Plant Cell Physiol. 37(2): 117-122 (1996)
JSPP © 1996

Acetyl-CoA Carboxylase in Higher Plants: Most Plants Other Than Gramineae Have Both the Prokaryotic and the Eukaryotic Forms of This Enzyme

Tomokazu Konishi [1,4], Kenji Shinohara [2], Kyoji Yamada [3] and Yukiko Sasaki [1,5]

[1] *Department of Food Science and Technology, Faculty of Agriculture, Kyoto University, 606-01 Japan*
[2] *Molecular and Cell Biology Section, Bio-Resources Technology Division, Forestry and Forest Products Research Institute, Inashiki, Ibaraki, 305 Japan*
[3] *Department of Biology, Faculty of Science, Toyama University, Toyama, 930 Japan*

The presence and the absence of a prokaryote type and a eukaryote type of acetyl-CoA carboxylase (EC 6.4.1.2; ACCase) were examined in members of 28 plant families by two distinct methods: the detection of biotinylated subunits of ACCase with a streptavidin probe, and the detection of the *accD* gene, which encodes a subunit of the prokaryotic ACCase, by Southern hybridization analysis. The protein extracts of all the plants studied contained a biotinylated polypeptide of 220 kDa, which was probably the eukaryotic ACCase. All the plants but those belonging to Gramineae also contained a biotinylated polypeptide of ca. 35 kDa, which is a putative subunit of the prokaryotic ACCase. In all plants but those in Gramineae, the ca. 35 kDa polypeptide was found in the protein extracts of plastids, while the 220 kDa polypeptide was absent from these plastid extracts. The plastid extracts of the plants in Gramineae contained the 220 kDa polypeptide, as did the homogenates of the leaves. Southern hybridization analysis demonstrated that all the plants but those in the Gramineae contained the *accD* gene. These findings suggest that most higher plants have the prokaryotic ACCase in the plastids and the eukaryotic ACCase in the cytosol. Only Gramineae plants might contain the eukaryotic ACCases both in the plastids and in the cytosol. The origin of the plastid-located eukaryotic ACCase in Gramineae is discussed as the first possible example of substitution of a plastid gene by a nuclear gene for a non-ribosomal component.

Key words: *accD* — Acetyl-CoA carboxylase (EC 6.4.1.2) — Biotinylated polypeptides — De novo synthesis of fatty acids — Gramineae.

Acetyl-CoA carboxylase (ACCase) catalyzes the first committed step in the fatty acid synthesis, namely, the formation of malonyl-CoA. Two forms of the enzyme have been found: a eukaryotic ACCase that is mainly present in the cytosol of animal and yeast cells and a prokaryotic ACCase that is found in bacteria (Wakil et al. 1983). These forms differ in the composition of the subunits; the eukaryotic ACCase is composed of a single multi-functional polypeptide, while the prokaryotic ACCase is composed of several subunits. In recent studies, cells of pea (*Pisum sativum*) (Konishi and Sasaki 1994, Alban et al. 1994) and maize (*Zea mays*) (Egli et al. 1993) were shown to contain two ACCases with different subcellular localization: one in the stroma of plastids and the other outside the plastids (for review, see Sasaki et al. 1995). The molecular mass of the detected ACCase suggests that outside the plastids these plants possess a eukaryotic ACCase. However, in their plastids, pea plants have a prokaryotic ACCase while maize and wheat appear to have another eukaryotic ACCase (Gornicki and Haselkorn 1993, Konishi and Sasaki 1994). It is unknown whether plants in other plant families contain the prokaryotic type or the eukaryotic type of ACCase in their plastids.

For identification of the ACCase in the plastids, we can easily detect the biotinylated subunit of ACCase in the protein extracts of plants. Both forms of ACCase contain biotinylated polypeptides, but they are unique in terms of molecular mass among the biotinylated proteins in pea leaves (Konishi and Sasaki 1994). Although higher plants contain several biotinylated enzymes (Wurtele and Nikolau 1992), these can be distinguished from ACCases, which yield characteristic bands on gels after SDS-PAGE.

An alternative way to identify the enzymes is to examine the presence of the *accD* (*zfpA*) gene in the plastid genome by Southern hybridization. This gene encodes transcarboxylase beta, which is one of the subunits of prokaryotic ACCase (Sasaki et al. 1993). The presence of an *accD* gene strongly suggests that a plant has the prokaryotic ACCase in its plastids. The gene is usually located between *rbcL* and *psaI*, and the nucleotide sequences of the gene from several plant species have been registered in the GenBank Nucleotide Sequence Database. They include genes from dicots: pea, *Cuscuta reflexa*, tobacco (*Nicotina*

Abbreviation: ACCase, acetyl-CoA carboxylase.
[4] Present address: Plant-Growth Regulation Laboratory, The Institute of Physical and Chemical Research (RIKEN), Hirosawa 2-1, Wako, 351-01 Japan.
[5] Present address: Laboratory of Plant Molecular Biology, School of Agricultural Sciences, Nagoya University, Chikusa-ku, Nagoya, 464-01 Japan.

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022

tabacum) and *Epifagus virginiana* (locus names: CHPSZFPA, CRZFPA, CHNTXX, EPFCPCG, respectively); from a fern: *Angiopteris lygodiifolia* (ALATPBS); from a liverwort: *Marchantia polymorpha*, from a moss: *Physcomitrella patens* (CHMPXX, CHPPZFTR); and from black pine (*Pinus thunbergii*) (PINCPTRPG). Additionally, in monocots, genes homologous to the tobacco *accD* gene have been detected in two Liliaceae plants (Katayama and Ogihara 1993b). By contrast, loss of the *accD* gene from some of the plastid genome has been suggested in several plants in Gramineae (Ogihara et al. 1991, Morton and Clegg 1993), Juncaceae and Cyperaceae (Katayama and Ogihara 1993a), Campanulaceae, Geraniceae, Lobeliaceae, Oleaceae (Downie and Palmer 1992). These findings suggest that members of some plant families lack the prokaryotic ACCase. However, the nucleotide sequences of plastid genomes of these plants have not been determined completely; rearrangement of the plastid genome could have resulted in a change in the *accD* locus. Additionally, nucleotide sequences similar to *accD* have been found in plastid genomes of several members of Gramineae (Hiratsuka et al. 1989, Ogihara et al. 1991, Morton and Clegg 1993). Furthermore, it is possible that *accD* might have been relocated to the nuclear genome, as is the cases for some genes for ribosomal components (Baldauf et al. 1990, Gantt et al. 1991). Taken together, these observations suggest that some plants in these families might contain the prokaryotic ACCase.

In this study, we surveyed the biotinylated polypeptides and the *accD* gene in higher plants that belong to 28 different families. Our findings suggest that most of the tested plants, including non-photosynthetic plants, contain the prokaryotic ACCase in their plastids and the eukaryotic ACCase in their cytosol. The only exceptions were plants in the Gramineae; they contained a eukaryotic ACCase in their plastids instead of the prokaryotic enzyme.

Materials and Methods

Plant materials—*Cuscuta japonica* Choisy, a parasitic plant, was cultivated in vitro (Furuhashi 1991). Seeds of *Arabidopsis thaliana* (L.) Heynh., black pine (*Pinus thunbergii* Parlatore), *Cyperus flavidus* Retz., geranium (*Pelargonium zonale* L'Herit.), *Juncus effusus* L., tobacco (*Nicotiana tabacum* L.) and tubers of ginger plant [*Zingiber officinale* (Willd.) Roscoe] and *Platycodon grandiflorum* (Jacq.) A. DC. were planted on vermiculite beds and grown at 25°C with illumination from fluorescent tubes (approximately 100 μE m^{-2} s^{-1}) for 16 h per day. Carrot (*Daucus carota* L.) and leek (*Allium tuberosum* Rottl.) were obtained from a local market. Other samples were collected from plants that were growing in the field: in Lake Biwa, in Midoro-ga-ike pond in Kyoto City, in the Kisaichi Botanical Gardens of Osaka City University and on the campus of Kyoto University.

Detection of biotinylated proteins—Biotinylated polypeptides were detected among the total proteins of young leaves as follows (Sasaki et al. 1993). Total proteins (approximately 10 μg) from each sample were separated by SDS-PAGE (5–15% polyacrylamide gradient gel) and blotted onto nitrocellulose membranes (Fig. 1A). Biotinylated polypeptides were probed with streptavidin-peroxidase (Sigma) and detected photochemically with ECL western blotting detection reagents (Amersham). Chloroplasts were isolated and purified on Percoll (Pharmacia) density gradients from leaves that had been kept in darkness for at least 8 h (Konishi and Watanabe 1993). Intactness of the chloroplasts (>90%) was checked by phase-contrast microscopy. Biotinylated polypeptides in the samples (approximately 2 μg Chl) were detected as described above (Fig. 1B).

Detection of the accD gene—Total DNA was extracted from leaves as described elsewhere (Sambrook et al. 1989). DNA (5 μg) was digested by *Hin*dIII, separated by 0.7% agarose gel electrophoresis and blotted onto a nitrocellulose membrane. The amount of plastid DNA in each lane on the blot was checked by hybridization with the tobacco *psaB* gene. The nucleotide sequence of the tobacco *psaB* gene was more than 90% homologous to that of genes of flowering plants in the GenBank Nucleotide Sequence Database, and 86% and 84% homologous to those of black pine and liverwort, respectively. The probe for *accD* gene was prepared as follows. Total DNA from pea seedlings was amplified by the polymerase chain reaction with the specific primers, 5'ATTCGGAAGAGGAAAAAGACC and 5'TTAGTTTTCATTTTCAGTCCA, and a 812-bp fragment was generated. The nucleotide sequence of the product exhibited of 82–70% homology to those of the other *accD* genes mentioned in the Introduction. The product was labeled with [^{32}P]dCTP using a Random Primer Labeling Kit (Takara) in accordance with the protocol from the supplier. After hybridization in 6× SSC at 60°C, the membrane was washed at 40°C in 0.5× SSC, 0.1% SDS. Autoradiography was performed with RX X-ray film (Fuji) at −80°C or with a Bioimage analyzer (BAS 2000 system, Fuji).

Results

Biotinylated polypeptides from higher plants—Using a streptavidin probe, we detected biotinylated polypeptides in the protein extracts from young leaves and chloroplasts of various plants (Fig. 1). The protein extracts from all the plants tested contained a biotinylated polypeptide of ca. 220 kDa (Fig. 1). This molecular mass is characteristic of the eukaryotic ACCases of many plant species (Harwood 1988, Egli et al. 1993, Gornicki and Haselkorn 1993, Alban et al. 1994, Ashton et al. 1994, Elborough et al. 1994, Konishi and Sasaki 1994). However, while the 220 kDa polypeptides were detected in extracts from whole leaves, they were not detected in extracts of plastids (Fig. 1B), as was the case for pea (Konishi and Sasaki 1994).

The protein extracts from all the plants, including the non-photosynthetic plant *Galeola septentrionalis* and the parasitic plant *Cuscuta japonica* but excluding plants in Gramineae, contained a major biotinylated protein of ca. 35 kDa (Table 1 and Fig. 1). The biotinylated protein was found in extracts of the chloroplasts of many of the plants tested (Fig. 1B and Alban et al. 1994, Konishi and Sasaki 1994). Though they differed somewhat in size, these proteins were the most plausible candidates for a subunit of the prokaryotic ACCase. Some of the protein samples con-

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022

Table 1 Detection of a biotinylated polypeptide of ca. 35 kDa from various plants

Class Family	Species	Common name	35 kDa [a]
Hepaticae			
Marchantiaceae	*Marchantia polymorpha* L.		Y
Cycadopsida			
Cycadaceae	*Cycas revoluta* Thunb.	cycad	Y
Coniferopsida			
Pinaceae	*Pinus thunbergii* Parlatore	black pine	Y
Diocotyledoneae			
Campanulaceae	*Platycodon grandiflorum* (Jacq.) A. DC.	balloon flower	Y
Convolvulaceae	*Cuscuta japonica* Choisy		Y
Cruciferae	*Arabidopsis thaliana* (L.) Heynh.		Y
Cucurbitaceae	*Cucumis sativus* L.	cucumber	Y
Geraniceae	*Pelargonium zonale* L'Herit.	geranium	Y
Leguminosae	*Pisum sativum* L.	pea	Y
Solanaceae	*Nicotiana tabacum* L.	tobacco	Y
Umbelliferae	*Daucus carota* L.	carrot	Y
Monocotyledoneae			
Amaryllidaceae	*Lycoris radiata* Herb.		Y
Araceae	*Pinellia ternata* (Thunb.) Breit.		Y
Commelinaceae	*Commelina communis* L.	dayflower	Y
Cyperaceae	*Cyperus flavidus* Retz.		Y
Dioscoreaceae	*Dioscorea japonica* Thunb.	Japanese yam	Y
Eriocaulaceae	*Eriocaulon hondoense* Satake		Y
Gramineae [b]			N
Hydrocharitaceae	*Hydrilla verticillata* (L. fil.) Caspary		Y
Iridaceae	*Iris laevigata* Fisch.	rabbit-ear iris	Y
Juncaceae	*Juncus effusus* L.		Y
Lemnaceae	*Spirodela polyrhiza* (L.) Schleid.		Y
Liliaceae	*Allium tuberosum* Rottl.	leek	Y
Musaceae	*Musa basjoo* Sieb.	Japanese banana	Y
Orchidaceae	*Galeola septentrionalis* Reichb. fil.		Y
Pontederiaceae	*Eichhornia crassipes* Solms-Laub.	water hyacinth	Y
Potamogetonaceae	*Potamogeton malaianus* Miq.		Y
Zingiberaceae	*Zingiber officinale* (Willd.) Roscoe	ginger plant	Y

[a] Y or N indicates that a plant contained or did not contain the biotinylated polypeptide of ca. 35 kDa, respectively.
[b] The following plants in the Gramineae were examined and none of them contained the biotinylated polypeptide of ca. 35 kDa: *Bromus catharticus* Vahl, *Coix lacryma-jobi* L., *Digitaria ciliaris* (Retz.) Koel., *Eleusine indica* (L.) Gaertn., *Eragrostis ferruginea* (Thunb.) Beauv., barley (*Hordeum vulgare* L.), maize (*Zea mays* L.), *Miscanthus sinensis* Anderss., *Oplismenus undulatifolius* (Arduino) Roemer et Schultes, *Pennisetum alopecuroides* (L.) Spreng., *Phragmites communis* Trin., *Phyllostachys heterocycla* (Carr.) Mitford, *Poa annua* L., rice (*Oryza sativa* L.), *Sasa palmata* (Bean) Nakai, *Setaria viridis* (L.) Beauv., wheat (*Triticum aestivum* L.), and *Zizania latifolia* Turcz.

tained multiple polypeptides of 35 kDa (Fig. 1A, lanes 2, 3, 4 and 7), suggesting the degradation of ACCase by proteases, as has been observed during extraction of the pea enzyme (Sasaki et al. 1993). None of the Gramineae plants tested contained biotinylated polypeptides of ca. 35 kDa, and all the plants that lacked such a polypeptide were members of Gramineae (Table 1 and Fig. 1).

Southern analysis of the accD gene—The *accD* gene was detected by Southern hybridization in the genomes of several plants, including those in Juncaceae (Fig. 2A, lane 6) and Cyperaceae (lane 7) but not Gramineae (lanes 2–5). Because of the divergence of the nucleotide sequences of *accD* genes, mild washing conditions and long exposure were used for the hybridization experiments. A band of a

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022

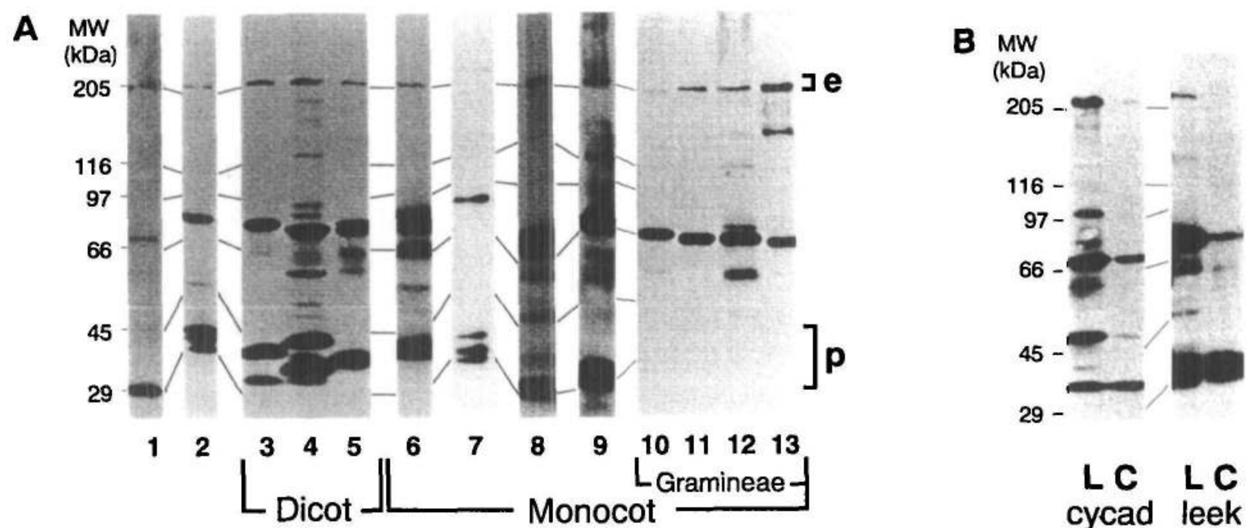

Fig. 1 Detection of biotinylated polypeptides in the protein extracts of various plants. Molecular mass standards are indicated on the left side. (A) Protein extracts of young leaves: lane 1, *Marchantia polymorpha*; lane 2, black pine. Lanes 3-5 were loaded with extracts of dicots: lane 3, *Arabidopsis thaliana*; lane 4, carrot; lane 5, tobacco. Lanes 6-13 were loaded with extracts of monocots: lane 6, *Hydrilla verticillata*; lane 7, *Cyperus flavidus*; lane 8, ginger plant; lane 9, *Galeola septentrionalis*. Lanes 10-13 were loaded with extracts of *Gramineae*: lane 10, *Poa annua*; 11, *Bromus catharticus*; 12, *Phyllostachys heterocycla*; 13, rice. The characters **e** and **p** indicate biotinylated subunits of the putative eukaryotic and prokaryotic ACCases, respectively. (B) Protein extracts of the leaves and chloroplasts of a cycad and leek: **L**, leaves; **C**, chloroplasts.

similar intensity was detected on the DNA blots from Juncaceae, Cyperaceae, black pine and cycad (lanes 6-9). However, even under the mildest washing conditions such as 4× SSC at 25°C, with longer exposure or with an alternative detection system (the Bioimage analyzer), we failed to detect any signals on the DNA blots from plants in Gramineae (data not shown). The *psaB* gene was detected in the genomes of all our samples in a control experiment, indicating that negative results were not due to the small quantities of DNA used in the experiments (Fig. 2B).

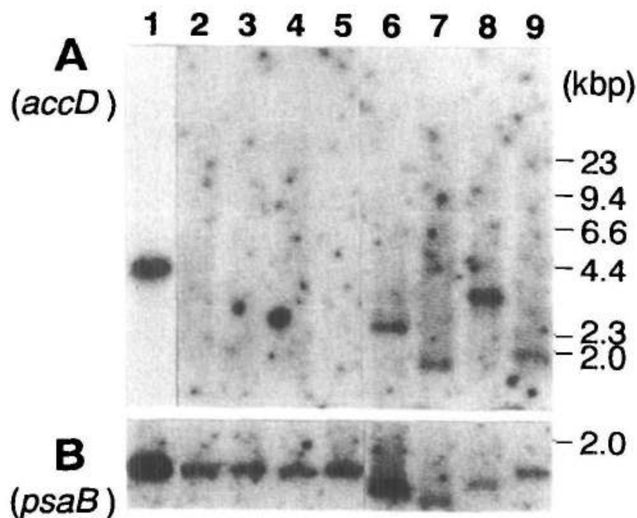

Fig. 2 Southern analysis of the *accD* gene. Total DNA was prepared from plants and probed with *accD* (A) and *psaB* (B). Molecular size standards are indicated on the right side of the panels. Lane 1, pea. Lanes 2-5, Gramineae: lane 2, wheat; lane 3, maize; lane 4, barley; lane 5, rice. Lane 6, *Juncus effusus*; lane 7, *Cyperus flavidus*, lane 8, black pine; lane 9, cycad. Exposure times for panel A were: lane 1, 20 min; lanes 2-5, 3 days; lanes 6-9, 24 h. Exposure time for the panel B was 10 h.

Discussion

A biotinylated polypeptide of ca. 220 kDa (Fig. 1A), detected in all the plants tested in this study, was identified as a eukaryotic ACCase from a comparison with data in earlier reports (Harwood 1988, Egli et al. 1993, Gornicki and Haselkorn 1993, Alban et al. 1994, Ashton et al. 1994, Elborough et al. 1994, Konishi and Sasaki 1994). Genes encoding the eukaryotic ACCase have been isolated from cDNA libraries of a variety of plant families (Gornicki and Haselkorn 1993, Ashton et al. 1994, Elborough et al. 1994, Roesler et al. 1994, Shorrosh et al. 1994). It is likely that all the plants possess the eukaryotic enzyme. However, the ca. 220 kDa polypeptides were not detected in plastids (Fig. 1B and Konishi and Sasaki 1994), with the exception of those of Gramineae; these results support the hypothesis that the eukaryotic ACCase is located in the cytosol (Roesler et al. 1994, Shorrosh et al. 1994).

All the plants except those in Gramineae contained the biotinylated polypeptide of ca. 35 kDa (Fig. 1 and Table 1). Although the plant extracts contained several biotinylated proteins, the 35 kDa polypeptide was the major poly-

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022

peptide detected in the chloroplast extracts (Fig. 1B). These results indicate that this polypeptide is a subunit of the prokaryotic ACCase, as was the case in pea (Sasaki et al. 1993). In accordance with these results, the results of Southern hybridization with probes for the *accD* gene (Fig. 2A and Katayama and Ogihara 1993b), together with nucleotide sequences of some plastid genomes (accession numbers: D17510, M81884, X04465, X15901, X70810, Z00044), suggest that all the plants except for those in Gramineae contained the *accD* gene. It appears, therefor, that all plants except those in Gramineae have the prokaryotic ACCase in their plastids.

We failed to detect the biotinylated polypeptide of 35 kDa (Table 1 and Fig. 1) and the *accD* gene (Fig. 2A) in any of the Gramineae tested. All the plants that did not contain a biotinylated polypeptide of ca. 35 kDa or the *accD* gene belonged to Gramineae (Table 1 and Fig. 2A). These results suggest that all the plants in Gramineae lack the prokaryotic ACCase; they seem to evolved from a common ancestral plant. The eukaryotic ACCase is inhibited by some graminicides, while the prokaryotic ACCase is not (Konishi and Sasaki 1994). The absence of the prokaryotic ACCase from plastids in Gramineae might explain the specific action of graminicides on this plant family as we suggested previously (Konishi and Sasaki 1994).

The genetic locus between *rbcL* and *psaI* in plastid genome is known as a hot spot for mutations in Gramineae (Hiratsuka et al. 1989, Ogihara et al. 1991, Downie and Palmer 1992, Katayama and Ogihara 1993a, b, Morton and Clegg 1993, Clegg et al. 1994). Thus, plants in Gramineae can be categorized into three classes according to the integrity of the *accD* gene. (1) Type 1 contains a short open reading frame(s), such as ORF 106 of rice (Hiratsuka et al. 1989). (2) Type 2 contains a sequence homologous to *accD* but lacks any open reading frames, for example, in the case of *Aegilops crassa* (Ogihara et al. 1991, Morton and Clegg 1993). (3) Type 3 completely lacks the similar sequence, as in the case of wheat (Ogihara et al. 1991, Morton and Clegg 1993). These variations in the *accD* locus suggest that reorganization of the plastid genome around this locus is still in progress in the Gramineae.

It has been reported that *accD* has been lost from the corresponding locus at the plastid genome of members of Juncaceae and Cyperaceae (Katayama and Ogihara 1993a) and from the plastid genomes of some members of Campanulaceae, Geraniceae, Lobeliaceae and Oleaceae (Downie and Palmer 1992). However, detection of the 35 kDa biotinylated polypeptide in some of these plant families (Table 1 and Fig. 1A) and of the *accD* gene in plants in the Juncaceae and Cyperaceae (Fig. 2A) suggests that they have a prokaryotic ACCase. The nucleotide sequences of *accD* genes that have been reported are rather diverse. Thus, detection of the gene by the Southern blot analysis required low-stringency condition. It is possible that the diversity of the nucleotide sequences prevented detection of the gene by hybridization analysis in some cases.

A eukaryotic ACCase seems to replace the prokaryotic ACCase in Gramineae plastids. The eukaryotic enzyme in the plastids must be encoded by the nuclear genome because no such gene has been found in the plastid genomes even in that of rice, whose complete nucleotide sequence had been determined (Hiratsuka et al. 1989). The eukaryotic ACCase in the plastids might have a different structure from that of the cytosolic counterpart. Indeed, in maize, these enzymes are immunologically distinguishable (Egli et al. 1993). The two eukaryotic ACCases could be encoded by distinct genes, both of which might have evolved from the same gene and diverged functionally during evolution. The replacement of the prokaryotic ACCase by the eukaryotic ACCase in plastids provides new evidence relevant to the evolution of plastid genomes. Plastid genomes seem to have been under selective pressure to be compact and to lose genes (Palmer 1993). Thus, many plastid proteins are encoded by nuclear genes that seem to have been relocated from the ancestral plastid genome. The relocation of the *tufA* gene of flowering plants (Baldauf et al. 1990) and that of the *rpl22* gene of leguminous plants (Gantt et al. 1991) to nuclear genomes suggest that the reduction in size of plastid genomes is still in progress. An alternative means of reducing the size of genomes is to replace a plastid-encoded protein by a nucleus-encoded one, as seems to be the case for a ribosomal protein (Bubunenko et al. 1994). The deletion of *accD* in the plastid genome and its replacement by a nuclear gene(s) in Gramineae may be the first example of such replacement in the case of a gene for a non-ribosomal component.

The authors thank Dr. Chiyomi Uematsu of Osaka City University, Dr. Hideya Fukuzawa and Dr. Reiichi Miura of Kyoto University for their generous gift of plant leaves and seeds, and Dr. Masahiro Sugiura of Nagoya University for a clone of the *psaB* gene. The authors also thank Dr. Chiyomi Uematsu for kind suggestions related to the nomenclature of the plants and Dr. Ryuichi Matsuno of Kyoto University for his encouragement. TK was the recipient of a fellowship from the Japan Society for the Promotion of Science for Japanese Junior Scientists.

References

Alban, C., Baldet, P. and Douce, R. (1994) Localization and characterization of two structurally different forms of acetyl-CoA carboxylase in young pea leaves, of which one is sensitive to aryloxyphenoxypropionate herbicides. *Biochem. J.* 300: 557–565.

Ashton, A.R., Jenkins, C.J.D. and Whitfeld, P.R. (1994) Molecular cloning of two different cDNAs for maize acetyl CoA carboxylase. *Plant Mol. Biol.* 24: 35–49.

Baldauf, S.L., Manhart, J.R. and Palmer, J.D. (1990) Different fates of the chloroplast *tufA* gene following its transfer to the nucleus in green algae. *Proc. Natl. Acad. Sci. USA* 87: 5317–5321.

Bubunenko, M.G., Schmidt, J. and Subramanian, A.R. (1994) Protein substitution in chloroplast ribosome evolution: a eukaryotic cytosolic protein has replaced its organelle homologue (L23) in spinach. *J. Mol.*

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022

Biol. 240: 28–41.

Clegg, M.T., Gaut, B.S., Learn, G.H., Jr. and Morton, B.R. (1994) Rates and patterns of chloroplast DNA evolution. *Proc. Natl. Acad. Sci. USA* 91: 6795–6801.

Downie, S.R. and Palmer, J.D. (1992) Use of chloroplast DNA rearrangements in reconstructing plant phylogeny. *In* Molecular Systematics of Plants. Edited by Soltis, P.S., Soltis, D.E. and Doyle, J.J. pp. 14–35. Chapman and Hall, New York.

Egli, M.A., Gengenbach, B.G., Gronwald, J.W., Somers, D.A. and Wyse, D.L. (1993) Characterization of maize acetyl-coenzyme A carboxylase. *Plant Physiol.* 101: 499–506.

Elborough, E.M., Simon, J.W., Swinhoc, R., Ashton, A.R. and Slabas, A.R. (1994) Studies on wheat acetyl CoA carboxylase and the cloning of a partial cDNA. *Plant Mol. Biol.* 24: 21–34.

Furuhashi, K. (1991) Establishment of a successive culture of an obligatory parasitic flowering plant, *Cuscuta japonica*, in vitro. *Plant Sci.* 79: 241–246.

Gantt, J.S., Baldauf, S.L., Calie, P.J., Weeden, N.F. and Palmer, J.D. (1991) Transfer of *rpl22* to the nucleus greatly preceded its loss from the chloroplast and involved the gain of an intron. *EMBO J.* 10: 3037–3078.

Gornicki, P. and Haselkorn, R. (1993) Wheat acetyl-CoA carboxylase. *Plant Mol. Biol.* 22: 547–552.

Harwood, J.L. (1988) Fatty acid metabolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 39: 101–138.

Hiratsuka, J., Shimada, H., Whittier, R., Ishibashi, T., Sakamoto, M., Mori, M., Kondo, C., Honji, Y., Sun, C.-R., Meng, B.-Y., Li, Y.-Q., Kanno, A., Nishizawa, Y., Hirai, A., Shinozaki, K. and Sugiura, M. (1989) The complete sequence of the rice (*Oryza sativa*) chloroplast genome: intermolecular recombination between distinct tRNA genes accounts for a major plastid DNA inversion during the evolution of the cereals. *Mol Gen Genet* 217: 185–194.

Katayama, H. and Ogihara, Y. (1993a) Distribution of structural alterations of grass chloroplast DNA in monocots. *Abstract of XV International Botanical Congress* p. 503. Yokohama.

Katayama, H. and Ogihara, Y. (1993b) Structural alterations of the chloroplast genome found in grasses are not common in monocots. *Curr. Genet.* 23: 60–165.

Konishi, T. and Sasaki, Y. (1994) Compartmentalization of two forms of acetyl-CoA carboxylase in plants and the origin of their tolerance toward herbicides. *Proc. Natl. Acad. Sci. USA* 91: 3598–3601.

Konishi, T. and Watanabe, A. (1993) Protein transport into thylakoid lumen—stromal processing and the energy requirement for the import of the precursor for the 23-kDa protein of PSII. *Plant Cell Physiol.* 34: 316–319.

Morton, B.R. and Clegg, M.T. (1993) A chloroplast DNA mutational hotspot and gene conversion in a noncoding region near *rbcL* in the grass family (*Poaceae*). *Curr. Genet* 24: 357–365.

Ogihara, Y., Terachi, T. and Sasakuma, T. (1991) Molecular analysis of the hot spot region related to length mutations in wheat chloroplast DNAs. I. Nucleotide divergence of genes and intergenic spacer regions located in the hot spot region. *Genetics* 129: 873–884.

Palmer, J.D. (1993) A genetic rainbow of plastids. *Nature* 364: 762–763.

Roesler, K.R., Shorrosh, B.S. and Ohlrogge, J.B. (1994) Structure and expression of an *Arabidopsis* acetyl-coenzyme A carboxylase gene. *Plant Physiol.* 105: 611–617.

Sambrook, J., Fritsch, E.F. and Maniatis, T. (1989) *Molecular Cloning: a Laboratory Manual.* Cold Spring Harbor Laboratory Press, New York.

Sasaki, Y., Hakamada, K., Suama, Y., Nagano, Y., Furusawa, I. and Matsuno, R. (1993) Chloroplast-encoded protein as a subunit of acetyl-CoA carboxylase in pea plant. *J. Biol. Chem.* 268: 25118–25123.

Sasaki, Y., Konishi, T. and Nagano, Y. (1995) The compartmentation of acetyl-CoA carboxylase in plants. *Plant Physiol.* 108: 445–449.

Shorrosh, B.S., Dixon, R.A. and Ohlrogge, J.B. (1994) Molecular cloning, characterization, and elicitation of acetyl-CoA carboxylase from alfalfa. *Proc. Natl. Acad. Sci. USA* 91: 4323–4326.

Wakil, S.J., Stoops, J.K. and Joshi, V.C. (1983) Fatty acid synthesis and its regulation. *Annu. Rev. Biochem.* 52: 537–579.

Wurtele, E.S. and Nikolau, B.J. (1992) Differential accumulation of biotin enzymes during carrot somatic embryogenesis. *Plant Physiol.* 99: 1699–1703.

(Received July 7, 1995; Accepted December 4, 1995)

Downloaded from https://academic.oup.com/pcp/article/37/2/117/1820226 by guest on 16 August 2022