

Biochemical and Folk Assessment of Variability of Andean Cultivated Potatoes¹

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*Isozyme markers were used to survey the genetic variability of non-bitter potatoes in 10 subsistence fields of Andean farmers at 3600–3850 m above sea level. Sixty-seven percent of the varieties were tetraploids corresponding to the species *Solanum tuberosum* ssp. *andigena*, 14% were triploids, probably corresponding to the species *S. × chaucha*, and 13% were diploids corresponding to the species *S. stenotomum*, *S. phureja*, and *S. goniocalyx*. The isozyme information served to determine the consistency of the folk naming system. We found a high degree of correspondence between farmer identification and electrophoretic phenotypes. The consistency of the folk system in electrophoretic terms depended on the farmer who was interviewed. The most common incongruity consisted of calling different electrophoretic phenotypes by the same variety name, leading to a slight underestimation of genetic variability present in the fields. The amount of variability observed in the sample of the Andean potato population was superior to that present in North American and European varieties. This was measured in terms of number of alleles, number of electrophoretic phenotypes and percent of heterozygosity. This finding supports the impression that a substantial amount of yet unexploited variability remains in Andean potato populations.*

*Evaluación bioquímica y popular de la variabilidad interespecífica de las papas cultivadas en los Andes. En este trabajo se da a conocer los resultados de un estudio genético sobre variedades de papa dulce en los Andes, realizada por medio de marcadores isoenzimáticos en parcelas de subsistencia localizadas entre 3600 y 3850 metros sobre el nivel del mar. Se encontró que 67% de las variedades muestreadas eran tetraploides de la especie *S. tuberosum* ssp. *andigena*, 14% triploides probablemente de la especie *S. × chaucha*, y 13% diploides de las especies *S. stenotomum*, *S. phureja* and *S. goniocalyx*. La información isoenzimática fue útil en la evaluación de la precisión del sistema folklórico para identificar variedades. Se encontró un alto grado de asociación entre el sistema de clasificación usado por el campesino para denominar sus variedades, y los fenotipos electroforéticos. La precisión del sistema de identidad folklórico en términos electroforéticos dependió del campesino entrevistado. La discrepancia mas frecuente entre los dos sistemas de nomenclatura consistió en llamar diferentes fenotipos electroforéticos con el mismo nombre varietal, lo que resultó en una subestimación de la variabilidad genética presente en los campos. El nivel de variabilidad observado en la muestra de papas de la población andina fue superior al observado en variedades norteamericanas y europeas. La variabilidad se midió en base al número de alelos, número de fenotipos electroforéticos y porcentaje de heterocigosidad. Estos resultados están de acuerdo con la impresión general de que todavía existe mucha variabilidad en variedades de papa andinas que no ha sido aún explotada.*

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Great intraspecific diversity of cultivated plants is one of the hallmarks of agricultural evolution, but this diversity presents numerous scientific issues. Why is there so much intraspecific diversity of cultivated species, and why is this exaggerated in certain regions? What is the contribution of ecological, agronomic, and human factors to the origin and maintenance of this diversity? What is the best way to describe and analyze this diversity? How is diversity affected by agricultural, economic and other changes?

Two primary steps in answering these questions are to understand the genetic base of the crop and to describe the ways in which farmers perceive and select crops so as to affect diversity. Investigating how and why farmers in centers of crop evolution maintain diversity can usefully begin with folk taxonomies and their relation to the genetics of the crop (Brush 1986). For whatever reason that diversity is maintained, farmers must have a specific means to accomplish this, and a folk nomenclature and taxonomy can be helpful toward this end. Folk nomenclature and taxonomies create labels and keys to distinguish morphological differences. The work of Boster (1985) on Aguaruna taxonomy of *Manihot esculenta* Cranz shows that folk taxonomy of great intraspecific variability can be understood as a means to maintain diversity and that diversity is sought for its own sake and not for a specific reason. Folk taxonomy allows Aguaruna cultivators to make distinctions that have no apparent utility, although culinary and pharmacological differences are noted between some folk varieties. Most important, there are no recognized agronomic characteristics incorporated into the Aguaruna folk taxonomy.

The fact that folk taxonomies are designed to satisfy cultural rather than agronomic reasoning forces the question of their utility for understanding the biological dynamics of a crop. It has been repeatedly shown that interspecific folk taxonomies are biologically accurate (Alcorn 1984; Berlin et al. 1974), but does this accuracy extend to the intraspecific level? Do folk identification and classification provide us with guides to estimating genotypic diversity? These questions are important because crop germplasm collections are often based to some degree on folk taxonomies. Geneticists at the International Potato Center have reduced the number of accessions in the Center's clonally propagated collection because of their conviction that extensive duplication existed. The idea of duplication derives, in part, from the notion that the folk taxonomies that underlie the original accession list are unreliable and tend toward overclassification.

Our article examines the identification of the cultivated potato (*Solanum tuberosum* L., Solanaceae) in reference to its cultivation in the Andes, its center of domestication. It reviews the means to classify the great intraspecific diversity of potatoes employed by farmers and geneticists. The article presents the use of biochemical markers as a way to cope with the great intraspecific diversity encountered in the Andean potato crop, and it correlates the identification of folk varieties and those determined by biochemical means.

VARIETAL CLASSIFICATION OF THE CULTIVATED POTATO

The diversity of the cultivated potato has posed an intriguing and challenging taxonomic problem for several generations of potato geneticists (Correll 1962; Hawkes 1979). Four ploidy levels ($2n = 2x = 24$ to $2n = 5x = 60$) comprise the

cultivated potatoes. Under the taxonomic system of Hawkes (1979), which is currently the most widely used, these four ploidy levels divide into eight cultivated species (four diploids, two triploids, one tetraploid, and one pentaploid). In Andean potato fields, the tetraploid *S. tuberosum* ssp. *andigena* (Juz. et Buk.) Hawkes is by far the most prominent, accounting for more than two thirds of the planted potatoes (Brush et al. 1981).

Ploidy and species level classification are of somewhat limited value for treating intraspecific diversity at the field level. While some plants in a typical field may be of different species or ploidy levels, most of them are of a single subspecies (*andigena*). Visual and agronomic distinctiveness may be greater within this subspecies than across the eight cultivated *Solanum* species. Because of the potato's predominantly asexual propagation, clonal distinctiveness is particularly important. This propagation works against the survival of products of genetic exchange and hybridization both between and within species. Somatic mutation is common and will not be revealed at the species or ploidy level. Polyploidization and hybridization may create different species and ploidies out of morphologically similar potatoes.

While the geneticist may be interested in describing potato populations, where species and ploidy level are meaningful, the farmers who actually manage the crop are concerned with the individual plant and variety. The selection, exchange, and maintenance of tubers is done at the variety level. This suggests that an understanding of population dynamics of the Andean potato must somehow include a more sophisticated treatment of the crop at the variety level than is allowed in the current taxonomic tools. However, varietal identification is plagued by such problems as somatic mutation, hybridization, and a daunting amount of data to be analyzed. The elaborate naming system of farmers is often viewed with skepticism by geneticists, partly because the specific knowledge base that determines folk classification is not formalized, and there is no easy way to estimate how consistent folk taxonomies are between individual farmers or between communities.

Nevertheless, we ignore varietal diversity and its identification by farmers at our own scientific peril since the actual dynamics of the potato crop are significantly determined at the varietal level. It has been firmly established for the potato and for other crops that folk identification and taxonomy are the keys to understanding the behavioral patterns that affect crop evolution (Boster 1984; Brush et al. 1981; Johns 1985). The Andean folk classification system for potatoes is based on tuber characteristics, cultivation, edibility, processing and frost resistance. Potato folk taxonomy helps determine cultivation practices that make the Andean potato fields dynamic evolutionary systems where new varieties and perhaps new species are generated by cross hybridization and introgression from related wild species (Jackson et al. 1977; Johns and Keen 1986).

Concern for the varietal level requires that new taxonomic techniques be mobilized, since the conventional ones used for the species and ploidy level description miss most of the intraspecific diversity. Further, the data requirements of using conventional morphological markers for variety identification are so large as to be essentially impossible. We have found that biochemical markers, specifically isozymes, provide effective tools for describing this great diversity.

APPLYING BIOCHEMICAL MARKERS TO ANDEAN POTATOES

Recent research in the Peruvian Andes by Brush indicates that a high degree of diversity is still maintained by peasant cultivators. Inventories of potatoes stored in households after harvest revealed that households in the Paucartambo area east of Cusco maintain an average of 9.6 distinct named varieties. Some households were found to maintain as many as 26 varieties, while others kept as few as a single variety. The traditional planting procedure in southern Peru fields is to sow as many as five small tubers in a single hole opened by the footplow. These tubers might comprise different varieties and even species of different ploidies. One reason for planting heterogeneous fields is to enhance the diet by having a mixture of flavors, textures, shapes, and colors. The great diversity and heterogeneity of these fields pose interesting problems of variety identification and classification by the farmers in order to maintain and conserve the original variability. A folk nomenclature based primarily on tuber morphology has been previously described (Brush et al. 1981).

In the last few years a number of biochemical markers useful for potato clone identification have been reported (Oliver and Zapater 1984; Quiros and McHale 1985; Stegemann and Loeschke 1977). In particular, isozyme markers are most useful as biochemical markers because of their known genetic basis and co-dominant expression (Quiros and McHale 1985). These have been used to follow up segregations in interploidy matings and to generate experimental data on the transmission of heterozygosity by the diploid strains with the ability to produce $2n$ gametes (Douches and Quiros 1987, 1988).

The objective of this article is to survey with isozyme markers the actual genetic variability of non-bitter potatoes in subsistence Andean fields at 3600–3850 m above sea level. This information serves to determine the accuracy of the folk classification system for potatoes in the Andes.

MATERIALS AND METHODS

Field sampling

Ten fields in a radius of 30 km and located between 3600 to 3850 m above sea level were sampled in the Province of Paucartambo, Department of Cusco, Peru (Table 1). After we sampled a single tuber from 200 plants in each field chosen at random, the tubers were bulked together in a pile according to tuber similarity. The farmer was asked to examine each pile, to regroup piles according to his criteria, and to name each unique group or individual tuber. Then, the tubers were washed and placed in paper bags identified by variety and by field. The only exception was the field at Maqopata (field number 10) where the farmer classified the tubers as they were harvested.

Because of the larger number of tubers, when a variety had more than 30 tubers per bag, a representative sample of 10–25 tubers was taken for the electrophoretic determination depending on the level of morphological heterogeneity present in the bag.

Isozyme analysis

Horizontal starch gel electrophoresis was employed to assay for nine enzyme systems disclosing 12 loci useful for genotyping the tubers of each variety (Douches and Quiros 1987; Quiros and McHale 1985). These are phosphoglucisomerase 1 (PGI-1), phosphoglucomutase 1 and 2 (PGM-1 and PGM-2), 6 phosphogluconase dehydrogenase 3 (6PGD-3), isocitrate dehydrogenase 1 (IDH-1), malate dehydrogenase 1 and 2 (MDH-1 and MDH-2), acid phosphatase 1 (APS-1), glutamate oxaloacetate

TABLE 1. FIELD LOCATION, ALTITUDE, FARMER NAME AND NUMBER OF TUBERS FOR *SOLANUM* SPECIES SAMPLED PER FIELD (PAUCARTAMBO, CUSCO, PERU).

Farmer	Location	Altitude (m)	Tubers
1 Jesus Amao	Colquepata	3650	70
2 Julio Amao	Colquepata	3600	47
3 Sebastian Mauri	Sipascancha Alta	3750	101
4 Trinidad Sandi	Mollamarca	3680	135
5 Gomercindo Champi	Mollamarca	3720	45
6 Augustin Turpo	Mollamarca	3750	37
7 Santos Chipa	Sispacancha Alta	3700	76
8 Hipolito Mamani	Carpapampa	3830	72
9 Pablo Mamani	Carpapampa	3780	62
10 Faustino Illa	Moqopata Alta	3850	185

transaminase 1 and 2 (GOT-1 and GOT-2), peroxidase 3 (PRX-3), and shikimic acid dehydrogenase (SKD-1).

For the electrophoretic assay a tuber eye was excised from a tuber and crushed in 75 μ l of 0.1 M Tris-HCl pH 7.0 buffer containing 2% glutathione as antioxidant. The extract was soaked into 3M filter paper wicks and subjected to electrophoresis.

Other tuber determinations

The following tuber characteristics are recorded: skin and flesh color, tuber eyes (color, depth, shape), skin texture, and shape. After the electrophoretic survey, chromosome counts were made for a representative tuber of electrophoretic phenotype. For this purpose the tubers were wrapped in moistened towels and introduced into covered plastic shoe boxes. Since most of the tubers were already sprouted, they formed roots readily at the base of the sprouts. The root tips were collected, fixed in alcohol-acetic acid (3:1), and stained with Feulgen.

Genetic parameters

Three parameters were determined in the Andean tuber population, percent heterozygosity (H), total number of alleles, and total number electrophoretic phenotypes in a per locus basis. These values were compared to those recorded in 24 North American and European potato cultivars: 'Russet Burbank', 'Norchip', 'Red Pontiac', 'Gold Rush', 'Kathadin', 'Rosa', 'Bintje', 'Sangre', 'Bel Rus', 'Pioneer', 'Atlantic', 'Monona', 'Targee', 'Nooksack', 'Shepody', 'Superior', 'Agassiz', 'Red Norland', 'Alpha', 'Centennial Russet', 'Bison', 'Lemhi', 'Sebago', and 'Red La Soda'.

Species identification

In an attempt to electrophoretically identify by specific allozymes the various species cultivated in the fields, six to 18 accessions of the species *S. stenotomum* Juz. et Buk., *S. goniocalyx* Juz. et Buk., *S. phureja* Juz. et Buk., *S. × chaucha* Juz. et Buk., and *S. tuberosum* ssp. *andigena* were electrophoretically surveyed. Also, 16 accessions of the bitter species *S. × juzepzukii* Buk. (3 \times) and 4 of *S. × curtilobum* Juz. et Buk. (5 \times) were included in the survey.

Comparison between folk and isozyme identification

An agreement index was developed to express a ratio of the proportion of tubers represented by the most numerous electrophoretic phenotype multiplied by the proportion of farms in the sample whose naming agrees with this phenotype. It is arrived at by comparing the number of tubers in the dominant sub-group with the total number of tubers in the group and the number of farmers agreeing on name with the total number of farmers who had that electrophoretic phenotype. A score of one indicates perfect congruence (six cases) and a score of zero indicates that there was no congruence across farms for the electrophoretic phenotypes found under a common name (11 cases).

TABLE 2. NUMBER OF VARIETIES REPORTED AND ACTUAL NUMBER OF ELECTROPHORETIC PHENOTYPES OBSERVED FOR *SOLANUM* SPECIES SAMPLED (PAUCARTAMBO, CUSCO, PERU).

Farmer	Sample size	Varieties reported	Phenotypes observed	Difference
1 Jesus Amao	70	11	15	4
2 Julio Amao	47	14	16	2
3 Sebastian Mauri	101	22	31	9
4 Trinidad Sandi	135	17	34	17
5 Gomercindo Champi	45	8	10	3
6 Augustin Turpo	37	11	10	-1
7 Santos Chipa	76	15	24	9
8 Hipolito Mamani	72	14	20	6
9 Pablo Mamani	62	16	17	1
10 Faustino Illa	185	43	36	-7

RESULTS AND DISCUSSION

Correspondence of folk names and electrophoretic phenotype

Two major results are evident from this research. First, there is an overall high degree of correspondence between farmer identification and electrophoretic phenotype. Second, the accuracy of the folk naming system in electrophoretic terms depended on the farmer doing the classification.

Two types of incongruity were evident within each field. The first type consisted in calling different electrophoretic phenotypes by the same variety name while the second type consisted in calling the same electrophoretic phenotypes by more than one variety name. The most common error of inconsistency was of the first type, leading to a general underestimation of the genetic variability present in the fields. In only two farms (numbers 6 and 10) more varieties than genotypes were observed. Table 2 summarizes the data on tuber identification from the 10 fields. The range of inconsistency in tuber identification went from 3% to 22%. The highest number of underestimated varieties (17 or 50%) was also observed in the same field (Trinidad Sandi, #4), while the lowest was observed for Pablo Mamani (#9) (1 or 5.9%), excluding the fields of Augustin Turpo (#6) and Faustino Illa (#10) where the number of varieties was overestimated. This wide variation represents, in part, lack of enthusiasm or desire by the farmer to spend the time to do an accurate identification, but it also indicates the wide range of skill and knowledge among farmers. Nevertheless, the inconsistency was justifiable in cases where the tubers were morphologically very similar as far as skin color and shape was concerned. However, slicing of the tubers revealed flesh color differences, which were further substantiated by electrophoretic differences.

A good example of this situation was observed for the variety *Yana Imilla* where three phenotypes were detected (Fig. 1-3). Although the distinction to us is enough to separate the three as different varieties, it is possible that the range of variation within *Yana Imilla* was not enough for the Andean farmer to consider them different entities. The consistency of variety names among fields was much lower than within fields, but the level of agreement is still about half. That is in cases where two farmers give the same name for tubers, they are naming similar

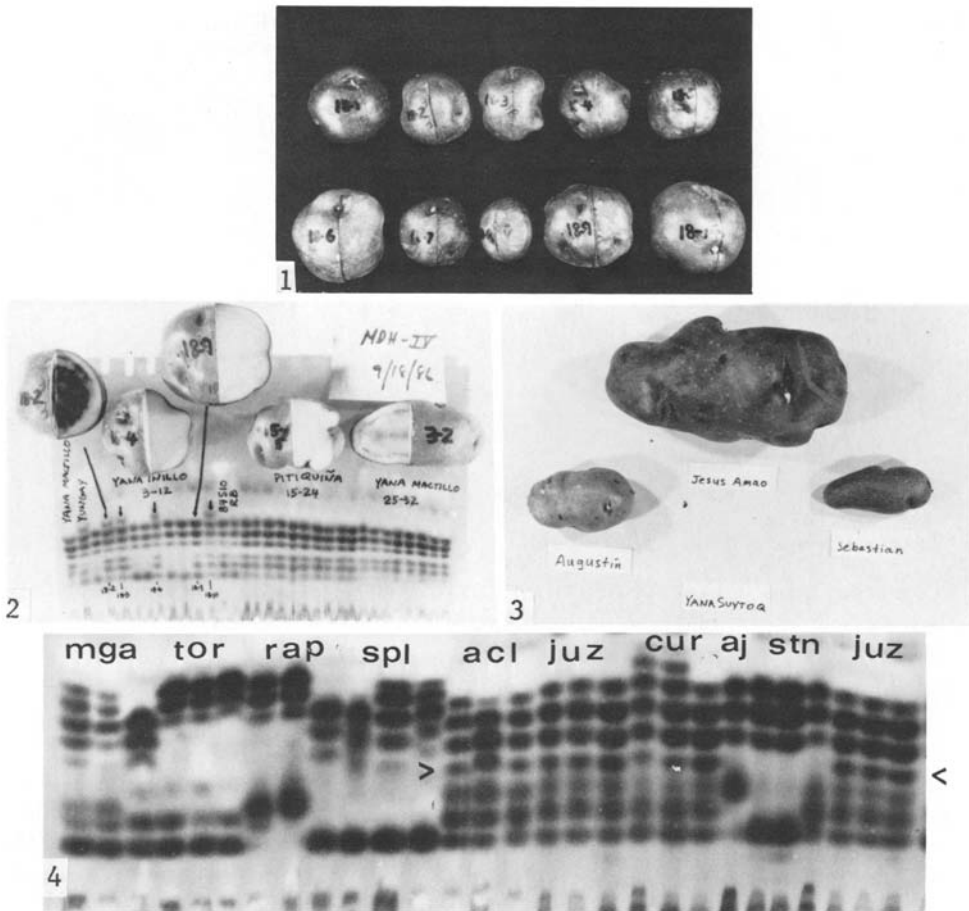


Fig. 1-4. Andean cultivated potatoes. **Fig. 1.** Example of inconsistent classification within *Solanum tuberosum* ssp. *andigena* collected in Paucartambo, Cusco, Peru. Morphologically similar tubers classified as *Yana Imilla*. **Fig. 2.** Example of inconsistent classification within *S. tuberosum* ssp. *andigena* collected in Paucartambo, Cusco, Peru. Sample *Yana Imilla* tubers disclosing three different phenotypes for flesh color and for the enzyme MDH. **Fig. 3.** Example of inconsistency in classification across three fields for the variety *Yana Suyt'u*. Three different morphotypes of *Solanum* species from Paucartambo, Cusco, Peru, with same name. **Fig. 4.** Discrimination of bitter from non-bitter potato species on the basis of the enzyme MDH. The bitter species *S. × juzepzukii* (*juz*) and *S. × curtilobum* (*cur*) carry the unique enzyme $Mdh-2^3$ also present in their ancestral species *S. acaule* (*acl*) (arrows). The non-bitter cultivated species and other wild species lack this unique isozyme [*mga* = *megistacrolobum*, *tor* = *toralaparum*, *rap* = *raphanifolium*, *spi* = *sparsipilum*, *aj* = *ajanhuiri*, *stn* = *stenotomum* (Huaman and Ross 1985)]. Three accessions per species are displayed, except for *ajanhuiri*, which includes only one accession.

electrophoretic phenotypes 50% of the time. Comparison between farms is difficult because of the common presence of different electrophoretic phenotypes within a single name. Among 32 named varieties that were found on more than one farm, 19 had more than one electrophoretic phenotype on at least one farm. The average for these multiple electrophoretic phenotypes was 2.9. A common pattern of inconsistency between farms was for agreement on a dominant electrophoretic

TABLE 3. AGREEMENT ACROSS FARMS ON IDENTIFICATION OF LIKE ELECTROPHORETIC PHENOTYPES OF *SOLANUM* SPECIES SAMPLED (PAUCARTAMBO, CUSCO, PERU).

A Variety	B No. tubers in dominant sub-group	C Total no. tubers	D No. farms in agreement	E Total no. farms w/phenotype	F Agreement index*
1	18	30	2	4	0.300
2	6	21	2	5	0.114
3	12	12	2	2	1.000
4	2	4	2	3	0.333
5	13	13	2	2	1.000
6	3	9	2	2	0.333
7	17	21	0	2	0.000
8	2	5	0	2	0.000
9	2	2	2	2	1.000
10	11	11	2	2	1.000
11	1	2	0	2	1.000
12	19	22	3	3	0.864
13	7	17	0	2	0.000
14	11	12	2	2	0.917
15	12	14	2	3	0.571
16	11	21	2	3	0.347
17	1	3	0	2	0.000
18	10	11	0	2	0.000
19	17	23	3	3	0.739
20	1	3	0	2	0.000
21	29	45	6	6	0.644
22	10	13	0	2	0.000
23	10	10	2	2	1.000
24	7	14	0	2	0.000
25	1	2	0	2	0.000
26	10	11	2	2	0.909
27	10	16	0	3	0.000
28	43	54	2	5	0.319
29	33	34	5	5	0.319
30	16	16	2	2	1.000
31	51	70	4	6	0.486
32	2	3	0	2	0.000
Avg. agreement index				0.43279304	
St. Dev.				0.41865658	

* Agreement Index (F) = (B/C)(D/E).

phenotype but disagreement on less dominant tubers. Eleven names with accessions from different farms had no multiple electrophoretic phenotypes, and in these cases there was congruence between the name and electrophoretic phenotype on six. Table 3 gives the results of a comparison between names and 32 electrophoretic phenotypes found across our sample of farms. This comparison expresses the dominance of a single electrophoretic phenotype and congruence between farms. An agreement index of one means that the same electrophoretic phenotype was given the same name on all farms where it was found. An index of zero indicates that a different name was given on each farm. Scores between zero and one result when only some farmers agreed on the name or when some electrophoretic phenotypes were given two or more names by the same farmer.

TABLE 4. TUBER NAMES BY ELECTROPHORETIC PHENOTYPE FOR *SOLANUM* SPECIES SAMPLED (PAUCARTAMBO, CUSCO, PERU).

	Name	No. tubers	Skin color
Phenotype 1			
Farm 10	<i>Yuraq</i> ("white") <i>K'usi</i>	76	white
	<i>Yana</i> ("black") <i>K'usi</i>	34	black
	<i>Huayro</i>	1	?
Farm 8	<i>Yuraq K'usi</i>	10	black
Phenotype 2			
Farm 10	<i>Soqowaqoto</i>	4	white
Farm 3	<i>Soqowaqoto</i>	2	white
Farm 4	<i>Yana Ch'eqepphoro</i>	6	black
	<i>Yuraq Ch'eqepphoro</i>	10	white
	<i>Wallichia</i>	1	?
Farm 6	<i>Ch'eqepphoro</i>	1	?
Phenotype 3			
Farm 10	<i>Yana K'usi</i>	29	black
Phenotype 4			
Farm 10	<i>Yuraq Waqoto</i>	1	?
Farm 4	<i>Alqa Qompis</i>	4	red
	<i>Qompis</i>	7	red
Phenotype 5			
Farm 3	<i>Onor Qompis</i>	8	red
Farm 4	<i>Alqa Warmi</i>	2	red
Farm 5	<i>Alqa Qompis</i>	9	red
	<i>Qompis</i>	6	red
Farm 6	<i>Qompis</i>	10	red

In the comparison of names and electrophoretic phenotypes across farms, two types of inconsistencies were, again, evident: the calling of different varieties by the same name and naming a variety by more than two names. This latter inconsistency may be hard to distinguish from synonymy, which is not an error. Synonyms are recognized by farmers and cannot be considered misclassifications.

The previous discussion began with a potato name found on more than one farm and then examined the electrophoretic phenotypes associated with that name. By beginning with the electrophoretic phenotypes and looking for associated names, a pattern of synonymy and some splitting is revealed. Table 4 shows the names for five electrophoretic phenotypes. For phenotype 2, for instance, the names *Soqowaqoto* and *Yuraq Ch'eqepphoro* appear to be synonyms. Farmer 4 split this phenotype into two names according to color, and he apparently erred in the *Wallichia* case.

Our examination of naming in comparison to electrophoretic phenotypes both on single farms and between farms clearly indicates that farmers err in naming principally by underestimating the degree of genetic diversity in their collections. There is far more lumping of different genotypes than splitting of like ones. However, an unexplained fact is that, although we found 104 electrophoretic phenotypes, farmers gave 100 names. This list includes synonyms and overesti-

TABLE 5. PLOIDY DISTRIBUTION AND SPECIES OF THE ELECTROPHORETIC PHENOTYPES OF *SOLANUM* SPECIES SAMPLED (PAUCARTAMBO, CUSCO, PERU).

Ploidy	Frequency %	Species
Diploids	13% (16/125)	<i>stenotomum</i> , <i>gonycalyx</i> , <i>phureja</i>
Triploids	14% (17/125)	<i>chaucha</i>
Tetraploids	67% (84/125)	<i>andigena</i>

mation errors of farmers #6 and 10. Our estimate of the actual number of discrete farmer names would be between 80 and 90. This suggests that there is less lumping than indicated in Table 3.

The system of folk identification is expected to be somewhat ambiguous because it is based in part on subjective descriptions. For example, the variety *Yana Kuwi Sullu* means literally "black guinea pig fetus." So depending on the criteria and imagination of the farmer, many of the black skinned tubers could be classified under the same variety name. A good example of this type of inconsistency can be appreciated in the variety *Yana Suyt'u* (Fig. 2). The prefix "yana" refers to black skin color, so Jesus Amao (#1) and Sebastian Mauri (#3) might have been right when they classified the tubers in the figure as *Yana Suyt'u*, although the morphological differences between the two are very distinct. The third farmer, Augustin (#6), might have been truly mistaken since he classified a pink skin tuber as black. However, "suyt'u," means long, which was an accurate description for all three tubers. This second name, of course, might have been used by Augustin as the main criterion to classify his tubers under this variety.

The chromosome counts revealed that the majority of the genotypes cultivated in the fields sampled at Paucartambo were tetraploids, most likely corresponding to *S. tuberosum* ssp. *andigena*. Cultivated diploid and triploid genotypes shared about the same frequency (Table 5). Although it was not possible to find specific allozymes to differentiate the species of the group *tuberosum*, it is safe to assume that the diploids included the species *S. stenotomum*, *S. phureja*, and *S. gonio-calyx*, while the triploids corresponded exclusively to *S. × chaucha*. On the other hand, specific allozymes were observed for the bitter species *S. acaule* Bitt., *S. × juzepzukii*, and *S. × curtilobum*. For example, the allozyme *Mdh-2*³ was observed in these three species supporting the hypothesis that the former species is ancestral to both the triploid *S. × juzepzukii* and the pentaploid *S. × curtilobum* (Hawkes 1979) (Fig. 4). So, on the basis of this unique marker, it was possible to conclude that non-bitter triploids were present in the fields sampled at Paucartambo.

No studies have been done in potatoes on the possible associations of specific isozyme loci and genes determining morphological traits such as tuber flesh or skin color. We did not observe in our survey any evidence of these associations for the isozyme loci and traits investigated. These traits include skin and flesh color and tuber shape. For example, the varieties *Yuraq K'usi* and *Yana K'usi* in Maqopata (#10) had the same electrophoretic phenotype for eight loci tested; however, the first is triploid and its skin is white, and the second is black and tetraploid. Therefore, it is likely that one might have been derived from the other by somatic mutation and chromosome doubling. A similar situation was observed for *Yuraq Ch'eqepphoro* and *Yana Ch'eqepphoro*, where the first one is a white

TABLE 6. GENETIC VARIABILITY IN THE ANDEAN POPULATION AND IN NORTH AMERICAN/EUROPEAN CULTIVARS OF *SOLANUM* SPECIES.

Loci	Andean population			North American/European cultivars		
	Alleles	Phenotypes	% H	Alleles	Phenotypes	% H
<i>Pgi-1</i>	3	4	36	2	2	20
<i>Pgm-1</i>	2	2	74	2	3	46
<i>Pgm-2</i>	3	4	4	3	2	52
<i>6pgd3</i>	3	5	81	2	2	92
<i>Idh-1</i>	3	3	44	—	—	—
<i>Mdh-1</i>	4	8	94	4	6	80
<i>Mdh-2</i>	2	2	25	2	2	8
<i>Aps-1</i>	3	4	39	—	—	—
<i>Got-1</i>	3	4	3	2	3	24
<i>Got-2</i>	5	7	2	—	—	—
<i>Prx-3</i>	3	4	58	3	3	52
<i>Sdh-1</i>	4	5	64	—	—	—
Total ^a	23	33	47%	20	24	44%

^a Excluding *Idh-1*, *Aps-1*, *Got-2*, and *Sdh-1* in the Andean population since these loci were not surveyed in the North American/European population.

tetraploid, and the second one is a black diploid. Another case was observed in two tetraploids of identical electrophoretic phenotype, *Yana Ruki* with black skin and *Yuraq Ruki* with white skin. “Ruki” is the local term for bitter varieties, probably indicating that these samples were misidentified. These observations indicate that skin color is independent of the eight isozyme loci studied.

There were also several cases where identical electrophoretic and morphological phenotypes for tubers of different ploidies were observed, indicating that these varieties might have originated directly by self polyploidization. Other situations included almost identical tubers and very similar electrophoretic phenotypes, making it very difficult to distinguish two or three varieties. For example, the tubers of *Qompis*, *Alqa Qompis*, and *Alqa Warmi* are very similar, and their genotypes are identical for 10 loci but different for the *Prx-1* or *Sdh-1* loci. *Qompis* and *Alqa Qompis* are heterozygous while *Alqa Warmi* is homozygous for these loci. Often the tubers of these varieties were classified as a single variety that was designated by one of the three names, indicating that the farmers understand them as synonyms.

In general we observed that morphologically distinguishable tubers differed in at least one isozyme locus, except in situations where somatic mutations for skin color or polyploidization were evident. In these situations, of course the isozyme technique was superfluous as an identification tool. However, the electrophoretic technique was useful to distinguish tubers that otherwise could be classified as belonging to the same variety. It provided an additional criterion for variety identification. The capability of the technique is expected to increase with the number of isozyme loci surveyed.

Genetic variability in Andean versus North American/European varieties

Although the sample size for both populations was highly unequal—24 North American/European clones against 830 Andean clones—it allowed us to obtain

a rough estimate of the variability in both populations. Furthermore, it is likely that the cultivars from the North American/European population covers pretty much the variability existing in that group, while the Andean population in spite of the larger sample covers only a fraction of all the variability present in the Andes. In any event, the amount of variability observed in the Andean population was superior for the three parameters measured: total number of alleles, total number of electrophoretic phenotypes, and percent of heterozygosity (% H) (Table 6). The largest difference was observed for the number of electrophoretic phenotypes. This increased variability in the primitive population was evident even when considering that 33% was composed by diploid and triploid tubers, while the other population was formed exclusively by tetraploids. An interesting finding in the Andean population was the high frequency of specific alleles at loci *Pgm-2* (allele 2), *Got-1* (allele 3), and *Got-2* (allele 4), reflected in a large number of homozygous genotypes. On the other hand, this was only observed for allele 3 of *Got-1* in the North American/European population. Additional research including a larger survey will be necessary to understand the significance of this observation.

The larger number of alleles and electrophoretic phenotypes in the Andean population, some of which are not represented in the North American/European populations, supports the impression that a substantial amount of yet unexploited variability remains in the primitive potato populations.

CONCLUSIONS

The use of isozymes as a basis for potato classification is advantageous to conventional taxonomies using plant morphological and general protein in several ways. It more closely approximates the genetic base of the potato. It is more easily quantified. It allows for a fuller treatment of intraspecific diversity. It provides a clearer picture of the relation between cultivated species and between cultivated and non-cultivated species.

Folk naming systems of the Andean potato are based on tuber characteristics and rarely include keys from other plant markers. The use of isozyme electrophoresis as a classification tool indicates that farmer identification corresponds with a high degree of accuracy to the actual biological diversity of Andean potato fields. There is, of course, a range of consistency among different farmers, depending on their interest and devotion to knowledge about their potato collection. While consistency within a particular household in classifying its potato collection has been demonstrated previously (Brush et al. 1981), this research suggests that interhousehold confusion over duplicate potatoes is not a major problem. Out of a relatively small sample of 10 fields, we identified 104 electrophoretic phenotypes, and among the 10 different collections there were 100 different names given by our informants. A comparison of electrophoretic and folk identification both within and between fields reveals that farmers may slightly underestimate the diversity of their fields. This finding bears on the debate of the degree of duplication found in the accessions collected from Andean potato fields. Our work leads us to conclude that duplication among accessions is not common. When duplication is found, it might be the result of sampling methods that are less proximate to the ultimate source of Andean potatoes. For instance, collections in markets, rather than in fields or in farmers' storage bins, might produce more duplication

and lead to an underestimation of the actual amount of diversity still extant in Andean potato agriculture.

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LITERATURE CITED

- Alcorn, J. B. 1984. Huastec Mayan ethnobotany. Univ. Texas Press, Austin.
- Berlin, B., D. E. Breedlove, and P. H. Raven. 1974. Principles of Tzeltal plant classification. Academic Press, New York.
- Boster, J. S. 1984. Inferring decision making from preferences and behavior: an analysis of Aguaruna Jivaro Manioc selection. *Human Ecol.* 12:343–358.
- . 1985. Selection for perceptual distinctiveness: evidence from Aguaruna cultivars of *Manihot esculenta*. *Econ. Bot.* 39:310–325.
- Brush, S. B. 1986. Genetic diversity and conservation in traditional farming systems. *J. Ethnobiol.* 6:151–167.
- , Carney, H. J., and Z. Huaman. 1981. Dynamics of Andean potato agriculture. *Econ. Bot.* 35:70–88.
- Correll, D. S. 1962. The potato and its wild relatives. Texas Research Foundation, Renner, TX.
- Douches, D. S., and C. F. Quiros. 1987. Use of 4x–2x crosses to determine gene-centromere map distances of isozyme loci in *Solanum* species. *Genome* 29:519–527.
- , and ———. 1988. Genetic recombination in a diploid synaptic mutant and a *Solanum tuberosum* × *S. chacoense* diploid hybrid. *Heredity* 60:183–191.
- Hawkes, J. G. 1979. Evolution and polyploidy in potato species. Pages 637–646 in J. G. Hawkes, R. N. Lester, and A. D. Skelding, eds., *The biology and taxonomy of the Solanaceae*. Linnean Soc. Symp. Ser. No. 7.
- Huaman, Z., and R. W. Ross. 1985. Updated listing of potato species names, abbreviations and taxonomic status. *Amer. Potato J.* 62:629–641.
- Jackson, M. T., J. G. Hawkes, and P. R. Rowe. 1977. The nature of *Solanum* × *chaucha* Juz. et Buk., a triploid cultivated potato of the South American Andes. *Euphytica* 26:775–783.
- Johns, T. A. 1985. Chemical ecology of the Aymara of western Bolivia: selection for glycoalkaloids in the *Solanum* × *ajanhui* domestication complex. Ph.D. diss., Univ. Mich., Ann Arbor, MI.
- , and S. L. Keen. 1986. Ongoing evolution of the potato on the Altiplano of western Bolivia. *Econ. Bot.* 40:409–424.
- Oliver, J. L., and J. M. Martinez-Zapater. 1984. Allozyme variability and phylogenetic relationships in the cultivated potato (*Solanum tuberosum*) and related species. *Pl. Syst. Evol.* 148:1–18.
- Quiros, C. F., and N. McHale. 1985. Genetic analysis of isozyme variants in diploid and tetraploid potatoes. *Genetics* 111:131–145.
- Stegemann, H., and V. Loeschcke. 1977. Das europäische Kartoffelsortiment und seine Indexierung. *Potato Res.* 20:101–110.