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Review

Wild *Manihot* species: botanical aspects, geographic distribution and economic value

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ABSTRACT. A total of 98 *Manihot* species have been recognized in the genus. All of them are native to the tropics of the New World, particularly Brazil and Mexico. The cultigen, *Manihot esculenta* Crantz (cassava), grows throughout the lowland tropics. Wild species vary in growth habit from acaulescent or short shrubs to tree-like. Because of their adaptations to different conditions, they are gene reservoirs for tackling many abiotic and biotic stresses such as improving root quality and resistance to diseases. They have been used successfully by the first author for improving protein content, seed-fertility, apomixis, resistance to mealy bug, and tolerance to drought. A table of the most important species from an economic viewpoint is presented.

Key words: Wild cassava; Natural habitat; Adaptation; Evolution

INTRODUCTION

Cassava, *Manihot esculenta*, grows throughout the lowland tropics. It is cultivated between 30° N and 30° S of the equator, in areas where the mean annual temperature is greater than 18°C (Nassar and Ortiz, 2007). This tuberous root crop ranks among the two most important staples of sub-Saharan Africa. It accounts for most of the cassava harvest worldwide, followed by Asia and South America. The main diversity center of *Manihot* species is Brazil.

In sub-Saharan Africa and Latin America, cassava is mostly used for human consumption whereas in Asia and parts of Latin America it is also used commercially for the production of animal feed and starch-based products. Cassava has been regarded as a crop adapted to drought-prone environments, where cereals and other crops do not grow well. It also grows well in poor soil.

Jennings and Iglesias (2002) provide an overview of the state of the art of cassava breeding as well as remaining challenges, whereas Nassar (2004b) and Nassar and Ortiz (2007) assess the impacts on cassava breeding programs worldwide. Although significant gains are reported in Africa (Dixon et al., 2003), there are pests and other constraints affecting crop yield.

Wild *Manihot* species are gene reservoirs for tackling abiotic and biotic stresses, as well as for improving the root quality of cassava. Most species are perennial and vary in growth pattern from nearly acaulescent subshrubs to small trees. The Universidade de Brasília (Brazil) maintains the most integrated living collection of *Manihot* species since the 1970s (Nassar, 1978a, 1981, 2002d,e). Such endeavor was undertaken because of genetic endowment used before in cassava breeding in relation to resistance to cassava mosaic disease (Nichols, 1947). These wild species proved to be potential sources for other traits such as high protein content (Jennings, 1959; Nassar and Costa, 1978) compared to low protein in cassava (Nassar and Dorea, 1982; Nassar and Marques, 2006). Restoring seed-fertility (Jennings, 1962; Nassar, 2004a), apomixis (Nassar et al., 1998a,c, 2000; Nassar, 2000b; Nassar and Collevatti, 2005), resistance to mealy bug, and tolerance to drought-prone environments (Nassar, 2000c) were useful characters gained from wild species. This review updates previous reports by Nassar (1999, 2000c, 2002f, 2004b) on wild *Manihot* species and focuses on different topics reviewed by us recently.

SPECIES DIVERSITY AND ORIGIN OF THE CROP

A total of 98 *Manihot* species have been recognized (Rogers and Appan, 1973), with one species (*Manihotoides pauciflora*) known in the closest related genus. Several of its attributes are not found in any *Manihot* species, including mono-flower inflorescences and leaves borne at the apex of short, condensed stems arising from branchlets. These primitive characters suggest *M. pauciflora* as a probable progenitor of all *Manihot* groups. Unfortunately, this species is on the verge of extinction (Nassar, 1999).

Cassava, a native crop of South America was domesticated in the Amazon by Brazilian Indians (Nassar, 1978a), although Ugent et al. (1986) cited evidence of domestication on the Peruvian coast earlier than 4000 B.C.E. The Coastal Peruvian and lowland Neotropical cassava types differ, and appear to be separated by several millennia, which suggests that the crop may have been domesticated more than once. Nassar (1978a, 2000a,c, 2003a,b) emphasized the idea

that *M. esculenta* species does not grow wild elsewhere. According to this author, domestication could have occurred from a natural hybrid between two species, and *M. pilosa* being perhaps one of the parents. Enlarged roots could have developed as a result of this hybridization.

The ability of cassava cultivars to set seed has been reduced since they evolved from wild *Manihot* species (Jennings, 1962) indicating that cassava has long been propagated asexually likely by cuttings. Conscious and unconscious farmers' selection for increasing the number and quality of cassava cuttings would act to favor plants with thicker stems (Nassar, 2002f; Elias et al., 2007). Thus, this selection for increased asexual propagation may have led to reduction in the degree of branching, which is regarded as one of the most striking differences between the cultigen and its wild ancestors (Nassar, 2002b). Although the cultigen is vegetatively propagated, farmers still incorporate plants from seedlings as planting stocks (Elias et al., 2001). The out-crossing rate ranged from 0.69 to 1 among eight cassava ethno-varieties, which indicates that they are preferentially allogamous (da Silva et al., 2003). Natural hybridization between cassava and wild *Manihot* relatives does occur, which coupled to weak interspecific barriers have led to an extremely heterozygous gene pool that may begin a sequence of hybridization followed by speciation (Nassar, 2002b, 2003b).

Comparative analysis between cassava and its wild relatives showed that epigeal germination was primitive in *Manihot*. Hypogeal germination was a feature of wild *Manihot* species because it confers better adaptation to the risky savanna environments, whereas epigeal germination and photosynthetic cotyledons evolved through domestication in cassava, since both traits provide the cultigen with fast initial growth in the farming systems (Pujol et al., 2005).

DISTRIBUTION AND NATURAL HABITAT

All *Manihot* species are native to tropical regions of the New World, particularly in Brazil and Mexico. The only species found in other tropical regions of the world are those that were introduced after Columbus' voyages to the American continent. The species of *Manihot* are sporadic in their distribution and rarely become dominant over the local vegetation. The majority of these species are in relatively dry regions, and only a few are found in the rain forest. Their typical habitats are openings in the forest as in the case of *M. anomala* (Nassar, 1978a,d,f). They are therefore heliophiles that grow only in the absence of shading. Many of these species (e.g., *M. pohlii*, *M. zehntneri* and *M. grahamii*) are weedy types capable of invading new agitated areas, and frequently found on limestone-derived and well-drained soils. Most species are damaged by frost with few exceptions (e.g., *M. grahamii* and *M. neusana*), whose native distribution includes areas with occasional frost.

Rogers and Appan (1973) classified *Manihot* species into 19 sections, varying from trees in the section *Glazioviannae* to subshrubs, nearly acaulescent, in the section *Stipularis*. The species in this latter section are also characterized by being more dioecious than monoecious, a condition reversed in all other *Manihot* species. Other sections, such as *Tripartitae* and *Graciles*, are perennial subshrubs with large woody roots, and whose stems frequently die back to the root crown in response to dry periods or fires (Nassar, 1980b).

There are four widely known centers of diversity for *Manihot* species: Mexico and northeast and central Brazil, plus southwest Brazil and Bolivia. Microcenters of diversity of these species exist within central Brazil where large numbers of species are concentrated in

small areas, i.e., <50 km in diameter (Nassar, 1978a,c, 1979b, 1980a, 1982, 1992). These microcenters arose from the frequent hybridization between species and the heterogenic topography of their habitats, which help isolate fragmented gene pools that lead to speciation. For example, Goiás Velho and Corumbá de Goiás are regarded as two micro-centers of cassava diversity (Nassar, 2003a), following Harlan's concept of geographic pattern of variation of cultivated crops (Harlan, 1951, 1971). Likewise, tree-like species such as *M. glaziovii* and *M. pseudoglaziovii* are found in northeastern Brazil, whereas short species and subshrubs are found in central Brazil.

The species within each *Manihot* section, their growth pattern and native distributions are provided by Rogers and Appan (1973). Central Brazil (southern Goiás and eastern Minas Gerais) is home to the largest *Manihot* diversity (38 of the 98 accepted species), whereas Mexico, the second largest center of diversity, harbors 17 *Manihot* species (Nassar, 1978a, 2000c). The third largest center of diversity is northeast Brazil with 16 species, whereas there are six species in south Mato Grosso and Bolivia that together are the fourth center of *Manihot* diversity.

The *M. esculenta* cultigen appears to be a complex species with multiple sites of initial domestication (Rogers and Fleming, 1973), although Allem (1994) proposed that *M. esculenta* derived from two primitive forms instead of being a cultigen, having 3 subspecies. However, Nassar (1978a, 2001a) did not agree with Allem's views that cassava arose from *M. flabellifolia*, and suggested insights into the putative ancestors of cassava (Haysom et al., 1994; Nassar, 2001a) that this species may be the result of a cassava crop-weed complex, as pointed out for other crops by Harlan and Wet (1965). Cytogenetics and DNA marker-aided research should be able to provide more insight.

GROWTH HABIT AND PLANT MORPHOLOGY

Procumbent, semi-herbaceous subshrubs, shrubs, and trees are found in *Manihot*. The branching pattern is typically dichotomous or trichotomous, having at the branching point a terminal inflorescence. Bark of the woody species is generally smooth. Many of the species are lacticiferous, and some species such as *M. glaziovii* (Ceará rubber) are cultivated in Brazil and elsewhere for rubber production (Rogers, 1965; Rogers and Appan, 1973). This species was used by Storey and Nichols in the 1930s in former Tanganyka (today continental Tanzania) to transfer resistance to cassava mosaic disease (Nichols, 1947; Nassar and Ortiz, 2007). Many species such as those in section Tripartitae have their stems adapted to dry periods; dieback to a root crown regularly and shed their leaves during the dry season. The majority of *Manihot* species are found on limestone-derived and well-drained soils (Nassar, 1995).

The majority of *Manihot* species are monoecious and a few are dioecious, which make them obligate out-crossers. In many species, they are protogeneous, i.e., pistillate flowers open before staminate flowers of the same inflorescence. Pollination is done by insects to whose bodies the sticky pollen adheres. Cross-pollination leads to the formation of extremely heterozygous gene pools. Being allopolyploid species, partially apomictic, and having weak barriers in addition to its allogamous nature, has led to the rapid speciation of this group and formation of the large number of species (Nassar et al., 1998b; Nassar, 1999, 2000c, 2001a,b, 2002a,c).

Table 1 lists the most important species from an economic viewpoint, along with their names and classification according to the monograph by Rogers and Appan (1973).

Table 1. Cassava most important species from economic viewpoint.

Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Heterophyllae	*M. tristis* Mueller von Argau	Brazil (Amapá, Roraima); Venezuela; Suriname	Shrubs (3 m), preference of granitic outcrops; bracts and bracteoles setaceous; leaf lobes obovate or elliptic; venation camptodromous, never craspedodromous	Used by Bolhuis (1953) as a possible source of protein	Endangered	
	M. pilosa Pohl	Brazil (Minas Gerais, São Paulo, Rio de Janeiro)	Tall, erect shrubs (3 m) to slender trees (10 m), it grows in sandy loam soils and among rocky outcrops; inflorescence moderately branched; ovary tomentose; leaf lobes entire	High affinity with *M. esculenta* (Rogers and Appan, 1973)	Endangered	
	M. leptopoda (Mueller von Argau) Rogers & Appan	Brazil (Rio de Janeiro)	Erect shrubs (2 m), it grows on granitic outcrops; all parts glabrous; lobe bases stiff; lobes held horizontally	Potencial to adaptation to granitic sandy regions (Rogers and Appan, 1973)	Endangered	

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Table 1. Continued.

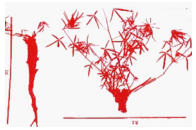
Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Quinquelobae	*M. alutacea* Rogers & Apan	Brazil (Goiás)	Shrubs (1.5 m); in rocky cerrado at summit of montain; texture of the leaf is like tanned leather; inflorescence racemose not subspicate; leaf lobes digiform; apices acute	Source of ornamental purpose. Source of adaptation to soil rich in calcium (Nassar, 1979a). Hybridizes with *M. reptans* (Nassar, 1979b)	Endangered	 
Graciles	*M. fruticulosa* (Pax) Rogers & Appan	Brazil (Goiás, Minas Gerais, Distrito Federal)	Slender subshrubs (0.5 m); inflorescence a lax raceme or a panicle; flowers evenly positioned in inflorescence; leaf lobes drooping	Source of edible roots (Nassar, 1985)	Medium	
	M. pentaphylla Pohl	Brazil (Pará, Goiás, Minas Gerais); Paraguay	Subshrubs to shrubs (to 2 m); all members occur in degraded, dry, interior, upland regions; leaf lobes linear or narrowly lanceolate; leaves 5 lobed; all parts glabrous	Source of tolerance to drought and soil rich in calcium (Nassar, 1978e)	Medium	
	M. gracilis Pohl	Brazil (Goiás, Minas Gerais, São Paulo, Distrito Federal); Paraguay	Subshrubs (1 m); inflorescence a lax raceme or a panicle; leaf lobes linear or narrowly lanceolate; leaves 3 lobed	Low HCN content (Nassar, 1978c)	Abundant	

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Table 1. Continued.

Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Sinuatae	*M. anomala* Pohl	Brazil (Pará, Mato Grosso, Goiás, Minas Gerais, São Paulo, Distrito Federal); Paraguay; Peru; Bolivia; Argentina	Shrubs (3 m); leaf lobes entire or shallowly pandurate; young leaf and bud color strong yellow-green	Forms enlarged roots, source of resistance to soil rich in calcium (Nassar, 1978e). Hybridizes with cassava and produces fertile hybrids (Nassar, 1989)	Abundant	
Glaziovianae	*M. glaziovii* Mueller von Argau	Brazil (Ceará, Paraíba, Bahia, Pernambuco)	Tall shrubs to trees (10 m), with copious latex; bracts and bracteoles setaceous; inflorescence a panicle; many flowered; median lobes obovate; basal lobes recurved	Commercial production of latex, ornamental (Rogers and Appan, 1973). Resistance to mosaic and brown streak (Nichols, 1947). Produces polyploid types (Nassar, 2004a). Source of apomixis (Nassar, 2007; Nassar and Ortiz, 2007)	Abundant	 
	M. pseudoglaziovii Pax & K. Hoffmann	Brazil (Ceará, Rio Grande do Norte, Paraíba)	Medium-sized trees (6 m), weedy habitat; inflorescence a panicle; few flowered; median lobes oblong; basal lobes straight	Minor latex supply (Rogers and Appan, 1973)	Abundant	
	M. dichotoma Ule	Brazil (Pernambuco, Bahia), plant introduced to several countries	Trees (3-12 m); inflorescence a raceme; staminated buds conical; leaves 5 lobed; lobes frequently pandurate	Tolerance to drought, rapid stem growth, leaves content showed double of carotin, five times of minerals and higher protein content (Nassar and Costa, 1978)	Abundant	

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Table 1. Continued.

Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Crotalariaeformes	*M. procumbens* Mueller von Argau	Brazil (Minas Gerais, São Paulo); Paraguay	Procumbent, weak-stemmed. Usually pubescent; in cerrado, low woods, and on sandstone slopes; bract and bracteole margins usually serrate; leaf lobes obovate or hastate	Tolerance to soil toxicity, particularly to magnesium (Nassar, 1978c)	Abundant	
	M. reptans Pax	Brazil (Goiás, Minas Gerais)	Procumbent, semiherbaceous shrubs (0.40 m); bract and bracteole margins usually entire; all parts glabrous; leaves usually 5 lobed, rarely 3 lobed	Resistance to *Xanthomonas manihotis* and to soil rich in calcium (Nassar, 1982)	Abundant	
Stipulares	*M. stipularis* Pax	Brazil (Goiás, Distrito Federal)	Very short, nearly acaulescent, subshrubs (0.20 m); on rocky banks; stipules foliaceous; lobes curved; stipule margin laciniate; more consistently dioecious than monoecius	Source to adaptation to soil rich in calcium and tolerance to soil toxicity (Nassar, 1985). It should make definite contributions to horticulture as a rock garden plant in warm climate (Rogers and Appan, 1973)	Medium	
	M. oligantha Pax	Brazil (Goiás)	Very short, nearly acaulescent, subshrubs (less than 0.15 m); among outcrops and rocky slopes; stipules setaceous; leaves 3-5 lobed, rarely 7 lobed; leaf lobes less than 1.5 cm wide	Source of high protein (Nassar, 1978e). Hybridizes with cassava and produces enlarged high protein roots (Nassar and Dorea, 1982)	Endangered	

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Table 1. Continued.

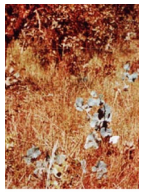
Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Peltatae	*M. peltata* Pohl	Brazil (Goiás)	Subshrubs (1 m); bracts and bracteoles setaceous; petiole attachment very peltate; leaf shallowly stellate	Source of use in ornamental purpose and source of tolerance to soil toxicity (Nassar, 1978a, 1985)	Endangered	 
Tripartitae	*M. neusana* Nassar	Brazil (Paraná)	Shrub with branches which tend to droop; fruit mottled; leaves pubescents; bracts and bracteoles foliaceous; leaf lobes obovate to lanceolate; leaf 3-5 lobed	Source of apomixis gene (Nassar, 2001b). Resistance to *Xanthomonas manihotis* (Nassar, 1985)	Almost extinted	
Caerulescentes	*M. caerulescens* Pohl	Brazil (Amapá, Pará, Piauí, Ceará, Goiás, Pernambuco, Maranhão, Mato Grosso, Minas Gerais, Rio de Janeiro); Paraguay	Tall shrubs to trees (+30 m); leaves 3-5 lobed; median lobes cuneate, obovate or elliptic; lobe apices obtuse, acute or cuspidate	Very tolerant to drought, enlarged and edible seeds (Nassar, 1986). Modest production of latex (Rogers and Appan, 1973)	Abundant	

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Table 1. Continued.

Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Peruvianae	*M. leptophylla* Pax	Brazil (Amazonas, Pará, Pernambuco, Acre); Ecuador; Peru	Vine-like shrub; inflorescence a panicle; petioles, midribs, peduncles, bracteoles, etc., sparsely pubescent; leaves frequently 5 lobed, sometimes 3 lobed	Extremelly tolerant to *Xanthomonas manihotis*; forms edible and enlarged seeds (Nassar, 1982). Hybridizes with cassava in nature (Nassar, 2000c).	Abundant	
Parvibracteatae	*M. pringlei* Watson	Mexico (Tamaulipas, San Luis Potosí)	Tall shrubs (3-4 m), unconsolidated sandy red lateritic soil; bracts and bracteoles foliaceous; fruits pedicels ascending	Very little HCN (Rogers and Appan, 1973)	Endangered	
	M. aesculifolia (Humbolt, Bonpland & Kunth) Pohl	Mexico (Sinaloa, Nayarit, Jalisco, Vera Cruz, Chiapas, Colima, Michoacan, Oaxaca, Guerrero, Mexico, Yucatan, Quinta Roo); Britsh Honduras; El Salvador; Nicaragua; Costa Rica; Panama	Erect tall shrubs (7 m), stems with white latex; leaf lobes oblong or oblong-pandurate; inflorescence a profusely branched panicle	Edible roots, ecotypic variability (Rogers and Appan, 1973). Hybridizes easily with cassava, produces enlarged roots (Nassar, 2004a)	Abundant	
	M. angustiloba (Torrey) Mueller von Argau	Mexico (Sonora, Chihuahua, Sinaloa, Baja California); USA (Arizona, Novo Mexico)	Erect shrubs (1-3 m), it grows in various habitats; leaf lobes more than 12 cm; seeds more than 1.25 cm long; fruit dehiscence loculicidal	Strong odor of HCN in all parts of the plant (Rogers and Appan, 1973)	Abundant	
	M. subspicata Rogers & Appan	Mexico (Coahuila, Nuevo Leon Tamaulipas)	Sprawling shrubs (1 m), it grows in limestone based, loose and rocky soil; inflorescence a subspicate raceme; secondary leaf lobe apices often dilated	Potencial to colonize disturbed areas, strong odor of HCN in the roots (Rogers and Appan, 1973)	Abundant	 

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Table 1. Continued.

Sections	Species	Habitat	Specific characters	Economic value	Danger of extintion/conservation	Photos of some cassava specie
Foetidae	*M. foetida* (Humbolt, Bonpland & Kunth) Pohl	Mexico	Tall trees, the largest seeds of genus; mature stems reddish brown; leaves constantly 3 lobed; median lobes obovate; ovary tomentose	Edible seeds (Nassar, 1984)	Endangered	
Carthaginenses	*M. carthaginensis* (Jacquin) Mueller von Argau	West Indies; Colombia; Venezuela; Trinidad and Tobago	Erect, tall shrubs (1.5 m) to small trees (5 m); root system not significantly spreading laterally; filaments less than 1.0 cm long	Source of tolerance to drought (Rogers and Appan, 1973)	Abundant	

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