Theor Appl Genet (1991) 81:13–20

THEORETICAL AND APPLIED GENETICS

Chloroplast DNA evolution in potato (*Solanum tuberosum* L.)

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Received April 14, 1990; Accepted July 13, 1990
Communicated by K. Tsunewaki

Summary. A deletion specific to chloroplast (ct) DNA of potato (*Solanum tuberosum* ssp. *tuberosum*) was determined by comparative sequence analysis. The deletion was 241 bp in size, and was not flanked by direct repeats. Five small, open reading frames were found in the corresponding regions of ctDNAs from wild potato (*S. tuberosum* ssp. *andigena*) and tomato (*Lycopersicon esculentum*). Comparison of the sequences of 1.35-kbp HaeIII ctDNA fragments from potato, tomato, and tobacco (*Nicotiana tabacum*) revealed the following: the locations of the 5′ ends of both rubisco large subunit (*rbcL*) and ATPase beta subunit (*atpβ*) mRNAs were probably the same as those of spinach (*Spinacia oleracea*); the promoter regions of the two genes were highly conserved among the four species; and the 5′ untranslated regions diverged at high rates. A phylogenetic tree for the three potato cultivars, one tomato cultivar, and one tobacco cultivar has been constructed by the maximum parsimony method from DNA sequence data, demonstrating that the rate of nucleotide substitution in potato ctDNA is much slower than that in tomato ctDNA. This fact might be due to the differences in the method of propagation between the two crops.

Key words: Potato – Chloroplast DNA – Sequence comparison – Nucleotide substitution rate – Evolution

Introduction

Comparative studies of DNA sequences make the construction of a phylogenetic tree possible, not only for closely related species, but also for varieties within a species. Two methods are used for inferring relationships from molecular data – the distance matrix method and the maximum parsimony method (Nei 1987). In the distance matrix method, a phylogenetic tree is constructed by considering the distance values either of the evolutionary relationships or among species (e.g., Fitch and Margoliash 1967), whereas the maxium parsimony method constructs a tree by minimizing the number of mutational changes for the entire tree (Fitch 1971; Goodman et al. 1974).

One of the most important discoveries in molecular evolution is the approximate constancy of the rate of synonymous nucleotide substitution (Miyata et al. 1980). Zurawski et al. (1984) reported that the rate of synonymous nucleotide substitution in chloroplast (ct) DNA was 1.1×10^{-9} site^{-1} year^{-1}, based on the assumption that barley and maize diverged 50 million years ago.

In chloroplast genome of higher plants, genes for the rubisco large subunit (*rbcl*) and the ATPase beta subunit (*atpβ*) are adjacent to one another and are independently transcribed to the opposite directions from a small intergenic region. The site of the 5′ ends of mRNAs of both genes were determined by several groups (tobacco: Shinozaki and Sugiura 1982; spinach: Zurawski et al. 1981, Mullet et al. 1985; maize: Erion 1985). However, the 5′ ends of *atpβ* mRNAs are different in tobacco and spinach.

Potato, tomato, and tobacco are closely related to each other. The genus *Lycopersicon*, to which tomato belongs, is distinguished from the genus *Solanum* by its pollen-shedding characters (Rick 1976). Close relationships between *Solanum* and *Lycopersicon* species are demonstrated by the digestion of ctDNAs with restriction endonucleases (Palmer and Zamir 1982; Hosaka et al. 1984). By this method, tuber-bearing *Solanum* species are classified into seven types (Hosaka 1986).

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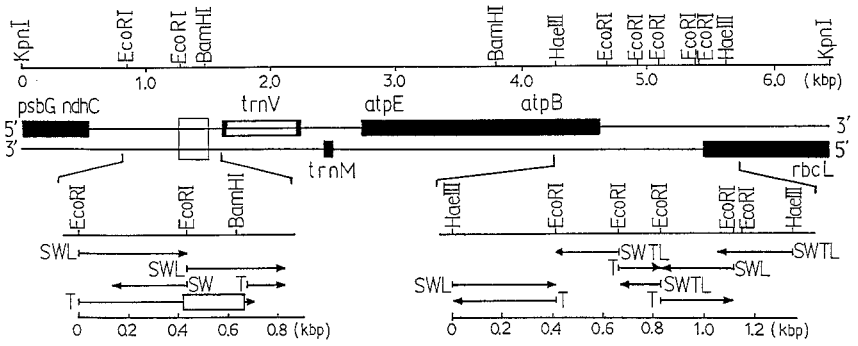


Fig. 1. Physical and genetic map of 6.20/6.45-kbp KpnI fragments. Coding regions of tobacco ctDNA (Shinozaki et al. 1986b) are shown by thick lines. The deletion found in ctDNA of ssp. *tuberosum* is indicated by open box. The lower part shows the sequencing strategy. The sequenced fragments are *S. tuberosum* ssp. *andigena* cv '150'. (S); ssp. *andigena* cv 'W553-4' (W); ssp. *tuberosum* cv 'Irish Cobbler' (T); *L. esculentum* cv 'Toko' (L). *Horizontal arrows* indicate the direction and extent of sequence analysis

Since little is known about molecular evolution in vegetatively propagated plants, we studied the potato chloroplast DNA sequences. In this paper we report the rates of nucleotide substitutions in potato, tomato, and tobacco ctDNAs. In addition, the evolution of tuber-bearing *Solanum* species and the origin of *S. tuberosum* ssp. *tuberosum* are discussed, based on the results obtained.

Materials and methods

Tubers of *Solanum tuberosum* L. ssp. *tuberosum* cv 'Irish Cobber' were obtained from the National Center for Seeds and Seedlings, Hokkaido Chuo Station, Japan. Tubers of *S. tuberosum* L. ssp. *andigena* cultivans 'W553-4' and '150' were obtained from the Potato Breeding Branch, National Agricultural Experiment Station, Simamatsu, Hokkaido, Japan. Seeds of *Lycopersicon esculentum* L. cv 'Toko' were purchased from Sapporo Konoyen, Japan.

Chloroplast DNAs were isolated according to the method of Palmer (1986). Restriction endonucleases BamHI, EcoRI, HaeIII, HincII, and KpnI were purchased from Nippon Gene, Tomaya, Japan. Chloroplast DNAs (0.2–0.3 μg per assay) were digested under the conditions recommended by the supplier of the restriction endonucleases.

Digested ctDNA fragments were inserted into appropriate sites of the phagemid Bluescript SK+ (Stratagne, California), using T4 DNA ligase, and were cloned in *E. coli* strain XL1-Blue (Stratagene, California). Recombinant plasmids were isolated by the boiling method (Holmes and Quigley 1981). Fragments to be subcloned for sequence analysis were eluted from agarose (Sigma Type II) after electrophoresis. The sequences of the inserts were determined by the dideoxy chain termination technique (Sanger et al. 1977), the strategies of which are shown in Fig. 1.

The DNA sequences determined were aligned to display maximal homology consistent with the fewest insertions or deletions. From these data, a phylogenetic tree for the three potato cultivars, one tomato cultivar, and one tobacco cultivar was constructed by the maximum parsimony method (Fitch 1971; Goodman et al. 1974; Nei 1987).

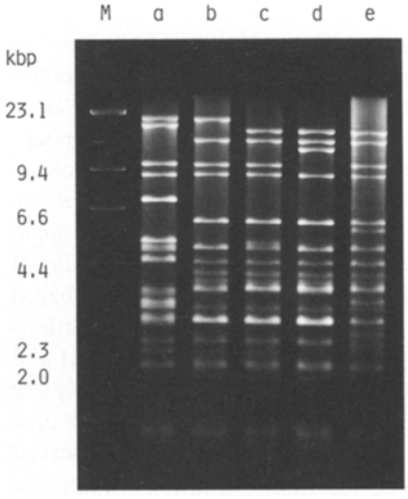


Fig. 2. BamHI restriction fragment patterns of ctDNAs from potato, tomato, and tobacco. The species are *Nicotiana tabacum* cv 'White Burley' (*a*); *Solanum tuberosum* ssp. *andigena* cv '150' (*b*); ssp. *andigena* cv 'W553-4' (*c*); ssp. *tuberosum* cv 'Irish Cobbler' (*d*); *Lycopersicon esculentum* cv 'Toko' (*e*). Fragments were separated by electrophoresis in a 0.8% agarose gel at 18 mA for 18 h. Lambda DNA HindIII fragments (*M*) were used as size markers

Results

Determination of the size and location of the deletion that characterizes the ctDNA of S. tuberosum ssp. tuberosum

The BamHI restriction fragment patterns of ctDNA from *S. tuberosum* ssp. *tuberosum* cv 'Irish Cobbler, ssp. *andigena* cv 'W553-4' and cv '150,' tomato cv 'Toko', and tobacco cv 'White Burley' were studied (Fig. 2). The results indicated that ctDNA of potato cultivars 'Irish Cobbler', 'W553-4', and '150' corresponded to the T, W, and S type of ctDNA reported by Hosaka (1986) and Hosaka and Hanneman (1987).

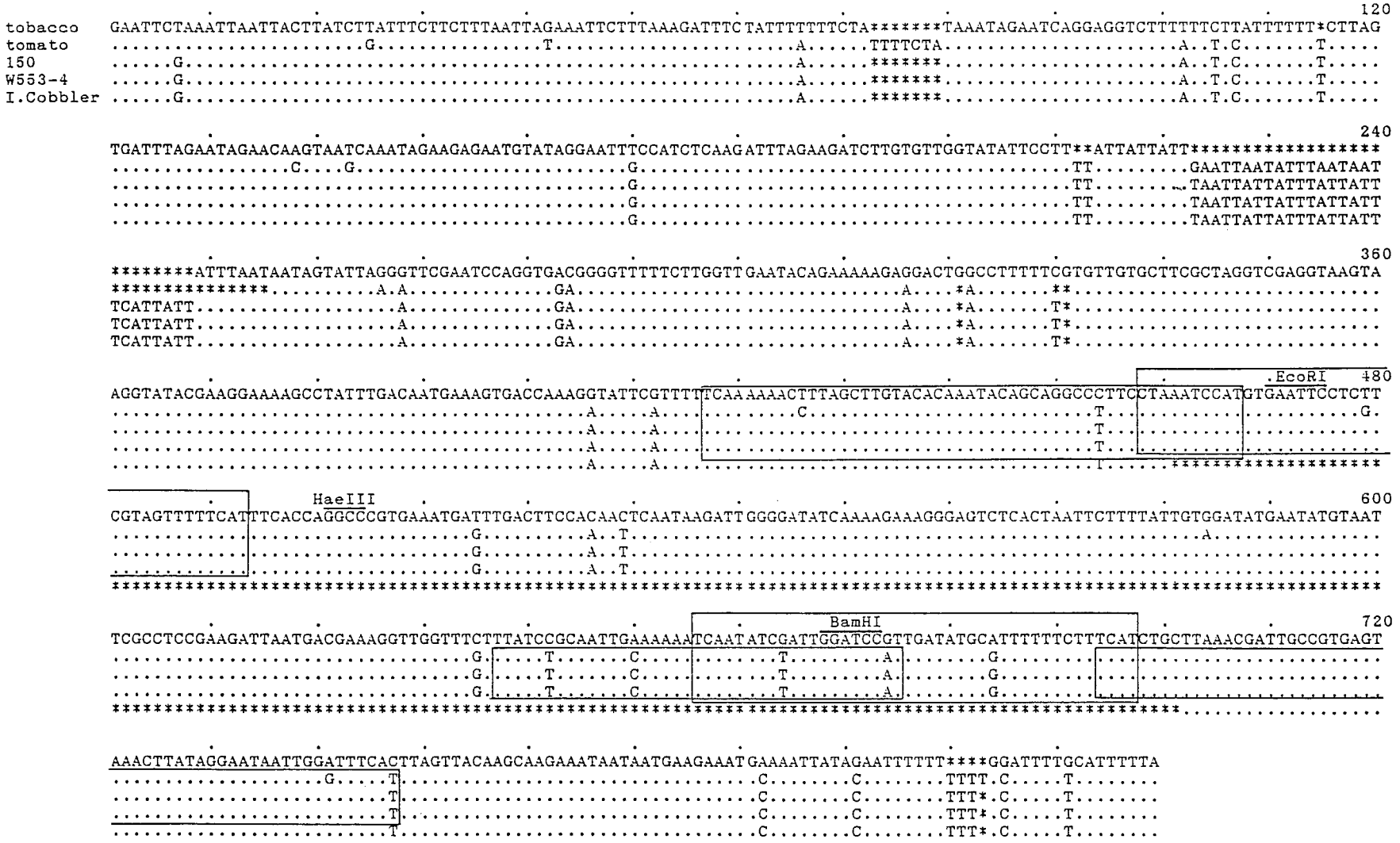


Fig. 3. Comparative sequences of the region containing the deletion found in ctDNA from ssp. *tuberosum*. The sequences are the 3′ flanking region of the *trnV-UAC* gene from *N. tabacum* (tobacco) (Shinozaki et al. 1986a), *L. esculentum* (tomato), *S. tuberosum* ssp. *andigena* cv '150' (150), ssp. *andigena* cv 'W553-4' (W553-4), ssp. *tuberosum* cv 'Irish Cobbler' (I. Cobbler). The sequences are aligned to display maximal homology consistent with the fewest insertions or deletions. The nucleotides in the sequence from tomato and potato that are homologous to the tobacco sequence are indicated by periods (.), and vacant positions are indicated by asterisks (*). The deletion found in cv 'Irish Cobbler' ctDNA is 241 bp (+461 to +701 from the start). Locations of the major restriction sites in the deleted region are overlined, and the sequences of five small ORFs are boxed

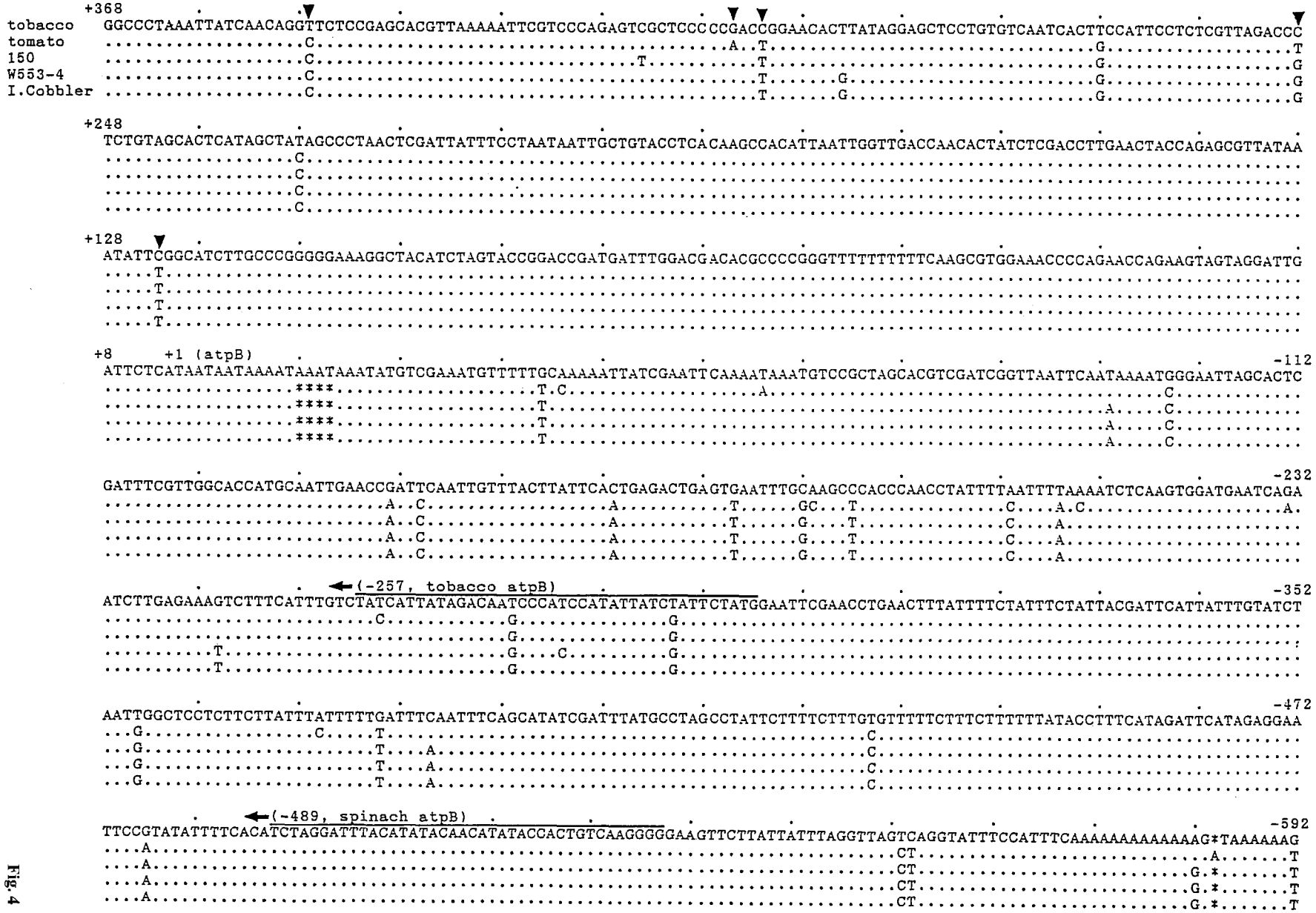
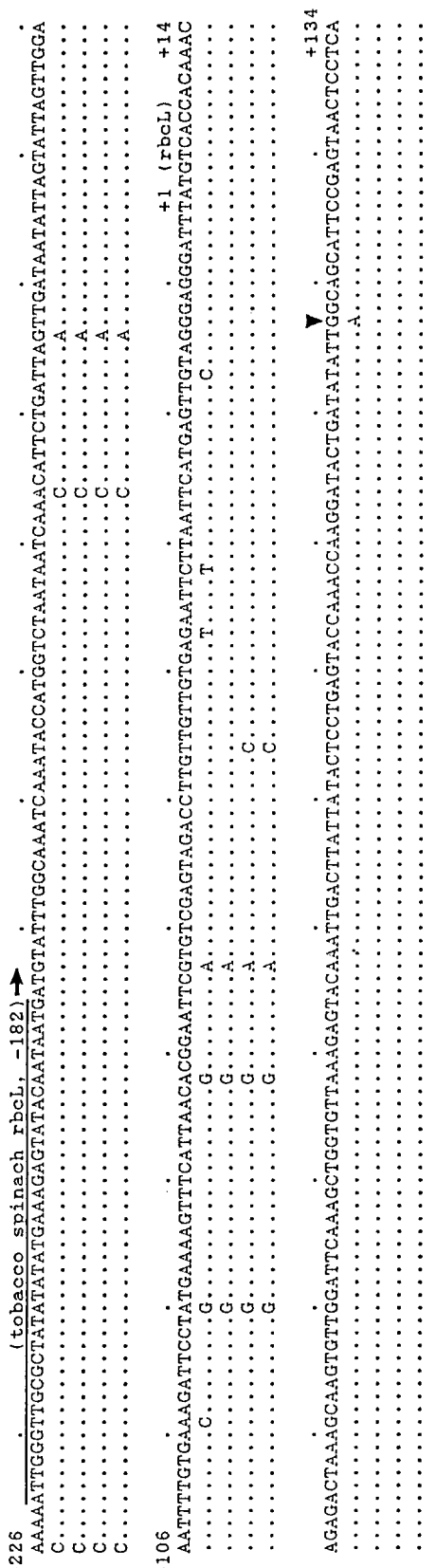

+368
tobacco GGCCCTAAATTATCAACAGGTTCTCCGAGCACGTTAAAAATTCGTCCCAGAGTCGCTCCCCCGACCGGAACACTTATAGGAGCTCCTGTGTCAATCACTTCCATTCCTCTCGTTAGACCC
tomato .....C.....A..T.....G.....T
150 .....C.....T.....T.....G.....G
W553-4 .....C.....T.....G.....G.....G
I.Cobbler .....C.....T.....G.....G.....G
+248
TCTGTAGCACTCATAGCTATAGCCCTAACTCGATTATTTCCTAATAATTGCTGTACCTCACAAGCCACATTAATTGGTTGACCAACACTATCTCGACCTTGAACTACCAGAGCGTTATAA
.....C.....
.....C.....
.....C.....
.....C.....
+128
ATATTCGGCATCTTGCCCGGGGGAAAGGCTACATCTAGTACCGGACCGATGATTTGGACGACACGCCCCGGGTTTTTTTTTTCAAGCGTGGAAACCCCAGAACCAGAAGTAGTAGGATTG
.....T.....
.....T.....
.....T.....
.....T.....
+8 +1 (atpB) -112
ATTCTCATAATAATAAAATAAATAAATATGTCGAAATGTTTTTGCAAAAATTATCGAATTCAAAATAAATGTCCGCTAGCACGTCGATCGGTTAATTCAATAAAATGGGAATTAGCACTC
.....****.....T.C.....A.....C.....
.....****.....T.....A.....C.....
.....****.....T.....A.....C.....
.....****.....T.....A.....C.....
-232
GATTTCGTTGGCACCATGCAATTGAACCGATTCAATTGTTTACTTATTCACTGAGACTGAGTGAATTTGCAAGCCCACCCAACCTATTTTAATTTTAAAATCTCAAGTGGATGAATCAGA
.....A..C.....A.....T.....GC...T.....C....A.C.....A.
.....A..C.....A.....T.....G....T.....C....A.....
.....A..C.....A.....T.....G....T.....C....A.....
.....A..C.....A.....T.....G....T.....C....A.....
(-257, tobacco atpB) -352
ATCTTGAGAAAGTCTTTCATTTGTCTATCATTATAGACAATCCCATCCATATTATCTATTCTATGGAATTCGAACCTGAACTTTATTTTCTATTTCTATTACGATTCATTATTTGTATCT
.....C.....G.....G.....
.....G.....G.....
.....T.....G....C.....G.....
.....T.....G.....G.....
-472
AATTGGCTCCTCTTCTTATTTATTTTTGATTTCAATTTCAGCATATCGATTTATGCCTAGCCTATTCTTTTCTTTGTGTTTTTCTTTCTTTTTTATACCTTTCATAGATTCATAGAGGAA
...G.....C.....T.....C.....
...G.....T....A.....C.....
...G.....T....A.....C.....
...G.....T....A.....C.....
(-489, spinach atpB) -592
TTCCGTATATTTTCACATCTAGGATTTACATATACAACATATACCACTGTCAAGGGGGAAGTTCTTATTATTTAGGTTAGTCAGGTATTTCCATTTCAAAAAAAAAAAAAAG*TAAAAAAG
....A.....CT.....A.....T
....A.....CT.....G.*.....T
....A.....CT.....G.*.....T
....A.....CT.....G.*.....T

Fig. 4



Hosaka et al. (1988) reported that the ctDNA of cultivated potato differed from the wild species by one deletion. DNA sequencing revealed a 241-bp deletion downstream of a *trnV-UAC* gene in the ctDNA of ssp. *tuberosum* cv 'Irish Cobbler' (Fig. 3). The location of the deletion was determined by reference to a tobacco gene map (Deno et al. 1982; Shinozaki et al. 1986b). The mechanism of deletion is unknown because the deleted region was neither part of a series of tandem repeats nor was it flanked by direct repeats.

Hosaka et al. (1988) expected that the deletion included a BamHI recognition site (GGATCC). This was confirmed by our sequence data (Fig. 3).

Open reading frames (ORFs) were sought in the deletion sequences by using the program "Search Open Reading Frame" (GENETYX, Software Development, Tokyo, Japan). There are two ORFs (13 and 14 codons) found within the corresponding deleted regions, and three additional ORFs (17, 12, and 18 codons) were found flanking the deletion on both sides of wild potato species.

Comparison of the intercistronic region between rbcL and atpβ genes in potato and tomato chloroplasts

The complete sequences of the 1.35-kbp HaeIII fragments from three cultivars of potato and from a tomato shown in Fig. 4 are compared with the sequence of the corresponding tobacco fragment (Shinozaki et al. 1986a). The size of the intercistronic region between the *rbcL* and *atpβ* genes was 813, 814, or 817 bp in potato, tomato, or tobacco ctDNA, respectively. The sequences of the promoter region of the *rbcL* gene in potato and tomato are completely homologous to those of tobacco (Shinozaki and Sugiura 1982) and spinach (Mullet et al. 1985). On the other hand, four nucleotide substitutions were detected within the promoter region of the *atpβ* gene of potato, as compared to that of tobacco (the 5′ end was located at −257 in Fig. 4), whereas complete se-

Fig. 4. Comparative sequences of the 1.35-kbp HaeIII fragments. The sequences are the intercistronic region between the *rbcL* and *atpβ* genes and their part of the coding regions from *N. tabacum* (tobacco) (Shinozaki et al. 1986a), *L. esculentum* (tomato), *S. tuberosum* ssp. *andigena* cv '150' (150), ssp. *andigena* cv 'W553-4' (W553-4), ssp. *tuberosum* cv 'Irish Cobbler' (I. Cobbler). The nucleotides in the sequences from tomato and three varieties of potato that are homologous to tobacco sequences are indicated by periods (.), and vacant positions are indicated by asterisks (*). The numbering is relative to the initiation codon of either *rbcL* or *atpβ* genes. The location identified as encoding the 5′ end of *rbcL* mRNA from both tobacco and spinach chloroplasts is indicated by an *arrow* (−182). The 5′ ends of *atpβ* mRNA that differ in location from tobacco (−256 or −257) and spinach (−489) mRNA are also indicated by an *arrow*. The promoter regions (the 5′ flanking sequences of the transcription initiation site) are *underlined*. Synonymous substitutions between tobacco and tomato are indicated by *triangles*

Table 1. Polytypic patterns and their frequencies of nucleotide substitutions and insert/deletions. Capital letters represent *N. tabacum* (N), *L. esculentum* (L), *S. tuberosum* ssp. *andigena* cv '150' (S), ssp. *andigena* cv 'W553-4' (W), ssp. *tuberosum* cv 'Irish Cobbler' (T). Informative mutations for determining topology and singular mutations are listed separately

Polytypic pattern[a]		Frequency	
		Nucleotide substitution	Insertion/deletion[b]
I.	Informative mutations		
a	(N, L)–(S, W, T)	4	–
b	(N, L, S)–(W, T)	3	–
II.	Singular mutations		
c	N–L–(S, W, T)	1	–
d	N	58	1^3, 2^1, 3^1, 4^1, 26^1
e	L	23	1^3, 7^1, 15^1
f	S	1	–
g	W	1	–
h	T	0	241^1
	Total	2,377 bp per species examined	

[a] A polytypic pattern (N, L)–(S, W, T) indicates that N and L share the same nucleotide, whereas S, W, and T share a different nucleotide

[b] x^y represents the fact insertion/deletion of X nucleotides in size are detected y times

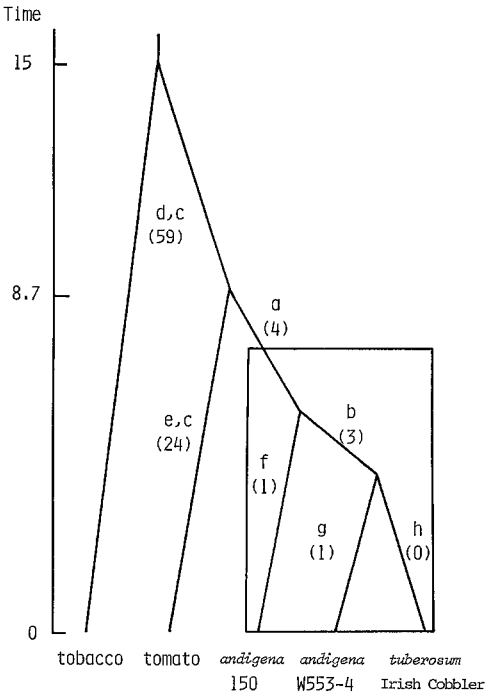


Fig. 5. Phylogenetic tree for tobacco, tomato, and three varieties of potato. The tree was reconstructed by the maximum parsimony method from the data presented in Table 1. In this tree, polytypic pattern (c), [N–L–(S, W, T)], is asumed to be the result of two independent mutations that occurred in the tobacco and tomato lineages. Number in *parentheses* indicate the frequency of nucleotide substitutions. The time of divergence between tobacco and tomato was inferred from the number of synonymous substitutions found in the coding regions of *rbcL* and *atpβ* genes (Fig. 4), and the time of divergence between potato and tomato was inferred from the total number of nucleotide substitutions in the tomato lineage (24) relative to those in the tobacco lineage (59). The ordinate scale is in million years. The generations inside the box are a combination of vegetative and sexual propagations; therefore, the relative time spans of each line inside the box cannot be inferred from the number of nucleotide substitutions

quence homology was conserved within the region of the promoter between potato and spinach (the 5′ end was located at −489 in Fig. 4).

Ten and 27 nucleotide substitutions were found in the 5′ untranslated leader sequences of the *rbcL* and *atpβ* genes, respectively, presenting a striking contrast to the conservation of the promoter regions among potato, tomato, and tobacco.

Construction of a phylogenetic tree from sequence data

One hundred and ten mutations (97 nucleotide substitutions and 13 insertions or deletions) were detected in 2,377 base pairs of corresponding ctDNA sequences, including a part of the 3′ *petD* gene (data not shown) among potato, tomato, and tobacco. However, only seven nucleotide substitutions were informative for determining topology. It was convenient to classify the mutations into different polytypic patterns for the construction of a maximum parsimony tree. There are eight different polytypic patterns listed in Table 1.

For example, a polytypic pattern (N, L) – (S, W, T) indicates that tobacco (N) and tomato (L) possess the same nucleotide, whereas potato cultivars '150' (S), 'W553-4' (W), and 'Irish Cobbler' (T) have a different nucleotide. A phylogenetic tree was constructed on the basis of the polytypic patterns a and b (Fig. 5). Since the polytypic pattern c required at least two substitutions for the entire tree, the two independent mutations had occurred within tobacco and tomato lineages.

From the restriction fragment patterns of ctDNA in Fig. 2, the putative ancestors within line (a) must have W-type ctDNA because tomato has a W-type-like ctDNA. Therefore, *Solanum* species having W-type ctDNA can be considered to range from the most primitive tuber-bearing *Solanum* to the latest cultivars of potato, such as *S. tuberosum* ssp. *andigena.*

Comparison of rates of nucleotide substitution between potato and tomato ctDNAs

The rates of nucleotide substitution appear to be approximately the same among different evolutionary lineages (Hayashida and Miyata 1983). However, our data demonstrate that the nucleotide substitutions in potato lineages are fewer than those in tomato lineage (Fig. 5).

For example, after the divergence between tomato and the potato cv '150', 24 nucleotide substitutions occurred in the lineage of tomato [line (c, e)], but onyl five occurred in the lineage of cv '150' [lines (a) and (f)]. These data indicate that the mutations have rarely been fixed in potato, in which chloroplast genomes have been transmitted to the next generations by means of vegetative propagation.

Discussion

Location of the 5′ ends of mRNAs for the rbcL and atpβ genes

It has been shown in chloroplasts that a typical promoter region, containing prokaryotic consensus '−35' and '−10' sequences, is highly conserved (Erion 1985; Zurawski and Clegg 1987). Since the promoter regions of the *rbcL* gene of tobacco (Shinozaki and Sugiura 1982) and spinach (Mullet et al. 1985) were identical to the promoters of potato and tomato in this paper, the 5′ ends of *rbcL* mRNA of both potato and tomato chloroplasts may be at the same location as in tobacco and spinach (−182 in Fig. 4). On the other hand, the location determined as the 5′ end of *atpβ* mRNA from tobacco (−257 in Fig. 4) could be considered the site of posttranscriptional processing, as Mullet et al. (1985) suggested, because four nucleotide substitutions were detected in the *atpβ* promoter region. It is probable that the actual 5′ ends of *atpβ* mRNA in ctDNAs of potato, tomato, and tobacco were at the same location as in spinach (−489 in Fig. 4), because the promoter regions were completely conserved.

Molecular evolution of potato ctDNA and the phylogenetic tree constructed from sequence data

The rate of synonymous substitution was reported to be relatively constant for all genes over a period of evolutionary time (Hayashida and Miyata 1983). Zurawski et al. (1984) reported that the synonymous substitution rate of ctDNA mutation was 1.1×10^{-9} site^{-1} year^{-1} based on the assumption that barley and maize diverged 50 million years ago. This rate was applied to our data to calculate the divergence time between tobacco and tomato. Using substitution at the third position of 177 codons (i.e., parts of *rbcL* and *atpβ* genes) in which the six synonymous substitutions were detected, divergence was calculated as having occurred 15 million years ago. Since the rate of substitution mutation was not the same in potato and tomato, the divergence time between the two species was inferred from the ratio of the total number of nucleotide substitutions of the tomato lineage (24) to the tobacco lineage (59). Divergence between potato and tomato was calculated to have occurred 8.7 million years ago.

Since nucleotide substitutions that occurred within lines (f), (h), and (g) were far less frequent than expected based on the tomato lineage [line (c, e)], the first appearance of tuber-bearing species of *Solanum* could be given within line (a), assuming that the tomato lineage was derived from non-tuber-bearing *Solanum*. The four nucleotide substitutions of line (a) occurred before the appearance of the first tuber-bearing *Solanum*. In this case, the time from the divergence of potato and tomato to the first appearance of tuber-bearing *Solanum* is calculated as 1.5 million years. Thus, the total period of line (a) is more than 1.5 million years because of the additional time for many generations to propagate themselves vegetatively. For this reason, the two divergence times of both ends of line (b) could not be inferred from our sequence data.

The method of propagation within line (b), including relatively recent ancestors of common potato, may have been by both vegetative and sexual means, by either selfing or crossing, or by a combinations of line (b) could be considered relatively frequent as compared to the three lines (f), (h), and (g). The observation that the wild species in the series Tuberosa can hybridize readily with one another and with cultivated diploids (Ugent 1970) is evident by the frequency of the nucleotide substitutions of line (b).

S. stenotomum is a cultivated diploid with the S-type ctDNA (Hosaka 1986), which is also found in ssp. *andigena* cv '150' (Fig. 1) and is considered to be the ancestor to all the modern, cultivated varieties of the potato (Simmonds 1976; Grun et al. 1977; Matsubayashi 1981). *S. stenotomum* as well as *S. tuberosum* appeared within line (a). Since the putative ancestors within line (a) must have contained W-type ctDNA, *S. stenotomum,* containing W-type ctDNA, exists somewhere even now.

Since both cv '150' and cv 'W553-4' are members of ssp. *andigena,* the time of appearance of ssp. *tuberosum* is within line (h). The deletion of 241 bp found in ctDNA of ssp. *tuberosum* had also occurred within line (h). The chronological order of the two events, the appearance of ssp. *tuberosum* and the 241-bp deletion in ctDNA, remains to be elucidated. The 241-bp deletion from ctDNA confirmed in this paper is one of the most useful characters for the investigation of the origin of *Solanum tuberosum* ssp. *tuberosum*.

Acknowledgements. We thank Dr. J. Obokata for his gift of tobacco ctDNA sequence data and technical advice, and Dr. S. Nishibe for providing tubers of potato. We also thank Drs. M. Burow and R. Chapman for critical reading of the manuscript and Dr. N. Murai for his encouragement. This work was conducted in the Gene Research Center, Hokkaido University, Sapporo, Japan, and was supported in part by a Grant-in-Aid for General Scientific Research(B) 01480040 from the Ministry of Education, Science, and Culture, Japan.

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