central – C and upper – U) in eight taro cultivars from Vanuatu: Vu 105 (1), Vu 360 (2), Vu 372 (3), Vu 384 (4), Vu 468 (5), Vu 1654 (6), Vu 1765 (7), and Vu 1822 (8).

high-energy phosphate bond in ATP is one of the central mechanisms within a cellular energy system. Maintenance of stable cytoplasmatic concentrations of inorganic P is essential for many enzyme reactions. This homeostasis is achieved by a transportation through the membrane and exchanges between various pools of P within the cells (Schachtman, Reid, & Ayling, 1998). In many ecosystems, P is often present in forms that are unavailable for plants and is therefore frequently one of the major limiting factors for plant productivity.

The mean content of P was the highest in the central part (0.162%), followed by the upper (0.153%), lower part (0.128%) and the marginal part (0.113%). There was no significant difference in the P mean contents between the central and upper parts (Fig. 2), whereas the difference in the P mean content between the central and marginal parts was 31%. The influence of the cultivar was relatively low (the percentage of variance that could not be explained by the variation amongst different corm sections and was related to differences amongst cultivars was 4.5%, Table 3). This result indicated that the accumulation of P was very similar in all the studied cultivars. Amongst the cultivars included in this study, Vu 372 exhibited the highest P contents in all parts of the corm. The distribution of P was similar in the majority of cultivars. The exceptions were two cultivars, Vu 384 and Vu 1822, which exhibited the highest P content in the upper part (Fig. 3). Our data agreed with the results of previously reported studies (Sefa-Dedeh & Agyir-Sackey, 2004), where the highest concentration of P was observed in the apical part (similar to the upper part of our study).

It accumulates in the cytoplasm, apoplast, nucleus and, specifically, in the vacuoles of cells (Schachtman et al., 1998), where the vacuoles act as a storage pool of inorganic P (Marschner, 1995). In starch granules, P is bound to the amylopectin fraction (Buléon, Cotte, Putaux, De Hulst, & Susini, 2014) and significantly affects its functional properties. The P contents of the defatted taro starches varied from 0.14 to 0.76 mg (100 g)$^{-1}$ (Aboubakar, Njintang, Scher, & Mbofung, 2008). Subramanian et al. (2011) studied the distribution of minerals in potato tubers, and their results reinforced the likelihood that most of the tuber phosphate being associated with starch; therefore, the P distribution is expected to resemble the starch distribution. In our study, the highest concentration of P was determined in the central and upper parts of taro corms which resemble the distribution of starch observed by Sefa-Dedeh and Agyir-Sackey (2004).

3.3.3. Calcium

Calcium is one of the essential minerals needed for building the bones and teeth of animals and humans. It plays a vital role in the functionings of nerves and muscles, and in the activations of a large number of enzymes. It is also needed for ensuring membrane permeability and immune defence. A deficiency of Ca can lead to disorders like rickets, osteoporosis, dentition, tachycardia, etc. (Mayes, 1996; Shapses, 2012). The highest mean values of Ca were determined in the marginal (980 mg kg^{-1}) and the lower parts (892 mg kg^{-1}) of the corms (Fig. 2). No significant differences were observed in the mean Ca contents between the marginal and the lower parts or between the lower, central and upper parts. Our data showed that the analysed cultivars did not present a uniform distribution of this mineral. The influence of the cultivar was high. Most of the unexplained variation was due to differences amongst the cultivars (Table 3). The cultivars Vu 372, Vu 468 and Vu 1822 accumulated more Ca in the marginal parts than in the other parts of the corms, whereas in Vu 105 and Vu 1654, the Ca levels were the highest in the lower parts. No significant difference in Ca content was observed between the lower and the marginal parts in Vu 360 (Fig. 3). Amongst the cultivars, large differences were observed in the average mean values of Ca. The cultivars with the highest accumulation were Vu 360 (581 mg kg^{-1}) and Vu 384 (1159 mg kg^{-1}).

There are distinct areas and compartments with high or very low Ca concentrations in plants (Marschner, 1995). High Ca concentrations are observed in the cell walls, exterior surface of the plasma membrane and compartments of the secretory pathway. Most of the soluble Ca in plants is located in vacuoles, especially in leaves. Ca bound to pectate in the middle lamella is essential for strengthening the cell wall and plays an important role in the structure and function of the cell membrane (White & Broadley, 2003). Ca is almost immobile in the phloem, and long-distance translocations take place via xylem. Little Ca is transported from the leaves to the phloem sink tissues, such as tubers, which consequently have low Ca concentrations (Karley & White, 2009). All parts of the raw taro plant are characterised by the presence of calcium oxalate (Noonan & Savage, 1999). Bradbury and Holloway (1988) reported that the concentration of oxalate decreases from the skin toward the centre of the corm. Similar results were reported by Sefa-Dedeh and Agyir-Sackey (2004), who showed that the distal section contained a higher level of calcium oxalate compared with the apical and middle sections. In order to explain our results, we also had to consider the investigation of the *in vivo* calcium transport path in the potato conducted by Busse and Palta (2006). Their investigation showed that water and Ca can be simultaneously transported from stolon roots to the tuber and no significant absorption Ca occurs from the soil through the periderm of tubers. Ca, along with water, is transported to the tuber from the roots on the stolon near the tuber, via the xylem. Redistribution through the phloem does not occur. The routes of Ca transportation are largely determined by the transpirational demand of the plant. Due to the very low transpirational demand of tuber, water tends to be routed to shoots. In order to explain the highest concentration of Ca in the marginal part of taro corm we have to consider that: (1) Ca is bound to the cell walls of thicker secretory cells, which are more common in the marginal and lower parts, (2) Ca, along with water, is transported to the corm from the roots connected to the corm exterior and (3) Ca is not mobile, it does not redistribute through the phloem. To explain the high concentration in the lower part we have to consider the early growth and development of corm. For vegetative propagation of our planting materials, we use headsets (the uppermost part of corm together with parts of the petioles). The initial concentration of Ca in this part is low, however, this is the part which develops the first roots (successively becomes the lower or basal part), enabling the beginning of the absorption of Ca and other minerals. As Ca is not a mobile mineral, it starts accumulating.

3.3.4. Magnesium and iron

Magnesium plays a role in hundreds of processes in the human body including activation of many enzymes like pyruvic acid carboxylase and pyruvic acid oxidase, myokinase, creatine kinase, and several others. It is required for normal muscular contractions, the building up of proteins, and the transmission of signals across nervomuscular junctions. Approximately 50% of body Mg is located in the bones (Vormann, 2012). In plants, it is involved in many enzymatic reactions, like those associated with energy transfer, phosphorylation/dephosphorylation, stabilization of nucleic acids and nucleotides, insertion of Mg into protoporphyrin (Maathuis, 2009). Mg is best known as the central element of the chlorophyll structure (White & Broadley, 2009). In plants well supplied with Mg only about 20% of the total Mg is bound to chlorophyll, whereas the remaining almost 80% are present in more mobile forms (Marschner, 1995). Mg plays a specific role in the phloem transportation of carbohydrates from the source to the sink organs. It is a good phloem mobile element and is readily translocated within plants to actively growing plant parts acting as sink (White & Broadley, 2009). During senescence of the potato, Mg is mobilized from the haulm and transported to the tubers (Marschner, 1995). When shoots become Mg deficient it can be released to the xylem (Karley & White, 2009). Adequate Mg supply to plants is of critical importance, especially during the reproductive growth stage. The photosynthate export from source into sink organs is impaired by Mg deficiency (Cakmak & Kirkby, 2008). The reduction of carbohydrate transport can cause the accumulation of carbohydrates in leaves and consequently the reduction of root growth. However, this does not appear in all crops. The studies of Hermans et al. (2005) showed that in sugar beet, under Mg deficiency, the shoot growth was more depressed than the root growth and carbohydrates started to accumulate in the leaves of the rosette, which were the lowest in the Mg concentration. The accumulation of carbohydrates in the above ground tissues restricts photosynthetic CO_2 fixation and enhances the formation of reactive oxygen species (Cakmak & Kirkby, 2008).

Mg tended to be more concentrated in the upper and the central part of the corm (Fig. 2), with mean values of 1068 mg kg^{-1} and 1124 mg kg^{-1}, respectively. No significant differences were observed between the Mg contents in the upper and the central parts. Additionally, no significant differences were observed between the Mg contents in the lower (906 mg kg^{-1}) and the marginal parts (902 mg kg^{-1}). The influence of the cultivar was very high (Table 3). The cultivars Vu 105 and Vu 1822 exhibited the lowest Mg contents (787 and 766 mg kg^{-1}, Higher concentration of Mg in the upper and the central parts can be explained by the mobility and translocation of this mineral. During growth, it is transported from the leaves to the main sink tissues – i.e., the parenchymatic tissue of the upper part of the corm which successively becomes the central part. The accumulation of Mg follows the development of the leaf area which increases until early maturity (in Vanuatu, until approximately 7 months after planting) and then starts to decrease. It is for this reason, at harvest, that one may expect much lower concentrations of this mineral in the upper part. However, during that time Mg is probably translocated to new faster growing plant parts acting as sink – i.e., fast developing side shoots (suckers).

Fe, like most minerals, is obtained primarily from the rhizosphere and its uptake in the potato, and most probably taro, belongs to the strategy I model. Plants first acidify the soil solution, iron is reduced from Fe^{3+} to the more available Fe^{2+} and finally transported into the plant using an iron specific transporter. Once Fe enters the symplast, Fe is bound to various chelators like citrate or nicotianamine in order to remain soluble (Kim & Guerinot, 2007). It travels symplastically into the outer layer of the vasculature, and finally into xylem parenchyma cells before entering the apoplast and being loaded into xylem cells for translocation and utilisation in the shoot (Samira, Stallmann, Massenburg, & Long, 2013). Fe is also transported through the phloem. It plays a substantial role in the structure of cytochromes; thus, its main function is its participation in redox reactions. Up to 80% of the cellular Fe is localised in the chloroplasts of rapid growing leaves and in thylakoids as the main structures of cytochromes; other Fe can be stored in plant cells in the stroma of plastids as phytoferritin (Cohen, Fox, Garvin, & Kochian, 1998; Hänsch & Mendel, 2009).

In general, the role of Fe is similar to the role of Mg. Both minerals are very important for photosynthesis; therefore, much of the Mg and Fe taken up will go to the green parts (leaves) and will not primarily be saved in older parts. In our study, the distribution pattern and accumulation of Fe was not significantly different from Mg, with the highest concentrations being observed in the upper (13.6 mg kg^{-1}) and central parts (13.8 mg kg^{-1}) of the corm. The lowest mean concentrations were observed in the marginal

(9.31 mg kg^{-1}) and the lower parts (9.73 mg kg^{-1}) (Fig. 2). Fe deficiency (ID) and Fe-deficiency anaemia are the most common nutritional disorders in humans throughout the world (Paesano et al., 2010). It is also reported that Fe deficiency has a negative impact on brain functioning in infants (Milman, 2011). Fe biofortification of major staple food plants like taro is therefore one of the crucial issues. Unfortunately, there are still many uncertainties about the physiological processes involved in Fe uptake and loading in different parts of corms.

3.3.5. Zinc, manganese and copper

Zinc is essential for human growth and development. It is used in the synthesis of hormones, enzymes, proteins and other components that promote physical and mental growth. Zinc is required for immune system, tissue repair and wound healing, optimum insulin action, reproduction, vision, taste, and behaviour. Amongst other disorders, Zn deficiency causes poor growth and retarded development (Mayes, 1996). The differences in mean Zn contents between the upper, central and the marginal parts of corm were not significant (Fig. 2). The only significant difference was determined in the lower part, which exhibited the lowest concentration (36.6 mg kg^{-1}). Zn is known for its catalytic function and structural role in enzyme reactions. Similar to Fe and Cu, Mn plays an important role in redox processes and is a cofactor activating approximately 35 different enzymes (Hänsch & Mendel, 2009). Manganese is needed in small amounts and therefore its deficiency in humans has rarely been reported. It is required for the proper metabolism of proteins, carbohydrates, and lipids. Mn participates in the activations of several important enzyme systems (Grider, 2012). The highest content of Mn was determined in the upper (12.72 mg kg^{-1}) and the marginal parts of the corm (11.71 mg kg^{-1}), although no significant differences were observed between these two parts (Fig. 2). Additionally, no significant differences were observed between the Mn contents in the central and the lower parts. The distribution of Zn and Mn in our study can be compared with the results obtained for the potato tubers (Subramanian et al., 2011). In the potato, they exhibited a dorsoventral polarity where the mineral content was higher in the slice of the tuber which was nearest the soil's surface (the corresponding parts of taro corm would be the marginal and upper parts). The copper metabolism is interlinked with the iron metabolism and is also significant in redox reactions (Hänsch & Mendel, 2009). Cu is constituent of several enzymes and is associated with the growth and formation of bones, absorption of iron during haemoglobin and myoglobin synthesis, and Fe utilisation. Cu deficiency simultaneously leads to a decrease in Fe content in some tissues (Araya, Olivares, & Pizarro, 2007). In plants, Cu is involved in many vital processes like photosynthesis, mitochondrial respiration, and carbon and nitrogen metabolisms. It is present in two oxidation states (Cu^{1+} and Cu^{2+}) and can function as a reducing or oxidising agent. This property makes copper also potentially toxic because its ions can catalyse the production of free radicals (Hänsch & Mendel, 2009). In agriculture, copper is frequently used as an antifungal agent and may be associated with serious environmental pollution, especially in vineyards. Our analysis indicated that, similarly to Mg and Fe, Cu exhibited the highest concentrations in the upper and the central parts, with mean values of 8.00 and 7.91 mg kg^{-1}, respectively. However, its content in the marginal part (6.36 mg kg^{-1}) was significantly higher than that in the lower part (4.38 mg kg^{-1}) (Fig. 2).

3.3.6. Chromium, cadmium and lead

Our study also involved the analyses of Cd, Pb, and Cr. Chromium is one of the crucial minerals which enables proper functioning of insulin (Morris, Kouta, Robinson, MacNeil, & Heller, 2000). It also participates in maintaining the configuration of RNA molecules (Eastmond, MacGregor, & Slesinki, 2008). Cd and Pb are known to be toxic to humans and may affect the functionings of several organs. Of major concern is the impairment of cognitive and behavioural development in infants and young children. Cadmium increases the production of free radicals in several organs and thus enhances lipid peroxidation which may cause tissue damage and cellular death (Méndez-Armenta et al., 2003). Cr, Cd and Pb are considered as non-essential elements for plants and can be toxic even at low concentrations. They can inhibit photosynthesis and disturb the mineral nutrition, water balance, membrane permeability and functioning of hormones (Mengel & Kirkby, 1987; Singh, Mahajan, Kaur, Batish, & Koli, 2013). Cd is one of the more dangerous metals due to its high mobility and small concentrations which can disturb plant growth and development. The studies of Cd absorption regarding potato plants conducted by Reid, Dunbar, and Mclaughlin (2003) showed that most of the Cd was absorbed by the basal roots, whereas the tubers, stolons and stolon roots contributed to only a minor fraction to the overall Cd absorption. Cd absorbed by roots from the soil (and also by leaves) was rapidly exported to other parts of the plant like stem and tubers. It was also found that Cd could not be transferred directly from the basal roots to the tubers via xylem without involving the phloem. This indirect transfer could be the main reason why we determined the highest concentrations of Cd in the central and the upper parts of the taro corms (0.091 mg kg^{-1} and 0.090 mg kg^{-1}, respectively) (Fig. 2). The concentrations of Pb and Cr were less than the limit of quantification (LOQ).

3.4. The contribution of taro consumption to the daily mineral intake

The percentages of recommended daily intakes (RDIs) based on an average consumption of 200 g of fresh taro corms per day were calculated for Ca, Cu, Fe, Mg, P, and Zn, in regard to children aged 4–8 years and adult females and males 19–50 years old. In these calculations, we considered the average mineral contents in the central part of taro corms and the current recommended daily allowance/acceptable intake (RDA/AI) values provided by the Food and Nutrition Board (National Academy of Sciences, 2004, available at http://www.iom.edu/~/media/Files/ActivityFiles/Nutrition/DRIs/DRI_Elements.pdf). The percentages of RDIs for children aged 4–8 years were: 33.2–52.6% for Mg, 2.91–5.35% for Ca, 12.5-21.5% for P, 30.4–80% for Zn, 5.2–9.2% for Fe, and 66.8–120.6% for Cu. For males aged between 19 and 50 years, the calculated values were: below 15% for Mg and P, and below 10% for Ca and Fe, whilst for females (of the same age) Mg and Fe were below 20% and 5%, respectively. The values calculated for Zn and Cu were notably higher and approached 35% and 46% respectively. These values need to be considered more as orientation values because they are based on the assumption of 100% absorptions of individual minerals. The absorptions of some minerals, however, can be reduced due to the presence of various antinutrients like phytic acid, fibres, certain tannins, oxalic acid, and lectins. The negatively charged phosphate in phytic acid binds the cations of Ca, Fe, K, Mg, Mn and Zn, and thus reduces their absorptions (Bohn, Meyer, & Rasmussen, 2008). There is also some competition between minerals; e.g., the absorption of Mn can be inhibited by the presence of excessive amounts of Ca and P in the diet (Soetan et al., 2010). Also, we did not take into account that significant amounts of minerals, especially P, Ca, K and Zn, as well as antinutrients (tannins, calcium oxalate and phytate) were lost during the boiling of corms. The exceptions can be Mg and Cu because their losses during boiling are not significant (Lewu, Adebola, & Afolayan, 2010b). Considering that the central part represents the largest part of the corm for consumption (according to our calculations approximately 75% after peeling), deep peeling did not significantly affect the daily intake of K, P, Mg, Zn, Fe and Cu, however, it may have reduced the intake of Ca.

For Cd, we calculated the percentage of the provisional tolerable weekly intake (PTWI). The PTWI recommended by FAO/WHO. (2010) is 7 μg kg^{-1} body weight. If we consider an adult person of 70 kg who consumes 200 g of fresh taro corms per day, his weekly intake of Cd will be 3.7–10.0% of PTWI.

4. Conclusion

The contents of eleven minerals were analysed for four main parts of taro corm: the upper, marginal, central and lower (basal) parts. The concentrations of most minerals (P, Mg, Fe, Cu, and Zn) were higher in the upper and the central parts. K was particularly accumulative in the central part, whereas its contents in other parts were lower but not significantly different. No significant differences were observed amongst the Zn concentrations in the upper, central, and marginal parts, whereas the basal part exhibited the lowest values. Mg, Fe, Cu and Cd tended to be more concentrated in the central and the upper parts. The highest concentrations of Ca were observed in the marginal part. Mn was more concentrated in the upper and marginal parts. The concentrations of Cr and Pb were less than the limit of quantification.

The results of our investigation suggest that the upper part, which plays a critical role in vegetative propagation based on headsets, is an important storage location for P, Mg, Zn, Fe, Mn, Cu and Cd. The central part, which is critical in human nutrition, is characterised by higher concentrations of K, P, Mg, Zn, Fe Cu and Cd. Ca, Zn and Mn are more concentrated in the marginal part, which is partly removed by peeling. Deep peeling can affect only Ca because Zn and Mn are also present in higher concentrations in the upper and/or central parts. The concentrations of the studied minerals in the lower part, which represents the oldest tissues and is the least important for human consumption, were observed to be relatively low, with the exception of Ca. The data obtained for daily intake of minerals showed that taro could be considered as a valuable source of Mg, Zn and Cu in the diets of children, and Zn and Cu in the diets of adult persons. On the other hand, it cannot satisfy the daily demands for Ca, Fe and P, and therefore it would be reasonable to combine taro with other foods. The concentrations of individually studied minerals exhibited relatively high differences amongst cultivars. This indicates that the concentration of a targeted mineral could be at least partly improved by genetic breeding, selection of the proper cultivar(s), and/or through the use of an appropriate peeling technique. If an essential mineral tends to be more concentrated in the marginal part, peeling should not be deep. The variations amongst cultivars also suggest that the selection of genotypes richer in minerals that are deficient in the diet (i.e., Fe, Mn and Zn) is possible, especially in developing countries. The data may also be useful in planning hybridization in taro breeding programs.

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