

## 1492 AND THE LOSS OF AMAZONIAN CROP GENETIC RESOURCES. II. CROP BIOGEOGRAPHY AT CONTACT.<sup>1,2</sup>

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**Clement, C.R.** (*Instituto Nacional de Pesquisas da Amazônia, Cx. Postal 478, 69011-970 Manaus, AM, Brasil*). 1492 AND THE LOSS OF AMAZONIAN CROP GENETIC RESOURCES. II. CROP BIOGEOGRAPHY AT CONTACT. *Economic Botany* 53(2): 203-216. 1999. *Fifty seven percent of the 138 cultivated plant species present in Amazonia at contact probably originated in the Amazon Basin and another 27% originated in lowland northern South America. The relationship between probable indigenous human population density and resultant agricultural intensification and crop diversity is used to propose the existence of a mosaic of crop genetic resource concentrations in Amazonia at contact, including two centers of diversity, four outlying minor centers, and five regions of diversity. This methodology is extrapolated to present a synthesis of South American crop genetic biogeography at contact.*

1492 e a perda dos recursos genéticos da Amazônia. II. A biogeografia dos cultivos no momento de contato. *Cinquenta e sete por cento das 138 espécies cultivadas na Amazônia no momento do contato provavelmente originaram na bacia amazônica e mais 27% originaram nas terras baixas do norte de América do Sul. A relação entre a densidade populacional indígena hipotética e a intensificação agrícola e a diversidade genética dos cultivos resultantes é usada para propor a existência de um mosaico de concentrações de recursos genéticos na Amazônia no momento de contato, incluindo dois centros de diversidade, quatro centros periféricos menores, e cinco regiões de diversidade. A mesma metodologia é extrapolada para apresentar uma síntese da biogeografia da diversidade genética dos cultivos na América do Sul no momento de contato.*

Key Words: Amazonia, centers of diversity, regions of diversity, South America

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Seventy nine (57%) of the 138 crops cultivated or managed in lowland northern South America at contact probably originated in the Amazon Basin and another 37 crops (27%) in adjacent parts of lowland South America (Clement, 1999). This represents 45% of the total for the Americas and has been largely ignored by most students of Neotropical crop diversity. In this paper, an hypothesis of Amazonian crop biogeography at contact is presented to place Amazonian diversity squarely in an integrated South American context.

The centers of crop genetic diversity proposed by Vavilov (1992c) and his successors are often related to the presence of advanced societies. In South America, the prehistory of many of these societies and possible centers of crop genetic diversity associated with them are being discovered, although they are still far from completely known (Pearsall 1992). In Amazonia, however, little archeological work with modern methods has been done (Meggers 1988; Pearsall 1992). Because of the lack of architectural artifacts, the rapid post-contact population decline and small recuperation, the vigor with which the forest recolonizes areas that humans abandon, and the catastrophic loss of crop genetic resources in the last 500 years (see Clement 1999), it is difficult to identify concentrations of crop genetic diversity in Amazonia today. These difficulties also help explain why Amazonia has been overlooked as

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<sup>2</sup> Dedicated to Victor Manuel Patiño, one of Latin America's foremost economic and ethnobotanists and fellow student of crop origins, domestication and biogeography.

a cradle of crop diversity by everyone except Sauer (1952), who recognized that it contained diversity but did not proceed to identify it as a major region of diversity.

A center of crop genetic diversity in NW Amazonia was proposed recently (Clement 1989). This area appears to have relied more heavily on fruit crops than was the case elsewhere in the Americas at contact (Patiño 1963:21-52). The pejibaye (*Bactris gasipaes*), for example, may have been a staple crop in this region [this inference is based on its degree of domestication (Clement 1988) and its importance to many societies as seen in their legends, myths, festivities and calendars (Patiño 1992)], supplemented by cassava (*Manihot esculenta*) and maize (*Zea mays*). Annual crops are the familiar pattern in the temperate zone and the biases of early and current biogeographers, anthropologists and archeologists toward the familiar is probably yet another reason that Amazonia has been ignored.

Why is the NW Amazonian center visible today and others are not? Possible explanations include the fact that the northwest divides the areas of Spanish and Portuguese authority in Amazonia and was one of the most difficult to access during the early post-contact centuries. Consequently, although also severely impacted by disease, missionization, and later by the rubber boom, many of the indigenous peoples survived and preserved their crop genetic heritage better than elsewhere in Amazonia. The special characteristics of NW Amazonia are not widely replicated in other areas. Therefore, other methods, based on hypotheses about early historical demography, current ideas of societal organization as a function of demography, carrying capacity of the various Amazonian ecosystems, and current knowledge of crop diversity and distribution, must provide clues to the biogeography of Amazonian crops at contact.

In this paper I review early hypotheses about South American crop biogeography, suggest how indirect evidence can be marshalled to identify possible concentrations of crop genetic resources at contact, present a hypothesis of Amazonian crop biogeography at contact, and extrapolate the methodology to provide a synthesis for South America as a whole. These hypotheses are all testable by archeological methods.

### **HYPOTHESES ON SOUTH AMERICAN CROP BIOGEOGRAPHY**

In this short review, I concentrate exclusively on South America. All of the authors mentioned, except Clement (1989) and Giacometti (1992), presented world-wide analyses and hypotheses, and all were also interested in the origins of agriculture. As far as possible, I avoid their discussion of the latter subject and concentrate exclusively on the biogeography of crop genetic diversity.

The first major student of world-wide crop biogeography was Alphonse de Candolle (1882). The information available on crop biogeography at that time was limited and taxonomic classification of crops was still relatively confused by an overabundance of synonymous names in many cultivated taxa. The genetics of biological species were also unknown then, so the limits of some species groups were unclear. De Candolle identified South America as the origin of numerous crops and in some cases identified probable sub-continental regions of origin, although he emphasized that his information might be unreliable for such fine definitions. His major contribution was to apply a multi-disciplinary approach, that is still applied today in expanded and modified form.

Forty years later, Nicolai I. Vavilov and his colleagues started exploring the mountains and adjacent lowlands of the Neotropics and incorporating these regions into their hypotheses of world-wide crop biogeography and agricultural origins. The recent translation of Vavilov's contributions to crop biogeography provides a fascinating record of the development of these hypotheses. Figure 1.b-f shows their development with respect to South America. Figure 1.a. is an approximation of the physical geography of South America.

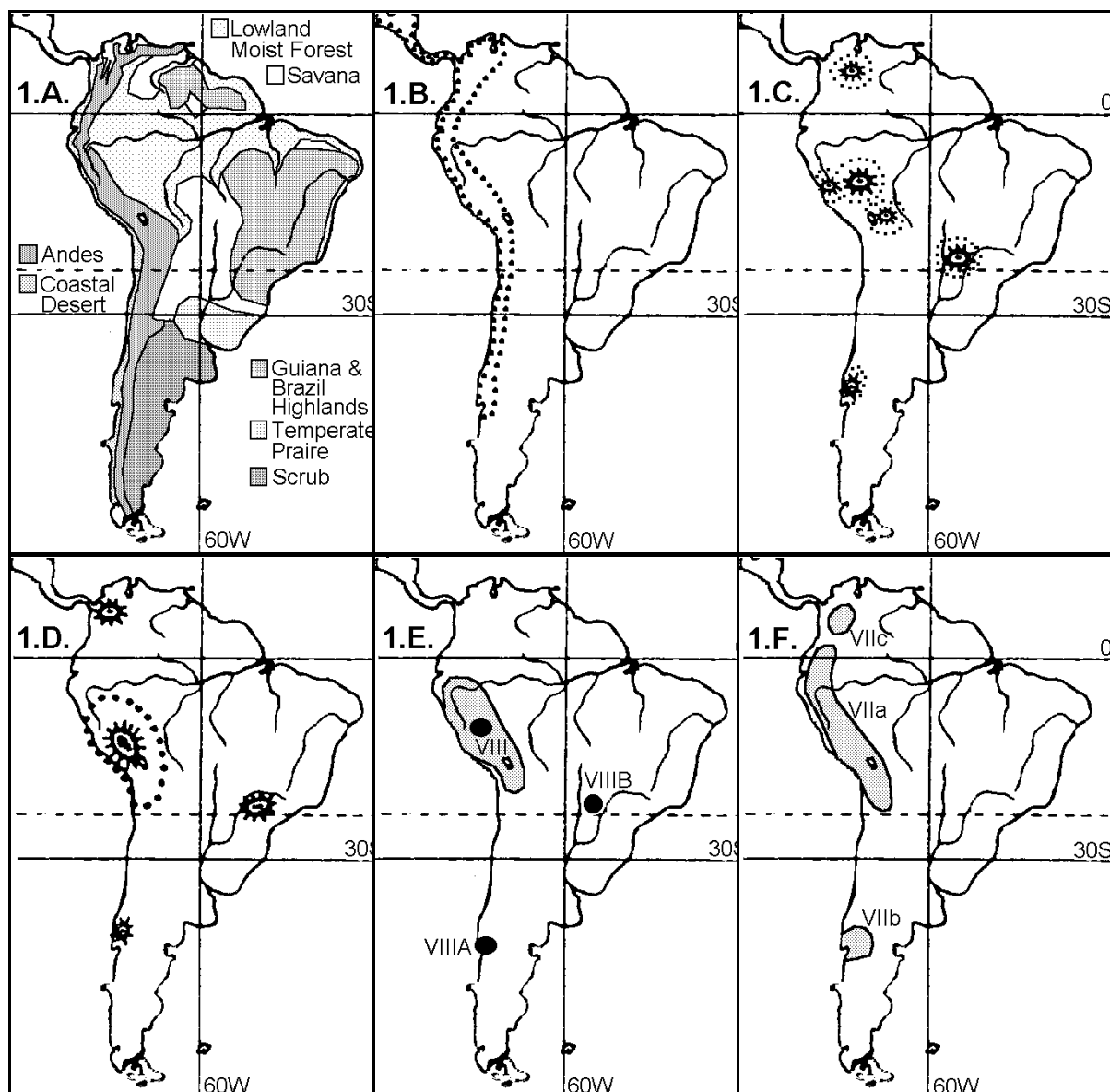


Figure 1. The development of Vavilov's hypotheses on the biogeography of crop genetic diversity in South America. A. Physical/vegetational geography. B. The first hypothesis (Vavilov, 1992a), with one center of origin. C. The second hypothesis (Vavilov, 1992e), with six centers of origin, each with a focus of type formation. D. The third hypothesis (Vavilov, 1992d), with one center of origin and four foci of type formation. E. The fourth hypothesis (Vavilov, 1992c), with one center of origin and three foci of type formation (the map in the 1992 version does not include VIIIB, but the text does). F. The final hypothesis (Vavilov, 1992f), with a three part center of origin.

The first hypothesis was essentially generated from the literature, according to Harlan (1992:49). A region of diversity extended along the Andean mountains and Central America, from Mexico to Chile. In South America it followed the Andes and immediately adjacent coast and interior lowlands (Figure 1.b.), from Venezuela to Chiloe Island, Chile (Vavilov 1992a). Vavilov always assumed a close relationship between crop genetic diversity and centers of advanced civilizations (Vavilov 1992b), which explains large sections of this

hypothesis. In South America he emphasized the Incas, the Chibcha (in the Colombian mid-to high-elevations), and the Araucanos (in Southern Chile).

As information collected by Soviet scientists became available, Vavilov generated more precise hypotheses. In 1929, he (1992e) hypothesized that there were six centers of crop diversity in South America, each containing a “focus of type formation.” By this, Vavilov meant the area in which a domesticated crop shows most clearly the traits subject to selection. These foci were: the Colombian highlands; the Peruvian coast; the mid-elevation Andes; the Peruvian-Bolivian high-elevation Andes; the area around Chiloe Island, Chile; and part of the Paraná-Paraguay river basins in southern Brazil (Figure 1.c.).

In 1931 the hypothesis was modified again (Vavilov 1992d), drawing all of the Peruvian-Bolivian foci into one center of diversity with a highland focus, while maintaining the Colombian, Chiloean and Brazilian foci (Figure 1.d.). The latter three foci were no longer parts of independent centers of diversity, however. The enlarged center of diversity covered parts of the Peruvian coast where the original hypothetical focus had been, as well as parts of the drainage systems of several upper Amazonian rivers, notably the Ucayali and the Huallaga. This appears to have been deliberate, as several Amazonian species were included in this center of diversity. Note also that position of the Brazilian focus was shifted slightly.

In 1935, Vavilov (1992c) published his major synthesis, *The Phyto-Geographical Basis of Plant Breeding*, in which he recognized only one center of diversity in South America, the Ecuador-Peru-Bolivia Andean center, with two associated foci, the Chiloe and the Brazil-Paraguay (Figure 1.e.). He does not explain why the Colombian focus was eliminated. For the first time, crop lists are presented for each center and focus; several Amazonian crops are included in the crop list for the center of diversity, as well as for the Brazil-Paraguay focus. This map is widely published as Vavilov's definitive statement.

Vavilov's final hypothesis was published in 1940, however. The Andean center of diversity was divided into three sections: the Bogotá focus, the Ecuador-Peru-Bolivia focus, and the Chiloe focus (Figure 1.f.). In this final version, the Brazil-Paraguay focus was eliminated, again without explanation. Unfortunately, Vavilov was imprisoned and died shortly thereafter.

The curious thing about the development of Vavilov's hypotheses with respect to South America is the shifting importance that he attributes to the Colombia and Brazil/Paraguay foci. It is unclear why these shifts occurred. It is clear, however, that he recognized the importance of the tropical lowlands, even though he visited only their periphery, at Belém, Pará, Brazil (Vavilov 1997). The continual inclusion of Chiloe Island and adjacent Chile is a fine example of bias towards annual crops, which were then and continue to be extremely important to world food security. Vavilov thought that Chiloe Island provided the *Solanum tuberosum* genotype best adapted to Europe; otherwise it only produced *Madia sativa* and *Bromus mango* (Vavilov 1992c), both essentially extinct in cultivation today.

Shortly afterwards, Darlington & Janaki Ammal (1945) published a map that they claimed was based on Vavilov's work (Figure 2.a.). The Andean center, however, was shifted north to include Colombia and exclude Bolivia. The Chiloe Island area was maintained. The Brazil-Paraguay area was expanded to encompass the Brazilian savannas, most of Amazonia, the Guiana highlands and most of the Orinoco River basin. No explanation was given. In 1956, Darlington (1973) accepted Kuptsov's (1955) proposed locations of the world's primary regions of agriculture and the regions into which they diffused after their initial development. In this map (3rd edition, 1973), Vavilov's Andean center equaled Kuptsov's primary region and the area of expansion included all of South America north of the Plata River.

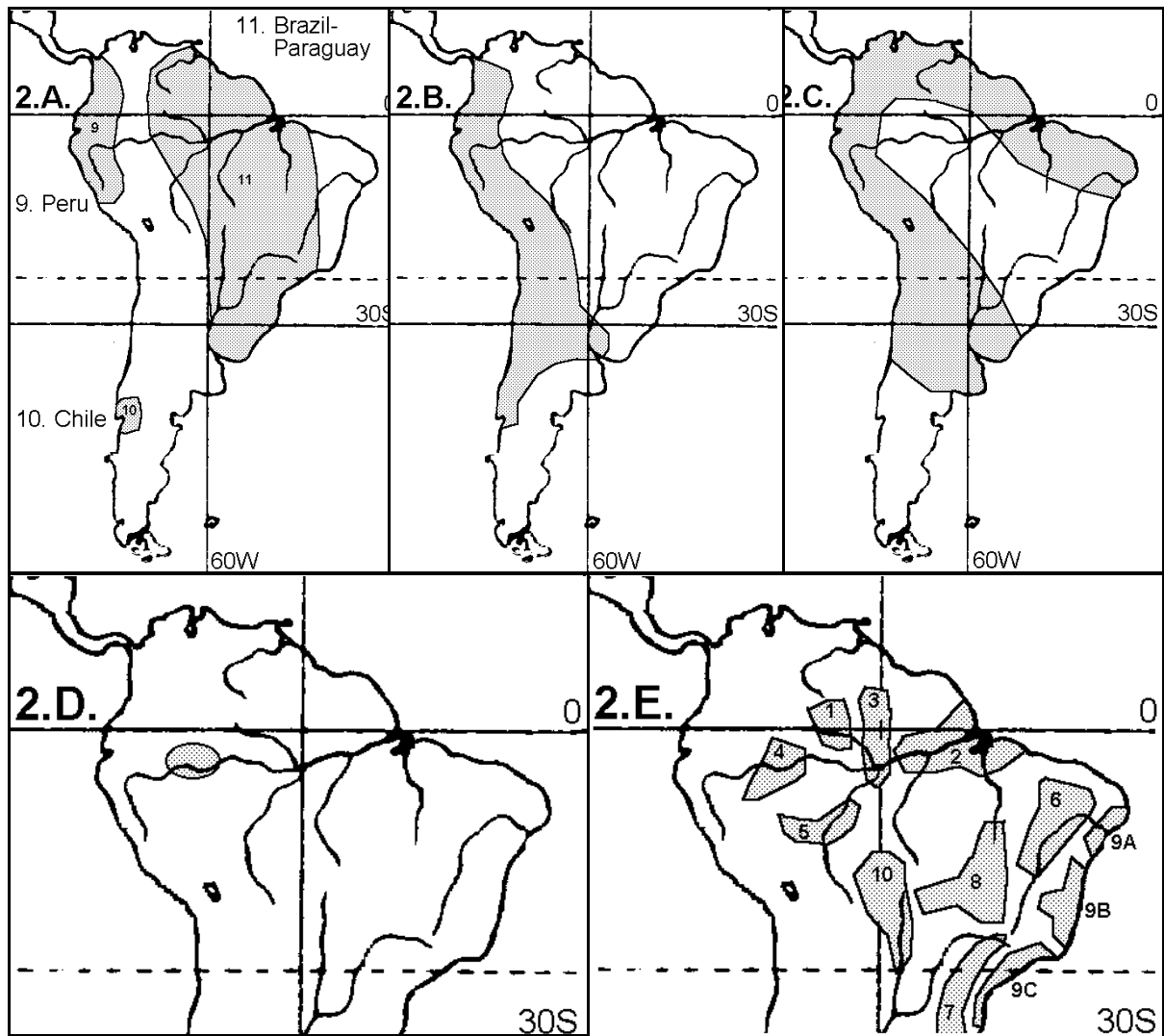


Figure 2. Post-Vavilovian development of South American biogeographic hypotheses. A. Darlington & Janaki Ammal's (1945) biogeography. B. Zhukovsky's (1968) South American megacenter. C. Harlan's (1971) South American non-center. D. Clement's (1989) Northwestern Amazonian center. E. Giacometti's (1992) centers of fruit biodiversity in Brazil.

In the early 1950's, Sauer (1952) suggested that several South American crops originated in Amazonia. He didn't attempt to delineate concentrations of crop genetic diversity, however, and is therefore seldom cited with respect to South American crop biogeography.

A decade later, Zhukovsky (1968, 1975) proposed that crop genetic diversity was so wide-spread in most of the world that 'megacenters' were a more appropriate approximation of crop biogeography. In South America, Zhukovsky's megacenter 10 (Figure 2.b.) was essentially equivalent to Vavilov's first hypothesis (1992a), with an extension to include northern Argentina.

At the same time, Brücher (1969) criticized Vavilov's hypothesis on the basis that many crops do not have centers of diversity that correspond with Vavilovian biogeography. In fact,

for Brücher, centers of diversity do not exist. Rather, each crop displays one or several centers of origin and an 'arc of diffusion' (Brücher 1990).

Immediately thereafter, Harlan (1971) proposed that some continents have centers and some don't. South America was an example of a non-center (Figure 2.c.), where agriculture was so widely distributed that no clear centers can be identified. For the first time the northeastern coast of South America, from Recife, Pernambuco, Brazil, across the mouth of the Amazon River and along the Guiana coast and highlands, was included in South American biogeography. Why was not clear. Chiloe Island was excluded for the first time, also without explanation. His subsequent books (Harlan 1975, 1992) failed to clarify these issues.

A decade later, Hawkes (1983) attempted to synthesize Vavilov's, Zhukovsky's and Harlan's ideas into a mosaic. In South America, Hawkes' scheme (1983:70-73) posited a nuclear center of agricultural origin in the Andes (essentially Vavilov's (1992c) Ecuador-Peru-Bolivia Andean center), surrounded by a region of diversity into which agriculture diffused [essentially Zhukovsky's megacenter (Zeven and Zhukovsky 1975)], and a couple of outlying minor centers (essentially Vavilov's Chiloean and Brazil/Paraguay foci). No map was presented. This synthesis appeared to offer great promise for further development, but was not elaborated further by Hawkes or other authors.

During the 1980s, work in Amazonia allowed me (Clement 1989) to propose a Vavilovian center of crop diversity in Northwestern Amazonia (Figure 2.d.), based principally on fruit crops, although various other crops were included as supporting evidence. At that time I also mentioned that there was more crop diversity north of the proposed center, as well as elsewhere in Amazonia.

In 1992, Harlan (1992) restated his conviction that South America is a non-center, but acknowledged that a complex mosaic of crop diversity was present in this and other non-centers. Unfortunately he did not elaborate on the form of this mosaic or present a map.

Also in 1992, Pearsall (1992) reviewed evidence from archaeology on the origin of crops in South America. She divided the western part of the continent into low, mid- and high elevation zones and provided exhaustive lists of crops found in many localities and their time-depths of first appearance. This data base provides considerable concrete evidence for the diffusion of crop biodiversity but is still incomplete, covering only a third of the continent.

Also in 1992, Giacometti (1992) proposed that there are 10 centers of fruit species diversity in Brazil (Figure 2.e.). Unfortunately, he did not distinguish between wild and domesticated fruit species, because his major objective was to identify areas for the *in situ* conservation of wild relatives of fruit crops and species with potential for future domestication. Giacometti's species lists can be used to identify those centers that probably had significant fruit crop genetic diversity, as opposed to fruit biodiversity, at contact: 1 - Upper Rio Negro/Northwestern Amazonia; 2 - Lower Amazon River and adjacent Atlantic coast; 4 - Solimões River/western Amazonia (an expansion of Clement's (1989) proposal); 9 - Atlantic forest, with three subsections; 10 - Brazil/Paraguay (essentially Vavilov's (1992c) focus of the same name). The other 5 centers are rich in fruit biodiversity and might once have been sites of endemic incipient domestication, but current information is too scarce to confirm them. All were populated to some degree and certainly contained some crop genetic diversity.

From this short review, it is clear that Pickersgill and Heiser's (1977) observation that the variety of hypotheses about the biogeography of crop genetic resources in South America is due principally to a lack of information remains true, even though significant advances have been made, especially in the Andes. It also seems clear that some type of mosaic will be

necessary to describe crop biogeography in the region. The question is how to characterize concentrations of diversity.

### DEFINING A CROP DIVERSITY MOSAIC

Since Vavilov's proposals, a mosaic of crop genetic diversity has been recognized in South America, although Vavilov never used this term. De Candolle, Brücher, and Harlan recognized the difficulty of identifying discrete centers; de Candolle for lack of firm data, Brücher and Harlan because modern research had already identified numerous crops with probable origins outside of Vavilov's mosaic. Hawkes (1983:71-72) was the first to specifically propose an hierarchical structure for this crop diversity mosaic. His hypothesis resolved part of the criticism raised by Harlan but it ignored two thirds of South America.

Most of the pre-1980s students of crop biogeography considered agricultural origins as integral to their hypotheses. Generally, they were also diffusionists, at least initially, believing that only a few peoples had the idea that lead to domestication and agricultural development, while others simply copied. The main exception is Brücher. In the mid- to late 1980s, however, the concept of a Neolithic revolution lost favor, being replaced by an evolutionary (Rindos 1984) or a situational (MacNeish 1992) hypothesis, or some synthesis of these (e.g., Harlan 1992). Some form of synthesis seems most likely, which means that agriculture probably originated in various places at various times in South America.

The evolutionary aspects of this synthesis suggest that the first steps towards agriculture were taken during the late Pleistocene, rather than the early Holocene. These first steps will be difficult to detect in the archeological record because they involve minor changes in land use, settlement behavior and plant population genetics. The sudden appearance of "domesticated" crops in the early Holocene archaeological record (e.g., *Manihot esculenta* and *Ipomoea batatas* in coastal Peru; Pearsall 1992) suggests that domestication started much earlier, e.g., during the late Pleistocene. Although these initial steps have not yet been identified archeologically, the final stages in the domestication continuum remain visible, even after 500 years of conquest and acculturation. Consequently, I develop here a mosaic without reference to agricultural origins, placing the emphasis instead on other cultural and biotic factors.

Specifically, I hypothesize that:

- a) an environment rich in biodiversity is likely to yield more crops than an environment poor in biodiversity, if humans are present to use the diversity (Lévi-Strauss 1950);
- b) humans continually experiment with plants in their environment and agricultural people will bring anything especially useful into domestication (cf Harlan 1992; Hawkes 1983; Rindos 1984), with the possible exception of perennials that are exceptionally abundant in their environment (e.g., buriti (*Mauritia flexuosa*), açai-do-Pará (*Euterpe oleracea*);
- c) the combination of swidden/fallow agriculture and micro-environmental heterogeneity in Amazonia allowed for rapid progress in domestication, because of small population sizes (genetic drift), inbreeding, selection, short generation spans, etc (Clement 1988) (This allows for the same type of extensive variation observed by Vavilov and others in mountainous regions);
- d) human societies accumulate useful plants by trade, stealth or during warfare (León 1987), as well as by domestication;
- e) the longer humans continuously occupy an area, the more crop diversity they are likely to create or accumulate (Vavilov 1992a);
- f) human population density correlates with the carrying capacity of the domesticated landscape, which is determined by the interaction between the physical environment and

human food procurement and processing technologies, social organization, agricultural intensification and the costs of these (W.M. Denevan, pers. com., 1995);

- g) agricultural intensification depended principally upon crop genetic diversity to produce reliably in a biotically aggressive environment like Amazonia, especially on the *terra firme*, but possibly less so on the *várzea* because periodic flooding could reduce pest populations;
- h) in any given locality, any or all of the above assumptions interact to maximize genetic diversity as social organization, agricultural intensification and population density increase;
- i) the rare observations about crops made by early chroniclers of ecological Amazonia can be deciphered (e.g., Patiño 1963, 1964) and no major changes in biogeography of most Amazonian crops occurred in the first 100 years after contact, i.e., until European colonization started;
- j) for crops that were not adopted by European settlers and not lost completely, current biogeography can provide another reasonably reliable guide to past biogeography. A major example is *Bactris gasipaes*, whose biogeography has been partially mapped in the last decade (Clement 1988; Mora Urpí 1992).

Like Hawkes (1983), I believe that a three-tiered hierarchy is useful. In the following hierarchy each tier is based exclusively on the expectation of crop genetic diversity, rather than on agricultural origins and diffusions, even though a significant portion of the diversity may not be present today (Clement 1999). I conserve the terminology developed during the last century, but define each term differently. The hierarchy includes the following levels:

- 1) Centers of diversity - relatively restricted areas with high concentrations of crop genetic resources at contact, including both species and landraces or cultivars. The high concentration may be due to one or more of the following factors: great time depth of human occupation; high human population densities and associated social organization and agricultural intensification; significant micro-environmental diversity that enhanced genetic diversification during domestication.
- 2) Minor centers of diversity - restricted areas with moderate to high concentrations of crop genetic resources at or before contact. The concentration is related to a specific cultural group with a significant agricultural technology and may be thought of as a center of accumulation during the centuries immediately pre-contact. These are hypothesized for the areas with earthworks, some of which were abandoned before contact.
- 3) Regions of diversity - extensive areas with moderate concentrations of crop genetic resources at contact. The concentration may be due to one or more of the factors mentioned for the centers of diversity but never acting intensively enough to attain high concentrations.

There were also areas with low concentrations of crop genetic resources at contact, because any area occupied by human populations with some form of agriculture or landscape management would have crop genetic resources. Concentrations were low in these areas because of a less favorable environment, low population densities, simpler social organization, and/or shorter occupation. An example is the Chiloe Island focus that Vavilov and subsequent students maintained. There were also areas that were essentially uninhabited by agricultural populations, e.g., the drier sections of the Brazilian northeast, the Argentinean pampas, etc.

### **BIOGEOGRAPHY OF AMAZONIAN CROP GENETIC RESOURCES**

At contact, there were probably two centers of diversity, four minor centers, and five or more regions of diversity in lowland northern South America east of the Andes. All exhibited



moderate or high population density, advanced social organization, and agricultural intensification. Many of them are not visible today, although some of the early chronicles attest to their existence. I discuss each concentration of diversity and attempt to build a crop list for each with emphasis on domesticates (see Clement 1999 for botanical families, probable origin, and uses). The major resource for this data set was Patiño (1963, 1964). I also assume that several crops were common to all areas: *Bixa orellana*, *Ananas comosus*, *Ipomoea batatas*, *Manihot esculenta*, *Zea mays*, *Gossypium barbadense*, *Genipa americana*, and *Nicotiana tabacum*. These lists are certainly incomplete. Confirmation and expansion of these crop lists by paleoethnobotanists will be a test of the soundness of these proposals.

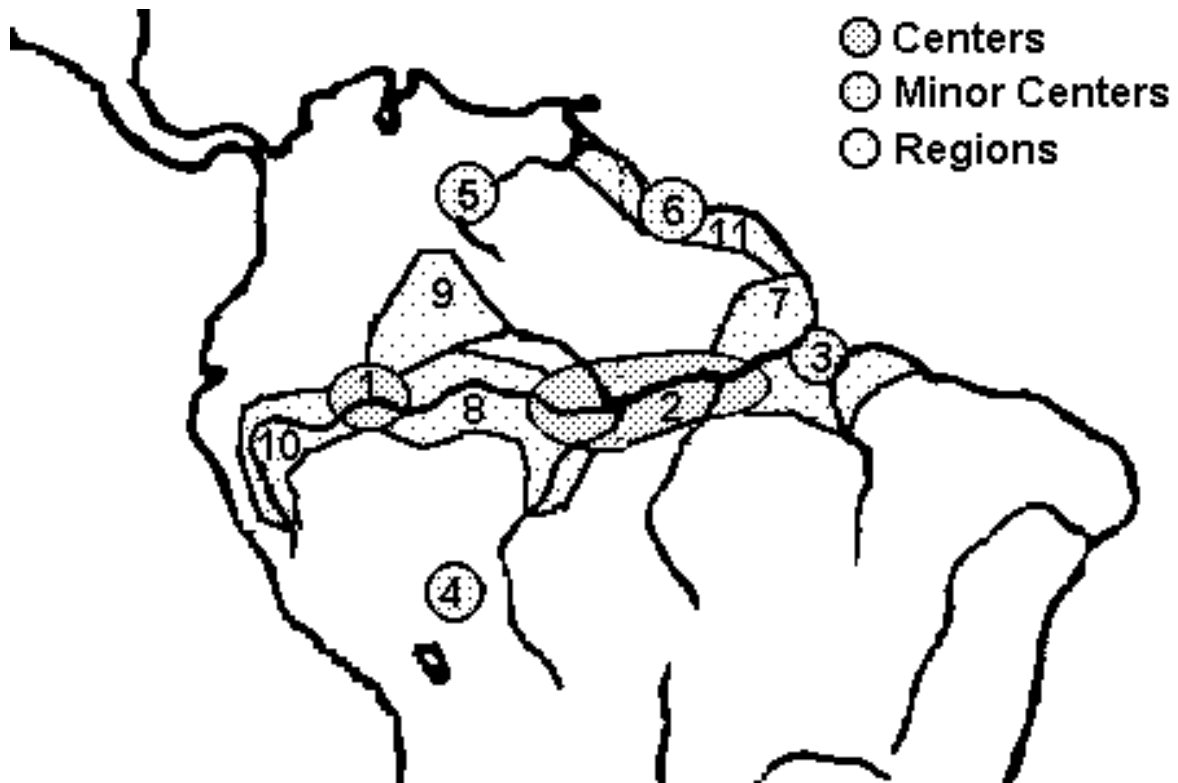


Figure 3. Biogeography of ecological Amazonia in 1500 AD. Centers of Diversity: 1. Northwestern Amazonia; 2. Central Amazonia. Minor Centers of Diversity: 3. Marajó Island; 4. Llanos de Mojo; 5. Middle Orinoco; 6. Guiana. Regions of Diversity: 7. Amazon Estuary; 8. Solimões; 9. Upper Negro/Orinoco; 10. Upper Amazon; 11. Guiana Coast.

1. The **Northwestern Amazonian Center** (Clement 1989). This center extends along the upper Amazon River from below the mouth of the Putumayo/Iça River in the east to above the mouth of the Napo River in the west, as well as extending up the Putumayo River to the northwest and the lower Javari River to the south. Population densities at contact were probably high, especially along the *várzeas* throughout this center. Environmental variation is also high, with outcroppings of Guiana shield remnants in the north of the center and extensive reworking of the Tertiary sediments by river meanders. This center is relatively well preserved, principally because of the large number of Amerindian societies still present in the area, especially in comparison with the Central Amazonian center. The crop list probably included the following domesticates: *Rollinia mucosa*, *Xanthosoma sagittifolium*, *Crescentia cujete*, *Canna edulis*, *Carica papaya*, *Cucurbita moschata*, *Dioscorea trifida*, *Erythroxylum coca* var. *ipadu*, *Poraqueiba sericea*, *Persea americana*, *Arachis hypogaea*,

*Canavalia ensiformis*, *Phaseolus vulgaris*, *Pachyrrhizus tuberosus*, *Calathea allouia*, *Bactris gasipaes* Putumayo landrace, *Pouteria caimito*, *Capsicum chinense*, *Solanum sessiliflorum* and other vegetables, condiments, drugs and poisons. A few of the semi-domesticates mentioned in Clement (1989) include: *Quararibea cordata*, *Inga edulis*, *Pourouma cecropiaefolia*, *Borojoa sorbilis*, and possibly other semi-domesticates and incipient domesticates.

2. The **Central Amazonian Center**. This center may have extended along the main stream of the Amazon River, from the Purus River in the west to the Tapajós River in the east, and included the lower sections of the Negro, Madeira and Tapajós Rivers. There were probably high population densities at contact, especially along the *várzeas* (Denevan 1992) and the greatest time depth detected in Amazonia to date - 11,000 BP (Roosevelt et al. 1996). There are large areas of terra preto do índio [an anthropogenic soil whose origin and importance is the subject of debate (Smith 1980; Meggers et al. 1988; Denevan 1996), but is generally associated with forests enriched with useful species (Smith 1995)] and Santarém area contains the oldest pottery yet found in the Americas - 8000 BP (Roosevelt et al. 1991). Lathrap (1977) and León (1987:29,31) hypothesized that this region may have been a nuclear center of agricultural origins. Giacometti (1992) recognized the eastern portion of this center as part of his lower Amazon center and the western portion as part of his Manaus/ Roraima center. A few annual and perennial crops are still clearly associated with this area, but in general it is severely eroded. The crop list probably included the following domesticates: *Rollinia mucosa*, *Xanthosoma sagittifolium*, *Crescentia cujete*, perhaps *Cucurbita moschata*, *Dioscorea trifida*, *Poraqueiba paraensis*, *Arachis hypogaea*, *Phaseolus vulgaris*, *Calathea allouia*, *Bactris gasipaes* Pará landrace, *Paullinia cupana* var. *sorbilis*, *Pouteria caimito*, *Capsicum chinense*, and other vegetables, condiments, drugs and poisons. Some of the semi-domesticates were: *Anacardium occidentale*, *Spondias mombin*, *Inga* spp., *Lonchocarpus utilis*, *Psidium guajava*, *Astrocaryum aculeata*, *Theobroma cacao*. Some of the important incipient domesticates were: *Caryocar villosum*, *Bertholletia excelsa*, *Lecythis pisonis*, *Hymenaea courbaril*, *Theobroma grandiflorum*, and *T. speciosum*. *Leersia hexandra* and/or *Oryza glumaepatula* may have been important cereal crops, although their placement along the domestication continuum is in doubt (Clement 1999).

At least four minor centers of diversity may have existed also. These were all related to the societies that built earthworks: Marajó Island, the Llanos de Mojos, the lower to middle Orinoco River, and the Guiana coastal lowlands. The societies that created the earthworks were either acculturated soon after contact and their agricultural technologies were lost, including their crops, or the societies responsible were no longer present at contact, although the area was inhabited, as occurred on Marajó Island (cf Meggers and Danon 1988). Consequently, crop lists for these areas are extremely conjectural; they will be filled in as archeological research advances at each site.

3. The **Marajó Island Minor Center**. Roosevelt (1991:25-26,113) identified the following domesticates: *Xanthosoma sagittifolium*, *Manihot esculenta*, *Zea mays*. Many of the domesticates of the Lower Amazonian Center were probably present as well. Among the semi-domesticates *Spondias mombin*, *Platonia insignis*, *Inga* spp., *Psidium guajava*, *Astrocaryum vulgare*, *Pouteria macrophylla* and/or *P. macrocarpa*, and *Theobroma cacao* were probably present. Roosevelt (1991:25) emphasizes the probable importance of *Leersia hexandra* on Marajó Island before and immediately after contact.

4. The **Llanos de Mojos Minor Center**. Zhukovsky's (1975) map of the South American megacenter suggests that this minor center is its only extension into the tropical lowlands, although there is no discussion. Its crop list probably included *Phaseolus vulgaris*, *P. lunatus*, possibly *Cucurbita moschata* and *C. maxima*, *Arachis hypogaea*, *Pachyrrhizus*

*tuberosus*, *Bactris gasipaes* (which may have originated nearby), *Passiflora edulis*, *Capsicum baccatum*, *Sicana odorifera* and other vegetables, condiments, drugs and poisons (Denevan's (1966) crop list confirms part of this list). Semi- and incipient domesticates may have included: *Inga* spp., *Bertholletia excelsa*, *Bunchosia armeniaca*, *Psidium guajava*, *Lucuma obovata*, *Theobroma bicolor*, *Caryocar glabrum*, *Hymenaea courbaril*, *Acrocomia sclerocarpa*, and others.

5. The **Middle Orinoco Minor Center**. This minor center has also not been surveyed for a paleoethnobotanical crop list. Down-river from the area with earthworks, Roosevelt (1980) discussed the arrival of *Zea mays* at about 2800 BP and how it supplanted *Manihot esculenta* as the major staple. Other domesticates from northern South America may have included: *Annona muricata*, *Xanthosoma sagittifolium*, *Ananas erectifolius*, possibly *Carica papaya*, *Dioscorea trifida*, *Canavalia ensiformis* and *C. plagioperma*, *Phaseolus vulgaris*, *Maranta arundinacea*, *Capsicum chinense*, and others.

6. The **Guiana Minor Center**. This minor center is proposed because of probable population density and presence of earthworks, and was probably influenced by both Amazonian and Caribbean crop complexes. Domesticates that may have been present were *Annona muricata*, *Xanthosoma sagittifolium*, *Crescentia cujete*, possibly *Carica papaya*, *Cucurbita moschata*, *Dioscorea trifida*, *Arachis hypogaea*, *Canavalia ensiformis* and *C. plagioperma*, *Phaseolus vulgaris*, *Gossypium hirsutum*, *Capsicum chinense* and others. Some important semi-domesticates were probably *Annona reticulata*, *Mammea americana*, *Byrsonima crassifolia*, *Psidium guajava*, and others, while incipient domesticates included *Caryocar nuciferum*, *Hymenaea courbaril*, *Melicoccus bijugatus* and others.

The five regions of diversity were the Amazon River estuary, the middle Solimões River, the upper Rio Negro and Orinoco Rivers, the upper Amazon River, including the Ucayali and the Huallaga Rivers, and the Guiana coast. All may have been densely populated at contact, with the possible exception of the upper Rio Negro and Orinoco River region, which has an apparently less favorable physical environment (Sponsel 1986).

7. The **Amazon Estuary Region** includes the estuary and adjacent Atlantic coast, both north and south. It was proposed by Giacometti (1992) as a center and is conserved here as a region of diversity. It encompasses the Marajó Minor Center and extends up-river to the Lower Amazonian Center. Most of the crops listed for the Lower Amazonian Center and the Marajó Minor Center occurred here also.

8. The **Solimões Region** extended from the Lower Amazonian Center in the east to the Northwestern Amazonian Center in the west and included the lower reaches of the Solimões River tributaries. This was the region occupied by the Machipara and Omagua chiefdoms at contact. It probably contained many of the crops from both centers and was in the process of creating its own advanced landraces of *Bactris gasipaes* and *Solanum sessiliflorum*, among others (Clement 1988; D. F. Silva Filho, INPA, 1998, pers. com.).

9. The **Upper Negro/Orinoco Region** probably extended from above modern Barcelos, on the Rio Negro, through the Casiquiare to the confluence of the Orinoco and Guaviare Rivers, perhaps even as far as the Meta River, in Venezuela, and included at least the lower reaches of the Inirida, Içana, and Vaupés River basins. Part of it was proposed by Giacometti (1992) as a center and is conserved here as a region of diversity. This region probably contained many of the crops of the Northwestern Amazonian Center, but was creating its own landraces. It contained at least two landraces of *Bactris gasipaes*, the Vaupés and the Inirida (Clement 1988), one of *Solanum sessiliflorum*, and was in the process of domesticating *Hevea* spp. for their seeds. This region is probably the origin of the Smooth Cayenne variety of *Ananas comosus*, possibly of *A. erectifolius*, and of *Paullinia cupana*.

10. The **Upper Amazon Region**, extended south from the Northwestern Amazonian Center along the Amazon River, and included the upper Napo River and Ucayali and Huallaga Rivers. As well as containing many of the crops of the Northwestern Amazonian center, it may have experienced considerable in-put from the mid-elevation Andean region. Because the upper Napo River is adjacent to a low section of the Andes, it may be where crops such as *Carica papaya* and *Persea americana* entered Amazonia from the northern Pacific coast. There are several landraces of *Bactris gasipaes*, only one of which (the Pampa Hermosa) has been adequately mapped (Clement 1988). It is probably where *Eugenia stipitata* originated (Clement 1989).

11. The **Guiana Coastal Region** probably extended from the Amazon Estuary Region in the south to the Orinoco River estuary in the north, and included the Guiana Minor Center. Consequently it probably contained many of the crops of the Guiana Minor Center and some of the Amazon Estuary Region, as well as crops from the Caribbean.

### A SOUTH AMERICAN SYNTHESIS

Assuming that these Amazonian concentrations of crop genetic diversity existed as mapped, how do they fit into a South American mosaic? In Figure 4, I extrapolate my thinking for Amazonia to the rest of the continent, although without supplying crop lists. Only a short justification is given for each South American concentration.

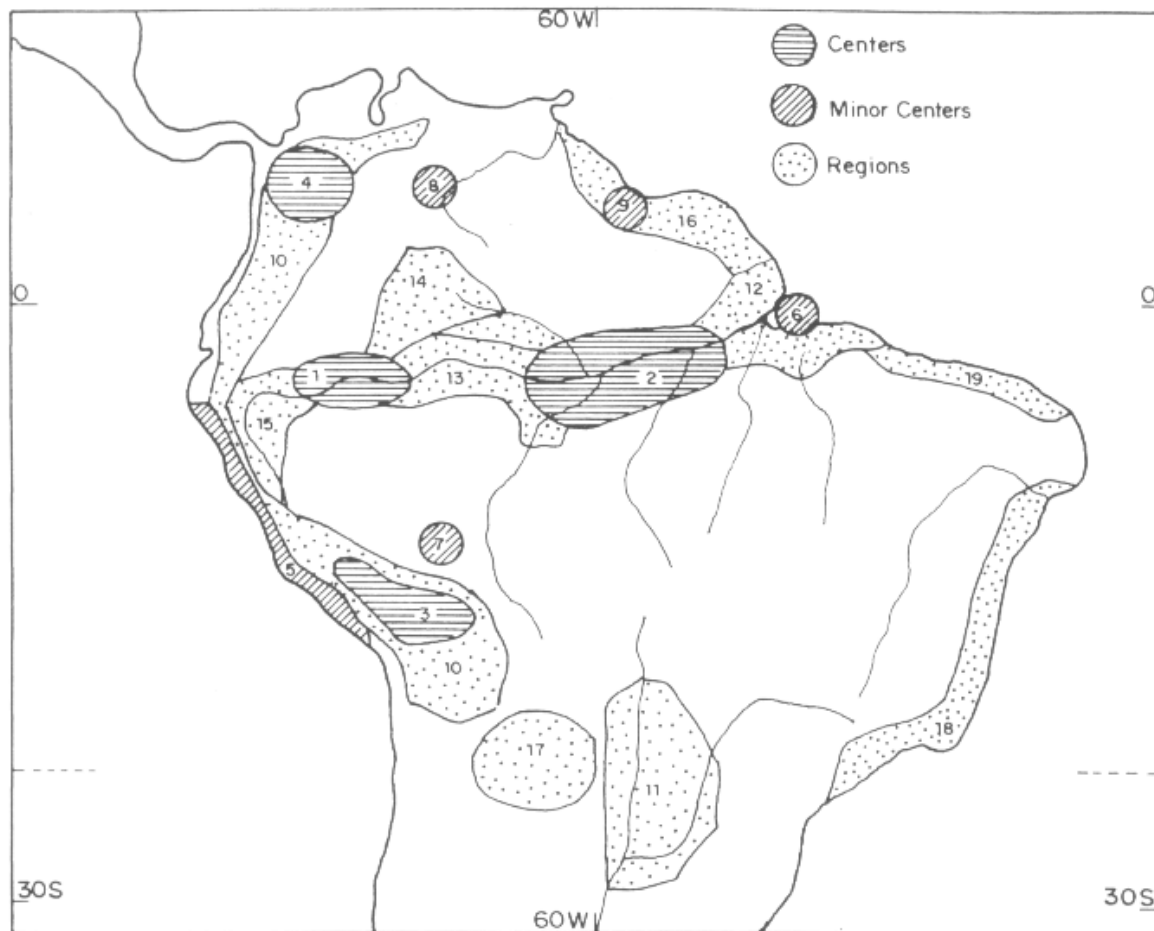


Figure 4. The biogeography of South America at contact. Centers of Diversity: 1. Northwestern Amazonia; 2. Central Amazonia; 3. Peru-Bolivia; 4. Colombia. Minor Centers

of Diversity: 5. Marajó Island; 6. Llanos de Mojos; 7. Middle Orinoco; 8. Guiana; 9. Peruvian Coast. Regions of Diversity: 10. Mid-elevation Andean Colombia-Ecuador-Peru-Bolivia; 11. Guaraní; 12. Amazon Estuary; 13. Solimões; 14. Upper Negro/Orinoco; 15. Upper Amazon; 16. Guianan Coast; 17. Northern Argentina; 18. Atlantic Forest; 19. Northeastern Brazilian Coast.

The Andean mosaic. Vavilov's (1992f) final approximation of two Andean centers serves as the basis for anchoring the Andean mosaic. The Colombian center is supported by analysis of maize races in South America (Brieger et al. 1958), as well as by the large number of crops that are restricted to the northern Andes (Patiño 1963, 1964). The Peru/Bolivia center was widely accepted before Harlan (1971) and is retained here because there are numerous crops that are endemic there or show exceptional variability there (Harlan 1992:217-236). Zhukovsky's 'megacenter' is transformed into a region of diversity, following Hawkes (1983), but is restricted to the mid-elevation Andes, because of the crop lists presented by Pearsall (1992) that are specific to the mid-elevations, rather than including the Llanos de Mojos and the NW Argentinean lowlands (see lowland mosaic below). Chiloe Island and adjacent mainland are not conserved because only two very minor crops occur there, and other crop genetic variation was probably insufficient to justify its status as a region of diversity. Part of the Peruvian coast is considered a minor center, following Vavilov's earlier proposal (1992e) and given the great number of species found in archaeological sites there (Pearsall 1992). This is definitely an area that accumulated crops, rather than developing them from endemic species, however, because all of the domesticates in the crop lists are non-native to the area.

The lowland, non-Amazonian mosaic. Vavilov's original Brazil/Paraguay focus is associated with high Guaraní population densities at contact and various crops (Vavilov 1992c) and is conserved here as the Guaraní region of diversity, in agreement with Giacometti (1992). Northwestern Argentina is another region of diversity, supported by maize (Brieger et al. 1958) and recent archaeological data (Pearsall 1992). Several sections of coastal Brazil were occupied by relatively dense Tupinamba populations at contact (Hemming 1978) and had efficient agriculture. Giacometti's (1992) suggestion for three centers is transformed into a single region of diversity, because there doesn't appear to be a break in crop distributions along the southeastern coast. Consequently, a region of diversity may have extended along the SE Brazilian coast, the Atlantic forest ecosystem, from modern São Paulo to Pernambuco, while a second extends from Piauí west to the Amazon along the NE coast, where cashew may have originated (Cundall 1995).

In fact, Brücher (1969) and Harlan (1971) were correct: South America has too much diversity to consider Vavilov's original hypothesis a sufficient characterization. Figure 4 also suggests that Brücher's arcs of diffusion were probably based on the distribution of human population densities along the major river systems, coasts and the Andes, where diffusion from one human population to the next facilitated crop distribution. Furthermore, most of the areas not included in this mosaic probably contained crop genetic resources, either at lower concentrations or at levels not yet identified. The hypothesis presented here will require considerable work to confirm, but even after 500 years the remains of the Amerindian heritage, both biological and archaeological, are impressive enough to permit this.

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