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1

Volume 103 February 1990 Page 1–130

Contents

1 Editorial

U. Lüttge and E. Schnepf

Botanica Acuta

2 Mistargeting: A Clue for Evolution of Protein Import? C. Sautter

5 Expansion of the "Coupled Translation-Membrane Model" of Circadian Rhythm of Prokaryotes E. J. de Groot and M. Schweiger

7 The Cellulose Synthase Problem H. U. Seitz and M. Emmerling

Review Article

9 Photoacoustic Spectroscopy and its Application in Plant Science C. Buschmann

Membranes and Transport

15 Implications of Control Theory for Homeostasis and Phosphorylation of Transport Molecules. U.-P. Hansen

24 Membrane Particles, Proteins and ATPase Activity of Tonoplast Vesicles of *Mesembryanthemum crystallinum* in the C-3 and CAM State R. Klink, H.-P. Haschke, D. Kramer, and U. Lüttge

32 Lipid Profiles of Leaf Tonoplasts from Plants with Different CO₂-Fixation Mechanisms. H.-P. Haschke, G. Kaiser, E. Martinoia, U. Hammer, T. Teucher, A. J. Dorne, and E. Heinz

39 The Plasma Membrane Ca²⁺-Pump of Plant Cells: A Radiation Inactivation Study Franca Rasi-Caldogno, Maria Chiara Pugliarello, C. Olivari, Maria Ida de Michelis, Grazia Gambarini, Paola Colombo, and G. Tosi

42 Changes in the Subcellular Distribution of Free Amino Acids in Relation to Light Conditions in Cells of *Chara corallina* T. Mimura, K. Sakano, and M. Tazawa

Metabolism, Photosynthesis

48 Regulation of the Synthesis of Isocitrate Lyase and the Corresponding mRNA in the Green Alga *Chlorogonium* A. Schmidt and K. Zetsche

54 Growth of *Anacystis* in the Presence of Thiosulphate and its Consequences for the Architecture of the Photosynthetic Apparatus F. Koenig

62 Photoinhibition of Photosynthetic Oxygen Production and its Recovery in the Subtidal Red Alga *Polyneura hilliae* W. Nultsch, J. Pfau, and K. Huppertz

68 The Effect of Phosphinothricin (Glufosinate) on Glutathione Synthesis in Plants A. Herold, C. Wendler, and A. Wild

Ecophysiology: Virus-Pathogen, Pollination, Photosynthesis

72 A Virus Infection in the Marine Brown Alga *Ectocarpus siliculosus* (Phaeophyceae) D. G. Müller, H. Kawai, B. Stache, and S. Lanka

83 Hummingbird Pollination in Two Species of *Vellozia* (Liliiflorae: Velloziaceae) in Southeastern Brazil M. Sazima and I. Sazima

87 On the Mechanism of Secondary Pollen Presentation in the Campanulales-Asterales-Complex P. Leins and Claudia Erbar

93 C₃- and C₄-Plants of the Xerophilic Vegetation in the Loess Hills of the Yellow River, Gansu-Province, NW-China. X.-C. Wang, U. Lüttge, and H. Ziegler

Developmental Biology

97 Flagellar Development During the Cell Cycle in *Chlamydomonas reinhardtii* P. Madey and M. Melkonian

103 Is Cell Elongation Regulated by Extracellular Auxin? Beate Knauth and D. Klämbt

107 Die Ontogenese der Salzdrüsen von *Limonium* (Plumbaginaceae) W. Wiehe and S.-W. Breckle

Biomechanics

111 Contributions to the Biomechanics of Plants (I) Th. Speck, H.-Chr. Spatz, and Dieter Vogellehner

123 Contributions to the Biomechanics of Plants (II) H.-Chr. Spatz, Th. Speck, and D. Vogellehner

A 1 Mitteilungen des Vorstandes der DBG

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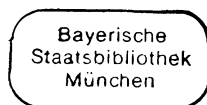
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598 Figures
65 Tables



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- No. 1 (February 1990) = Page 1–130
 No. 2 (May 1990) = Page 131–222
 No. 3 (August 1990) = Page 223–322
 No. 4 (November 1990) = Page 323–434
- 291** Distribution and $\delta^{13}\text{C}$ Values of Portulacaceae Species of the High Andes in Northern Chile
Mary Kalin Arroyo, E. Medina, and H. Ziegler
- 190** Peroxisomes in the Alga *Vaucheria* are Neither of the Leaf Peroxisomal Nor of the Glyoxysomal Type
K. Backeshoff and H. Stabenau
- 149** Activities of Photosystems I and II in *Chlamydomonas segnis* Adapted and Adapting to Air and Air-enriched with Carbon Dioxide
S. S. Badour and B. R. Irvine
- 296** Primary Phloem Development in the Shoot Apex of *Rhizophora mangle* L. (Rhizophoraceae)
H.-D. Behnke and K. Richter
- 9** Photoacoustic Spectroscopy and its Application in Plant Science
C. Buschmann
- 349** Ultrastructural Observations of *Papaver rhoeas* Mature Pollen Grains
M. Cresti, C. Milanesi, P. Salvatici, and A. C. Van Aelst
- 4** Expansion of the "Coupled Translation-Membrane Model" of Circadian Rhythm of Prokaryotes
E. J. de Groot and M. Schweiger
- 183** Diurnal Nitrogenase Modification in the Cyanobacterium *Anabena variabilis*
Anneliese Ernst, Yong-Ding Liu, Sabine Reich, and P. Böger
- 174** Comparison of Properties of the Proteolytic Degradation of Unassembled Nuclear-encoded Subunits of Ribulose-1,5-bisphosphate Carboxylase and of the Coupling Factor of Photophosphorylation CF₁
J. Feierabend, C. Bergmann, and S. Otto
- 258** Sequence Characteristics and Transcripts of *rbcS* Genes from *Brassica napus*: Temporal and Spatial Expression during Crucifer Seedling Morphogenesis
C. Fiebig, F. Kretschmar, I. Sprenger, and G. Link
- 311** The Localization of Lead in the Lichen *Ramalina duriaei* (De Not.) Bagl.
J. Garty and Heide-Birgitt Theiss
- 323** Molecular Aspects of the Self-incompatibility Systems of *Brassica* and *Nicotiana*
T. Gaude and Chr. Dumas
- 360** Flowers and Beetles in the South American Tropics
G. Gottsberger
- 15** Implications of Control Theory for Homeostasis and Phosphorylation of Transport Molecules
U.-P. Hansen
- 32** Lipid Profiles of Leaf Tonoplasts from Plants with Different CO₂-Fixation Mechanisms
H.-P. Haschke, G. Kaiser, E. Martinoia, U. Hammer, T. Teucher, A. J. Dorne, and E. Heinz
- 372** Karyological Differentiation in Sapindaceae with Special Reference to *Serjania* and *Cardiospermum*
W. Hemmer and W. Morawetz
- 131** *Auriculora byssomorpha*, a Tropical Lichen with a Remarkable Developmental Morphology
A. Hensen and A. Titze
- 68** The Effect of Phosphinothricin (Glufosinate) on Glutathione Synthesis in Plants
A. Herold, C. Wendler, and A. Wild
- 281** Isoenzyme Variation in Asian Beans
Vello Jaaska and Vilve Jaaska
- 384** Developmental Aspects of Ultrastructure and Histochemistry of the Stylar Transmitting Tissue of *Nicotiana sylvestris*
M. K. Kandasamy and U. Kristen
- 140** Biochemical Taxonomy of Symbiotic *Chlorella* Strains from *Paramecium* and *Acanthocystis*
E. Kessler and V. A. R. Huss
- 24** Membrane Particles, Proteins and ATPase Activity of Tonoplast Vesicles of *Mesembryanthemum crystallinum* in the C-3 and CAM State
R. Klink, H.-P. Haschke, D. Kramer, and U. Lüttge
- 103** Is Cell Elongation Regulated by Extracellular Auxin?
Beate Knauth and Dieter Klämbt
- 54** Growth of *Anacystis* in the Presence of Thiosulphate and its Consequences for the Architecture of the Photosynthetic Apparatus
F. Koenig
- 197** Oligomeric Forms of Glycolytic Enzymes in *Chlorella* Grown in Different Light Qualities
W. Kowallik, N. Grotjohann, and G. Ruyters
- 250** The Supramolecular Structure of Photosystem II – Phycobilisome-Complexes of *Porphyridium cruentum*
W. Lange, C. Wilhelm, W. Wehrmeyer, and E. Mörschel
- 87** On the Mechanism of Secondary Pollen Presentation in the Campanulales-Asterales-Complex
P. Leins and Claudia Erbar
- 1** Editorial
U. Lüttge and E. Schnepf
- 305** Effect of Lateral Root Formation on the Vascular Pattern of Barley Roots
M. Luxová
- 97** Flagellar Development During the Cell Cycle in *Chlamydomonas reinhardtii*
P. Madey and M. Melkonian

- 399 Malate Uptake into Isolated Vacuoles from *Catharanthus roseus* Cells: Role of the Membrane Potential
G. Marigo and Huguet Bouyssou
- 203 PP_i-ase-Activated ATP-Dependent H⁺ Transport at the Tonoplast of Mesophyll Cells of the CAM Plant *Kalanchoë daigremontiana*
Gisela Marquardt-Jarczyk and U. Lüttge
- 343 Antibiotics, Sugars, and Amino Acids in Nectar of *Rhododendron* and *Piptanthus* Species from Nepal
M. Martini, Angela Schmid, and D. Hess
- 223 In Pursuit of the Elusive Mechanism of Cell Surface Motility
D. Menzel
- 42 Changes in the Subcellular Distribution of Free Amino Acids in Relation to Light Conditions in Cells of *Chara corallina*
T. Mimura, K. Sakano, and M. Tazawa
- 408 Subcellular Distribution of Free Amino Acids in Relation to Protein Synthesis in Cells of *Chara corallina*
T. Mimura, K. Sakano, Y. Moriyasu, and M. Tazawa
- 72 A Virus Infection in the Marine Brown Alga *Ectocarpus siliculosus* (Phaeophyceae)
D. G. Müller, H. Kawai, B. Stache, and S. Lanka
- 62 Photoinhibition of Photosynthetic Oxygen Production and its Recovery in the Subtidal Red Alga *Polyneura hilliae*
W. Nultsch, J. Pfau, and K. Huppertz
- 226 Potential Consequences of Virus Infection for Shade-Sun Acclimation in Leaves
C. B. Osmond, J. A. Berry, S. Balachandran, C. Büchen-Osmond, P. F. Daley, and R. A. J. Hodgson
- 274 Characterization of CF₁ from the Diatom *Odontella sinensis*
P. G. Pancic, K. V. Kowallik, and H. Strotmann
- 143 Hypersensitive Reaction of Nodule Cells in the *Glycine* sp./*Bradyrhizobium japonicum*-Symbiosis Occurs at the Genotype-Specific Level
M. Parniske, Christa Zimmermann, P. B. Cregan, and D. Werner
- 430 Assimilate Partitioning in the Variegated *Coleus* Leaf
Martina Plomann and W. Eschrich
- 266 Phosphate Activates the Phosphoenolpyruvate Carboxylase from the C₄ Plant *Amaranthus viridis* L.
F. E. Podestá, C. S. Andreo, and A. A. Iglesias
- 39 The Plasma Membrane Ca²⁺-Pump of Plant Cells: A Radiation Inactivation Study
Franca Rasi-Caldogno, Maria Chiara Pugliarello, C. Olivari, Maria Ida de Michelis, Grazia Gambarini, Paola Colombo, and G. Tosi
- 168 Blue Light-Dependent Chloroplast Differentiation in Cultured Plant Cells: Evidence for Transcriptional Control of Plastid Genes
G. Richter and N. Ottersbach
- 424 Import of ¹⁴C-Photosynthate by Developing Leaves of Sugarcane
Kay Robinson-Beers, Th. D. Sharkey, and R. F. Evert
- 155 Analysis of the Molecular Organization of Photosystem I during Light-Dependent Chloroplast Differentiation in Mutant C-6D of *Scenedesmus obliquus*
S. Römer, K. Humbeck, and H. Senger
- 355 Outward Extension of Spinules in Exine of *Centrolepis aristata* (Centrolepidaceae)
J. R. Rowley and Anita Dunbar
- 404 Tetrathiofulvalene Radical Cation – A New Potent Inhibitor of Anion Transport in a Green Alga
Renata Rybová, L. Nešpůrková, O. Ryba, and K. Janáček
- 2 Mistargeting: A Clue for Evolution of Protein Import?
C. Sautter
- 83 Hummingbird Pollination in Two Species of *Vellozia* (Liliiflorae: Velloziaceae) in Southeastern Brazil
M. Sazima and I. Sazima
- 327 Light/Dark Modulation: Regulation of Chloroplast Metabolism in a New Light
Renate Scheibe
- 392 Exchange of Metabolites in *Cyanophora paradoxa* and its Cyanelles
R. Schlichting, W. Zimmer, and H. Bothe
- 48 Regulation of the Synthesis of Isocitrate Lyase and the Corresponding mRNA in the Green Alga *Chlorogonium*
A. Schmidt and K. Zetsche
- 235 The Distribution of a Phytochrome-Like Protein in the Fern *Psilotum nudum*. An Immunoblotting Analysis of an Early Ancestor of all Vascular Plants
H. A. W. Schneider-Poetsch, Gabriele John, and Birgit Braun
- 7 The Cellulose Synthase Problem – A Report from the 5th Cell Wall Meeting held in Edinburgh 1989
H. U. Seitz and M. Emmerling
- 230 Recent Molecular Approaches to the Physiology of the Plasma Membrane Proton Pump
R. Serrano
- 335 Isotopic Fractionation of Hydrogen in Plants
B. N. Smith and H. Ziegler
- 270 The Compatibility of D-Pinitol and 1D-1-O-Methyl-Muco-Inositol with Malate Dehydrogenase Activity
Christiane Sommer, Barbara Thonke, and Marianne Popp

- 123** Contributions to the Biomechanics of Plants. II. Stability Against Local Buckling in Hollow Plant Stems
H.-Chr. Spatz, Th. Speck, and D. Vogellehner
- 111** Contributions to the Biomechanics of Plants. I. Stabilities of Plant Stems with Strengthening Elements of Different Cross-Sections Against Weight and Wind Forces
Th. Speck, H.-Chr. Spatz, and D. Vogellehner
- 415** X-Ray Microprobe Analyses of Vacuoles of Spruce Needle Mesophyll, Endodermis and Transfusion Parenchyma Cells at Different Seasons of the Year
R. Stelzer, H. Lehmann, D. Kramer, and U. Lüttge
- 315** Thallus Formation of the Cyanobacterial Lichen *Peltigera didactyla* from Soredia under Laboratory Conditions
Elfie Stocker-Wörgötter and R. Türk
- 244** The Supramolecular Organization of Photosynthetic Membranes of the Thallus Stage of *Porphyra leucosticta* Thuret. (Bangiales, Rhodophyta) Visualized by Freeze-Fracture
I. Tsekos and H.-D. Reiss
- 214** Neutral Red as a Redox Dye Induces K⁺ Efflux and Current-Voltage Changes in *Eremosphaera, Lemna*, and Guard Cells
C. I. Ulrich, K. Köhler, M. Baier, and W. Hartung
- 93** C₃- and C₄-Plants of the Xerophilic Vegetation in the Loess Hills of the Yellow River, Gansu-Province, NW-China
X.-C. Wang, U. Lüttge, and H. Ziegler
- 240** Temporal Pattern of Gene Expression in Cotyledons of Mustard (*Sinapis alba* L.) Seedlings
A. Wennig, A. Batschauer, B. Ehmman, and E. Schäfer
- 366** Bird-Flowers: Hovering Versus Perching Exploitation
Chr. Westerkamp
- 107** Die Ontogenese der Salzdrüsen von *Limonium* (Plumbaginaceae) – The Ontogenesis of the Salt Glands of *Limonium* (Plumbaginaceae)
W. Wiehe and S.-W. Breckle
- 162** Regulation of LHCa-Polypeptide-Biosynthesis in the Phototropic Green Alga *Chlamydomonas stellata*
W. Wiessner, B. Kohnke, K. Kloppstech, D. Mende, A. Radunz, and J. Winter
- A 1–A 8** Mitteilungen des Vorstandes der DBG
- A 9–A 20** Mitgliedsverzeichnis der DBG
- A 21–A 22** Mitteilungen des Vorstandes der DBG

Author's Index

VI

- A**
Andreo, C. S. 266
Arroyo, Mary Karin 291
- B**
Backeshoff, K. 190
Badour, S. S. 149
Baier, M. 214
Balachandran, S. 226
Batschauer, A. 240
Behnke, H.-D. 296
Bergmann, C. 174
Berry, J. A. 226
Böger, P. 183
Bothe, H. 392
Bouyssou, Huguette 399
Braun, Birgit 235
Breckle, S.-W. 107
Büchen-Osmond, C. 226
Buschmann, C. 9
- C**
Colombo, Paola 39
Cregan, P. B. 143
Cresti, M. 349
- D**
Daley, P. F. 226
de Groot, E. J. 4
de Michelis, Maria Ida 39
Dorne, A. J. 32
Dumas, Chr. 323
Dunbar, Anita 355
- E**
Ehmann, B. 240
Emmerling, M. 7
Erbar, Claudia 87
Ernst, Anneliese 183
Eschrich, W. 430
Evert, R. F. 424
- F**
Feierabend, J. 174
Fiebig, C. 258
Förster, B. 214
- G**
Gambarini, Grazia 39
Garty, J. 311
Gaude, T. 323
Gottsberger, G. 360
Grotjohann, N. 197
- H**
Hammer, U. 32
Hansen, U.-P. 15
Hartung, W. 214
Haschke, H.-P. 24, 32
Heinz, E. 32
Hemmer, W. 372
Henssen, A. 131
Herold, A. 68
Hess, D. 343
Hodgson, R. A. J. 226
Humbeck, K. 155
Huppertz, K. 62
Huss, V. A. R. 140
- I**
Iglesias, A. A. 266
Irvine, B. R. 149
- J**
Jaaska, Vello 281
Jaaska, Vilve 281
Janáček, K. 404
John, Gabriele 235
- K**
Kaiser, G. 32
Kandasamy, M. K. 384
Kawai, H. 72
Kessler, E. 140
Klämbt, D. 103
Klink, R. 24
Klopstech, K. 162
Knauth, Beate 103
Köhler, K. 214
Koenig, F. 54
Kohnke, B. 162
Kowallik, K. V. 274
Kowallik, W. 197
Kramer, D. 24, 415
Kretzschmar, F. 258
Kristen, U. 384
- L**
Lange, W. 250
Lanka, S. 72
Lehmann, H. 415
Leins, P. 87
Link, G. 258
Liu, Yong-Ding 183
Lüttge, U. 1, 24, 93, 203, 415
Luxová, M. 305
- M**
Madey, P. 97
Marigo, G. 399
Marquardt-Jarczyk, Gisela 203
Martini, M. 343
Martinoia, E. 32
Medina, E. 291
Melkonian, M. 97
Mende, D. 162
Menzel, D. 223
Milanesi, C. 349
Mimura, T. 42, 408
Morawetz, W. 372
Moriyasu, Y. 408
Mörschel, E. 250
Müller, D. G. 72
- N**
Nešpůrková, L. 404
Nultsch, W. 62
- O**
Olivari, C. 39
Osmond, C. B. 226
Ottersbach, N. 168
Otto, C. 174
- P**
Pancic, P. G. 274
Parniske, M. 143
Pfau, J. 62
Plomann, Martina 430
Podestá, F. E. 266
Popp, Marianne 270
Pugliarello, Maria Chiara 39
- R**
Radunz, A. 162
Rasi-Caldogno, Franca 39
Reich, Sabine 183
Reiss, H.-D. 244
Richter, G. 168
Richter, K. 296
Robinson-Beers, Kay 424
Römer, S. 155
Rowley, J. R. 355
Ruyters, G. 197
Ryba, O. 404
Rybová, Renata 404
- S**
Sakano, K. 42, 408
Salvatici, P. 349
Sautter, C. 2
Sazima, I. 83
Sazima, M. 83
Schäfer, E. 240
Scheibe, Renata 327
Schlichting, R. 392
Schmid, Angela 343
Schmidt, A. 48
Schneider-Poetsch, H. A. W. 235
Schnepf, E. 1
Schweiger, M. 4
Seitz, H. U. 7
Senger, H. 155
Serrano, R. 230
Sharkey, Th. D. 424
Smith, B. N. 335
Sommer, Christiane 270
Spatz, H.-Chr. 111, 123
Speck, Th. 111, 123
Sprenger, I. 258
Stabenau, H. 190
Stache, B. 72
Stelzer, R. 415
Stocker-Wörgötter, Elfie 315
Strotmann, H. 274
- T**
Tazawa, M. 42, 408
Teucher, T. 32
Theiss, Heide-Birgitt 311
Thonke, Barbara 270
Titze, A. 131
Tosi, G. 39
Tsekos, I. 244
Türk, R. 315
- U**
Ullrich, C. I. 214
- V**
Van Aelst, A. C. 349
Vogellehner, D. 111, 123
- W**
Wang, X.-C. 93
Wehrmeyer, W. 250
Wendler, C. 68
Weng, A. 240
Werner, D. 143
Westerkamp, Chr. 366
Wiehe, W. 107
Wiessner, W. 162
Wild, A. 68
Wilhelm, C. 250
Winter, J. 162
- Z**
Zetsche, K. 48
Ziegler, H. 93, 291, 335
Zimmer, W. 392
Zimmermann, Christa 143

A

- Acanthocystis* 140–142
Acetabularia circadian rhythm 5–6
 acetate, effect on isocitrate lyase synthesis 48–53
 acetate-photoassimilation 162–167
 acetylandromedol 343–348
 action spectrum of photoinhibition 62–67
 activation of ATP-dependent H⁺ transport 203–213
 albino tissue 430–434
 algae, blue-green 183–189
 brown 72–82
 chlorococcal 214–221
 diatoms 274–280
 green 48–53, 97–102, 149–154, 155–161, 162–167, 197–202, 214–221, 404–407
 red 62–67, 244–249, 250–257
Amaranthus viridis 266–269
 amino acids
 in floral nectar 343–348
 subcellular distribution 42–47, 408–414
 N-terminal sequences 274–280
Anabaena 183–189
Anacystis nidulans 54–61
 Andes, Portulacaceae species 291–295
 anion pump 404–407
Annona 360–365
 antibiotics, in floral nectar 343–348
Arabidopsis 230–234
 ascocarp ontogeny 131–139
 Asian beans, isoenzyme variation 281–290
 assimilate partitioning 430–434
 Asteraceae secondary pollen presentation 87–92
 ATP binding site (non-consuming) 15–23
 ATPase 24–31, 39–41, 203–213, 230–234
Auricularia byssomorpha 131–139
 auxin binding protein 103–106
 auxin secretion 103–106
 auxin-induced cell elongation 103–106

B

- beetle pollination 360–365
 “bending effectivity” 111–123
 biochemical taxonomy, of *Chlorella* strains 140–142
 biomechanics, of plants 111–122, 123–130
 bird-pollination 83–86, 366–371
 blue light, dependence of chloroplast differentiation on 168–173
 blue/red light effects 197–202
Bradyrhizobium japonicum 143–148

- Brassica* 68–71, 258–265, 323–326
 Brunoniaceae, secondary pollen presentation 87–92
 buthionine sulfoximine 68–71

C

- C₃ metabolism 24–31, 32–38, 335–342
 C₄ metabolism 93–96, 266–269, 335–342
 δ¹³C-values 291–295, 335–342
 Ca²⁺ dependence, of K⁺-efflux 214–221
 Ca²⁺-pump 39–41
 callose synthase 7–8
 calmodulin, activation of Ca²⁺-ATPase 39–41
 CAM, see crassulacean acid metabolism
 Campanulaceae, secondary pollen presentation 87–92
Cardiospermum 372–383
Carludovica 360–365
Catharanthus roseus 399–403
 cell cultures, *Chenopodium rubrum* 168–173
 cell cycle, flagellar development during 97–102
 cell elongation, auxin-induced 103–106
 cell surface motility, mechanism 223–225
 cell wall, nacreous 296–304
 cellulose synthase 7–8
 centrifugation, silicone oil layer 392–398
Centrolepis 355–359
Ceratotropis 281–290
 CF₁-subunit, of chloroplast H⁺-ATPase 274–280
Chara 42–47, 408–414
 China 93–96
Chlamydomobryns 162–167
Chlamydomonas eugametos 5–6, 97–102, 149–154, 223–225
Chlorella 140–142, 197–202
Chlorogonium elongatum 48–53
 chlorophyll a/b binding protein 240–243
 chloroplast(s) 42–47, 408–414
 differentiation 155–161, 168–173, 174–182
 enzymes, light/dark modulation 327–334
 H⁺-ATPase 274–280
 metabolism 327–334
 chromosome banding patterns 372–383
 chromosome numbers 372–383
 circadian rhythm 5–6
 C:N-ratio 183–189
 CO₂-adaptation 149–154

- coleoptile growth, auxin regulated 103–106
Coleus 430–434
 coupled translation-membrane model 5–6
 coupling factor, of photophosphorylation (CF₁) 174–182
 crassulacean acid metabolism (CAM) 24–31, 32–38, 203–213, 291–295, 335–342
 crucifer development 258–265
 cyanelles 392–398
 cyanobacteria 54–61, 183–189
 cyanobacterial lichens 315–321
Cyanophora paradoxa 392–398
 cycloheximide, inhibition of flagellar development 97–102

D

- deuterium, isotopic fractionation 335–342
 5,5-dimethylxozolidine-2,4-dione (DMO) uptake 214–221
 diurnal growth 183–189

E

- Ectocarpus siliculosus* 72–82
 endosymbiosis 392–398
 energy dispersive microanalysis 415–423
Eremosphaera viridis 214–221
 evolution 327–334, 360–365
 exine 355–359

F

- Fe-protein modification 183–189
 flagellar development 97–102
 flagellar membrane 223–225
 floral biology 83–86
 flower(s), adaptation of 360–365
 flower-birds 366–371
 fluorescence, chlorophyll 155–161
 FPLC Superose 6 separation 197–202
 freeze-fracture 24–31, 244–249, 250–257
 freeze-substitution 349–354
 functional anatomy, plant stems 111–122, 123–130
 functional morphology 355–359

G

- gene cloning 230–234
 gene expression 258–265
 temporal pattern 240–243
 generative cell 349–354
 glucan synthase II 7–8
 glufosinate, effect on glutathione synthesis 68–71
 glutathione synthesis 68–71
 glyceollin 143–148
Glycine max 143–148
 glycolate metabolism 190–196

glycolytic enzymes 197–202

Goodeniaceae, secondary pollen presentation 87–92

growth control, ATPase 230–234

guard cells, current-voltage changes 214–221

HH⁺ transport 203–213H⁺-ATPase 230–234, 274–280

halophytes 93–96, 107–110

heat production 9–14, 364

hemiangiocarpy 131–139

heterocysts 183–189

histochemistry 311–314, 384–391

homeostasis, control theory 15–23

Hordeum vulgare 32–38, 305–310

hovering birds 366–371

hummingbirds 83–86, 366–371

Hydrodictyon reticulatum 404–407

hydrogen, isotopic fractionation 335–342

hypersensitive reaction in root nodules 143–148

I

immunoblot analysis, phytochrome 235–239

inorganic nitrogen sources 140–142

interphase nuclei 372–383

intracellular perfusion 42–47

intracellular pH 214–221

intramembranous particles 24–31, 244–249

ion localization 415–423

isocitrate lyase, synthesis 48–53

isoenzyme variation, in Asian beans 281–290

isotop fractionation 335–342

KK⁺-efflux 214–221*Kalanchoë daigremontiana* 24–31, 32–38, 203–213

karyosystematics, tropical woody plants 372–383

L

laboratory cultures of lichens 315–321

lateral root formation 305–310

lead localization in lichens 311–314

leader sequences 2–4

leaf development 424–429

Lecanorales, systematics of 131–139

Lemna gibba 214–221

LHC, see light-harvesting complex

lichen(s) 131–139, 311–314, 315–321

light, effect on isocitrate lyases synthesis 48–53

intensity adaptation of cyanobacteria 54–61

light-harvesting complex 155–161, 162–167

light/dark modulation 327–334

Limonium 107–110

lipid composition, leaf tonoplasts 32–38

Lobeliaceae secondary pollen presentation 87–92

loess area, vegetation 93–96

long wavelength antenna 155–161

M

magnesium, vacuolar concentration 415–423

maize coleoptiles 103–106

malate dehydrogenase 270–273

malate transport 399–403

mechanical loads on plants 111–122

Mehler reaction 149–154

Melicoccus bijugatus 380

membrane particles 24–31, 244–249, 250–257

membrane potential 399–403

membrane redox system 214–221

Mesembryanthemum crystallinum

24–31, 32–38, 203–213, 270–273

metabolite exchange 392–398

methionine sulfoximine 68–71

microtubules 349–354

mistargeting 2–4

monoclonal anti-phytochrome antibody 235–239

motility, gliding 223–225

mRNA 258–265

abundance 240–243

of isocitrate lyase 48–53

level 168–173

light-mediated accumulation 240–243

multigene family 258–265

mutagenesis, yeast H⁺-ATPase 230–234**N**

nacreous cell wall 296–304

naphthylphthalamic acid 103–106

nectar, floral 343–348

neutral red 214–221

New World flowers 366–371

Nicotiana 323–326, 384–391

nitrogen sources, inorganic 140–142

nitrogenase 183–189

nodes, hollow plant stems 123–130

O*Odontella sinensis* 274–280

Old World flowers 366–371

oligomerization, glycolytic enzymes 197–202

β-oxidation 190–196

oxygen evolution 9–14

oxygen evolution complex, 23 kDa subunit of 240–243

oxygen production, photosynthetic 62–67

P*Papaver* 349–354*Paramecium* 140–142

perching birds 366–371

Peltigera 314, 315–321peroxisomes, of *Vaucheria* 190–196

pathogen, interaction with plant 143–148

pH, intracellular 214–221

Phaeophyceae 72–82

Phaseolus 281–290*Philodendron* 360–365

phloem, development 296–304 loading 430–434

translocation 430–434

unloading 424–429, 430–434

phosphate activation 266–269

phosphoenolpyruvate 266–269

phosphoenolpyruvate carboxylase 266–269

phosphofructokinase 197–202

phosphonothricin 68–71

phosphorus, vacuolar concentration 415–423

phosphorylation and transport 15–23

photoacoustic spectroscopy 9–14

photoinhibition of photosynthesis 62–67

photomorphogenesis 258–265

photosynthate import 424–429

photosynthesis 9–14, 62–67, 250–257, 335–342

anoxygenic 54–61

application of photoacoustic spectroscopy 9–14

CO₂ adaptation 149–154

photoinhibition 62–67

photosystems 54–61, 149–154, 155–161, 226–229, 250–257

photosystem II-phycoobilisome complex, model 250–257

phycoobilisomes 250–257

phylogeny, of cyanobacteria 54–61

phytoalexin 143–148

phytochrome 235–239

Picea abies 415–423

pigment-protein complexes 155–161, 162–167

Piptanthus nepalensis 343–348

pistil, putative receptor molecules 323–326

plant(s), biomechanics of stems 111–122, 123–130

plasma membrane, Ca²⁺-pump 39–41

proton pump 230–234
 redox system 404–407
 plastid genes, transcriptional control 168–173
 plastids in sieve elements 296–304
 pollen 87, 349–354, 355–359
 of *Centrolepis aristata* 355–359
 secondary presentation 87–92
 tube nutrition 384–391
 pollen-pistil recognition 324, 325
 pollination biology 83–86,
 343–348, 360–365, 366–371
 polyglucan synthesis 392–398
Polyneura hilliae 62–67
Porphyra 244–249
Porphyridium cruentum 250–257
 Portulacaceae 291–295
 potassium, vacuolar concentration 415–423
 PP_iase 203–213
 prokaryotes, circadian rhythm 5–6
 protease 174–182
 protein degradation 174–182
 synthesis 408–414
 transport, through membranes 2–4
 proton pump, plasma membrane 230–234
 protoplast preparation 32–38
Psilotum nudum 112, 235–239
 pyruvate kinase 197–202

R

radiation inactivation 39–41
Ramalina duriaei 311–314
Raphanus sativus 11, 39–41, 62
 recovery after photoinhibition 62–67
 red algae 62–67, 244–249,
 250–257
 redox modification, covalent 327–334
 redox system, plasmalemma 404–407
 regulation, of ATPase activity 230–234
 chloroplast metabolism 327–334
 isocitrate lyase synthesis 48–53
 LHCa-polypeptide biosynthesis 162–167
 regulatory extra-peptides, evolution of 327–334
 reprogramming, of parent stelar parenchyma 305–310
Rhizobium fredii 143–148
Rhizophora mangle 270–273,
 296–304
 rhodizonate, lead localization 311–314
Rhododendron 343–348
 Rhodophyceae 62–67, 244–249,
 250–257

ribulose-1,5-bisphosphate carboxylase oxygenase 174–182,
 226–229, 330
 small subunit of 240–243,
 258–265
 root, vascular system 305–310
 lateral root formation 305–310
 nodules 143–148

S

Saccharum species 424–429
 salt gland, of *Limonium* 107–110
 Sapindaceae 372–383
Scenedesmus obliquus 155–161
Secale cereale 174–182
 second moments of area 111–122
 secretion 103–106, 384–391
 self-incompatibility 323–326
Serjania 372–383
 shade-sun acclimation, effects virus infection 226–229
 SID, see strong ion concentration difference
 sieve elements 296–304
 sieve element plastids 296–304
 silicone oil layer centrifugation 392–398
Sinapis alba 68–71, 240–243,
 258–265
 sink-to-source transition 424–429
 spruce needles, ultrastructure 415–423
 stable isotopes, fractionation 335–342
 stelar parenchyma, reprogramming 305–310
 stem, biomechanics, functional anatomy 111–122, 123–130
 stress, mechanical on plant stems 111–112, 123–130
 strong ion concentration difference 214–221
 stylar transmitting tissue 384–391
 sucrose synthesis 392–398
 sugars, in floral nectar 343–348
 sulfur, vacuolar concentration 415–423
 surface potential 399–403
 symbiosis 140–142
Glycine sp./*Bradyrhizobium japonicum* 143–148
 synthesis, of glutathione 68–71
 of isocitrate lyase 48–53
 of polyglucans 7–8, 392–398
 of protein 408–414
 of sucrose 392–398
 systematics, of Lecanorales 131–139

T

temporal pattern, of gene expression 240–243

N-terminal amino acid sequences 274–280
 tetrathiafulvalene radical cation 404–407
 thallus formation, lichens 315–321
 thiosulphate, effect on growth of *Anacystis* 54–61
 thylakoid membrane 250–257
 composition 54–61
 molecular organization 149–154
 supramolecular organization 244–249
 tonoplast 24–31, 32–38, 203–213
 ATPase 24–32
 H⁺ transport into 203–213
 lipid profiles of leaf 32–38
 transcription complex 168–173
 transcriptional control, plastid genes 168–173
 transmembrane transport 15–23
 transtonoplastic potential 309–403
 transverse reinforcements, hollow plant stems 123–130
 Trochilidae 83–86, 367–368
 tropical woody plants, karyosystematics 372–383

U

ultrastructure 244–249, 250–257,
 296–304, 349–354
 spruce needles 415–425
 stylar transmitting tissue 384–391
 unit size, PSI 155–161

V

vacuolar concentration, of magnesium 415–423
 of phosphorus 415–423
 of potassium 415–423
 of sulfur 415–423
 vacuole 42–47, 399–403, 408–414
 amino acid concentration 42–47
 variegated leaves 430–434
 vascular pattern 305–310
Vaucheria 190–196
 vegetative cell 349–354
 Velloziaceae 83–86
Vigna 281–290
 virus infection, of *Ectocarpus* 72–82
 effect on shade-sun acclimation in leaves 226–229
 vitamin B₁₂ requirements 140–142

X

X-ray microanalysis 415–423
 xerophytes 93–96

Y

yeast H⁺-ATPase 230–234

Z

Zea mays coleoptile elongation 103–106

In this first issue of 1990, *BOTANICA ACTA* would like to thank all readers, subscribers, members of the German Botanical Society, authors, associate editors, and reviewers for their continued interest and support. Thanks to the joint efforts of all involved, *BOTANICA ACTA* can start its third year optimistically. Progress has been made towards attaining international recognition as a journal serving all branches of plant science. The number of manuscripts received increased considerably: in 1987 and 1988 a total of 99 manuscripts were submitted, in 1989 alone, 121 papers were received. The quality was high; the average rejection rate at present amounts to just under 30%. However, much still remains to be done and the editors and publishers will continue to seek ways of improving our journal. We are also happy to welcome 12 new Associate Editors who will either be responsible for additional fields of plant science or will increase our expertise in areas where we receive rather more contributions.

Special thanks are due to the many referees who donated their valuable time to help us evaluate all the papers submitted to *BOTANICA ACTA* including solicited review articles and contributions to *BOTANICA ACTA*. The members of the Editorial Board are named in each issue whereas the referees remain anonymous. While not abolishing this principle of anonymity, we would like, at intervals, to convey our sincere thanks to these people by name. Hence, after its first two years *BOTANICA ACTA* expresses its gratitude to the following scientists who have put their expert knowledge at our disposal to maintain and improve the high scientific quality of our journal:

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Hypersensitive Reaction of Nodule Cells in the *Glycine* sp./*Bradyrhizobium japonicum*-Symbiosis Occurs at the Genotype-Specific Level*

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Abstract

Three *Glycine* genotypes, *G. max* cv. Williams, *G. soja* PI 468397, and *G. soja* PI 342434 in combination with the two rhizobial strains *Bradyrhizobium japonicum* USDA 123 and *Rhizobium fredii* USDA 193 were analysed for phytoalexin concentration in the nodules. In the nodules of PI 468397/*B. japonicum* USDA 123 a very strong glyceollin I accumulation occurred around 30 d.p.i. Ultrastructural analysis of these nodules revealed several symptoms of a severe plant defense response associated with plant cell death (hypersensitive reaction): The cytoplasm of the infected cells was degraded and organelles had vanished. The cell walls of the infected cells showed remarkable thickening. This plant defense response could only be observed in this strain/genotype interaction. The same strain did not elicit a phytoalexin accumulation in the other plant genotypes tested, indicating that this response occurs at the genotype-specific level. This special character of *G. soja* PI 468397 is heritable as indicated by glyceollin I analysis of the nodules formed by F1 hybrids of PI 468397 x Williams inoculated with *B. japonicum* USDA 123. The genotype/strain specific occurrence of the hypersensitive response in root nodules resembles the race/cultivar specific incompatibility of several plant-pathogen interactions. This specificity, together with the phenomenon of the HR itself, points out the close physiological relationship between the late stages of the root nodule symbiosis and a plant/pathogen interaction.

Key words

Glycine, *Rhizobium*, *Bradyrhizobium*, glyceollin, hypersensitive reaction, phytoalexin, root nodules.

Abbreviations and Symbols

d.p.i.:	day after infection
PBM:	peribacteroid membrane
PHB:	poly- β -OH-butyrat
HR:	hypersensitive reaction
RIA:	radioimmunoassay
TEM:	transmission electron microscopy

Introduction

Glycine max forms nitrogen fixing nodule symbioses with its microsymbiont *Bradyrhizobium japonicum*. A few years ago, Keyser et al. (1982) described a new genus of fast growing rhizobia, *Rhizobium fredii*, with the ability to nodulate soybeans. As a rule one might state, that *R. fredii* strains form a less effective symbiosis with *G. max* than the slow growing *Bradyrhizobia* (Keyser and Cregan, 1984), although a few exceptions to this rule have been detected recently (Dowdle and Bohlool, 1985; Dowdle and Bohlool, 1987). Interestingly, a poorly effective strain of *R. fredii* has been shown to establish a highly effective symbiosis after mutation (Buendia-Claveria et al., 1988).

In the midwestern USA, indigenous *Bradyrhizobium* strains of serocluster 123 occupy most nodules of field grown soybeans (Ellis et al., 1984; Moawad et al., 1984). These strains of *B. japonicum* are highly competitive but form less than optimal nitrogen fixing symbioses with the commercially used cultivars of *G. max* (Caldwell and Vest, 1970; Ham, 1980). Highly effective strains of *B. japonicum* like USDA 110, are outcompeted by these strains even when inoculated at very high rates (Caldwell and Vest, 1970; Ham et al., 1971). Several approaches have been tried to circumvent this problem. Cregan and Keyser (1986) and Cregan et al. (1989) reported genotypes of *G. max* that restrict nodulation of the indigenous strains and thereby enable inoculum strains to nodulate better (Cregan et al., 1988; Keyser et al., 1988). Another strategy was based on the use of *G. soja* genotypes that form ineffective symbioses with slow growing rhizobia (Keyser and Cregan, 1984). These genotypes form highly effective symbioses with *R. fredii* strains. Using the genetic factors responsible for this "inverse" nodulation behaviour in combination with *R. fredii* inoculum might be a strategy to improve nitrogen fixation of *G. max* in the field even in the presence of *Bradyrhizobium* serocluster 123.

One of these *G. soja* genotypes is PI 468397 from the People's Republic of China. This genotype forms an effective symbiosis with *R. fredii* USDA 193, originally isolated from this genotype (Keyser and Cregan, 1984). On the other hand, the symbiosis with *B. japonicum* USDA 123 is Fix⁻. In addition, *R. fredii* USDA 193 has been shown to

be a much better competitor for nodulation on this genotype than *B. japonicum* strains (Cregan and Keyser, 1988).

In order to use the genetic factors of this genotype for breeding new *G. max* cultivars one has to understand better the physiological and genetic reasons for the observed change in compatibility. In this paper we give evidence that the incompatibility of PI 468397 with *B. japonicum* is accompanied by a severe plant defense reaction in the nodules. This plant reaction has striking similarities with a hypersensitive reaction (HR) described for several host-pathogen interactions (Klement, 1982) in terms of phytoalexin accumulation, plant cell death and degradation. The ability of PI 468397 to produce an HR when infected with USDA 123 is heritable as suggested by observation of the nodules of PI 468397 crossed with *G. max* cv. Williams.

Materials and Methods

White plastic pots (18 cm diameter at top) which had been soaked overnight in a sterilizing solution of Rocall were filled with autoclaved vermiculite. Experimental design consisted of a randomized complete block with a split plot arrangement of treatments and two replications. Whole plots (pots) were a factorial of two inoculation treatments (USDA 123 and USDA 193) \times 9 harvest dates and subplots were the three *Glycine* genotypes Williams, PI 342434 and PI 468397. The vermiculite was wetted with a nitrogen-free nutrient solution (Cregan and Keyser, 1988) and one "hill" of Williams, and two hills each of the *G. soja* genotypes were planted per pot at a depth of 1.5–2 cm. The seeds were subsequently inoculated with 1 ml of stationary broth culture per hill of either USDA 123 or USDA 193 and covered. The surface of the vermiculite was then covered with a 1.0 cm layer of autoclaved perlite to serve as a dry barrier to contamination by extraneous rhizobia. Four pots, otherwise treated as described above, were planted and left uninoculated. Nodules were harvested at 19, 21, 25, 27, 31, 33, 35, 38, and 40 d.p.i.

The radioimmunoassay specific for glyceollin I was performed as described by Hahn et al. (1985) except that solid-phase-bound anti-rabbit serum (Tecova, F.R.G.) was used to precipitate the glyceollin I-antibody. For electron microscopic studies, plants were grown in modified Leonard jar assemblies filled with perlite (Leonard, 1943). Nodules were fixed with glutaraldehyde, stained with osmium tetroxide, embedded in Epon and post-stained with uranyl acetate and lead citrate as described previously (Werner and Mörschel, 1978).

Results

Glyceollin I content of root nodules does not correlate with ineffectiveness of a given genotype/strain interaction

Three *Glycine* genotypes and two *Rhizobium/Bradyrhizobium* strains were included in this study (Table 1).

G. max cv. Williams formed effective nodules when inoculated with *B. japonicum* USDA 123 (Keyser and Cregan, 1984) (Table 1). These nodules contained only very low amounts of the phytoalexin glyceollin I (Fig. 1). When cv. Williams was inoculated with the fast growing *R. fredii* USDA 193, only small, ineffective nodules were formed. The nodules developed very late, i.e. there were no nodules found on the 19th d.p.i. The nodules of this host/strain combination contained very low amounts of glyceollin

Table 1 Effectiveness and glyceollin I content of nodules of the genotype/strain interactions used in this study.

Interaction	Nitrogen fixation	Glyceollin I accumulation
<i>G. max</i> cv. Williams / <i>B. japonicum</i> USDA 123 / <i>R. fredii</i> USDA 193	+ -	- -
<i>G. soja</i> PI 342434 / <i>B. japonicum</i> USDA 123 / <i>R. fredii</i> USDA 193	+ -	- -
<i>G. soja</i> PI 468397 / <i>B. japonicum</i> USDA 123 / <i>R. fredii</i> USDA 193	- +	+ -

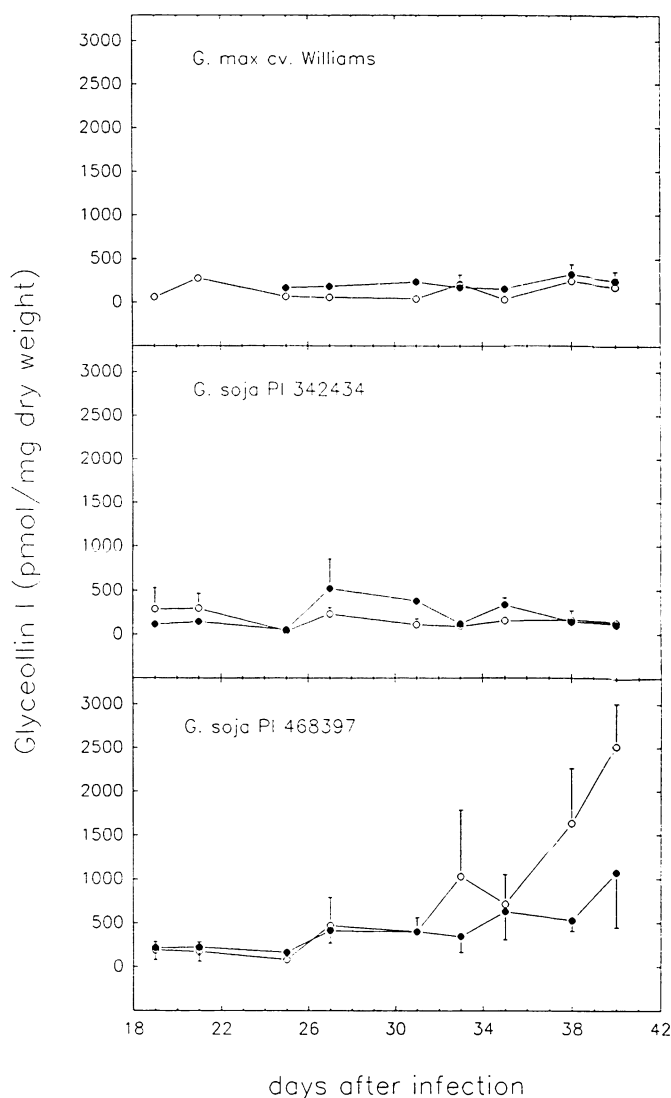


Fig. 1 Glyceollin I content of nodules formed by three *Glycine* genotypes in combination with *B. japonicum* USDA 123 (○) or *R. fredii* USDA 193 (●).

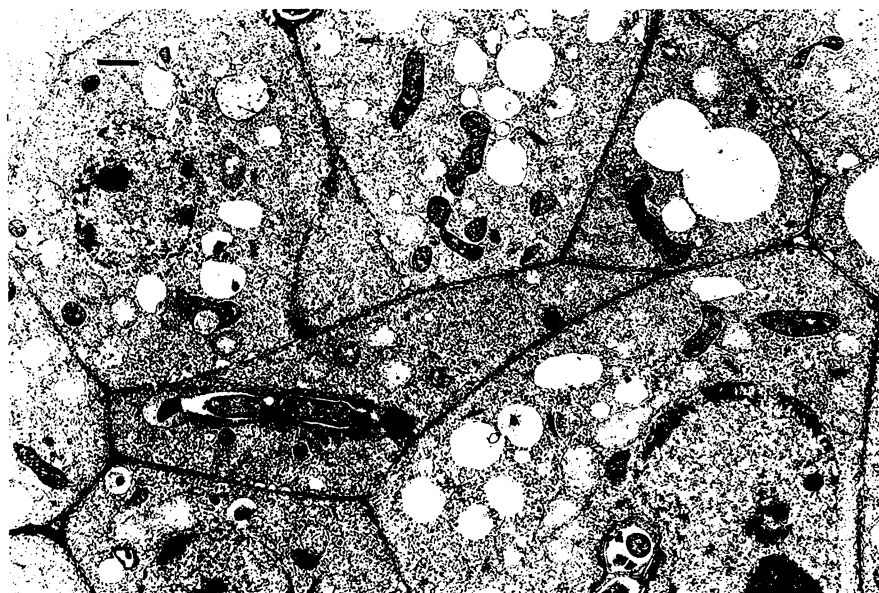
I (Fig. 1). *G. soja* PI 342434, a genotype that has a nodulation behaviour similar to commercially grown *G. max* cultivars, formed effective nodules with *B. japonicum* USDA 123. Glyceollin I content of these nodules was low (Fig. 1). *G. soja* PI 342434 in combination with *R. fredii* USDA 193

formed an ineffective symbiosis. Only low levels of glyceollin I were detected in these nodules (Fig. 1).

The symbiotic effectiveness and glyceollin I accumulation by *G. soja* PI 468397 contrasted with the two other *Glycine* genotypes. This genotype formed Fix⁻ nodules with the slow growing *B. japonicum* USDA 123. These nodules had a smooth surface and a green color, indicating the lack of leghemoglobin. In these nodules very high concentrations of glyceollin I could be found 33 days p.i. indicating a plant defense reaction. In contrast, this accumulation did not occur in nodules formed with *R. fredii* 193, rather normal effective nodules resulted from inoculation with this strain.

Nodules of G. soja PI 468397/B. japonicum USDA 123 exhibit several symptoms of a plant-pathogen interaction

We studied the developing nodules of the PI 468397/*B. japonicum* USDA 123 interaction in more detail by using TEM. At day 12 after infection, many infection threads were found in the meristematic plant cells (Fig. 2). Bacteria were enclosed by a thick layer of matrix material. Only few, if any, released bacteria could be detected in the plant cells at this developmental stage. Instead, vacuolar structures were observed in the meristematic cells. At day 15 p.i. (Fig. 3) many released bacteria could be found in the plant cells. They were surrounded by a peribacteroid membrane (PBM). In these early stages, no obvious differences to a fully compatible interaction could be observed at the fine structural level (for TEM analysis of effective nodule development see Bassett et al. (1977a); Werner and Mörschel (1978); Roth and Stacey (1989)).



Figs. 2–5 Electron micrographs of nodules of the *G. soja* PI 468397/*B. japonicum* USDA 123 interaction at different developmental stages. Each bar represents 1 μ m.

Fig. 2 Meristematic nodule cells at the 12th d.p.i. contained infection threads with thick matrix material around the bacteria. Little or no released bacteria were visible.

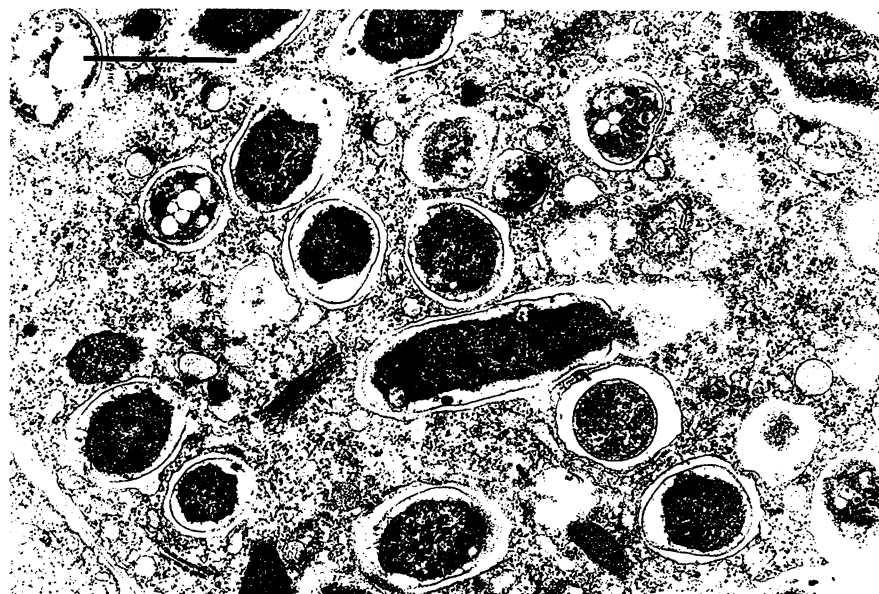


Fig. 3 Part of an infected plant cell at the 15th d.p.i. Bacteroids surrounded by a PBM and plant organelles such as dictyosomes and mitochondria were visible in the plant cells.

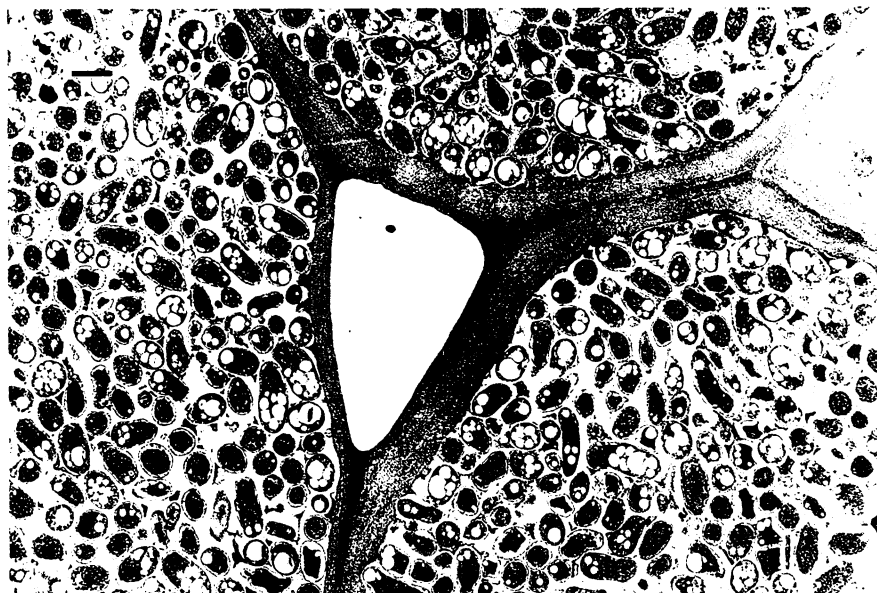


Fig. 4 Infected plant cells at the 29–33th d.p.i. showed massive cell wall thickening. Bacteria inside the plant cells accumulated large amounts of PHB and had reached higher cell densities than in the earlier stages. They were no longer surrounded by a PBM nor by any other intact plant structure indicating that plant cells were dead.

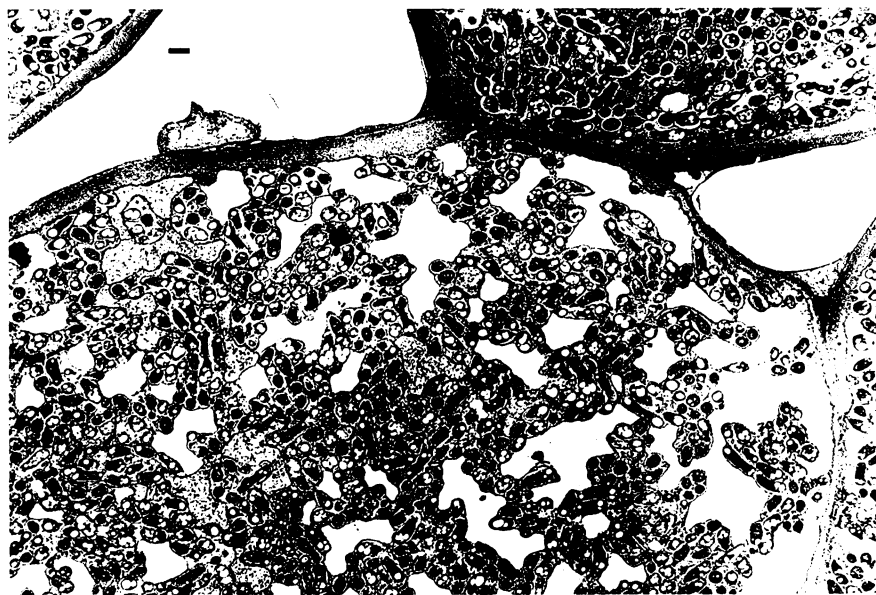


Fig. 5 Infected plant cell at the 29–33th d.p.i. contained bacteroids, plant organelles and vacuolar structures indicating plant cell lysis. Bacteroids contained large PHB-granules.

In contrast to an effective interaction, at day 29–33 p.i. a number of infected plant cells had been subjected to severe degradation as indicated by the complete lack of plant organelles (Fig. 4). The bacteria were no longer enclosed by a PBM. We conclude from these observations, that these plant cells are dead at this stage of development. Cell death and degradation are typical features of the hypersensitive reaction of a plant cell (Klement, 1982). Another marker of a plant defense response on the ultrastructural level is the observed thickening of cell walls. Interestingly, a major portion of the bacteria inside the degraded plant cells looked structurally intact suggesting that they were still alive.

Apart from this cell type another type of development occurred in nodules of this age (Fig. 5). Here, most of the plant organelles remained present but some irregular vacuolar structures were seen. We interpret this cell

type as a developmental precedent of the terminal stage described in Fig. 4.

*Hypersensitive plant reaction to
B. japonicum USDA 123 in PI 468397
is heritable*

In order to determine if the nodulation features of PI 468397 are inherited when hybridised with cultivar Williams, we analysed the glyceollin I content of the nodules of the F₁-generation of this cross (Table 2). Interestingly, all plants of the F₁-generation produced two types of nodules on their root systems when inoculated with *B. japonicum* USDA 123: small green ineffective (nodule type 2 in Table 2) and normal looking effective ones (type 1). Visual estimates made at harvest indicated that 60 to 90 percent of the nodules on F₁ plants were of the green ineffective type. The ineffective nodules contained glyceollin I in

Table 2 Glyceollin I content of nodules of *B. japonicum* USDA 123 formed with *G. soja* PI 468397, *G. max* cv. Williams and F1-hybrids.

Genotype	Nitrogen fixation	Glyceollin I content (pmol/mg dw)
<i>G. max</i> cv. Williams	+	175
<i>G. soja</i> PI 468397	-	2518
F1, nodule type 1	+	79
F1, nodule type 2	-	2323

the same order of magnitude as the nodules of the PI 468397 parent genotype indicating that this character is heritable.

Discussion

The *G. soja* genotype PI 468397 has some unusual nodulation properties in comparison to the commercial cultivars of *G. max* and several other genotypes of *G. soja*, e.g. PI 342434. First, it forms ineffective nodules with all *B. japonicum* strains tested so far (Keyser and Cregan, 1984). Second, it forms a highly effective symbiosis with *R. fredii* USDA 193. Third, it nodulates preferentially with *R. fredii* USDA 193 instead of *B. japonicum* USDA 123.

In this paper we demonstrate that the ineffective symbiosis of PI 468397 with *B. japonicum* USDA 123 leads to a plant defense reaction in the later stages (i.e. about day 30 p.i.) of the symbiosis. Until day 15 p.i. no obvious difference to a fully compatible interaction could be observed by TEM or by glyceollin I analysis. Only in later stages of the interaction is *B. japonicum* USDA 123 recognized as a pathogen. The phytoalexin glyceollin I is accumulated in the nodules and a hypersensitive reaction of the infected plant cells could be observed at the ultrastructural level. Glyceollin accumulation is believed to be an important early defense reaction of *G. max* towards the fungal pathogen *Phytophthora megasperma* f. sp. *glycinea* (Ebel and Grisebach, 1988). Glyceollin I concentration in the nodules of *G. soja* PI 468397/*B. japonicum* USDA 123 is in the same order of magnitude as in soybean root tissue infected with *P. megasperma* (compare to Hahn et al., 1985). It should be mentioned that phytoalexin accumulation may not only be elicited by biotic factors but also by abiotic stresses such as the presence of heavy metals (Darvill and Albersheim, 1984; Ebel, 1986).

However, phytoalexin accumulation was only observed in the PI 468397/USDA 123 interaction and in none of the other genotype/strain combinations tested. The elicitation of the plant defense response seems to be a highly specific event for which a certain strain/genotype combination is needed.

Cultivars of *G. max* accumulate large amounts of glyceollin I in the nodules only when infected with specific strains of *B. japonicum* like USDA 24 or a *nifA* deletion mutant of USDA 110 (Werner et al., 1980; Werner et al., 1985; Parniske et al., in preparation). Other ineffective strains fail to elicit a hypersensitive response of the infected nodule cells. These results confirm the observations of Werner et al. (1985) that phytoalexin accumulation is not simply a consequence of the ineffectivity of the symbiosis.

The strong genotype/strain dependence of the HR-phenomenon in nodule cells suggests a very specific recognition process between the two partners in the later stages of nodule development.

The genotype/strain specific occurrence of the HR in nodule cells resembles the cultivar/race specific incompatibility of several host-pathogen-interactions. The close physiological relationship between the early recognition process in the *Rhizobium*-legume symbiosis and that of a pathogenic interaction has been mentioned by several authors (Vance, 1983; Djordjevic et al., 1987; Djordjevic et al., 1988; Keen and Staskawicz, 1988; Rolfe and Gresshoff, 1988). The recognition process that decides between a symbiotic and a pathogenic development does not only work in the early stages (i.e. infection of the root hairs) of the symbiotic interaction. Even infected nodule cells may perform a hypersensitive reaction. Compatible rhizobia must have evolved mechanisms to circumvent the elicitation of a HR in the early as well as in the late stages of the symbiotic interaction.

The term "hypersensitive response" with respect to soybean root nodule tissue was first used by Bassett et al. (1977b). These authors describe a "selective autolysis" of the infected cells which has a greater effect on the bacteria than on the host cell. The latter remains alive during this process. They also compared this specific type of autolysis with that occurring during senescence. In order to better distinguish between different types of ineffective nodule developments, we suggest that the term "hypersensitive response" should only be used if host cell death occurs. As a consequence, we think that the term "early senescence" would better fit the reaction type described by Bassett, because host cells stay alive and that "hypersensitive response" more appropriately describes the reaction of *G. soja* PI 468397 to *B. japonicum* 123 that results in host cell death.

Factors that lead to advantages in competition act in the early stages of the host-microsymbiont interaction. Cregan and Keyser (1988) observed a better competitiveness of *R. fredii* USDA 193 in comparison to *B. japonicum* USDA 123 on PI 468397. We think that this phenomenon cannot be explained by the observed defense reaction of this genotype towards USDA 123 because it occurs in the later stages of the symbiosis. However, we have not yet determined whether *B. japonicum* elicits a higher glyceollin I accumulation in the root hairs during the infection process. Using the very sensitive RIA-technique we will attempt to answer this next question.

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