



The primary gene pool of cassava (*Manihot esculenta* Crantz subspecies *esculenta*, Euphorbiaceae)

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Summary

The primary gene pool (GP-1) of a crop is composed of gene reservoirs that cross easily with the domesticated, while the crosses regularly produce fertile offspring. The GP-1 is further subdivided into cultivated and wild gene pools. The cultivated gene pool encompasses commercial stocks of the crop, as well as landraces. The wild GP-1 of the crop comprises putative ancestors and closely related species that show a fair degree of fertile relationships with the domesticate. Two South American wild subspecies of cassava (*M. flabellifolia* and *M. peruviana*) were proposed as natural members of the wild GP-1 of the crop. Another Brazilian species (*M. pruinosa*) is morphologically so close to both wild subspecies that it may turn out as another member of the wild GP-1.

Introduction

The origins of cassava have long been obscure. Three of the most important questions to answer concern the botanical origin, i.e. the wild species from which cassava has descended, the geographical origin, i.e. the area where the progenitor evolved in the geological past, and the agricultural origin, i.e. the area of initial cultivation of the wild ancestor by Amerindians (Allem, 2000). This study is concerned with the botanical origin of the crop. The core of the argument rests on the assumption that the discovery of a living wild ancestor would in all likelihood clarify the taxonomy of cassava. In turn, should a find such as this happen, it may provide insights on the ancestry of the crop (the evolution of the ancestor and its phylogenetic relationships with related species), the area of its initial domestication, as well as inferences on the composition of the gene pools of the crop. If it can be proven that cassava is not only known in cultivation, but also has living wild forms, the crop is no longer a cultigen, but instead becomes an indigen, i.e. a plant known to encompass both wild and cultivated populations.

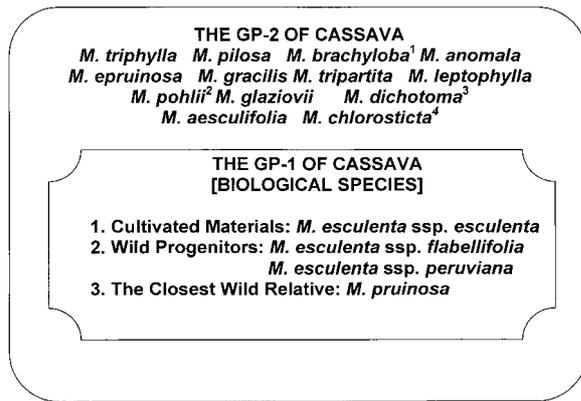
Studies on the taxonomy of the genus *Manihot* in Brazil led unexpectedly to progress in matters with a bearing on the origins and phylogeny of cassava. Accumulated empirical knowledge derived from field

experience culminated with the formulation of a preliminary sectional classification in which the Brazilian species were arranged in 16 groups (Allem, 2000). The classification proposed was thought to mirror, to some extent, some degree of phyletic kinship between the species. Group VI in particular of that classification, the *M. esculenta* ssp. *esculenta* species complex, has been tested extensively by the scientific community, through genetic studies and phylogenetic investigations. This in turn led to the formulation of a cladistic species concept for cassava.

Three major areas contributed with relevant inputs toward the botanical origin of cassava: 1. taxonomy, with the definition of the taxonomic species; 2. biosystematics, through interspecific crosses, which led to the definition of the biological species (gene pools); 3. molecular genetics, with the definition of the cladistic species. Each one is reviewed briefly below.

Materials and methods

The study reviewed past and recent literature dealing with the origin of cassava in three major fields, viz. taxonomy, biosystematics, and molecular genetics. Papers from fields not directly concerned to the scope of the communication (e.g. archaeology and an-



¹These three species suggested by Allem (1999).

²These six species deduced from Bai et al. (1993).

³These two species deduced from Nichols (1947).

⁴These two species deduced from Roa et al. (1997).

Figure 1. The primary (GP-1) and secondary (GP-2) gene pools of cassava.

thropology) were not reviewed, but a number of such titles appear in Allem (2000). The study discusses, on the basis of bibliography, three species concept, the taxonomic species concept, the biological species concept, and the phylogenetic species concept.

Results

The taxonomic species concept

The controversy on the origin of a crop may eventually be settled with the find of a living ancestor. This fact normally equates with the discovery of the morphological species. This happened for cassava (Allem, 1994a). The author advanced the hypothesis that the crop is composed of three taxa, while descending from two wild plants relatively common in much of Amazonia. The classification divided cassava into three subspecies, the domesticate *M. esculenta* Crantz ssp. *esculenta* (all cultivated genotypes) and two wild plants, *M. esculenta* Crantz ssp. *flabellifolia* (Pohl) Ciferri (the likely ancestor) and *M. esculenta* ssp. *peruviana* (Muell. Arg.) Allem. The view that wild populations of *M. flabellifolia* Pohl are likely to have led to the genesis of modern commercial cultivars and landraces of cassava (Allem, 1994b) has been reaffirmed more recently (Allem, 1999). Independent studies on the subject reached similar conclusions (Roa et al., 1997; Olsen & Schaal, 1999).

Species thought to be involved in the ancestry of cassava were reviewed more recently (Allem, 1999).

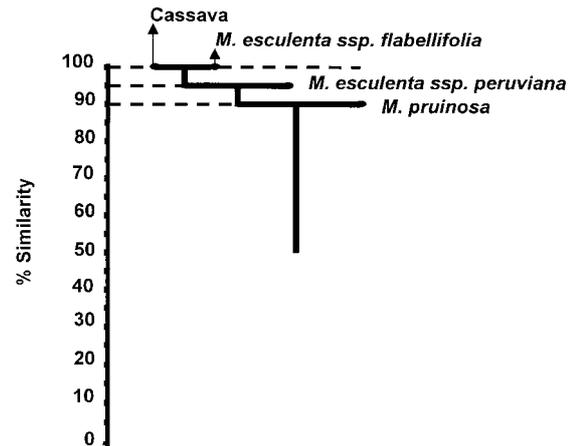


Figure 2. Phenogram of cassava and its closest allies and empirically-deduced phylogenetic relationships between species. Figures are just illustrative and serve as a frame of reference. The assumption is that *M. pruinosa* and the two wild strains of cassava descend from a common stock.

One of them (*M. esculenta* ssp. *flabellifolia*) is regarded as the progenitor of modern cultivars and folk varieties and thus becomes part of the wild primary gene pool of the crop (Figure 1). Another neotropical Brazilian species (*M. pruinosa* Pohl) is regarded as the nearest species to the GP-1 of cassava. *M. pruinosa* is most difficult to separate, on morphological grounds, from the wild strain *M. esculenta* ssp. *flabellifolia* (Figure 2). Three other Brazilian species, *M. pilosa* Pohl, *M. triphylla* Pohl, and *M. brachyloba* Mueller Arg. are thought to be linked, to some degree, to the cassava species complex (Allem, 1999, 2000). In particular, *M. pilosa* and *M. triphylla* are morphologically rather close to cassava, while both present very similar vegetative and floral parts. However, there is little substantive evidence, at present, to justify the inclusion of any of the three species in the wild GP-1 of cassava (but see comments on *M. triphylla* in discussion).

The biological species concept (BSC)

The BSC defines the species as a closed gene pool, i.e. species limits are defined on the basis of degrees of genetic compatibility and fertility relationships shown by taxa (Dobzhansky, 1937). The concept was continuously perfected by Mayr (1969, 1982) who insisted that the core of the BSC rests on degrees of fertility relationships existing between taxa, i.e. the species is reproductively isolated from other related gene pools. The decisive criterion to circumscribe a species and to keep it distinct through reproductive isolation is

Table 1. Results of crosses between cassava and *Manihot saxicola* in Indonesia between 1942–1949. Source: adapted from Bolhuis (1969)

Female parent	Male parent	Flowers pollinated	Fruit-set	Success %	Seed-set	Success %
<i>M. saxicola</i> ¹	<i>M. esculenta</i>	335	125	37.3	76	20.2
<i>M. esculenta</i>	<i>M. saxicola</i>	96	47	48.9	80	56.7

¹ Seeds of *M. saxicola* came from Surinam. The species is now a synonym of *M. esculenta* subspecies *flabellifolia*.

Table 2. Results of crosses between cassava and *Manihot melanobasis* in Tanzania around 1955. Source: adapted from Jennings (1959)

Female parent	Male parent	Flowers pollinated	Seed-set	Success %
<i>M. melanobasis</i> ¹	<i>M. esculenta</i>	125	225	60
<i>M. esculenta</i>	<i>M. melanobasis</i>	253	592	78

¹ The Tanzanian material originated in Surinam. *M. melanobasis* is now a synonym of *M. esculenta* ssp. *flabellifolia*, the progenitor of cassava.

its fertility status relative to another gene pool, this underlined the cytogenetic component of the BSC. Application of the BSC has been much used for cultivated plants, as well as in plant breeding, where it is much utilized under the names of primary, secondary and tertiary gene pools (Baker, 1970; Harlan, 1970; Harlan & de Wet, 1971).

Several workers carried out experimental biosystematic crosses between cassava and wild species of *Manihot*. The results offered the first appraisals on degrees of fertility relationships and presumed genetic distances between species. Such results of experimental taxonomy became the foundation of the primary and secondary gene pools of cassava.

The hypothesis that *M. flabellifolia* may indeed be the ancestor of cassava received strong support from biosystematic crosses carried out long before in Africa and Asia. The pioneering research was that of Nichols (1947) who crossed *M. saxicola* Lanjouw (a synonym of *M. flabellifolia*) and cassava in Tanzania and obtained good results. Further crosses between the crop and the ancestor took place in Java in the interval 1942–1949 (Bolhuis, 1953). The results were so exceptional (Table 1) that they drew a comment from the writer: ‘particularly striking is the high percentage of success which is far in excess of the percentages found in crosses within the species *M. utilisissima* (= *M. esculenta*). It makes it even questionable as to whether *M. saxicola* is sufficiently different from *M. utilisissima* to consider it as a separate species, since both crosses have such a high percentage of success’ (Bolhuis,

1969). Cassava and the progenitor were also crossed in Tanzania around 1955 and over one hundred F1 fertile hybrids were produced (Jennings, 1957, 1963). The most incisive remarks suggesting a common phyletic origin between cassava and the wild species were reserved for Nichols’ substitute, Derek Jennings (1959): ‘the fertility of *M. melanobasis* (= *M. flabellifolia*) and its hybrids is relatively very high’ (and) ‘in view of the readiness with which the two species intercross, however, it is doubtful whether their separation as distinct species is justified. Bolhuis reached the same conclusion for *M. saxicola* and cassava, which also intercross very easily. Lanjouw noted that *M. melanobasis* has much in common with *M. saxicola*. He suggested that the latter species may be an ancestor of cassava. It appears from the data presented here that *M. melanobasis* could also be a closely related ancestor of cultivated cassava’ (Table 2).

The combined results in Africa and Asia suggested that the wild species tested belonged to the GP-1 of cassava or, in other words, that they were a biological species since both crossed easily and F1 hybrids were regularly fertile. Interestingly enough, crosses within cassava itself gave disappointing results. Nichols (1947) summarized the matter thus: ‘low seed fertility is a striking feature within this species’. Much in the same tone, Bolhuis (1969) concluded that intraspecific crosses in cassava with a percentage of success higher than 10% were rarely achieved.

Trials of crossing cassava with other *Manihot* species offered the first insights on the GP-2 of the crop,

Table 3. Results of crosses between two cassava cultivars and seven Brazilian *Manihot* species. Source: Bai et al. (1993)

Female parent	Male parent	Flowers pollinated	Fruit-set (%)	Seed-set (%)
TMS 30555	<i>M. anomala</i> – 7	115	18.26	17.97
TMS 42025	<i>M. anomala</i> – 7	133	16.54	14.28
TMS 30555	<i>M. epruinosa</i> – 46	338	11.24	9.17
TMS 42025	<i>M. epruinosa</i> – 34	228	21.05	7.90
TMS 30555	<i>M. tristis</i> – 39–3 ¹	878	32.46	27.26
TMS 42025	<i>M. tristis</i> – 39–3 ¹	1870	14.06	7.50
TMS 30555	<i>M. gracilis</i> – 26	93	21.50	17.92
TMS 30555	<i>M. tripartita</i> – 24	50	26.00	21.33
TMS 42025	<i>M. leptophylla</i> – 1	667	1.94	1.44
TMS 42025	<i>M. pohlii</i> – 1	161	9.32	8.28

¹ *M. tristis* is a synonym of the progenitor of cassava.

Table 4. Results of interspecific crosses between cassava and three *Manihot* species. Source: adapted from Roa et al. (1997)

Female parent	Male parent	Crosses	Seed-set
<i>M. esculenta</i> ssp. <i>flabellifolia</i> ¹	<i>M. esculenta</i> ssp. <i>esculenta</i>	16	thousands ²
<i>M. aesculifolia</i> ³	<i>M. esculenta</i> ssp. <i>esculenta</i>	2	5
<i>M. chlorosticta</i> ⁴	<i>M. esculenta</i> ssp. <i>esculenta</i>	14	1 to 148

¹ It is the ancestor of cassava.

² Crosses included backcrosses.

³ Species regarded by some writers as the closest wild relative of cassava.

⁴ Mexican species; hybrid seeds showed strong dormancy.

i.e. crossing is possible but gene transfer may be difficult, as predicted by Harlan & de Wet (1971), while F1 hybrids tend to be sterile and to show poor chromosome pairing or univalents. Nichols (1947) placed in this category the Brazilian species *M. glaziovii* Muell. Arg. and *M. dichotoma* Ule. Bai et al. (1993) suggested seven Brazilian species as prospective members of the GP-2 (Table 3); one of them (*M. tristis* Muell. Arg.) showed fertility rates above average (the species is now a synonym of the ancestor *M. flabellifolia*). Roa et al. (1997) crossed three species with cassava; once more, the putative ancestor of cassava gave the highest results, while two Central American species qualified for the GP-2 of the crop (Table 4).

Data on the taxonomic species concept of cassava came to entwine with biosystematic data involving crosses between cassava and its wild progenitor. Biosystematics recorded the unusual high degree of fertility and genetic relationships existing between the crop and the putative progenitor (Bolhuis, 1953, 1969; Jennings, 1959; Roa et al., 1997). These trials provided the preliminary delimitation of the biological species of cassava.

The delimitation of the GP-2 of cassava has made lesser progress as few species have been tested for genetic compatibility. Biosystematic crosses conducted between the crop and a number of wild species, however, suggest a dozen of them as components of the GP-2, the majority are Brazilian species (Figure 1).

The cladistic species concept

The morphological species concept and the biological species concept of cassava enlightened important aspects on the origin of the crop. Phylogenetic studies of the species and its wild relatives happened more recently. Several writers investigated the phylogeny of cassava, while simultaneously tested the hypothesis on the origin of cassava, i.e. the view that *M. flabellifolia* is the progenitor of the crop. The interpretation of their results are shown in Table 5.

Discussion

Research on degrees of crossability between cassava and wild species was decisive in establishing the

Table 5. Molecular and biochemical tests conducted on the phylogeny and origin of cassava

Reference	Marker	Support Allem's 1994a hypothesis
Carvalho et al. (1993)	RFLP/RAPD	moderate (+)
Fregene et al. (1994)	CpDNA/rDNA	moderate (-)
Carvalho et al. (1995)	RAPD	moderate (+)
Schaal et al. (1995)	rDNA/RAPDs	moderate (-)
Brondani (1996)	Isozymes	strong (+)
Schaal et al. (1997)	RAPD	strong (-)
Second et al. (1997)	AFLP	moderate (-)
Bonierbale et al. (1997)	AFLP	strong (+)
Roa et al. (1997)	AFLP	strong (+)
Olsen & Schaal (1998)	Nuclear DNA	strong (+)
Cabral et al. (2000)	SSRs	strong (+)
Second (1998)	RFLP	strong (-)
Roa et al. (1998a)	AFLP	strong (+)
Roa et al. (1998b)	SSRs	strong (+)
Olsen & Schaal (1999)	G3pdh	strong (+)

primary gene pool of the crop, this ultimately contributed to tracing down more firmly the origin of cassava. A further link became established when genetic markers linked the cladistic species and the biological species: 'the species relationships illustrated by AFLP are supported by preliminary data on crossability' (Roa et al., 1997). Convergent morphological, biosystematic, and molecular results strengthened the hypothesis (Allem, 1994a) on the origin of cassava, i.e. 'clear evidence from multiple sources suggest that *Manihot esculenta* ssp. *flabellifolia* (*peruviana*) represent the wild ancestors of cassava' (CBN, 2000).

M. esculenta subspecies *flabellifolia* is an example that the biological species and the taxonomic species may eventually coincide in practice. Interspecific crosses offered a first view on how fertility relationships are structured in the genus. This enabled the build-up of the GP-1 and the build-up of a tentative GP-2 of cassava (Figure 1). The dendrogram of cassava and its closest allies (Allem, 2000) can now be upgraded to a phenogram. Because the intuitive hypothesis on the phylogeny of cassava received support from specific molecular studies, the phenogram virtually amounts to an evolutionary cladogram (Figure 2).

Two further points are worth recording. First, *M. pruinosa* has been suggested as a presumable member of the wild GP-1 of cassava (Allem, 1999). A preliminary molecular study gave some support to

the view (Second et al., 1997), while another related study backed the hypothesis strongly (Olsen & Schaal, 1999). Second, a parallel molecular study concluded that *M. triphylla* stands closer to cassava than the wild subspecies *M. esculenta* ssp. *peruviana* (Cabral et al., 2000). Of the five *Manihot* species tested in that study, *M. pilosa* turned out to be phylogenetically the most distant from cassava. If pending biosystematic crosses between cassava and *M. triphylla* lend support to the above molecular results, *M. triphylla* may eventually join the wild GP-1 of the crop.

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