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BRIEF COMMUNICATION

Characterization of the photosynthetic pathway of some tropical food yams (*Dioscorea* spp.) using leaf natural ^{13}C abundance

D. CORNET[*,+], J. SIERRA[**], and R. BONHOMME[**]

Centre de Coopération International en Recherche Agronomique pour le Développement,
Unité de Recherche en Amélioration des Plantes à Multiplication Végétative, IITA, 08BP0932 Cotonou, Benin Republic[*]
Institut National en Recherche Agronomique, INRA, UR135, Agropédoclimatique de la zone caraïbe,
Petit-Bourg, F-97170, France[**]

Abstract

A total of 23 genotypes belonging to seven tropical food yams and two wild relative species of different origin and coming from two sampling ecological zones (the Republic of Benin in Africa and Guadeloupe in the Caribbean) was analysed for their ^{13}C content. The δ^{13}C values for all yam samples (from –25.39 and –30.07 ‰) indicated that all species had a C_3 photosynthetic type.

Additional key words: cultivar differences; *Zea*.

Plant productivity is dependent on several environmental and biological factors. One of the most important factors is photosynthesis. Since the discoveries by Kortschak *et al.* (1965) and Hatch and Slack (1966) of the C_4 carboxylation mechanism, the photosynthetic pathway of plant species has received much attention (Downton 1975, Raghavendra and Das 1978, Rowan and Russell 1998). The metabolic type of most important food crops is now well documented (Rowan and Russell 1998). The differences between the photosynthetic pathways of C_3 and C_4 plants result in different behaviours in terms of radiation (Black 1973), water (Downes 1969, Winslow *et al.* 2003), and nitrogen use efficiency (Brown 1978, Sinclair and Horie 1989, Gastal and Lemaire 2002).

Dioscorea is a monocotyledon (Ayensu 1972) belonging to the Dioscoreale order. It is grown throughout the tropical world for food, pharmaceutical products, and ornamental foliage plants. It is an important food crop (more than 40 kg per inhabitant per year) in at least 10 countries (from Nigeria to Jamaica and the Solomons) accounting for 155 million inhabitants (FAO 2004). Even though some yam species are sometimes cited as a C_3 plant, it has never been verified (Orkwor *et al.* 1998, Voortman *et al.* 1999, Basinger 2002). These authors inferred the information from a higher phylum or from the sparse photosynthesis measures available on yams (Kpeglo *et al.* 1982, Bhagsari 1988, Johnston and Onwueme 1998, Onwueme and Johnston 2000). To our knowledge, no study has been conducted on the metabolic type of major yam species. Although no publication reports the presence of a C_4 species among the Dioscoreaceae family, the wide diversity of origins within the genus could possibly contain some. Indeed the genus includes more than 600 different species (Knuth 1924) adapted to different ecosystems: *D. trifida* is indigenous to tropical America, *D. rotundata* is native to West Africa, *D. alata* is indigenous to Melanesia, *D. elephantipes* is native to semi-arid bush of South Africa, and *D. opposita* originated in temperate East Asia (China). This paper focuses on identifying the photosynthetic pathway of the most common tropical food yams and some wild relatives (*D. prahensilis* and *D. burkiliana*).

Plants with different photosynthetic pathways/types (*i.e.* C_3, C_4, and CAM) can be differentiated based on their natural ^{13}C content. ^{13}C screening is a simple test for determining the photosynthetic type and was widely used as criterion for C_3 and C_4 classification (Li *et al.* 2006, Marchese *et al.* 2006).

^{13}C was determined in the leaves of nine yam species and 23 genotypes from two locations (Table 1). The species studied originated from three different continents (Africa, Asia, and South America). For each genotype

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[+]Corresponding author; fax: +229-35-05-56, e-mail: denis.cornet@cirad.fr

Table 1. Carbon isotope values of yam species grown in Benin Republic and Guadeloupe. $\delta^{13}C$ = carbon isotope composition, S_x = standard deviation.

Species	Origin	Botanical section	Yam Type	Variety	Sample origin	$\delta^{13}C$‰ (S_x)
Dioscorea alata	Melanesia	Enantiophyllum	Cultivated	Florido	Benin	–28.45 (0.19)
				Florido	Guadeloupe	–27.77 (0.26)
				Plimbite		–26.66 (0.01)
				Boutou		–26.56 (0.35)
				Kinabayo		–27.74 (0.29)
				Oriental		–28.41
				Belep		–27.90 (0.17)
Dioscorea bulbifera	South East Asia and Africa	Opsophyton	Wild	Wild	Benin	–27.57 (0.19)
				Adon Gwada	Guadeloupe	–25.39
			Wild	Wild	Benin	–27.40
			Breeding material	Code 6	Guadeloupe	–27.44 (0.16)
Dioscorea burkiliana	West Africa	Enantiophyllum	Wild	Wild	Benin	–30.07 (0.38)
Dioscorea cayenensis	West Africa	Enantiophyllum	Cultivated	«Igname jaune»	Guadeloupe	–27.83 (0.04)
Dioscorea dumetorum	West Africa	Lasiophyton	Cultivated	Leffe	Benin	–28.20 (0.20)
Dioscorea esculenta	South East Asia	Combilium	Cultivated	«Pas possible»	Guadeloupe	–27.52 (0.41)
Dioscorea prahensilis	West Africa	Enantiophyllum	Wild	Wild	Benin	–28.17
Dioscorea rotundata	West Africa	Enantiophyllum	Cultivated	Kpouna	Benin	–29.86 (0.23)
				Gnidou	Benin	–29.58 (0.11)
				Kokoro	Benin	–29.19 (0.01)
				Klatchi	Benin	–29.76 (0.02)
				Grande Savane	Guadeloupe	–27.55 (0.06)
Dioscorea trifida	Guyana, Amazonian basin	Macrogynodium	Breeding material	Code 7	Guadeloupe	–28.01 (0.01)
			Breeding material	Code 5	Guadeloupe	–29.15 (0.68)
Zea mays			Cultivated		Benin	–12.27 (0.04)

two measurements were realized on the same sample. For each sample at least ten leaves were collected randomly on more than two plants per genotype six months after planting. The leaves were oven dried to constant mass at 75 °C, ground finely, and then sub-sampled in two for isotopic analysis. The carbon isotope of a maize cultivar was determined for C_4 plant control.

^{13}C was determined by an element analyser (*Carlo Erba EA 1110*, *Carlo Erba Strumentazione*, Milan, Italy) connected to a mass spectrometer (*Thermo-Finnigan Delta*^{plus}, *Termo-Quest*, Bremen, Germany) through a *ConFlo II* Interface (*Thermo-Finnigan*) in the CNRS Laboratory (Vernaison, France). The deviation of sample ^{13}C content ($\delta^{13}C$) [‰] from that in the PDB standard ($R_{standard}$) (Balesdent 1996) was calculated as:

$$\delta^{13}C = (\frac{R_{sample}}{R_{standard}} - 1) \times 1000$$

where R is the $^{13}C/^{12}C$ ratio. Bender (1971) and Smith and Epstein (1971) showed that plants utilizing the C_3 pathway had $\delta^{13}C$ values from –22 to –34 ‰, while those utilizing the C_4 pathway from –6 to –19 ‰.

$\delta^{13}C$ values of yam samples ranged from –25.4 to –30.1 ‰ corresponding to a C_3 photosynthetic type, while maize had a $\delta^{13}C$ of –12.3 ‰ (Table 1). Mean standard deviation on $\delta^{13}C$ measurement was 0.20 ‰, while mean standard deviation between genotypes was 1.16 ‰. For the group of species *D. alata*, *D. bulbifera*, and *D. rotundata,* a paired *t*-test revealed significant ($p<0.05$) difference between $\delta^{13}C$ values of samples coming from Benin and Guadeloupe (with respectively +0.9, +1.1, and +2.1 ‰ for *D. alata*, *D. bulbifera*, and *D. rotundata* coming from Guadeloupe).

Although the large differences in $\delta^{13}C$ values among C_3 and C_4 plant types make the results easy to interpret, the small differences among C_3 yam samples are harder to explain. O'Leary (1988) showed that interpretations based on differences smaller than 1 ‰ should be made with caution. He also reported that differences in ploidy levels, like those occurring within the *Dioscorea* genus, are not responsible for differences in $\delta^{13}C$ value.

These smaller differences could be explained by environmental differences between the two locations (growth temperature or irradiance) reflecting the functional plasticity of the species (O'Leary 1988, Hultine and Marshall 2000). Small differences also occur between species (from –27.0 to –30.1 ‰ for *D. bulbifera* and *D. burkiliana*, respectively). However, the absence of complementary observations, like specific leaf area and stomatal density suggested by Hultine and Marshall (2000), did not permit an interpretation of these results.

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