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The greater yam (*Dioscorea alata* L.): a review of its phytochemical content and potential for processed products and biofortification

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CRediT authorship contribution statement. V. Lebot wrote the first draft of the manuscript. F. Lawac supervised the maintenance and characterisation of VARTC greater yam germplasm in different studies reviewed here. L. Legendre supervised students involved in greater yam analytical researches who contributed to this review. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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The greater yam (*Dioscorea alata* L.): a review of its phytochemical content and potential for processed products and biofortification

Abstract

The greater yam (*Dioscorea alata* L.) is the most widely distributed yam species in the world. In many countries, its cultivation is expanding because of its ease of preparation, taste and nutritional properties. The greater yam has been the object of significant research studies conducted by independent teams in distant countries, and aiming at characterising its complex chemical composition in major compounds and in secondary metabolites. Here, we conduct a detailed and comprehensive literature review regarding the chemical composition and functional properties of the greater yam. We also review briefly the botanical, phylogeny and genetic information on *D. alata*, as well as the antioxidant, antimicrobial and anti-inflammatory properties of its phytochemicals, and its use as a staple food, or in processed products. One of the objectives of this review is also to compile the information needed by genetic improvement programs interested in the biofortification of the greater yam.

Keywords: allantoin, anthocyanins, caryatin, catechins, dioscin, dioscorin, flavonoids, organic acids

1. Introduction

Cultivated yams (*Dioscorea* spp.) provide the staple food for millions of people in tropical countries. Eleven species are cultivated but only three are major food crops (*D. alata*, *D. cayenensis* and *D. rotundata*), while the eight others (*D. bulbifera, D. dumetorum, D. esculenta, D. nummularia, D. oppositifolia, D. pentaphylla, D. polystachya, D. trifida*) are often referred to as the "minor yams" (Degras, 2013). The underground storage organs are tubers, renewed and produced annually. They are harvested every season and replanted vegetatively using tuber pieces. Once harvested, the yam tubers can be stored for 4–6 months in ambient tropical conditions without deterioration of their excellent nutritional properties (Asiedu and Sartie, 2010). According to the FAO database, the world production was 75 million tonnes of yam tubers in 2021, cultivated over 8.8 million hectares, mainly in the 'yam belt' of West Africa where four countries (Nigeria, Benin, Ghana, Côte d'Ivoire) account for more than 90 % of the global production (FAOSTAT, 2022). It is estimated that 60% of the yam production is sold locally towards urban markets, or for exports within African countries and to Europe and North America (Scott, 2021). With the present international cereal crisis, many developing countries, especially in Africa, are looking at locally cultivated crops as possible alternatives to feed growing cities and there is an interest on yams.

The greater yam (*Dioscorea alata* L., also called water- or winged-yam) is the most widely cultivated yam species in the world. It is preferred because of its ease of cultivation and its adaptation to non-staking conditions (Neina, 2021). It has an attractive tuber shape, a delicate taste and long postharvest life. Just like other *Dioscorea* spp., the stems, petioles and leaves are non-edible. Throughout West Africa, *D. alata* is increasingly popular as a high-value crop for urban markets and in Côte d'Ivoire it accounts for 70% of the national production. It is important in the Pacific Islands, especially in Melanesia (Papua New Guinea, the Solomon Islands, Vanuatu, New Caledonia and Fiji), and in the Caribbean, where it has considerable cultural significance. It is grown in South America, in India, and in parts of upland Asia including China, but also in Japan, the Philippines and Indonesia.

In most countries, its cultivation is expanding because of its ease of preparation, taste and nutritional properties. Compared to cassava (*Manihot esculenta*) and other tropical root crops, yam cultivation is relatively intensive and local prices are higher but consumers' attachment to its taste is such that it is in high demand. In Asian cities, the greater yam is increasingly sought by urban dwellers because of its reputation as a healthy food. Fresh tubers are consumed mostly as boiled yam. They are peeled, cut into pieces and cooked for 10–20 min, depending on the cultivar. In most countries, they are accompanied by other vegetables. In West Africa, pounded yam (*fufu*) is prepared from pieces of boiled tubers pounded in a mortar until it forms a thick and elastic paste, eaten in the form of balls, with sauce and meat (Honfozo et al., 2019). However, as a result of urbanization, diets are rapidly changing and there is nowadays a trend towards the consumption of more processed yam-based foods, such as ready-to-use flours, or ready-to-cook peeled pieces of tubers in vacuum-sealed plastic bags.

Because of its wide international distribution, *D. alata* has been the object of significant research studies around the world, conducted by independent teams in distant countries, and aiming at characterising its complex chemical composition in major compounds and in secondary metabolites. In the present study, we intend to conduct a detailed and comprehensive literature review regarding the chemical composition and functional properties of the greater yam tuber. One of the objectives of this review is to compile the necessary information needed by genetic improvement programs interested in the biofortification of *D. alata*. We will also briefly review the botanical and genetic information on this species, as well as the physiological properties of the greater yam phytochemicals, and its use as an unprocessed or processed food.

2. Materials and methods

Five databases were consulted: Google Scholar, Medline (PubMed), Science direct, Web of Science and Agritrop. The six key words: '*Dioscorea*', '*alata*', 'chemical', 'nutritional', 'composition', and 'constituents' were entered to obtain lists of references from 1980 to 2022. All references mentioning at least '*Dioscorea*' in their title were studied and if sufficient information was obtained from their abstracts, the papers were selected and downloaded (or obtained through authors' institutions subscriptions). All papers were read and analysed to confirm their relevance to this review criteria (*D. alata*, chemical composition, functional properties, phytochemicals, physiological properties, unprocessed and processed food). Those with uncertainties regarding the taxonomical identification of *D. alata* and its cultivars, were not retained. Unless mentioned purposely, all statements and figures reported in the present review refer exclusively to *D. alata*, the greater yam.

3. Botanical characteristics

3.1. Taxonomy

Dioscoreales are an order of the monocotyledons. Their most diverse and important genus is *Dioscorea*, the type genus of the family Dioscoreaceae which includes about 600 species (Govaerts et al., 2007). Yam species are used for their pharmacologically active compounds in traditional medicine (Adomènienè and Venskutonis, 2022) and have high therapeutic potential (Obidiegwu et al., 2020). Most species are harvested from the wild for their bioactive compounds but such activity is threatening their fragile natural resources. Yams produce tubers but unlike the Irish potato (*Solanum tuberosum*), these tubers have no buds or eyes. Tuber germination occurs from a bud within the cambium in the tuber skin. The root system of the plant is very superficial. Several thick and long roots develop rapidly after the planted piece of tuber has sprouted. The stems are unable to support the heavy weight of the leaves and have to climb by twining on trees or on artificial stakes. The direction of twining, anticlockwise or clockwise, is a characteristic of each taxonomic section within the genus. *Dioscorea alata* belongs to the Enantiophyllum section (with *D. cayenensis* and *D. rotundata*) and twines to the right (clockwise) (Degras, 2013).

The name *alata* comes from its winged stems (Fig. 1). The stem cross-section is square with the corners being under the form of wings represented by a thin membrane of approximately 1 to 6 mm in width. All intraspecific classification systems based on morphological descriptions have failed to produce a clear structure. Cultivars can be classified by their ploidy levels, diploids, triploids and tetraploids, with diploids being the most common. Higher ploidy levels tend to produce larger tubers. These tubers weight an average of 3–5 kg/plant in 6–9 months, depending on cultivars. They present all sorts of shapes and the flesh colour can vary from homogeneous white or yellow to a deep purple. The shape of the leaves is very variable in size and form, with some being rounded, elongated, uplifted or sharply pointed. Tetraploids have leaves larger than diploids. The greater yam, just like all *Dioscorea* spp., is dioecious with male and female flowers on different plants. Many cultivars flower only rarely and, even more rarely, produce fertile seeds. The sex ratio is unbalanced and there are more male than female plants (Abraham and Nair, 1990). The fruits are dry dehiscent capsules (1–3 cm long) that can host up to six seeds but this is very unusual. Some cultivars produce bulbils in the axils of the leaves. These bulbils can be used for the propagation of the plant.

3.2. Phylogeny

Dioscorea alata processing is hypothesised to have started about 10,000 BP in New Guinea although starch grains were found on stone tools discovered on archaeological sites of New Guinea and dating 46,000 BP (Summerhayes et al., 2010). Its exact geographical origin is unknown and it could have been domesticated more than once in different regions. DNA markers have been used to elucidate this long standing enigma, with sometimes very conflicting results. For decades *D. alata* was thought to result from hybridization between two Asian species (*D. hamiltonii* and *D. persimilis*) but these two taxa are synonyms (Wilkin et al., 2007). AFLP markers revealed that *D. alata* shares a common genetic background with *D. nummularia*, a species found only in eastern Indonesia and Melanesia. Melanesia is also the centre of diversity of the greater yam where hundreds of cultivars exist (Malapa et al., 2005). DNA phylogeny confirmed that *D. alata* is closer to *D. hamiltonii* and to *D. nummularia* (Hsu et al., 2013; Couto et al., 2018). However, DNA markers studies also revealed that *D. alata* was closer to *D. calcicola*, *D. fordii*, *D. glabra*, while *D. hamiltonii* and *D. nummularia* were quite distant from this group (Viruel et al., 2018; Soto-Gomez et al., 2019). Surprisingly, in India, DNA markers indicated that *D. alata* was closer to *D. oppositifolia* than to *D. hamiltonii* (Padhan et al., 2019) while in China it was found to be closely related to *D. persimilis*, *D. polystachya* (also called *D. japonica, D. opposita* or *D. oppositifolia*) and *D. glabra* (Xia et al., 2019). These different studies revealed that some taxa are so close that they might not be different species, a conclusion that only adds to the overall confusion. The greater yam is clearly an Asian species but it is mainly cultivated in Africa.

3.3. Genetic diversity

When Austronesians originating from South Borneo (Kalimantan) colonized Madagascar approximately 2000 years ago, they probably introduced the greater yam, along with bananas (*Musa* spp.), and taro (*Colocasia esculenta*). However, recent studies suggested that transmissions via Northeast Africa was most likely (Power et al., 2019). From there, these crops could have been introduced to East Africa, central Africa, and to West Africa. *Dioscorea alata* imported from the Portuguese trading base on the island of São Tomé in the Guinea Gulf, was introduced and cultivated in the Caribbean at the end of the 16th century (Degras, 2013). AFLP markers could not differentiate Asian, African and Melanesian cultivars of *D. alata*, indicating their very ancient geographical distribution as clones over long distances (Malapa et al., 2005). Melanesian cultivars introduced in Benin contributed significantly to a broadening of the genetic base (Adoukonou-Sagbadja et al., 2014).

Another study in Nigeria found diversity within 100 accessions (97 hybrids and three cultivars) (Agre et al., 2019). A global survey of 643 accessions from Asia, Africa, the Caribbean and the Pacific, confirmed that diploids are more frequent than triploids and tetraploids, and that domestication occurred independently in Asia and in the Pacific with a narrow genetic base introduced in Africa (Sharif et al., 2020). In China, the DNA analysis of 142 accessions concluded that this region might have been an isolated domestication centre for the greater yam (Wu et al., 2019).

4. Nutritional composition

4.1. Consumers' preferences

The chemical composition depends mainly on the cultivar and there is significant variation within different countries (Table 1). The greater yam nutritional profile is excellent with low fat and high fibres content. Considering its high moisture content, the greater yam is comparatively less able to satisfy energy requirements than other tropical root crops: cassava and sweet potato (*Ipomoea batatas*), taro and cocoyam (*Xanthosoma sagittifolium*), but its proteins, minerals and vitamins contents are much higher (Ogidi et al., 2017). Local knowledge claims that there is variation between different cultivars for the culinary and palatability properties with some being suitable for certain preparations while others are not. Some cultivars need to be cooked much longer than others (Udensi et al., 2008). Just like for other root crops, the texture in the mouth is usually determined by various co-factors but mostly by softness of the cell walls, dry matter and starch contents (Champagne et al., 2009). In West Africa, cultivars most appreciated characteristics for boiled yam are raw tuber appearance (absence of rootlets), ease of peeling, white or yellow flesh colour, no oxidation during peeling and cooking, viscosity of cooking water and the ease of breaking the yam piece with a fork after cooking. Boiled yam must have a good aroma and the ease to chew is also considered as a high-quality characteristic. Mealiness, colour and taste are the most important variables contributing to general preference among consumers (Honfozo et al., 2021). In Melanesia, greater yam cultivars with good eating quality are characterised by high dry matter, starch and amylose content (Lebot et al., 2006). In Guadeloupe, West Indies, consumers consider the origin, taste, texture, external damage, and tuber size as important attributes characterizing cultivars quality (Barlagne et al., 2017).

In West Africa, greater yam is popular for producing boiled yam but some studies reported that due to their chemical composition, most local cultivars are unsuitable for pounded yam. For pounded yam, consistency, colour and stickiness are the most important variables contributing to general preference (Egesi et al., 2003). Tests were therefore conducted to compare *D. alata* to *D. rotundata*, the most preferred species for pounded yam, in order to assess its potential (Baah et al., 2009). It appeared that some cultivars present characteristics similar to *D. rotundata*, especially regarding the starch, amylose and fibres content but the texture of the greater yam flesh is usually not as firm. There is a strong interrelationship between final viscosity, setback and peak viscosity of the paste and the springiness, stickiness, cohesiveness and hardness of the pounded yam samples in both yam species (Otegbayo et al., 2006; 2021). In Ghana, greater yam cultivars presented significantly higher protein contents with higher peak time and pasting temperature when compared with the local yam *D. rotundata*. However, the dry matter and starch contents, swelling power and pasting viscosities were lower than the *D. rotundata* cultivar *Pona* highly appreciated for pounded yam (Wireko-Manu et al., 2011). A comparative study conducted in Nigeria with several *D. rotundata* cultivars revealed that the only *D. alata* cultivar assessed (*Kpetè*) for pounded yam was unsuitable (Honfozo et al., 2021).

Adeola et al. (2012) have shown that blanching of greater yam at 70°C for 10 min resulted in instant pounded yam of significantly higher sensory qualities compared to the one blanched at 70°C for only 5 min. Instant pounded greater yam blanched for 10 min compared fairly well with *D. rotundata* and it was concluded that it can be used to produce an acceptable instant pounded yam. When studying the pasting and sensory characteristics of the greater yam to assess its suitability for *amala*, a popular darkish paste prepared from slightly fermented flour, sensory results showed that greater yam was equally good if not better in texture and paste colour (Wireko-Manu et al., 2013a). Obviously, in West Africa, some cultivars are suitable for pounded yam or *amala* while others are not but it has been shown that genetically improved genotypes of *D. alata* in Nigeria have potential to satisfy consumers' requirements (Ukpabi et al., 2008). In Côte d'Ivoire, it has been suggested that the success and rapid adoption of *C18*, a greater yam cultivar introduced from Cameroon, was due to its ability to produce an appreciated pounded yam (Kouakou et al., 2012).

4.2. Starch

Starch is by far the major component of the greater yam tuber and it can represent up to 85% dry weight (d.w., Table 1). Some cultivars with 40% dry matter content have been identified and they usually correspond to late maturing types with a growth cycle up to ten months. But these extreme values are often not appreciated as they present a very dry texture in the mouth. The effect of different cooking techniques (open pan, pressure cooking and steaming) on the nutritionally important starch fractions and the extent of in vitro starch digestibility of greater yam tuber, has been investigated using controlled enzymatic digestion with pancreatin and amyloglucosidase. Steaming resulted in significant increase in total starch content and rapidly available glucose value. Cooking significantly decreased the amylose content but no significant difference was observed between the three techniques. It was suggested that pressure cooking is the best technique for cooking greater yam as it led to lower rapidly available glucose value (Ahmed and Urooj, 2008).

When it is processed into flour greater yam nutritional value is comparable to cereals (Trèche, 1998). In Ghana, it has been shown that when the cultivar *Akaba* is used, its flour has physicochemical, functional and pasting characteristics comparable to the best *D. rotundata* cultivar

(*Pona*) (Tortoe et al., 2017). Greater yam starch is easily extracted by grinding, filtering and successive sedimentation steps in water. However, non-starch polysaccharides present in the mucilage can render the operation complex and trap the starch grains thus reducing the yield of pure starch (Alves et al., 1999). Among all yam species, *D. alata* presents the larger starch grains with diameter of the granules up to 90 µm (Daiuto et al., 2005; Zhu, 2015). Compared with potato starch, the greater yam starch has lower swelling and solubility values (at 90°C) and both varied among five cultivars from 13.8–16.0 and 7.3–13.5 respectively (Amani et al., 2004). In Jamaica, significant variation between cultivars was also observed in the solubility, phosphorous content, crude fat content and gelatinization temperatures of the different cultivars starches and it was thought that their differing characteristics may fit different nutritional applications (Riley et al., 2006).

Finally, ten greater yam cultivars starches were analysed in Nigeria. Their swelling power was found to be in the category of high restricted-swelling starch (9.21–11.03% for flours and 9.49–13.80% for starches). It was observed that this characteristic is desirable for noodles and composite blends with cereals. The pasting temperature for flours (78.05–86.13°C) and for starches (80.38–86.15°C) and the pasting time for flours (4.44–5.17 min) and for starches (4.53–5.17 min) are adequate. Cultivars pasting properties of flours and starches confirmed that they represent a useful resource for food processing. However, the results presented significant differences among cultivars (Oke et al., 2013a). The suitability of five different cultivars starches for extrusion was also investigated and it was observed that due to its high starch content, the greater yam starch has a great potential as a food ingredient in extruded products and can be used for snacks, pre-gelatinized flours and breakfast cereals (Oke et al., 2013b). A study was conducted to clarify the effects of tempering, acid hydrolysis and low-citric acid-substitution on the chemical and physico-chemical properties of starches of four Nigerian *Dioscorea* spp., including greater yam. It was shown that relevant and suitable applications of the modified starches may be developed with a view of using them in industrial production, or as additives for specific purposes in foods (Falade and Ayetigbo, 2017).

4.3. Amylose

Starch granules with high amylose content absorb limited water content during cooking. The amylose content varies greatly (13.7–43.5% d.w.) (Table 1) and the amylose (A) versus starch (S) ratio is a palatability trait. Preferred cultivars for boiled tubers have a high A/S ratio (> 0.18) and cultivars with poor eating quality are characterized by low A/S ratio < 0.16, high mineral and high protein content (Lebot and Malapa, 2012; Ehounou et al., 2021). In Vanuatu, cultivars with very high amylose content are often preferred for a highly appreciated traditional dish called *laplap*, a sort of pudding prepared by grinding the tuber into a fine paste prior to cooking to produce an elastic starchy gel. It was observed that starch content correlated positively with dry matter content. Mineral, and protein contents correlated positively with each other, but correlated negatively with d.w. and starch. It is thought, however, that the age of the tuber has an effect on the amylose content for a given cultivar. A higher amylose content was observed in tubers harvested at full maturity than when harvested earlier (Huang et al., 2006). The post-harvest storage period (up to 4–6 months for *D. alata*) can also decrease the amylose content (Brunnschweiler et al., 2005). The ratio of amylose to amylopectin content of *D. alata* starch affects the starch properties and functional characteristics such as crystallinity and digestibility (Zhu, 2015; Harijono et al., 2016a).

4.4. Sugars

Urban consumers in West Africa and in Asia are looking for a compact shape, smooth tuber skin, a non-oxidizing white flesh, no bitterness and low sweetness (Baah et al., 2009). Sugars are responsible for the browning of the fried greater yam (Wireko-Manu et al., 2011). The reducing sugars content also determines the formation of acrylamide during high temperature cooking. With the processing of *D. alata* into fried products, low reducing sugars content is an important quality trait (Oluwole et al., 2017). Some cultivars present very low reducing sugar content and could therefore be appropriate for processing into chips or French-fries (Lebot et al., 2018a). The analysis of 216 cultivars from Vanuatu revealed a mean sugar content of 2.53% d.w., composed of sucrose (1.66%), glucose (0.36%) and fructose (0.51%). Forty cultivars from India, cultivated within the same plot, presented comparable mean values, with respectively 1.58, 0.27 and 0.51% d.w. Interestingly, improved hybrids presented very low soluble sugars values (1.33% d.w.) compared to cultivars from Vanuatu (2.53%) or India (2.36%) grown together within the same plot. These hybrids were first selected on their tolerance to anthracnose (*Colletotrichum gloeosporioides*) and tuber shape but also on their taste after boiling (Lebot et al., 2018a). Total soluble sugar content is an important trait and low sweetness is often favoured. Nevertheless, in Melanesia, a few cultivars are appreciated because of their sweet taste, which is confirmed analytically by the high sugar content (up to 5.71% for *Maligni*) (Lebot et al., 2006). In Taiwan, the crude lipid and fibre contents decreased with storage time but the reducing sugar contents increased during storage, regardless the different storage temperatures tested (Chou et al., 2006). In Ghana, it was shown that the tuber maturity, the time of harvest and the length of storage have significant impact on the physicochemical and pasting characteristics and tuber quality. However, sugars, along with dry matter content, starch, amylose, swelling power and pasting viscosities, were also impacted during storage. The greater yam tubers can be stored for up to five months without significant negative changes on tuber quality (Wireko-Manu et al., 2013b).

4.5. Proteins and amino acids

The greater yam cultivars present significant variation in protein content (4.1–20% d.w., Table 1). Very high protein content are found (15–20%) but they usually correspond to poor quality cultivars (Lebot and Malapa, 2012). Dioscorins represent approximately 85% of the total soluble protein content (Lin et al., 2009). Dioscorins are easily purified proteins and are found in high concentrations in some greater yam cultivars. These proteins have various physiological properties including antioxidant, immunomodulatory, estrogenic, angiotensin I-converting enzyme inhibiting, carbonic anhydrase and trypsin inhibiting, chitinase, insecticide, anti-mite, lectin and anti-proliferative activities and have therapeutic potential (Zhang et al., 2019).

It has been suggested that dioscorins are worth developing as healthy or functional foods (Lu et al., 2011). When comparing the antioxidant activities of dioscorins from greater yam, using the DPPH (2,2-diphenyl-1-picryl-hydrazyl-hydrate) and hydroxyl radicals scavenging activity assays, reducing power test and anti-lipid peroxidation test, it was found that *D. alata* dioscorin presented a higher antioxidant activity than *D. polystachya*, a species known for its high dioscorin content. This is due to the variation in amino acid composition and protein blends (Liu et al., 2006). The potential of *D. alata* dioscorin for the activation of the innate and adaptive immune systems was confirmed (Fu et al., 2006).

Dioscorin is essential for the process of tuberization (Liu et al., 2017). A proteome map of *D. alata* tuber has been developed in order to gain an overview of the biochemical pathways and their association to morphological changes in tuber development. Tuber growth is accompanied by dioscorin depletion along with sugar mobilization which is controlled by the oxidation-reduction (or redox) status of the tuber (Sharma et al., 2017). Growth-specific markers for tuber germination (ascorbate peroxidase, monodehydroascorbate reductase, invertase) and for tuber formation (sucrose synthase) were validated by enzyme activity assays (Sharma and Deswal, 2021).

Raman spectroscopy has been used to show that in greater yam the secondary structure of dioscorin A (molecular weight [MW] ~ 33 kDa) is mostly made of alpha-helices whereas that of dioscorin B (MW ~ 31 kDa) is significantly different (Liao et al., 2006). The major amino acids (phenylalanine, tyrosine, methionine, tryptophan and cysteine) complex exhibited a clear difference between dioscorins A and B. They exhibit antioxidant, antihypertensive and immunomodulatory properties and can protect airway epithelial cells against mite allergen. They also show some enzyme activities, and present minor trypsin-inhibitor activity (Liu et al., 2016). Essential amino acids were determined in China from nine cultivars with the following contents (in g/100g yam proteins): Threonine (3.88–7.81% proteins), Valine (1.32–2.98%), Methionine (0.40–2.97%), Isoleucine (1.64–4.47%), Leucine (2.16–4.73%), Phenylalanine (1.77–5.45%), Lysine (3.92–8.11%), Histidine (1.87–4.80%), and non-essential amino acids: Asparagine (2.51–9.93%), Serine (3.10–8.37%), Glutamine (7.70–11.98%), Proline (1.99–4.15%), Glycine (1.60–4.72%), Alanine (3.29–7.72%), Tyrosine (0.38–2.15%), Arginine (7.96–13.43%) (Wu et al., 2016). Tryptophan (another essential amino acid) was quantitated in 101 cultivars from India and Vanuatu with values varying from 0.0–369.2 mg/100 g d.w. (Muñoz-Cuervo, 2015).

4.6. Fibres

Greater yam cultivars are rich in dietary fibres (1–12% d.w.) (Table 1). The fibres are very useful for the digestive system and adequate fibre content increases water holding capacity, aids in regular bowel movement, and accelerates the intestinal transit. Whole brown rice is often reported to be a food with high fibre content with 5% d.w. Many greater yam cultivars present higher value with some having total dietary fibres around 10% which is comparable to the whole wheat flour (approx. 12%). Not surprisingly then, a daily diet rich in greater yam can contribute significantly to dietary fibres requirements satisfaction. It has been suggested that if greater yam is not ideal for the sticky and cohesive yam products such as pounded yam or *fufu*, it could be due partly to its relatively high fibres content. However, it is also observed that cultivars combining high amylose and total dietary fibre contents could be useful in diets for diabetics and health conscious consumers (Wireko-Manu et al., 2013c).

4.7. Minerals

The greater yam is a good source of dietary minerals such as calcium, iron, zinc and phosphorus, which are known to be beneficial for health. Total minerals content vary from 2.7 to 8.1% d.w., depending on cultivars and country of origin (Table 1). Consumption of greater yam can contribute significantly to the daily need in calcium (Ca) with values ranging from 25 to 75 mg/100 g f.w. Zinc is considered as an essential micro nutrient in healthy diets and greater yam appears to be a good source with values up to 4.3 mg/100 g. Phosphorus, magnesium, potassium and iron are also in significant amount, indicating that greater yam is a good source with nonetheless tremendous variation between cultivars. Potassium is the most important mineral. In Nigeria, a range of 775 to 1850 mg/kg of potassium has been reported (Otegbayo et al., 2018) and confirms previous values of 1157–2016 mg/kg d.w. of potassium in different cultivars of *D. alata* (Baah et al., 2009) which suggests that greater yam contributes significantly to consumers potassium needs. In Sri Lanka, the most predominant minerals in local cultivars were K (4750–5120 µg/g), Mg (170–210 µg/g), Na (40–260 µg/g), Zn (9.82–15.95 µg/g) and Fe (23.47–25.63 µg/g) with, however, clear significant differences observed among different accessions (Kalasinghe et al., 2018).

The effects of boiling, steaming and baking the greater yam tuber pieces have been investigated to assess their impact on their nutrients. It appears that total crude protein contents tend to decrease with cooking, but the differences were not statistically significant. Crude fat, crude fibre, starch and total sugar contents were unaffected. However, the water-soluble minerals leached out during boiling, thus causing a reduction in the mineral content of boiled tuber pieces. Furthermore, the three cooking methods significantly reduced the vitamin C content in the tuber pieces (Wanasundera and Ravindran, 1992). Minerals content is impacted by post-harvest storage. A study conducted in Côte d'Ivoire to assess changes up to six months after harvest has shown that minerals content of cultivar *Bété bété* tuber significantly decreased during storage. (Kouakou Dje et al., 2010).

4.8. Organic and fatty acids

A preliminary survey of five greater yam cultivars from Papua New Guinea identified organic acids as malic acid and citric acid with, respectively 123 and 127 mg/100 g f.w. and in four cultivars from the Solomon, respectively 87 and 157 mg/100 g f.w. (Holloway et al., 1989). In Côte d'Ivoire the greater yam cultivar *Bété bété* is widely cultivated and appreciated and its organic acids were analysed: gallic acid and tannins (1380 mg/100 g d.w.), citric acid (1130 mg/100 g), ascorbic acid (880 mg/100 g), tartaric acid (1013 mg/100 g), sulfanilic acid (12 mg/100 g) and fumaric acid (4 mg/100 g). The content of all these compounds decreased significantly after boiling tuber pieces for more than 20 min. (Didier et al., 2014). A survey conducted on 91 cultivars planted together within a common plot in Vanuatu, to control possible environmental effects, identified not less than fourteen organic acids (Fig. 2) and quantitated them using GC-MS (Table 2) (Mercier, 2013). Organic acids represented approximately 2.9% d.w. among cultivars and fatty acids represented 0.21% d.w. Oxalic acid is an anti-nutritional factor but the 91 cultivars presented very low values (18.41 mg/100 g). The detection of malonic acid is rather surprising as it can be toxic when in high content but the values were low (59.02 mg/100 g). Citric acid was by far the most important organic acid because of its positive influence on taste perception and kidney functioning. Its mean content was variable (CV= 30.03%) but quite high (2668.87 mg/100 g), content at which it can play an essential role against tuber flesh browning. The dominant fatty acids were oleic acid (mean 19.29 mg/100 g d.w.) and linoleic acid (116.04 mg/100 g) (Table 2).

4.9. Mucilage

The greater yam tuber flesh is rich in mucilage. Three Taiwanese cultivars (*Tainong 1, Tainong 2*, and var. *purpurea,* a purple-fleshed cultivar) were studied to compare their properties. It was concluded that their mucilages presented different antioxidant activities against DPPH (2,2-diphenyl-1-picryl-hydrazil-hydrate) radicals, hydroxyl radicals and superoxide radicals. Furthermore, the purification process was able to partially increase the antioxidant activity of the mucilage polysaccharides. Greater yam mucilaginous polysaccharides may act as important radical scavengers and antioxidants (Lin et al., 2005). The purified mucilage is composed of arabinose, galactose, glucose and rhamnose. This mucilage has a significant effect on the gelatinisation properties of the greater yam starch. The addition of mucilage was tested and resulted in a significant increase in peak viscosity of the starch. It has been shown that compared to the starch alone, the addition of mucilage resulted in a slight decrease of swelling power for greater yam starch (Huang et al., 2010).

5. Bioactive compounds

The greater yam is rich in useful and healthy secondary metabolites: phenolic acids, flavonoids, and anthocyanins. Their antioxidant activities is, however, highly dependent on the drying process and the extraction solvent used to prepare the samples prior to testing, as well as on the analysed part of the tuber (Chung et al., 2008) and the analytical technique used. A preliminary HPLC screening of twenty different cultivars revealed significant variations with seven anthocyanins, five flavonols (including quercetin-3-glc(pyr) and quercetin-3'-glc,6'-acet), four flavanols and two phenolic acids (Champagne et al., 2011). GC-MS profiling aiming to assess the potential of metabolomics was conducted on the polar and lipophilic extracts from tubers of 49 cultivars belonging to four *Dioscorea* spp., including five cultivars of *D. alata*. Not less than 123 metabolites were identified in greater yam cultivars and these cultivars were chemically differentiated from the three other species using multivariate analyses on these metabolites (Price et al., 2017). HP-TLC allowed high throughput analysis of the most important metabolites in several hundreds of cultivars (Lebot et al., 2018a, b; 2019) (Table 3).

5.1. Phenolic compounds

When compared to other cultivated yam species, there is a prevalence of phenolic compounds in the greater yam irrespective of the cultivar (Ozo et al., 1984). The total phenolic content of its ethanol and water extracts were determined in India to assess the antioxidant potential of one cultivar. The ethanolic extract contained large amounts of flavonoids, flavonols, proanthocynidins and phenolic compounds, and exhibited reducing power and free radical quenching properties. The in vitro free radical quenching potential of crude extracts of tubers were found comparable to those of the pure standard compounds (gallic acid, ascorbic acid, quercetin and catechin). However, the individual compounds responsible for the antioxidative activity were not identified (Narkhede et al., 2013). In India, phenolic acids and flavonoids (21 compounds) were quantified in a greater yam ethanol extract and kaempferol (9.219 mg/100 g d.w.) and myricetin (4.613 mg/100 g d.w.) were detected as the major constituents, while the other identified phenolics were less than 1 mg/100 g d.w. (Chaudhury et al, 2018). Another study on a purple-fleshed cultivar from China reported the presence of quercetin dehydrate, kaempferol, ferulic, sinapic, caffeic and p-coumaric acid and vanillic acid. The total phenolic content was highest in the proximal and mid sections of the tuber and lowest in the distal wetter section (Zhang et al., 2018).

In Sri Lanka, a widely distributed cultivar (*Raja ala*) has been studied to analyse the effect of boiling on its antioxidant activity. Different treatments were compared: an extract of the raw tuber flesh used as control, boiled yam extract prepared with water used in boiling and boiled yam extract prepared with fresh water. The boiled yam prepared using fresh water had significantly lower antioxidant activity than the other treatments based on the total phenol, monomeric anthocyanin and the total antioxidant capacity (TAC) measured by FRAP (Ferric Reducing Antioxidant Power) and reducing power assays. It also had significantly lower DPPH radical scavenging capacity, total flavonoid and condensed tannin content compared to the raw yam extract. Discarding of water used for boiling resulted in significant loss of water soluble antioxidants compounds. It is then recommended that minimal water should be used, and not discarded, to retain the maximum antioxidants when cooking *Raja ala* (Abeynayake and Sivakanesan, 2014). Another study conducted with *Raja ala* in Sri Lanka, comparing boiling and pressure cooking using antioxidant assays, suggested that a higher amount of antioxidants are present in the cooking water when the tuber pieces are boiled rather than pressure cooked. However, as the overall results showed that the cooking water of both methods is a good source of bioactive compounds, it was recommended to further investigate these compounds to find alternative uses of the waste cooking water (Amarasekara and Wickramarachchi, 2021

In Côte d'Ivoire, it was suggested that the reduced oxalate content in boiled *Bété bété* cultivar could present a positive impact as the reduction of oxalate levels was expected to enhance the bioavailability of essential minerals and to reduce consumers' risk of kidney stones formation. Boiling also decreased significantly tannin contents to levels too low to cause any adverse effect. Furthermore, reduced phytates values in boiled yam tubers were expected to enhance the bioavailability of protein and dietary minerals (Facchinetti, 2021). Storage was also found to reduce significantly total phenolic compounds, which were higher in proximal parts of the tubers (Kouakou Dje et al., 2010). In Taiwan, the antioxidant activity of the greater yam was found to significantly decline in both the reducing power after three weeks and for the DPPH radical-scavenging activity after eleven weeks of storage at room temperature and 17°C (Chou et al., 2006).

5.2. Flavonoids

Two cultivars from Nigeria were analysed using HPLC and were shown to contain (+)-catechin, the procyanidin dimers B-l and B-3, and two other procyanidins, most probably a trimer and tetramer. The presence of cyanidin-3-monoglucoside was confirmed (Ozo et al., 1984). It has been shown that in Benin, tuber flesh browning correlates with total phenol and dry matter contents and is probably due to catechins (Akissoé et al., 2005). Gallocatechin, epigallocatechin or catechin- and epicatechin-gallate have been reported in freeze-dried cultivars tuber samples using HPLC (Champagne et al., 2011). Catechins were found in greater yam cultivars from India and hybrids (means of 5.31 and 3.11 mg/g d.w. respectively). Cultivars from Vanuatu presented values lower than Indian accessions and hybrids (respectively 4.87, 5.07 and 5.69 mg/g) but significant variation was observed within each geographical origin, as shown by the high standard deviations. Catechin and epicatechin were the most important catechins but two unknown catechins (Cat1 and Cat2) were also detected (Lebot et al., 2018a) (Table 4).

In India, Padhan et al. (2019) found the total flavonoids content of the greater yam to be significantly lower compared to eight wild *Dioscorea* spp. with overall values ranging from 0.62 to 0.85 mg/g d.w. In Sri Lanka, flavonoids content of two cultivars were 5.2 mg/100 g d.w. for *Raja ala* and 9.8 mg/100 g d.w. for *Higur ala* (Senanyake et al., 2012). In Bangladesh, HPLC analysis of a local cultivar methanolic extract identified 19 metabolites (Table 3) but the antioxidant and antibacterial activities of the extract were thought to be due to myricetin (Anisuzzman et al., 2016). In India, HPLC analysis of dried flours from greater yam tubers collected in West Bengal identified 21 compounds, kaempferol being the most important compound with 9.2 mg/100 g d/w. It was concluded that the regular intake of greater yam containing kaempferol at such high content is thereby reducing the risk of cardio vascular diseases, cancer, arteriosclerosis (Chaudhury et al., 2018) (Table 3).

The flavonols caryatin ($C_{17}H_{14}O_7$) and 3′ -O-methylcaryatin are present in some cultivars with contents reaching up to 179 and 241 µg/g d.w. respectively. It appears that these substances are the main contributor of the antioxidant activity when using the ABTS assay. Caryatin alone explained over 90 % of the total antioxidant activity of a tuber methanol extract (Fel et al., 2021).

5.3. Anthocyanins

When comparing the greater yam to other tropical root and tuber crops, the greater yam presented highest total anthocyanins content compared to other crops (Table 5). Great variation in total anthocyanin contents was measured in 20 cultivars with thirteen HPLC peaks identified as anthocyanins including seven major ones. Despite obvious differences in composition, particular attention was paid to one component that represented more than 50% of the total anthocyanin peaks area in all cultivars (Champagne et al., 2011). In Taiwan, purple-fleshed cultivars contain substantial amounts of anthocyanins, mostly cyanidin or peonidin acylated glycosides (Fang et al., 2011). Five different pigments from purple-fleshed tubers were separated by HPLC-MS and the anthocyanin fraction was collected for evaluation. Their anti-inflammatory effects were investigated at different concentrations in the mice. It was found that 80 µg/kg of anthocyanins produced potent anti-inflammatory effects in the mouse model for inflammatory bowel disease. It was suggested that these anthocyanins may be applied as a potential food supplement (Chen et al., 2017a).

In China, the analysis of a purple-fleshed cultivar allowed the separation and identification of cyanidin 3-gentiobioside, alatanin C, cyanidin 3-ferulyl gentiobioside, cyanidin 3-sinapylgentianoside, peonidin 3-gentiobioside and alatanin 2. The dominant anthocyanin in this cultivar was alatanin C and accounted for about 46.3% of the total anthocyanins (He et al., 2015). In the Philippines, the cultivar *Ubi* is grown to satisfy the colorant needs of the ice cream industry. Alatanin A, B and C have been confirmed as the major anthocyanins in cultivars grown in the Philippines (Yoshida et al., 1991; Moriya et al., 2015). In two Thai purple-fleshed cultivar, the major anthocyanin found was also alatanin C (cyanidin 3-(6-sinapoyl gentiobioside) (Srivichai and Hongsprabhas, 2020).

The transcriptome of tubers from a purple-fleshed cultivar and a white-fleshed cultivar of greater yam has been conducted along with molecular markers. Genes encoding chalcone isomerase, flavanone 3-hydroxylase, flavonoid 3′-monooxygenase, dihydroflavonol 4-reductase, leucoanthocyanidin dioxygenase, and flavonol 3-O-glucosyltransferase were found to be significantly up-regulated in the purple-fleshed cultivar suggesting that they are potentially associated with tuber flesh colour and their expression was confirmed by qRT-PCR. It was suggested that the key genes associated with the purple-flesh trait would provide valuable information on the molecular process of regulating pigment accumulation and that this information could be used to genetically manipulate white-fleshed cultivars to convert them into purple flesh (Wu et al., 2015).

Steaming of a purple-fleshed cultivar increased phenolic contents from 85.36 to 167.22 mg/100 g d.w. GAE (gallic acid equivalent) and raised anthocyanin level from 36.09 to 57.28 mg/100 g d.w. CGE (cyanidin-3-glucoside equivalent) (Imanningsih et al. 2013). Steam-cooking did not affect the antioxidant capacity of the purple-fleshed cultivar. It was found that it could help to retain phenolic compounds in purple yam while making them more available for consumption. The responses to heat and O_2 of phenolic compounds were thought to be influenced by the contents of indigenous phenolic compounds and flavonoids prone to PPO (polyphenol oxidase) activities (Cakrawati et al., 2021).

The greater yam is a good source of antioxidants but most often they are consumed after boiling and pounding and these cooking methods impact directly the chemical composition of the food. The total phenol, total flavonoid, anthocyanin and tannin contents have been measured before and after boiling. The total phenol and anthocyanins contents of the boiled yam are significantly lower. As most antioxidants are water soluble compounds, the discarding of the water after boiling results in significant losses. Hence, processing of yam with minimal water that is not discarded should be recommended to get the maximum benefit from these water soluble compounds (Abeynayake and Sivakanesan, 2014).

5.4. Carotenoids

An HPLC analysis of 17 cultivars from Vanuatu detected seven major peaks including lutein, all-trans-β-carotene and zeaxanthin (Champagne et al., 2010). Five cultivars analysed using HPLC in Indonesia presented five major peaks and three were identified as lutein, all-trans-β-carotene and zeaxanthin with 23.75 to 132.12 µg/100 g d.w. (Nadia et al., 2015). Distinct species-specific carotenoids of five cultivars from Nigeria have been analysed (including all-trans-β-carotene and βcarotenes epoxides) and multivariate analyses succeeded to differentiate them from 46 cultivars belonging to four other cultivated yam species. Overall, the β-carotene contents of all 46 cultivars were low (96.3–326 µg/100 g d.w.) compared to plants rich in such compounds (e.g., carrots or sweet potato). However, the five greater yam cultivars presented greater α-tocopherol with greater β-carotene content and had significantly more provitamin A activity than *D. rotundata* cultivars. Greater yam cultivars also had noticeable quantities of 13-cis-β-carotene. But if the β-carotene epoxides are included, then provitamin A content of some cultivars could be comparable to rich plants but their provitamin A activity in humans remains unknown (Price et al., 2018). In India, the β-carotene content ranged between 0.97 and 1.88 µg/g d.w. in fifteen cultivars (Patel et al., 2019).

A comprehensive survey conducted on 101 cultivars from Vanuatu and India (planted together within the same plot) using acetone and hydro-alcoholic (ethanol) extraction identified 56 distinct compounds with HPLC, including fifteen carotenoids, one indol (tryptophan), four phenolic acids, seven hydroxycinnamic acids, fifteen flavanols/flavanones, eight flavonols/flavones, four anthocyanins, and two unknown compounds (Muñoz-Cuervo, 2015). Cluster analysis showed that the cultivars rich in carotenoids and anthocyanins form separated clusters and are differentiated from others (Fig. 3) due to the positive correlations existing between the different compounds of these two groups (Fig. 4).

5.5. Saponins

Saponins exist in most *Dioscorea* spp. (Sautour et al., 2007). They are often associated to bitter taste. Their abundance in some greater yam cultivars is thought to contribute to poor tuber quality (Ezeocha and Ojimelukwe, 2012). Yam saponins have been shown to present different properties including blood pressure-lowering, anti-inflammation, antifungal and have been shown to inhibit thrombosis in mice (Li et al., 2010). After hydrolysis, these saponins are converted into a steroidal aglycone called diosgenin, which is used as a source of steroid hormones by the pharmaceutical industry (Jesus et al., 2016). The major yam saponins are dioscin, gracillin, protodioscin and protogracillin. Dioscin is the most important and well documented saponin. It presents antitumor activity, suppresses cancer cells growth, and is cytotoxic towards leukemia and cervical carcinoma cells. Dioscin is also efficient against gastric cancer, breast cancer, alcoholic liver fibrosis and obesity. It could be used for the treatment of acute lung injury and renal ischemia injury. Overall, not less than fourteen physiological activities are well documented for dioscin (Yang et al., 2019).

Dioscin has been detected in greater yam cultivars from Taiwan (Yang et al., 2003), from China with contents varying from 0.06 to 0.09% d.w. (Wu et al. 2019) but not in *D. alata* cultivars from Japan (Nakayasu et al., 2015). However, Shan et al. (2020) could not detect it in two cultivars from China. Diosgenin has been identified in a greater yam cultivar from India (Shah and Lele, 2012; Cynthia et al., 2019) and China (Yang et al., 2019). Several studies report the presence of dioscin or diosgenin in cultivars extracts (Kaur et al., 2021; Harijono et al., 2016b; Jesus et al., 2016). However, a comprehensive review of saponins present in *Dioscorea* spp. did not report dioscin in *D. alata*, nor other saponins (Sautour et al., 2007). Kwon et al. (2015) analysed fifteen accessions and breeding lines in Nigeria and did not detect dioscin in greater yam. Dioscin, protodioscin, gracillin and protogracillin were not detected in 550 accessions representative of a wide geographical diversity (Lebot 2018ab; 2019). It is quite clear that the domestication process, which has led to the selection of the present cultivars, has favoured genotypes with low saponins and catechins contents. It is therefore unclear if the presence of dioscin (and diosgenin) is genetically controlled in the greater yam, with some primitive cultivars presenting dioscin while it is absent from more improved ones. Or, if these discrepancies are due to analytical artefacts, an insufficient coverage of the genetic diversity, or, and most likely, to taxonomic misidentifications which are quite frequent among *Dioscorea* spp.

5.6. Allantoin

Allantoin (an ureide, hydantoin) is one of the most interesting secondary metabolites found in the greater yam. It has remarkable antihypertensive action and has a dose-dependent ability to decrease plasma glucose and increase plasma β-endorphin levels in diabetic rats that is not observed in normal rats (Niu et al., 2010). It is safe and non-toxic and it has been suggested that it could be developed as a new therapeutic agent (Chen et al., 2014). It is reported that allantoin improves the smoothness of the skin, promote cell proliferation and contributes to rapid wound healing (Go et al., 2015). In Taiwan, allantoin has been shown to protect the stomach tissues and inhibit the growth of tumours. It has anti-diabetic effect, can modulate oxidative stress and antioxidant activities; it can improve kidney and liver functions while maintaining insulin and glucose levels. Allantoin was quantified in *D. opposita* (syn. *D. polystachya*), a species known to present high allantoin content with values ranging from 13.68 to 18.65 mg/g d.w. (Liu et al., 2016). An analysis of 208 cultivars and hybrids from Nigeria, India, Vietnam, Papua New Guinea, and Vanuatu, revealed values ranging from 9.42 to 29.1 mg/g d.w. of allantoin in *D. alata* (Lebot et al., 2019a). In China, allantoin varies from 6.20 mg/g to 14.9 mg/g d.w. in nine local cultivars (Wu et al., 2016) and allantoin content was shown to be highly correlated with starch content (Shan et al., 2020).

5.7. Antinutritional compounds

The oxalate content is small compared to other root crops (Bradbury and Holloway, 1988; Mercier, 2013). One of the major alkaloids in yam is dioscorine, a toxic isoquinuclidine alkaloid with molecular formula $C_{13}H_{19}O_2N$ but so far dioscorine has been reported only in wild yams, especially in *D. hispida* and not in *D. alata*. However, among the different antinutrients which have been identified in *D. alata* cultivars in Nigeria are alkaloids, saponins, flavonoids, and tannins but their contents were significantly reduced in the boiled tubers (Ezeocha and Ojimelukwe, 2012). Senanayake et al. (2012) recorded alkaloid contents of 0.94, 1.64 and 1.89 mg/100 g in greater yam cultivars (*Raja ala*) and (*Hingur ala*) in Sri Lanka.

Low levels of antinutritional compounds were identified in seven greater yam cultivars from Nigeria (IITA): alkaloids (0.12–0.55% d.w.), trypsin inhibitor (24–49 TIU/g) and heamagglutinin (1.22–5.75 Hu/g), phytic acid (0.22–0.28% d.w.), tannins (54.75–176.09 mg/100 g), hydrogen cyanide (9.6–12 mg/kg d.w.) (Udensi et al. 2010). In India, total oxalate contents were significantly low after boiling and the loss of oxalates was greater with boiling (40–50%) compared to steaming (20–25%) and baking (12–15%) (Wanasundera and Ravindran, 1992; 1994).

In Côte d'Ivoire, the antinutritional compounds analysed in the raw flour and boiled flour of the cultivar *Bété bété* were quantitated to assess the impact of the time of cooking (30 min.). The total oxalate, soluble oxalate, tannins and phytates were, 650, 397, 138 and 840 mg/100 g d.w., respectively, while these values decreased to 345, 144, 84, 529 mg/100 g d.w., with total compounds decreasing from 333 to 152 mg/100 g d.w. (Didier et al., 2014). In Nigeria, the presence of tannins, phytates and oxalates ranging from 56–1970 mg/kg, 270.7–379.4 mg/kg and 487–671 mg/kg d.w., respectively, were recorded in 43 cultivars from five yam species including greater yam. Using spectrophotometry methods, cyanide was also reported in *D. alata* sampled from Yogyakarta, Indonesia, but at extremely low levels (0.049 mg/100 g) compared to cassava (0.1098 mg/100 g) (Widiastuti et al., 2017).

5.8. Browning and polyphenol oxidase (PPO)

When the greater yam is processed into flour, there is tremendous variation between cultivars with some being non-oxidizing while others turn brown in a few seconds after cutting the fresh tuber into pieces. It has been suggested that the browning in raw and processed tubers results from enzymatic polyphenol oxidase (PPO) and peroxidase activities. In Benin, where yam tubers are processed to obtain a flour, whole tubers or pieces are traditionally blanched at an intermediate temperature (60–75°C) before drying. There is no significant variation in phenol content during blanching but it increases during drying. This is a problem as sun drying of the tubers into dried chips is the traditional process in West Africa. The flesh of the fresh tuber of cultivar *Florido* is usually white but *amala* (a popular paste in Benin) made from dried flour, turns brown during processing and the quality of the final product is therefore not acceptable. It was found that there is a relationship between the *amala* browning and the total phenol content of the flour: the higher the phenol content, the darker the final product (Akissoé et al., 2005).

Total catechins values are significantly correlated with the colour of the flour indicating that they contribute to the browning of the greater yam flesh tuber. Catechins were not detected in cultivars from Vietnam and Papua New Guinea and only 25 cultivars from Vanuatu (over a total of 216 analysed) presented catechins in low values. Most local cultivars from Nigeria presented catechins but the highest mean value was found in hybrids (Table 4). The presence of catechins in high amounts in greater yam cultivars can be considered as a wild trait. Most high quality cultivars present low or no catechins, while hybrids between parents originating from distant genepools, present high catechins. High catechins content, along with hairy tubers, poor shape, spines at the base of the stems, are deleterious traits resulting from true seeds. Some cultivars from Nigeria present high levels of catechins which could explain the browning of their flour or puree. This might indicate that these clonally introduced cultivars are very ancient (Lebot et al., 2018b).

Oxidation is most obvious when new hybrids are produced through conventional cross-pollination since a high proportion of oxidizing tubers is found among progenies. When recently created hybrids were analysed in Guadeloupe (West Indies), it was found that the genotype susceptibility to browning depends on the total phenolics and catechins contents of the pulp but also on the degree of polymerization of the flavanols. It was observed that cultivars tolerant to browning were those with high levels of procyanidins and these compounds are known to reduce PPO activity. Hybrids susceptible to browning were found to present high levels of catechins which are a good substrate to PPO (Rinaldo et al., 2022).

Different analytical techniques detect different compounds in methanolic greater yam extracts. Table 3 present the most important compounds ranked in decreasing order of values quantitated by HPLC (Anisuzzman et al., 2016; Chaudhury et al., 2018), GC-MS (Price et al., 2017), and HP-TLC (Lebot et al., 2018ab, 2019). Independently of the country of origin and the technique used, catechins were detected in greater yam tubers. It is, however, difficult to compare these results as different studies analysed different cultivars.

6. Biological activity and health benefits

There are numerous reports, especially from India and China, indicating that the greater yam boiled tubers have different health-beneficial activities, including anti-gonorrhoea, anti-leprosy, anti-inflammatory, anti-rheumatism. It is also known of being purgative, diuretic, to prevent cancer, reduce blood sugar, and diabetes. Most of these reported properties are found in ethno-botanical surveys (Jadhav et al., 2011; Sakthidevi and Moran, 2013; Dey and Chaudhuri, 2014). Several studies have confirmed the antioxidant activity of the different extracts obtained from the greater yam tuber with different solvents using the FRAP, TEAC assays, O_2 and DPPH-scavenging activities, as well as metal chelating assays. Methanolic extracts of the raw tuber were shown to present high antioxidant activity (Anisuzzman et al., 2016). It is thought that the acetone extract contains potent antiproliferative properties. A study performed on two cancer cell lines, has shown that the extract displayed anticancer properties resulting in the initiation of apoptosis, the death of cancer cells. It was suggested that the greater yam may serve as a source for new anticancer compounds (Wallace et al., 2021). Powders or flours prepared from dried tubers also presented high antioxidant activity (Adedayo et al., 2012; Das et al., 2012; Chaudury et al., 2020; Guo et al., 2004; Larief and Dirpan, 2018; Ratnanningsih et al., 2018). These studies, however, did not succeed to isolate the compounds responsible for such remarkable activity. A few of greater yam physiological properties have been tested in cell or animal experimental studies. Experiments conducted with mice have shown that methanolic extracts has significant antidepressant and anxiolytic activities (Ruhul Amin et al., 2018).

6.1. Cardioprotective properties

In Taiwan, cultivar *Tainong no. 1* is often used in traditional medicine. A study was conducted to test the antihypertensive potential of dioscorin, the protein extracted from fresh tubers purchased from wholesalers (and representing about 90% of its water soluble proteins). Among the pharmacological products used in the treatment of hypertension, angiotensin converting enzyme (ACE) inhibitor presents a low rate of adverse side effects and is among the preferred antihypertensive agents used when treating patients. Purified dioscorin was used for the determination of ACE inhibitory activities and was found to be dose-dependent of these inhibitory activities. It was therefore concluded that greater yam consumption might contribute to hypertension control (Hsu et al., 2002).

Elevated plasma homocysteine is considered to be a risk factor for cardiovascular diseases. It can be induced by excessive oral intake of methionine which causes an increase in plasma oxidation markers and a decrease in antioxidant capacity in humans. A study was conducted with rats fed with methionine to see if a diet based on cultivar *Tainung no. 2* in Taiwan could have a beneficial effect on rats. After 12 weeks of freeze-dried powder feeding, the results indicated that elevated plasma homocysteine (induced by methionine) could be reversed by greater yam feeding which also resulted in significant antioxidative effects (Chang et al., 2004). In Taiwan, powdered greater yam and liquid products, were used to analyse their health benefits and to investigate the potential antihypertensive activity they might have on spontaneously hypertensive rats (SHR) fed with such products during 30 days. It was found that both type of products have significant antihypertensive activities toward SHRs (Liu et al., 2009). Another study explored how it could protect the heart from doxorubicin (DOX)-induced oxidative stress leading to cardiotoxicity in vivo. It was conducted by feeding greater yam extracts given to experimental mice. The extract decreased the cardiac levels of thiobarbituric acid, reactive oxygen species, and inflammatory factors. The extracts also played a role in increasing the activities of glutathione peroxidase and superoxide dismutase, thus improving the DOX-induced alterations in the heart tissue of DOX-treated mice. This study concluded that the greater yam has significant cardioprotective properties against DOX-induced damage via its multiple effects on antioxidant, anti-inflammatory, and antiapoptotic activities. Some ethanol extracts contain more than 20% diosgenin, a compound known to significantly improve the cardiac damage induced by DOX. Hence, diosgenin may be responsible for the antioxidant, anti-inflammatory, or antiapoptotic activities of the extracts but its overall contribution to greater yam cardioprotective benefices remains to be determined (Chen et al., 2017a).

6.2. Protection of postmenopausal symptoms

The greater yam has been traditionally used to treat menopausal symptoms in Taiwan. A first study was conducted to clarify its effects on lipids, antioxidant status, and sex hormones in postmenopausal women. Twenty-four healthy postmenopausal women were asked to replace their rice diet with 390 g of boiled tuber pieces in two of three meals per day for 30 days. It was observed that after ingestion, there were significant increases in serum concentrations of estrone (+26%), sex hormone binding globulin (SHBG) (+9.5%), and significant increase in estradiol (+27%). Urinary concentrations of the genotoxic metabolite of estrogen, 16-hydroxyestrone decreased significantly by 37%. Plasma cholesterol concentration decreased significantly by 5.9%. Lag time of low-density lipoprotein oxidation prolonged significantly by 5.8% and urinary isoprostane levels decreased significantly by 42%. It was concluded that replacing two thirds of rice with boiled greater yam tubers for 30 days improves the status of sex hormones, lipids, and antioxidants and that these positive effects might reduce the risk of breast cancer and cardiovascular diseases in postmenopausal women (Wu et al., 2005). Cheng et al., (2007) purified and identified new compounds from cultivar *Tainung no. 2* ethyl acetate extract: hydro-Q_9 chromene and γ-tocopherol-9, together with four known compounds, RRR-R-tocopherol, coenzyme Q_9, cycloartane, and 1-feruloylglycerol. Five of these compounds were shown to have estrogenic activity. It was concluded that the results provide evidence for the beneficial effect for menopausal women.

A second study was conducted in Taiwan with cultivar *Tainung no. 2* to assess the effect on the bone density of ovariectomised female mice. After 12 weeks of feeding the mice with yam flour, the uterine weight, and indices of bone mass were recorded. *Tainung no. 2* prevented loss of bone mineral density and improved bone calcium status without stimulating uterine hypertrophy in mice. It was concluded that *Tainung no. 2* may be beneficial for postmenopausal women for preventing bone loss (Chen et al., 2009). A third Taiwanese study examined greater yam efficacy in the treatment of menopausal symptoms on 50 women. An evident improvement was recorded for feeling tense, nervous or excitable, insomnia, musculoskeletal pain as well as on the blood hormone profile among women (Hsu et al., 2011). Finally, a fourth study showed that greater yam proteins presented potential to upregulate the translational levels of estrogen receptor beta, thus possibly reducing the risk of ovarian cancer (Lu et al. 2016). For this latter biological activity, the bioactive proteins were identified as the bioactive compounds directly contributing to the mechanisms underlying the beneficial effects of greater yam although no bioguided fractionation was conducted to assign the activity to a specific protein or protein class.

6.3. Anti-microbial activity

The effects of the greater yam on intestinal microflora and intestinal enzymes activities, as well as antioxidant protection against lipopolysaccharide (LPS)-induced oxidative damage, have been examined by feeding mice with boiled yam. It was observed that the intake significantly modified the mice intestinal microflora. Colony numbers of *Bifidobacterium* and *Lactobacillus* increased while the colony numbers of *Clostridium perfringens* decreased. An elevated activity of leucine aminopeptidase and lipase were observed while sucrase and maltase were increased only in mice treated with high yam diet. It was therefore concluded that the intake of greater yam significantly alleviated LPS-induced oxidative damage by decreasing lipid oxidation level. It is known that LPS stimulates immune responses by interacting with membrane receptors to induce the production of cytokines such as tumour necrosis factors. However, the greater yam being rich in dietary fibres, polyphenols, and flavonoids, it may contribute to the observed gastrointestinal function and antioxidant protection and is therefore beneficial for intestinal health and oxidation prevention (Hsu et al., 2006). In Orissa, India, the inhibitory potential and antibacterial activity of an extract were tested against *Salmonella typhimurium, Vibrio cholerae, Shiegella flexneri, Streptococcus mutans* and *Streptococcus pyogenes* to test its. It was concluded that the extract is highly active against *S. pyogenes* (Kumar et al., 2017). Although the mechanisms responsible for such activities are not clearly identified, they might be related to the diverse polyphenols and flavonoids present in greater yam.

6.4. Anti-inflammatory activity

The assessment of the immune system stimulation potentialities of an hydro-methanolic extract demonstrated that the greater yam can actively polarize the lymphocyte population towards the expression of an immune response. The tuber extract also presented mitogenic activity as evidenced by the in vitro proliferation of lymphocytes (Dey and Chaudhuri, 2014). The hydro-methanol extract has been shown to significantly down-regulate the pro-inflammatory signals in a gradual manner compared to a reference control using murine lymphocytes for 48 h (with different concentrations from 0–80 mg/mL). The extract was then analysed to clarify its chemical composition in order to identify the compounds involved. HPLC analysis identified gallic acid, 4-hydroxy benzoic acid, syringic acid, p-coumaric acid, and myricetin. GC-MS analysis identified azulene, phenol, 2,4-bis(1,1-dimethylethyl), pentadecanoic acid, methyl ester, n-hexadecanoic acid, octadecadienoic acid, indolizine, bumetrizole, cinnamyl cinnamate and squalene. It was concluded that the extract significantly down-regulated the pro-inflammatory signals in a gradual manner compared with control (0 mg/mL) and that the various bioactive compounds identified present anti-inflammatory activities contributing to the overall bioactivity (Dey et al., 2016). A greater yam diet on mice fed with 50% raw lyophilized yam for 21 days produced a remarkable effect on the mucosal enzyme activities in the small intestine and lipid metabolism of adult mice and showed constant improvement in the cholesterol profile of the liver and plasma of mice (Chen et al., 2003). Another team also observed an increase in faecal excretions of neutral steroid and bile acids whereas absorption of fat was reduced (Yeh et al., 2007).

Anthocyanins separated by HPLC-MS from a purple-fleshed cultivar were studied for their anti-inflammatory effects at different concentrations and compared with the standard colitis treatment, 5-aminosalicylic acid, in a trinitrobenzenesulfonic acid (TNBS)-induced colitis mouse model. Different parameters, including body weight change, disease activity index and intestinal histology were measured to determine the anti-inflammatory effects of these anthocyanins. Only 8 µg of anthocyanins per kilogram of body weight produced potent anti-inflammatory effects in the mouse model. It was concluded that these anthocyanins may be applied as a potential food supplement in inflammatory bowel disease therapy (Chen et al., 2017b).

It has been shown that the consumption of a small amount of Chinese cultivar *Tainong no. 1* could be helpful in stimulating macrophage function and immunomodulatory effect on the mucosal-associated lymphocyte tissues (Lin et al., 2009). *Tainong no. 1* was also identified as representing a potential for hypertension control due to its high dioscorin content (Hsu et al., 2006). In Taiwan, *Tainung no. 2* has also been reported to possess many functional properties because of its high dioscorin content. Boiling and deep-frying caused dioscorin denaturation resulting in loss of dioscorin solubility but freeze-drying resulted in higher total phenol content, antioxidative capacity, and dioscorin stability (Liu and Lin, 2009). Finally, it is known that chronic kidney disease is increasing in industrialized countries due to various disorders such as obesity, diabetes, and peripheral artery disease. The greater yam extract has been evaluated for its fibrosis regulatory effect and, using in vitro experiments, it was demonstrated that the extract attenuates induced kidney damage and renal fibrosis (Liu et al., 2012). Various bioactive compounds, including anthocyanins, organic acids, flavonoids and dioscorin, have been detected in greater yam extracts exhibiting anti-inflammatory activity. However, the relative contribution of these substances to the overall activity and the cellular mechanisms responsible for such beneficial effects remain to be elucidated.

6.5. Anti-diabetic activity

In Nigeria, the occurrence of diabetes has been observed to increase, especially in urban areas due to excessive weight gain which might be due to increased food intake and blood glucose level. The greater yam is known to possess anti-diabetic properties which could help in managing body weight. It was observed that when different groups of rats were treated with greater yam extracts there was a clear reduction in food intake and weight gain. The food intake, blood glucose level and body weight were found to be significantly reduced in a dose-dependent manner when compared with the control group. The weight loss might be due to increased satiety or to the reduction in the fasting blood glucose level. It was also observed that the reduction in body weight might be due to the phenolic compounds present in the tubers (Olubobokun et al., 2013). Water soluble polysaccharides extracted from purple and yellow-fleshed cultivars were tested and exhibited blood glucose lowering properties in hyperglycemia condition in rats with the purple extract having a slightly higher effect. It was suggested that the greater yam could be used to develop foods aiming at controlling blood glucose levels for diabetic persons (Estiasih et al., 2018).

In India, an ethanolic extract from Tamil Nadu was tested for hypoglycemic activity in normal rats (100 and 200 mg/kg for 21 days). The treatment showed a highly significant reduction in blood glucose levels and the extract did not produce hypoglycemic activity at both dose levels in normal rats. In induced diabetic rats, the body weight of rats treated with extracts showed a significant increase after 21 days. A reduction in plasma triglyceride and cholesterol in rats resulted from a diet supplemented with 40% greater yam was found significant. The tuber extract showed reduction in blood glucose level as well as increased body weight in rats treated with streptozotocin and alloxan, respectively. The study concluded that the ethanolic extract presented significant antidiabetic activity (Maithili et al., 2011).

A study conducted in Indonesia, showed that three cycle of autoclaving-cooling treatment were able to increase resistant starch and dietary fibre content in greater yam flour, thus able to decrease blood glucose level. After four week experiment, it was found that the modified flour presented the ability to decrease blood glucose level in hyperglycemic rats and to inhibit glucose absorption in meal tolerance tests and increase short chain fatty acids formation. It was concluded that the greater yam has significant hypoglycemic activity (Rosida et al., 2016). It is also known to possess various biological activities beneficial in the control of glycaemia in diabetic patients (type II diabetes mellitus, T2DM). Finally, another study aiming at determining the antioxidant, α-amylase and α-glucosidase activities, glycemic index, and blood glucose concentration of dough meals developed from flours blends including greater water yam found a clear free radical scavenging activity and ferric ion reducing power as the supplementation increased with greater yam (Adeloye et al., 2021). All studies were based on results obtained from rodent models of diabetes and have shown that the consumption of greater yam and/or its extracts improved glycaemia. Changes in body weight and adiposity were observed and it was concluded that the consumption of boiled tubers or extracts is beneficial for improving blood glucose. The molecular mechanisms at stake remain unknown and there is a need to conduct trials on human subjects to clarify their roles in the beneficial effects of the greater yam (Alharazi et al., 2021).

It is difficult to narrow down to a single compound the beneficial effects of the greater yam. However, there is strong evidence that dioscorin plays a major role in the greater yam biological activity and health benefits but dioscorin may not act alone and synergies of action are possible with additional bioactive substances. The greater yam is rich in various polyphenols and it has been shown that these compounds alleviate the side effects of metabolic disorders. Their action has been described as alleviating intestinal oxidative stress, improving inflammatory status, and improving intestinal barrier function. It is known that polyphenols regulate intestinal functions, including the gut microbiota, and are therapeutic agents for various metabolic disorders (Niwano et al., 2022).

7. Future developments

Freshly peeled greater yam tuber slices prepared in vacuum-sealed transparent plastic bags are commercialised in most tropical cities around the world. The portions are sliced into 2–4 cm thick pieces and dipped in a solution of 1% metabisulphite to prevent oxidation. These slices are then precooked at 40°C for 15 min and frozen at -40°C for 30 min and can then be stored in a freezer at -3 to -5°C. This product is ready to be cooked and eaten. The use of metabisulphite improves the colour greatly and avoids discoloration for up to 3 months of storage.

7.1. Flours

The greater yam flour is prepared from peeled fractions of dried tubers. This type of product could have industrial potential (Harijono et al., 2017). However, after 24 weeks of storage in plastic bags, a reduction in the breakdown viscosity is observed indicating breakdown of starches during storage. As the final viscosity gives the ability of flours to form viscous paste after cooking and cooling, long term storage results in a significant reduction of final viscosity (Adebowale et al., 2017). The greater yam flour is quite convenient for consumers in West African cities. The flour is stirred into boiling water and cooked for a few minutes in order to obtain a thick viscous paste similar to the one obtained with pounded boiled yam (Baah et al., 2009). This product is developing and farmers have to adapt by adopting the right cultivars rich in starch and dry matter which might be different from those preferred for boiled and pounded yam. In Nigeria, tubers are processed into flour by peeling, slicing, parboiling in hot water (40–60°C for 1–3 h), soaking, and sun drying. Soaking time is a factor impacting quality. When comparing one cultivar of greater yam with *D. rotundata*, it was found that after the 18 h soaking, the acceptability, taste, texture colour, and appearance of greater yam were significantly different from *D. rotundata*. The main reason was the low peak viscosity compared to *D. rotundata* indicating the carbohydrates of *D. rotundata* flour would not breakdown as easily and quickly as for the greater yam. Peak viscosity is an important parameter for flour processors looking for good starch paste with good capacity to resist shear stress and heating (Obadina et al., 2014).

Unfortunately, the sun drying process has a significant negative impact on the vitamins content of high quality flour (Adebowale et al., 2018). In Indonesia, a purple-fleshed cultivar processed into flour after steaming retained its colour. The substitution of wheat flour with purple greater yam flour up to 40% allowed the production of wet noodles with adequate quality (Lavlinesia et al., 2019). Their similarities to other commercial starches or flours could be useful for noodles, snacks and baby food products (Salda et al., 1998). The incorporation of greater yam flour in bread (25% yam flour/75% wheat flour) has been shown to significantly increase the antioxidant capacity of the blended bread with potential for health-promoting foods. It seems that the substitution with yam flour in a bread formulation does not interfere with bread acceptability (Hsu et al., 2004). When compared to other cultivated yam species, *D. alata* flour has greater ability to withstand shear at high temperatures and higher cooked paste stability, indicating that its flour can be targeted for industrial uses because of its hot paste stability (Wahab et al., 2016).

In Indonesia, a study showed that the purple-fleshed cultivar flour is more adapted to the production of cookies (Yalindua et al., 2021). Likewise, plain bread made with wheat flour substituted with purple yam flour has increased levels of anthocyanins, total phenol, and antioxidant activity whereas decreased the volume expansion rate. Wheat bread made with 30% purple yam flour, roasting at 180°C, resulted in good bread volume development and high antioxidant activity (Tamaroh and Sudrajat, 2021). On the other hand, gluten-free muffins can be prepared directly from purple-fleshed cultivar by incorporating pectin as a hydrocolloid (compared to xanthan or guar gums). It gives high springiness to the muffin and after sensory evaluation, it is the best and obtained the highest sum of ranks for appearance, colour, taste, and overall acceptability (Gunasekara et al., 2021).

Flakes are produced by drum drying of cooked and mashed yam. Peeled tubers are steamed for 60 min and pulverized into flours of particle sizes of approximately 100–200 µm to result in a steamed yam flour with optimum characteristics. The flour is vacuum-sealed or packaged hermetically to extend product life. As the microbial load is close to nil and the moisture content around 7%, the shelf life can be almost 1 year. This product is easily cooked in less than 5 min with boiling water. It is has all the characteristics of pounded yam with a creamy white colour. The required target level required of elasticity is obtained by adding more or less water during the cooking process (Iwuhoa 2004).

7.2. Resistant and modified starches

The greater yam presents the potential to be used for flour with resistant starch (RS) because it has high amylose content. RS is considered to present health benefits (Harijono et al., 2016c). However, if the starch paste appears to be thermostable during heating, it also presents setbacks after cooling. Starch thermal and material properties vary considerably among cultivars but it is stable at high temperatures and within a low pH range when pregelatinized. It can be combined with cassava starch to improve its functionality (Alves and Grossmann, 1998). As greater yam starch has a high viscosity under heat treatment, it could be used as substitute for modified starches in UHT foods and in canned baby foods (Amani et al., 2002). It also present mechanical shearing under slightly acidic conditions and has therefore potential in some acidic food products which also require thermal processing. Potential industrial uses have been suggested such as biodegradable film, edible antimicrobial film, tablet and capsule formulation (Zhu, 2015).

Heat-moisture treatment (HMT) submits starch or flour to a moisture content of 10–35% and heat of 90–120 °C. At these conditions, gelatinization of starch does not occur and the process leads to changes in functional properties of starch without destroying its granular structure. In Malaysia, when purple-fleshed cultivar flour was submitted to HMT, the physicochemical and functional properties of the flour changed significantly. When the moisture level increased, a reduction in amylose content, gelatinization enthalpy, swelling capacity and carbohydrate leaching was observed. HMT was found to allow the flour to be used in products requiring high thermal stability with minimum changes in starch granules as well as in products requiring low cooking loss such as noodles (Mustapha et al., 2019).

Hydroxypropylation is used in the starch industry to modify starches properties. It is based on the etherification of starch with propylene oxide in the presence of alkaline catalyst, which lowers gelatinization temperature and increases paste clarity, and solubility in cold water. Hydroxypropylation of greater yam starch results in very good physicochemical, morphological and functional parameters. It is thought that it could be widely utilized and could offer new opportunities on the global starch market (Arueya and Ojesanmi, 2019).

The greater yam starches are also interesting as additives, especially for yogurts. In Nigeria, sensory evaluation revealed that yoghurt produced from acetylated greater yam starch was superior to commercial cassava flour. It presents good starch qualities but acid-thinned greater yam starch presented the best results indicating that it could be adopted for industrial uses (Awolu and Olofinlae, 2016). Two different cultivars were analysed in Ghana for their potential as thickening agent in yogurts. The starches were found of suitable quality with a long shelf life due to their low acidity and their light colour was a plus for a new product. The cultivar *Akaba* was found to present an overall acceptability higher than the control, indicating that greater yam starches could be used thicken yogurts to produce transparent, creamy texture, sweet taste, flavour, and consistency (Tortoe et al., 2019). In Colombia, the addition of greater yam starch improved the physicochemical characteristics of yogurt, maintained an intense white colour while presenting a preference at the sensory level, compared to pectin, the commercial stabilizer. During three weeks of storage, yogurt with yam starch at 0.1% w/w showed a decrease in syneresis (separation of liquid from gel), while in yogurts with pectin, syneresis remained practically constant in this period. In the first week of storage, yogurts with yam starch showed a decrease in acidity (Pérez et al., 2021).

7.3. Anthocyanins extracts

The production of anthocyanins extracts for the food processing industries is of interest. A comparative study has shown that the highest yield of anthocyanin extract from purple-fleshed cultivar flour was obtained when MeOH solvent was used (247 mg/100 g extract). As expected, anthocyanin and total phenolic contents were found to be highly correlated with antioxidant activity (RSA% and FRAP) (Tamaroh et al., 2018). It is possible to obtain ethanolic anthocyanin-rich extracts by ultrasound-assisted extraction (UAE). The optimum extraction occurs at 60 °C for 10 min with ethanol: water (80:20). An economic evaluation study found that the production cost decreased from US$ 950 /kg to US$ 124 /kg when the extractor capacity increased from 5 l to 500 l. The extraction of anthocyanins from purple yam by UAE is economically feasible when the selling price is above US$ 170 /kg (Ochoa et al., 2020).

7.4. Other processed uses

The greater yam can also be used for replacing fat in industrial sausages. Sausages with 5% yam added had no significant difference in colour, flavour, hardness, juiciness, and overall acceptability with the control. Such replacement results in sausages with 22% less fat content (Tan et al. 2007). Hydrocolloids are hydrophilic polymers that have multi functionalities such as thickener, gelling agent, stabilizer, but their world market is constrained by price instability and shortage of raw materials. The mucilage of *D. alata* represents an interesting source of hydrocolloids but its extraction is constrained by its high viscosity and high water-binding capacity of its glycoprotein that inhibits the separation of mucilage from starch. In Indonesia, the effect of different salt types on water to tuber ratios during mucilage extraction were compared to optimize mucilage yield. A water to tuber ratio of 4:1 with addition of $CaCl_2$ salt resulted in the best mucilage yield (1.58% f.w.) with high purity (low starch content) (Fortuna et al., 2020).

Diverse processing possibilities have been discovered around the world for the greater yam but the major constraint remains the mechanization of the tuber peeling process. Lye-peeling has been proposed as a possible solution in the early 1970s in Puerto-Rico (Rivera-Ortiz and González, 1972) but has not been adopted since. Ease of peeling the tubers is highly variable and some cultivars are more adapted than others but in all countries nowadays peeling is still done by-hand. Unless this constraint is eliminated, processing will remain expensive and will result in non-competitive products.

7.5. Food security and biofortification

There is tremendous chemical variation within cultivars and there is therefore scope for biofortification, an approach often favoured for crops playing and important role for food security. The greater yam being mostly cultivated for the fresh food markets, mainly in West Africa, it would appear interesting to improve existing contents in selected metabolites, such as carotenoids, anthocyanins or allantoin through conventional breeding techniques. There are a few breeding programmes working on the genetic improvement of the greater yam. They are located in the yam belt countries of Nigeria, Benin, Ghana and Côte d'Ivoire with the International Institute of Tropical Agriculture (IITA, Ibadan, Nigeria) coordinating the activities. Three other programmes are based in Guadeloupe (West Indies) under the leadership of INRAE and CIRAD, in CTCRI (Trivandrum, Kerala, India) and in VARTC

(Santo, Vanuatu). Improvement is conducted through successive cycles of phenotypic recurrent selection. However, *D. alata* being dioecious, with rare female plants, erratic flowering, and variable ploidy levels, progress is rather slow. As the greater yam is highly heterozygous, when hybrids are created, many wild traits, including tuber flesh oxidation and poor palatability are dominant among progenies (Lebot et al., 2019b; Rinaldo et al., 2022).

Existing traditional cultivars present outstanding nutritional and chemical properties and it is quite possible that it will be difficult for breeders to reach comparable chemotypes through conventional breeding. Most breeding programmes are presently working on anthracnose resistance and are eliminating, through successive clonal evaluations, progenies with poor quality traits. But so far no improved genotype has been widely distributed and adopted by farmers. At present, growers are working mostly with ancient cultivars clonally introduced from distant sources. It has been estimated that there are 4,524 accessions of *D. alata* maintained in 28 countries germplasm collections (Lebot and Dulloo, 2021). In the 1970s, international germplasm collections were made under the USDA programme based in Mayaguez (Puerto Rico) and elite cultivars were selected (Martin et al., 1975) and internationally distributed. When *Florido* was introduced from Puerto Rico to Côte d'Ivoire, it was rapidly adopted (Doumbia et al., 2004). When *C18* was introduced from Cameroon to Côte d'Ivoire, the adoption rate was also spectacular (Kouakou et al., 2012). These two well documented cases indicate that, in West Africa, producers are eager to test new cultivars. Unfortunately, the hundreds of cultivars existing in Asia and in the Pacific are not transferred to West Africa where is concentrated more than 90% of the world yam production. There is an urgent need to standardise the analytical protocols in order to conduct comprehensive assessment of these cultivars and to select the most promising ones prior to their safe transfer to West Africa. Technical constraints hindering accurate comparisons might result from pedoclimatic variation between countries (and studies) due to genotype × environment interactions. Major compounds and secondary metabolites are known to be impacted quantitatively by environmental factors and ontogeny.

8. Conclusion and perspectives

This review highlighted the remarkable chemical composition of the greater yam and the diverse physiological properties of its phytochemicals. Of all root and tuber crops, the greater yam has higher minerals and vitamins content and is the richest in proteins (mostly dioscorins) and these have well documented physiological properties. Its nutritional composition is excellent with extremely low fat and high fibres and carbohydrates content. Most cultivars present high levels of secondary metabolites (allantoin, carotenoids, anthocyanins, organic acids, flavonoids), all with beneficial effects on human health. However, this review has emphasized the scope of variation existing within and between countries and the highly variable results obtained by independent teams analysing different cultivars. All cultivars are clones of hybrids and *D. alata* is highly heterozygous. Comparison of data obtained in different environments is therefore difficult without and accurate identification of genotypes and the control of environmental factors. Although the greater yam is mostly cultivated in Africa where it has been clonally introduced, many research studies have been conducted in Asia, the area of origin of the species, where cultivars present greater genetic diversity. This review also confirmed the complexity of consumers' taste and preferences, and the need for adequate chemotypes for processed products. Over the forthcoming decades, the yam belt countries will witness tremendous population growth and pressure on the land in a context of climate change. There is an urgent need to introduce to West Africa new cultivars for direct clonal distribution to growers. And to compose base populations for genetic improvement with sufficient genetic diversity and chemical variation to allow breeding programmes to develop new hybrids with suitable characteristics.

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Figure captions:

Fig. 1. *Dioscorea alata*, the greater yam: a) foliage; b) close-up of young leaves of two different cultivars, one with anthocyanin pigmentation; c) male and female inflorescences developing into capsules after successful pollination; d) tubers for sale on a local market; e) popular cultivar *Florido*, with compact tuber shape, smooth skin surface and appreciated taste with white flesh and no oxidation; f) cultivar with elongated tuber shape, g) purple-fleshed cultivar; h) cross-section of a tuber showing anthocyanin pigmentation; i) white-fleshed cultivar with tinges of anthocyanins (photos by V. Lebot).

Fig. 2. GC-MS chromatogram of methylated organic acids extract of *D. alata* cultivar (acc. no. Da1335 from Vanuatu) after methylation. 1: caprylic acid (internal check). 2: oxalic; 3: malonic; 4: 2-methoxy dimethyl succinate; 5 & 6: glucose derivatives; 7: mallic; 8: pentadécanoic; 9: palmitic; 10: heptadecanoic; 11: citric; 12: stearic; 13: oleic; 14: linoleic; 15: α-linolenic; 16: arachidic.

Fig. 3. Neighbour joining tree on a data matrix of 101 cultivars x 56 compounds (15 carotenoids, 1 indol (tryptophan), 4 phenolic acids, 7 hydroxycinnamic acids, 15 flavanols/flavanones, 8 flavonols/flavones, 4 anthocyanins, and 2 unknown compounds). The *D. alata* cultivars rich in carotenoids (orange numbers) and those rich in anthocyanins (purple numbers) are differentiated.

Fig. 4. PCA analysis of 101 cultivars (blue dots) x 56 compounds (red lines) showing the positive correlations between 15 carotenoids (C nos) including all-trans-β-carotene (beta) (yellow ellipse), towards axis 1 and the 4 anthocyanins (An1, 2, 3, 4, in blue ellipse), towards axis 2.

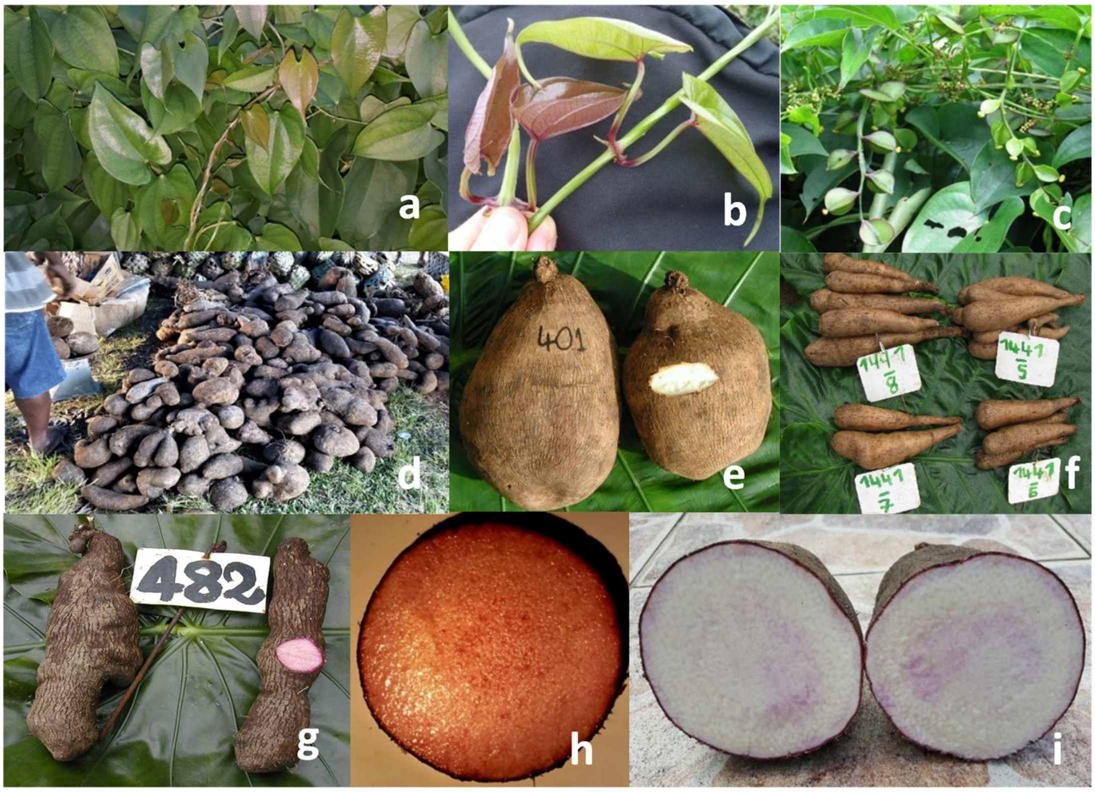

Fig. 1

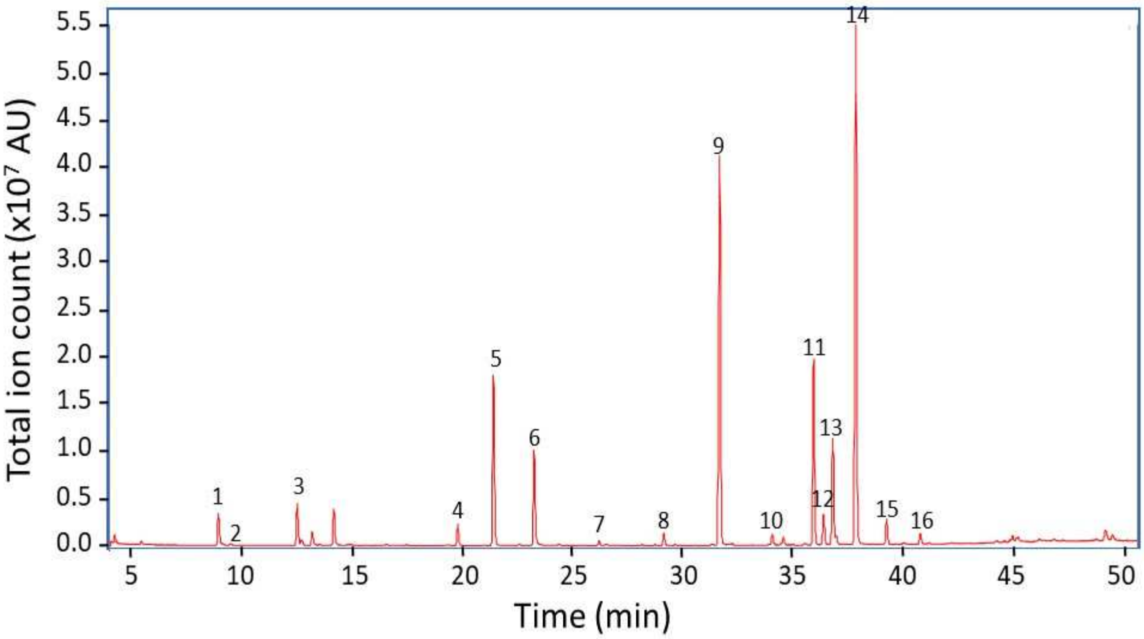
Total ion count (x10⁷ AU)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
5
10
15
20
25
30
35
40
45
50
Time (min)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Fig. 2

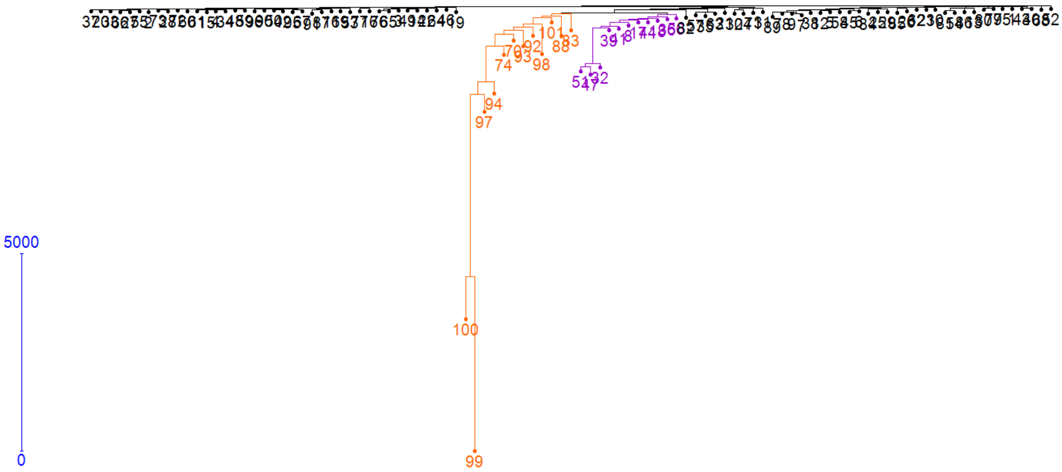
5000
0
100
99
97
94
74
98
88

Fig. 3

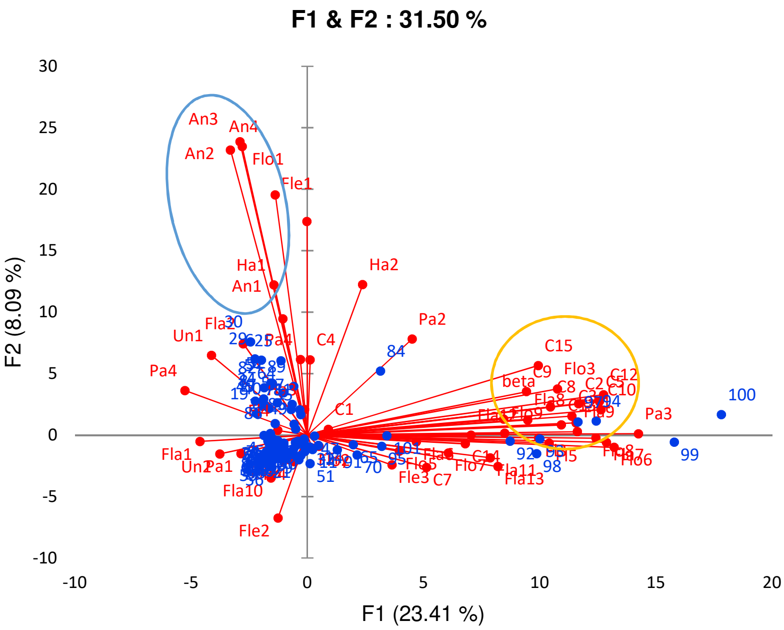
F1 & F2 : 31.50 %
F2 (8.09 %)
F1 (23.41 %)
30
25
20
15
10
5
0
-5
-10
-10
-5
0
5
10
15
20
An3
An4
An2
Flo1
Fle1
Ha1
An1
Ha2
Pa2
Un1
Pa4
C4
84
C1
C15
beta
C9
Flo3
C12
C10
C8
Pa3
100
99
Fla1
Un2
Pa1
Fla10
Fle2
Fle3
C7
Flo7
Fla11
Fla13
98
Flo6
51
70

Fig. 4

Table 1
Nutritional composition of *D. alata* cultivars from different geographical origins

	Ghana[1,2]	Nigeria[3,4]	India[5,6,7]	Sri Lanka[8]	China[9]	Indonesia[10]	New Caledonia[11]	Vanuatu[12,13]
Cultivars analysed (*n*)	*18*	*16*	*15*	*7*	*9*	*15*	*131*	*216*
Dry matter (% f.w.)	20.7–43.5	19.1–33.8	29.9–34.9	22.5–35.5		17.5–33.2	15.1–40.7	13.7–31.4
Starch (% d.w.)	60.4–77.6	60.3–74.4	40.7–85.0	75.6–84.3	64.4–80.6	70.6–83.0	56.5–83.2	58.8–85.0
Amylose (% d.w.)	21.7–31.6	26.7–32.3						13.4–17.2
Sugars (% d.w.)	2.43–6.91	3.60–11.0	2.16–7.52	0.90–1.50				0.60–10.6
Proteins (% d.w.)	5.10–9.10	4.10–11.0	2.56–3.10	2.02–10.20	6.40–9.70	1.30–3.00	4.90–12.4	6.30–21.0
Dietary fibre (% d.w.)	1.59–1.75	4.10–11.0	1.10–4.10	1.80–2.00	0.67–1.19	6.70–11.6		1.05–11.98
Fat (% d.w.)	0.81–0.82	0.86–1.86	0.80–2.32	1.53–1.56		0.00–0.29		
Minerals (% d.w.)	6.19–6.29	2.90–4.10	1.89–7.06	2.80–3.80		0.85–1.44	2.90–4.70	2.67–8.14
Ca (mg/100 g d.w.)	26.0–53.5	27.0–41.0	62.6–78.0	8.15–8.13	31.6–45.3	15.6–62.0	2.00–10.0	
P (mg/100 g d.w.)	273–219	88.0–190		117–194		329–700	100–320	
Mg (mg/100 g d.w.)	40.0–41.5	39.0–59.5		64.7–74.6	38.7–47.8	16.8–43.1		
Na (mg/100 g d.w.)	8.3–13.1	8.40–13.1		52.0–78.7		39.5–48.2		
K (mg/100 g d.w.)	622–642	1055–2010		1157–2016		2250–4830		
Fe (mg/100 g d.w.)		0.36–3.48		9.90–10.9	8.30–22.2	1.40–13.4		
Cu (mg/100 g d.w.)		1.20–1.60		6.30–6.90	4.20–4.70			
Zn (mg/100 g d.w.)	1.00–1.76	1.00–1.40	3.40–4.30	1.07–2.11	8.20–25.9	0.43–2.83		
Mn (mg/100 g d.w.)		0.50–2.20	3.10–4.30					
Vit. A (mg/100 g d.w.)		1.68–2.60[14]	0.97–1.88					
Vit. B_1 (mg/100 g d.w.)		0.36–0.57						
Vit. B_2 (mg/100 g d.w.)		0.44–1.75						
Vit. B_6 (mg/100 g d.w.)		2.36–2.92						
Vit. C (mg/100 g d.w.)		23.0–30.9	13.0–24.7	13.0–24.7				
Oxalates (mg/100 g d.w.)	45.0–50.0	50.2–64.9	48.0–78.0	48.3–78.1		12.7–44.9*		0.49–57.5*

[1]Wireko-Manu et al., 2011, 2013c; [2]Polycarp et al., 2012; [3]Baah et al., 2009; [4]Adebowale et al., 2018; [5]Patel et al., 2019; [6]Padhan et al., 2018; [7]Behera et al., 2009, [8]Wanasundera & Ravindran, 1994; [9]Wu et al., 2016; [10]Fauziah et al., 2020; [11]Lebot et al., 1998; [12]Lebot & Malapa, 2012; [13]Lebot et al., 2018a. [14]Price et al., 2018, *oxalic acid.

Table 2
Organic acids quantitated using GC-MS in 91 cultivars of *D. alata* from Vanuatu cultivated within a common plot to avoid environmental factors (in mg/100 g d.w.) (Mercier, 2013; Muñoz-Cuervo, 2015)

acid	min	max	mean	sd	cv%
oxalic	0.49	57.55	18.41	11.11	60.35
malonic	7.81	210.4	59.0	37.5	63.61
fumaric	0.1	0.65	0.24	0.10	40.49
succinic	0.13	1.55	0.71	0.26	36.90
malic	33.1	548.3	198.6	106.4	53.58
citric	698.5	5497.3	2668.9	801.5	30.03
pentadecanoic	2.25	13.35	5.93	2.25	37.92
palimitic	38.51	70.9	52.71	7.77	14.73
heptadecanoic	1.38	7.58	4.00	1.26	31.41
stearic	2.44	25.17	7.23	4.41	61.09
oleic	7.71	52.6	19.3	7.25	37.58
linoleic	69.9	178.4	116.0	19.4	16.70
linolenic	3.54	22.31	9.03	3.65	40.44
arachidic	1.27	4.74	2.34	0.58	24.61

Table 3
Comparison of compounds quantitated in methanolic extracts of *D. alata* cultivars by different analytical techniques (compounds are ranked in decreasing order of importance).

Anisuzzman et al., 2016 HPLC Bangladesh (n=1)	Chaudhury et al., 2018 HPLC India (n=1)	Price et al., 2017* GC-MS Nigeria (n=5)	Lebot et al., 2018ab, 2019a HP-TLC Nigeria, India, Vietnam, Papua New Guinea, Vanuatu (n=550)
Myricetin	Kaempferol	Sucrose	Allantoin
trans-cinnamic acid	Myricetin	Inositol, scyllo	Sucrose
Kaempferol	Syringic acid	Malic acid	Fructose
Ellagic acid	Quercetin	Glucose isomer 1	Glucose
p-Coumaric acid	Gallic acid	L-Serine	Chlorogenic acid
Vanillin	Chlorogenic acid	Phosphate	Gallic acid
Epicatchin	Ellagic acid	Xylulose isomer 1	Caryatin
Syringic acid	Caffeic acid	Citric acid	Epicatechin
Vanillic acid	Apigenin	Fructose isomer 1	Catechin
Gallic acid	p-Hydroxy benzoic acid	Galactose isomer 1	Catechin derivative 1
Arbutin	Sinapic acid	Fructose isomer 2	Catechin derivative 2
Hydroquinone	Ferulic acid	L-Threonine	
(+)-catechin	Rutin	Itaconic acid	
Caffeic acid	Naringenin	Pyroglutamic acid	
Trans-ferulic acid	Salicylic acid	L-Aspartic acid	
Rutin hydrate	Naringin	Glucose isomer 2	
Benzoic acid	p-Coumaric acid	GABA	
Rosmarinic acid	Vanillic acid	Monostearin	
Quercetin	Catechin	L-Alanine	
	Protocatechuic acid	1-Monopalmitin	
	Gentisic acid	Fumaric acid	
		Trehalose	
		L-Valine	
		Hexadecanoic acid	
		2-Piperidone-amino	
		L-Proline	
		Maleic acid	
		Glycine	
		Linoleic acid	
		Galactose isomer 2	
		Ethanolamine	
		cis-Aconitic acid	
		Glycerol	
		Gluconic acid	
		L-Isoleucine	
		Allantoin	
		Octadecanoic acid	
		b-Sitosterol	
		5-Hydroxytryptophan	
		L-Leucine	
		Catechin	

*123 compounds were detected, only major ones are listed here

Table 4
Comparison of *D. alata* cultivars from Vanuatu and India (and their hybrids) mean values for phenolic acids and catechins with two *Dioscorea* spp. Values are in mg/g d.w. (±standard deviations). All cultivars were cultivated within a common plot (adapted from Lebot et al., 2018a).

Origin	Vanuatu (VU)	India (IN)	Hybrids (INxVU)	*D. bulbifera* tub*	*D. bulbifera* bul**	*D. nummularia*
Cultivars *n*	*216*	*40*	*128*	*26*	*26*	*36*
CGA[1]	2.23 ± 2.2	2.56 ± 2.3	2.32 ± 1.7	2.09 ± 2.5	4.25 ± 4.6	1.75 ± 1.6
Caryatin	0.91 ± 0.4	1.15 ± 1.0	1.65 ± 1.4	0.61 ± 0.5	3.35 ± 2.8	5.67 ± 3.6
Gallic acid	1.73 ± 1.5	1.34 ± 1.1	1.72 ± 1.7	1.62 ± 1.1	2.35 ± 2.3	2.12 ± 1.1
Cat1[2]	0.03 ± 0.3	0.92 ± 1.3	0.74 ± 1.3	0.81 ± 0.3	5.21 ± 3.5	1.12 ± 1.4
Cat2[2]	0.04 ± 0.2	0.64 ± 1.1	0.46 ± 0.6	1.26 ± 0.8	4.34 ± 3.0	0.71 ± 1.0
Catechin	0.14 ± 0.4	1.61 ± 2.2	0.91 ± 1.0	2.14 ± 1.9	4.92 ± 5.0	0.53 ± 0.4
Epicatechin	0.45 ± 0.4	2.14 ± 2.4	1.00 ± 2.2	2.75 ± 0.8	10.71 ± 4.7	1.25 ± 1.2

[1]chlorogenic acid, [2]unknown catechins but most likely gallocatechin, epigallocatechin or catechin- and epicatechin-gallate as reported by Champagne et al. (2011). *tub= tubers, **bul= bulbils

Table 5
Comparison of *D. alata* with 9 tropical root and tuber crop (134 accessions) for total anthocyanin content represented by cultivars maxima (in mg/100 g CGE, d.w. = dry weight, f.w. = fresh weight, CGE=cyanidin-3-glucoside equivalent) (adapted from Champagne et al., 2011).

Species	d.w. (mg 100 g^{-1})	f.w. (mg 100 g^{-1})
D. alata	93.32	26.6
Alocasia macrorrhyza	n.d.	n.d.
Colocasia esculenta	26.56	3.32
D. bulbifera (tubers)	64.17	11.53
D. bulbifera (bulbils)	34.84	6.11
D. cayenensis	n.d.	n.d.
D. esculenta	6.39	1.55
D. pentaphylla	n.d.	n.d.
I. batatas	40.95	12.53
M. esculenta	n.d.	n.d.
Xanthosoma sagittifolium	37.77	7.44