

CONSERVATION OF THE GENETIC RESOURCES OF CASSAVA (*MANIHOT ESCULENTA*) DETERMINATION OF WILD SPECIES LOCALITIES WITH EMPHASIS ON PROBABLE ORIGIN

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Wild species of Manihot are progenitors of cassava. They constitute valuable genetic reservoirs with genes of new characters. Study of geographic distribution of wild Manihot species showed concentration of wild species in a number of centers in South and Central America. Considering Vavilov's concept of centers of diversity based on the Age and Area hypothesis of Willis, and Harlan's theory of Introgression, and by studying Indian immigrations in Pre-Columbian times, it is assumed that northern Amazonia is the place of domestication of cassava and that Goiás is the primary center of diversity of Manihot species as a "biological group".

Many reports have referred to wild species of *Manihot* as carriers of useful characters that do not exist in cassava (*M. esculenta* Crantz). Resistance to mosaic and high protein content have been discovered in *M. glaziovii* and *M. tristis* var. *saxicola*, respectively (Nichols, 1947; Bolhuis, 1953). It seems that there is a richness of useful genes in wild *Manihot* species still not discovered. At the same time, these wild species are threatened by extinction, due to changes of environment and destruction of their natural habitats. Frankel and Bennett (1970) reported extinction of many wild species in different places, some wild *Triticum* from Palestine and African rice from West Africa. Thus, it is obviously essential to collect wild species of *Manihot* and maintain them in cultivation.

MATERIALS AND METHODS

From May to July 1975 I made a trip to northeastern Brazil to collect seeds of wild species of *Manihot*. The trip covered three states: Pernambuco, Ceará and Bahia. Geographical distribution of *Manihot* species was

studied in Roger and Appan (1973) and in Martius' Flora Brasiliensis (1874). *Manihot* specimens collected by the expedition of Reading University and deposited at IPA herbarium Recife were also examined.

RESULTS AND DISCUSSION

Table I lists the wild species of *Manihot* that were collected from different localities of northeastern Brazil. Localities of the species are indicated in Maps 1, 1a, 1b, and 1c. It is apparent that western Pernambuco and central Bahia have the greatest variability in *Manihot*. It may be worthy of mention here that certain species reported by Reading University Expedition to occur in some localities could not be collected from these places. An example: specimens of *M. glaziovii* collected from about 12 km west of Ibimirim, PE. Unfortunately, it was found that vegetation in that place had been cleared and the land cultivated by mamona. Unlike most *Manihot* species, *M. glaziovii* grows in large numbers and not as sporadic plants. Extinction of some wild *Manihot* species from their rural habitats may be due to another factor. The majority of these species are poisonous to grazing animals because of the presence of HCN. They are known among people of "Nordest" as "maniçoba", i.e., the poisonous cassava. Because of this fact, many plants are exterminated by farmers.

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TABLE I
Wild Species of *Manihot* Collected from Different
Localities in Northeastern Brazil

Species	Locality
<i>M. caerulea</i> Pohl	Araripina, PE
<i>M. heptaphylla</i> Ule	Seabra, BA
<i>M. dichotoma</i> Ule	Jequie, BA
<i>M. catingae</i> Ule	Itaberaba, BA
<i>M. brachyandra</i> Pax et Hoffmann	Petrolina, PE
<i>M. maracasensis</i> Ule	Itambé, BA
<i>M. epruina</i> Pax et Hoffmann	Belmonte, BA
<i>M. pseudoglaziovii</i> Pax et Hoffmann	Pentecoste, Fortaleza, CE
<i>M. glaziovii</i> Mueller	Arcoverde, Ouricuri, Serratalhada, PE
<i>M. jacobinensis</i> Mueller	Vitoria da Conquista, BA
<i>M. quinquefolia</i> Pohl	Senhor do Bonfim, Juazeiro, BA

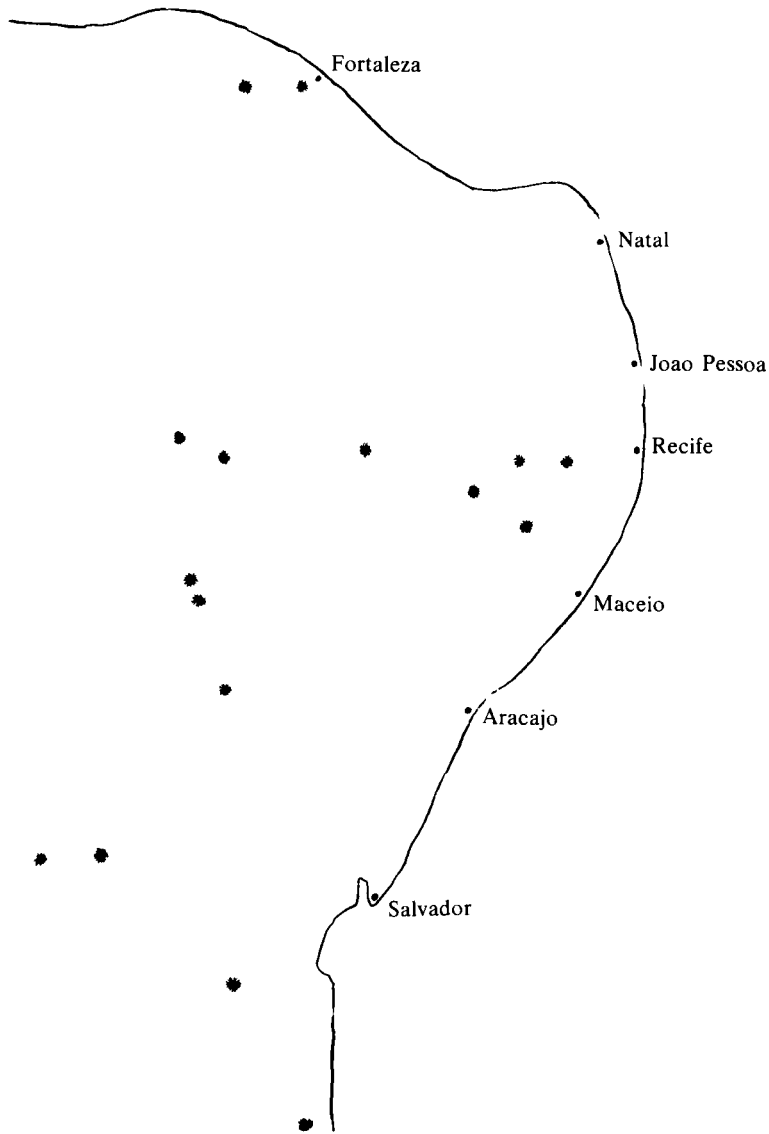
By studying geographic distribution of *Manihot* species in both Rogers & Appan (1973) and Martius (1874) combined with localities determined on this trip, it became possible to present a map of concentration of wild species (Map 2, 2a). It shows that central Brazil (southern Goias and western Minas Gerais) has about 38 wild species of the total 98 species recognized. Thus, this region includes the largest number of wild *Manihot* species and represents the highest diversity. In this region the following species occur:

M. acuminatissima Mueller
M. sparsifolia Pohl
M. pruinosa Pohl
M. alutacea Rogers et Appan
M. divergens Pohl
M. cecropiaefolia Pohl
M. triphylla Pohl
M. pentaphylla Pohl
M. anomala Pohl
M. procumbens Mueller
M. crotalariaeformis Pohl
M. pusilla Pohl
M. longepetiolata Pohl
M. tomentosa Pohl
M. purpureo-costata Pohl
M. attenuata Mueller
M. orbicularis Pohl
M. tripartita (Sprengel) Mueller
M. pilosa Pohl
M. sagittato-partita Pohl
M. falcata Rogers et Appan
M. quinqueloba Pohl
M. violacea Pohl

M. irwinii Rogers et Appan
M. mossamedensis Taubert
M. fruticulosa (Pax) Rogers et Appan
M. gracilis Pohl
M. warmingii Mueller
M. reptans Pax
M. stipularis Pax
M. oligantha Pax
M. nana Mueller
M. stricta Baillon
M. salicifolia Pohl
M. weddelliana Baillon
M. peltata Pohl
M. janiphoides Mueller
M. handroana N. D. Cruz

The second center of diversity is southwestern Mexico. It includes

M. pringlei Watson
M. aesculifolia Pohl
M. oaxacana Rogers et Appan
M. rhomboidea Mueller
M. walkerae
M. walkerae Croizat
M. divisiae Croizat
M. michaelis McVaugh
M. websterae Rogers et Appan
M. auriculata McVaugh
M. rubricaulis I. M. Johnson
M. chlorosticta Standley & Goldman
M. subspicata Rogers et Appan
M. caudata Greenman
M. angustiloba (Torrey) Mueller
M. tomatophylla Standley
M. foetida Pohl



Map. 1. (*) Localities of *Manihot* species collected from northeastern Brazil.

The third center of diversity is north-eastern Brazil, which includes

M. zentneri Ule
M. surinamensis Rogers et Appan
M. quinquefolia Pohl
M. pseudoglaziovii Pax et Hoffmann
M. maracasensis Ule
M. catingae Ule
M. brachyloba Mueller
M. quinquepartita Huber
M. caerulescens Pohl
M. marajoara Chermont de Miranda

M. tristis Mueller
M. glaziovii Mueller
M. epruinosa Pax et Hoffmann
M. brachyandra Pax et Hoffmann
M. dichotoma Ule
M. leptophylla Pax
M. reniformis Pohl
M. heptaphylla Ule

Fourth center of diversity is western South Mato Grosso and Bolivia. It includes the following species:



Map 1a. Localities of *Manihot* species in Ceara state. (*) Collected samples; *M. pseudoglaziovii* (centro Agronomico, Fortaleza, sides of Federal Road 90 km W Fortaleza to Itapaje and from Experimental Station at Pentecoste).

M. guaranitica Choda et Hassler
M. pruinosa Pohl
M. jacobinsis Mueller
M. condensata Rogers et Appan
M. xavantinsis Rogers et Appan
M. flemingiana Rogers et Appan

Vavilov (1920) showed that variation in cultivated plants is confined to relatively few restricted areas or centers. He set up (1920) six main geographic centers for cultivated plants and later (1935) increased their number to about ten. He assumed that cassava has its center of diversity in the Brazilian-Bolivian center. Vavilov proposed that centers of diversity are places of origin of cultivated plants. Since this exposition of centers of

diversity in the 1920's, much more information has been gathered, and it has become clear that not all centers of diversity represent centers of origin.

Thanks to Harlan (1961), it was shown that more than one center of diversity may be formed for a given crop through introgression. This phenomenon explained why in many cases we find centers of diversity for a given crop very far from areas of much diversity of wild relatives. Since Harlan proposed this theory (giving a convincing example of the evolved species of *Helianthus*) much evidence has supported it. Dobzhansky (1973) stated many conspicuous cases, such as formation of species of *Iris*, *Eucalyptus*, *Liatris*, *Penstemon*,



Map 1b. Localities of *Manihot* species in Pernambuco state. *M. glaziovii*: side of road Fazenda Nova-Caruaru, 3 km E Arcoverde in direction of Resquera and 2 km NE Serratalhada. *M. brachyandra*: arredores de Petrolina. *M. caerrulescens*: roads of Experimental Station of IPA at Araripina.

and *Tragopogon*.

Thus, this phenomenon serves as a model for what apparently happened in formation of these four centers of diversity of *Manihot*. Assuming that cassava was domesticated for the first time in one place, then carried by Indians through their immigrations, there could then result an extensive hybridization between the cultivated species and local wild ones, giving rise to numerous new species through introgression.

Cassava does not grow wild. The large variation of cassava cultivars due to maintaining them by vegetative reproduction over hundreds of years makes it difficult to designate definite characters for *M. esculenta*. Thus, it is believed that this species did not arise by natural selection. Hybrids between some wild species may have been domesticated and maintained afterwards through vegetative reproduction. Surely if these cultivars were left to sexual reproduction and left subjected to natural selection, it would have led to different populations with specific gene pools depending mainly on local environments.

Our assumption is that domestication included some natural hybrids and that the selected plants were maintained by vegetative

reproduction for hundreds of years. This assumption is supported by the fact that many experimental crosses and observations led to frequent hybridity of cultivars of *M. esculenta* and local wild species (Abraham, 1975; Bolhuis, 1953; Cruz, 1968; Jennings, 1957; Lanjouw, 1939; Magoon et al., 1966; Nichols, 1947). It seems that in this genus systems of genetic and cytologic barriers are not yet well established. Another support may come from Schmidt's (1951) statement about the very rapid response of selection in different wild species to increase starch content in tubers and tuber formation through low number of generations. It seems that many different wild species have the potentiality to increase tuber formation and starch content. I observed two tree species of *Manihot* (*M. epuinosa* and *M. brachyandra*) frequently grown in door-yards at Goiania with considerable tuber production. These two species are natives of Bahia. It seems that they were carried by people of this state immigrating to central Brazil. This immigration was common during the last thirty years due to the rapid development of Goias. This assumption that domestication included hybrids and did not include a certain wild species has been referred to by Rogers (1963),



Map 1c. Localities of *Manihot* species in Bahia state.

M. heptaphylla: 1 km N Seabra.

M. maracasensis: 4 km E Itambe on sides of F. Road.

M. quinquefolia: 9 km N Senhor do Bonfim and 5 km W Juazeiro.

M. jacobinensis arredores da Vitoria da Conquista.

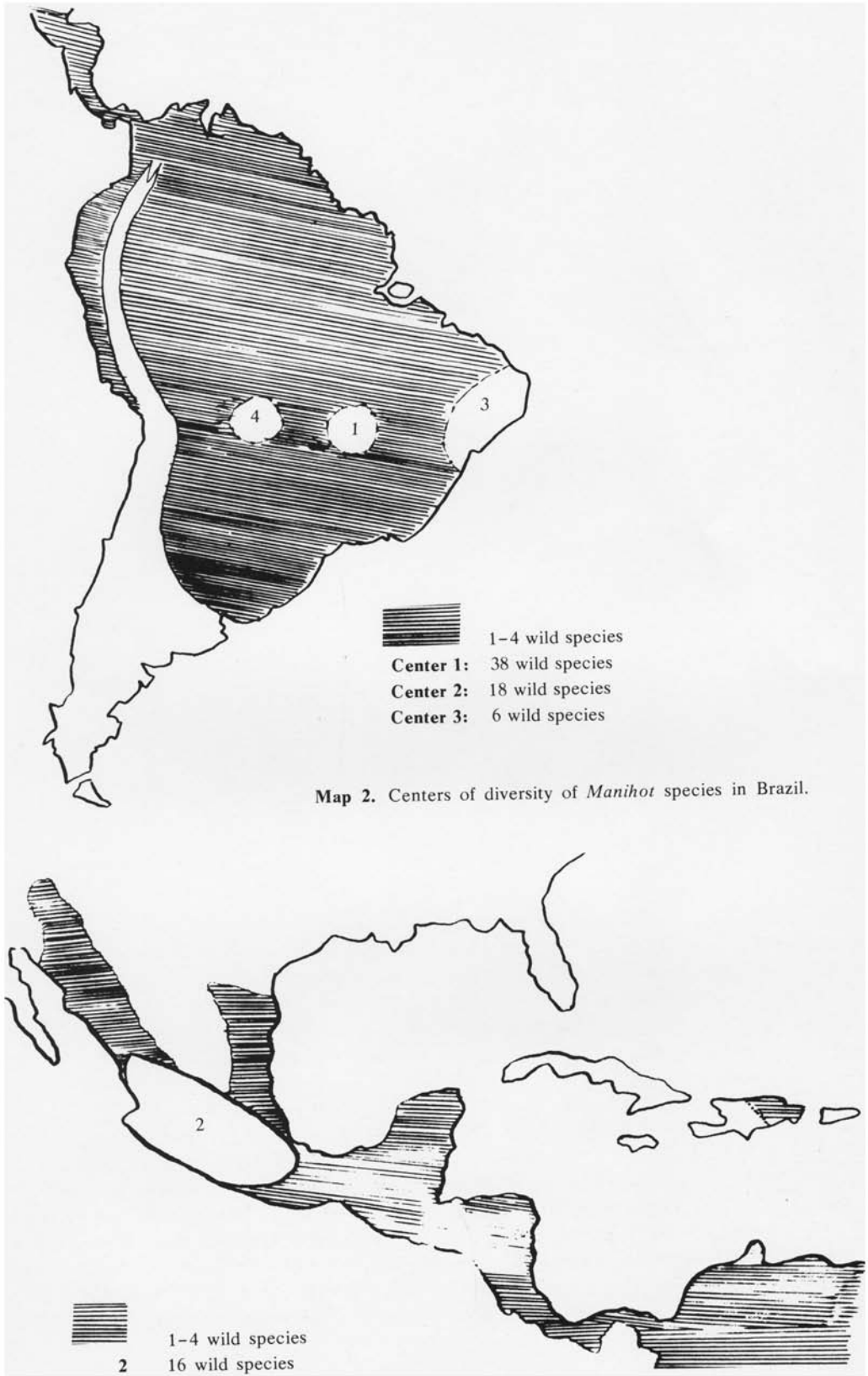
M. dichotoma: 6 km NW Jequie on sides of Estad. Road.

M. epruinosa: 3 km W Experimental Station of CEPLAC.

using the expression “species complexity”.

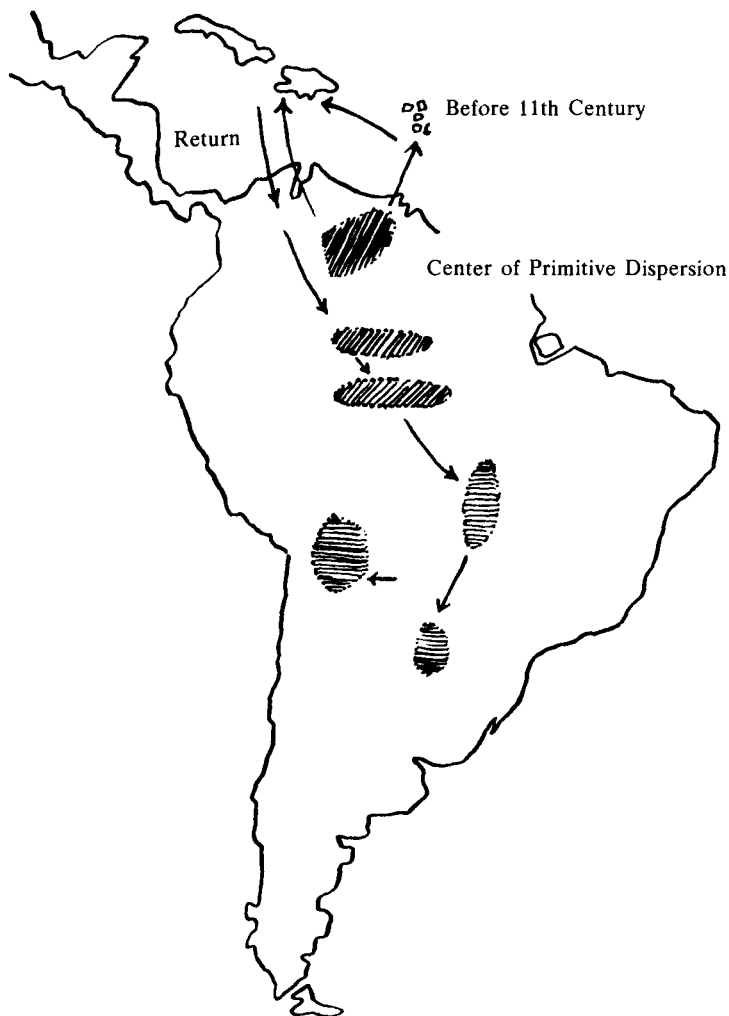
The place of domestication still needs much discussion. I prefer to use “place of domestication” and not “center of origin”, as it is obvious that this crop has not been brought to existence as a wild species by means of natural selection. Studying the history of ethnological groups in Brazil and their immigrations throws light on the subject. It is reported that the Aruak who lived in North Amazonia more than a thousand years ago (Schmidt, 1951) knew cassava and practised a developed agri-

culture. Their name in the Indian language means “people who eat tubers”. It is seen from numerous reports that they cultivated cassava many centuries before Columbus. The Aruak were obliged to immigrate in the 11th century (Map 3) to Central America, crossing the Caribbean and establishing themselves for some time in the West Indies. Many reasons were given to explain their immigration — probably escaping from enemies; possibly looking for a place where man does not die. But the most important reason given was that



Map 2. Centers of diversity of *Manihot* species in Brazil.

Map 2a. Center of diversity of *Manihot* spp. in Mexico. (After Rogers & Appan, 1973.)

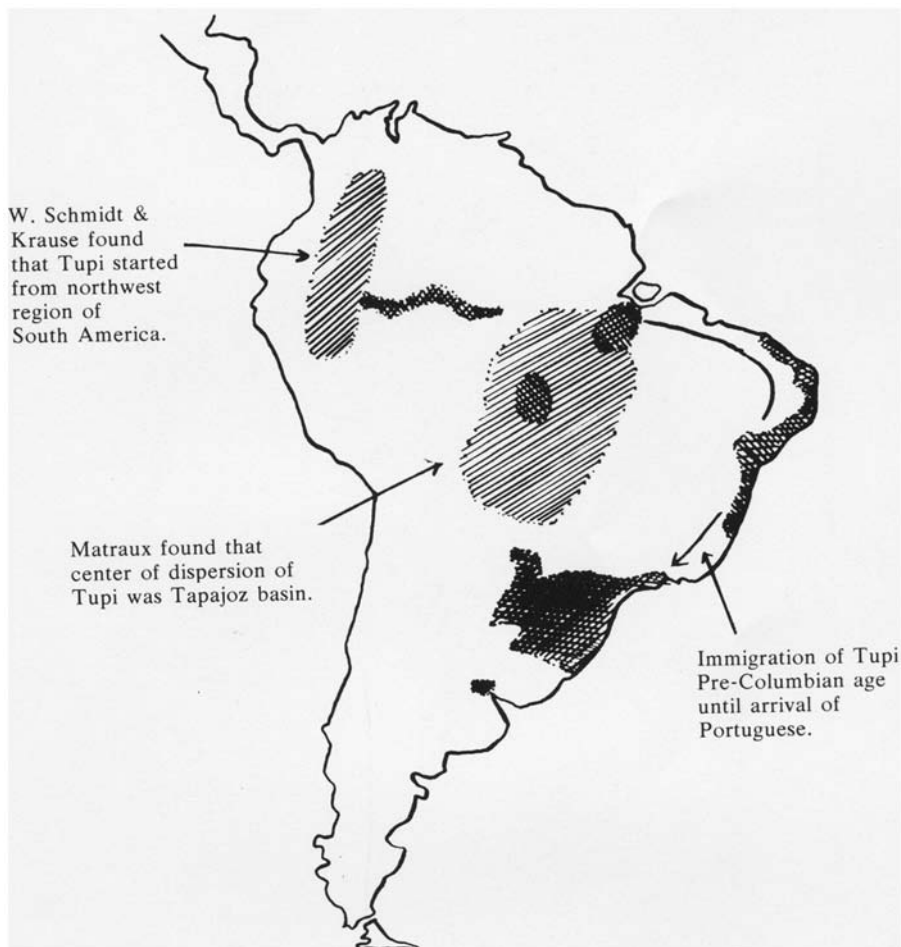


Map 3. Immigrations of the Aruak. (After Schmidt, 1951.)

they were searching for a better soil to cultivate cassava. However, this immigration coincides with the formation of a center of diversity of Mexico. Cassava carried by the Aruak to Mexico would be expected to hybridize with local wild species creating a center of diversity. The fact of the Aruak continuing on to the Planalto Boliviano and to central Brazil agrees with the existence of the two centers of diversity in these regions (Map 3). The northeastern Brazilian center of diversity is believed to be the result of immigration of the Tupi-Guarani group (Map 4).

We must still determine which of these four centers constitutes the primary center of diversity of *Manihot*. In other words, *Manihot*

as a "biological group" must have passed their differentiation in a certain region from which species spread to other regions. It could seem that central Brazil with its enormous number of species of *Manihot* is the primary center. Indeed, this region is an ancient area long available for growth of the angiosperms (Map 5). Considering Stebbins' explanation (1950) of Vavilov's interpretation of diversity patterns may be useful here: that Vavilov's concept is an elaboration of Willis' Age-and-Area hypothesis, i.e., that the longer a given biological entity occupies an area, the more variability it will produce. Thus this region, with its enormous variability of *Manihot* species, might constitute its primary center of

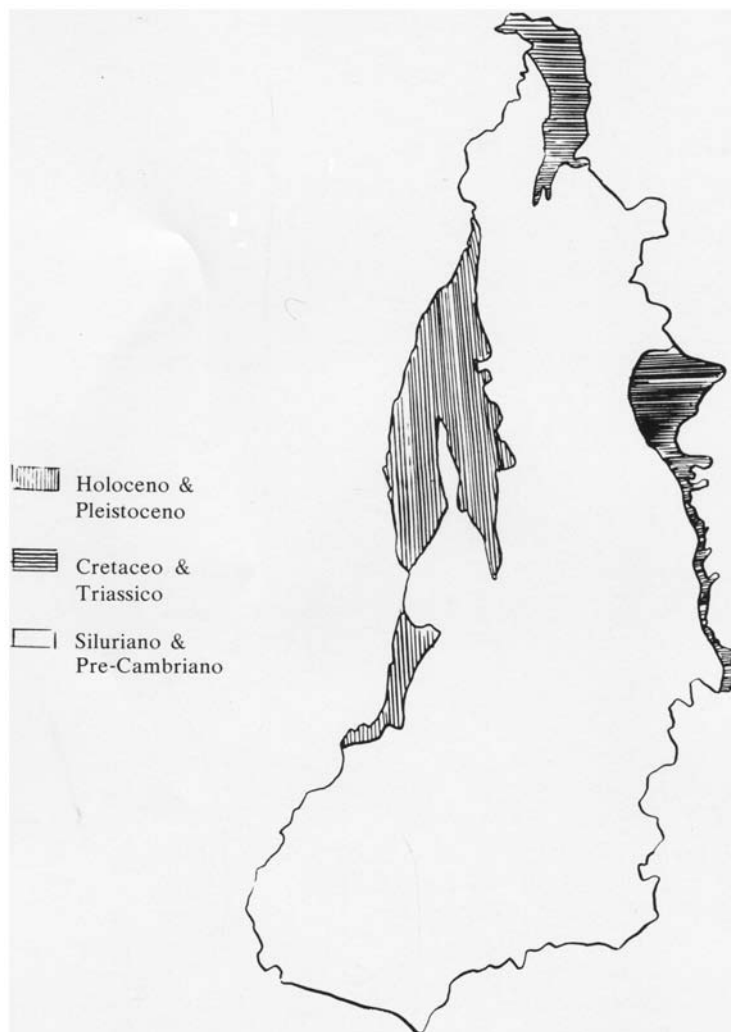


Ma. 4. Immigrations of Tupi-Guarani. Area of dispersion of tribes Tupi in the early 11th century. (After Schmidt, 1951.)

diversity. This assumption finds support in the fact that species which exhibit the most primitive characters are restricted to this region: *M. stipularis* Pax, *M. pusilla* Pohl, *M. longipetiolata* Pohl with their dioecious inflorescences and *M. stricta* Baillon, *M. purpureo-costata* Pohl and *M. salicifolia* Pohl with their nonlobed and sessile leaves.

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Map 5. Geological map of the State of Goiás. (After "Secretaria do Planejamento e Coordenacao", Goiás 1967.)

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