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► To cite this version:

Vincent Lebot, Floriane Lawac, Laurent Legendre. The greater yam (*Dioscorea alata* L.): A review of its phytochemical content and potential for processed products and biofortification. *Journal of Food Composition and Analysis*, 2023, 115, pp.104987. 10.1016/j.jfca.2022.104987 . hal-03870052

HAL Id: hal-03870052

<https://hal.inrae.fr/hal-03870052>

Submitted on 23 Feb 2024

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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.

Funding. This review did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. IAEA (Vienna, Austria) financial support to the Food Quality Laboratory of the Department of Agriculture in Vanuatu (project no. NHE2018001) is greatly appreciated.

Acknowledgements. Special thanks are due to Mrs Elisha Tekak for laboratory assistance in preparing *D. alata* flour samples and their methanolic extracts. Technical contribution of Philip Tjiobang, Edilbert Telukluk, Bennomy Bulememe, Georges Ruruely, and Emmanuel Sowan for conducting the germplasm harvest and morpho-agro characterisation in VARTC, Santo, Vanuatu, is greatly appreciated. Special thanks are due to Ismaël Muñoz-Cuervo, Pierre-Edouard Mercier (Université de Lyon 1), Anne-Marie Perrois and Valérie Serre (Lycée Simone Weil, Le Puy en Velay, France) for conducting the HPLC and GC-MS analyses of phenolics, organic and fatty acids.

Declaration of Competing Interest. The authors declare no conflict of interest or competing interests. The authors have no relevant financial or non-financial interests to disclose.

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,

37 especially in Africa, are looking at locally cultivated crops as possible alternatives to feed growing
38 cities and there is an interest on yams.

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

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

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

68

69 **2. Materials and methods**

70

71 Five databases were consulted: Google Scholar, Medline (PubMed), Science direct, Web of
72 Science and Agritrop. The six key words: '*Dioscorea*', '*alata*', 'chemical', 'nutritional',
73 'composition', and 'constituents' were entered to obtain lists of references from 1980 to 2022. All

74 references mentioning at least '*Dioscorea*' in their title were studied and if sufficient information was
75 obtained from their abstracts, the papers were selected and downloaded (or obtained through authors'
76 institutions subscriptions). All papers were read and analysed to confirm their relevance to this review
77 criteria (*D. alata*, chemical composition, functional properties, phytochemicals, physiological
78 properties, unprocessed and processed food). Those with uncertainties regarding the taxonomical
79 identification of *D. alata* and its cultivars, were not retained. Unless mentioned purposely, all
80 statements and figures reported in the present review refer exclusively to *D. alata*, the greater yam.

81

82 **3. Botanical characteristics**

83

84 *3.1. Taxonomy*

85

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

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

111 cm long) that can host up to six seeds but this is very unusual. Some cultivars produce bulbils in the
112 axils of the leaves. These bulbils can be used for the propagation of the plant.

113

114 3.2. Phylogeny

115

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

135

136 3.3. Genetic diversity

137

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

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

154

155 **4. Nutritional composition**

156

157 *4.1. Consumers' preferences*

158

159 The chemical composition depends mainly on the cultivar and there is significant variation within
160 different countries (Table 1). The greater yam nutritional profile is excellent with low fat and high
161 fibres content. Considering its high moisture content, the greater yam is comparatively less able to
162 satisfy energy requirements than other tropical root crops: cassava and sweet potato (*Ipomoea*
163 *batatas*), taro and cocoyam (*Xanthosoma sagittifolium*), but its proteins, minerals and vitamins
164 contents are much higher (Ogidi et al., 2017). Local knowledge claims that there is variation between
165 different cultivars for the culinary and palatability properties with some being suitable for certain
166 preparations while others are not. Some cultivars need to be cooked much longer than others (Udensi
167 et al., 2008). Just like for other root crops, the texture in the mouth is usually determined by various
168 co-factors but mostly by softness of the cell walls, dry matter and starch contents (Champagne et al.,
169 2009). In West Africa, cultivars most appreciated characteristics for boiled yam are raw tuber
170 appearance (absence of rootlets), ease of peeling, white or yellow flesh colour, no oxidation during
171 peeling and cooking, viscosity of cooking water and the ease of breaking the yam piece with a fork
172 after cooking. Boiled yam must have a good aroma and the ease to chew is also considered as a high-
173 quality characteristic. Mealiness, colour and taste are the most important variables contributing to
174 general preference among consumers (Honfozo et al., 2021). In Melanesia, greater yam cultivars with
175 good eating quality are characterised by high dry matter, starch and amylose content (Lebot et al.,
176 2006). In Guadeloupe, West Indies, consumers consider the origin, taste, texture, external damage, and
177 tuber size as important attributes characterizing cultivars quality (Barlagne et al., 2017).

178 In West Africa, greater yam is popular for producing boiled yam but some studies reported that
179 due to their chemical composition, most local cultivars are unsuitable for pounded yam. For pounded
180 yam, consistency, colour and stickiness are the most important variables contributing to general
181 preference (Egesi et al., 2003). Tests were therefore conducted to compare *D. alata* to *D. rotundata*,
182 the most preferred species for pounded yam, in order to assess its potential (Baah et al., 2009). It
183 appeared that some cultivars present characteristics similar to *D. rotundata*, especially regarding the
184 starch, amylose and fibres content but the texture of the greater yam flesh is usually not as firm. There

185 is a strong interrelationship between final viscosity, setback and peak viscosity of the paste and the
186 springiness, stickiness, cohesiveness and hardness of the pounded yam samples in both yam species
187 (Otegbayo et al., 2006; 2021). In Ghana, greater yam cultivars presented significantly higher protein
188 contents with higher peak time and pasting temperature when compared with the local yam *D.*
189 *rotundata*. However, the dry matter and starch contents, swelling power and pasting viscosities were
190 lower than the *D. rotundata* cultivar *Pona* highly appreciated for pounded yam (Wireko-Manu et al.,
191 2011). A comparative study conducted in Nigeria with several *D. rotundata* cultivars revealed that the
192 only *D. alata* cultivar assessed (*Kpetè*) for pounded yam was unsuitable (Honfozo et al., 2021).

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

205

206 4.2. Starch

207

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

219 When it is processed into flour greater yam nutritional value is comparable to cereals (Trèche,
220 1998). In Ghana, it has been shown that when the cultivar *Akaba* is used, its flour has
221 physicochemical, functional and pasting characteristics comparable to the best *D. rotundata* cultivar

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

232 Finally, ten greater yam cultivars starches were analysed in Nigeria. Their swelling power was
233 found to be in the category of high restricted-swelling starch (9.21–11.03% for flours and 9.49–
234 13.80% for starches). It was observed that this characteristic is desirable for noodles and composite
235 blends with cereals. The pasting temperature for flours (78.05–86.13°C) and for starches (80.38–
236 86.15°C) and the pasting time for flours (4.44–5.17 min) and for starches (4.53–5.17 min) are
237 adequate. Cultivars pasting properties of flours and starches confirmed that they represent a useful
238 resource for food processing. However, the results presented significant differences among cultivars
239 (Oke et al., 2013a). The suitability of five different cultivars starches for extrusion was also
240 investigated and it was observed that due to its high starch content, the greater yam starch has a great
241 potential as a food ingredient in extruded products and can be used for snacks, pre-gelatinized flours
242 and breakfast cereals (Oke et al., 2013b). A study was conducted to clarify the effects of tempering,
243 acid hydrolysis and low-citric acid-substitution on the chemical and physico-chemical properties of
244 starches of four Nigerian *Dioscorea* spp., including greater yam. It was shown that relevant and
245 suitable applications of the modified starches may be developed with a view of using them in
246 industrial production, or as additives for specific purposes in foods (Falade and Ayetigbo, 2017).

247

248 4.3. Amylose

249

250 Starch granules with high amylose content absorb limited water content during cooking. The
251 amylose content varies greatly (13.7–43.5% d.w.) (Table 1) and the amylose (A) versus starch (S)
252 ratio is a palatability trait. Preferred cultivars for boiled tubers have a high A/S ratio (> 0.18) and
253 cultivars with poor eating quality are characterized by low A/S ratio < 0.16 , high mineral and high
254 protein content (Lebot and Malapa, 2012; Ehounou et al., 2021). In Vanuatu, cultivars with very high
255 amylose content are often preferred for a highly appreciated traditional dish called *laplap*, a sort of
256 pudding prepared by grinding the tuber into a fine paste prior to cooking to produce an elastic starchy
257 gel. It was observed that starch content correlated positively with dry matter content. Mineral, and

258 protein contents correlated positively with each other, but correlated negatively with d.w. and starch. It
259 is thought, however, that the age of the tuber has an effect on the amylose content for a given cultivar.
260 A higher amylose content was observed in tubers harvested at full maturity than when harvested
261 earlier (Huang et al., 2006). The post-harvest storage period (up to 4–6 months for *D. alata*) can also
262 decrease the amylose content (Brunnschweiler et al., 2005). The ratio of amylose to amylopectin
263 content of *D. alata* starch affects the starch properties and functional characteristics such as
264 crystallinity and digestibility (Zhu, 2015; Harijono et al., 2016a).

265

266 4.4. Sugars

267

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

291

292 4.5. Proteins and amino acids

293

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

302 It has been suggested that dioscorins are worth developing as healthy or functional foods (Lu et al.,
303 2011). When comparing the antioxidant activities of dioscorins from greater yam, using the DPPH
304 (2,2-diphenyl-1-picryl-hydrazyl-hydrate) and hydroxyl radicals scavenging activity assays, reducing
305 power test and anti-lipid peroxidation test, it was found that *D. alata* dioscorin presented a higher
306 antioxidant activity than *D. polystachya*, a species known for its high dioscorin content. This is due to
307 the variation in amino acid composition and protein blends (Liu et al., 2006). The potential of *D. alata*
308 dioscorin for the activation of the innate and adaptive immune systems was confirmed (Fu et al.,
309 2006).

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

317 Raman spectroscopy has been used to show that in greater yam the secondary structure of dioscorin
318 A (molecular weight [MW] ~ 33 kDa) is mostly made of alpha-helices whereas that of dioscorin B
319 (MW ~ 31 kDa) is significantly different (Liao et al., 2006). The major amino acids (phenylalanine,
320 tyrosine, methionine, tryptophan and cysteine) complex exhibited a clear difference between
321 dioscorins A and B. They exhibit antioxidant, antihypertensive and immunomodulatory properties and
322 can protect airway epithelial cells against mite allergen. They also show some enzyme activities, and
323 present minor trypsin-inhibitor activity (Liu et al., 2016). Essential amino acids were determined in
324 China from nine cultivars with the following contents (in g/100g yam proteins): Threonine (3.88–
325 7.81% proteins), Valine (1.32–2.98%), Methionine (0.40–2.97%), Isoleucine (1.64–4.47%), Leucine
326 (2.16–4.73%), Phenylalanine (1.77–5.45%), Lysine (3.92–8.11%), Histidine (1.87–4.80%), and non-
327 essential amino acids: Asparagine (2.51–9.93%), Serine (3.10–8.37%), Glutamine (7.70–11.98%),
328 Proline (1.99–4.15%), Glycine (1.60–4.72%), Alanine (3.29–7.72%), Tyrosine (0.38–2.15%),
329 Arginine (7.96–13.43%) (Wu et al., 2016). Tryptophan (another essential amino acid) was quantitated

330 in 101 cultivars from India and Vanuatu with values varying from 0.0–369.2 mg/100 g d.w. (Muñoz-
331 Cuervo, 2015).

332

333 4.6. *Fibres*

334

335 Greater yam cultivars are rich in dietary fibres (1–12% d.w.) (Table 1). The fibres are very useful
336 for the digestive system and adequate fibre content increases water holding capacity, aids in regular
337 bowel movement, and accelerates the intestinal transit. Whole brown rice is often reported to be a food
338 with high fibre content with 5% d.w. Many greater yam cultivars present higher value with some
339 having total dietary fibres around 10% which is comparable to the whole wheat flour (approx. 12%).
340 Not surprisingly then, a daily diet rich in greater yam can contribute significantly to dietary fibres
341 requirements satisfaction. It has been suggested that if greater yam is not ideal for the sticky and
342 cohesive yam products such as pounded yam or *fufu*, it could be due partly to its relatively high fibres
343 content. However, it is also observed that cultivars combining high amylose and total dietary fibre
344 contents could be useful in diets for diabetics and health conscious consumers (Wireko-Manu et al.,
345 2013c).

346

347 4.7. *Minerals*

348

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

363

364 The effects of boiling, steaming and baking the greater yam tuber pieces have been investigated to
365 assess their impact on their nutrients. It appears that total crude protein contents tend to decrease with
366 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

367 causing a reduction in the mineral content of boiled tuber pieces. Furthermore, the three cooking
368 methods significantly reduced the vitamin C content in the tuber pieces (Wanasundera and Ravindran,
369 1992). Minerals content is impacted by post-harvest storage. A study conducted in Côte d'Ivoire to
370 assess changes up to six months after harvest has shown that minerals content of cultivar *Bété bété*
371 tuber significantly decreased during storage. (Kouakou Dje et al., 2010).

372

373 4.8. Organic and fatty acids

374

375 A preliminary survey of five greater yam cultivars from Papua New Guinea identified organic
376 acids as malic acid and citric acid with, respectively 123 and 127 mg/100 g f.w. and in four cultivars
377 from the Solomon, respectively 87 and 157 mg/100 g f.w. (Holloway et al., 1989). In Côte d'Ivoire the
378 greater yam cultivar *Bété bété* is widely cultivated and appreciated and its organic acids were
379 analysed: gallic acid and tannins (1380 mg/100 g d.w.), citric acid (1130 mg/100 g), ascorbic acid (880
380 mg/100 g), tartaric acid (1013 mg/100 g), sulfanilic acid (12 mg/100 g) and fumaric acid (4 mg/100 g).
381 The content of all these compounds decreased significantly after boiling tuber pieces for more than 20
382 min. (Didier et al., 2014). A survey conducted on 91 cultivars planted together within a common plot
383 in Vanuatu, to control possible environmental effects, identified not less than fourteen organic acids
384 (Fig. 2) and quantitated them using GC-MS (Table 2) (Mercier, 2013). Organic acids represented
385 approximately 2.9% d.w. among cultivars and fatty acids represented 0.21% d.w. Oxalic acid is an
386 anti-nutritional factor but the 91 cultivars presented very low values (18.41 mg/100 g). The detection
387 of malonic acid is rather surprising as it can be toxic when in high content but the values were low
388 (59.02 mg/100 g). Citric acid was by far the most important organic acid because of its positive
389 influence on taste perception and kidney functioning. Its mean content was variable (CV= 30.03%) but
390 quite high (2668.87 mg/100 g), content at which it can play an essential role against tuber flesh
391 browning. The dominant fatty acids were oleic acid (mean 19.29 mg/100 g d.w.) and linoleic acid
392 (116.04 mg/100 g) (Table 2).

393

394 4.9. Mucilage

395

396 The greater yam tuber flesh is rich in mucilage. Three Taiwanese cultivars (*Tainong 1*, *Tainong 2*,
397 and var. *purpurea*, a purple-fleshed cultivar) were studied to compare their properties. It was
398 concluded that their mucilages presented different antioxidant activities against DPPH (2,2-diphenyl-
399 1-picryl-hydrazil-hydrate) radicals, hydroxyl radicals and superoxide radicals. Furthermore, the
400 purification process was able to partially increase the antioxidant activity of the mucilage
401 polysaccharides. Greater yam mucilaginous polysaccharides may act as important radical scavengers
402 and antioxidants (Lin et al., 2005). The purified mucilage is composed of arabinose, galactose, glucose
403 and rhamnose. This mucilage has a significant effect on the gelatinisation properties of the greater yam

404 starch. The addition of mucilage was tested and resulted in a significant increase in peak viscosity of
405 the starch. It has been shown that compared to the starch alone, the addition of mucilage resulted in a
406 slight decrease of swelling power for greater yam starch (Huang et al., 2010).

407

408 **5. Bioactive compounds**

409

410 The greater yam is rich in useful and healthy secondary metabolites: phenolic acids, flavonoids,
411 and anthocyanins. Their antioxidant activities is, however, highly dependent on the drying process and
412 the extraction solvent used to prepare the samples prior to testing, as well as on the analysed part of
413 the tuber (Chung et al., 2008) and the analytical technique used. A preliminary HPLC screening of
414 twenty different cultivars revealed significant variations with seven anthocyanins, five flavonols
415 (including quercetin-3-glc(pyr) and quercetin-3'-glc,6'-acet), four flavanols and two phenolic acids
416 (Champagne et al., 2011). GC-MS profiling aiming to assess the potential of metabolomics was
417 conducted on the polar and lipophilic extracts from tubers of 49 cultivars belonging to four *Dioscorea*
418 spp., including five cultivars of *D. alata*. Not less than 123 metabolites were identified in greater yam
419 cultivars and these cultivars were chemically differentiated from the three other species using
420 multivariate analyses on these metabolites (Price et al., 2017). HP-TLC allowed high throughput
421 analysis of the most important metabolites in several hundreds of cultivars (Lebot et al., 2018a, b;
422 2019) (Table 3).

423

424 *5.1. Phenolic compounds*

425

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

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

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

468

469 5.2. Flavonoids

470

471 Two cultivars from Nigeria were analysed using HPLC and were shown to contain (+)-catechin,
472 the procyanidin dimers B-1 and B-3, and two other procyanidins, most probably a trimer and tetramer.
473 The presence of cyanidin-3-monoglucoside was confirmed (Ozo et al., 1984). It has been shown that
474 in Benin, tuber flesh browning correlates with total phenol and dry matter contents and is probably due
475 to catechins (Akissoé et al., 2005). Gallocatechin, epigallocatechin or catechin- and epicatechin-gallate
476 have been reported in freeze-dried cultivars tuber samples using HPLC (Champagne et al., 2011).
477 Catechins were found in greater yam cultivars from India and hybrids (means of 5.31 and 3.11 mg/g

478 d.w. respectively). Cultivars from Vanuatu presented values lower than Indian accessions and hybrids
479 (respectively 4.87, 5.07 and 5.69 mg/g) but significant variation was observed within each
480 geographical origin, as shown by the high standard deviations. Catechin and epicatechin were the most
481 important catechins but two unknown catechins (Cat1 and Cat2) were also detected (Lebot et al.,
482 2018a) (Table 4).

483 In India, Padhan et al. (2019) found the total flavonoids content of the greater yam to be
484 significantly lower compared to eight wild *Dioscorea* spp. with overall values ranging from 0.62 to
485 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*
486 and 9.8 mg/100 g d.w. for *Higur ala* (Senanyake et al., 2012). In Bangladesh, HPLC analysis of a
487 local cultivar methanolic extract identified 19 metabolites (Table 3) but the antioxidant and
488 antibacterial activities of the extract were thought to be due to myricetin (Anisuzzman et al., 2016). In
489 India, HPLC analysis of dried flours from greater yam tubers collected in West Bengal identified 21
490 compounds, kaempferol being the most important compound with 9.2 mg/100 g d/w. It was concluded
491 that the regular intake of greater yam containing kaempferol at such high content is thereby reducing
492 the risk of cardio vascular diseases, cancer, arteriosclerosis (Chaudhury et al., 2018) (Table 3).

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

497

498 5.3. Anthocyanins

499

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

512 In China, the analysis of a purple-fleshed cultivar allowed the separation and identification of
513 cyanidin 3-gentiobioside, alatanin C, cyanidin 3-ferulyl gentiobioside, cyanidin 3-sinapylgentianoside,
514 peonidin 3-gentiobioside and alatanin 2. The dominant anthocyanin in this cultivar was alatanin C and

515 accounted for about 46.3% of the total anthocyanins (He et al., 2015). In the Philippines, the cultivar
516 *Ubi* is grown to satisfy the colorant needs of the ice cream industry. Alatanin A, B and C have been
517 confirmed as the major anthocyanins in cultivars grown in the Philippines (Yoshida et al., 1991;
518 Moriya et al., 2015). In two Thai purple-fleshed cultivar, the major anthocyanin found was also
519 alatanin C (cyanidin 3-(6-sinapoyl gentiobioside) (Srivichai and Hongsprabhas, 2020).

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

529 Steaming of a purple-fleshed cultivar increased phenolic contents from 85.36 to 167.22 mg/100 g
530 d.w. GAE (gallic acid equivalent) and raised anthocyanin level from 36.09 to 57.28 mg/100 g d.w.
531 CGE (cyanidin-3-glucoside equivalent) (Imanningsih et al. 2013). Steam-cooking did not affect the
532 antioxidant capacity of the purple-fleshed cultivar. It was found that it could help to retain phenolic
533 compounds in purple yam while making them more available for consumption. The responses to heat
534 and O₂ of phenolic compounds were thought to be influenced by the contents of indigenous phenolic
535 compounds and flavonoids prone to PPO (polyphenol oxidase) activities (Cakrawati et al., 2021).

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

544

545 5.4. Carotenoids

546

547 An HPLC analysis of 17 cultivars from Vanuatu detected seven major peaks including lutein, all-
548 trans- β -carotene and zeaxanthin (Champagne et al., 2010). Five cultivars analysed using HPLC in
549 Indonesia presented five major peaks and three were identified as lutein, all-trans- β -carotene and
550 zeaxanthin with 23.75 to 132.12 μ g/100 g d.w. (Nadia et al., 2015). Distinct species-specific
551 carotenoids of five cultivars from Nigeria have been analysed (including all-trans- β -carotene and β -

552 carotenes epoxides) and multivariate analyses succeeded to differentiate them from 46 cultivars
553 belonging to four other cultivated yam species. Overall, the β -carotene contents of all 46 cultivars
554 were low (96.3–326 $\mu\text{g}/100\text{ g d.w.}$) compared to plants rich in such compounds (e.g., carrots or sweet
555 potato). However, the five greater yam cultivars presented greater α -tocopherol with greater β -carotene
556 content and had significantly more provitamin A activity than *D. rotundata* cultivars. Greater yam
557 cultivars also had noticeable quantities of 13-cis- β -carotene. But if the β -carotene epoxides are
558 included, then provitamin A content of some cultivars could be comparable to rich plants but their
559 provitamin A activity in humans remains unknown (Price et al., 2018). In India, the β -carotene content
560 ranged between 0.97 and 1.88 $\mu\text{g}/\text{g d.w.}$ in fifteen cultivars (Patel et al., 2019).

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

569

570 5.5. Saponins

571

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

584 Dioscin has been detected in greater yam cultivars from Taiwan (Yang et al., 2003), from China
585 with contents varying from 0.06 to 0.09% d.w. (Wu et al. 2019) but not in *D. alata* cultivars from
586 Japan (Nakayasu et al., 2015). However, Shan et al. (2020) could not detect it in two cultivars from
587 China. Diosgenin has been identified in a greater yam cultivar from India (Shah and Lele, 2012;
588 Cynthia et al., 2019) and China (Yang et al., 2019). Several studies report the presence of dioscin or

589 diosgenin in cultivars extracts (Kaur et al., 2021; Harijono et al., 2016b; Jesus et al., 2016). However,
590 a comprehensive review of saponins present in *Dioscorea* spp. did not report dioscin in *D. alata*, nor
591 other saponins (Sautour et al., 2007). Kwon et al. (2015) analysed fifteen accessions and breeding
592 lines in Nigeria and did not detect dioscin in greater yam. Dioscin, protodioscin, gracillin and
593 protogracillin were not detected in 550 accessions representative of a wide geographical diversity
594 (Lebot 2018ab; 2019). It is quite clear that the domestication process, which has led to the selection of
595 the present cultivars, has favoured genotypes with low saponins and catechins contents. It is therefore
596 unclear if the presence of dioscin (and diosgenin) is genetically controlled in the greater yam, with
597 some primitive cultivars presenting dioscin while it is absent from more improved ones. Or, if these
598 discrepancies are due to analytical artefacts, an insufficient coverage of the genetic diversity, or, and
599 most likely, to taxonomic misidentifications which are quite frequent among *Dioscorea* spp.

600

601 5.6. Allantoin

602

603 Allantoin (an ureide, hydantoin) is one of the most interesting secondary metabolites found in the
604 greater yam. It has remarkable antihypertensive action and has a dose-dependent ability to decrease
605 plasma glucose and increase plasma β -endorphin levels in diabetic rats that is not observed in normal
606 rats (Niu et al., 2010). It is safe and non-toxic and it has been suggested that it could be developed as a
607 new therapeutic agent (Chen et al., 2014). It is reported that allantoin improves the smoothness of the
608 skin, promote cell proliferation and contributes to rapid wound healing (Go et al., 2015). In Taiwan,
609 allantoin has been shown to protect the stomach tissues and inhibit the growth of tumours. It has anti-
610 diabetic effect, can modulate oxidative stress and antioxidant activities; it can improve kidney and
611 liver functions while maintaining insulin and glucose levels. Allantoin was quantified in *D. opposita*
612 (syn. *D. polystachya*), a species known to present high allantoin content with values ranging from
613 13.68 to 18.65 mg/g d.w. (Liu et al., 2016). An analysis of 208 cultivars and hybrids from Nigeria,
614 India, Vietnam, Papua New Guinea, and Vanuatu, revealed values ranging from 9.42 to 29.1 mg/g
615 d.w. of allantoin in *D. alata* (Lebot et al., 2019a). In China, allantoin varies from 6.20 mg/g to 14.9
616 mg/g d.w. in nine local cultivars (Wu et al., 2016) and allantoin content was shown to be highly
617 correlated with starch content (Shan et al., 2020).

618

619 5.7. Antinutritional compounds

620

621 The oxalate content is small compared to other root crops (Bradbury and Holloway, 1988;
622 Mercier, 2013). One of the major alkaloids in yam is dioscorine, a toxic isoquinuclidine alkaloid with
623 molecular formula $C_{13}H_{19}O_2N$ but so far dioscorine has been reported only in wild yams, especially in
624 *D. hispida* and not in *D. alata*. However, among the different antinutrients which have been identified
625 in *D. alata* cultivars in Nigeria are alkaloids, saponins, flavonoids, and tannins but their contents were

626 significantly reduced in the boiled tubers (Ezeocha and Ojmelukwe, 2012). Senanayake et al. (2012)
627 recorded alkaloid contents of 0.94, 1.64 and 1.89 mg/100 g in greater yam cultivars (*Raja ala*) and
628 (*Hingur ala*) in Sri Lanka.

629 Low levels of antinutritional compounds were identified in seven greater yam cultivars from
630 Nigeria (IITA): alkaloids (0.12–0.55% d.w.), trypsin inhibitor (24–49 TIU/g) and heamagglutinin
631 (1.22–5.75 Hu/g), phytic acid (0.22–0.28% d.w.), tannins (54.75–176.09 mg/100 g), hydrogen cyanide
632 (9.6–12 mg/kg d.w.) (Udensi et al. 2010). In India, total oxalate contents were significantly low after
633 boiling and the loss of oxalates was greater with boiling (40–50%) compared to steaming (20–25%)
634 and baking (12–15%) (Wanasundera and Ravindran, 1992; 1994).

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

645

646 5.8. Browning and polyphenol oxidase (PPO)

647

648 When the greater yam is processed into flour, there is tremendous variation between cultivars with
649 some being non-oxidizing while others turn brown in a few seconds after cutting the fresh tuber into
650 pieces. It has been suggested that the browning in raw and processed tubers results from enzymatic
651 polyphenol oxidase (PPO) and peroxidase activities. In Benin, where yam tubers are processed to
652 obtain a flour, whole tubers or pieces are traditionally blanched at an intermediate temperature (60–
653 75°C) before drying. There is no significant variation in phenol content during blanching but it
654 increases during drying. This is a problem as sun drying of the tubers into dried chips is the traditional
655 process in West Africa. The flesh of the fresh tuber of cultivar *Florido* is usually white but *amala* (a
656 popular paste in Benin) made from dried flour, turns brown during processing and the quality of the
657 final product is therefore not acceptable. It was found that there is a relationship between the *amala*
658 browning and the total phenol content of the flour: the higher the phenol content, the darker the final
659 product (Akissoé et al., 2005).

660 Total catechins values are significantly correlated with the colour of the flour indicating that they
661 contribute to the browning of the greater yam flesh tuber. Catechins were not detected in cultivars
662 from Vietnam and Papua New Guinea and only 25 cultivars from Vanuatu (over a total of 216

663 analysed) presented catechins in low values. Most local cultivars from Nigeria presented catechins but
664 the highest mean value was found in hybrids (Table 4). The presence of catechins in high amounts in
665 greater yam cultivars can be considered as a wild trait. Most high quality cultivars present low or no
666 catechins, while hybrids between parents originating from distant gene pools, present high catechins.
667 High catechins content, along with hairy tubers, poor shape, spines at the base of the stems, are
668 deleterious traits resulting from true seeds. Some cultivars from Nigeria present high levels of
669 catechins which could explain the browning of their flour or puree. This might indicate that these
670 clonally introduced cultivars are very ancient (Lebot et al., 2018b).

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

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

685

686 **6. Biological activity and health benefits**

687

688 There are numerous reports, especially from India and China, indicating that the greater yam
689 boiled tubers have different health-beneficial activities, including anti-gonorrhoea, anti-leprosy, anti-
690 inflammatory, anti-rheumatism. It is also known of being purgative, diuretic, to prevent cancer, reduce
691 blood sugar, and diabetes. Most of these reported properties are found in ethno-botanical surveys
692 (Jadhav et al., 2011; Sakthidevi and Moran, 2013; Dey and Chaudhuri, 2014). Several studies have
693 confirmed the antioxidant activity of the different extracts obtained from the greater yam tuber with
694 different solvents using the FRAP, TEAC assays, O₂ and DPPH-scavenging activities, as well as metal
695 chelating assays. Methanolic extracts of the raw tuber were shown to present high antioxidant activity
696 (Anisuzzman et al., 2016). It is thought that the acetone extract contains potent antiproliferative
697 properties. A study performed on two cancer cell lines, has shown that the extract displayed anticancer
698 properties resulting in the initiation of apoptosis, the death of cancer cells. It was suggested that the
699 greater yam may serve as a source for new anticancer compounds (Wallace et al., 2021). Powders or

700 flours prepared from dried tubers also presented high antioxidant activity (Adedayo et al., 2012; Das et
701 al., 2012; Chaudury et al., 2020; Guo et al., 2004; Larief and Dirpan, 2018; Ratnanningsih et al.,
702 2018). These studies, however, did not succeed to isolate the compounds responsible for such
703 remarkable activity. A few of greater yam physiological properties have been tested in cell or animal
704 experimental studies. Experiments conducted with mice have shown that methanolic extracts has
705 significant antidepressant and anxiolytic activities (Ruhul Amin et al., 2018).

706

707 *6.1. Cardioprotective properties*

708

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

717 Elevated plasma homocysteine is considered to be a risk factor for cardiovascular diseases. It can
718 be induced by excessive oral intake of methionine which causes an increase in plasma oxidation
719 markers and a decrease in antioxidant capacity in humans. A study was conducted with rats fed with
720 methionine to see if a diet based on cultivar *Tainung no. 2* in Taiwan could have a beneficial effect on
721 rats. After 12 weeks of freeze-dried powder feeding, the results indicated that elevated plasma
722 homocysteine (induced by methionine) could be reversed by greater yam feeding which also resulted
723 in significant antioxidative effects (Chang et al., 2004). In Taiwan, powdered greater yam and liquid
724 products, were used to analyse their health benefits and to investigate the potential antihypertensive
725 activity they might have on spontaneously hypertensive rats (SHR) fed with such products during 30
726 days. It was found that both type of products have significant antihypertensive activities toward SHRs
727 (Liu et al., 2009). Another study explored how it could protect the heart from doxorubicin (DOX)-
728 induced oxidative stress leading to cardiotoxicity in vivo. It was conducted by feeding greater yam
729 extracts given to experimental mice. The extract decreased the cardiac levels of thiobarbituric
730 acid, reactive oxygen species, and inflammatory factors. The extracts also played a role in increasing
731 the activities of glutathione peroxidase and superoxide dismutase, thus improving the DOX-induced
732 alterations in the heart tissue of DOX-treated mice. This study concluded that the greater yam has
733 significant cardioprotective properties against DOX-induced damage via its multiple effects on
734 antioxidant, anti-inflammatory, and antiapoptotic activities. Some ethanol extracts contain more than
735 20% diosgenin, a compound known to significantly improve the cardiac damage induced by DOX.
736 Hence, diosgenin may be responsible for the antioxidant, anti-inflammatory, or antiapoptotic activities

737 of the extracts but its overall contribution to greater yam cardioprotective benefices remains to be
738 determined (Chen et al., 2017a).

739

740 6.2. Protection of postmenopausal symptoms

741

742 The greater yam has been traditionally used to treat menopausal symptoms in Taiwan. A first
743 study was conducted to clarify its effects on lipids, antioxidant status, and sex hormones in
744 postmenopausal women. Twenty-four healthy postmenopausal women were asked to replace their rice
745 diet with 390 g of boiled tuber pieces in two of three meals per day for 30 days. It was observed that
746 after ingestion, there were significant increases in serum concentrations of estrone (+26%), sex
747 hormone binding globulin (SHBG) (+9.5%), and significant increase in estradiol (+27%). Urinary
748 concentrations of the genotoxic metabolite of estrogen, 16-hydroxyestrone decreased significantly by
749 37%. Plasma cholesterol concentration decreased significantly by 5.9%. Lag time of low-density
750 lipoprotein oxidation prolonged significantly by 5.8% and urinary isoprostane levels decreased
751 significantly by 42%. It was concluded that replacing two thirds of rice with boiled greater yam tubers
752 for 30 days improves the status of sex hormones, lipids, and antioxidants and that these positive effects
753 might reduce the risk of breast cancer and cardiovascular diseases in postmenopausal women (Wu et
754 al., 2005). Cheng et al., (2007) purified and identified new compounds from cultivar *Tainung no. 2*
755 ethyl acetate extract: hydro-Q₉ chromene and γ -tocopherol-9, together with four known compounds,
756 RRR-R-tocopherol, coenzyme Q₉, cycloartane, and 1-feruloylglycerol. Five of these compounds were
757 shown to have estrogenic activity. It was concluded that the results provide evidence for the beneficial
758 effect for menopausal women.

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

773

774 6.3. Anti-microbial activity

775

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

793

794 6.4. Anti-inflammatory activity

795

796 The assessment of the immune system stimulation potentialities of an hydro-methanolic extract
797 demonstrated that the greater yam can actively polarize the lymphocyte population towards the
798 expression of an immune response. The tuber extract also presented mitogenic activity as evidenced by
799 the in vitro proliferation of lymphocytes (Dey and Chaudhuri, 2014). The hydro-methanol extract has
800 been shown to significantly down-regulate the pro-inflammatory signals in a gradual manner
801 compared to a reference control using murine lymphocytes for 48 h (with different concentrations
802 from 0–80 mg/mL). The extract was then analysed to clarify its chemical composition in order to
803 identify the compounds involved. HPLC analysis identified gallic acid, 4-hydroxy benzoic acid,
804 syringic acid, p-coumaric acid, and myricetin. GC-MS analysis identified azulene, phenol, 2,4-bis(1,1-
805 dimethylethyl), pentadecanoic acid, methyl ester, n-hexadecanoic acid, octadecadienoic acid,
806 indolizine, bumetrizole, cinnamyl cinnamate and squalene. It was concluded that the extract
807 significantly down-regulated the pro-inflammatory signals in a gradual manner compared with control
808 (0 mg/mL) and that the various bioactive compounds identified present anti-inflammatory activities
809 contributing to the overall bioactivity (Dey et al., 2016). A greater yam diet on mice fed with 50% raw
810 lyophilized yam for 21 days produced a remarkable effect on the mucosal enzyme activities in the

811 small intestine and lipid metabolism of adult mice and showed constant improvement in the
812 cholesterol profile of the liver and plasma of mice (Chen et al., 2003). Another team also observed an
813 increase in faecal excretions of neutral steroid and bile acids whereas absorption of fat was reduced
814 (Yeh et al., 2007).

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

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

838

839 6.5. *Anti-diabetic activity*

840

841 In Nigeria, the occurrence of diabetes has been observed to increase, especially in urban areas due
842 to excessive weight gain which might be due to increased food intake and blood glucose level. The
843 greater yam is known to possess anti-diabetic properties which could help in managing body weight. It
844 was observed that when different groups of rats were treated with greater yam extracts there was a
845 clear reduction in food intake and weight gain. The food intake, blood glucose level and body weight
846 were found to be significantly reduced in a dose-dependent manner when compared with the control
847 group. The weight loss might be due to increased satiety or to the reduction in the fasting blood

848 glucose level. It was also observed that the reduction in body weight might be due to the phenolic
849 compounds present in the tubers (Olubobokun et al., 2013). Water soluble polysaccharides extracted
850 from purple and yellow-fleshed cultivars were tested and exhibited blood glucose lowering properties
851 in hyperglycemia condition in rats with the purple extract having a slightly higher effect. It was
852 suggested that the greater yam could be used to develop foods aiming at controlling blood glucose
853 levels for diabetic persons (Estiasih et al., 2018).

854 In India, an ethanolic extract from Tamil Nadu was tested for hypoglycemic activity in normal rats
855 (100 and 200 mg/kg for 21 days). The treatment showed a highly significant reduction in blood
856 glucose levels and the extract did not produce hypoglycemic activity at both dose levels in normal rats.
857 In induced diabetic rats, the body weight of rats treated with extracts showed a significant increase
858 after 21 days. A reduction in plasma triglyceride and cholesterol in rats resulted from a diet
859 supplemented with 40% greater yam was found significant. The tuber extract showed reduction in
860 blood glucose level as well as increased body weight in rats treated with streptozotocin and alloxan,
861 respectively. The study concluded that the ethanolic extract presented significant antidiabetic activity
862 (Maithili et al., 2011).

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

880 It is difficult to narrow down to a single compound the beneficial effects of the greater yam.
881 However, there is strong evidence that dioscorin plays a major role in the greater yam biological
882 activity and health benefits but dioscorin may not act alone and synergies of action are possible with
883 additional bioactive substances. The greater yam is rich in various polyphenols and it has been shown
884 that these compounds alleviate the side effects of metabolic disorders. Their action has been described

885 as alleviating intestinal oxidative stress, improving inflammatory status, and improving intestinal
886 barrier function. It is known that polyphenols regulate intestinal functions, including the gut
887 microbiota, and are therapeutic agents for various metabolic disorders (Niwano et al., 2022).

888

889 **7. Future developments**

890

891 Freshly peeled greater yam tuber slices prepared in vacuum-sealed transparent plastic bags are
892 commercialised in most tropical cities around the world. The portions are sliced into 2–4 cm thick
893 pieces and dipped in a solution of 1% metabisulphite to prevent oxidation. These slices are then
894 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
895 to -5°C. This product is ready to be cooked and eaten. The use of metabisulphite improves the colour
896 greatly and avoids discoloration for up to 3 months of storage.

897

898 *7.1. Flours*

899

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

917 Unfortunately, the sun drying process has a significant negative impact on the vitamins content of
918 high quality flour (Adebowale et al., 2018). In Indonesia, a purple-fleshed cultivar processed into flour
919 after steaming retained its colour. The substitution of wheat flour with purple greater yam flour up to
920 40% allowed the production of wet noodles with adequate quality (Lavlinesia et al., 2019). Their
921 similarities to other commercial starches or flours could be useful for noodles, snacks and baby food

922 products (Salda et al., 1998). The incorporation of greater yam flour in bread (25% yam flour/75%
923 wheat flour) has been shown to significantly increase the antioxidant capacity of the blended bread
924 with potential for health-promoting foods. It seems that the substitution with yam flour in a bread
925 formulation does not interfere with bread acceptability (Hsu et al., 2004). When compared to other
926 cultivated yam species, *D. alata* flour has greater ability to withstand shear at high temperatures and
927 higher cooked paste stability, indicating that its flour can be targeted for industrial uses because of its
928 hot paste stability (Wahab et al., 2016).

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

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

945

946 *7.2. Resistant and modified starches*

947

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

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

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

973 The greater yam starches are also interesting as additives, especially for yogurts. In Nigeria,
974 sensory evaluation revealed that yoghurt produced from acetylated greater yam starch was superior to
975 commercial cassava flour. It presents good starch qualities but acid-thinned greater yam starch
976 presented the best results indicating that it could be adopted for industrial uses (Awolu and Olofinlae,
977 2016). Two different cultivars were analysed in Ghana for their potential as thickening agent in
978 yogurts. The starches were found of suitable quality with a long shelf life due to their low acidity and
979 their light colour was a plus for a new product. The cultivar *Akaba* was found to present an overall
980 acceptability higher than the control, indicating that greater yam starches could be used thicken
981 yogurts to produce transparent, creamy texture, sweet taste, flavour, and consistency (Tortoe et al.,
982 2019). In Colombia, the addition of greater yam starch improved the physicochemical characteristics
983 of yogurt, maintained an intense white colour while presenting a preference at the sensory level,
984 compared to pectin, the commercial stabilizer. During three weeks of storage, yogurt with yam starch
985 at 0.1% w/w showed a decrease in syneresis (separation of liquid from gel), while in yogurts with
986 pectin, syneresis remained practically constant in this period. In the first week of storage, yogurts with
987 yam starch showed a decrease in acidity (Pérez et al., 2021).

988

989 *7.3. Anthocyanins extracts*

990

991 The production of anthocyanins extracts for the food processing industries is of interest. A
992 comparative study has shown that the highest yield of anthocyanin extract from purple-fleshed cultivar
993 flour was obtained when MeOH solvent was used (247 mg/100 g extract). As expected, anthocyanin
994 and total phenolic contents were found to be highly correlated with antioxidant activity (RSA% and
995 FRAP) (Tamaroh et al., 2018). It is possible to obtain ethanolic anthocyanin-rich extracts by

996 ultrasound-assisted extraction (UAE). The optimum extraction occurs at 60 °C for 10 min with
997 ethanol: water (80:20). An economic evaluation study found that the production cost decreased from
998 US\$ 950 /kg to US\$ 124 /kg when the extractor capacity increased from 5 l to 500 l. The extraction of
999 anthocyanins from purple yam by UAE is economically feasible when the selling price is above US\$
1000 170 /kg (Ochoa et al., 2020).

1001

1002 *7.4. Other processed uses*

1003

1004 The greater yam can also be used for replacing fat in industrial sausages. Sausages with 5% yam
1005 added had no significant difference in colour, flavour, hardness, juiciness, and overall acceptability
1006 with the control. Such replacement results in sausages with 22% less fat content (Tan et al. 2007).
1007 Hydrocolloids are hydrophilic polymers that have multi functionalities such as thickener, gelling
1008 agent, stabilizer, but their world market is constrained by price instability and shortage of raw
1009 materials. The mucilage of *D. alata* represents an interesting source of hydrocolloids but its extraction
1010 is constrained by its high viscosity and high water-binding capacity of its glycoprotein that inhibits the
1011 separation of mucilage from starch. In Indonesia, the effect of different salt types on water to tuber
1012 ratios during mucilage extraction were compared to optimize mucilage yield. A water to tuber ratio of
1013 4:1 with addition of CaCl₂ salt resulted in the best mucilage yield (1.58% f.w.) with high purity (low
1014 starch content) (Fortuna et al., 2020).

1015 Diverse processing possibilities have been discovered around the world for the greater yam but the
1016 major constraint remains the mechanization of the tuber peeling process. Lye-peeling has been
1017 proposed as a possible solution in the early 1970s in Puerto-Rico (Rivera-Ortiz and González, 1972)
1018 but has not been adopted since. Ease of peeling the tubers is highly variable and some cultivars are
1019 more adapted than others but in all countries nowadays peeling is still done by-hand. Unless this
1020 constraint is eliminated, processing will remain expensive and will result in non-competitive products.

1021

1022 *7.5. Food security and biofortification*

1023

1024 There is tremendous chemical variation within cultivars and there is therefore scope for
1025 biofortification, an approach often favoured for crops playing an important role for food security. The
1026 greater yam being mostly cultivated for the fresh food markets, mainly in West Africa, it would appear
1027 interesting to improve existing contents in selected metabolites, such as carotenoids, anthocyanins or
1028 allantoin through conventional breeding techniques. There are a few breeding programmes working on
1029 the genetic improvement of the greater yam. They are located in the yam belt countries of Nigeria,
1030 Benin, Ghana and Côte d'Ivoire with the International Institute of Tropical Agriculture (IITA, Ibadan,
1031 Nigeria) coordinating the activities. Three other programmes are based in Guadeloupe (West Indies)
1032 under the leadership of INRAE and CIRAD, in CTCRI (Trivandrum, Kerala, India) and in VARTC

1033 (Santo, Vanuatu). Improvement is conducted through successive cycles of phenotypic recurrent
1034 selection. However, *D. alata* being dioecious, with rare female plants, erratic flowering, and variable
1035 ploidy levels, progress is rather slow. As the greater yam is highly heterozygous, when hybrids are
1036 created, many wild traits, including tuber flesh oxidation and poor palatability are dominant among
1037 progenies (Lebot et al., 2019b; Rinaldo et al., 2022).

1038 Existing traditional cultivars present outstanding nutritional and chemical properties and it is quite
1039 possible that it will be difficult for breeders to reach comparable chemotypes through conventional
1040 breeding. Most breeding programmes are presently working on anthracnose resistance and are
1041 eliminating, through successive clonal evaluations, progenies with poor quality traits. But so far no
1042 improved genotype has been widely distributed and adopted by farmers. At present, growers are
1043 working mostly with ancient cultivars clonally introduced from distant sources. It has been estimated
1044 that there are 4,524 accessions of *D. alata* maintained in 28 countries germplasm collections (Lebot
1045 and Dulloo, 2021). In the 1970s, international germplasm collections were made under the USDA
1046 programme based in Mayaguez (Puerto Rico) and elite cultivars were selected (Martin et al., 1975)
1047 and internationally distributed. When *Florido* was introduced from Puerto Rico to Côte d'Ivoire, it
1048 was rapidly adopted (Doumbia et al., 2004). When *C18* was introduced from Cameroon to Côte
1049 d'Ivoire, the adoption rate was also spectacular (Kouakou et al., 2012). These two well documented
1050 cases indicate that, in West Africa, producers are eager to test new cultivars. Unfortunately, the
1051 hundreds of cultivars existing in Asia and in the Pacific are not transferred to West Africa where is
1052 concentrated more than 90% of the world yam production. There is an urgent need to standardise the
1053 analytical protocols in order to conduct comprehensive assessment of these cultivars and to select the
1054 most promising ones prior to their safe transfer to West Africa. Technical constraints hindering
1055 accurate comparisons might result from pedoclimatic variation between countries (and studies) due to
1056 genotype × environment interactions. Major compounds and secondary metabolites are known to be
1057 impacted quantitatively by environmental factors and ontogeny.

1058

1059 **8. Conclusion and perspectives**

1060

1061 This review highlighted the remarkable chemical composition of the greater yam and the diverse
1062 physiological properties of its phytochemicals. Of all root and tuber crops, the greater yam has higher
1063 minerals and vitamins content and is the richest in proteins (mostly dioscorins) and these have well
1064 documented physiological properties. Its nutritional composition is excellent with extremely low fat
1065 and high fibres and carbohydrates content. Most cultivars present high levels of secondary metabolites
1066 (allantoin, carotenoids, anthocyanins, organic acids, flavonoids), all with beneficial effects on human
1067 health. However, this review has emphasized the scope of variation existing within and between
1068 countries and the highly variable results obtained by independent teams analysing different cultivars.
1069 All cultivars are clones of hybrids and *D. alata* is highly heterozygous. Comparison of data obtained in

1070 different environments is therefore difficult without and accurate identification of genotypes and the
1071 control of environmental factors. Although the greater yam is mostly cultivated in Africa where it has
1072 been clonally introduced, many research studies have been conducted in Asia, the area of origin of the
1073 species, where cultivars present greater genetic diversity. This review also confirmed the complexity
1074 of consumers' taste and preferences, and the need for adequate chemotypes for processed products.
1075 Over the forthcoming decades, the yam belt countries will witness tremendous population growth and
1076 pressure on the land in a context of climate change. There is an urgent need to introduce to West
1077 Africa new cultivars for direct clonal distribution to growers. And to compose base populations for
1078 genetic improvement with sufficient genetic diversity and chemical variation to allow breeding
1079 programmes to develop new hybrids with suitable characteristics.

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1081 **References**

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- 1593

1594 **Figure captions:**

1595

1596

1597 **Fig. 1.** *Dioscorea alata*, the greater yam: a) foliage; b) close-up of young leaves of two different
1598 cultivars, one with anthocyanin pigmentation; c) male and female inflorescences developing into
1599 capsules after successful pollination; d) tubers for sale on a local market; e) popular cultivar *Florido*,
1600 with compact tuber shape, smooth skin surface and appreciated taste with white flesh and no
1601 oxidation; f) cultivar with elongated tuber shape, g) purple-fleshed cultivar; h) cross-section of a tuber
1602 showing anthocyanin pigmentation; i) white-fleshed cultivar with tinges of anthocyanins (photos by V.
1603 Lebot).

1604

1605 **Fig. 2.** GC-MS chromatogram of methylated organic acids extract of *D. alata* cultivar (acc. no.
1606 Da1335 from Vanuatu) after methylation. 1: caprylic acid (internal check). 2: oxalic; 3: malonic; 4: 2-
1607 methoxy dimethyl succinate; 5 & 6: glucose derivatives; 7: mallic; 8: pentadécanoic; 9: palmitic; 10:
1608 heptadecanoic; 11: citric; 12: stearic; 13: oleic; 14: linoleic; 15: α -linolenic; 16: arachidic.

1609

1610 **Fig. 3.** Neighbour joining tree on a data matrix of 101 cultivars x 56 compounds (15 carotenoids, 1
1611 indol (tryptophan), 4 phenolic acids, 7 hydroxycinnamic acids, 15 flavanols/flavanones, 8
1612 flavonols/flavones, 4 anthocyanins, and 2 unknown compounds). The *D. alata* cultivars rich in
1613 carotenoids (orange numbers) and those rich in anthocyanins (purple numbers) are differentiated.

1614

1615 **Fig. 4.** PCA analysis of 101 cultivars (blue dots) x 56 compounds (red lines) showing the positive
1616 correlations between 15 carotenoids (C nos) including all-trans- β -carotene (beta) (yellow ellipse),
1617 towards axis 1 and the 4 anthocyanins (An1, 2, 3, 4, in blue ellipse), towards axis 2.

1618

1619

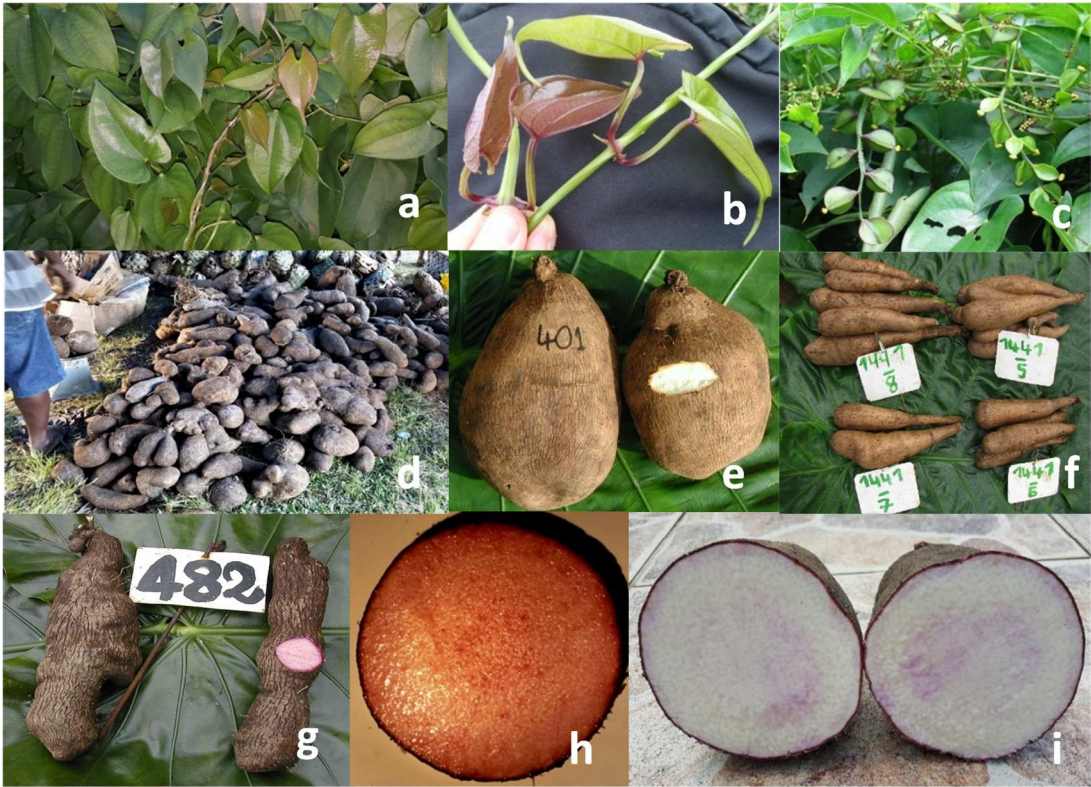


Fig. 1

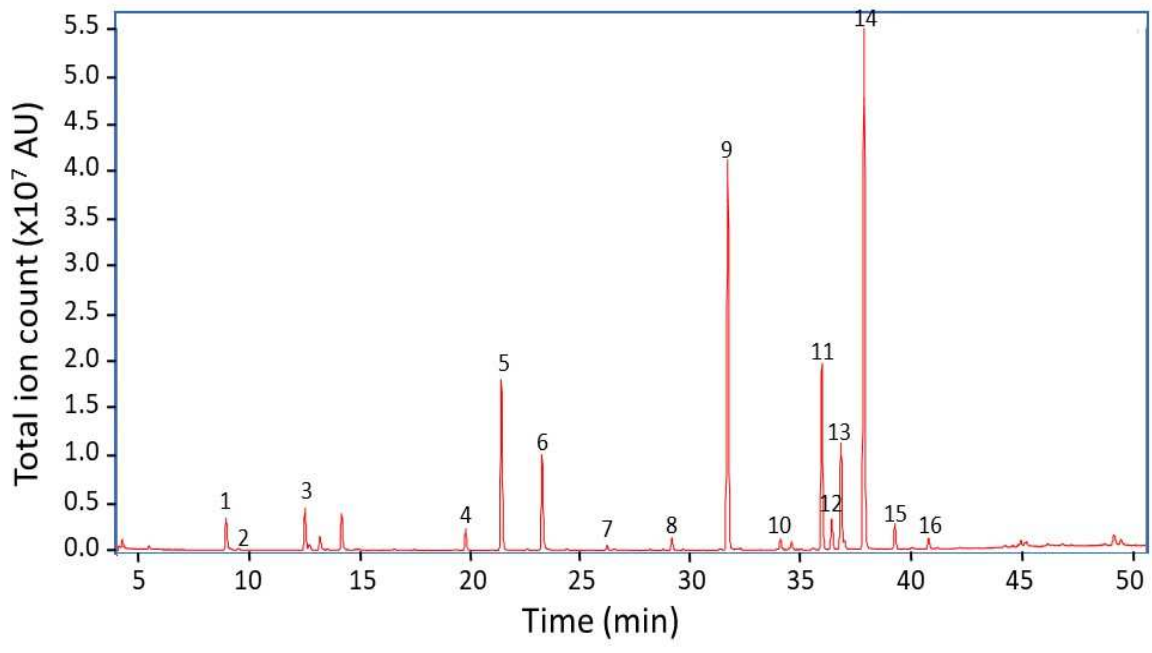


Fig. 2

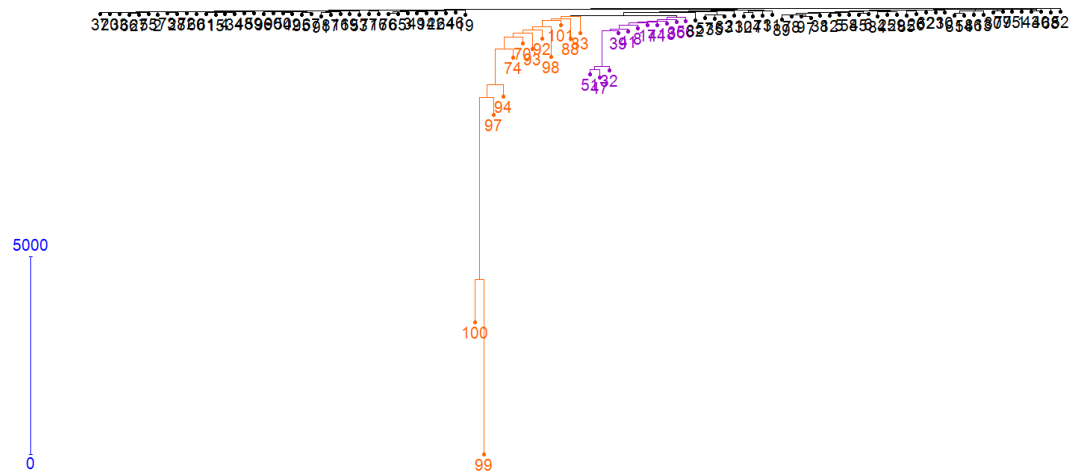


Fig. 3

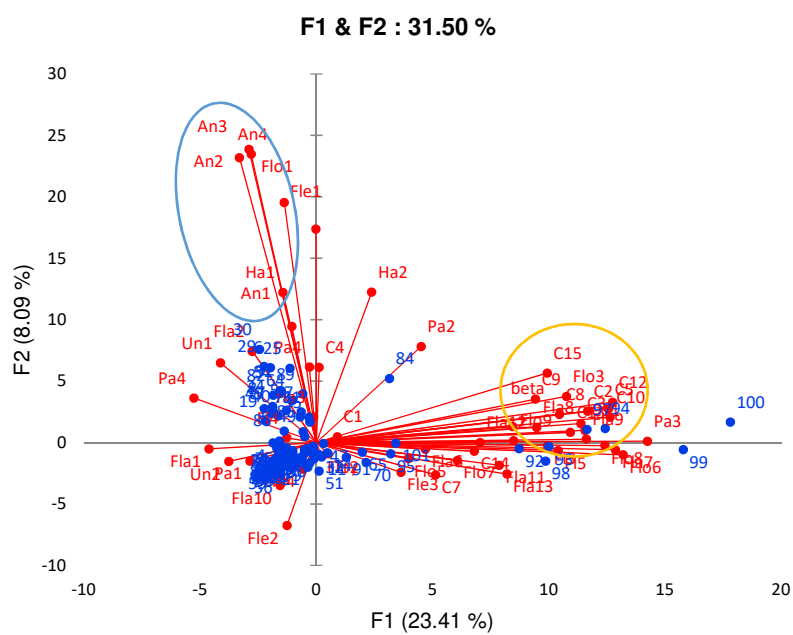


Fig. 4

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 (<i>n</i>)	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*

¹Wireko-Manu et al., 2011, 2013c; ²Polycarp et al., 2012; ³Baah et al., 2009; ⁴Adebowale et al., 2018; ⁵Patel et al., 2019; ⁶Padhan et al., 2018; ⁷Behera et al., 2009; ⁸Wanasundera & Ravindran, 1994; ⁹Wu et al., 2016; ¹⁰Fauziah et al., 2020; ¹¹Lebot et al., 1998; ¹²Lebot & Malapa, 2012; ¹³Lebot et al., 2018a. ¹⁴Price 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
palmitic	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
<i>trans</i> -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. (\pm standard deviations). All cultivars were cultivated within a common plot (adapted from Lebot et al., 2018a).

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

¹chlorogenic acid, ²unknown catechins but most likely gallicocatechin, 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)
<i>D. alata</i>	93.32	26.6
<i>Alocasia macrorrhiza</i>	n.d.	n.d.
<i>Colocasia esculenta</i>	26.56	3.32
<i>D. bulbifera</i> (tubers)	64.17	11.53
<i>D. bulbifera</i> (bulbils)	34.84	6.11
<i>D. cayenensis</i>	n.d.	n.d.
<i>D. esculenta</i>	6.39	1.55
<i>D. pentaphylla</i>	n.d.	n.d.
<i>I. batatas</i>	40.95	12.53
<i>M. esculenta</i>	n.d.	n.d.
<i>Xanthosoma sagittifolium</i>	37.77	7.44