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The origin of the cultivated tetraploid potato based on chloroplast DNA

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Summary. By using restriction enzyme analysis of chloroplast DNA, a geographical cline from the Andean region to coastal Chile was found for the tetraploid potato (*Solanum tuberosum*). This supports the Andean origin of Chilean ssp. *tuberosum*. One of the relic cultivars of the early introduction of potato to Europe had ssp. *andigena* type chloroplast DNA. Its derivatives were largely lost in the mid-19th century due to the late blight epidemic and were replaced by ssp. *tuberosum* originally introduced from Chile. Therefore, the present common potato has the same type chloroplast DNA as Chilean ssp. *tuberosum*.

Key words: Chloroplast DNA – Potato – *Solanum tuberosum* – Origin – Restriction endonuclease

Introduction

The tetraploid domestic potato is classified as *Solanum tuberosum* L., consisting of two subspecies, ssp. *tuberosum* and ssp. *andigena* (Hawkes 1956). Subspecies *tuberosum* is divided into the common potato and Chilean ssp. *tuberosum*, the latter of which is cultivated on the southern coast and islands of southern Chile (Chiloé region). According to Hawkes (1956), both ssp. *tuberosum* types were independently selected as long-day adapted types from ssp. *andigena* in Europe and Chile. Bukasov (1933, 1966) suggested an independent origin for each subspecies and that Chilean ssp. *tuberosum* was introduced to Europe. Subspecies *andigena* is grown from Venezuela to northern Argentina and is especially variable in morphological and physiological characteristics from central Peru to central Bolivia. It is also grown in Costa Rica, Guatemala and Mexico, but was probably taken to those countries by the Spaniards after the conquest (Hawkes 1972). The usefulness of ssp. *andigena* in potato improvement has been recognized and it has been used to broaden the genetic base for varietal improvement (Glendinning 1969; Cubillos and Plaisted 1976; Tarn and Tai 1977). Some workers have reported cytoplasmic differences between subspecies based on yield trials of progeny from reciprocal crosses (Hoopes et al. 1980), electropherograms of Fraction 1 protein (Gatenby and Cocking 1978), nuclear-cytoplasmic male sterility (Grun 1973) and chloroplast DNA (ctDNA) restriction fragment patterns (Hosaka et al. 1984). However, Buckner and Hyde (1985) reported the same ctDNA restriction fragment pattern for material from both subspecies. Thus, controversy is raised not only over the origin, but also over the cytoplasmic differentiation of the potato.

In previous papers (Hosaka 1986; Hosaka et al. 1988), relationships of ctDNA types among cultivated potato species and their wild relatives were described (Fig. 1). Subspecies *andigena* had either A type (four accessions) or S type (one accession) ctDNA, while ssp. *tuberosum* had T type ctDNA (Hosaka 1986). T type is a unique ctDNA differing by one physical deletion from W type ctDNA (Hosaka et al. 1988) and was found only in ssp. *tuberosum*, which includes the common potato and Chilean ssp. *tuberosum*. From these studies, no conclusion could be reached on the phylogenetic relationship between ssp. *andigena* and ssp. *tuberosum*.

In this paper, ctDNA types of diverse accessions of *S. tuberosum* ssp. *andigena* and ssp. *tuberosum* were determined, and the relationship of the subspecies and the origin of the common potato are discussed.

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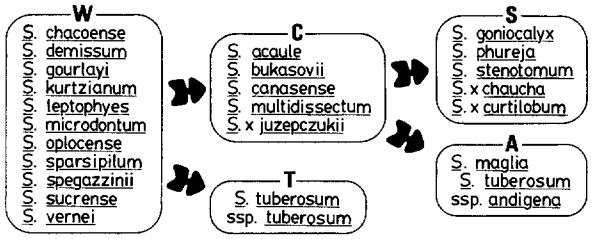

Fig. 1. Relationships of ctDNA types, cited from Hosaka (1986) with a modification that T type ctDNA was derived from W type ctDNA with one physical deletion (about 400 bp) (Hosaka et al. 1988). Other ctDNA types differ from one another by a single change each in the *Bam*HI or *Hin*dIII restriction fragment pattern

Materials and methods

The *S. tuberosum* plant materials used are listed in Table 1. Fresh leaves were usually collected from several plants per accession in the field at Sturgeon Bay, Wisconsin, USA. Species identification for Chilean potatoes were performed by Drs. K.A. Okada, Instituto Nacional de Technologia Agropecuaria, Estacion Experimental Agropecuaria, Balcarce, Argentina, and J.P. Hjerting, Copenhagen University, Botanic Garden, Denmark, in the summer of 1986 at Sturgeon Bay. Some hybrid seeds of (Myatt's Ashleaf × 4nAA) × 4nAC were a kind gift from Prof. P. Grun, Pennsylvania State University, USA. The original female parent, cv "Myatt's Ashleaf", was obtained from Scotland via Dr. J.L. Hardie in the early 1970s (P. Grun 1986, personal communication). CtDNA extraction and restriction enzyme

Table 1. Chloroplast DNA type. All accessions except those mentioned below were supplied by the Inter-Regional Potato Introduction Project (IR-1), Sturgeon Bay, Wisconsin, USA. The accessions prefixed with T-AY were collections of the 1971 "Expedition of Cultivated Plants in the Andean Areas", Kyoto University, Japan. Cvs "Chona" and "Huilcana" were supplied by A. Contreras M., Universidad Austral de Chile, Valdivia, Chile. Restriction fragment patterns, on which ctDNA type determination was based, were cited from Buckner and Hyde (1985) for cv "Kennebec", and Shepard et al. (1983) for cv "Russet Burbank"

Origin	CtDNA type	Accession
1. *S. tuberosum* ssp. *andigena*		
Mexico	A	PI 243343, PI 281035, PI 281036, PI 285008, PI 285014
Guatemala	W	WRF 1758
Costa Rica	A	PI 230475
Colombia	A	PI 243365, PI 243394, PI 243425, PI 243442, PI 247338, WRF 1756, WRF 1768
	C	PI 243361
Ecuador	A	PI 229894, PI 230470, PI 230471, PI 237208, PI 243399, PI 243409
Peru	A	PI 214426, PI 214427, PI 214430, PI 214436, PI 232045, PI 232839, PI 232841, PI 232842, PI 281052, PI 281064, PI 281081, PI 281093, T-AY-5, T-AY-19, T-AY-22, T-AY-28
	S	PI 214422, PI 230496, T-AY-6
	C	PI 230499, PI 232840, PI 281061, PI 292073
Bolivia	A	PI 233982, PI 233984, PI 233985, PI 233989, PI 233994, PI 233996, PI 234002, PI 255491, PI 258898, PI 280943, PI 280944, PI 280957, PI 280961, PI 280964, PI 280989, PI 280990, PI 281000
	S	PI 233987, PI 233988, PI 255505, PI 280963
	C	PI 233990, PI 233999, PI 234000, PI 258879, PI 258881, PI 258936, PI 280968
	W	PI 265882, PI 281014, WRF 1865
Argentina	A	PI 209426, PI 255504, PI 255507, PI 280863, PI 280865, PI 280869, PI 280871, PI 280888, PI 280902, PI 280907, PI 280915, PI 280932, PI 280960, PI 280982, PI 500056, PI 500060
	S	PI 280896, PI 280905, PI 280910, PI 280929, PI 280967
	C	PI 280903, PI 280908, PI 500057, PI 500058
	W	PI 209415, PI 255503, PI 280914, PI 280923
	T	PI 209421, PI 280936, WRF 1586
Chile		
(Coastal)	T	WRF 1605, WRF 1745
(Arica)	A	PI 245931, PI 245937
(Arica)	S	PI 245928, PI 245935
2. *S. tuberosum* ssp. *tuberosum*		
Chile	A	PI 245783, PI 245815
	W	WRF 1624
	T	PI 133667, PI 208563, PI 245320, PI 245816, PI 245317, PI 245792, PI 245800, WRF 1610, WRF 1611, WRF 1616, WRF 1617, WRF 1621, WRF 1743, WRF 1746, WRF 1748, WRF 1750, WRF 1752, WRF 1754, WRF 2282, Chona, Huilcana
Europe	T	May Queen, Up-to-date
America	T	Early Rose, Garnet Chili, Irish Cobbler, Katahdin, Kennebec, Norland, Russet Burbank

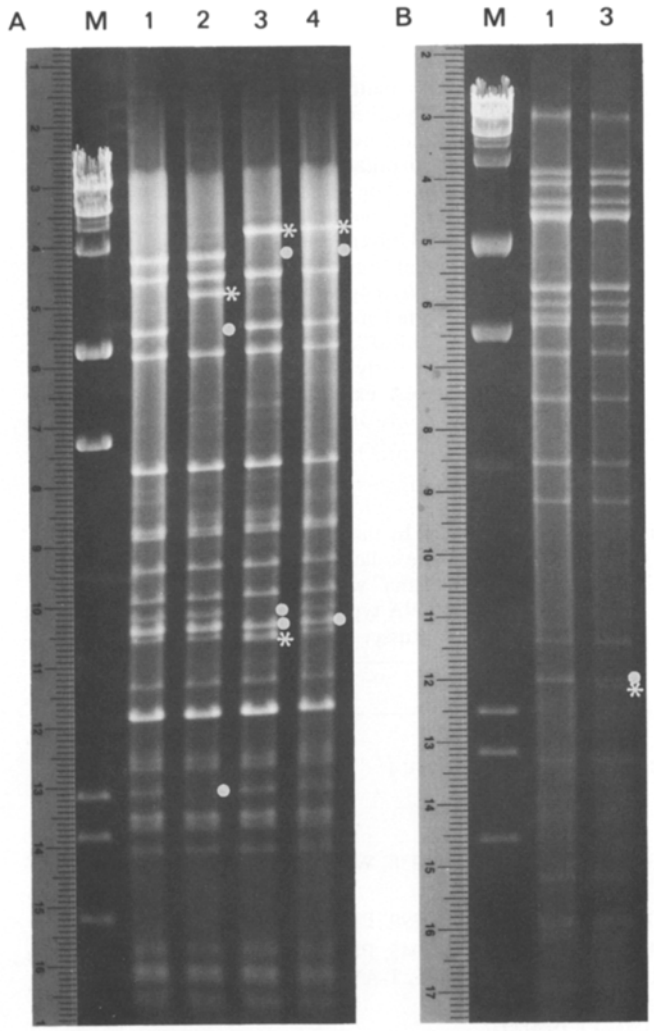

Fig. 2A and B. Restriction fragment patterns of **A** *Bam*HI and **B** *Hin*dIII digests of potato ctDNA. Fragment changes were compared with the type 1 pattern. A loss or gain of a fragment is shown by a *circle* or *asterisk*, respectively. A mixture of *Hin*dIII and *Kpn*I digests of λDNA was used as a marker DNA (M). **A** type 1, ssp. *tuberosum* (WRF 1624); type 2, ssp. *tuberosum* (WRF 1617); type 3, ssp. *tuberosum* (PI 245783); type 4, ssp. *andigena* (PI 280903). **B** type 1, ssp. *andigena* (PI 280903); type 3, ssp. *andigena* (PI 245928)

analysis methods have been described elsewhere (Hosaka and Hanneman 1987). CtDNA type was determined by a simple method discussed in another paper (Hosaka and Hanneman 1988), i.e., each ctDNA was digested by *Bam*HI restriction endonuclease, then only undetermined ctDNA were subject to a second digestion by either *Hin*dIII or *Pvu*II.

Results

The ctDNAs from 33 accessions of ssp. *tuberosum* and 113 accessions of ssp. *andigena* were analyzed (Table 1). The *Bam*HI and *Hin*dIII restriction fragment patterns are shown in Fig. 2, in which each pattern type is designated by the same numbering system used in previous papers (Hosaka et al. 1984; Hosaka 1986). The ctDNA showing type 2 or type 3 *Bam*HI restriction fragment patterns was determined as T or A type ctDNA, respectively. The ctDNA exhibiting a type 4 pattern was digested by *Hin*dIII, confirming a C or S type ctDNA (showing 1 or 3 *Hin*dIII type, respectively). Nine ctDNAs had a type 1 *Bam*HI pattern. Of those nine, six accessions (PI 209415, PI 265882, PI 280923, WRF 1624, WRF 1758 and WRF 1865) were confirmed as W type by *Pvu*II digestion, but the remaining three accessions (PI 255503, PI 280914 and PI 281014) were not available for analyses. They may have been other W derivative types, but were included with the W type in this paper for convenience (Table 1).

Out of 113 accessions of ssp. *andigena*, 70 (62%) had A type ctDNA, 14 (12%) had S type, 16 (14%) had C type, eight (7%) had W type, and five (4%) had T type (Table 1). All ssp. *tuberosum* varieties from Europe and America have T type ctDNA. In 24 accessions of Chilean ssp. *tuberosum*, 21 (88%) accessions had T type ctDNA, two (8%) had A type ctDNA, and one (4%) had W type ctDNA. This indicates the polymorphism of the ctDNAs in *S. tuberosum*, particularly in ssp. *andigena*.

The *Bam*HI restriction fragment pattern of WRF 2288 (PI 209421 × PI 292084) has been reported to be the same as that of cv "Kennebec" (Buckner and Hyde 1985; B. Buckner 1986, personal communication). The WRF 2288 (data not listed in Table 1) and its original female parent, PI 209421, were confirmed by the present study to have T type ctDNA (Table 1). The ctDNA of Myatt's Ashleaf hybrid has A type ctDNA which is typical of that of ssp. *andigena*.

In Fig. 3, geographical distribution of the ctDNA types are shown, indicating an obvious geographical cline of the ctDNA types. In the Andes, from the north to the south, the frequency of A type ctDNA decreases gradually, and other ctDNA types, C, S and W, become more frequent, culminating in Argentina with 50% A, 12.5% C, 15.6% S, 12.5% W and 9.4% T. Across the Andean highlands, in coastal Chile, 88% of tetraploid potatoes (including ssp. *tuberosum* and ssp. *andigena*) have T type ctDNA.

Discussion

CtDNA variation in the tetraploid potato

Polymorphic ctDNA was found in the cultivated tetraploid potato, *S. tuberosum*, particularly in ssp. *andigena*, although ctDNA is generally thought to be remarkably conservative. The reason for such polymorphisms in potato is attributed to its cultivated nature and vegetative propagation. Any ctDNA types detected in ssp. *andigena* are not ssp. *andigena*-specific, but are found in other

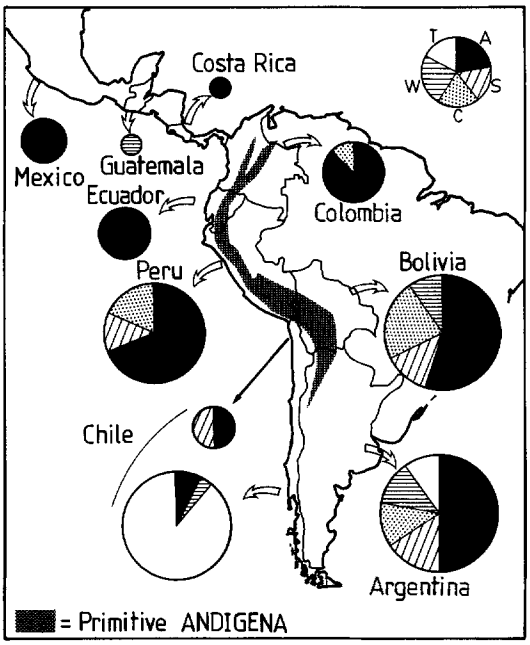

Fig. 3. Distribution of ctDNA types in *S. tuberosum*. The percentage of accessions of each ctDNA type are indicated by the *area occupied in a given circle*. The Chilean potatoes are shown by two groups, coastal, or southern Chilean potatoes and those of the province of Arica, or northern Chile. For the former group, ssp. *tuberosum* and ssp. *andigena* were combined and shown here. The distribution area of primitive ssp. *andigena* is cited from Hawkes (1978)

cultivated and wild species (Fig. 1). This does not necessarily mean that different ctDNA types were induced by mutation after ssp. *andigena* arose, but could indicate that ssp. *andigena* may have arisen many times by hybridization and introgression. At least in this sense, ssp. *andigena* is a collective subspecies.

Once ssp. *andigena* with a different ctDNA occurred, it could be maintained under cultivation. The origin of the ctDNA diversity of ssp. *andigena*, however, remains unknown as to whether it originated from different species with different ctDNA, or from the cultivated diploid population in which polymorphisms may have already existed. This will be discussed further in an accompanied paper (Hosaka and Hanneman 1988).

Phylogenetic relationship between ssp. andigena and ssp. tuberosum

As shown in Fig. 3, geographical cline of the ctDNA types lies between ssp. *andigena* and ssp. *tuberosum*. This genetic cline of ctDNA suggests that Chilean ssp. *tuberosum* originated from ssp. *andigena*, as suggested by Hawkes (1956). The following evidence supports the above-mentioned idea: (1) Subspecies *tuberosum*-specific T type ctDNA has not been discovered in any wild species (Fig. 1); (2) some ssp. *andigena* accessions have T type ctDNA, while some ssp. *tuberosum* accessions have A type ctDNA (Table 1), demonstrating an obvious link between both subspecies; and (3) ssp. *andigena*, collected from the Arica region of the northern boundary of Chile with Bolivia or Peru, has A or S type ctDNA (Fig. 3), indicating that the Chilean tetraploid was not brought from the northern part of Chile but from the Argentine boundary. Another factor preventing their immigration is the Atacama desert.

Bukasov (1933, 1966) suggested the independent origin for Chilean ssp. *tuberosum* and ssp. *andigena*. His idea, however, cannot explain why intermediate accessions exist. Even if these accessions were presumed to have originated as hybrids between ssp. *tuberosum* and ssp. *andigena* after both had differentiated, it could not explain the ancestral species of Chilean ssp. *tuberosum*. Bukasov (1933, 1966) suggested that *S. molinae* or *S. leptostigma* was the ancestral species of Chilean ssp. *tuberosum*, but these species have been recognized as escaped forms from Chilean ssp. *tuberosum* (Hawkes 1956). In fact, those accessions classified as *S. molinae* or *S. leptostigma* have T type ctDNA (Hosaka 1986).

Recently, Ugent et al. (1987) proposed a unique idea that Chilean ssp. *tuberosum* originated from a Chilean wild species, *S. maglia*. They found 13,000-year-old tuber skins, recovered from the archaeological site of Monte Verde in southern Chile, and identified them as those of *S. maglia*, based on the comparative morphology of starch grains. This, along with the close morphological resemblance of *S. maglia* to Chilean ssp. *tuberosum*, led them to conclude that Chilean ssp. *tuberosum* originated through many years of human selection from chromosome-doubled forms of diploid *S. maglia*. But, ctDNA data do not support this concept because *S. maglia* has A type ctDNA (Hosaka 1986), indicating a closer relationship to ssp. *andigena* than to Chilean ssp. *tuberosum*. Therefore, no species having T type or its primitive W type ctDNA has been discovered in coastal Chile except for Chilean ssp. *tuberosum*. Our conclusion is that Chilean ssp. *tuberosum* was derived directly from ssp. *andigena* from the Andean highlands of the Chile-Argentine boundary.

Origin of the European, or the common, potato

In the 16th century, the first potato was brought into Europe (Salaman 1949; Hawkes 1967). Bukasov (1933, 1966) stated that the first European potato was Chilean ssp. *tuberosum* because of the long-day adaptability of the Chilean ssp. *tuberosum* that can easily form tubers in Europe. Later, Salaman (1937, 1946) and Hawkes (1956) proposed a different idea. They morphologically investigated old descriptions, drawings and herbarium specimens that had been maintained in Europe since the first introduction and indicated a gradual morphological

change from ssp. *andigena* to ssp. *tuberosum*. Combined with other historical records, they concluded that ssp. *andigena* was first introduced into Europe, then it was selected for long-day adaptation becoming ssp. *tuberosum*. Simmonds (1964) simulated this change by measuring leaf characters.

In the present study, the ctDNA of Myatt's Ashleaf hybrid was analyzed and determined as A type ctDNA. The cytoplasm of this hybrid was derived from the cv "Myatt's Ashleaf", one of the relics of the first European potato (Salaman 1926). Therefore, this evidence strongly supports the idea of Salaman (1937, 1946) and Hawkes (1956) that the first European potato was ssp. *andigena*. Further, taking into account the relatively high frequency of A type ctDNA in the northern Andes, the place of origin for introduction into Europe might have been the northern Andean region, as suggested by Salaman (1946) on the basis of leaf shape similarity.

Based on the ctDNA determination, the history of the potato after the first introduction to Europe is proposed as follows: ssp. *andigena*, which was brought from the northern Andes, prevailed in Europe, and was selected for long-day adaptation. In the 1840s, late blight was introduced into Europe and destroyed almost all existing varieties. For this reason, the American variety, cv "Rough Purple Chili" and its derivatives, replaced the old European varieties (Salaman 1949; Hawkes 1967). Cv "Rough Purple Chili" was selected from Chilean ssp. *tuberosum*, as mentioned by C.E. Goodrich, who introduced it. It has the same factors conditioning cytoplasmic sterilities as the northern-grown common potato (Grun et al. 1977). It also must have had the same ctDNA type as the northern-grown common potato, for the cv "Garnet Chili" (selfed progeny from cv "Rough Purple Chili") and the cv "Early Rose" (selfed progeny from cv "Garnet Chili") both have T type ctDNA, the same as Chilean ssp. *tuberosum* (Table 1). Thus, the common potato at present has T type ctDNA.

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