

Chapter 1

The Origins and Taxonomy of Cassava

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Introduction

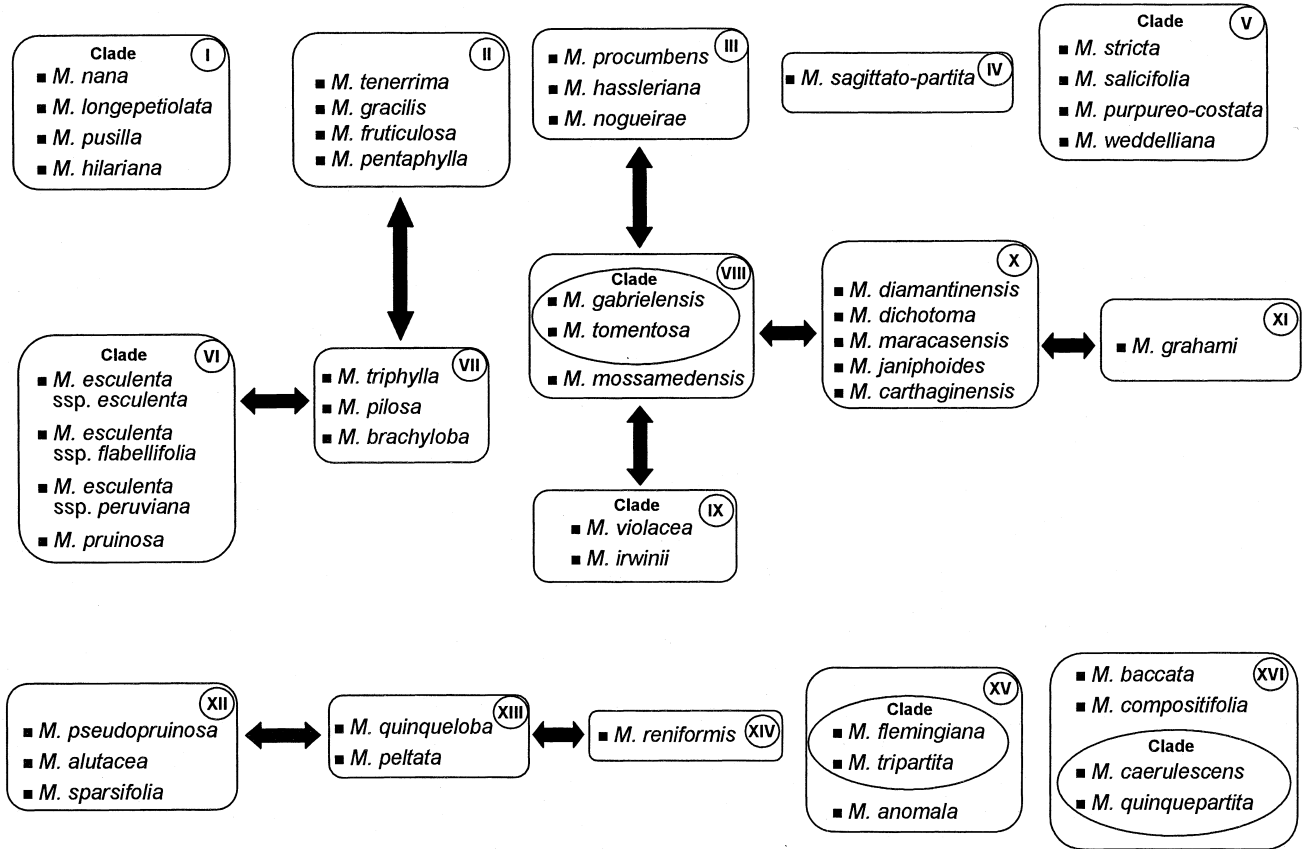
The origins of cassava (*Manihot esculenta* Crantz subspecies *esculenta*) have long been obscure. The three important questions to answer concern the botanical origin, (i.e. the wild species from which cassava descends), the geographical origin, (i.e. the area where the progenitor evolved in the geological past) and the agricultural origin (i.e. the area of initial cultivation of the wild ancestor by Amerindians). The core of the above argument rests on the assumption that if there is a living wild ancestor, its discovery would be likely to indicate the taxonomy of cassava. In turn, this would indicate the ancestry of the crop (the evolution of the ancestor and its phylogenetic relationships with related species) and the cradle of domestication. Current knowledge on the three topics shows that studies on the botanical origin of cassava have progressed far and stand on firm ground, those on the geographical origin have progressed and conjecture on the area where cultivation began has recently experienced a renewed surge following the appearance of novel ideas.

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 classification in which the Brazilian species were arranged in groups. The model of classification proposed was thought to mirror some degree of phyletic kinship between the species (Fig. 1.1). A number of the prospective clades proposed in Fig. 1.1 (e.g. the *Manihot nana* group; the *Manihot salicifolia* group, etc.) match remarkably closely with former taxonomic classifications advanced for the same groups in earlier classic treatments including that of Rogers and Appan (1973). Group VI in particular, the *M. esculenta* group, has been tested extensively by the scientific community through genetic studies and phylogenetic investigations, which in turn influenced cladistic and taxonomic classifications. This group is particularly highlighted in the present review. No attempt has been made in Fig. 1.1 to suggest that the sequence of groups presented represents evolution towards greater complexity, although there is a tendency in the model to progress from herbaceous to tree species.

The Botanical Origin of Cassava

Until 1982 there was a tendency in the literature to assume that cassava has no known ancestry (a comprehensive historical background on how this arose appears in



Allem, 1994a). In March 1982, however, a wild population indistinguishable on morphological grounds from the domesticate was found in the central Brazilian state of Goiás and led to an announcement that cassava grows in the wild (Allem, 1987). The communication proved a watershed in the historiography of cassava, since it established a link between that particular wild population and the botanical origin of the crop. Several publications doubted the find and raised the possibility that feral cassava had been regarded as wild material (Bretting, 1990; Heiser, 1990; Bertram, 1993). The conviction was that wild populations of *Manihot flabellifolia* are likely to have led to the genesis of modern commercial cultivars and landraces of cassava (Allem, 1994b). The author has recently reaffirmed this position (Allem, 1999) and other studies point to a similar conclusion (Roa *et al.*, 1997; Olsen and Schaal, 1999). In so doing, the author followed Alphonse de Candolle's 1882 view that the occurrence of a crop in wild habitats amounts to the find of the wild ancestor; a view not held by Vavilov and others (Harris, 1990).

A further elaboration of the 1987 announcement resulted in the formal recognition of three subspecies within the crop (Table 1.1). This view contrasts with that of others who considered that the crop had no traceable ancestor and was instead the

by-product of indiscriminate introgression involving a number of wild relatives (Rogers, 1963, 1965; Harlan, 1965; Pickersgill, 1977; Bretting, 1990; Heiser, 1990; Sauer, 1994).

The original study of Rogers (1963) on the closest wild relatives of cassava did not greatly emphasize a hybrid origin for the domesticate (Table 1.2). However, this was stressed later and the postulation of introgression of wild genes into cassava became the norm in all subsequent publications on the subject (Rogers, 1965, 1972; Rogers and Appan, 1973; Rogers and Fleming, 1973). The paper of Rogers (1965) is particularly enlightening and offers insights into how interspecific hybridization came to be considered responsible for most of the difficulty found in establishing the proper separation of species in the genus. Rogers and Fleming (1973) stated that the amount of variation found in many native species of *Manihot* was due to introgression with cassava since the gene flow was certainly bi-directional. Rogers and Appen (1973) provided a number of amendments for species on the grounds that 'over a period of years phenotypic variation takes place [inside the introgressed hybrid] which expands the circumscription of such a species'. Rogers had been influenced by previous theories on the origins of crops, i.e. that crops could arise and evolve through periodic infusions of germplasm from adjacent weedy relatives (Harlan, 1961,

Fig. 1.1. (*opposite*) Phenetic relationships of Brazilian *Manihot* species. Empirically compelling phylogenetic kinships, deduced on the basis of phenetic and ecogeographic similarities, are presented as clades, which are thought to reflect common ancestry. From Allem (1995), modified. Arrows indicate strong phenetic similarity existing between groups of species. Within groups, a clade means strict morphological, geographical and ecological relationships recorded between the species concerned. The true number of Brazilian species is estimated around 47–50. A unique species of liana with simple and entire leaves from the Atlantic coast forest of the state of Bahia besides another kin species from the state of Mato Grosso (both belonging to Group V) await description. A number of new varieties and subspecies also await description. Some discrepancies are expected in phenetic and phylogenetic systems. For example, morphology determined the placement of *Manihot nogueirae* in Group III; however, the geography and ecology of the species recommend its inclusion in Group I and, in addition, *M. nogueirae* and *M. nana* seem to be hybridizing in the Federal District as discovered through isozyme studies (G. Second, Brasília, 1995, personal communication). A considerable number of traditional species (e.g. *Manihot orbicularis*, *Manihot glaziovii*, *Manihot stipularis*, etc.) do not appear in Fig. 1.1 as they will become synonymous of other species in the near future. Davis and Heywood (1963) remark that certain genera have undergone a modest level of differentiation where only groups of phenetically related species can be recognized. This applies to *Manihot*, a genus where infrageneric categories such as section are difficult to draw for many species. Pax (1910) recognized 11 sections for the genus while Rogers and Appan (1973) acknowledged 19 sections. The view is that a number of the sections devised by Rogers and Appan are artificial, thus echoing Croizat (1943) who denounced Pax's system as unworkable from the taxonomic standpoint.

Table 1.1. The subspecies of cassava.^a

Basionym	Novel status	Category
<i>M. esculenta</i> Crantz	<i>M. esculenta</i> Crantz ssp. <i>esculenta</i>	Cultivated stock
<i>M. flabellifolia</i> Pohl	<i>M. esculenta</i> Crantz ssp. <i>flabellifolia</i> (Pohl) Cifferi	Wild strain
<i>M. peruviana</i> Mueller	<i>M. esculenta</i> Crantz ssp. <i>peruviana</i> (Mueller) Allem	Wild strain

From Allem (1994a).

^aBecause cassava is known to include cultivated and wild forms, the species is no longer a cultigen but ranks as an indigen instead. The definitive infraspecific classification of the species is in preparation. There is a real possibility that two other species (e.g. *Manihot leptophylla*) join the extensive synonymy of the complex. In addition, a further wild variety with smooth fruits found in May 1994 and so far only known from the northern Brazilian Amazonian state of Tocantins awaits description.

Table 1.2. Species of *Manihot* regarded close to cassava on the basis of morphology, ecology and geography.

Species	Range
<i>M. carthaginensis</i>	All countries bordering the Caribbean
<i>M. aesculifolia</i>	Mexico; Central America
<i>M. grahami</i>	Brazil, Paraguay, Uruguay, Argentina
<i>M. flabellifolia</i>	Brazil, Paraguay, Uruguay, Argentina
<i>M. saxicola</i> ^a	Guiana, Surinam, Venezuela

From Rogers (1963).

^aA synonym of *M. esculenta* ssp. *flabellifolia* (see Allem, 1994a).

1970; Harlan and de Wet, 1963, 1965). Rogers assumed this had happened in *Manihot*. However, Harlan's concept of a weed meant either an intra-specific category, or a sibling species (Harlan, 1965) and not necessarily a distinct species. Harlan's standpoint focused mostly on intra-specific hybridization and drew on the fact that distinct populations of a species normally carry different peaks of adaptive norms. The record suggests that *persistent* artificial hybrids of *Manihot* are extremely difficult to obtain (Nichols, 1947; Jennings, 1963); Magoon *et al.* (1970) provide the sole available report on the unsuccessful fate of hybrid seeds. Natural hybrids are indeed a fact in the genus as assessed through the occurrence of individuals showing morphological intermediaries. This has been recorded in five instances involving populations in central Brazil (A.C. Allem, unpublished). However, these natural hybrids occur together

with their parents which makes interpretation easier and there is no evidence from herbarium specimens that hybrid speciation (the spread of an intermediate form over a significant geographical area) occurs with *Manihot*.

Rogers and Appan (1973) regarded a species native to Mexico and Mesoamerica as the closest morphologically to cassava: 'as evident from the computer analyses the closest wild relative of *M. esculenta* is *M. aesculifolia* (H.B.K.) Pohl'. Bertram (1993) later commented that 'the section *Parvibracteatae* also contains the wild species *Manihot aesculifolia* which is closest to cassava in morphological terms' [and] 'the morphological similarity of *Manihot aesculifolia* to cassava is striking'. Bertram adds '*M. aesculifolia* and *M. carthaginensis* are genetically closest to cassava', and also 'several factors point clearly to these two species – *M. carthaginensis* and *M. aesculifolia* – as putative ancestors of the crop'. It has also been suggested that the cultivation of cassava in the Caribbean area resulted from the domestication of the wild species *Manihot carthaginensis* (Reichel-Dolmatoff, 1986).

Sophisticated research on the ancestry of cassava drew initially on North American species. Investigation on the phylogeny, through the use of restriction fragment length polymorphism (RFLP) analyses of chloroplast DNA, made use of 12 species from Central America and North America and *M. carthaginensis* from South America. The outcome was inconclusive (Bertram and Schaal, 1993). Subsequently, an increasing number of authors have become involved in the controversy involving the cassava species complex and novel data have appeared. Molecular studies carried out to unravel the ancestry of cassava discussed the

hypothesis on the origin of the crop on a regular basis. The results were diverse but, overall, supported the view of *M. flabellifolia* as the progenitor of the crop (Table 1.3).

Species thought to be involved in the ancestry of cassava were reviewed more recently (Allem, 1999). One of them (*M. esculenta* ssp. *flabellifolia*) is regarded as the wild progenitor of modern cultivars and thus becomes part of the primary gene pool of the crop (Fig. 1.2). Another Brazilian species (*Manihot pruinosa*) is regarded as the nearest species to the GP1 of cassava and is difficult to separate from the wild strain *M. esculenta* ssp. *flabellifolia* on morphological grounds (Fig. 1.3). The study also included the Brazilian *Manihot pilosa* and *Manihot triphylla* as species close to cassava and pointed out the close vegetative and floral similarities between them. Earlier, *M. pilosa* had been found to be the closest wild relative of cassava (Grattapaglia *et al.*, 1987) but the checklist of species did not include *M. flabellifolia*. From parallel molecular studies it was concluded that *M. triphylla* stands closer to

cassava than the wild subspecies *M. esculenta* ssp. *peruviana* and *M. pilosa* is the most distant of all five species tested (Cabral *et al.*, 2000). If the biosystematic crosses now being done back up the above molecular results, *M. triphylla* may eventually join the wild GP1 of the crop.

Data on the taxonomic species concept of cassava came to entwine with earlier views which, through biosystematic crosses between cassava and its wild progenitor, had recorded the unusual high degree of fertility and genetic relationships holding between the two species (Bolhuis, 1953, 1969; Jennings, 1959; Roa *et al.*, 1997; Tables 1.4, 1.5 and 1.6). Such investigations provided a preliminary delimitation of the biological species of cassava. A synthesis became possible when results of molecular biology supplemented existing systematic and biosystematic data. Tests carried out with genetic and biochemical markers strongly suggested that a preliminary delimitation of the phylogenetic (cladistic) species of cassava was in prospect (cf. Table 1.3 below).

Table 1.3. Molecular and biochemical tests carried out to test Allem's (1987/1994a) hypothesis on the origin of cassava.^a

Authority	Marker	Degree of support
Carvalho <i>et al.</i> (1993)	RFLP/RAPD	Moderate (+)
Fregene <i>et al.</i> (1994)	CpDNA/rDNA	Moderate (-)
Carvalho <i>et al.</i> (1995)	RAPD	Moderate (+)
Schaal <i>et al.</i> (1995)	rDNA/RAPDs	Moderate (-)
Brondani (1996)	Isozymes	Strong (+)
Schaal <i>et al.</i> (1997)	RAPDs	Strong (-)
Second <i>et al.</i> (1997)	AFLP	Moderate (-)
Bonierbale <i>et al.</i> (1997)	AFLP	Strong (+)
Roa <i>et al.</i> (1997)	AFLP	Strong (+)
Olsen and Schaal (1998)	Nuclear DNA	Strong (+)
Second (1998)	SSRs	Strong (+)
Roa <i>et al.</i> (1998a)	RFLP	Strong (-)
Roa <i>et al.</i> (1998b)	AFLP	Strong (+)
Olsen and Schaal (1999)	SSRs	Strong (+)
Cabral <i>et al.</i> (2000)	G3pdh	Strong (+)
Schaal and Olsen (2000)	G3pdh	Strong (+)
Roa <i>et al.</i> (2000)	SSRs	Strong (+)
Colombo <i>et al.</i> (2000)	RAPD/AFLP	Strong (+)
Olsen and Schaal (2001)	SSRs	Strong (+)
Olsen (2002)	G3pdh	Strong (+)

^aSupport for *M. flabellifolia* as the progenitor of cultivated cassava (Haysom *et al.* (1994) concluded that *M. flabellifolia* is not native to South America. The conclusion was in complete disagreement with the taxonomic history and geographical distribution of the species. The possibility cannot be ruled out that misidentified germ plasm used in the experiment, accounted for the flawed conclusion.

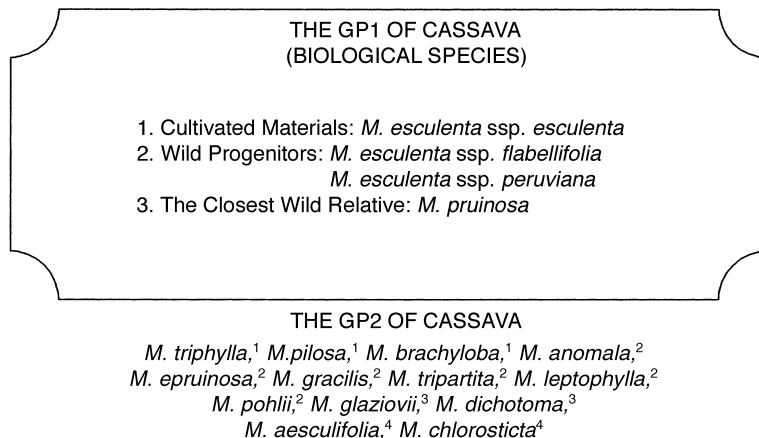


Fig. 1.2. The primary (GP1) and secondary (GP2) gene pools of cassava. From Allem *et al.* (2000).

¹These three species suggested by Allem (1999).

²These six species deduced from the text of Bai *et al.* (1993).

³These two species deduced from the text of Nichols *et al.* (1947).

⁴These two species deduced from the text of Roa *et al.* (1997).

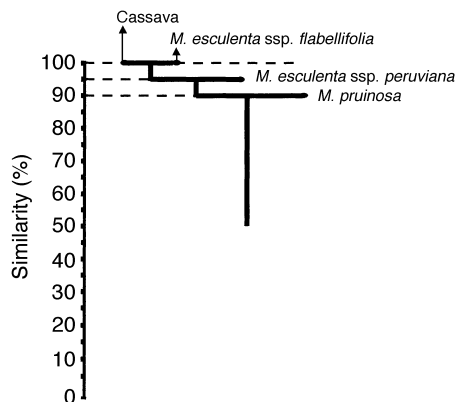


Fig. 1.3. Phenogram of cassava and its closest allies and empirically deduced phylogenetic relationships between species. Figures are merely illustrative and serve as a frame of reference. The assumption is that *M. pruinosa* and the two wild strains of cassava descend from a common stock. From Allem *et al.* (2000).

The Geographical Origin of Cassava

In this section geography is used in the sense of phylogeny, i.e. the area where evolution and divergence of the progenitor occurred and the pertinent phylogenetic relationships with other species. This standpoint differs from that of most authors who traditionally equate the geography of a crop with the area of domestication.

As argued in the preceding section, the view is that *M. pruinosa* and *M. esculenta* ssp. *flabellifolia* descend from a common primeval stock. Some pertinent questions apply. Did the ancestor of both species evolve in the Brazilian Cerrado savannah? Or was it the reverse, i.e. the ancestor evolved in the Amazon, spread to the Cerrado vegetation and then diverged to give *M. pruinosa* and *M. esculenta* ssp. *flabellifolia* and only then did the latter return to the Amazon? Both Cerrado and Amazonia are quite old types

Table 1.4. Results of crosses between cassava and *Manihot saxicola* in Indonesia between 1942 and 1949.

Female parent	Male parent	Flowers pollinated	Fruit-set	Success (%)	Seed-set	Success (%)
<i>M. saxicola</i> ^a	<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

Adapted from Bolhuis (1969).

^aSeeds of *M. saxicola* came from Surinam. The species is a synonym of *M. esculenta* ssp. *flabellifolia*.

Table 1.5. Results of crosses between cassava and *Manihot melanobasis* in Tanzania around 1955.

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

Adapted from Jennings (1959).

^aThe Tanzanian material originated in Surinam. *M. melanobasis* is a synonym of *M. esculenta* subspecies *flabellifolia*.

Table 1.6. Results of interspecific crosses between cassava and three *Manihot* species.

Female parent	Male parent	Crosses	Seed-set
<i>M. esculenta</i> ssp. <i>flabellifolia</i>	<i>M. esculenta</i> ssp. <i>esculenta</i>	16	Thousands ^a
<i>M. aesculifolia</i> ^b	<i>M. esculenta</i> ssp. <i>esculenta</i>	2	5
<i>M. chlorosticta</i> ^c	<i>M. esculenta</i> ssp. <i>esculenta</i>	14	1 to 148

Adapted from Roa *et al.* (1997).

^aCrosses included backcrosses.

^bNorth American and Meso-American species regarded by some writers as the closest wild relative of cassava.

^cMexican species; hybrid seeds showed strong dormancy.

of vegetation and the latter has experienced notable natural catastrophies over the last 100,000 years, during the Pleistocene period, which led to repeated extinctions (Prance, 1978; Simpson and Haffer, 1978). The answer to the question, 'is the Cerrado older than the Amazon?' may provide unique insights into the early evolution of the progenitor. If the Cerrado vegetation arose earlier than the Amazonian forest, this biome may hold the answer regarding the ancestry of cassava. The Brazilian state of Goiás, mainly composed of the Cerrado vegetation, is the primary centre of diversity of species in Brazil. *M. pruinosa* occurs exclusively in Goiás and Mato Grosso states and thrives in open forests ('Cerradão'), eventually overlapping sympatrically with *M. esculenta* ssp. *flabellifolia* in these sites. The working hypothesis is that, because most of the biological diversity of the genus *Manihot* in Brazil is concentrated in the Federal District and in the neighbouring state of Goiás, the original stock that gave birth to *M. pruinosa* and *M. esculenta* ssp. *flabellifolia* may have arisen in the lax forests of the Central Brazilian savannah, afterwards differentiated into the two species and only then did the latter colonize the Amazon.

Discoveries concerning *M. pruinosa* and *M. esculenta* ssp. *flabellifolia* have a bearing on

the phylogeny of cassava. The species share a common geography, ecology, morphology and life form, but no one disputed their taxonomic ranking or challenged them as distinct species for more than 150 years, since the original descriptions made by the Austrian botanist Johann Baptist Emanuel Pohl in 1827. The strict morphological kinship between *M. esculenta* ssp. *flabellifolia* and *M. pruinosa* is undisputable. Biosystematic trials will determine the degree of fertility between them and with cassava. Planned trials will also reveal whether *M. pruinosa* is part of the GP1 of cassava (and so joining *M. flabellifolia* and *M. peruviana*) or whether it belongs to the secondary (GP2) gene pool. If, as seems likely, *M. flabellifolia* is part of the gene pool of cassava, then *M. pruinosa* is certainly the wild species most closely related to the crop. Pioneering molecular data support the latter view (Second *et al.*, 1997; Olsen and Schaal, 1998) and later more elaborate studies further strengthened it (Olsen and Schaal, 1999). The fact that *M. pruinosa* and *M. esculenta* ssp. *flabellifolia* seem to descend from a common stock has implications both for the early evolution of cassava and for its agricultural origin. Among others, this may expand or narrow the areas eligible for consideration as the cradle of domestication.

The Agricultural Origin of Cassava

Cassava is an ancient crop species. Lathrap (1970) estimates that domestication began 5000–7000 years BC and the estimate receives support from archaeological finds in the Amazon (Gibbons, 1990). By the time the first Europeans reached the New World, the crop was already cultivated in all of neotropical America (Patiño, 1964). The antiquity of the domesticate receives further support from two related facts. First, cultivation from vegetative propagules (vegeculture) is assumed to be an older practice than seed-culture (Harris, 1967, 1971a; Lathrap, 1973, 1977). Second, the great importance of manioc in American aboriginal swidden type of cultivation is the result of a combination of ecological factors, which favoured the growth of the plant, and cultural factors – the latter principally in the form of tradition drift which played a determinant role in the retention and further spread of the crop among ancient Amerindian societies (Albuquerque, 1969; Harris, 1971b; Lathrap, 1973; Moran, 1975).

Since Pohl (1827) suggested Brazil as the place of origin of cassava, i.e. the place of initial domestication, investigators have spent over a hundred years considering the issue, without reaching a definitive and consensual conclusion. Attempts to review the evidence on the origin of the crop produced no hard facts (Renvoize, 1972). Historically, ‘origin’ meant the quest for the agricultural origin of the crop as the sole concern had to do with the original place of domestication. In other words, writers were neither concerned with the tracking down of a presumed ancestry of the crop nor with the raising of such a possibility. However, anything short of speculation on the cradle of domestication had to consider first the discovery of the wild progenitor. The consequence of this would be to narrow the candidacy of eligible areas for the initial cultivation of manioc (Table 1.7).

The view has been expressed that ‘the domestication of manioc was perhaps even easier [relative to yams]. It can be reproduced by stem cuttings. All that is necessary is to cut off a branch and place it in the ground during the rainy season and tubers will be produced’ (Harlan, 1975). This view is premature and somewhat misleading since it considers the propagation of the crop rather than its domestication

which, as a process, was certainly more complicated. Initially it is likely to have been difficult to select for easy rooting, since the percentage of survival of wild stem-cuttings of the ancestor averages only 10% (Allem and Goedert, 1991). Two examples can be cited on how cassava was probably domesticated in pre-Columbian America. On the 14 May 1986, Embrapa’s collecting team stopped at a petrol station in the municipality of Cacoal (11°28’S, 61°21’W), Brazilian state of Rondônia. A pump attendant commented on seeing the wild stakes of the progenitor being carried and told the team that he knew the material by the names ‘mandioca-brava’ (wild cassava) and ‘mandioca-do-mato’ (bush cassava). It was a common weed by the roadsides and inside food crop plantations. The roots were reportedly highly toxic and fresh leaves could kill pigs. Shortly after the family arrived from the Brazilian southern state of Paraná in 1982, his father cleared a plot of virgin forest and this turned the wild *Manihot* into an aggressive weed. The father planted some stakes of the species and within a year the family was harvesting roots of considerable size. Mr Adelicio, the clerk, said that only flour could be made from the roots because of their toxicity, while stem-cuttings were said to root with relative facility. This may have been an exaggeration as wild conspecific forms of the domesticate have been reported to root with great difficulty (Lanjouw, 1939, with the Surinamese *Manihot saxicola* and Jennings, 1963, with *Manihot melanobasis* from Guyana). A second example on how manioc was possibly first domesticated came on the 26 May 1986 through a report obtained in the vicinity of the municipality of Vila Rica (09°58’S, 51°00’W), Brazilian state of Mato Grosso. Two riders came by and looked closely at the attempts of the team to dig up some roots of a wild population of *M. esculenta* ssp. *flabellifolia*. They were asked about the plant. Both replied it was a native of the area and thrived at the edge of woods and that it was common practice for local dwellers to prune it back as cattle appreciated it and consumed the fresh leaves. The plant produced swollen roots but people did not eat them. An interesting story followed. They had heard that a few local inhabitants had once planted cuttings of the wild cassava and that the F1 generation usually gave very unsatisfactory results. Starting with the F2 generation, however, the plant was already

Table 1.7. Areas suggested by authors as the likely cradle where the domestication of manioc first took place.^a

Cradle of domestication	Source
Brazil	Pohl (1827)
Brazil	Mueller (1874)
Eastern tropical Brazil	de Candolle (1884)
Brazil	Pax (1910)
Peru	Cook (1925)
Brazil	Lanjouw (1932)
Northern Amazonia	Schmidt (1951)
Brazil – central Paraguay	Vavilov (1951)
Venezuelan savannahs	Sauer (1952)
South America	Anderson (1954)
Peru or Mexico	Rogers (1963) ^a
Brazil	Jennings (1963)
Southern Mexico, Guatemala, Honduras	Rogers (1965), Rogers and Appan (1970)
Eastern Venezuela	Reichel-Dolmatoff (1965)
Peru	Lanning (1967)
Mexico and Central America	Schwerin (1970)
Northern Amazonia	Lathrap (1970)
North America	Rogers (1972)
Amazonia	Spath (1973)
Central America and north-eastern Brazil	Purseglove (1976)
Amazonia	Schultes (1979)
Mesoamerica	Jennings (1979)
Brazilian states of Goiás, Mato Grosso and Rondônia	Allem (1997)
Brazilian states of Mato Grosso and Rondônia	Olsen and Schaal (1998, 1999)

^aBertram (1993, p. 98) reports ‘He [Rogers] is reported to have backed away from this position later (Stone, 1984), but maintained a sense that Central American species may have had role in the evolution of cassava (D. Rogers, personal communication).’

‘amansada’ (tamed) and started producing tuberous roots of fair size. The riders remarked that people could only make flour from the roots because they were poisonous if not processed. An additional related example from Africa seems to give support to the above version. A rare ethnobotanical report on the agronomic behaviour of the conspecific *M. melanobasis* shows that domestication from the wild is a real possibility for woody forms of the genus: ‘its roots are usually fibrous, but large tuberous roots have been obtained from plants that have been left in the ground for long periods’ (Jennings, 1957). Jennings (1959) later specifies this time as ‘many years’. A second edible taxon of *Manihot* (still undescribed nomenclaturally to science and apparently a hybrid between cassava and the Brazilian species *Manihot glaziovii*) is harvested after staying at least 3 years in the ground while optimal harvest is reached in 7 years, hence the

common name ‘mandioca-de-sete-anos’ (7-year cassava; Allem and Hahn, 1991).

Manipeba: the Transitional Link Between the Wild Ancestor and Cultivated Cassava?

What can properly be regarded as the transitional link between the two wild strains of cassava and the domesticate was found in northeastern Brazil in July–August 1985. The find offered for the first time insights on how domestication and evolution of the crop might have proceeded in pre-Columbian times. First, there was the record that a climbing cassava landrace called ‘manipeba’ existed in northeastern Brazil and yielded every 6 years (Albuquerque, 1969). It was also hinted that such a material would reveal an as yet undescribed

second edible species in the genus. During a collection in the area (A.C. Allem, unpublished) it was discovered that the names 'manipeba-branca' and 'manipeba-preta' were used for modern cassava varieties in southern Ceará and northeastern Bahia. In the municipality of Mari, state of Paraíba, the name 'manipeba-graúda' was being applied to another distinct edible 'species' of *Manihot* (see the above remarks on 'mandioca-de-sete-anos'). However, in a few rural households of Paraíba the name manipeba was found associated with a distinctly primitive architectural indigenous landrace of cassava. Such a plant is virtually unknown to breeders of cassava. The following was found relative to this unique plant. In places of northeastern Brazil, manipeba nearly always refers to a primitive and rustic folk variety of cassava. Many agriculturalists know the name but few grow the plant in their backyards because it is uneconomic to do so. Those who do cultivate it do so on account of social tradition. In the few households where manipeba was found growing, the number of individual plants ranged from one to six (eventually eight). It seemed as if people were relying on the plant as reserve against times of famine in a region chronically plagued by drought. Soon it was realized that social tradition was the chief factor behind its cultivation. People raising manipeba showed a sort of special consideration for the plant. Invariably, with pride, they described the landrace as highly productive which, in turn, suggested optimal mass selection performance as decisive to its retention. What may be called a plantation of manipeba was found at only two sites. The first was in the municipality of Bento Fernandes (05°42'S, 35°48'W) state of Rio Grande do Norte, where about 100 individuals were being raised on a small farm. The second plantation was found in the municipality of Sapé (07°12'S, 35°14'W) state of Paraíba, where about 50 individuals were being grown. On botanical grounds, landraces of manipeba are exceedingly close to wild plants of *M. esculenta* ssp. *flabellifolia*. They share basically the same type of inflorescence and leaf morphology. Significantly, as observed for specimens of *M. esculenta* ssp. *flabellifolia* in the wild, the internodes of manipeba are widely spaced 6–8 cm apart along the stem. The discovery was significant in the path leading to domestication

since it was the first time that undomesticated characters were found present in a cultivated folk variety of the crop. The particularly strong evidence suggested that, under domestication, agronomic characteristics may differentiate prior to the differentiation of botanical characters (advanced cultivars of cassava normally show the leaf scars clustered closely together and very prominent, whereas those of manipeba and the wild strain are virtually absent). The habit of manipeba is invariably that of a low to medium tall shrub, highly branched and always semi-decumbent to decumbent, often crawling on the ground. Agronomically, landraces of manipeba correspond to bitter cassava, i.e. show high levels of cyanogenic glucosides and the roots are highly poisonous if not processed. The roots are used solely to make flour and a type of bread known as 'beiju'. It takes, on average, between 4 and 5 years to produce high-quality roots, another indication of its primitive state. This explains why the landrace is so little exploited regionally for few people are willing, or can afford, to wait so long. If harvested less than 3 years from planting, the roots of manipeba are said to be watery. The quality of its flour, however, according to local reports, is unsurpassed. Moreover, local people say that manipeba is 'boa de goma' (good starch yielder). Of relevance was the information that genotypes of manipeba, unlike those of modern cultivars of cassava, successfully withstand fire and competition from the surrounding native vegetation. The primitive variety persists in abandoned areas even though other varieties of cassava do not.

The existence of manipeba bridges the architectural and agronomic gap between wild forms of cassava and the crop. Its existence also suggests how domestication may have proceeded in primeval times and illustrates that a substantial part of the variation inherent within cassava may be the direct result of human selection. Manipeba stands as the perfect archetype of very primitive varieties of manioc. Such an ancient landrace, given its ethnobotanic importance in shedding light on likely routes leading to the domestication and cultivation of the domesticate, should necessarily be included in worldwide representative collections. Regrettably, there is a trend in northeastern Brazil for such interesting germplasm to be displaced

by the distribution and spread of improved materials.

Summing up, if the hypothesis of Allem (1994a) is valid, i.e. the progenitor of cassava is restricted to parts of the South American neotropical mainland and a number of places thought of in the recent past as likely cradles and prospective centres of initial domestication are obligatorily ruled out as sites where cultivation first began (pertinent examples in Table 1.7 include, among others, Honduras, Guatemala and Mexico). The assumption is that cassava was domesticated straight from the wild and therefore, because the crop is vegetatively propagated, present cultivated forms should preserve a maximum purity from the early days, i.e. the cultivated forms are expected to have very similar botanical morphologies as the living ancestor. That is the main reason why *M. esculifolia*, and also *M. carthaginensis*, are considered unlikely to have contributed genes to cassava, i.e. the wingless fruit sculpturing of these species and the morphology of their seeds (resembling a tick) are very different in shape from those of cassava. Cassava shares these very characters with the wild ancestor.

Other progenitors might have been involved in the evolution of cassava but evidence is lacking. For example, it is known that many pubescent cassava cultivars occur in Peru (S.K. Hahn, personal communication) and some of them may have descended from domesticated stocks of *M. peruviana*, thus conferring legitimacy to Cook's (1925) hypothesis that cassava may have been domesticated in eastern Peru, an area indeed inhabited by the subspecies *M. esculenta* ssp. *peruviana*. Dr Hahn reported to the author in 1993 that perhaps the true figure is 200–300 pubescent Peruvian cultivars but he did not remember whether any particular cultivar bore pubescent ovaries or fruits, traits associated with the wild strain *M. esculenta* ssp. *peruviana*.

As pertinently speculated by Spath (1973), cassava may have been domesticated asynchronously at several sites in the Amazon. Consistent with the view that cassava may have originated in the Brazilian Amazon, there have been two recent theories whose greater interest lies in the fact that reasons were for the first time advanced on why cassava is expected to have been domesticated in a particular area.

First, there was the report by Allem (1997), who argued in favour of the central Brazilian state of Goiás and the westernmost Brazilian states of Mato Grosso and Rondônia as likely cradles of initial domestication of the crop. This was on the grounds that populations of both wild strains are particularly dense in these areas; the idea was that stocks drew the attention of local Amerindians who proceeded to tame the wild plant, the stocks probably spotted inside the Indians' household plantations rather than in the bushwood. Second, Olsen and Schaal (1999) elected the Brazilian states of Mato Grosso and Rondônia as a putative cradle of domestication on the basis of the fact that strong genome congruity has been documented between local wild populations of *M. esculenta* ssp. *flabellifolia* and modern cultivars of *M. esculenta* ssp. *esculenta*. However, equally legitimate claims hold that the domestication of cassava may have taken place in northern Brazilian Amazonia through the activities of Arawak tribes (Schmidt, 1951; Stone, 1984; Fig. 1.4). Allem (1997) advanced the view that perhaps the ultimate key as to the cradle of domestication of cassava may lie with the study of migration patterns of South American Amerindians in pre-Columbian times and specific scholarly studies on this theme (e.g. Schmidt, 1951; Migliazza, 1982) may hold the answer to this intriguing question.

Whatever the future of this active area of research, the increasing prospect is that manioc was domesticated in part of the Amazon, possibly in the Brazilian forest areas, rather than in the savannah. One possibility is that the ancestor of cassava evolved in the Brazilian Cerrado before reaching the Amazon. Domestication, however, seems to have happened in the Amazon and a further element may shed additional light on the subject. An Amazonian origin in the rain forest might explain an apparent paradox recorded by investigators. Why is it that cassava stops all photosynthetic functions and the stomata close whenever atmospheric humidity decreases, even though there is plenty of water in the soil (El-Sharkawy and Cock, 1984; El-Sharkawy *et al.*, 1984)? An origin in the humid Amazon, where the relative humidity of the air is rarely less than 70% (Bastos, 1972), may explain such behaviour.

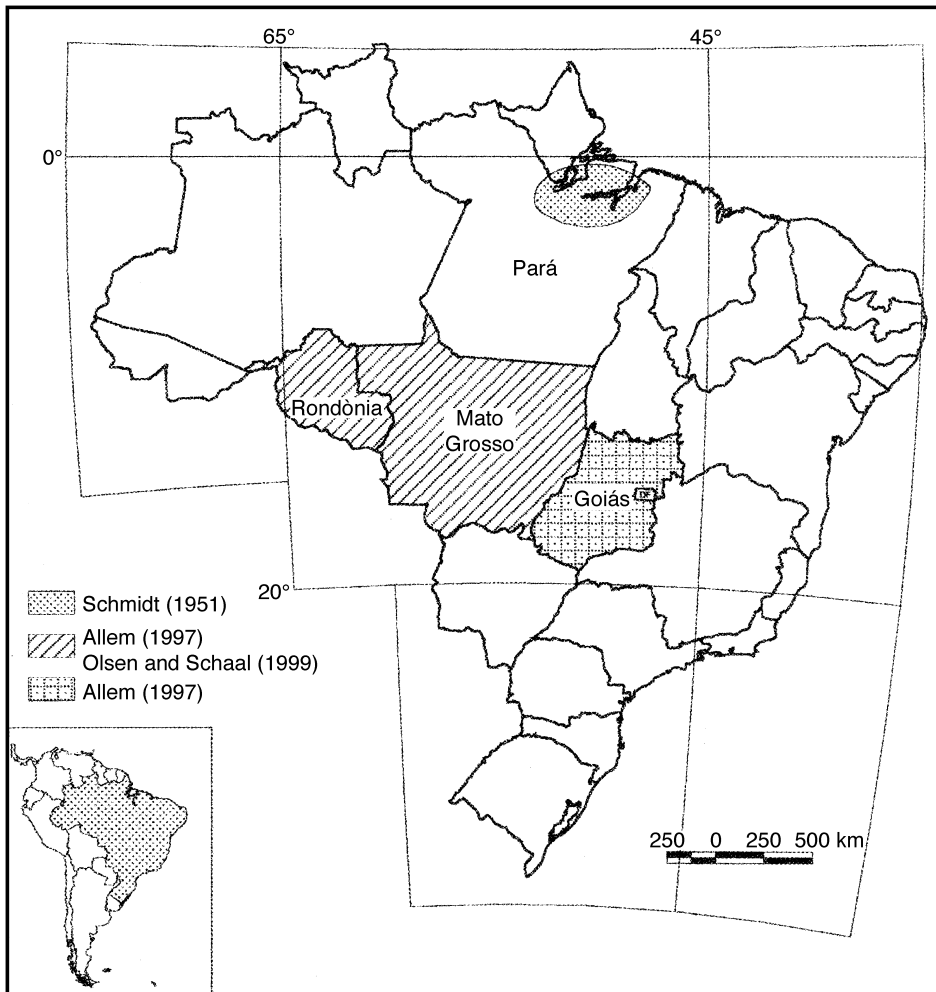


Fig. 1.4. Three putative areas of initial domestication in the Brazilian neotropics as suggested by Schmidt (1951), Allem (1997) and Olsen and Schaal (1999). Whether cassava was first domesticated in northern Brazilian Amazonia, or, somewhere in Brazil's westernmost states of Rondônia and Mato Grosso is controversial. However, if domestication did occur in Brazil it must have occurred along the periphery of the Amazon forest since the wild ancestor does not spread inside the tall forest of 'terra firme' (dry upland forest) which covers up to 90% of the Amazon. The referral of the collection Michael Goulding 80 (MG 86406) to *M. esculenta* ssp. *flabellifolia* in Allem's (1994a) study, supposedly the only specimen of the subspecies to have ever been collected in central Amazonia (Manaus area), was a mistake and is corrected here. The species in question is *Manihot brachyloba*, which ranges over much of Amazonia, in the interior and along its periphery. So far the wild progenitor of cassava has been collected in the Brazilian Amazon solely along the periphery of the forest (A.C. Allem, unpublished). Apparently, the ancestor did not penetrate the interior on account of soil type, i.e. it is absent in areas dominated by oxisols and ultisols, which occupy 90% of the Amazonian area. The large frequency of populations of *M. esculenta* ssp. *flabellifolia* and *M. esculenta* ssp. *peruviana* in northwestern Brazilian Amazonia (e.g. states of Mato Grosso and Rondônia) seems to associate with the presence of alfisols, in the Amazon they show a superficial sandy layer. The collection Allem and Silva 4477 (CEN), 31st Jan 1995, Brasil, state of Maranhão, 36 km (river Peritoró) SE of Peritoró along BR-316 highway heading for Caxias, is *M. esculenta* ssp. *flabellifolia*. The specimen was found close to the municipality of Caxias in Maranhão, an area inside northern Amazonia. However, Caxias is only 75 km away from Teresina,

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Fig. 1.4. (continued) the capital of the neighbouring northeastern state of Piauí, a state largely covered by the xerophilous vegetation known as Caatinga. This suggests that collection 4477 comes from the eastern most part of the Brazilian Amazon, thus corresponding to its outskirts.

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