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Michelly de Cristo-Araújo

Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil, michelly_araujo@yahoo.com.br

Vanessa Maciel dos Reis

Laboratório de Evolução Aplicada; Instituto de Ciências Biológicas; U. Federal do Amazonas Manaus, Brazil, reis.vm@gmail.com

Doriane Picanço Rodrigues

Laboratório de Evolução Aplicada; Instituto de Ciências Biológicas; U. Federal do Amazonas Manaus, Brazil, prdoriane@msn.com

Charles R. Clement

Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil, cclement@inpa.gov.br

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Michelly de Cristo-Araújo

Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
michelly_araujo@yahoo.com.br

Vanessa Maciel dos Reis

Laboratório de Evolução Aplicada; Instituto de Ciências Biológicas; U. Federal do Amazonas Manaus, Brazil
reis.vm@gmail.com

Doriane Picanço Rodrigues

Laboratório de Evolução Aplicada; Instituto de Ciências Biológicas; U. Federal do Amazonas Manaus, Brazil
prdoriane@msn.com

Charles R. Clement

Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
cclement@inpa.gov.br

Abstract

The peach palm (*Bactris gasipaes* Kunth) is the only Neotropical palm domesticated by Native Americans. Its place of origin as a crop (*B. gasipaes* var. *gasipaes*) has been debated for more than a century, with three hypotheses currently in discussion: southwestern Amazonia; northwestern South America; or multiple origins in the distribution of the wild relatives (*B. gasipaes* var. *chichagui*). The small amount of archaeological data available supports the second hypothesis, but they contrast dramatically with the molecular-genetic analyses that support the first or the third, depending on how they are interpreted. On morphological grounds, two of the three types of var. *chichagui* are plausible candidates for wild ancestral populations. All the molecular-genetic analyses have identified a deep division between the landraces of cultivated peach palm in western Amazonia to Central America and those in southwestern to eastern Amazonia. The first analysis using isoenzymes linked the Tembe population (Bolivia) with the Pará landrace (eastern Amazonia), and these were distant from the western landraces. Multiple RAPD and SSR analyses identified the same deep division, which was interpreted by the group of researchers in Brazil as a single domestication in southwestern Amazonia with two dispersals, while another group working in Costa Rica interpreted it as three domestication events. Analysis with nuclear markers does not allow discrimination among the hypotheses, because gene flow may occur via pollen and seed. A new analysis with two sequences from the chloroplast genome, which has maternal inheritance and is therefore more appropriate to test the hypothesis, suggests that the cultivated peach palm was domesticated once in southwestern Amazonia, with two dispersals. One dispersal started in the upper Ucayali River basin, in southeastern Peru, and then throughout western Amazonia, northwestern South America and southern Central America. Another dispersal started in the upper Madeira River basin and then along the Madeira River into eastern Amazonia. New explorations in southwestern Amazonia are critical to identify the exact location of the original events.

Keywords: *Bactris gasipaes*, molecular markers, genetic analysis, origin, dispersal

Introduction

The origin of domesticated peach palm (*Bactris gasipaes* var. *gasipaes*) from wild populations (var. *chichagui*) remains a matter of speculation, with three hypotheses currently under consideration: a single domestication event in southwestern Amazonia (Clement, 1995) or northwestern South America (Morcote-Rios & Bernal, 2001); or multiple domestication events in the distribution of the wild populations (Mora-Urpí, 1993, 1999). Clement defended the parsimonious option, as most domesticates have been shown to have arisen from single events, and SW Amazonia as the area of origin in accordance with Huber's (1904) proposal about hybridization between wild types in that region. Morcote-Rios & Bernal worked from archaeological information and the distribution of type 3 *chichagui* to defend a northwestern domestication. Mora-Urpí defended multiple events given the wide distribution of wild peach palm populations, and frequent phenotypic similarities between wild and adjacent domesticated populations. However, these similarities have been shown by Couvreur *et al.* (2006) to be partially due to hybridization.

The recent revision of *Bactris* (Henderson, 2000) gathered the wild populations into var. *chichagui*, and the domesticated populations and landraces into var. *gasipaes*, finally permitting phylogenetic hypotheses. Within var. *chichagui*, Henderson identified three types, without attributing synonyms or describing their distribution, which was done by Clement *et al.* (2009a). Type 1 occurs in southern and southwestern Amazonia, and has very small fruits (1 to 2 g). Type 2 occurs in northern South America, has very small fruits (1 to 2 g) and is not involved in the origin of domesticated peach palm. Type 3 has a disjunctive distribution, from southwestern to western Amazonia, and from southwestern Ecuador to western Colombia to southern Central America, and has small fruits (3 to 10 g, rarely 15 g). Ferreira (1999) used a cladistic analysis of morphological and anatomical traits of the species closest to *B. gasipaes* to show that all cultivated peach palm populations have seed shape and germinal pore positioning similar to types 1 and 3, effectively eliminating type 2 populations. This conclusion was supported with molecular-genetic analyses by Hernández *et al.* (2011).

Over the last two decades, molecular markers have been brought to bear on the question of the origin of the domesticated landraces. The first study was by Rojas-Vargas *et al.* (1999), who found a deep dichotomy in their dendrogram, which separated populations in southern and eastern Amazonia from those in northwestern South America and Central America. This dichotomy recurs in all studies with all molecular markers, such as those of Rodrigues *et al.* (2004) and Cristo-Araújo *et al.* (2010), both of which used Randomly Amplified Polymorphic DNA (RAPD), and Reis (2009) and Hernández *et al.* (2011), who used Simple Sequence Repeats (SSR), with variable numbers of landraces and wild populations. The western side of the dichotomy is quite complex, given the large number of landraces in northwestern South America and northwards. Hernández *et al.* (2011) propose that this complexity arose from three domestication events in that region, one in Amazonia, one in western South America and one in Central America. Clement *et al.* (2010) reviewed the full set of molecular evidence and maintained the more parsimonious hypothesis: a single domestication event in southwestern Amazonia with two dispersals, which represent the two main branches in the molecular-genetic analyses. As Hernandez *et al.* (2011) observe, the exact shape of any dendrogram depends upon the populations included, the molecular marker used, the statistical methods and the algorithm used to generate a dendrogram. We add that this is especially true for nuclear DNA markers, which are biparentally inherited and suffer recombination during meiosis. Analysis with chloroplast DNA, which is almost always maternally inherited in angiosperms, avoids the problems of recombination and biparental inheritance, and is more appropriate for the kind of phylogeographic analysis (Avice, 2004) that can contribute more to identifying the location of the domestication event(s) that gave rise to peach palm's landraces. In this study we use more sophisticated statistical analyses and more SSR markers to examine the nuclear data, and provide the first analysis of a peach palm chloroplast sequence to address the origin of peach palm.

Methods

The genetic material used is from the Peach Palm gene bank, maintained by the National Research Institute for Amazonia (INPA), in Manaus, Brazil. Its complete molecular characterization (Rodrigues *et al.*, 2004; Cristo-Araújo *et al.*, 2010) allowed the creation of a Core Collection (CC) that represents the genetic resources of peach palm available in Brazil: Juruá (2 accessions); Pará (5); Guatuso (2); Cauca (2); Pastaza (1); Taira (1); Utilis (2); Vaupés (2); not designated populations (5); var. *chichagui* types 1 and 3 (4); Putumayo (4); Solimões (3); Pampa Hermosa (4); and hybrid populations (3). These 40 accessions represent the majority of the genetic diversity of the whole bank (375 accessions), with the minimum of repetition (Cristo-Araújo, 2008). Two *Bactris* species, *B. riparia* and *B. simplicifrons*, were used as outgroups to provide a basis for comparison, since *B. riparia* is a close relative and *B. simplicifrons* is a distant relative of peach palm (Couvreur *et al.*, 2007; Henderson, 2000).

The analyses were conducted using two types of molecular markers that access the variation contained in DNA (genetic variability), which allows us to compare individuals, populations, landraces or species, and thus profile each of them in terms of the amount and distribution of this variation, with the ultimate goal of clarifying the origin, domestication and distribution of peach palm. Microsatellite markers access extremely variable regions of the genome and can distinguish between homozygotes and heterozygotes, and so are called co-dominant markers. What characterizes the polymorphism of this type of marker is the number of repetitions that exist of the simple sequence repeat (SSR) units (Avisé, 2004). These markers are good for examining general relationships among samples. Chloroplast DNA sequences are much less variable, but important because the chloroplast is generally inherited from the maternal parent. Hence, it is distributed in seeds and permits examination of possible dispersal routes. The chloroplast sequences used were *psbJ-petA* and *psaI-accD* (Shaw *et al.*, 2007), because these are more informative than other potential alternatives.

Each marker type was analyzed separately. The SSR information was used to generate basic molecular genetic parameters, such as number of alleles, observed and expected heterozygosities and degree of inbreeding, and then the information was used to simulate the probable number of genetic groupings with the Structure program (Pritchard *et al.*, 2000). This analysis uses Monte Carlo probability methods to compare allele frequencies within and among possible groups to identify the number of groups that are most likely in the dataset. This can then be compared to the *a priori* number of groups based on our previous knowledge of peach palm landraces. Once we have an idea of the groupings, the genetic distances among the groups (landraces) can then be analyzed to study the phylogenetic relationships among them, which help identify probable origins. When the genetic distances are used to construct phylogenetic trees (dendrograms), an idea of origins and dispersals is generated. The chloroplast sequence information was used to study the relationship among haplotypes, the number of specific combinations of individual differences in the chloroplast sequences. A haplotype network was generated with Phylogenetic Network v.4.5.1.6 (<http://www.fluxus-engineering.com>), as this type of network permits examination of relationships that may be reticulate, i.e., descent may be confused by hybridization among different populations and landraces, a very common situation in domesticated plants and animals.

Results

Relations among samples using nuclear microsatellites

The analysis with Structure identified the best number of clusters as $K = 2$, with some indication that it could be $K = 4$. The simulation with $K = 2$ separated the Pará landrace, the populations of the upper Madeira River, and the var. *chichagui* type 1 from the other samples. Subsequent simulations with $K = 4$ showed the formation of four groups: southwestern-to-eastern Amazonia (Pará landrace, upper Madeira River populations and var. *chichagui* type 1); southwestern-to-western Amazonia (Pampa Hermosa landrace, Ucayali River populations and var. *chichagui* type 3); northwestern Amazonia to western South America (Putumayo, Vaupés, Cauca, Pastaza and Juruá landraces); and Central America (Utilis landrace).

The dendrograms based on shared allele distances (DAS; not shown) and the distances of Nei (1978) (Figure 1) showed the separation of two groups: one composed of landraces and populations of Central America and western Amazonia, and another made up of the Pará landrace, upper Madeira River populations and var. *chichagui* type 1. These groupings were expected after the analysis with Structure.

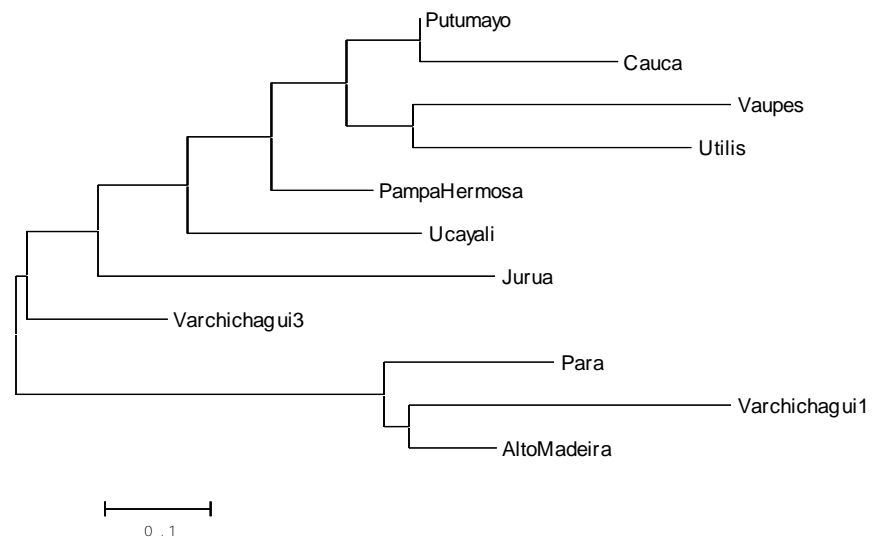


Figure 1. Dendrogram based on Nei's genetic distances (1978) and using the Neighbor-Joining algorithm, showing the genetic relationships among seven landraces, the upper Madeira River and Ucayali River populations of peach palm, and two wild populations (var. *chichagui* type 1 and 3) represented in the Core Collection and maintained in the peach palm gene bank at INPA, Manaus, Amazonas, Brazil (Reis, 2009).

Relations among samples using cpDNA

The *psbJ-petA* sequence contains 700 base pairs of DNA, of which 81 were variable (11.5%); the other sequence only distinguished *B. simplicifrons* from *B. gasipaes-riparia*. The network analysis identified two clusters, with *B. simplicifrons* as an outgroup (Figure 2). One cluster was smaller and contained most of the Pará landrace accessions (66%), all accessions of the upper Madeira River and the Juruá landrace, some Putumayo landrace accessions (28%), one of the Solimões landrace accessions, the *B. riparia* accessions and an individual of *chichagui* type 1. The other larger cluster included all the western landraces and populations, one individual of the Pará landrace, two individuals of *chichagui* type 1, which was not expected, and the *chichagui* type 3 accessions. The distance between these clusters is considerable, although less than the distance between the *B. simplicifrons* and the eastern cluster, which was expected given the phylogenetic distance of *B. simplicifrons* within *Bactris* (Couvreur *et al.*, 2007).

A maximum parsimony dendrogram of relationships also contained two

large clusters (not shown). The separation between clusters was very consistent (100%). Inside the smaller cluster, the relationship between the Pará landrace and the upper Madeira populations was highly consistent (95%). Another individual of the upper Madeira and a *chichagui* type 1 individual complete the group. The other cluster contained the western landraces and populations, with one highly consistent sub-cluster and several reasonably consistent sub-clusters.

These two analyses with a sequence from the chloroplast genome suggest that the cultivated peach palm was domesticated once in southwestern Amazonia, because of the relationships among *B. simplicifrons*, *B. riparia*, *B. gasipaes* var. *chichagui* type 1, and the upper Madeira River populations and the Pará landrace. The western landraces and the Ucayali River populations are all differentiated by a single 12-base pair sequence from the Pará landrace and associated populations, and this difference essentially corresponds to the deep division in the SSR dendrogram (Figure 1).

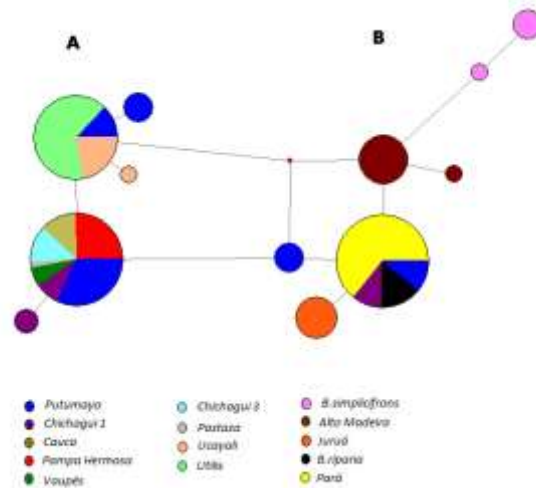


Figure 2. Network of chloroplast sequence samples in the peach palm Core Collection using the Median-Joining algorithm (Bandelt *et al.*, 1999). Each colored dot represents a plant with a unique haplotype (combination of distinct base pairs). The landraces and populations are color coded.

Discussion

The analyses with nuclear microsatellites confirmed previous analyses that showed a deep split between the southwestern-to-eastern Amazonian landraces, on one hand, and the western Amazonian to Central American landraces on the other (Rojas-Vargas *et al.*, 1999; Rodrigues *et al.*, 2004; Cristo-Araújo *et al.*, 2010; Hernández *et al.*, 2011). As mentioned, however, these markers alone are insufficient for determining if the split represents two or more domestication events, as suggested by Mora-Urpí (1993, 1999) and Hernández *et al.* (2011), or one event with two dispersal routes, as suggested by Rodrigues *et al.* (2004) and Cristo-Araújo *et al.* (2010). The chloroplast sequence analysis suggests that there was only one domestication event with two dispersals, although more sequences will be necessary to confirm this.

These molecular analyses are incapable of answering other important questions, such as when and how this all took place. Clement (1988) hypothesized that domestication started in the early Holocene, based on the dramatic differences in fruit sizes between var. *chichagui* type 1 (1 to 2 g) and the Vaupés landrace of var. *gasipaes* (mean > 70 g, maximum 200 g), and the fact that selection was probably mostly unconscious and propagation was by seeds. Clement *et al.* (2009b) described the reasoning in greater detail and cross-referenced it with indigenous and peasant practices, showing how the domestication may have proceeded. There is great need for anthropologists and ethnobotanists to dig into indigenous perceptions and practices of peach palm management to tease out mechanisms that will permit a better understanding of this process.

Conclusions

These new analyses support the parsimonious hypothesis of a single domestication event in southwestern Amazonia. Whether this occurred in the upper Madeira River basin or the upper Ucayali River basin is still uncertain, although the former is more likely. Two dispersals resulted in the landrace complex found today. One occurred along the Ucayali River and cultivated peach palm was dispersed throughout western Amazonia, northwestern South America and southern Central America. The other occurred along the Madeira River basin and the cultivated peach palm was dispersed along the Madeira River to eastern Amazonia.

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