FOLK TAXONOMY AND EVOLUTIONARY DYNAMICS OF CASSAVA: A CASE STUDY IN UBATUBA, BRAZIL¹

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J. B. M. Sambatti (Agronomy and Range Science, One Shields Avenue. Hunt Hall. University of California, Davis, CA 95616; ibsambatti@ucdavis.edu), P. S. Martins (In Memoriam) and A. Ando (Genetics and Plant Breeding Department of the ESALO/USP, Piracicaba-Brazil; ando@cena.usp.br). FOLK TAXONOMY AND EVOLUTIONARY DYNAMICS OF CASSAVA: A CASE STUDY IN UBATUBA, BRAZIL, Economic Botany 55(1):93-105, 2001, A survey was conducted of Caicara farmers from Ubatuba in the Brazilian coastland between São Paulo and Rio de Janeiro States regarding the folk-taxonomy for cassava (Manihot esculenta Crantz) landraces they cultivate and cassava evolutionary dynamics in swidden cultivation. The accuracy of their folk taxonomy was assessed. Cluster analysis was used to make comparisons between names given by the farmers to sampled individuals and their isozyme phenotypes obtained with four isozyme systems. Interviews with farmers were done and ethnobiological data collected. These farmers possess a loose taxonomic system and tend to underestimate cassava genetic diversity in their gardens. However, classification skills vary considerably among them. The accuracy of their taxonomy along with the results of interviews with farmers and ethnobiological data are discussed in light of a proposed evolutionary dynamics model for cultivated cassava and its ecology in tropical swidden cultivation.

TAXONOMY POPULAR E DINÂMICA EVOLUCIONÁRIA DA MANDIOCA: UM ESTUDO DE CASO EM UBA-TUBA, BRASIL. A taxonomia local e a dinâmica evolutiva da mandioca foram estudadas na agricultura de corte, queima e abandono entre agricultores caiçaras de Ubatuba-SP, Brazil. Avaliou-se, através de análise de agrupamentos, a acurácia da taxonomia local comparandose nomes dados pelos agricultores a indivíduos amostrados com seus fenótipos isoenzimáticos obtidos a partir de quatro sistemas. Entrevistas com os agricultores e coleta de dados etnobiológicos também foram realizadas. Estes agricultores possuem uma taxonomia pouco acurada e tendem a sub-estimar a diversidade genética da mandioca em suas roças. Entretanto, a habilidade de classificação de etnovariedades varia consideravelmente de agricultor para agricultor. Este fato em conjunto com os dados etnobiológicos e o resultado das entrevistas são discutidos à luz de um modelo proposto para a dinâmica evolutiva e da ecologia da mandioca cultivada neste sistema de agricultura.

Key Words: cassava; landraces; swidden cultivation; crop evolution; farmer selection; folk taxonomy; Brazil.

Cassava (*Manihot esculenta* Crantz, Euphorbiaceae) is perhaps the most important crop in swidden cultivation in the lowland tropical Americas. Traditional farmers classify cassava diversity in a culturally transmitted way defined as folk taxonomy in Quiros et al. (1990). A multitude of names for cassava varieties within folk taxonomy reflects the large genetic diversity of cassava. Some studies have assessed cassava intraspecific diversity in traditional agriculture systems using folk taxonomy to make inferences about the actual intraspecific diversity. Kerr and Clement (1980) and Kerr and Posey (1984), for example, used the folk taxonomy of Amazon indigenous people to highlight the amount of genetic diversity of cassava that they managed. However, the underlying assumption that folk taxonomy accurately represents the actual diversity is untested. Farmers may underestimate (Quiros et al. 1990) or overestimate the actual cassava genetic diversity. Moreover, some variability in terms of ability to distinguish cultivars may exist among farmers of the same region.

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Ouiros et al. (1990) observed a regional consistency between folk taxonomy and isozyme variation of potato varieties in Peru, whereas Salick. Cellinese and Knapp (1997), by comparing morphological phenotypes with folk taxonomy of cassava of the Amuesha Indians, observed a lack of consistency in this taxonomy among Indian families. Varietal names may differ among regions, among communities, and even among families. Therefore comparing whether farmers coherently classify their own plant collections vis-à-vis actual genetic differences is necessary. Understanding this system of classification is important not only due to its ethnobotanical implications but also because the skills with which farmers recognize and manage a given amount of diversity may have important evolutionary consequences for a given crop plant population.

CASSAVA EVOLUTIONARY DYNAMICS

Cassava (Manihot esculenta) is a species domesticated by the tropical American indigenous peoples. However, its center of origin remains controversial (Dominguez, Ceballos, and Fuentes 1984; Martins 1994). The Brazilian northeast (Hawkes 1991), the Amazon Basin (Schmidt 1951), Mexico (Rogers 1972), Venezuela (Sauer 1976), and recently the southern border of the Amazon Basin (Olsen and Schaal 1999) have been suggested as possible centers of origin of cassava. The possibility that cassava was domesticated in different places simultaneously cannot be discounted. Jennings (1979) pointed out that the process of cassava domestication involved selection for root size, growth habit, number of stems, and ability of clonal propagation through stem cuttings. The enormous amount of diversity found in cultivated cassava in tropical areas apparently contrasts with its propagation system, which is based only on stem cuttings. Although it has not lost its sexual reproductive ability (Graner 1942a; Iglesias et al. 1994; see also Boster 1984; Jennings 1979; Martins 1994; Salick, Cellinese, and Knapp 1997), cassava is propagated exclusively through clones by humans (Martins 1994).

The possibility of both sexual and clonal propagation provides adaptive advantages to cassava (and many other tropical crop species that share a mixed reproductive system) in traditional agriculture. On one hand, favorable genotypes can be maintained through many generations by clonal reproduction. On the other hand, new genotypes are constantly being created by mutation and recombination during sexual reproduction (Kerr and Clement 1980; Martins 1994). In fact, cassava is believed to have high rates of outcrossing (Gulick, Hershey and Alcazar 1983; Martins 1994) and interspecific crosses between *Manihot esculenta* and wild relatives are possible (Gulick, Hershey, and Alcazar 1983; Lefèvre and Charrier 1993; Nassar 1989). Nevertheless, the existence and viability of these interspecific crosses have yet to be demonstrated in nature.

Understanding evolutionary dynamics of cassava in swidden cultivation demands the definition of a spatio-temporal scale within which evolutionary phenomena may be approached. One garden, a set of different gardens of one farmer, a community of farmers, and a whole region each have relevance in the evolutionary dynamics of cultivated cassava. The garden. however, can be seen as a well-delimited population in which selective pressures are applied, and where intraspecific as well as interspecific hybridizations may occur. Thus, the garden may be seen as an important evolutionary unit of cassava in swidden cultivation. Using the garden as the evolutionary spatio-temporal unit, a model of evolutionary dynamics of cassava (modified from Cury 1993) is proposed. In this model, besides the maintenance of a set of cultivars by clonal reproduction, new genotypes are generated by crossings between different clones, selfing, and possibly by interspecific hybridization. Seeds from these sexual reproduction events are stored in soil seed banks and can eventually germinate, becoming new genotypes that may be incorporated consciously and/or unconsciously into the original set of cultivars a farmer possesses. These new genotypes are subject to natural selection, selection based on visible, conspicuous traits or perceptual selection (sensu Boster 1985), and conscious selection in a broader sense. This model is showed schematically in Fig. 1. Johns and Keen (1986) similarly described the evolutionary dynamics of potato in the Bolivian Altiplano. Salick (1992) proposed a model for the evolutionary dynamics of cocona (Solanum sessiliflorum Dunal) to describe how balanced selection plays a role in maintaining polymorphism of this species (spiny and spineless plants) in the Peruvian Amazon. Jennings (1979) used a model for cassava domestication in which sexual reproduction along



Fig. 1. Model of evolutionary dynamics of cassava having the garden as the evolutionary unity.

with clonal reproduction is considered as an important feature of cassava evolution. The proposed model attempts to show how this double reproductive system can affect cassava evolution in the context of swidden cultivation, considering also how farmers' attitudes related to cassava cultivation are crucial for the evolution of cassava.

In the present work we present evidence that supports the role of sexual reproduction in generating new genotypes in swidden cultivation. Conscious selection is directly related to the degree of accuracy with which farmers classify their collections. This is a major issue in determining the role that farmers' conscious selection plays in the evolution of their own collection of plants. The assessment of farmer taxonomy and their attitudes along the cassava life cycle described in the proposed model are also a focus of this work.

MATERIAL AND METHODS

UBATUBA—COASTLAND OF SÃO PAULO, BRAZIL AND THE CULTIVATION OF CASSAVA

The traditional inhabitants of the Brazilian southeast coast are the Caiçara people. They are a mixture of African, indigenous, and Portuguese cultures and are basically fishermen and farmers. Their agricultural tradition includes cassava cultivation using techniques inherited from former São Paulo indigenous people (Papy 1957), that used swidden cultivation as the major agricultural system. The north coast of the São Paulo State is covered by Atlantic rainforest and it is in this ecosystem where the Caiçaras practice their agriculture. The Caiçara community of this region is comprised of small villages associated with different beaches along the coast. These villages are, on average, 10 km apart from one another along the road Rio-SanECONOMIC BOTANY

Landrace and code	Frequency in the sample (%)	Landrace and code	Frequency in the sample (%)
	Farm	ner DF (n = 62)	
Landi-Preto (LP)	9, 7	Mucaé-Roxo (MR)	1, 6
Paranaense (P)	17, 7	Landí-Bravo (LB)	3, 2
Carioca (C)	9, 7	Mucaé-Ferro (MF)	1, 6
Campista (CA)	19, 3	Landí-Ferro (LF)	1, 6
Roxinha (RO)	4, 8	Mucaé-Bravo (MB)	1, 6
Maricá (M)	17, 7	Rama-Branca (RB)	1, 6
		Nonidentif. (NI)	8, 1
	Farm	her AG (n = 52)	
Amarelinha (AM)	13, 4	Mata-Fome (MT)	5, 8
Dois-Irmãos (2I)	38, 4	Mandioca-Doce (MD)	1, 9
Landí (LA)	11, 5	Landizinho (LD)	1, 9
Aipi-Rosa (AR)	17, 3	Rama-Preta (RP)	9, 6
	Farn	ner FA (n = 45)	
Aipi-Preta (AP)	2, 2	Rosinha (R)	13, 3
Maricá (M)	82, 2	Zumira (Z)	4, 4
	Farn	her FO $(n = 34)$	
Maricá (M)	79, 4	Zumira (Z)	8, 8
Roxinha (RO)	5, 9	Dois-Irmãos (21)	2, 9
Santa Helena (SH)	2, 9		_, -

TABLE 1. FREQUENCY OF LANDRACES SAMPLED IN THE GARDENS OF FOUR FARMERS. THE LANDRACE NAMES ARE WRITTEN AS GIVEN BY THE FARMERS.

tos (BR-101). However, some farmers live in the forest or apart from the villages, where they have a house and one or more gardens in which cassava is cultivated.

Four farmers from three different village/ beaches-Puruba, Ubatumurim, and Fazenda da Caixa-were chosen and one garden of each farmer was studied. The villages' UTM coordinates (see http://mcmcweb.er.usgs.gov/drg/mercproj/), zone 23, are respectively: x = 507000, y = 7417500; x = 509600, y = 7419600; x = 515400, y = 7416900. These villages are found within 30 km along the coast and are separated from each other by about 10 km. Farmer names were abbreviated-DF, AG, FA, and FO-and each abbreviation represents the farmer and the respective garden. Farmer DF has his gardens in Puruba, farmer AG in Ubatumirim and farmers FA (the only woman) and FO in the Fazenda da Caixa. Although they are somewhat distant, these farmers know each other. Cassava plants were sampled in each garden (see Table 1). The sampling consisted of walking through the garden in a grid design and cutting a 60 cm stem from a plant every five steps. The farmer followed the sampling and identified each sampled plant using his own classification system. The

samples were planted in plastic sacks with three replications per sample in a greenhouse with automatic irrigation at the School of Agriculture of the University of São Paulo-ESALQ/USP-in Piracicaba, São Paulo State. Young leaves were harvested to carry out starch-gel electrophoresis. Among ten enzyme systems tested, four were chosen based on the presence of polymorphism and resolution: SKDH, LAP, and MDH with a morpholin citrate buffer (Clayton and Tretiak 1972), and PGI with a lithium borate buffer (Scandalios 1969). The gels were interpreted and transformed into presence-absence data. Matrices including the data of all systems were constructed. These matrices were the raw material for the construction of distance matrices using the percent disagreement index by the program Statistica 99. This index compares the number of noncoincident electrophoretic bands between two individuals against the total number of bands, and it is the complementary of the simple matching similarity index (see Manly, 1994). The distance matrices were used for the construction of dendrograms using the UPGMA method (Manly 1994). Since each individual was named, it was possible to have an idea of the accuracy of farmers' classification, based on



Fig. 2. Phenotype patterns of each isozyme system found among all sampled individuals. Front line of migration at the position 1.0.

the isozyme phenotypes. The dendrograms were constructed with the program Statistica 99.

The information was complemented with interviews conducted with the farmers whose gardens were sampled, and with 10 other farmers who cultivate or who had cultivated cassava in different parts of the region. The questions were asked during informal talks and addressed the following:

(1) What are the uses of these landraces? Are there observable phenotypic differences among those that are cultivated for the same purpose?

(2) Can seed-originated plants be recognized?



Fig. 3. Dendrogram showing the distribution of names through the isozyme phenotypes using individuals sampled from and named by farmer DF Codes as in Table 1. Cophenetic correlation coefficient—0.94.

Can phenotypic differences between seed-originated plants and those that are regularly planted be identified?

(3) Are cassava seedlings often observed after slashing the forest that covers old abandoned gardens?

(4) Have they already named some landrace originated from seed?

(5) What do they do when receive a landrace from another farmer?

(6) Are there pests in cassava gardens?

Additional questions were also asked addressing other problems and will be discussed elsewhere.

RESULTS

CLASSIFICATION OF LANDRACES BY INDIVIDUAL FARMERS

The isozyme phenotype patterns found among the samples for the four systems are shown in Fig. 2.

Farmer DF's classification (see Table 1 and Fig. 3) shows a clear coherence with the isozyme phenotypes since a given name tends not to appear in different isozyme groups. The isozyme systems were not able to discriminate between Campista and Maricá. On the other hand, landrace Paranaense is clearly distinguished from Carioca. Landraces whose names bear



Fig. 4. Dendrogram showing the distribution of names through the isozyme phenotypes using individuals sampled from and named by farmer AG. Codes as in Table 1. Cophenetic correlation coefficient—0.88.

Landí and Mucaé were scattered among different phenotypes, although these phenotypes clustered into groups with phenotypically similar individuals. Landraces that bear *bravo* in their names cluster very well. The name bravo is associated with bitter landraces, which are usually thought to be poisonous due to the presence of HCN. Yet, this correlation is imperfect (Nye 1991). These landraces are only used for making flour. Whatever meaning bravo may have, Fig. 3 shows that for farmer DF it is taxonomically more significant than Landí or Mucaé. However, based on the available data it is impossible to assert whether or not this feature is due to some kind of conscious selection.

Although farmer AG consistently discriminated between landraces Rama-Preta, Mata-Fome, and Amarelinha, his landraces Dois-Irmãos, Landí, and Aipi-Rosa were scattered among different phenotypic classes (Fig. 4). It suggests that he had difficulties in identification of landraces. Actually, he acknowledged these difficulties in classification when consulted about it. His lower classification accuracy was also evidenced by the fact that he identifies only one type of Landí, whereas DF uses an additional taxonomic level to classify his Landí landraces.

Farmer FA discriminated the landraces Maricá and Zumira consistently (Fig. 5). However, similarly to AG, the landrace Rosinha was scattered among relatively distant phenotypic classes. In contrast, for farmer FO the landrace Zumira was scattered among different phenotypes, whereas Maricá and Roxinha were classified consistently (Fig. 6).

The names Landí and Mucaé seem to be very



Fig. 5. Dendrogram showing the distribution of names through the isozyme phenotypes using individuals sampled from and named by farmer FA. Codes as in Table 1. Cophenetic correlation coefficient—0.97.

old in the region. Schmidt (1958) listed these names as cultivated landraces in his book. Moreover, all interviewed farmers recognized the names. On the other hand, the landraces Paranaense, Carioca, and Campista were barely known to farmers other than DF, which suggests that they were more recently introduced. Indeed, these names indicate an outside origin, since Paranaense and Carioca make reference to places in the States of Rio de Janeiro and Paraná, far away from Ubatuba.

SEED-ORIGINATED PLANTS AND INCORPORATION OF NEW GENOTYPES INTO FARMERS' COLLECTIONS

The majority of farmers interviewed are aware of plants originated from seeds. They can recognize them since these plants produce taproots instead of the characteristic secondary root pattern observed in plants originated from stem cuttings. Sometimes they notice their cotyledons at the seedling stage as well. However, by taking



Fig. 6. Dendrogram showing the distribution of names through the isozyme phenotypes using individuals sampled from and named by farmer FO. Codes as in Table 1. Cophenetic correlation coefficient—0.99.

only aerial parts into account, an adult seed-originated plant is indistinguishable from clonal propagated plants. Thus, noticing whether or not a particular individual is originated from a seed is not straightforward in the field. This is an important fact to bear in mind because when farmers cut stems for assembling a new garden, it does not necessarily involve digging up roots, which may cause the unconscious propagation of seed-originated plants.

In the same way farmer DF accurately recognized differences among landraces, he also demonstrated the ablity to recognize phenotypic differences between seed-originated plants and currently cultivated ones. This became evident when he described how he recognized a seedoriginated plant and matched its morphology with the general features of a known landrace. Yet, he observed that root color did not match with the root color he usually saw in that particular landrace. This would be expected since many perceptual traits such as leaf width and root suberous pellicle color (Graner 1942b), leaf vein color (Hershey and Amaya 1984), and stem color, growing habit, root parenchyma color and leaf shape (Hershey and Ocampo 1989) possess Mendelian inheritance. Segregation following a cross rearranges particular combinations of these traits found in the parents. Farmer DF is the only interviewed farmer who is concerned in marking and evaluating plants originated from seeds based on the simple criterion of relative productivity. He also evaluates, based on the same criterion, landraces that he receives from other farmers. It is only after these evaluations that he decides whether or not these new landraces will be incorporated into his collection.

The farmers' concerns regarding seed-originated plants varied considerably. Farmer AG stated that seed-originated plants and the plants he currently has in his collection are the same and did not demonstrate interest in distinguishing phenotypic differences between them. It follows that he probably incorporates recombinant seed-originated plants unconsciously into his gardens. However, farmer AG evaluates landraces that come from other farmers following the criterion of relative productivity before incorporating them into his collection. In farmer FA's garden, a seedling was observed, which was unintentionally weeded because it was out of stand. Another farmer, whose garden was not included in the study, stated that he usually weeds plants originated by seeds that are out of stand.

NAMES ASSOCIATED WITH PERCEPTUAL TRAITS AND ISOZYME VARIATION

Some landraces—Amarelinha (vellow). Rama-Preta (Black-Stem), Roxinha (Purple), and Rosinha (pink)-were clearly named after perceptual traits. Amarelinha has yellow roots, Rama-Preta has a dark petiole and leaf veins, Roxinha has purple young leaf and stems, and Rosinha has pink young stems. Names such as Vassourinha (little broom) with narrower lobules can also be included as a common name used currently among farmers, although not represented in this sample. Names like those are also common among farmers not only in this region of the São Paulo coast, but also in other regions in the Brazilian southeast. The isozyme phenotypic composition of these landraces varies considerably. Whereas Amarelinha, Rama-Preta, and Roxinha are composed of one isozyme phenotype within samples from individual gardens, Rosinha is composed of different phenotypes even within the FA collection. It is noticeable how some of these landraces seem to be discriminated more easily, even by farmers who showed some inconsistencies of classification, e.g., landrace Rama-Preta by farmer AG. Landrace identification by farmers involved observation of leaf surface, stem, and petiole but not root characteristics. The case of landrace Amarelinha is interesting in this respect. Farmer AG classified it consistently. The name makes reference to the root color, which is a trait he did not consider for classification purposes during the sampling process. Regardless of whether there are other traits that help its identification. farmer AG planted this landrace in a restricted place in the garden, which may have made the identification easier.

CONSISTENCY OF LANDRACE CLASSIFICATION ACROSS FARMERS

The existence of some common names allowed the assessment of the classification consistency across farmers. Landrace Maricá showed the same isozyme phenotype across farmers DF, FA, and FO (data not shown in Fig. 7). However, this does not seem to be the rule. As shown in Fig. 7, other landraces whose names are common among farmers do not have the same isozyme phenotypes. The

Unweighted pair-group average Percent disagreement



Fig. 7. Dendrogram showing the consistency of classification of landraces across farmers. The farmer abbreviations from where the individual was sampled were added to the name codes (Table 1). ZFO is Zumira sampled from FO, ZFA is Zumira sampled from farmer FA, RFA is Rosinha from farmer FA, ROFO is Roxinha from farmer FO and RODF is Roxinha from farmer DF Landrace Maricá was not included because the individuals possess basically the same isozyme phenotype across farmers. The landraces Landí have unique abbreviations. Cophenetic correlation 0.84.

landraces Roxinha (RO) between DF and FO, Zumira (Z) between FA and FO, and the Landís types (LA, LD, LF, LB, LP) between DF and AG possess different isozyme phenotypes across farmers, even though some of them, such as FA and FO, live in the same beach/ village. Equally noteworthy is how the landraces Landí-Preta (LP), Rama-Preta (RP), Aipí-Preto (AP), and Roxinha (RO), whose names that suggest dark perceptual traits (*preto* (black) and *roxo* (purple)), were similar for isozymes and formed a clear cluster in the dendrogram of Fig. 7.

CHRISTENING LANDRACES

A new genotype—either a seed plant or an imported individual from another place—can be named differently if the phenotypic differences observed by the farmer are strong enough to make him discriminate it as a different landrace. The criteria for this are subjective. In other words, for different farmers the same phenotypic difference may have a different weight. The landrace Mucaé-Roxo

(see Table 1) was cited by farmer DF as a case of a landrace originated from a seed plant and christened by an older farmer from the same beach/village of DF. As farmer DF described, this farmer identified a seed-originated plant of the landrace Mucaé noticing at the same time sufficient phenotypic differences to christen it as Mucaé-Roxo. Although it was not said which differences made him decide to christen the landrace, presumably it has something to do with color since plants possessing purple leaves, stems, petiole and/or external root pellicle are common. These differences were also enough for other farmers-as is the case of DF-to adopt the name associated with this particular genotype.

Considering the whole picture, dendrograms may be considered to be a reflection of several forces acting on cassava populations, including conscious selection, natural selection, sampling effects, crossings, and exchange with other farmers. Therefore, it is appropriate seeing these forces from the farmer perspective in an attempt to understand how they may influence the evolutionary dynamics and the genetic structure of the cassava population.

DISCUSSION

AMPLIFICATION OF GENETIC DIVERSITY

Genetic diversity may be amplified through two basic processes: mutation and/or recombination. Recombination is the faster process provided that there is sexual reproduction and preexisting genetic diversity. The most direct pieces of evidence that recombinants are effectively incorporated in cassava gardens in this region is the presence of seed plants in the gardens, and the attitudes of the farmers in relation to these plants revealing conscious or unconscious incorporation of them into their collections. As indirect evidence, we have the association of perceptual traits with different genotypes and the fact that some names encompass groups of similar genotypes, as is the case of the several Landis in the farmer DF's collection. A very similar pattern was observed by Elias et al. (2000) in Guvana.

Based on information from farmers about the landraces Landí, Mucaé-probably old landraces in the region-and Campista, Paranaense, and Carioca-probably more recently introduced in the region-we can understand the process whereby cassava diversity is generated within gardens. The landraces Landí and Mucaé possess not only greater isozyme diversity but also a greater number of names at the subvarietal level than Campista, Paranaense, and Carioca. There are at least two hypotheses to explain the genetic uniformity observed in the presumed recently introduced landraces. (1) Introduction may have caused a bottleneck effect and consequently, these landraces are now represented by only one genotype. These landraces could have been named as Carioca, Campista, and Paranaense either before or after incorporation into farmer DF's collection. This could also be the case of the landrace Rama-Preta in Farmer AG's collection. (2) They might be improved clones, which by definition are composed by only one genotype. In either case, there has not been enough time for new recombinants to appear, which could have amplified the genetic diversity of these landraces to levels similar to those found in Mucaé and Landí. In contrast, old landraces have been in the region for many generations of farmers. As recombinants were appearing in their gardens, they classified them as current landraces. Eventually differences became conspicuous enough for observant farmers to label the landrace with another name. This is a possible explanation for the existence of names for subvarieties Landí-Preto, Landí-Roxo, and Mucaé-Roxo. Therefore, since landraces Landí and Mucaé are older in the region, more time for the process of amplification of genetic diversity to take place elapsed compared to the landraces more recently introduced, such as the landraces Maricá. Paranaense. Carioca. and Campista. The additional taxonomic levels recognized by farmer DF for the traditional landraces Landí and Mucaé compared to the introduced landraces Paranaense. Carioca, Maricá, and Campista may be also seen as an evidence that the processes of genetic diversity amplification have not produced new genotypes in these presumed recently introduced landraces. Consequently, there has been no need for new names for variants arising in these landraces.

The inclusion of new genotypes from recombination events is not only a function of recombination rates alone but also a function of the intensity and type of selection against these recombinants. In other words, regardless of the number of seeds that are produced through crossing events, natural selection as well as artificial selection will regulate the effective rate of incorporation of new recombinants into farmers' gardens. Variation in the intensity of selection will influence the variation of effective incorporation of new genotypes into the gardens and the quality of these genotypes among farmers. This quality is certainly different if we consider the degree of consciousness with which farmers incorporate new recombinants into their gardens.

Evolutionary Implications of Folk Taxonomy

The diversity of cassava recognized by farmers tends to underestimate the actual diversity, a similar result to that obtained by Quiros et al. (1990) in their work with Andean potato. Nevertheless, the power of isozyme systems in discriminating the landraces may alter this trend, as was the case with farmer DF. The variation in the accuracy with which farmers discriminate their genetic material has important evolutionary implications because it is closely related to the level of conscious selection that is applied on the cassava population.

Boster (1985) argued that farmers select to increase the possibilities of perceptual characters as a way to enhance their power of discriminating different cultivars. For him this has the following consequences: (1) the overall range of variation in important taxonomic characters is increased; (2) large perceptual gaps between cultivars on these taxonomic characters are gradually filled or, in other words, the possibility of different combination of perceptual traits used as taxonomic labels are reduced with time: (3) important taxonomic characters of the cultivar species wide tend to vary independently of one another; (4) geographic races defined by taxonomic characters are absent; and (5) the important taxonomic characters that distinguish cultivars in a local inventory vary independently from one another just as the characters of the species-wide collection of cultivars do. Among the Aguaruna Indians of Peru, Boster showed that the most important characters used for discriminating different cassava cultivars are petiole color, leaf shape, and stem color, which agrees with what was observed in the present work. In fact, some landraces sampled for the present work conspicuously support Boster's arguments, as is the case of landraces Amarelinha (yellow), Rama-Preta (black-stem), Roxinha (purple), and Rosinha (pink). In addition, Boster (1985) showed that cultivars that were similar in these traits were more prone to be confused.

Utilizing perceptual characters to identify different landraces is especially important for crops whose economically important organ is hidden from daily view. This is the case with cassava and allows a given cultivar to be recognized as a distinct type even before a high yield, a pleasant taste, or some other useful characteristic is observed (Boster 1985). However, this is only possible because clonal propagation makes the clone a large linkage group, since its propagation system circumvents recombination. This characteristic may be paralleled to the modern techniques of marker assisted selection, in which quantitative traits controlled by many genes (such as production) are selected through the assessment of QTLs (quantitative trait loci), or markers linked with genes that contribute for these quantitative traits. In contrast, if the proposed model of evolutionary dynamics holds, eventual recombination through crosses allows

some gene independence. In this case, the advantage of using perceptual traits as labels for whole genotypes can thus be lost if the farmer does not realize that recombination takes place and the adaptation of a given landrace may be reduced with the inclusion of inferior genotypes into the group of genotypes that composes this landrace. Inferior genotypes can be thought of as genotypes that deviate from the optimum in the farmer's point of view. If, for example, root production concerns farmers, less productive genotypes are those that should be eliminated. In this sense, the most adapted genotype is also the one that produces more in the farming environment. Since it is the farmer who decides which genotype is planted and which should be discarded, the recognition of better-adapted genotypes is important. Differences between the abilities of AG and DF in recognizing and evaluating seed-originated plants, and differences between their respective accuracy in terms of taxonomic skills in general are reflected in their respective garden dendrograms, but might also be reflected in the efficiency with which these farmers use the available resources. If this indeed happens and farmer AG keeps reproducing inferior genotypes because he cannot differentiate the less productive from the more productive ones, the efficiency of his agriculture is probably lower compared to the one of farmer DF who has a better understanding of the genotype composition of his garden.

On the other hand, regardless of the criterion farmers use to select individuals for planting in their gardens, the frequency of neutral traits such as isozymes is governed by mutation and genetic drift. Considering the examples of landraces named after perceptual traits such as Roxinha or Rosinha and provided that recombination took place, theoretically any isozyme phenotype may be a Roxinha or Rosinha, once the individual possesses purple young leaf and stems, and pink young stems respectively.

Thus, Boster's (1985) arguments can be illustrated in light of the presented evolutionary dynamics model. Through experience a farmer may learn to associate a certain landrace with a certain environmental condition. For example, purple-stemmed plants (Roxinha) may appear to be more productive in sandy soils in a particular region. However, if recombination occurs, perceptual traits may become genetically independent from adaptive traits. It can be imagined, for example, that a Roxinha adapted to clay soils (instead of sandy soil) might exist in other regions. Hence, as Boster (1985) pointed out, the utility of a taxonomic system for a group of farmers is limited to a certain geographic region. It may also explain why Salick, Cellinese, and Knapp (1997) found that for the Amuesha Indians in Peru a large proportion of the common names given to cassava was unique to the particular extended family cultivating the variety. In contrast, some names shared by different families were given to diverse phenotypes. Finally, the rather low consistency of names across the farmers studied reinforces the trend described by Salick, Cellinese, and Knapp (1997) and the predictions of Boster's (1985) work.

The degree of similarity in agronomic traits among individuals belonging to a genetically heterogeneous landrace was not assessed in this work. The evaluation of their similarities is certainly an urgent subject for future work and will contribute to the understanding of the importance of perceptual selection in relation to selection based on agronomic traits in defining landraces.

SEED BANK, SEED PLANT LIFE HISTORY, AND FARMER SELECTION

As mentioned before, natural as well as artificial selection plays a major role in the incorporation of new recombinants into farmers' gardens. Based on the model of evolutionary dynamics (Fig. 1), natural selection in cassava occurs predominantly in individuals originating from seeds that experience selection episodes (Arnold and Wade 1984) similar to those in wild species. Indeed, by tracing life-history events of these individuals it is possible to understand how selection operates on them. After being dispersed, a seed may or may not find an adequate site to germinate and establish. The seed can germinate at any time, especially if it possesses dormancy. There are some dormancy types where environmental factors trigger the germination of the seeds (Begon, Harper, and Towsend 1996). This is likely the case with cassava seeds, as they germinate when the garden is open. This is also consistent with the fact that cassava wild ancestors are forest gap colonizers and heliophytes (Gulick, Hershey, and Alcazar 1983; Jennings 1979). The existence of a seed bank implies that the farmer recurrently cultivates an area, such that older gardens can produce a seed bank. Many farmers, including farmer DF, noticed the presence of cassava seedlings even in gardens abandoned for over 20 years, in agreement with the observations of Salick, Cellinese, and Knapp (1997). If a seed germinates, the plant is subjected to intraspecific competition from other plants. The intensity of competition is probably dependent on the position relative to other plants planted by the farmer and the time of germination in relation to that of the cultivated plants. At this time, the farmer may notice a seedling or a small plant and influence its survivorship and reproduction. Since the behavior of farmers with respect to these plants varies, human selective pressures at this stage are rather erratic. Seed-originated plants are subject to herbivory at all stages of their development. They may also possess relatively low rooting capacity and will not be propagated by humans, because all artificial propagation is via stem cuttings. This can be interpreted as a selective pressure against seed-originated individuals that cannot be propagated in the cultivation system. Therefore, once an individual originated from seed has established, and if this individual is a strong enough rooter to be propagated clonally, the sieve of natural selection is strongly reduced. The farmer needs only to evaluate productivity or some other factor of interest, since these factors will reflect the whole range of selective pressures that the individual had to overcome. Nevertheless, evaluating the performance of seed-originated plants is not commonly practiced by the farmers consulted in this study. Variation in this respect is closely related to their ability of recognizing differences between seedoriginated plants and the clonal plants of their collections. Farmers who do not recognize differences do not find it necessary to evaluate seed-originated plants since they consider these plants the same as the others they have in their collections. The majority of farmers consulted only evaluate the performance of landraces imported from other places before incorporating them into their collections.

According to the farmers consulted, cassava can be severely affected by leaf-cutter ants, wild pigs, and a sort of soil fungus (Saporén) that causes root decay. However, they all believed that these deleterious agents are generalists. In other words, these agents show no preference for one or another landrace and, if this is true, their action has probably little or no evolutionary consequences on the cassava populations. Even though there might be small preferences among the pests for one or another landrace, the fact that farmers do not notice it suggests that pests may not affect the desired composition of landraces a farmer wants to have in his garden.

BREEDING AND VARIATION OF FARMERS CLASSIFICATION SKILLS AMONG THE CAIÇARAS

Farmers on the São Paulo Coast demonstrated in general a rather loose classification system whose main consequence is an ineffective conscious selection. It might seem at first sight that farmers' conscious selection does not play a major role in the evolutionary dynamics of cassava populations. However, there is variability in farmer skills not only in relation to the classification system but also in relation to the degree of awareness concerning the phenotypic differences among landraces, seed plants, and introduced landraces. Salick, Cellinese, and Knapp (1997) described the importance of the Shaman of the Amuesha Indians in the maintenance and development of cassava landraces. The Shaman position seems to be a specialized job done by the most skilled individual in the community. On the other hand, the Caiçara community does not possess such a kind of specialization. It is possible to learn how these differences in individual classification skills can be important to the whole community by proposing some testable hypotheses.

First of all, if farmers who are less skilled at classifying germplasm end up cultivating cassava less efficiently, these farmers are presumably the ones who most introduce landraces from other farmers because they are always searching for more productive genotypes. If this happens, the turnover of landraces in less-skilled farmers' collections must be higher than the turnover in more-skilled farmers' collections. It can also be hypothesized that the flow of landraces among farmers is asymmetric, occurring predominantly from skilled farmers to lessskilled farmers. Skilled farmers would behave in these communities as a sort of breeder who, similarly to the Amuesha Shaman, maintains old varieties and provides new genotypes to the whole community, although among the Caiçaras, this function is not explicit.

EVOLUTIONARY MODEL AND APPROPRIATE SCALE OF STUDY

The existence of recombinants within gardens, the recognition of seed-originated individuals by the farmers, and the patterns observed in the dendrograms support the validity of the underlying model of evolutionary dynamics of cassava. The large number of genotypes that are usually found in traditional gardens (Boster 1984, 1985; Kerr and Clement 1980; Salick, Cellinese, and Knapp 1997) can be viewed as a balance between the rate of genotype addition through introduction from other farmers, recombination and mutation, and rates of genotype extinction through selection and random processes. It is important that we understand the mechanisms that determine these rates. However, another spatio-temporal scale must be chosen to study them thoroughly. Exchange of genotypes among farmers is not a local phenomenon. Moreover, the rates with which new genotypes are generated by recombination and particularly by mutation are probably low in any given garden. Conversely, if we consider a set of gardens from different farmers organized as a metapopulation (Husband and Barrett 1996), even a rare, favorable mutation may play an important role in generating genetic diversity because the entire population is amplified and consequently the likelihood of this rare event is also amplified. It follows that if indeed a favorable genotype appears in a garden, regardless of the mechanism that generated it, it will spread faster or slower throughout the region depending on the amount of material exchanged by farmers.

The understanding of how phenomena on different spatio-temporal scales interact and influence one another is a common challenge in ecology. The present study addressed evolutionary and ecological events on a local scale, but it is expected that the results have some significance on a much broader scale, particularly when the goal is the understanding of the large amounts of genetic diversity observed in cassava in light of its evolutionary dynamics.

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LITERATURE CITED

- Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution 38(4):709–719.
- Begon, M., J. L. Harper, and C. R. Towsend. 1996. Ecology: individuals, populations and communities. 3rd Ed. Blackwell Science, Oxford.
- Boster, J. S. 1984. Classification, cultivation, and selection of Araguaruna cultivars of *Manihot esculenta* (Euphorbiaceae). Advances in Economic Botany 1:34–47.
- Boster, J. S. 1985. Selection for perceptual distinctiveness: evidence from Aguaruna cultivars Manihot esculenta. Economic Botany 39(3):310–325.
- Clayton, J. W., and D. N. Tretiak. 1972. Aminecitrate buffers for PH control in starch gel eletrophoresis. Journal of the Fisheries Research Board of Canada 29:1169–1172.
- Cury, R. 1993. Dinâmica evolutiva e caracterização de germoplasma de mandioca (*Manihot esculenta* Crantz) na agricultura autóctone do sul do Estado de São Paulo. Piracicaba, 103 p. Dissertação (Mestrado)-Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo.
- Dominguez, C. E., L. F. Ceballos, and C. Fuentes. 1984. Morfologia de la planta de yuca. *In Domin*guez, C.E. *Yuca*: investigacion, producion y utilizacion. Cali: CIAT. p. 29–49.
- Elias, M., O. Panaud, and T. Robert. 2000. Assessment of genetic variability in a traditional cassava (*Manihot esculenta* Crantz) farming system, using AFLP markers. Heredity 85(3):219–230.
- Graner, E. A. 1942a. Notas sobre o florescimento e frutificação da mandioca. Bragantia 2(1):1-12.
- ———. 1942b. Genética de Manihot. I Hereditariedade da forma da folha e da coloração da película externa das raízes em Manihot utilissimum Pohl. Bragantia 2(1):1–12.
- Gulick, P., C. Hershey, and J. E. Alcazar. 1983. Genetic resources of cassava and wild relatives. Rome: International Board for Plant Genetic Resources (IBPGR). 56p.
- Hawkes, J. G. 1991. Centros de diversidad genética vegetal en Latinoamérica. Diversity 7(1/2):7–9.
- Hershey, C., and A. Amaya. 1984. Genética, citogenética, estrutura floral y tecnica de hibridacion de la yuca. *In* Dominguez. C.E. Yuca: Investigacion, producion y utilizacion. Cali: CIAT, p.113– 125.

—, and N. Ocampo.1989. Yuca—Boletin informativo 13(1):1–5.

- Husband, B., and S. C. H. Barret. 1996. A metapopulation perspective in plant population biology. Journal of Ecology 84:461–469.
- Iglesias, C. A., C. Hershey, F. Calle, and A. Bolaños. 1994. Propagating cassava (*Manihot esculenta*) by sexual seed. Experimental Agriculture 30:283–290.

- Jennings, D. L. 1979. Cassava. Pages 81–84 in N.W. Simmonds, Evolution of crop plants. Longman, London.
- Johns, T., and S. L. Keen. 1986. Ongoing evolution of the potato on the altiplano of eastern Bolivia. Economic Botany 40(4):409-424.
- Kerr, W. E., and C. R. Clement. 1980. Práticas agrícolas de conseqüências genéticas que possibilitaram aos índios da Amazônia uma melhor adaptação às condições ecológicas da região. Acta Amazônica 10(2):251–261.
 - , and D. A. Posey. 1984. Informações adicionais sobre a agricultura dos Kayapó. Interciência: 9(6):392–400.
- Lefèvre, F., and A. Charrier. 1993. Heredity of seventeen isozyme loci in cassava (*Manihot esculenta* Crantz). Euphytica 66:171–178.
- Manly, B. F. J. 1994. Multivariate statistical methods: a primer. Chapman & Hall, London.
- Martins, P. S. 1994. Biodiversity and agriculture: patterns of domestication of brazilian native plant species. Anais da Academia Brasileira de Ciências 66: 219–224.
- Nassar, N. M. A. 1989. Broadening the genetic base of cassava, *Manihot esculenta* Crantz, by interspecific hybridization. Canadian Journal of Plant Science 69(3):1071–1073.
- Nye, M. M. 1991. The mis-measure of manioc (*Manihot esculenta*, Euphorbiaceae). Economic Botany 45(1):47–45.
- **Olsen, K. M., and B. A. Schaal.** 1999. Evidence on the origin of cassava: phylogeography of *Manihot esculenta*. Proceedings of the National Academy of Science USA, 96:5586–5591.
- Papy, L. 1957. À margem do império do café: a fachada atlântica de São Paulo. Boletim Geográfico, 15:139–165.
- Quiros, C. F., S. B. Brush, D. S. Douches, K. S. Zimmerer, and G. Huestis. 1990. Biochemical and folk assessment of variability of Andean cultivated potatoes. Economic Botany 44(2):254–266.
- **Rogers, D. J.** 1972. Some further considerations on the origin of *Manihot esculenta* Crantz. Tropical Root and Tuber Crops Newsletter 6:4–10.
- Salick, J. 1992. Crop domestication and evolutionary ecology of cocona (*Solanum sessiliflorum* Dunal). Pages 247–285 in M. K. Hecht, et al. eds., Evolutionary biology. Plenum Press, New York.
- , N. Cellinese, and S. Knapp. 1997. Indigenous diversity of cassava: generation, maintenance, use and loss among Amuesha, Peruvian upper Amazon. Economic Botany 51(1):6–19.
- Sauer, J. 1952. Agricultural origin and dispersal. American Geographic Society, New York.
- Scandalios, J. G. 1969. Genetic control of multiple molecular forms of enzymes in plants: a review. Biochemical Genetics 3:37–39.
- Schmidt, C. B. 1958. A mandioca: contribuição para o conhecimento de sua origem. Boletim da Agricultura 25:73–128.