

# BIOCHEMISTRY AND METABOLISM OF PLANT LIPIDS

---

Proceedings of the 5th International Symposium on the Biochemistry and  
Metabolism of Plant Lipids held in Groningen, The Netherlands, June 7-10,  
1982.

*Editors*

J.F.G.M. Winternans

*and*

P.J.C. Kuiper



1982

ELSEVIER BIOMEDICAL PRESS  
AMSTERDAM · NEW YORK · OXFORD

# DEVELOPMENTS IN PLANT BIOLOGY

## VOLUME 8

---

### Other volumes in this series:

- Volume 1 Plant Mitochondria  
G. Ducet and C. Lance editors, 1978
- Volume 2 Chloroplast Development  
G. Akoyunoglou and J. H. Argyroudi-Akoyunoglou editors, 1978
- Volume 3 Advances in the Biochemistry and Physiology of Plant Lipids  
Lars-Åke Appelqvist and Conny Liljenberg editors, 1979
- Volume 4 Plant Membrane Transport: Current Conceptual Issues  
R. M. Spanswick, W. J. Lucas and J. Dainty editors, 1980
- Volume 5 Plant Cell Cultures: Results and Perspectives  
F. Sala, B. Parisi, R. Cella and O. Ciferri editors, 1980
- Volume 6 Biogenesis and Function of Plant Lipids  
P. Mazliak, P. Benveniste, C. Costes and R. Douce editors, 1980
- Volume 7 Plasmalemma and Tonoplast: Their Functions in the Plant Cell  
D. Marmé, E. Marrè and R. Hertel editors, 1982

© 1982 Elsevier Biomedical Press B.V.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior permission of the copyright owner.

ISBN for this volume: 0-444-80457-9

ISBN for the series: 0-444-80081-6

Published by:

Elsevier Biomedical Press B.V.

P.O. Box 211

1000 AE Amsterdam, The Netherlands

Sole distributors for the USA and Canada:

Elsevier Science Publishing Company Inc.

52 Vanderbilt Avenue

New York, N.Y. 10017

Library of Congress Cataloging in Publication Data

**International Symposium on the Biochemistry and Metabolism of Plant Lipids (5th : 1982 : Groningen, Netherlands)**  
Biochemistry and metabolism of plant lipids.

(Developments in plant biology ; v. 8)

Bibliography: p.

Includes indexes.

1. Plant lipids--Congresses. 2. Plant lipids--Metabolism--Congresses. I. Wintermans, J. F. G. M. II. Kuiper, P. J. C. (Pieter Jan Cornelis) III. Title. IV. Series.

QK898.L56I56 1982 581.19'247 82-13952

ISBN 0-444-80457-9 (Elsevier Science Pub. Co.)



Printed in the Netherlands

## CONTENTS

Dedication	v
Preface	vii
<b>BIOCHEMISTRY AND METABOLISM OF FATTY ACIDS</b>	
Biosynthesis of fatty acids in a leaf cell P.K. Stumpf, T. Shimakata, K. Eastwell, D.J. Murphy, B. Liedvoegel, J.B. Ohlrogge and D.N. Kuhn	3
Separation of component enzyme activities of fatty acid synthetase from barley chloroplasts J.D. Mikkelsen and P.B. Høj	13
Partial purification and characterization of fatty acid synthetase from barley chloroplasts P.B. Høj and J.D. Mikkelsen	17
Metabolism of oleoyl-CoA in cell fractions of soybean cell suspension cultures M. Kates and G. Ferrante	21
Fatty acid binding proteins in <i>Avena sativa</i> seedlings F. Spener and I. Tober	25
Stability of palmitoyl-CoA hydrolase from carrot P. Baardseth and E. Slinde	29
Solubilization of components involved in the microsomal oleate desaturase of potato tubers M. Christ, A. Jolliot, P. Rustin and J-C. Kader	35
Effect of calcium on the biosynthesis of linoleic and linolenic acids during the growth of a calcifuge plant ( <i>Lupinus luteus</i> L.) B. Citharel, A. Oursel and P. Mazliak	39
Shuttle of fatty acids between pea leaf chloroplasts and microsomes, mediated by a phospholipid transfer protein D. Drapier, J-P. Dubacq, A. Trémolières, C. Vergnolle, M. Julienne and J-C. Kader	43
A poly-unsaturated octadecanoic acid derivative, a major fatty acid in sporophores of <i>Cantharellus cibarius</i> Fr. L.J. De Kok, P.J.C. Kuiper and A.P. Bruins	47
The biosynthesis of photosynthetic membrane lipid precursors in higher plants and its integration with photosynthetic carbon assimilation D.J. Murphy	51

Biosynthesis of linoleic acid by cell-free extracts of sunflower seeds C.P. Rochester and D.G. Bishop	57
On the chloroplastic acyl-CoA synthetase J. Sanchez	61
Influence of the culture time on the lipid content of the cells of <i>Taphrina insititiae</i> and its fatty acid composition M.S. Sancholle and A. Schneider	65
Biosynthesis of epicuticular lipids as analyzed with the aid of gene mutations in barley P. von Wettstein-Knowles	69
On the nature and further metabolism of the products of the microsomal elongase(s) from leek epidermal cells C. Cassagne and R. Lessire	79
Retro-inhibition of the stearyl-CoA synthetase by stearyl-CoA in <i>Allium porrum</i> epidermal cell microsomes R. Lessire, P. Moreau and C. Cassagne	83
BIOSYNTHESIS AND METABOLISM OF PLANT MEMBRANE LIPIDS	
Biosynthesis and metabolism of phospholipids P. Mazliak, A. Jolliot and C. Bonnerot	89
Properties of phospholipid exchange proteins from germinated castor bean endosperms T. Tanaka and M. Yamada	99
Phospholipid transfer proteins from maize seeds and spinach leaves J-C. Kader, D. Douady, M. Julienne, M. Grosbois, F. Guerbette and C. Vergnolle	107
Studies on chloroplast lipid metabolism: stimulation of phosphatidylglycerol biosynthesis and analysis of the radioactive lipid S.A. Sparace and J.B. Mudd	111
The arsenolipids of aquatic plants A.A. Benson and P. Nissen	121
The presence of phospholipid transfer proteins in filamentous fungi L. Chavant and J-C. Kader	125
Synthesis of phospholipids in synchronous phototrophic cultures of <i>Rhodospseudomonas sphaeroides</i> T. Knacker, N.J. Russell and J.L. Harwood	129
Characterization of root plasma membranes prepared by partition in an aqueous polymer two-phase system T. Lundborg, A.S. Sandelius, S. Widell, C. Larsson, C. Liljenberg and A. Kylin	133

- Phospholipid metabolism in plant mitochondria III. CDP-choline:  
diacylglycerol cholinephosphotransferase compared to NADPH:  
cytochrome *c* reductase  
T.S. Moore, Jr. 137
- De novo*-biosynthesis of galactolipid molecular species by  
reconstituted enzyme systems from chloroplasts  
M. Frentzen, E. Heinz, T. McKeon and P.K. Stumpf 141
- Studies on the localization of enzymes involved in galactolipid  
metabolism in chloroplast envelope membranes  
A-J. Dorne, M.A. Block, J. Joyard and R. Douce 153
- In vivo* synthesis of lipids in the blue-green alga, *Anabaena*  
*variabilis*  
N. Murata and N. Sato 165
- De novo* synthesis, desaturation and acquisition of monogalactosyl  
diacylglycerol by chloroplasts from "16:3"- and "18:3"-plants  
E. Heinz and P.G. Roughan 169
- Galactolipid biosynthesis in *Brassica napus* and *Vicia faba*; a  
comparison of lipid biosynthesis in 16:3- and 18:3-plants  
J.P. Williams, M. Khan and K. Mitchell 183
- Correlation between glycerol-3-phosphate uptake and lipid synthesis  
in spinach chloroplasts  
A. Sauer and K-P. Heise 187
- UDP-galactosyl-1,2-diacylglycerol galactosyltransferase activity  
in developing oat leaf plastids  
B. Gillanders, J.A. Taylor and R.O. Mackender 191
- Some observations on the biosynthesis of galactolipids by  
intact chloroplasts  
J.W.M. Heemskerk, G. Bögemann and J.F.G.M. Wintermans 197
- In vitro* synthesis of glyceroglycolipids in the blue-green alga,  
*Anabaena variabilis*  
N. Sato and N. Murata 201
- In vitro* demonstration of the path for  $\alpha$ -linolenic acid synthesis  
by *Avena* plastids  
J-I. Ohnishi and M. Yamada 205
- Heterocyst glycolipid biosynthesis during 7-azatryptophan induced  
heterocyst differentiation in the cyanobacterium *Anabaena*  
*cylindrica*  
M.T. Mohy-Ud-Dhin, W.J. Krepski and T.J. Walton 209
- Effect of light on lipid metabolism of tissue cultures  
A.R. Gemmrich 213
- EPTC (S-ethyl dipropylthiocarbamate) modifies the composition of  
membrane lipids in mature bean chloroplasts *in vivo*  
L. Eronen and J. Bahl 217

## XII

### BIOSYNTHESIS AND METABOLISM OF SEED LIPIDS

- Fat metabolism in seeds: role of organelles  
H. Beevers 223
- Composition and lipid biosynthesis *in vivo* in oil bodies of  
olive tree fruit  
L.M. Daza and J.P. Donaire 237
- Acyl-CoA synthetase, acyltransferase and acyl-CoA thioesterase  
activities of oil bodies from avocado mesocarp  
M. Mancha and J.M. Garcia 243
- Lipid biosynthesis in the developing mustard seed: metabolism  
of endogenous and exogenous fatty acids  
K.D. Mukherjee 247
- Characterization of fatty acid synthesis in a cell free system  
from developing oil seed rape  
A. Slabas, P. Roberts and J. Ormesher 251
- The control of the triacylglycerol composition in the micro-  
somes of developing oil seeds  
K. Stobart, S. Stymne and G. Glad 257

### CATABOLISM OF PLANT LIPIDS

- Lipoxygenases, properties and mode of action  
J.F.G. Vliegenthart, G.A. Veldink, J. Verhagen,  
S. Slappendel and M. Vernooy-Gerritsen 265
- Lipoxygenase as effected by free radical metabolism: senescence  
retardation by the xanthine oxidase inhibitor allopurinol  
Y.Y. Leshem and G. Barnes 275
- Liposoluble fluorescent compounds as indication of lipid  
peroxidation during aging of plants  
M.N. Merzlyak, V.B. Rumyantseva and M.V. Gusev 279
- Action of boron *in vivo* on fatty acid content and lipoxygenase  
activity in cotyledons during germination of the sunflower  
seeds  
A. Belver, L.M. Daza and J.P. Donaire 283
- Factors affecting the stability of lipoxygenase activities of  
pea seeds during their preparation  
R. Douillard and E. Bergeron 287
- Lipoxygenase in higher plants: a non-mitochondrial enzyme  
J. Dupont, P. Rustin and C. Lance 293
- Molecular properties of potato tuber lipolytic acyl hydrolase  
P.J. Walcott, J.R. Kenrick and D.G. Bishop 297
- Partial purification and properties of a lipolytic acyl hydrolase  
from *Phaseolus multiflorus* leaves  
F. Depery, P. Schürmann and P.A. Siegenthaler 301

Changes in tobacco lipid composition during senescence and effect of ripening accelerators K. Gruiz and P. Biacs	305
Phosphatidylcholine degradation by solvents R.E. Wilkinson	309
FUNCTION OF LIPIDS AS RELATED TO THE STRUCTURE OF PLANT CELL MEMBRANES	
Lipid organization and barrier functions of membranes J. de Gier, C.J.A. van Echteld, A.T.M. van der Steen, P.C. Noordam, A.J. Verkleij and B. de Kruijff	315
Structural configuration of plant membrane lipids and their role in the organisation of chloroplast thylakoid constituents P.J. Quinn, K. Gounaris, A. Sen and W.P. Williams	327
Physical properties of thylakoid lipids A.A. Foley and J.L. Harwood	331
Restoration by phospholipids of the CDP-choline transferase activity of potato microsomes treated by phospholipase C - examination of ultrastructural rearrangements A. Jolliot, J. Olive, E. Bimont, A-M. Justin and P. Mazliak	335
The role of membrane fluidity in the maintenance of chloroplast function D.G. Bishop, J.R. Kenrick, J.M. Coddington, S.R. Johns and R.I. Willing	339
Fluidity dependence of the proton permeability of membranes from root phospholipid mixtures M. Rossignol and C. Grignon	345
Transmembrane distribution and function of lipids in spinach thylakoid membranes: rationale of the enzymatic modification method P-A. Siegenthaler	351
Lipid topography of thylakoid membranes M.D. Unitt and J.L. Harwood	359
Lipid content of chloroplast thylakoids and regulation of photosynthetic electron transport D.J. Chapman, P.A. Millner, R.C. Ford and J. Barber	363
Role of phosphatidylglycerol containing trans-hexadecenoic acid in oligomeric organization of the light-harvesting chlorophyll protein (LHCP) A. Trémolières, J-P. Dubacq, J-C. Duval, Y. Lemoine and R. Remy	369
Lipoprotein association in chlorophyll containing complexes isolated by non-ionic detergents T. Guillot-Salomon, C. Tuquet, N. Farineau, J. Farineau and M. Signol	373



Influence of $\beta$ -carotene antibodies on the photosynthetic electron transport in chloroplasts of higher plants and in thylakoids of the blue green alga <i>Oscillatoria chalybea</i> A. Radunz and K.P. Bader	377
Lipid composition and ultrastructure of potato tuber amyloplasts and amylochloroplasts A.S. Sandelius and C. Liljenberg	385
The importance of monogalactosyldiglyceride for the structure of the prolamellar body E. Selstam, G. Lindblom, I. Brentel and M. Ryberg	389
Galactolipid and lecithin monolayers at the air/water interface M. Tomoaiia-Cotişel, E. Chifu, A. Sen and P.J. Quinn	393
On phospholipid as part of the crude essential oil from orange fruits K. Knobloch, F. Gemeinhardt, E. Ziegler and H. Brandauer	397
ECOLOGICAL AND PHYSIOLOGICAL FACTORS AS RELATED TO PLANT LIPID METABOLISM	
Adaptation of thylakoid membranes of wheat seedlings to low temperature L. Vigh	401
Modification of phospholipase D activity during frost hardening of winter rape plants E. Sikorska and A. Kacperska	415
Effect of sodium chloride on the biosynthesis of unsaturated fatty acids of sunflower plants ( <i>Helianthus annuus</i> L.) M. Ellouze, M. Gharsalli and A. Cherif	419
Biochemical and ultrastructural changes in plastids from various alfalfa cultivars growing under salt-stress F. Harzallah-Skhiri, T. Guillot-Salomon and M. Signol	423
The physical state of lipids of the leaves of cucumber genotypes as affected by temperature I. Horváth, L. Vigh, J. Woltjes, P.R. van Hasselt and P.J.C. Kuiper	427
Drought induced frost resistance in wheat correlates with changes in phospholipids H. Huitema, J. Woltjes, L. Vigh and P. van Hasselt	433
The effect of temperature on phospholipid biosynthesis in rye roots A.J. Kinney, D.T. Clarkson and B.C. Loughman	437
Effect of water stress on lipid composition of oat seedling root cell membranes C. Liljenberg and M. Kates	441
Temperature effect on phospholipids and fatty acid content of germinating seeds E. Palacios-Alaiz, J. Velez and M.T. Alsasua	445

Effects of water stress on lipid and fatty acid composition of cotton leaves A.T. Pham Thi, C. Flood and J. Vieira da Silva	451
The effect of salinity on phospholipid content and composition of two <i>Plantago</i> species, differing in salt tolerance C.E.E. Stuiver, L.J.de Kok, A.E. Hendriks and P.J.C. Kuiper	455
Changes in the cuticular transpiration rate and in the composition of the epicuticular wax of oat seedlings induced by water stress M. Svenningsson and C. Liljenberg	459
Effects of temperature and cytokinin on the metabolism of fatty acids in cell suspensions of <i>Nicotiana tabacum</i> M. Gawer, A-M. Justin, A. Sansonetti and P. Mazliak	463
Correlation between oleic acid content and cell elongation in <i>Vigna radiata</i> and <i>Vigna sinensis</i> J-P. Dubacq, R. Goldberg, G. de March, R. Prat, A. Trémolières and A. Lecharny	467
Abscisic acid induced changes in physical state and lipid composition of plant membranes T. Farkas, G. Nemezc and B. Singh	471
Effects of phytochrome on the incorporation of different radiolabelled precursors into phospholipids of etiolated bean hypocotyls E. Hartmann and I. Grasmück	475
Evidence for the interaction of membrane lipids and the plant photoreceptor, phytochrome B.R. Jordan	479
Light regulation of lipid metabolism and a peroxisomal activity in sunflower and <i>Phaseolus nil</i> cotyledons F. Tchang, A. Oursel, A. Lecharny, A. Connan, D. Robert, A. Trémolières and P. Mazliak	483
<b>BIOSYNTHESIS AND METABOLISM OF ISOPRENOID COMPOUNDS</b>	
Cytoplasmic and plastidic isoprenoid compounds of oat seedlings and their distinct labelling from <sup>14</sup> C-mevalonate H.K. Lichtenhaler, T.J. Bach and A.R. Wellburn	489
The biosynthesis of isoprenoid compounds in the chloroplast from the compartmental view G. Schultz, J. Soll and E. Fiedler	501
Polyprenoid biosynthesis in chloroplasts and chromoplasts K. Kreuz and H. Kleinig	507
Function of plastids in terpene biosynthesis M. Gleizes, C. Bernard-Dagan, J.P. Carde, G. Pauly and A. Marpeau	511

Inhibition of mevalonate biosynthesis and of plant growth by the fungal metabolite mevinolin T.J. Bach and H.K. Lichtenthaler	515
Cell structure and volatile terpene compounds: is there a relationship? J-P. Carde, G. Pauly and C. Chéniclet	523
Biosynthesis of biologically important meroterpenoid quinones and chromanols D.R. Threlfall	527
Formation of the aromatic moieties of prenylquinones in the stroma of spinach chloroplasts E. Fiedler and G. Schultz	537
Taxonomic and phylogenetic implications of lipid and quinone compositions in phototrophic microorganisms J.F. Imhoff	541
Distribution and levels of ubiquinone homologues in higher plants S. Schindler and H.K. Lichtenthaler	545
Herbicide action on carotenogenesis in a photosynthetic cell-free system I.E. Clarke, P.M. Bramley, G. Sandmann and P. Böger	549
Intracellular and intraplastidic distribution of the carotenoids phytoene and lycopene in herbicide - treated seedlings of radish ( <i>Raphanus sativus</i> L.) K.H. Grumbach and G. Britton	555
Biosynthesis and degradation of chlorophylls in relation to the developmental stages of a plastid K.H. Grumbach, P. Mungenast and J. Ritz	559
Localization of $\beta$ -carotene in chlorophyll a-proteins and changes in its levels during short-term high light exposure of plants U. Prenzel and H.K. Lichtenthaler	565
Effect of saponins and sterols on the membrane composition of <i>Trichoderma viride</i> P. Biacs and K. Gruiz	573
Evolution and metabolism of amyrins and sterols during the growth of lettuce seedlings ( <i>Lactuca sativa</i> ) P. Doireau, P. Duperon, A. Verger and R. Duperon	577
Metabolism of cortisol in etiolated mung bean seedlings J.M.C. Geuns	581
Building units of prolamellar bodies: an open question J. Kesselmeier and U. Laudenschlag	585
Author index	591
Subject index	595
Index of plant names	605

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

G SCHULTZ, J. SOLL AND E. FIEDLER

Botanisches Institut, Tierärztliche Hochschule Hannover, FRG

### 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).

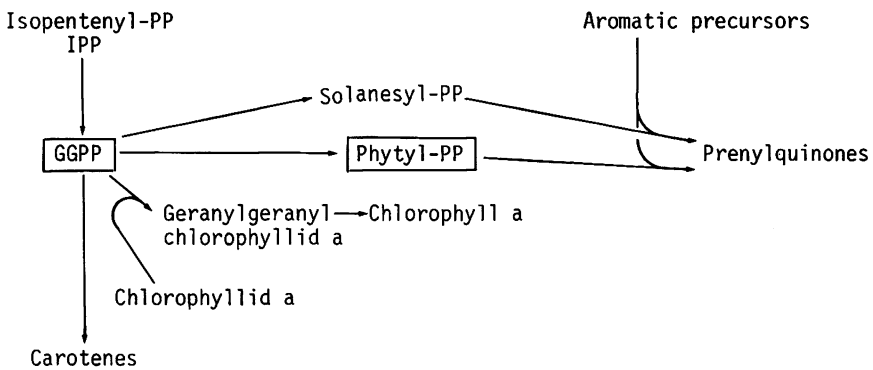


Fig. 1. Pattern on biosyntheses of isoprenoidic compounds in chloroplasts.

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;  $\alpha$ T  $\alpha$ -tocopherol; Trp tryptophan; Tyr tyrosine.

## THE SHIKIMATE PATHWAY AND ITS INVOLVEMENT IN PRENYLQUINONE SYNTHESIS

If intact spinach chloroplasts were illuminated, label from  $^{14}\text{CO}_2$  is incorporated into aromatic amino acids and the prenylquinones  $\alpha\text{T}$  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).

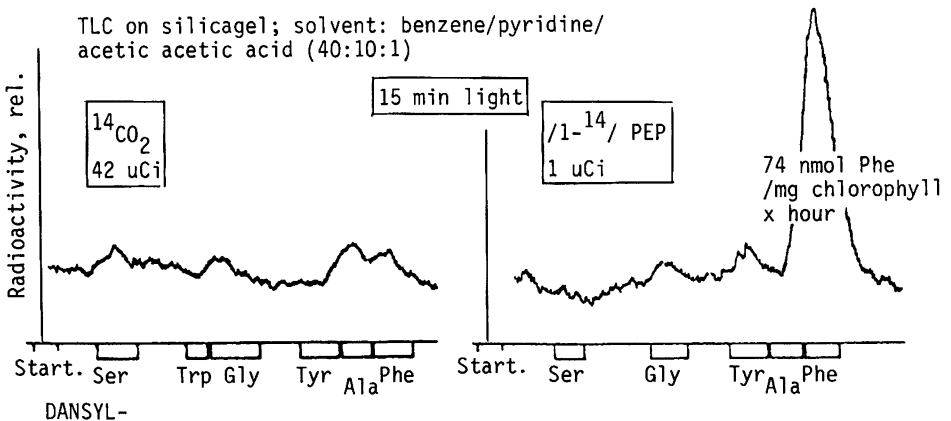


Fig. 2.  $^{14}\text{C}$ -Incorporation from  $^{14}\text{CO}_2$  and  $/1-^{14}\text{C}/$  PEP into amino acids by intact spinach chloroplasts (5). For details in experimental conditions see (4).

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  $\alpha\text{T}$  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  $\alpha\text{T}$  and PQ-9 was elucidated by Soll et al. (12) (see Fig. 4 and (13)). The site of  $\alpha\text{T}$  synthesis is exclusively the envelope membrane, that of PQ-9 the thylakoid membrane, too (12).

Additionally, the phylloquinone (vitamin  $\text{K}_1$ ) synthesis occurs in chloroplasts. 1,4-Dihydroxy-2-naphthoate is formed from chorismate via o-succinyl-

benzoate  $\rightarrow$  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.

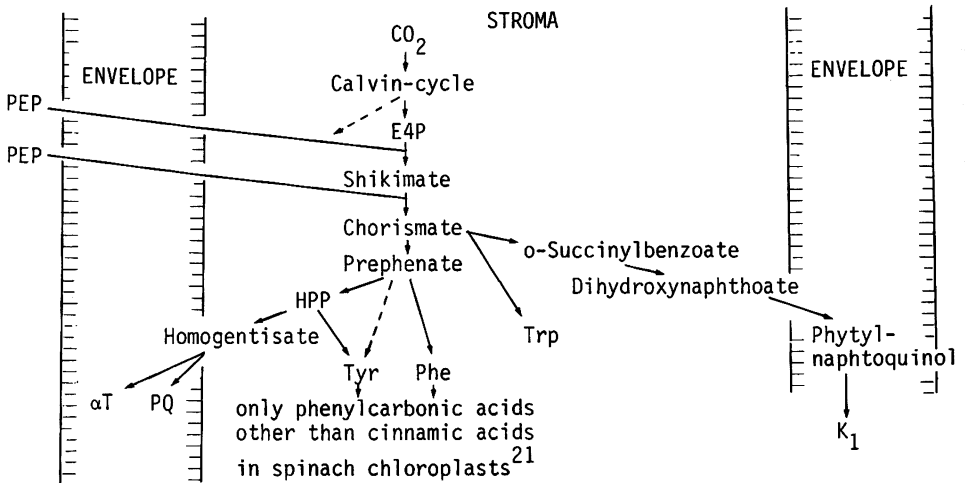


Fig. 3. Metabolic ways related to shikimate pathway in spinach chloroplasts

#### PLASTIDIC ISOPRENOID SYNTHESIS: 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 <sup>14</sup>C from <sup>14</sup>CO<sub>2</sub> 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)).

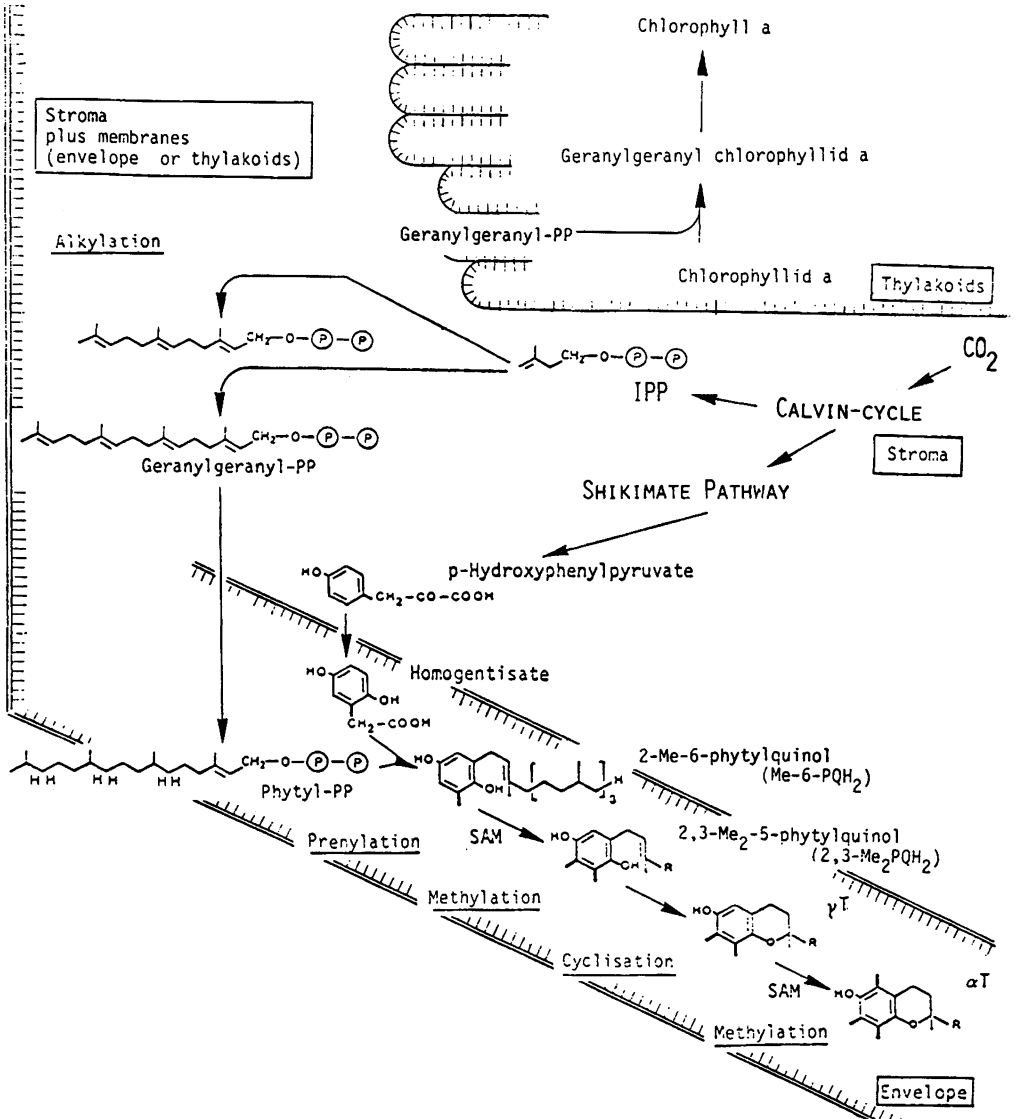


Fig. 4. Compartmental view on syntheses of isoprenoid compounds in chloroplasts

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)).

#### ACKNOWLEDGEMENTS

Financial support by the Deutsche Forschungsgemeinschaft is gratefully acknowledged.

#### REFERENCES

1. Goodwin, T.W. (1958) *Biochem. J.* 68, 26 P and 70, 612.
2. Schultz, G. and Bickel, H. (1977) in: *Proceedings of the 5th Hungarian Bioflavonoid Symposium, Mátrafüred/Hungary*, Farkas, L. et al. eds., Elsevier, Amsterdam, pp. 271 - 284.
3. Bickel, H., Palme, L. and Schultz, G. (1978) *Phytochemistry* 17, 119 - 124.
4. Buchholz, B. and Schultz, G. (1980) *Z. Pflanzenphysiol.* 100, 209 - 215.
5. Scharf, H. and Schultz, G., unpublished.
6. for review see: Heldt, H.W. (1976) in: *The Intact Chloroplast*, Barber, J. ed., Elsevier-North Holland, Amsterdam, pp. 215 - 234.
7. Kleinig, H. and Liedvogel, B. (1980) *Planta* 150, 166 - 169.
8. Bickel, H. and Schultz, G. (1979) *Phytochemistry* 18, 498 - 499.
9. for review see: Threlfall, D.R. and Whistance, G.R. (1971) in: *Aspects of Terpenoid Chemistry and Biochemistry*, Goodwin, T.W. ed., Academic Press, London, pp. 335 - 404.
10. Whistance, G.R. and Threlfall, D.R. (1970) *Biochem. J.* 117, 593 - 600.
11. Fiedler, E., Soll, J. and Schultz, G. (1982) submitted.
12. Soll, J., Kemmerling, M. and Schultz, G. (1980) *Arch. Biochem. Biophys.* 204, 544 - 550.
13. Soll, J. and Schultz, G. (1980) in: *Biogenesis and Function of Plant Lipids*, Mazliak, P., Benveniste, P., Costes, C. and Douce, R. eds., Elsevier-North Holland, Amsterdam, pp. 341 - 344.
14. Meganathan, R., Bentley, R. and Taber, H. (1981) *J. Bacteriol.* 145, 328-332.
15. Heide, L. and Leistner, E. (1981) *FEBS Letters* 128, 201 - 204.
16. Bryant, R.W. and Bentley, R. (1976) *Biochemistry* 15, 4792 - 4796.
17. Thomas, G. and Threlfall, D.R. (1974) *Phytochemistry* 13, 807 - 813.
18. Hutson, K.G. and Threlfall, D.R. (1980) *Phytochemistry* 19, 535 - 537.



19. Schultz, G., Ellerbrock, B.H. and Soll, J. (1981) *Eur. J. Biochem.* 117, 329 - 332.
20. Kaiping, S. and Schultz, G., in preparation.
21. Schultz, G. and Bitsch, A., unpublished.
22. Bickel, H. and Schultz, G. (1976) *Phytochemistry* 15, 1253 - 1255.
23. Beyer, P., Kreuz, K. and Kleinig, H. (1980) *Planta* 150, 435 - 438.
24. Kleinig, H. and Liedvogel, B. (1981) 3. Arbeitstagung "Pflanzliche Lipide" Ulm, 2. - 3. 10. 1981, Abstract.
25. Block, M.A., Joyard, J. and Douce, R. (1980) *Biochim. Biophys. Acta* 631, 210 - 219.
26. Block, M.A., Joyard, J. and Douce, R. (1981) 6th International Symposium on Carotenoids, Liverpool, 26. - 31. 7. 1981, Abstract.
27. Porter, J.W., Spurgeon, S.L. and Pan, D. (1980) in: *Biogenesis and Function of Plant Lipids*, l.c., pp. 321 - 330.
28. Clarke, J.E., Sandmann, G., Bramley, P.M. and Böger, P., *FEBS Letters* 140, 203
29. Soll, J. and Schultz, G. (1981) *Biochem. Biophys. Res. Commun.* 99, -206  
907 - 912.
30. Rüdiger, W., Benz, J. and Guthoff, C. (1980) *Eur. J. Biochem.* 109, 193-200.
31. Benz, J., Wolf, C. and Rüdiger, W. (1980) *Plant Sci. Letters* 19, 225 - 230.
32. Schultz, G., Bickel, H., Buchholz, B. and Soll, J. (1981) in: *Photosynthesis, Vol. V. Chloroplast Development*, Akoyunoglou, G. ed., Balaban International Science Services, Philadelphia, pp. 311 - 318.