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THE BIOSYNTHESIS OF ISOPRENOID COMPOUNDS IN THE CHLOROPLAST FROM THE COMPARTMENTAL VIEW

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INTRODUCTION

Since the isotopic studies of Goodwin's group (1) it has been proved that chloroplasts are autonomic in the synthesis of the isoprenoid moiety in chlorophylls, prenylquinones and carotenoids. In contrast to the endoplasmic reticulum with farnesyl-PP, in chloroplasts GGPP is the central prenyl-PP, which is elongated (solanesol) hydrogenated (phytol) or bound in tail-to-tail-condensation (carotenoids) (Fig. 1).

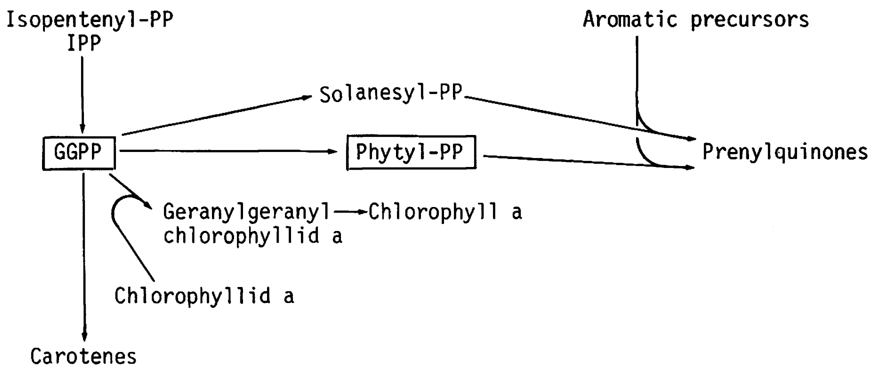

Fig. 1. Pattern on biosyntheses of isoprenoidic compounds in chloroplasts.

The survey presented here deals with the intra-organelle localization of the biosyntheses of isoprenoidic compounds and their primary processes, especially the shikimate pathway in the synthesis of prenylquinones. The studies were done by using purified spinach chloroplasts and their subfractions.

Abbreviations: E4P erythrose-4-phosphate; GGPP geranylgeranyl-PP; HPP 4-hydroxyphenylpyruvate; KDAHP 2-keto-3-deoxy-arabinoheptulonate-7-P; PEP phosphoenolpyruvate; Phe phenylalanine; PQ-9 plastoquinone-9; αT α-tocopherol; Tryp trypthophan; Tyr tyrosine.

THE SHIKIMATE PATHWAY AND ITS INVOLVEMENT IN PRENYLQUINONE SYNTHESIS

If intact spinach chloroplasts were illuminated, label from $^{14}CO_2$ is incorporated into aromatic amino acids and the prenylquinones αT and PQ-9 (2, 3). The syntheses were enhanced by external PEP (4) (for the effect on the synthesis of aromatic amino acids see Fig. 2 (5)). Whether PEP is synthesized in the chloroplasts, too, and to what extent is under investigation. It is obvious, that PEP predominately originates from the cytosol and is transferred across the envelope membrane by the phosphate translocator (6, 7). In the chloroplast stroma, KDAHP of the shikimate pathway is formed from E4P of the Calvin-cycle and PEP mentioned above. Just recently, enzymes of this pathway housed in the chloroplast stroma have been characterized (see Fiedler et al., Proc. of this Symposium). The synthesis of aromatic amino acids is centrally regulated by a feedback of Tryp on a step between shikimate and chorismate, whereas Phe and Tyr controls only their own synthesis (8, 4).

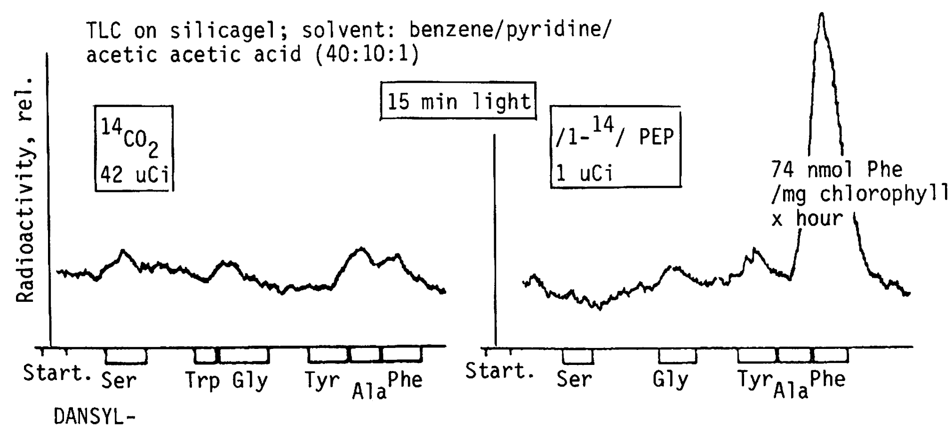

Fig. 2. ^{14}C-Incorporation from $^{14}CO_2$ and /1-^{14}C/ PEP into amino acids by intact spinach chloroplasts (5). For details in experimental conditions see (4).

The involvement of shikimate pathway in prenylquinone formation was first demonstrated by Threlfall's group (9). Homogentisate is the aromatic intermediate in the synthesis of αT and PQ-9 (10). It is formed from 4-hydroxyphenylpyruvate by a dioxygenase which mainly occurs in the chloroplast stroma (11).

The sequence of the steps in the biosynthesis of αT and PQ-9 was elucidated by Soll et al. (12) (see Fig. 4 and (13)). The site of αT synthesis is exclusively the envelope membrane, that of PQ-9 the thylakoid membrane, too (12).

Additionally, the phylloquinone (vitamin K_1) synthesis occurs in chloroplasts. 1,4-Dihydroxy-2-naphthoate is formed from chorismate via o-succinylbenzoate ⟶ CoA-ester of o-succinylbenzoate (14, 15). The naphthoate synthesis, studied in bacteria by Bentley's group (16), was verified in higher plants, too (17, 18). Schultz et al. (19) could demonstrate that 1,4-dihydroxy-2-naphthoate is prenylated by phytyl-PP to form 2-phytyl-1,4-naphthoquinol. The only site of the reaction is the envelope membrane. In the final step of the phylloquinone synthesis, the naphthoquinol is methylated by SAM at the thylakoid membrane (20). Addition of stromal phase is essential.

In Fig. 3 the situation of shikimate pathway in chloroplast is summarized.

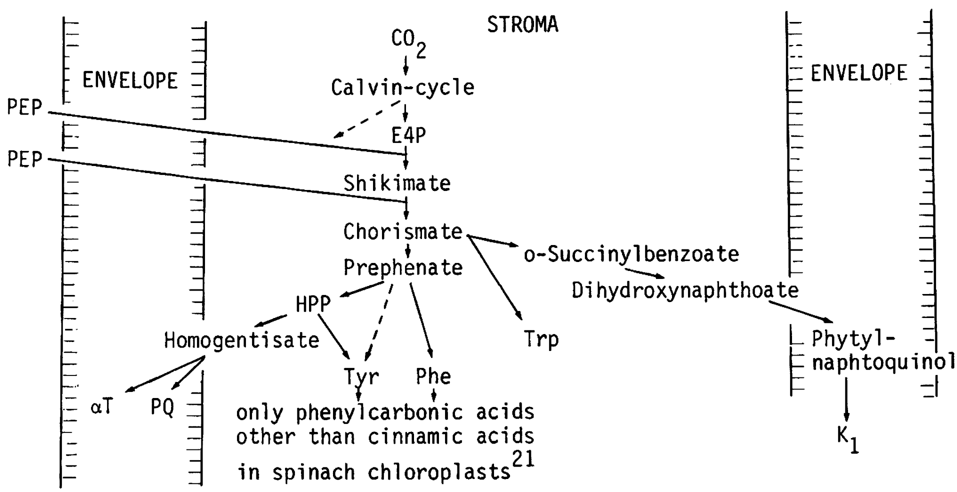

Fig. 3. Metabolic ways related to shikimate pathway in spinach chloroplasts

PLASTIDIC ISOPRENOID SYNTHESES: THE PHYTOL SYNTHESIS

Concerning the isoprenoid synthesis in plastids, there are some conflicting data. Although spinach chloroplasts are autonomic in isoprenoid synthesis (compare (1)) and incorporate ^{14}C from $^{14}CO_2$ into carotene (22), in chromoplasts of Narcissus pseudonarcissus GGPP, phytoene and carotene are formed only from IPP (23) but not from acetate (24).

The prenyltransferase reaction to yield the polyprenyl-PP s occurs in the stromal phase. It is enhanced by addition of envelope or thylakoid membranes (25) (for solanesyl-PP only envelope and stroma (26)). From the present knowledge on carotenoid synthesis, the multienzyme system forming phytoene from IPP via GGPP (27) differs from the prenyltransferase mentioned above. The desaturation and the cyclization in carotenoid synthesis are performed by other enzyme systems (27) (for the carotenoid biosynthesis in the blue-green algae Aphanocapsa see (28)).

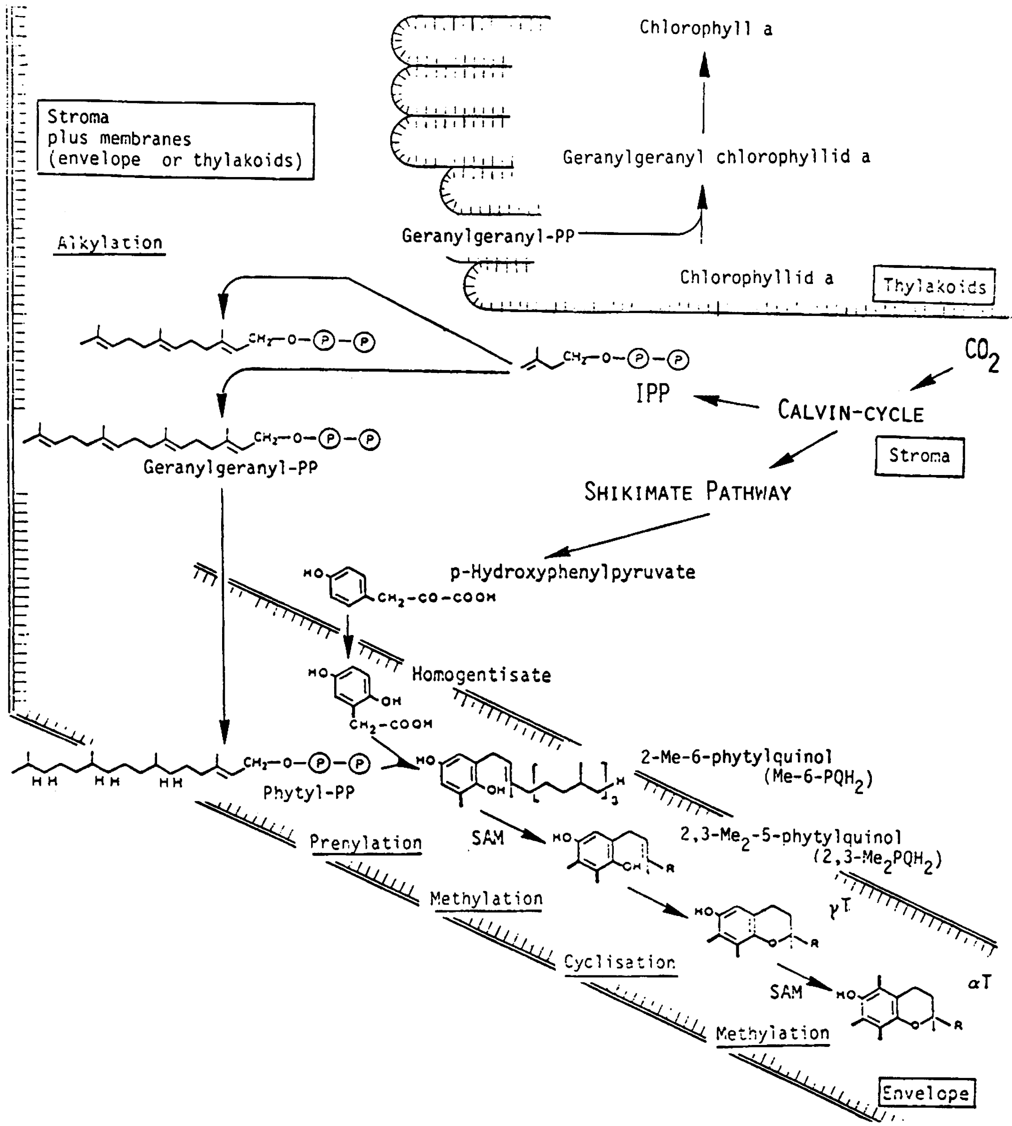

Fig. 4. Compartmental view on syntheses of isoprenoid compounds in chloroplasts

In chlorophylls, tocopherols and phylloquinone, the isoprenoid moiety is phytol. There are two pathways for its synthesis, first the direct hydrogenation of GGPP to form phytyl-PP in the envelope membrane as revealed by Soll et al. (29) , second the esterification of chlorophyllid a by GGPP in the thylakoid membranes and subsequent hydrogenation of GG-chlorophyllid a to yield chlorophyll a as shown by Rüdiger's group (30, 31). The hydrogenation is a 3-step-reaction (31): NADPH seems to be involved (29).

In Fig. 4 a survey on intra organelle localization of systems in isoprenoid compounds is given (for further references see (32)).

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