# THE NATURE OF *SOLANUM* × *CHAUCHA* JUZ. ET BUK., A TRIPLOID CULTIVATED POTATO OF THE SOUTH AMERICAN ANDES

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SUMMARY

The variation in *Solanum* × *chaucha* JUZ. et BUK. (2n = 3x = 36) was studied using 114 accessions from the Potato Collection maintained by the International Potato Center. These accessions represented less than 5% of the collection originally screened for ploidy. Twenty morphological characters of the tubers, inflorescences and leaves were scored. The accessions were grouped into 20 morphotypes on the basis of the tuber characters. Two qualitative characters, red-anther tip and sky-blue flowers were diagnostic of 4 morphotypes, but the variation of the quantitative characters overlapped among morphotypes, and were of limited value. Electrophoretic separation of tuber proteins in 7.5% polyacrylamide gels generally confirmed the morphotype groupings. It is concluded that each of the morphotypes represents a single genotype, and these are named according to the International Code of Nomenclature for Cultivated Plants. The variation within *S.* × *chaucha* apparently has been restricted by its hybrid origin.

INTRODUCTION

*Solanum* × *chaucha* JUZ. et BUK., a triploid (2n = 3x = 36) cultivated potato species, is found throughout the Andean region of Peru and Bolivia, and it has been found as far south as northern Argentina (HAWKES & HJERTING, 1969). BUKASOV (1939) considered that *S.* × *chaucha* was derived from *S. phureja* JUZ. et BUK. Based on morphological and genetical evidence, HAWKES (1963) stated that *S.* × *chaucha* was a hybrid between tetraploid *S. tuberosum* L. ssp. *andigena* (JUZ. et BUK.) HAWKES and diploid *S. stenotomum* JUZ. et BUK.

The taxonomic position of *S.* × *chaucha* was simplified by HAWKES (1963), who reduced to synonymy all the triploid species (with the exception of *S. juzepczukii* BUK.) which had been described earlier (HAWKES, 1944; JUZEPCZUK & BUKASOV, 1929). The Russians, following the taxonomic methods of BITTER, had afforded taxonomic rank to each minor variant, even though the diagnostic characters which were employed to differentiate them were insignificant. For example, OCHOA (1951) pointed out that some of the characters which were used to differentiate *S. mamilliferum* JUZ. et BUK. ( = *S.* × *chaucha*) were to be found in both tetraploid clones, as well as other triploids.

Lack of fertility inhibits sexual reproduction between triploids and most new clones must come from a 4x–2x cross. Once a new genotype is produced, the intervention of man may maintain the clone in the population. HAWKES (1963) was of the opinion that if each clone was to be given taxonomic rank and included in *S.* × *chaucha*, all variants should be regarded as nothomorphic forms of the one species. To name all separately would be to end up with taxonomic absurdity.

Triploids are generally morphologically indistinguishable from tetraploids, and diploids, although HAWKES (1963) stated that they had corolla lobes which were in general about three times as broad as long when spread out flat. OCHOA (1952, 1964, 1965) had many problems accommodating the variation of triploids into a system of classification. Often it was impossible to distinguish the triploids, as they fell within the range of variation of both tetraploids and diploids, themselves highly polymorphic, and as UGENT (1966) pointed out, overlapping in many characters. The main diagnostic character of the triploids was their chromosome number. MARKS (1966b) stated that the relative abundance of triploids, and the variation within the species suggested fairly free hybridisation between the putative parents. Yet the experimental evidence (MARKS, 1966a; HANNEMAN & PELOQUIN, 1968) from inter-ploidy crossability, 4x–2x, apparently refutes this, in that the formation of triploids was uncommon.

As a result of intensive collecting efforts, the International Potato Center (CIP) has accumulated a large number of primitive potato cultivars from Peru and Bolivia. The present study was undertaken to assess the variation in *S.* × *chaucha* clones in the CIP collection. In addition, an attempt was made to group clones into morphotypes. The morphotype is conceived as plants which are similar or apparently phenotypically identical, without implying genetic sameness. In order to be certain of this, more tests would have to be conducted, such as electrophoresis of tuber proteins and disease reaction. The efficiency of electrophoretic studies in identifying variation has been emphasised by a number of workers (ZWARTZ, 1966; STEGEMANN et al., 1973), and the technique has been shown to be exact enough to separate different varieties of *S. tuberosum* ssp. *tuberosum*. In the end, therefore, if all tests show identical patterns or results within a morphotype, we can be reasonably certain that similar morphotypes are the phenotypic expressions of identical genotypes.

Crossability studies between primitive tetraploid and diploid varieties from the Andean region (JACKSON et al., 1977) showed that triploids could be produced from crosses involving the diploid species *S. stenotomum* ssp. *stenotomum*, and ssp. *goniocalyx* (JUZ. et BUK.) HAWKES, and *S. phureja*. Thus no attempt was made to define the progenitors of *S.* × *chaucha*. Rather an evaluation was made of the extent of variation within the species and its consequences from an evolutionary point of view.

MATERIALS AND METHODS

Potato clones from the CIP Collection were used in this study. The collection is maintained at Huancayo, alt. 3380 m, in the central Andes of Peru, and only material grown at this location was observed. The chromosome number of each accession

Fig. 1. Morphotypes of *S.* × *chaucha*.
L to R, first row: Duraznillo, Huayro, Garhuash Shuito, Puca Shuito, Yana Shuito.
L to R, second row: Komar Ñahuichi, Pishpita, Surimana, Piña, Manzana, Morhuarma.
L to R, third row: Tarmeña, Ccusi, Yuracc Incalo.
L to R, fourth row: Collo, Rucunag, Hayaparara, Rodeñas.

was determined by a root-tip squash, following the technique of TARN (1967).

*Morphology.* Twenty morphological characters of the tubers, inflorescences and leaves were scored. A complete list is given by JACKSON (1975). Five plants per accession and two leaves and inflorescences per plant were scored.

*Disc-electrophoresis.* Tuber proteins were separated electrophoretically in 7.5% polyacrylamide gels, pH 8.5. Approximately 10 g of freshly sliced tubers were frozen in polyethylene bags at −30°C for 24 h. The slices were allowed to thaw at room temperature, and the tuber sap was expressed. It was centrifuged at 3500 rev/min for 20 min at 3°C, and the supernatant carefully decanted and stored in glass vials at −30°C. The upper and lower gels were prepared from stock solutions, and the electrophoretic separation of the proteins carried out following the general methods of DAVIS (1964). Banding homologies were established by running mixed extracts, and comparing the composite patterns with those from individual clones. Electrophoretic patterns were also obtained in 7.5% gels, pH 4.3. using a β-alanine acetic acid buffer (pH 4.3).

RESULTS

*Morphology.* One-hundred and fourteen accessions were identified as triploids. These accessions represented less than 5% of those initially screened for ploidy and species status. On the basis of tuber characters (Table 1) it was possible to group the accessions into 20 morphotypes. Each morphotype was named using its common varietal name, a term used to describe the tuber, or the locality of collection. The 'Huayro', 'Duraznillo' and 'Shuito' morphotypes comprised 72% of all the collections. Six morphotypes, 'Pishpita', 'Rucunag', 'Piña', 'Surimana', 'Collo', and 'Komar Ñahuichi' were represented by only a few accessions each, and nine morphotypes had only a single accession (Fig. 1).

'Duraznillo' and 'Huayro' differed only in tuber shape. With respect to depth of eyes, skin and flesh colour and vascular pigmentation in the tuber flesh, they were very similar. The fusiform tubers of the three 'Shuito' morphotypes were distinguishable only on the basis of skin colour, namely yellow, red and yellow, and purple and yellow. The 'Surimana' tubers were also fusiform, but the skin had distinct patches of red and yellow.

Both the 'Pishpita' and 'Piña' morphotypes had very distinct tubers. 'Komar Ñahuichi', 'Rucunag' and 'Collo' had very dark purple tubers, but there were some differences in tuber shape, and especially the colour of the sprouts and the tuber flesh. Two clones, 'Hayaparara' and 'Rancas' both had the common name *Huayro*. The former could be distinguished from 'Duraznillo' on account of its darker, almost purple skin colour, its purple sprout and the presence of purple pigmentation in the yellow tuber flesh. The relationship of 'Rancas' to either 'Huayro' or 'Duraznillo' did not seem to be clear, and consequently it was separated as a distinct morphotype.

The range of variation of the metrical characters overlapped considerably and it was not possible to differentiate one morphotype from another solely on the basis of these characters. Overall differences in leaflet length/breadth ratios for both leaflets

Table 1. Summary of tuber characteristics for twenty morphotypes of *S. × chaucha*.

| Morphotype | Number of accessions | Shape | Skin | Eyes | Sprout | Flesh | Pigmentation |
|---|---|---|---|---|---|---|---|
| Duraznillo | 16 | Round | Red | Medium | Red | Yellow | Red vascular ring |
| Huayro | 29 | Oval-oblong | Red | Medium | Red | Yellow | Red vascular ring |
| Garhuash Shuito | 8 | Fusiform | Yellow | Shallow | White, speckled pink | White | Absent |
| Puca Shuito | 24 | Fusiform | Red and yellow | Shallow | Pink | White | Absent |
| Yana Shuito | 4 | Fusiform | Purple and yellow | Shallow | Purple | White | Absent |
| Pishpita | 8 | Round-oblong | Purple, yellow halos around eyes | Medium | White, speckled purple | White | Absent |
| Rucunag | 4 | Round-oval | Purple-black | Deep | Purple | White | Purple |
| Piña | 3 | Pineapple-shaped | Reddish-purple | Deep, marked eyebrow | Purple | Cream | Purple |
| Surimana | 3 | Fusiform | Red, yellow around eyes | Shallow | White | White | Absent |
| Komar Ñahuichi | 3 | Oblong, wedge-shaped | Purple | Medium deep | White, speckled purple | White | Absent |
| Collo | 3 | Round-uveous | Purple, black | Deep | Purple | White | Purple |
| Manzana | 1 | Round-uveous | Cream, peach coloured | Deep | White | White | Absent |
| Ccusi | 1 | Round | Red, underlying black skin | Deep | White | White | Absent |
| Tarmeña | 1 | Wedge-shaped, oblong | Red, underlying black skin | Medium | Purple | Cream | Purple |
| Yuracc Incalo | 1 | Round | Cream-yellow | Deep | White | White | Absent |
| Colquepata | 1 | Round | Mottled red and yellow | Medium | Red | Cream | Absent |
| Rodeñas | 1 | Roundish | Yellow, speckled purple | Deep | White, speckled purple | White | Absent |
| Morhuarma | 1 | Round | Mottled red and yellow | Deep | Red | Cream | Red |
| Hayaparara | 1 | Round | Dark red – purple | Medium | Purple | White | Purple |
| Rancas | 1 | Round | Reddish | Medium | Red | Cream | Absent |

measured were not great, and the number of pairs of lateral and interjected leaflets was also variable. None of the floral metrical characters was diagnostic of any morphotype. The corolla lobes varied from just under twice as broad as long (L/B = 0.55) to three times broader (L/B = 0.33). This was in contrast to the suggestion of HAWKES (1963) for the identification of *S.* × *chaucha* triploids. Some of the discrete characters which were scored, such as ovary wall pigmentation, peduncle or calyx shape were certainly typical of some of the morphotypes, and most accessions of each morphotype manifested the same vegetative and floral characters. However, these characters were not unique.

On the other hand, two characters, namely sky-blue flowers and a red pigmentation of the anther tip were diagnostic of 'Pishpita' and the three 'Shuito' morphotypes respectively. The flower colour of the other triploids was reddish-purple or magenta, and in the field, it was extremely difficult to detect subtle differences in intensity and hue, even between those clones with purple and those with red tubers.

*Disc-electrophoresis.* Protein spectra were examined from all accessions, with the exception of the single accession morphotype 'Rancas'. In basic gels (pH 8.5) a total of 21 protein bands was separated (Fig. 2). Accessions were characterised and grouped together on the basis of greatest similarity of protein spectra. It was found that identical morphotypes had identical protein band spectra.

In general, the grouping of accessions following electrophoresis supported the morphotype differentiation. Likewise, the grouping of accessions under conditions
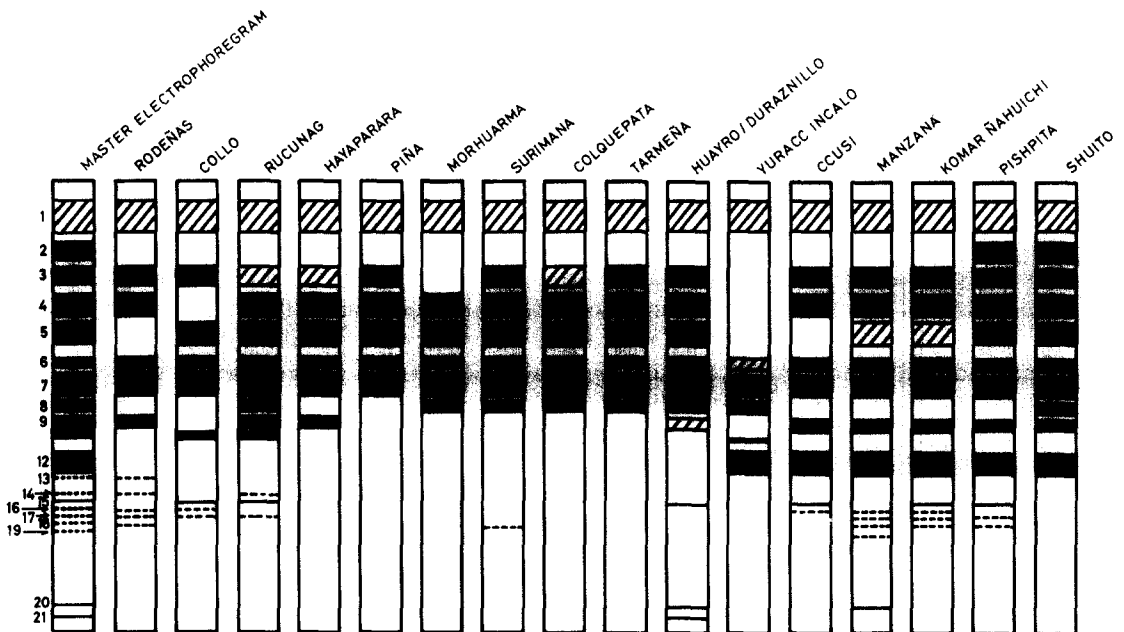


Fig. 2. Electrophoregrams of *S.* × *chaucha* morphotypes. Faint or diffuse bands are indicated by dotted lines and cross-hatching.

of pH 8.5 were confirmed by the results from protein separation in polyacrylamide gels of pH 4.3.

A number of faint bands were separated, and these were not seen in every gel within a particular group. It is known that minor fluctuations during electrophoretic separation of protein, or slight overheating can cause proteins to break down into their individual monomers. Some of the faint bands may have been artefacts produced during the separation of the proteins.

Two protein bands, 6 and 7, were common to all accessions, and therefore of no taxonomic value. The two main electrophoretic groups were separated on the presence or absence of Band 12. A further sub-division was made within the group with Band 12 on the occurrence of Band 2. All 'Shuito' morphotypes had Bands 2 and 12. Some variation was apparent with regard to Bands 8 and 9, but this could not be correlated with differences in skin colour of the different morphotypes. 'Pishpita' was distinguished from 'Shuito' because Band 8 did not occur in any of the eight accessions. 'Komar Ñahuichi', 'Ccusi' and 'Manzana' had similar protein spectra, but could not be confused morphologically. The electrophoretic pattern of 'Yuracc Incalo' was completely different from the others in this group.

The other group included 'Huayro', 'Duraznillo', 'Surimana', 'Piña', 'Rucunag', and 'Collo', as well as the single clones 'Tarmeña', 'Colquepata', 'Rodeñas', 'Morhuarma' and 'Hayaparara'. Bands 8, 9, 20 and 21 were found in both 'Duraznillo' and 'Huayro', and their electrophoretic patterns suggested a close relationship. The 'Piña' accessions had identical patterns. Although the patterns of 'Colquepata', 'Morhuarma' and 'Tarmeña' were similar, tuber differences were marked. 'Rucunag' had Bands 3 to 11, as well as Band 15. The presence of Bands 10 and 11 was typical of 'Collo', although Bands 4, 8 and 9 were absent. The pattern of 'Rodeñas' was distinct from those of the other morphotypes.

GEOGRAPHICAL DISTRIBUTION OF THE MORPHOTYPES

All accessions were found in the Andes of Peru, with the exception of 'Collo', which was restricted to northern Bolivia. The 'Huayro', 'Duraznillo' and the three 'Shuito' morphotypes were extremely widespread, and were found from the north of Peru, south to the Lake Titicaca Basin. There was a concentration of samples from north-central Peru, reflecting only that more collections had been made from that region.

The 'Pishpita' accessions came from the central Andes of Peru. Accessions of this morphotype were given specific rank by HAWKES (1944) using the name *S. coeruliflorum* ( = *S.* × *chaucha*) and its distribution has not changed since then. 'Surimana' and 'Komar Ñahuichi' were sampled only in the south of Peru. Two 'Piña' accessions came from the central Andes, and one from Cusco market in the south of the country. Accessions of 'Rucunag' were found in the central and northern part of Peru. Clones represented by single accessions were distributed apparently at random throughout Peru.

DISCUSSION

The usefulness of floral and vegetative characters in clarifying the variation pattern within *S. × chaucha* was generally limited. Although trends of variation were apparent in some of the metrical characters, they were not so clear-cut as to facilitate the separation of one morphotype from another. Only two of the discrete characters were diagnostic of four of the morphotypes, namely sky-blue flowers of 'Pishpita' and red anther-tip of 'Shuito'. On the other hand, the importance of the tuber characters has been stressed and confirmed; only on the basis of tuber characters was it possible to differentiate all 20 morphotypes. In accordance with ROGERS & FLEMING (1973), the present study has shown that the most important morphological characters which can be assessed in a vegetatively reproducing crop such as the potato, are those relating to the tubers. Other vegetative and floral characters may be considered as 'secondary' since man has undoubtedly selected potatoes on the basis of the tubers only (JACKSON et al., 1977), although some selection according to disease reaction in the field must also occur. The type of morphological variation which is manifested by the flowers and haulms is therefore presumably somewhat fortuitous. Although certain haulm types can be recognised as typical of certain varieties, there was not a strong relationship between morphotype groupings using tubers and most other characters.

The electrophoretic survey was employed to analyse only qualitative differences between triploid accessions with regard to protein spectra. It has been argued that proteins deserve more taxonomic weighting because, derived directly from DNA, they are the building blocks of evolution and variation. The value of protein data from electrophoresis lies in the additional taxonomic information which they provide. It would be unwise to erect a system of classification of triploid cultivars based solely on protein characters. Likewise a classification based solely on tuber characters may be dangerous, since some similarities could perhaps represent the results of parallel evolution. This is to be expected if man selects tubers which fall within a known range of morphological variation. This idea is supported by the presence in the CIP collection of tetraploid varieties called *Huayro* which have tubers similar to 'Huayro' discussed in this paper.

Since there was generally a good correlation between tuber morphology and electrophoretic protein patterns, it is therefore fairly safe to assume that each morphotype represents a single clone. Following the International Code of Nomenclature for Cultivated Plants (1969), Articles 5 and 10, these clones can be regarded as cultivars of *S. × chaucha*, and named accordingly. It is proposed that the morphotype names be used as the cultivar names; e.g. 'Duraznillo' would be named *S. × chaucha* cv. Duraznillo.

We do not claim that the cultivars named here are the only ones that may be found in *S. × chaucha*. However, it seems unlikely that there are any other triploid cultivars that are as widely distributed or as popular as cv. Huayro or cv. Puca Shuito. Other random triploids probably exist, but our study of the CIP Collection leads us to believe that we have observed the majority of the cultivars which are in existence at the present time.

The amount of variation apparently within the species is limited, especially when it is remembered that five cultivars (cv. Huayro, cv. Duraznillo, cv. Garhuash Shuito,

cv. Puca Shuito and cv. Yana Shuito) comprise over 70% of all accessions studied. The report of MARKS (1966b) of great variation within Group Chaucha (= *S.* × *chaucha*) would appear to be unfounded therefore. His reports of a 'triploid block' following 4x–2x hybridisation in cultivated potatoes are generally supported by JACKSON et al. (1977), who found that a number of tetraploid clones yielded triploids more readily in this type of cross than did other tetraploids, confirming that the ability to form triploids was genotype dependent (KESSEL & ROWE, 1975). This present study has indicated that there is no contradiction between the low numbers of triploids which have been reported from experimental crosses, and the number of triploid cultivars which have been found, or could be expected to be found, in the field.

The wide geographical distribution of the Huayro, Duraznillo and Shuito cultivars suggests that they may be superior clones, and that their consumer acceptability is high. The widespread nature of some of the triploids may have led MARKS (1966b) and others to believe that the variation of *S.* × *chaucha* was higher than it really is. It is unlikely that the widespread cultivars have originated independently many times; rather man has increased those genotypes for which he noted a particular useful quality. Following selection, it is likely that mutations have occurred. For example, the skin colour differences of the three Shuito cultivars can be explained in terms of single-gene mutations (HOWARD, 1970).

The fact that there are few triploid cultivars is not surprising when one considers the combined effects of inter-ploidy crossability and the selection of new genotypes by man. Triploids have originated from crosses between the diploid and tetraploid gene-pools, but the 'triploid block' and the high self-fertility of the tetraploids are barriers to the production of triploids in the field. It is difficult to demonstrate that new triploid genotypes are entering the population, although the potential for hybridisation undoubtedly exists, since the Quechua Indians plant their potato varieties in great mixtures (JACKSON et al., 1977). Although many millions of potential tetraploids are formed each year in the form of true seed, there are no data to show how many actually enter the population each year, and are eventually selected by man. Undoubtedly, some seedlings have sufficient vigour to grow to maturity. In the case of the triploids, therefore, their low formation following inter-ploidy hybridisation, their chances of survival in the natural environment are low, even when the vast majority of tetraploid seedlings do not survive, and their subsequent selection by man is dependent upon many factors. Thus the pattern of variation and the nature of *S.* × *chaucha* can be placed into perspective. This triploid species is hybridogenic between the tetraploid and diploid gene-pools and consequently the variation pattern is narrow. By their very composition, the potato fields of the Quechua Indians can be considered as a dynamic evolutionary system whereby variability is released at both the tetraploid and diploid levels, leading occasionally to the formation of triploids whose survival is dependent upon man.

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