



Carotenoid profiling of yams: Clarity, comparisons and diversity

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ABSTRACT

Screening carotenoids of elite accessions of yam (*Dioscorea* spp.) used in the global yam breeding program has been conducted to quantitatively determine the carotenoid composition of the crop. Comparisons to previous data reporting carotenoid levels in yam has been made, in order to deduce greater perspectives across multiple studies. Characterisation of complex species and accession-specific profiles have shown a rich base of diversity that can inform breeding strategies. Key findings include; (i) the identification of accessions rich in β -carotene which can aid provitamin A biofortification, (ii) Data disputing the commonly held belief that yellow Guinea yam (*D. cayennensis*) has higher β -carotene content than that of white Guinea yam (*D. rotundata*), and (iii) the tentative identification of C₂₅-epoxy-apocarotenoid persicaxanthin with potential implications for tuber dormancy.

1. Introduction

Yams (*Dioscorea* spp.) are a staple starchy tuber for 60–100 million people (Mignouna, Abang, & Asiedu, 2003). Whilst production costs are greater, in low technology farming systems yams have a higher yield and/or production value than other starchy tropical staples (Oke, 1990). Yams have preferred organoleptic qualities to other carbohydrate sources (Bhattacharjee et al., 2011). The relatively long dormancy period ensures yam tubers have a longer shelf life, even without refrigeration (Knoth, 1993), and so yams are vital for year-round food-security in growing regions. Favourable sensorial traits, better storage qualities and socio-economic importance have led yam to being considered as an agricultural commodity of superior economic value to alternative starchy crops (Osunde, 2008). In the growing regions, demand outstrips supply and it has been noted that, as income increases, consumers shift from cassava to yam (Sanginga, 2015). Despite these consumer preferences, yam is understudied when compared to other tropical root and tuber crops. Recent research on tropical crops has involved biofortification efforts, including enhancing provitamin A

through increasing amounts/biosynthesis of β -carotene. Approaches have involved capturing natural diversity and targeted breeding, e.g., the HarvestPlus program (www.harvestplus.org), the CGIAR research program on roots, tubers and bananas (CGIAR-RTB) (www.rtb.cgiar.org) and for taro; or through genetic modification such as for GoldenRice (www.goldenrice.org), BioCassava Plus (Sayre et al., 2011), Bananas21 (www.banana21.org) and the Next Generation Biogreen21 Program (sweet potato) (Park et al., 2015).

Vitamin A deficiency is prevalent in yam-growing regions. Increasing the provitamin A carotenoid content of yams has been cited as a key nutritional improvement and especially desired by females, offering a gender-equal breeding option (Abdoulaye et al., 2015). However, improvements in the provitamin A content of *Dioscorea* are in early stages and behind that of cassava and sweet potato and not even included in the HarvestPlus Program. As incomes in low-income food-deficit countries (LIFDC) rise, consumers may switch from the provitamin A enriched sweet potato or cassava to yams, which is currently inadequately consumed. In addition to provitamin A activity, other carotenoids have key roles in nutrition and health, such as lutein and

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zeaxanthin for eye-health, antioxidant activities and potential chemopreventative effects (Fraser & Bramley, 2004).

Understanding carotenoid biosynthesis is vital to understand plant development, due to their essential role in photosynthesis and as precursors of various signalling molecules and hormones (Hou, Rivers, León, McQuinn, & Pogson, 2016), such as abscisic acid (ABA), strigolactones and apocarotenoids, which regulate many cellular processes, including fruit ripening, environmental interactions and especially may be important for yam tuber dormancy, which is less understood and contrasts with the model tuberous crops, such as potato and cassava.

Contributing to the delay/absence in biofortification efforts on yams could be the lack of literature regarding carotenoid compositions of different species and where available, reports are conflicting. Historically, yams have been considered to be low in β -carotene. The most widely cultivated species are the Guinea yams, comprising the white variety *D. rotundata* and yellow variety *D. cayennensis*. *D. cayennensis* is reported to have higher carotenoid content (Bhattacharjee et al., 2011; Gedil & Sartie, 2010; Lebot, 2008), whilst *D. rotundata* is preferred by farmers and consumers. A few studies have showed that β -carotene is the major carotenoid of *D. cayennensis* (Ukom, Ojmelukwe, & Alamu, 2016; Ukom, Ojmelukwe, Ezeama, Ortiz, & Aragon, 2014), yet, other reports show β -carotene is of minor presence in the species (Champagne et al., 2010) and that the major carotenoids are xanthophyll esters (Martin & Ruberte, 1975). Recent work has shown varieties of *D. dumetorum* with estimated vitamin A activity at levels similar to that of enhanced cassava genotypes (Ferede, Maziya-Dixon, Alamu, & Asiedu, 2010). However, studies on other varieties of the species have found low carotenoid content (Ukom et al., 2014). The same holds true for the species *D. alata* and *D. bulbifera*, where reports conflict regarding carotenoid compositions and quantities of β -carotene (Inocent, Ejoh, Issa, Schweigert, & Tchouanguep, 2007; Lako et al., 2007; Martin, Telek, & Ruberte, 1974; Ukom et al., 2016).

Comprehensive and comparative studies between different *Dioscorea* species could potentially be improved by following Metabolomic Society Initiatives (MSI), (Salek, Steinbeck, Viant, Goodacre, & Dunn, 2013) and community recommendations (Ferne et al., 2011) on reported parameters regarding analytical methods, such as sample storage conditions, e.g., frozen, fresh or freeze-dried materials; saponification or non-saponification of extracts and compound identification parameters. Champagne et al. (2010) published the only broad species study of carotenoid composition in *Dioscorea* to date. The work highlighted genotype diversity and emphasised the importance of future study and potential for biofortification in yams. However, the authors noted the study was exploratory and due to the complex nature of profiles, identification of major carotenoids was lacking for species including *D. cayennensis*, *D. bulbifera* and *D. alata*.

In the present study, detailed comparative cross-species carotenoid profiling has been undertaken on tuber of elite accessions routinely used in yam breeding, to provide clarity regarding the carotenoid compositions of different *Dioscorea* spp. The technique also allowed simultaneous fingerprint profiling of other isoprenoids, including tocopherols and quinones. Results showed diverse species-specific profiles and the analysis of elite accessions has identified those with high provitamin A content, putative blocks in the carotenoid biosynthetic pathway and tentative identification of the C₂₅-epoxy-apocarotenoid persicaxanthin, which may play a role in tuber dormancy. The investigation serves as a foundation to develop breeding strategies towards nutritional improvement of yams and a potential approach to elucidate mechanisms of dormancy.

2. Materials and methods

2.1. Reagents

All reagents were of analytical standard supplied as follows: CHCl₃, EtOAc, HCl, MeOH and MTBE (Fluka, Loughborough, UK); DCM (VWR

International, Leighton Buzzard, UK); meta-chloroperoxybenzoic acid (mCPBA), NaOH, Tris, NaCl, KOH, water, ammonium acetate and formic acid (Sigma-Aldrich, Gillingham, Dorset, UK).

2.2. Plant material

Accessions covering four species of *Dioscorea* were grown in field conditions of the Yam Breeding Unit of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. The field plot design was controlled and plants grown between June 2013 and Feb. 2014. Tubers were harvested and shipped to the Royal Holloway University of London (RHUL), United Kingdom for further analysis. For standard extractions tubers from three biological replicates per accession were sectioned laterally and longitudinally into 12; and 6 representative sections per tuber frozen in liquid nitrogen (Price, Bhattacharjee, Lopez-Montes, & Fraser, 2017). Sections were freeze-dried (Lyovac GT2, Leybold-Heraeus, Chessington, UK); skin peeled and ground (via a cryogenic mill; SPEX CertiPrep Freezer/Mill 6750, Stanmore, UK) to a homogenous powder prior to extraction. All samples were stored at -80°C prior to further processing.

2.3. Preparation of standards

Standards were prepared using treatment with mCPBA (Rodriguez & Rodriguez-Amaya, 2007) and/or dilute HCl (Meléndez-Martínez et al., 2009). For epoxidation 10 mg of carotenoid stock and 1 mg of mCPBA were stirred at room temperature (RT) for 2 h in DCM and washed with NaOH (5%) followed by washing twice with water and dried using a centrifugal evaporator (Genevac EZ-2 Plus, SP Scientific, Suffolk, UK). Standards were re-suspended in EtOAc, volume adjusted to ensure well resolved spectra and aliquots (100 μL) taken. For furanoid rearrangement, 1 μL of HCl (0.1 mM) was added to the aliquots. Compounds were identified with comparison to reported retention times, spectra and elution orders (Meléndez-Martínez et al., 2009; Rodriguez & Rodriguez-Amaya, 2007; de Rosso & Mercadante, 2007). Tangerine tomato (*Solanum lycopersicum* var. Tangella) was extracted to provide reference for ζ -carotene, phytoene and phytofluene. Additionally, β -zeacarotene, ζ -carotene, phytoene and phytofluene were extracted from *Phycomyces blakesleeanus* mutant S442. In brief, lyophilised mycelia from 7-day-old cultures of S442 grown on Sutter agar were ground in a tissue lyser II (Qiagen, Manchester, UK) at 30 rpm for 8 min and 10 mg extracted thrice using MeOH: CHCl₃ (1:1), incubated for 1 h on ice and phase separated via addition of water. Organic phases were pooled, dried under centrifugal evaporation and stored at -80°C prior to further processing.

2.4. Extraction of carotenoids

Carotenoids were extracted following a modified protocol (Fraser, Pinto, Holloway, & Bramley, 2000), whereby 200 mg of lyophilised tissue were extracted in 15-mL borosilicate glass test tubes (Fisherbrand, Loughborough, UK). To each sample, 6 mL of chilled (-20°C) MeOH:CHCl₃ (1:2) were added, vortexed (VELP Scientifica ZX3 Advanced Vortex Mixer, Usmate (MB), Italy) and incubated for 15 min at -20°C . Subsequently, 2 mL of ice cold 100 mM Tris-HCl buffer containing 1 M NaCl (pH 7.5) were added. Samples were vortexed, centrifuged at 3250g for 5 min at 4°C to facilitate phase separation, and the organic phase removed using a glass Pasteur pipette. Repeated extractions were undertaken until material was exhausted of visible colour (typically 1–2 extractions). Organic phases were dried using a centrifugal evaporator (no lamp) and stored at -80°C before further processing. Saponification involved the addition of (2 mL) methanolic KOH (10%), vortexing and incubation at 40°C (Techne Dri-Block DB-2A; Cole-Parmer, Stone, UK) for 15 min, followed by addition of chilled (-20°C) CHCl₃ (4 mL) and phase separation by addition of water (2 mL). Saponified samples were then processed as per normal

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