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## 1.1 THE PRIMARY GENE POOL OF CASSAVA (*MANIHOT ESCULENTA* CRANTZ)

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### ABSTRACT

A crop gene pool comprises three distinct categories of gene suppliers, primary, secondary, and tertiary gene pools. The primary gene pool (GP-1) is composed of gene reservoirs that cross easily with the domesticate and the crosses produce fertile offspring regularly. The secondary (GP-2) and tertiary (GP-3) gene pools comprise gene sources that cross with variable degrees of difficulty with the crop species, this implies less close genetic distances. The GP-1 is further subdivided in cultivated and wild gene pools. The cultivated gene pool englobes comercial stocks of the crop besides indigenous landraces and folk varieties of the domesticate. The wild GP-1 of a 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*) are natural members of the wild GP-1 of the species. Another Brazilian species (*M. pruinosa*) is so close morphologically to the two wild subspecies of cassava that it may turn out another member of the wild GP-1 of the indigen. The GP-2 of cassava is more difficult to delimit as few species have been tested for genetic compatibility. Biosystematic crosses carried out between the crop and a number of wild species suggest a dozen of them as components of the GP-2, the majority are Brazilian species.

### INTRODUCCION

Studies on the origin of crop species may involve different disciplines. This fact tends to create interdisciplinary interactions. The aftermath is an expansion of knowledge of the concerned subject.

Such an interchange happened for cassava and enlightened the subject of its origin. Three major areas contributed relevant inputs related to the botanical origin of the crop. 1. Taxonomy, with the definition of the taxonomic species; 2. Biosystematics, through interspecific crosses, with the definition of the biological species (gene pools); 3. Molecular genetics, with the definition of the cladistic species.

There have been many hypotheses on the origin of cassava, the first ones were advanced by Pohl (1827), Mueller (1874), and de Candolle (1884). The three suggested Brazil as the likely place of origin of manioc. Their reasoning concentrated on the original place of domestication of the crop. Speculations on the cradle of the crop (place of initial domestication) accounted for most of the publications on the issue over the last one hundred and fifty years.

The information that cassava does have an origin (Allem, 1994) prompted a renewed surge of interest in the area with different writers testing the novel hypothesis. Molecular studies and biosystematic trials produced a more comprehensive insight of the issue besides securing proper scientific perspective of the controversial subject. The result was a gradual lessening of dissent from the mainstream as the expanding knowledge tended to shape consensual synthesis.

## MATERIALS AND METHODS

The study reviewed the 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 anthropology) were not included in the revision. The combined use of the select compilation meant merely at strengthening the case on the origin of cassava, this implying that the taxonomic point of view runs independently. The study discusses the species concept. Although five categories of species have been proposed (Grant, 1981), the review focuses on two classes of species only, the taxonomic species concept (MSC) and the biological species concept (BSC).

## RESULTS

**The taxonomic species concept.** Over thirty authors proposed several places of the neotropic where cassava could have been domesticated first.

Inferences on the ancient cradle were however dependent on the discovery of the botanical origin of the crop. Once discovered a putative living wild ancestor, this might lead to sound inferences as to the area (or areas) where domestication by Amerindians took place. Crop origins are often solved when there happens the find of an ancestor, this normally equating to the existence of a morphological species. This materialized for cassava with the recent hypothesis (Allem, 1994) that the crop is composed of three taxa and descends from two wild plants relatively common in much of Amazonia. The classification divided cassava into three subspecies, *M. esculenta* Crantz ssp. *esculenta* (all cultivated genotypes), *M. esculenta* Crantz ssp. *flabellifolia* (Pohl) Ciferri and *M. esculenta* ssp. *peruviana* (Muell. Arg.) Allem, the latter two wild plants. The 1994 proposal had to be verified as to the question: "is it true?". Two distinct methodologies were available to test the hypothesis, biosystematic crosses and molecular markers.

**The biological species concept.** The BSC defines that the species is 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; Mayr, 1940). The concept was continuously perfected by Mayr (1969, 1982, 1992) 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 its fertility status relative to another genepool, this underlined the cytogenetic component of the BSC.

Application of the BSC to flowering plants could result in huge amounts of nameless variation, the result would be chaos (Harlan 1970). The concept has been however of much use in the realm of cultivated plants (Baker 1970) besides plant breeding, where it is much utilized under the names of primary, secondary and tertiary gene pools (Harlan and 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 became the foundation of the primary and secondary gene pools of cassava.

The hypothesis that *M. flabellifolia* Pohl is 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 recorded very good results (Table 1). Further crosses between the crop and the ancestor took place in Java in the interval

**Table 1.** Results of crosses between cassava, three *Manihot* species and a hybrid in Tanzania. Source: Nichols (1947).

Female Parent	Male Parent	Flowers Pollinated	Seeds Expected	Seedlings Obtained	Success (%)
<i>M. glaziovii</i>	<i>M. esculenta</i>	83	249	1	0.4
<i>M. esculenta</i>	<i>M. glaziovii</i>	370	1110	20	1.8
<i>M. dichotoma</i>	<i>M. esculenta</i>	50	150	16 <sup>1</sup>	10.7
<i>M. esculenta</i>	<i>M. dichotoma</i>	296	888	16	1.8
<i>M. esculenta</i>	<i>M. esculenta</i> x <i>dichotoma</i>	250	750	3 <sup>2</sup>	0.4
<i>M. esculenta</i> x <i>dichotoma</i>	<i>M. esculenta</i>	NA	NA	NA	NA
<i>M. saxicola</i>	<i>M. esculenta</i>	NA	NA	13 <sup>3</sup>	NA

1. F1 generation sterile.

2. One individual fully sterile, another fully fertile, and another pollen sterile.

3. F1 hybrids flowered prolifically and showed high fruit-set and seed-set.

1942-1949 (Bolhuis, 1953). The results were so exceptional (Table 2) that drew the writer's comment: "particularly striking is the high percentage of success which is far in excess of the percentages found in crosses within the species *M. utilissima* (= *M. esculenta*). It makes it even questionable as to whether *M. saxicola* is sufficiently different from *M. utilissima* to consider it as a separate species, since both crosses have such a high percentage of success" (Bolhuis, 1969:84). Cassava and its 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' (1959:158; 161): "the fertility

**Table 2.** Results of crosses between cassava and *Manihot saxicola* in Indonesia between 1942-1949. Source: Bolhuis (1969).

Female Parent	Male Parent	Flowers Pollinated	Fruit-Set	Success %	Seed-Set	Success %
<i>M. saxicola</i> <sup>1</sup>	<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*.

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 3).

**Table 3.** Results of crosses between cassava and *Manihot melanobasis* in Tanzania around 1955. Source: Jennings (1959).

Female Parent	Male Parent	Flowers Pollinated	Seed-Set	Success %
<i>M. melanobasis</i> <sup>1</sup>	<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.

The combined results in Africa and Asia strongly suggested that the wild species 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 (1947:188) summarized the matter thus: “low seed fertility is a striking feature within this species” (Table 4). Likewise, Bolhuis (1969) concluded that intraspecific crosses with a percentage of success higher than 10% were rarely achieved (Table 5). Such a divergence within cassava is not restricted to differences in fertility relationships between genotypes. Genetic divergence has been reported for cultivars of cassava from Nigeria, Colombia, and Thailand (Schaal et al., 1995:65) and seeds of

**Table 4.** Results of crosses between cassava cultivars in Tanzania. Source: Nichols (1947).

Number of Crosses	Fertility (%)	Mean
27	zero to 56	13.6
32	zero to 55	14.6

distinct varieties of cassava show distinct physiological performances (Antonieta Salomão, pers. comm.).

**Table 5.** Results of crosses between cassava cultivars in Indonesia. Source: Bolhuis (1969).

Year	Pollinations	Seeds Expected	Seeds Harvested	Success %
1937	2344	7032	none	nil
1939	17689	53067	3588	6.7
1940	19565	58695	3672	6.2
1941	13969	41907	4307	10.2

Trials crossing cassava with other *Manihot* species offered the first insight on the GP-2 of the crop, i.e. crossing is possible but gene transfer may be difficult and F1 hybrids tend to be sterile besides frequently showing poor chromosome pairing or univalents (Harlan and de Wet, 1971). Nichols (1947) identified the Brazilian species *M. glaziovii* and *M. dichotoma* (Table 1). Bai et al. (1993) singled out seven Brazilian species (Table 6), one of them (*M. tristis*) standing out with above average figures (the species is now a synonym of the ancestor *M. flabellifolia*). Roa et al. (1997) crossed three species with cassava; once more, the ancestor of cassava gave the highest results and two Central American species qualified for the GP-2 of the crop (Table 7).

**The phylogeny of cassava (the cladistic species).** The MSC and the BSC defined for cassava became fairly convincing pieces of knowledge when their premises were taken together. The ultimate test on the origin of

**Table 6.** Results of crosses between two cassava cultivars and seven Brazilian *Manihot* species. Source: Bai et alii (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 <sup>1</sup>	878	32.46	27.26
TMS 42025	<i>M. tristis</i> - 39-3 <sup>1</sup>	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

cassava was however reserved for molecular genetics. Independent writers tested the hypothesis through the use of different markers. Overall results were supportive of the idea and fair to strong marks were conferred to the theory (Table 8).

**Table 7.** Results of interspecific crosses between cassava and three *Manihot* species. Source: Roa et alii (1997).

Female Parent	Male Parent	Crosses	Seed-Set
<i>M. esculenta</i> ssp. <i>flabellifolia</i> <sup>1</sup>	<i>M. esculenta</i> ssp. <i>Esculenta</i>	16	thousand <sup>2</sup>
<i>M. aesculifolia</i> <sup>3</sup>	<i>M. esculenta</i> ssp. <i>esculenta</i>	2	5
<i>M. chlorosticta</i> <sup>4</sup>	<i>M. esculenta</i> ssp. <i>esculenta</i>	14	1 to 148

1. It is the ancestor of cassava.

2. Crosses include backcrosses.

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

4. Mexican species; hybrid seeds showed strong dormancy.

**Table 8.** Molecular tests carried out to test the hypothesis on the origin of cassava.

SOURCE	MARKER	DEGREE OF SUPPORT [Allem's 1994 Hypothesis]
Carvalho et alii (1993)	RFLP/RAPD	fair (+)
Fregene et alii (1994)	CpDNA/rDNA	fair (-)
Carvalho et alii (1995)	RAPD	fair (+)
Schaal et alii (1995)	rDNA/RAPDs	fair (-)
Brondani (1996)	ISOZYMES	strong (+)
Schaal et alii (1997)	RAPDs	strong (-)
Second et alii (1997)	AFLP	fair (-)
Roa et alii (1997)	AFLP	strong (+)
Olsen and Schaal (1998)	NUCLEAR DNA	strong (+)
Cabral et alii (1998)	SSRs	strong (+)
Second (1998)	RFLP	strong (-)
Roa et alii (1998a)	AFLP	strong (+)
Roa et alii (1998b)	SSRs	strong (+)

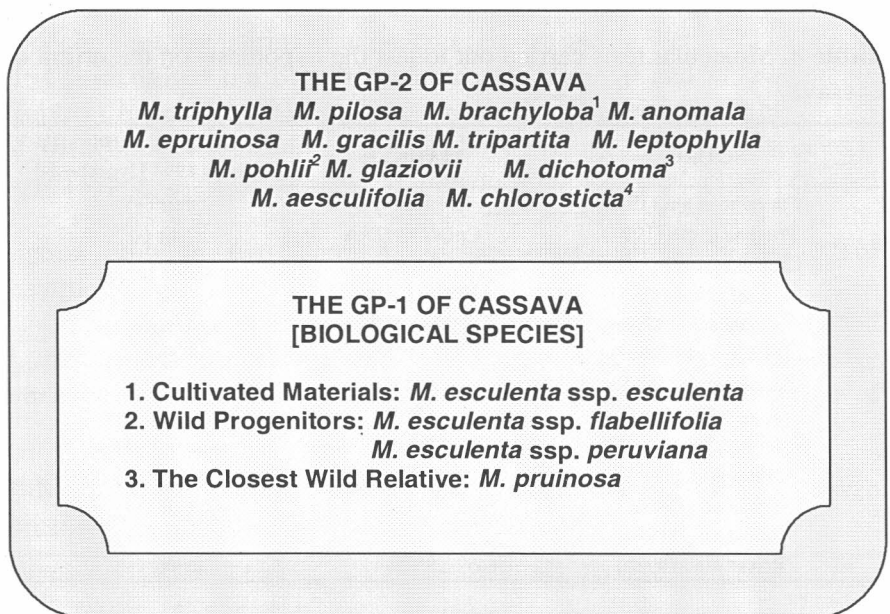
## DISCUSSION

Research on degrees of crossability between cassava and wild species was decisive in establishing the primary gene pool of the crop, this ultimately contributed to tracing more firmly the origin of cassava. A further link was established when genetic markers bound the cladistic species and the biological species: "the species relationships illustrated by AFLP are supported by preliminary data on crossability" (Roa et al., 1997:748).

Convergent morphological, biosystematic, and molecular results strengthened the hypothesis on the origin of cassava. The combination of different fields equated to a synthesis of knowledge.

*Manihot esculenta* subspecies *flabellifolia*, the wild ancestor, is an example that the biological species and the taxonomic species may eventually coincide in their circumscriptions.

Interspecific crosses offered a view on how fertility relationships are structured in the genus. This enabled the build-up of the GP-1 and GP-2 of cassava (Figure 1). The dendrogram of cassava and its closest allies (Allem, 1995) can now be upgraded to a phenogram. Because the hypothesis on the phylogeny of cassava is strongly backed by molecular data, the phenogram virtually amounts to an evolutionary cladogram (Figure 2).



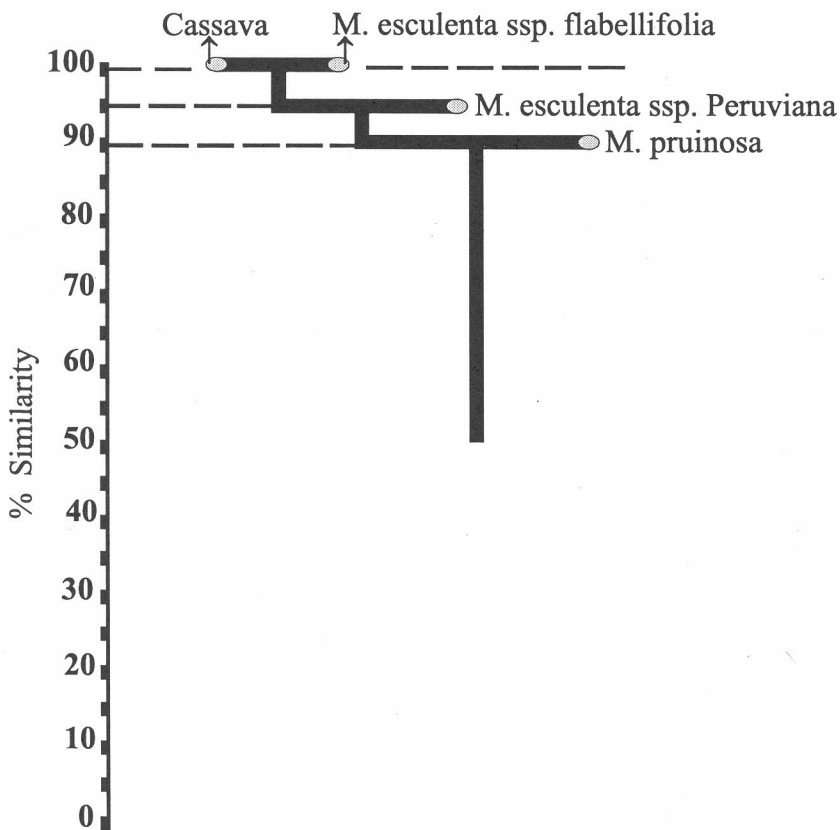
**Figure 1.** The GP-1 and GP-2 of cassava. <sup>1</sup>These three species suggested by Allem (in press). *M. triphylla* is closer to cassava than *M. esculenta* ssp. *peruviana* and *M. pilosa* (Cabral et al., 1998). If biosystematic crosses confirm the molecular results, *M. triphylla* may join the wild GP-1 of the crop.

<sup>2</sup>These six species deduced from Bai et al. (1993).

<sup>3</sup>These two species deduced from Nichols (1947).

<sup>4</sup>These two species deduced from Roa et al. (1997).





**Figure 2.** Phenogram of cassava and its closest allies and deduced phylogenetic relationships between species. <sup>1</sup> *M. pruinosa* has been suggested as a putative member of the wild GP-1 of cassava (Allem, in press). Preliminary molecular studies supported the view (Second et al., 1997; Olsen and Schaal, 1998).

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## REFERENCES

- Allem A.C. 1994. The origin of *Manihot esculenta* Crantz (Euphorbiaceae). Genetic Resources and Crop Evolution 41:133-150.
- Allem A.C. 1995. Evolutionary relationships of Brazilian *Manihot* species.

- Lecture delivered at the “*Manihot* taxonomy and conservation workshop” held at CIAT, Cali, Colombia, 7-11 November 1995 (unpublished).
- Bai K.V., Asiedu R. & Dixon A.G.O. 1993. Cytogenetics of *Manihot* species and interspecific hybrids. In: Roca, W.M. and Thro, A.M. (eds.) 1993. Proceedings of the First International Scientific Meeting of the Cassava Biotechnology Network, pp.51-55, Cartagena, Colombia, 25-28 August 1992. Cali, Colombia: Centro Internacional de Agricultura Tropical, 1993. Working Document no.123.
- Baker H.G. 1970. Taxonomy and the biological species concept in cultivated plants. In: Frankel, O.H. and Bennett, E. (eds.) 1970. Genetic Resources in Plants: their Exploration and Conservation, pp.49-68. IBP Handbook n.11. Blackwell, Oxford.
- Bolhuis G.G. 1953. A survey of some attempts to breed cassava varieties with a high content of protein in the roots. *Euphytica* 2:107-112.
- Bolhuis G.G. 1969. Intra and interspecific crosses in the genus *Manihot*. In: Proceedings of the First International Symposium on Tropical Root Crops, 1967, pp.81-88. University of the West Indies. St. Augustine, Trinidad.
- Brondani C. 1996. Variação isoenzimática de três espécies do gênero *Manihot* (Euphorbiaceae) relacionadas morfológicamente à mandioca (*Manihot esculenta* Crantz). *Pesq. agropec. bras.* 31:287-289.
- Cabral G.B., Carvalho L.J.C.B. & Schaal B.A. 1998. Relationship analysis of closely related species to cassava (*Manihot esculenta* Crantz) based on microsatellite-primed PCR. (Proceedings of the Fourth Scientific Meeting of the Cassava Biotechnology Network, in press).
- Carvalho L.J.C.B., Cascardo J.M.C., Limeira P.S., Ribeiro M.C.M. & Fialho J.F. 1993. Study of DNA polymorphism in *Manihot esculenta* Crantz and related species. In: Roca, W.M. and Thro, A.M. (eds.) 1993. Proceedings of the First International Scientific Meeting of the Cassava Biotechnology Network, pp.56-61, Cartagena, Colombia, 25-28 August 1992. Cali, Colombia: Centro Internacional de Agricultura Tropical, 1993. Working Document no.123.
- Carvalho L.J.C.B., Buso G.M.C., Brondani C., Allem A.C., Fukuda W.M.G. & Sampaio M.J.A.M. 1995. Study on interspecific evolutionary relationships and intraspecific characterization of cassava germplasm at Cenargen/Embrapa. In: Thro, A.M. (ed.) 1995. Proceedings of the Second International Scientific Meeting of the Cassava Biotechnology Network, pp.163-174, Bogor, Indonesia, 22-26 August 1994. Cali,

- Colombia: Centro Internacional de Agricultura Tropical, 1995. Working Document no. 150.
- de Candolle A. 1884. Origin of cultivated plants. Kegan Paul, Trench, London.
- Dobzhansky, T. 1937. Genetics and the origin of species. Columbia University Press, New York.
- Fregene M.A., Vargas J., Ikea J., Angel F., Tohme J., Asiedu R.A., Akoroda M.O. & Roca W.M. 1994. Variability of chloroplast DNA and nuclear ribosomal DNA in cassava (*Manihot esculenta* Crantz) and its wild relatives. Theor. Appl. Genet. 89:719-727.
- Grant V. 1981. Plant speciation. 2nd. ed. Columbia University Press, New York.
- Harlan J.R. 1970. Evolution of cultivated plants. In: O.H. Frankel and E. Bennett (Eds), Genetic Resources in Plants: their Exploration and Conservation, pp.19-32. Blackwell, Oxford.
- Harlan J.R. & de Wet J.M.J. 1971. Towards a rational classification of cultivated plants. Taxon 20:509-517.
- Jennings D.L. 1957. Further studies in breeding cassava for virus resistance. East Afr. Agr. J. 22:213-219.
- Jennings D.L. 1959. *Manihot melanobasis* Muell. Arg. – a useful parent for cassava breeding. Euphytica 8:157-162.
- Jennings D.L. 1963. Variation in pollen and ovule fertility in varieties of cassava, and the effect of interspecific crossing on fertility. Euphytica 12:69-76.
- Mayr E. 1940. Speciation phenomena in birds. Amer. Nat. 74:249-278.
- Mayr E. 1969. The biological meaning of species. Biol. J. Linn. Soc. 1:311-320.
- Mayr E. 1982. The growth of biological thought: diversity, evolution, and inheritance. The Belknap Press of Harvard University Press, Cambridge. 974 p.
- Mayr E. 1992. A local flora and the biological species concept. Amer. J. Bot. 79:222-238.
- Mueller J. 1874. Euphorbiaceae. In: C.F.P. von Martius, Flora Brasiliensis 11(2):293-750.
- Nichols R.F.W. 1947. Breeding cassava for virus resistance. East Afr. Agr. J. 12:184-194.
- Olsen K.M. & Schaal B.A. 1998. Evolution in the cassava species complex: phylogeography and the origins of cultivated cassava. (Proceedings of the Fourth International Scientific Meeting of the Cassava Biotechnology Network, in press).
- Pohl, J.E. 1827. Plantarum Brasiliae icones et descriptiones. 1:1-136. Pls. 1-100. Vindobonae.
- Roa A.C., Maya M.M., Duque M.C., Tohme J., Allem A.C. & Bonierbale

- M.W. 1997.  
 AFLP analysis of relationships among cassava and other *Manihot* species. *Theor. Appl. Genet.* 95:741-750.
- Roa A.C., Maya M.M., Chavarriga P., Duque M.C., Mesa E., Bonierbale M.W., Tohme J., Kochert G. & Iglesias C. 1998a. In search of the closest relatives of cassava: a morphological and molecular approach. (Proceedings of the Fourth International Scientific Meeting of the Cassava Biotechnology Network, in press).
- Roa A.C., Chavarriga P., Duque M.C., Bonierbale M.W., Thome J., Kochert G. & Iglesias C. 1998b. Microsatellites as a tool for assessing genetic diversity in *Manihot* species. (Proceedings of the Fourth Scientific Meeting of the Cassava Biotechnology Network, in press).
- Schaal B., Olson P., Prinzie T., Carvalho L.J.C.B., Tonukari N.J. & Heyworth D. 1995. Phylogenetic analysis of the genus *Manihot* based on molecular markers. In: Thro, A.M. (ed.) 1995. Proceedings of the Second International Scientific Meeting of the Cassava Biotechnology Network, pp.62-70, Bogor, Indonesia, 22-26 August 1994. Cali, Colombia: Centro Internacional de Agricultura Tropical, 1995. Working Document no. 150.
- Schaal B., Carvalho L.J.C.B., Prinzie T., Olsen K., Hernandez M., Cabral G. & Moeller D. 1997. Phylogenetic relationships and genetic diversity in *Manihot* species. *African Journal of Root and Tuber Crops* 2(1-2):147-149.
- Second G., Allem A.C., Mendes R.A., Carvalho L.J.C.B., Empeaire L., Ingram C. & Colombo, C. 1997. Molecular markers (AFLP)-based *Manihot* and cassava numerical taxonomy and genetic structure analysis in progress: implications for their dynamic conservation and genetic mapping. *African Journal of Root and Tuber Crops* 2(1-2):140-147.
- Second G. 1998. *Manihot glaziovii*, an example for a proposed dynamic conservation of cassava genetic resources. (Proceedings of the Fourth International Scientific Meeting of the Cassava Biotechnology Network, in press).