

45 Progress in Botany

Morphology Physiology Genetics
Taxonomy Geobotany

Fortschritte der Botanik

Morphologie Physiologie
Genetik Systematik Geobotanik

45

Progress in Botany

Morphology · Physiology · Genetics
Taxonomy · Geobotany

Fortschritte der Botanik

Morphologie · Physiologie · Genetik
Systematik · Geobotanik

Editors/Herausgeber

Karl Esser, Bochum

Klaus Kubitzki, Hamburg

Michael Runge, Göttingen

Eberhard Schnepf, Heidelberg

Hubert Ziegler, München



Springer-Verlag

Berlin Heidelberg New York Tokyo 1983

Vorwort

Der Senior unserer Herausberggemeinschaft HEINZ ELLENBERG hat sich leider aus der Redaktion zurückgezogen. Nach dem Tode von ERNST GÄUMANN hatte er 1963 (ab Band 26) zusammen mit ERWIN BÜNNING die Herausbergerschaft der "Fortschritte der Botanik" übernommen. Seiner Aufgeschlossenheit und auch seiner Initiative ist die dann später erfolgte Erweiterung des Herausbergremiums und die damit verbundene inhaltliche Umgestaltung zu verdanken.

In seiner nunmehr fast zwanzigjährigen Betreuung des Abschnittes "Geobotanik" hat er dazu beigetragen, daß dieses Teilgebiet zu einer wesentlichen Säule unserer Reihe geworden ist.

Herausgeber und Verlag möchten ihm für seine Redaktionsarbeit danken und hoffen, daß Herr ELLENBERG ihnen auch weiterhin in alter Freundschaft verbunden bleibt.

An seiner Stelle hat von diesem Band ab Herr MICHAEL RUNGE die Schriftleitung des Kapitels Geobotanik übernommen.

Die Herausgeber

With 23 Figures

ISBN 3-540-12997-9 Springer-Verlag Berlin Heidelberg New York Tokyo
ISBN 0-387-12997-9 Springer-Verlag New York Heidelberg Berlin Tokyo

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically those of translation, reprinting, re-use of illustrations, broadcasting, reproduction by photocopying machine or similar means, and storage in data banks. Under § 54 of the German Copyright Law where copies are made for other than private use a fee is payable to "Verwertungsgesellschaft Wort", Munich.

© by Springer-Verlag Berlin Heidelberg 1983. Library of Congress Catalog Card Number 33-15850.

Printed in Germany

The use of registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Offsetprinting and bookbinding: Brühlsche Universitätsdruckerei, Giessen
2131/3130-543210.

List of Editors

Section A: Professor Dr. E. SCHNEPF, Zellenlehre, Universität
Heidelberg, Im Neuenheimer Feld 230, D 6900 Heidelberg

Section B: Professor Dr. H. ZIEGLER, Institut für Botanik und Mikro-
biologie, Technische Universität München, Arcisstr. 21,
D 8000 München 2

Section C: Professor Dr. Dr. h.c. K. ESSER, Lehrstuhl für Allgemeine
Botanik, Ruhr-Universität, Postfach 10 2148,
D 4630 Bochum 1

Section D: Professor Dr. K. KUBITZKI, Institut für Allgemeine
Botanik und Botanischer Garten, Universität Hamburg,
Ohnhorststr. 18, D 2000 Hamburg 52

Section E: Professor Dr. M. RUNGE, Lehrstuhl für Geobotanik,
Systematisch-Geobotanisches Institut der Universität,
Untere Karspüle 2, D 3400 Göttingen

Contents

A. MORPHOLOGY

I. Cytology

a) General and Molecular Cytology. By ANTHONY W. ROBARDS ...	1
1. Root Hairs	1
a) Development and Structure of Root Hairs	1
b) Microbial and Other Associations with Root Hairs ..	3
2. Cytoplasmic Streaming	6
a) General Experimental Effects on Cytoplasmic Streaming	7
b) Effects of Cytochalasin B on Cytoplasmic Streaming	8
c) Effects of Light and of Growth Regulators on Cytoplasmic Streaming	9
d) The Role of Calcium in Cytoplasmic Streaming	10
e) General Observations on Cytoplasmic Streaming	11
3. Calmodulin	12
References	14
b) Special Cytology: Cytology and Morphogenesis of Higher Plant Cells - Phloem. By H.-D. BEHNKE	18
1. Flowering Plants	18
a) Sieve Elements	18
α) Cell wall, microtubules, plasmalemma, plasmatic connections, sieve pores	19
β) Vacuole and Tonoplast	21
γ) Nucleous	21
δ) Plastids and Mitochondria	21
ε) Endomembrane System	21
ζ) P(phloem)-proteins	22
η) Microfilaments	24
b) Companion Cells and Phloem-Parenchyma Cells	24
c) Fibers and Other Elements of Phloem	25
d) Phloem Regeneration After Wounding and Host-Parasite Contact Between Vascular Plants	25
α) Phloem Regeneration	25
β) Host-Parasite Contact	26
e) Effects of Viruses, Mycoplasmas and Other Agents on Phloem Structure and Differentiation	27
2. Conifers and Other Gymnospermae	28
a) Sieve Cells	28
b) Strasburger Cells	29

VIII Contents

3. Ferns and Fern Allies	29
4. Mosses and Liverworts	30
5. Algae	31
References	31

II. Morphologie und Anatomie der höheren Pflanzen:

a) Vergleichende Morphologie des Vegetationskörpers Von WOLFGANG HAGEMANN

36

1. Allgemeines	36
2. Meristeme	38
a) Sproßscheitelmeristeme	38
b) Randmeristeme	39
c) Wurzelmeristeme	40
d) Anlegung der Leitbündelsysteme	41
3. Blattorgane	43
4. Verzweigung und Wuchsformen	45
a) Allgemeines	45
b) Farne	46
c) Dikotyle Bäume	46
d) Sträucher und Kräuter bei Dikotylen	47
e) Monokotylen	48
5. Wurzeln	48
Literatur	50

b) Reproductive Structures of the Flowering Plants

By PETER K. ENDRESS

54

1. General, Textbooks	54
2. Flowers	54
a) Initiation, Ontogeny, Phyllotaxis, Symmetry	54
b) Perianth	56
c) Androecium	56
d) Gynoecium	56
e) Systematic and Evolutionary Aspects	59
a) Fossil Flowers	59
b) Recent Groups	59
3. Fruits and Seeds	61
4. Inflorescences	62
5. Methods	63
References	63

B. PHYSIOLOGY

I. Phloem Loading and Unloading. By EWALD KOMOR

68

1. Introduction	68
2. Transfer of Solute to the Sieve Tube	68
3. Uptake of Solute by the Sieve Tube	70
4. Long-distance Transport of Solutes	71
5. Unloading of Solutes	72
6. Conclusions	73
References	74

II. Mineral Nutrition: Salinity. By ULRICH LÜTTGE	76
1. Present Demand and Support	76
2. Salt Exclusion and Inclusion on the Root and Whole-Plant Levels	80
3. Salt Elimination by Salt Hairs and Salt Glands	82
4. Tissue Culture	84
References	
III. Photosynthesis. Photosystems in Green Plants and Green Bacteria. By J. AMESZ	89
1. Introduction	89
2. Oxygen Evolution	89
a) The Reaction Center of Photosystems II	90
b) Architecture of the Photosynthetic Apparatus in Chloroplasts in Relation to Electron Transport ...	93
c) The Role of Manganese in Oxygen Evolution	95
d) Protein Constituents	96
3. Charge Separation and Electron Transport in Green Bacteria	96
a) Chlorobiaceae	99
b) Chlorolexaceae (gliding green bacteria)	100
c) Conclusion	101
References	
IV. Metabolism of Inorganic Nitrogen Compounds By HERMANN BOTHE	106
1. Nitrogen Fixation	106
a) N_2 -Fixation by Free-Living Microorganisms	108
b) Symbiotic N_2 -Fixation	110
2. Nitrate Reduction	110
a) Assimilatory Nitrate Reduction	112
b) Dissimilatory Nitrate Reduction	113
3. Nitrification	114
References	
V. Secondary Plant Substances. Aspects of Carotenoid Biosynthesis. By HORST-ROBERT SCHUTTE	120
1. Introduction	120
2. Formation of Phytoene	121
3. Desaturation of Phytoene	122
4. Cyclization and Formation of Xanthophylls	124
5. Enzymology	127
6. Carotenoid Biosynthesis and Light	129
7. Unusual Carotenoids	131
References	
VI. Growth. By NIKOLAUS AMRHEIN	136
1. General Reviews	136
2. Gibberellins	136
a) Chemistry	137
b) Methods of Isolation and Determination	138
c) Occurrence	

X Contents

d) Biosynthesis and Metabolism	138
e) Action	143
α) Gibberellin-Induced Elongation	143
β) Gibberellin Action in the Aleurone Layer	145
3. Brassinolide	148
4. Triacontanol	149
5. Cytokinins	150
a) Chemistry and Analytical Methods	150
b) Occurrence	151
α) Cytokinins in Tumors	151
β) Cytokinins in Nontransformed Tissues	152
γ) Cytokinin-active Nucleotides in tRNA	152
δ) Synthetic Cytokinins	153
c) Biogenesis and Metabolism	153
d) Action	155
α) The Quest for Receptors	155
β) Effects on Membranes and Ion Fluxes	156
γ) Effects on DNA, RNA, and Protein Synthesis	157
References	158

C. GENETICS

I. Replication. By WALTER NAGL

166

1. Introduction	166
2. DNA Polymerases	166
3. Regulation of Initiation	167
4. Differential DNA Replication	168
5. DNA Replication and Chromatin Structure	169
References	170

II. Recombination, New and Classical Approaches at the Higher Plant Level. By GERHARD WENZEL

174

1. Introduction	174
2. Asexual Recombination	174
a) Somaclonal Variation	174
b) Transfer of Genetic Information	177
α) Somatic Hybridization	178
β) Gene Transfer by Vectors	179
γ) Research on Controlling Elements	181
c) Sister Chromatid Exchange	182
3. Sexual Recombination	182
a) Recombination During Classical Breeding in Cereals	182
b) Situation in Interspecific Hybrids	183
c) Mapping of Other Crops	184
References	184

III. Mutation: Higher Plants. By WERNER GOTTSCHALK

189

1. Methods for Inducing Gene Mutations and Chromosome Aberrations	189
a) Mutagenic Chemicals	189
b) The Response of Mutagens to Other Substances	191

2. Gene Mutations	191
3. Chromosome Mutations	193
a) Translocations in Natural Populations	193
b) Experimentally Produced Translocations	193
4. Genome Mutations	194
a) Methods for Inducing Polyploidy	194
b) Natural Autopolyploids	195
c) The Genomic Constitution of Allopolyploid Species	195
d) Experimentally Produced Allopolyploids	196
e) Trisomics and Related Forms	196
f) Haploids and Polyhaploids	197
References	198

IV. Function of Genetic Material: Genetics of Proteins and Nucleic Acids in Flowering Plants. By R. BLAICH

1. Function of Genes Coding for Enzymes	202
a) Alcohol Dehydrogenase	202
b) Other Enzymes	203
c) Enzyme Regulation and Metabolism	204
2. Genetics of Nonenzymatic Plant Proteins	205
a) Actin Gene of a Higher Plant	205
b) Leghemoglobins of Legumes	205
c) Zein Storage Protein	206
d) Wheat Endosperm Proteins	206
e) Storage Proteins in Legume Seeds	207
3. Genetics of Nucleic Acids	207
a) Ribosomal RNA	207
b) Messenger RNA	208
c) Transfer RNA and Aminoacyl tRNA Synthase	208
References	209

V. Extranuclear Inheritance: Plastid Genetics

By RUDOLF HAGEMANN and MICHAEL METZLAFF

1. Introduction	212
2. New Nomenclature of Plastid Genes	212
3. New Data on Physical Mapping of Plastid Genes (1981-1983)	212
a) General and Evolutionary Aspects	212
b) Physical Mapping of Plastid Protein Genes	214
c) Physical Mapping of rRNA and tRNA Genes	216
4. Sequencing of Plastid Genes	217
a) Sequencing of Protein Genes	217
b) Sequencing of rRNA and tRNA Genes	219
5. Introns and Gene Overlapping	221
a) Introns in Plastid Genes	221
b) Overlapping Genes	221
6. Expression of Plastid Genes in <i>Escherichia coli</i> Cells	222
7. Hybrid Variegation in Higher Plants	222
References	224

XII Contents

VI. Population Genetics

By KLAUS WÖHRMANN and VOLKER LOESCHCKE	228
1. Introduction	228
2. Enzyme Polymorphism	228
a) Some Problems in Assessing the Amount Genetic Variation	228
α) Cryptic Variation	228
β) Null Alleles	229
γ) Pseudopolymorphism	229
δ) Developmental Expression of Isozyme Pattern	229
b) Breeding Structure	229
c) The Causes of Evolutionary Change	230
α) Mutation	230
β) Migration	230
γ) Drift	231
δ) Selection	231
d) Multilocus Associations	232
e) Polygenic Inheritance	232
f) Varying Environments	233
g) Geographic Variation	233
3. Selection Components and Demography	234
4. Coevolution	235
a) Host-Parasite Interactions	236
b) Competition	237
References	238

D. TAXONOMY

I. Evolution and Classification of Seed Plants

By HANS-HELMUT POPPENDIECK	242
1. Introduction	242
2. Problems of Classification	243
a) Phylogenetics, Phenetics, and Classification	243
α) Cladistic Approaches	243
β) Numerical Phenetics	245
γ) Final Decisions	245
b) Data Banks	246
c) Critique of Higher Order Systematics	246
3. Morphology	247
a) General Aspects	247
b) Vegetative Structures Including Anatomy and Micromorphology	248
c) Floral Characters	249
d) Palynology and Embryology	251
4. Karyology and Cytogenetics	252
5. Chemical Systematics	254
a) Phytochemical Evidence	254
b) Interpretation of Chemical Data	256
c) Flower Color Evolution	257
d) Ecological Significance of Secondary Compounds	257
6. Evolution	258
a) Populations and Species	258
α) Patterns of Variation	259
β) Gene Flow and Mating Systems	259
γ) Divergence of Populations	259
δ) Hybridization	260

ε) Evolution Within Apomictic Groups	260
ζ) Further Studies Within Larger Groups	261
b) Sexual Differentiation and Pollination System	261
c) Dispersal and Related Plant-Animal Interactions ..	262
α) Dispersal Anachronisms	262
β) Interaction with Frugivores	263
γ) Interactions with Ants	263
d) Diversity and Rarity	264
e) Ecological Aspects	265
f) Geographical Aspects	266
α) Disjunctions	267
β) Exemplary Studies	267
7. Plants and Man	268
8. Origin of Angiosperms	270
9. Evolution and Classification of Larger Groups	271
a) Gymnosperms	271
b) Angiosperms, General Aspects	272
c) Monocotyledons	274
d) Leguminosae	275
10. Seed Plant Systematics on the Family Level and Below	277
References	283

II. Paläobotanik. Von FRIEDEMANN SCHAARSCHMIDT

1. Allgemeines	298
2. Thallophyta	298
3. Bryophyta	299
4. Psilophyta	299
5. Lycophyta	300
6. Sphenophyta	302
7. Filicophyta	303
8. Pteridospermae	305
9. Cycadophyta	307
10. Ginkgophyta	307
11. Coniferophyta	308
12. Angiospermae	310
Literatur	314

E. GEOBOTANY

I. Areal- und Florenkunde (Floristische Geobotanik)

Von ECKEHART J. JÄGER

1. Forschungstrends	318
2. Zusammenfassende Darstellungen	318
3. Floristische Grundlagen	319
a) Neufunde	319
b) Floren des mediterran-orientalischen Gebietes	319
c) Floren von Nordamerika	320
d) Floren von Mittel- und Südamerika	321
4. Kartierung	323
5. Florenvergleich und Florengebietsgliederung mit numerischen Methoden	325
a) Florenvergleich	325
b) Florengebietsgliederung mit Computer	325

XIV Contents

c) Konventionelle Florengebietsgliederungen	326
d) Numerische Methoden und Vikarianz-Bio- geographie	326
6. Rekonstruktion der Ausbreitungsgeschichte (Chorogenese)	327
a) Ursprungszentren, Brückenwanderung und Ferntransport	327
b) Paläogeographie und Arealentwicklung	328
c) Glaziale Arealveränderungen in den Tropen	328
d) Arealentwicklung der sommergrünen Laubwald- pflanzen	329
e) Eiszeit-Überdauerung auf Nunatakkern	329
f) Karyogeographische Beiträge zur Areal- entwicklung	330
Literatur	330
 <u>II. Vegetation Science (Sociological Geobotany)</u>	
By RÜDIGER KNAPP	336
1. Fundamental Perspectives, Books, Monographs and Bibliographies	336
2. General Results and Methods	337
a) Theoretical Foundations of Community Structure ...	337
b) Life Forms and Vegetation	338
c) Vegetation and Herbivory	338
d) Island Vegetation and Isolated Plant Community Stands	338
3. Vegetation Mapping	339
4. Arctic Vegetation	340
5. Boreal and Temperate Vegetation: Recent Changes	340
a) Anthropogenic Changes in Boreal Vegetation	340
b) Changing European Aquatic and Littoral Vegetation	341
c) Temperate Urban Vegetation	341
6. Temperate and Meridional Forest Vegetation	342
a) Deciduous Forests of Eastern North America	342
b) Meridional and Temperate Forests in Japan	342
7. Tropical Vegetation	343
a) Tropical Rain Forests	343
b) Mangrove Vegetation	344
References	344
 <u>III. Ecosystem Research (Ecological Geobotany)</u>	
By WOLFGANG SCHMIDT	351
1. General	351
2. Productivity	352
a) Photosynthesis	352
α) Modelling	352
β) Carbon Fixation Pathways	353
γ) Relations to Environmental Factors	353
δ) Leaf Area Index and Chlorophyll Content	354
b) Respiration	355
c) Carbon Cycle	355
d) Biomass and Net Primary Production	355
α) Algae and Aquatic Ecosystems	355
β) Fungi, Lichens and Mosses and Their Communities	356

γ) Herbs and Grasses in Different Ecosystems, Mainly Grasslands	356
δ) Woody Plants and Forest Ecosystems	359
ε) Methods	362
3. Energy and Water Balance	362
a) Energy Content	363
b) Energy Flow and Allocation	363
α) Energy Efficiency	363
β) Biomass and Energy Allocation	364
c) Transpiration and Water Cycle	365
d) Radiation Balance	365
4. Mineral Cycle	365
a) General	365
b) Litter Fall	366
c) Decomposition	366
α) General and Methods	367
β) Grasslands and Herb Communities	368
γ) Forest Ecosystems	369
d) Mineral Cycle	369
α) General	370
β) Aquatic Ecosystems	370
γ) Grasslands and Herb Communities	371
δ) Forest Ecosystems	373
5. Ecosystems Development	373
a) Succession	373
α) Forest Succession	374
β) Fire Succession	375
γ) Old-Field Succession	375
δ) Other Ecosystems	376
b) Stability and Man's Influence on Ecosystem Structure and Processes	376
α) Grazing and Trampling Effects	377
β) Effects of Acid Precipitation	378
γ) Heavy Metals and Other Chemical Factors	378
References	391
<u>Subject Index</u>	391

A. Morphology

I. Cytology

a) General and Molecular Cytology

By ANTHONY W. ROBARDS

This contribution presents some recent information on the general topic of cytoplasmic streaming, with some specific comments about the role of calmodulin, which may well be involved in regulatory mechanisms of cytoplasmic streaming, in plants. It also concerns itself with the structure and growth of root hairs, which have often been used to study intracellular movements.

1. Root Hairs

a) Development and Structure of Root Hairs

The asymmetric division leading to the formation of a trichoblast was noted by GUNNING et al. (1978) to be predicted by the presence of a pre-prophase band of microtubules in *Hydrocharis* roots. This division in passed acropetally along every cell in the dermatogen layer, pre-prophase bands being noted up to eight cells in advance of the last completed division. KAWATA and CHUNG (1979), studying the crown roots of rice plants, found that the length of trichoblasts could not be distinguished from that of other epidermal cells. However, trichoblasts had more E.R., mitochondria, and ribosomes than other epidermal cells. ROTHBERG and CUNNINGHAM (1978) observed membrane transformation in the roots hairs of *Raphanus*, which they found to elongate at a rate of about 0.1 mm h^{-1} (cf. COOPER and BROWN, below). Numerous vesicles were found adjacent to the plasmalemma and complex interfoldings of the wall were noted, which expanded as the cells grew. Freeze-etching, to reveal intramembrane particles, indicated the possibility of membrane flow, small Golgi vesicles having 1250 to 1400 7-8 nm diameter p-face particles μm^{-2} .

SORAN and LAZAR-KEUL (1978) investigated the relationship between growth and length of barley root hairs and the rate of streaming within them. In young root hairs there was a good correlation between growth and increase in streaming rate but after the end of the grand period of growth this relationship is lost. The continuing increase in streaming rate must then be sought in biochemical changes rather than in the physical strain of the cytoplasm during growth.

The surface area of root hairs is obviously a critical parameter in relation to uptake capacity and yet it is often a difficult value to obtain. SMITH et al. (1979) made measurements on root hairs of *Zostera* and *Halodule* from estuarine sediments. The root hair basal cells of *Zostera* had an average exposed surface area of $7.98 \times 10^{-3} \text{ mm}^2$. The average *Zostera* root and root hair surface areas were 48.2 and 138.8 mm^2 per root respectively. *Halodule* roots and root hairs were shorter than those of *Zostera* with areas of 34.8 and 19.2 mm^2 per root respectively.

The subject of root hair wall synthesis has been a matter of particular interest, as these plant cells elongate rapidly and are relatively accessible to study. SEAGULL (1978a,b,c) and SEAGULL and HEATH (1980a) have made a detailed study of the events surrounding root hair wall synthesis and deposition in *Raphanus*. Cortical microtubular arrays were analysed from reconstructions of serial thin sections by SEAGULL and HEATH (1980a) to test further and extend the hypotheses concerning the relationship between microtubular orientation and the direction of microfibril deposition (SEAGULL and HEATH, 1979a). Approximately 25 μm behind the tip of the root hair, microfibrils change from a random to an orientated arrangement. It was confirmed that microtubules increase in number, from the tip, until they reach a plateau at about 25 μm . They also change in length from having approximately 60% less than 1.0 μm long in the tip to approximately 40% less than 1.0 μm long at 60 μm behind the tip. They maintain a pattern of angular deviation from the longitudinal axis of the cell which is similar to the angular deviation of cell-wall microfibrils, and they maintain a constant (approximately 70% of tubules) close (within 50 nm) proximity with the plasma membrane. There is a low (approximately 20%) degree of intermicrotubule proximity (within 50 nm of each other) but some variable long range (> 50 nm) association. Fixation with glutaraldehyde in a "complete microtubule polymerization medium", or pretreatment with cytochalasin B, caused an approximate twofold increase in the proportion of long microtubules in the tip region and microtubules within 50 nm of one another.

Bridges were seen joining microtubules to the plasmalemma. Microfilaments ranging from single fibres to large bundles, paralleled the microtubules and treatment with 1% dimethylsulphoxide, while not affecting microtubules, increased the observed number of microfilaments. It was concluded that there were too few long microtubules to coordinate cell-wall microfibril orientation and, further, microtubule orientation did not change within the first 60 μm from the tip although microfibrillar orientation shifts from a random arrangement to an orientated one. The suggestion was made that actin bridges between long and short microtubules might produce a meshwork which would allow a few long microtubules to direct the synthesis of many microfibrils, thus resulting in an orientated microfibrillar deposition. A population of single, actin-like microfilaments was found specifically associated with the cortical microtubules of root hairs (SEAGULL and HEATH, 1979a). Extensive filament bundles were not specifically associated with the tubules although close proximity was observed. The addition of tannic acid to the fixative (SEAGULL and HEATH, 1979a,b,c) preserved more microtubule-associated microfilaments but did not reveal any extra non-microtubule-associated microfilaments. The tannic acid increased the apparent microfilament diameter in proportion to its concentration in the fixative.

SASSEN et al. (1981) studied wall texturing in hairs of *Equisetum*. They identified two general types of wall texture in root hairs: that in terrestrial plants where there is a fibrillar texture, and that in aquatics where the arrangement is helicoidal. *Equisetum* was found to be an exception as the primary wall had randomly arranged microfibrils and the secondary wall was helicoidal. The microtubules ran more or less longitudinally and no clear correlation between microfibrillar and microtubular orientation was found. BROWN (1981) and COOPER and BROWN (1981) experimentally altered microfibril deposition in *Raphanus*, using the wall brightener *Calcofluor*. They found that, when growing root hairs were treated with *Calcofluor*, the tips became rounded although cyclosis was unimpeded; when the *Calcofluor* concentration in the medium dropped below a certain threshold level, normal tip growth resumed. COPPER and BROWN (1981) showed that the growth rate of radish root

hairs was about 0.05 to 0.1 mm h⁻¹ and that this rate was reduced by inhibitors of cellulose synthesis such as coumarin and 2-6-dichlorobenzonitrile, which eventually caused the hair tips to burst. Cyclosis continued up to the time of bursting. Prolonged treatment with *Calcofluor* resulted in the deposition of acid- and alkali-resistant masses, possibly callose, at the tips of the hairs. It was suggested from these, and other, experiments that *Calcofluor* prevents the lateral aggregation of cellulose chains, thus impeding crystallisation.

If root hairs are functional in nutrient uptake and transport, then their connections to adjacent cells are of some importance. VAKHMISTROV and KURKOVA (1979), KURKOVA (1981) and VAKHMISTROV et al. (1981) have addressed themselves to this problem. In the aquatic plant *Trianea* it was found (VAKHMISTROV and KURKOVA, 1979) that the highest frequency of plasmodesmata was on the inner tangential wall of the hair cell where there were more than 17 times as many plasmodesmata as in the equivalent position in hairless epidermal cells (see also HARRIS 1979, for *Equisetum* trichoblasts). Similarly (VAKHMISTROV et al. 1981), the frequency of plasmodesmata in root hairs was twice as great as that in other epidermal cells of *Raphanus*. A comparison between the data from *Trianea* and *Raphanus* led VAKHMISTROV et al. to conclude that, whereas in the aquatic species the root hairs provided a preferential channel for K⁺ uptake, root hairs conferred no special advantages in the absorption of ions by the terrestrial plant.

Using 3,3'-diaminobenzidine, ZAAR (1979) studied the distribution of peroxidase activity in root hairs of *Lepidium* and found it to be high in the dictyosomes and associated vesicles, in ribosomes on E.R. cisternae and in the cell wall. It was proposed that the peroxidase in the root hairs is synthesised in the E.R. and dictyosome cisternae, packaged into vesicles and transported to the tip region of the hairs. Peroxidase activity seemed to be stimulated by stress incubation in distilled water and was 20 times higher in the root hairs than in cells of the root body.

b) Microbial and Other Associations with Root Hairs

Numerous recent papers have concerned themselves with structural changes related to the penetration of root cells by fungi or during the formation of mycorrhizal associations with roots. AIST and ISRAEL (1977) reported the formation of papillae on root hair cell walls during host cell penetration by the fungus *Olpidium brassicae*. Most papillae were initiated after the penetration tubes had appeared from the zoospore cysts and were attached to the tubes, but some were produced before tube development and were attached to the host walls. Although "tube" and "wall" papillae were initiated at about the same absolute time after inoculation, cysts which induced wall papillae were significantly later than other cysts in producing tubes. Failure of some tubes to penetrate was clearly unrelated to papillae formation. The penetration efficiency of cysts that induced wall papillae was merely half that of cysts that induced only tube papillae. AIST (1977) also found that mechanical wounding of root hairs of *Brassica oleracea* prior to incubation with zoospores of a compatible fungus produced localized wall appositions resembling those commonly induced by fungal attack. These induced appositions were effective in preventing fungal penetration at wound sites.

TURGEON and BAUER (1982) followed the early events during infection of *Glycine* and *Rhizobium*. They found that bacteria became attached to

4 Morphology

epidermal cells and root hairs within minutes of inoculation and marked root hair curling occurred within 12 h. Light microscopy revealed infection threads within 24 h in short, tightly curled root hairs which had not emerged at the time of inoculation. Infection threads, apparently originated in pockets, formed by contact of the cell wall of the curled root hair with itself. By 48 h, the infection threads had progressed to the base of the root hair but had not penetrated into the cortex. Increase in cortical cell cytoplasm and mitotic activity occurred in advance of thread penetration. A nodule meristem developed in the outer cortex next to the infected root hair by 4 days and was accompanied by cell division across the cortex.

The pattern of calcium localization in clover root hair cells associated with the infection process was studied by SETHI and REPORTER (1981) using the Ca^{2+} -binding antibiotic, chlorotetracycline. Some hairs from the immature zone showed increased Ca fluorescence distributed through most of the wall and these cells had "notched" side walls typical of cells infected with bacteria. Maturing roots hairs, with growing infection threads, similarly showed increased fluorescence especially around the site of origin of the infection thread and at the tip of the root hair.

HIGASHI and ABE (1980) used scanning electron microscopy to study *Rhizobium trifolii* infection sites on root hairs of *Trifolium repens*. Three morphological types of root hair retaining infection threads were recognized. The bacteria were strongly attached between the surfaces of two cell walls in one of the following ways: between surfaces of a root hair curled back on itself; between a protruberance from a root hair and its cell surface; or between two root hair tips clinging together. The structural basis for infection of root hairs of *Trifolium* by *Rhizobium* was investigated by CALLAHAM and TORREY (1981). Most infected root hairs had in common an enclosed region at the site of thread origin formed by specialized root hair growth or contacts with, in every case studied, a degradation of the root hair wall at the site of thread origin within the enclosure. The thread wall is a new layer formed by the apposition of material by the host cytoplasm near the penetrated wall and surrounding the break as encapsulation of the invading rhizobia. Rhizobial enzymes probably provide for degradative penetration of the root hair cell wall. Localized concentrated activity of hydrolytic enzymes as well as protection from cell lysis is probably favoured by physical constraints provided by the deformed root hair enclosures.

BHUVANESWARI et al. (1981) determined that the roots of four different leguminous plants were only transiently susceptible to nodulation by *Rhizobium*. Initially susceptible regions of host roots became progressively less susceptible if inoculation was delayed by a few hours. Apparently, a fast-acting regulatory mechanism prevents overnodulation. Nodulation in white clover may occur in two distinct phases: in addition to the transient susceptibility of pre-emergent and developing root hair cells, there appeared also to be an induced susceptibility of mature clover root cells brought about by a substance exuded from the bacterial cells.

NEWCOMB et al. (1978) made a detailed study of the structure and host-actinomycete interactions in developing root nodules of *Comptonia*. They found that the fungus enters the host via a root hair infection and then the hyphae perforate the root cortical cells by a local degradation of host cell walls and penetration of the host cytoplasm. WERKER and KISLEV (1978) demonstrated small drops of mucilaginous material near the tips of root hairs of several *Sorghum* species. Electron microscopy demonstrated that the secretion was made up from two dis-