Molecular Phylogenetics and Evolution 53 (2009) 329–334

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Short Communication

Phylogeography and the origin of cassava: New insights from the northern rim of the Amazonian basin

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ARTICLE INFO

Article history:
Received 12 December 2008
Revised 20 April 2009
Accepted 4 May 2009
Available online 10 May 2009

Keywords:
Domestication
G3*pdh*
Guianas
Hybridization
Introgression

1. Introduction

The origin of cassava (*Manihot esculenta* Crantz) is still unclear, although several recent studies have addressed this issue (Fregene et al., 1994; Roa et al., 1997, 2000; Olsen and Schaal, 1999, 2001; Elias et al., 2000; Olsen, 2004). Rogers and Appan (1973) postulated that cassava was a "compilo-species", *i.e.*, the result of hybridization events between several species, among them *Manihot aesculifolia* (Kunth) Pohl, a species endemic to Central America. On the other hand, Allem hypothesized the crop to be issued from a single species, *Manihot esculenta*, with two subspecies found only in the wild: *Manihot esculenta* ssp. *flabellifolia* (Pohl) Ciferri and *Manihot esculenta* ssp. *peruviana* (Muell. Arg.) Allem (Allem, 1994; Allem et al., 2001). These wild taxa together have a broad ecological range, from southwestern Amazonia to the savannas of the Guianas.

Molecular studies have favored the latter scenario, generally showing that cassava was domesticated only once, in South America, with no contribution from the Mesoamerican species pool, or at least not from *M. aesculifolia* (Roa et al., 1997, 2000; Olsen and Schaal, 1999, 2001; Olsen, 2004). Study of this and seven other Mesoamerican species (A. Duputié, unpublished data) show that all are only distantly related to cassava, excluding the possibility that cassava was domesticated in Central America. These studies, however, suffer several limitations. First, they have considered only a limited sample of domesticated cassava accessions. Second, they overlooked a part of the range of *Manihot esculenta* ssp. *flabellifolia*: while the taxon is distributed on an arc partially circling the Amazon basin, from eastern Bolivia westwards to central Brazil eastwards, and in the Guianas and eastern Venezuela northwards, these studies considered only samples from Brazil, thereby excluding any possibility of testing the hypothesis that cassava could have more than one center of domestication. Yet, several other crops have been shown to have been domesticated twice (*e.g.*, the common bean, Gepts et al., 1986).

The present study aims at filling some of these gaps. Olsen and Schaal (1999) sampled accessions of *M. esculenta* ssp. *flabellifolia* and the closely related species *M. pruinosa* Pohl from Brazil and 20 accessions of cultivated cassava from the CIAT core collection, a collection constituted with the goal of representing cassava's genetic and morphological diversity worldwide (Hershey et al., 1994). We combined their sample of wild *Manihot* with samples of *Manihot esculenta* ssp. *flabellifolia* from the northern rim of the Amazonian basin, to cover most of the range of this taxon. Furthermore, to test the hypothesis that cassava could have more than one center of domestication, we also broadened the sample of domesticated cassava to include landraces cultivated in the Guianas, thus filling an acknowledged gap in earlier studies (Olsen and Schaal, 2001). Even though these samples all come from the same region,

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1055-7903/$ - see front matter © 2009 Published by Elsevier Inc.
doi:10.1016/j.ympev.2009.05.003

it has been shown that cassava genetic diversity in a single village in Guyana can be comparable to that in the CIAT (International Center for Tropical Agriculture) core collection (Elias et al., 2000). Finally, we included samples of two additional wild species from South America and two outgroups. Specifically, we addressed the following questions: (i) Was cassava domesticated only once? (ii) Did post-domestication gene flow play a role in shaping the crop's diversity in French Guiana?

2. Material and methods

2.1. Plant material

Six wild *Manihot* species have been described in the Guianas (Rogers and Appan, 1973; Allem, 1999). They include rainforest vines, and shrubs of savanna and savanna-forest ecotone. Within the latter, several taxa have been named, some of doubtful distinctness. One of them, *M. surinamensis* Rogers and Appan, was synonymized with *M. esculenta* ssp. *flabellifolia* by Allem (1994). We sampled populations of this taxon (i) in coastal regions of French Guiana, where human activity is relatively high, and (ii) in rock-savanna islands on inselbergs located in the densely forested south of French Guiana, where recent gene flow with the domesticate or presence of escapees from cultivation are both highly unlikely. Sampling locations are presented in Fig. 1 and detailed in Supplementary Table 1.

One population (SM) was formerly in sympatry with domesticated cassava, which is no longer cultivated in the site. Natural hybridization has been shown to occur between the two taxa (Duputié et al., 2007), and we sampled individuals of domesticated, wild and intermediate phenotype (4, 4 and 3 individuals, respectively). Only the three individuals of wild phenotype which were found to be purely wild individuals in another study (Duputié et al., 2007) were included in this analysis. Individuals of domesticated or intermediate phenotype were analyzed as supplementary individuals.

Our sample of domesticated cassava includes 37 plants (belonging to 31 landraces) from French Guiana and 49 plants (16 landraces and 33 seedlings) from the Amerindian village of Rewa, Guyana. Sampling details are given in Supplementary Table 2.

Two individuals of *Manihot glaziovii* Muell. Arg. and three of *M.* aff. *quinquepartita* Huber ex Rogers and Appan were included, together with three individuals found in the Monts d'Arawa, initially determined as two different species (*M.* aff. *quinquepartita* and *M. brachyloba* Muell. Arg.). These species are more distantly related to cassava (Chacón et al., 2008).

Two outgroup specimens were collected in French Guiana: *Cnidoscolus urens* (L.) Arthur, and *Jatropha gossypiifolia* L.

2.2. DNA sequences

We sequenced a 962-bp long portion of the nuclear gene G3*pdh*, encompassing four exons and three introns, one of which contains a minisatellite region, as described by Olsen and Schaal (1999). The sequences of the 28 G3*pdh* haplotypes already identified by Olsen and Schaal (1999) were obtained from GenBank (Accession Nos. AF136119–AF136149).

DNA was extracted from dried leaves using DNeasy Plant kit (Qiagen GmbH). PCR amplification of the G3*pdh* region was performed as described in Olsen and Schaal (1999) and sequencing reactions were performed using classical protocols with products from Applied Biosystems, on an ABI 310 monocapillary sequencer. We sequenced the two haplotypes of heterozygotes at the G3*pdh* locus together, using the "haplotype subtraction" approach (Clark, 1990), as did Olsen and Schaal (1999). Alignment was done using

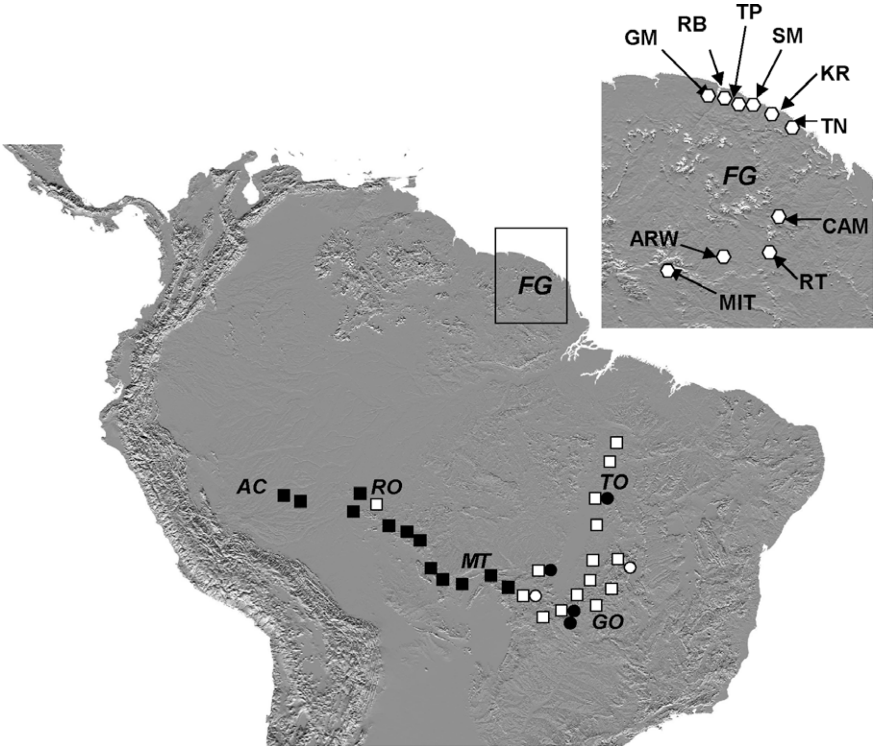

Fig. 1. Populations of the wild relative of cassava sampled in the Guianas (hexagons), and populations of *M. esculenta* subsp. *flabellifolia* (squares) and of *M. pruinosa* (circles) studied by Olsen and Schaal (1999). Shades of grey indicate elevational contours. Abbreviations: Brazilian states: Acre (AC), Goías (GO), Mato Grosso (MT), Rondônia (RO), Tocantins (TO); French Guiana (FG); populations in French Guiana: Grand Macoua (GM), Roche Blanche (RB), Trou Poissons (TP), Savane Manuel (SM), Kourou (KR), Tonate (TN), Camopi (CAM), Roche Touatou (RT), Monts d'Arawa (ARW), Petit Mitaraka (MIT). Filled symbols represent populations containing G3*pdh* haplotypes shared with domesticated cassava.

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