
Contents

Organisms: Diatoms

Living Inside a Glass Box – Silica in Diatoms

F. Brümmer

1	Introduction	3
2	Silica in Protozoa, Sponges and Higher Plants	4
2.1	Phaeodaria	4
2.2	Choanoflagellates	4
2.3	Silicoflagellates	4
2.4	Sponges	5
2.5	Plants	5
3	Living in a Glass Box – the Diatoms	5
4	Biosilicification in Diatoms	7
5	Conclusion	8
	References	9

Components and Control of Silicification in Diatoms

Mark Hildebrand and Richard Wetherbee

1	Introduction	11
2	Features of Diatom Cell Walls and Terminology	12
3	Transport of Silicic Acid into the Diatom Cell	13
4	Intracellular Silicic Acid Transport	19
5	Micromorphogenesis vs. Macromorphogenesis	20
5.1	Micromorphogenesis – the Nanostructure of Diatom Biosilica	20
5.2	Control of Micromorphogenesis	34
6	Macromorphogenesis – the Formation of Large-Scale Silicified Structures in the Diatom Cell Wall	35
7	The Silica Deposition Vesicle – the “Black Box” in the Process of Silicification	47
8	Conclusions and Future Prospects	49
	References	51

The Phylogeny of the Diatoms

W.H.C.F. Kooistra, M. De Stefano, D.G. Mann, and L.K. Medlin

1	Introduction	59
2	Approaches to Reconstruct Phylogenies	60
3	The Diatom Silica Frustule	63
3.1	Morphology of the Silica Frustule	63
3.2	Taxonomy Based on Characteristics of the Silica Frustule	67
3.3	The Phylogeny Inferred from Nuclear SSU rDNA Sequences	69
3.4	Phylogenetic Relevance of Taxonomy and Frustule Characters	69
3.4.1	The Radial Centrics	72
3.4.2	The Bipolar Centrics	72
3.4.3	The Bipolar Centric Toxarium	74
3.4.4	The Araphid Pennates	76
3.4.5	The Position of Pseudohimantidium	77
3.4.6	The Raphid Pennates	77
4	Phylogenetic Signal in Diatom Chloroplast Structure	78
5	Phylogenetic Signal in the Life Cycle and Auxospore Ontogeny	80
5.1	Gamete Formation	80
5.2	Auxospore Development	82
6	The Phylogenetic Position of the Diatoms Within Heterokonta	83
6.1	The Ancestry of the Diatoms	83
6.2	Origin of Pigmented Heterokontophyta and the End Permian Mass Extinction	84
6.3	Origin of the Silica Cell Wall Within Heterokonta	85
7	Historical Ecology	86
8	Palaeontology and Phylogeny	89
9	Conclusions	92
	References	92

Silicon – a Central Metabolite for Diatom Growth and Morphogenesis

V. Martin-Jézéquel and P.J. Lopez

1	Introduction	99
2	Silicon Uptake and Transport: Regulation and Influencing Factors	99
2.1	Uptake, Transport and Soluble Pools	99
2.2	Energy Requirement	105
2.3	Factors Affecting the Uptake and Transport Processes	105
3	Link Between Silicon Metabolism, Growth and Cell Division	106

3.1	Coupling Between Silicon Metabolism and Cell Growth	106
3.2	Cell-Cycle Regulation	107
4	Diatom Morphogenesis	109
4.1	Overview of the Morphogenesis Process	109
4.2	Differentiation Programs Involving Silicon Morphogenesis	111
5	Morphological Plasticity and Variation	112
5.1	Size Reduction and Polymorphism	112
5.2	Impact of Growth Conditions and Environment	115
5.2.1	Light, Major Nutrients and Temperature	115
5.2.2	Salinity and Osmotic Stress	116
5.2.3	Trace Elements and Pollutants	117
6	Regulatory Mechanisms in Silicon Metabolism and Morphogenesis	119
	References	120

Organisms: Higher Plants

Functions of Silicon in Higher Plants

J.F. Ma

1	Introduction	127
2	Beneficial Effects of Silicon in Different Plant Species	128
2.1	Si-Accumulating Plants Versus Si Nonaccumulating Plants	128
2.2	Accumulation Process of Si in Si-Accumulating Plants	128
2.3	Effect of Si on the Growth of Si-Accumulating Plants	130
2.4	Effect of Si on the Growth of Si Nonaccumulating Plants	133
3	Functions of Si in Higher Plants	134
3.1	Stimulation of Photosynthesis	134
3.2	Alleviation of Physical Stress	135
3.2.1	Radiation Damage	135
3.2.2	Water Stress	135
3.2.3	Climatic Stress	137
3.3	Improvement of Resistance to Chemical Stress	138
3.3.1	Nutrient Imbalance Stress	138
3.3.1.1	Phosphorus Deficiency and Excess	138
3.3.1.2	N Excess	139
3.3.2	Metal Toxicity Stress	140
3.3.2.1	Mn and Fe Toxicity	140
3.3.2.2	Na Excess	141
3.3.2.3	Al Toxicity	141
3.4	Increase in Resistance to Abiotic Stress	141
3.4.1	Disease	141
3.4.2	Pests	145
4	Conclusion	145
	References	145

Silicon in Plants

D. Neumann

1	Introduction	149
2	Silicon in Monocots	149
2.1	SiO ₂ Deposits in Monocots	150
2.2	Silicic Acid in Monocots	150
3	Si in Dicots	154
4	Si in Cell Walls	156
5	Formation of SiO ₂ Deposits in Plants	157
6	Uptake and Long-Distance Transport	158
	References	158

Organisms: Sponges

Silica Deposition in Demosponges

M.J. Uriz, X. Turon, and M.A. Becerro

1	Introduction	163
2	The Cells Involved	170
3	The Axial Filament	172
4	Extracellular Versus Intracellular Silica Deposition: the Role of Membranes	178
5	The Process of Silica Polymerization	180
6	Environmental Factors Modulating Silica Deposition	184
7	The Future	188
	References	189

Molecular Mechanism of Spicule Formation in the Demosponge

Suberites domuncula: Silicatein – Collagen – Myotrophin

W.E.G. Müller, A. Krasko, G. Le Pennec, R. Steffen, M. Wiens,

M.S.A. Ammar, I.M. Müller, and H.C. Schröder

1	Introduction	195
2	Sponges	195
3	Spiculogenesis	197
3.1	The Model Test System: Primmorphs	197
3.2	Effect of Silicon on the Spicule Formation	200
3.3	Silicon-Responsive Genes	200
3.3.1	Silicatein	200
3.3.2	Collagen	201
3.3.3	Myotrophin	203
3.4	Effect of Silicon on Silicon-Responsive Genes	205
3.5	Inhibition of Biosilica Formation by Germanium	206
3.6	Proposed Pathway for Spicule Formation	207

4	Expression of Silicatein in Primmorphs and in Sponge Tissue	208
5	Biosilica Formation	210
5.1	Silicatein cDNA Expression	210
5.2	Silicatein Enzyme Assay	211
6	Effect of Iron	213
6.1	Effect of Iron on the Expression of Ferritin, Septin and Scavenger Receptor in Primmorphs	214
7	Conclusion	214
	References	217

Biotechnology

Biotechnological Advances in Biosilicification

J.L. Sumerel and D.E. Morse

1	Introduction	225
2	Silicon Transport in Diatoms	227
3	Proteins Closely Associated with the Silica Wall of Diatoms	230
4	Polycationic Peptides and Polyamines Accelerate Silica Condensation	231
5	Employing Silica-Condensing Peptides to Fabricate Nanostructured Devices	234
6	Polycondensation-Catalyzing, Structure-Directing Catalytic Proteins from Sponge Biosilica	236
7	Structure-Directing Polycondensation-Catalyzing Diblock Copolypeptides	239
8	Gene Expression During Sponge Development	240
9	The Biological Precursor for Silica Synthesis	241
10	Recognition of Inorganic Compounds Using Phage Display	241
11	Future Prospects	244
	References	245

Silicase, an Enzyme Which Degrades Biogenous Amorphous Silica: Contribution to the Metabolism of Silica Deposition in the Demosponge *Suberites domuncula*

H.C. Schröder, A. Krasko, G. Le Pennec, T. Adell, M. Wiens, H. Hassanein, I.M. Müller, and W.E.G. Müller

1	Introduction	249
2	Siliceous Spicule Turnover	250
3	Screening for Silica Degrading Enzymes	251
3.1	The Model Test System: Primmorphs	251

3.2	“Differential Display” of Transcripts	252
3.3	Cloning of the Gene Encoding the Silicase	253
3.3.1	Silicase	254
3.3.2	Phylogenetic Analysis of Silicase	255
4	Cloning of a Marker Gene of the Intermediary Metabolism	255
5	Preparation of Recombinant Silicase	258
6	Enzymatic Activities of Recombinant Silicase	258
6.1	Carbonic Anhydrase Activity	259
6.2	Silicase Activity	260
7	Expression of Silicase in Response to Silicon	261
8	Proposed Mechanism of Action of Silicase	262
9	Conclusion	265
	References	266

Studies of Biosilicas; Structural Aspects, Chemical Principles, Model Studies and the Future

C.C. Perry, D. Belton, and K. Shafran

1	Terminology	269
2	Introduction	269
3	Structural Chemistry of Biosilicas	271
4	Organic Matrix-Controlled Silica Production in Biological Organisms	274
5	The Chemistry of Silica Formation	276
5.1	Silica Chemistry in Aqueous Solution	276
5.1.1	Effects of pH and M^+ Ion Identity on Speciation in Aqueous Solution	280
5.2	Silica Chemistry in Non-Aqueous Solution	285
6	Solution Additives and Model Precipitation Reactions	286
6.1	Rationale for Use of Model Precipitation Reactions; Experimental Approaches	287
6.2	Studies of the Effect of Biosilica Extracts on the In Vitro Formation of Silica	288
6.3	Biomimetic Studies of Silica Precipitation	289
7	Other Areas of Interest	290
7.1	Transport	290
7.2	The Significance of Hypervalency in Biological Silicon Chemistry	291
8	Future Directions	293
8.1	Molecular Engineering in Diatoms	293
8.2	Isolation and Identification: Labelling	293
8.3	Theoretical Studies	294
9	Conclusions	295
	References	296

Silicon Biomineralisation: Towards Mimicking Biogenic Silica Formation in Diatoms

E.G. Vrieling, S. Hazelaar, W.W.C. Gieskes, Q. Sun, T.P.M. Beelen,
and R.A. van Santen

1	Introduction	301
2	Biochemical and Physico-Chemical Characteristics of Diatomaceous Silica	303
2.1	Organic Composition	303
2.2	Chemical Aspects	304
2.2.1	Principles of Silica Synthesis	304
2.2.2	Silica Synthesis in Diatoms	307
2.3	Nanoscale Structure	310
2.3.1	Specific Surface Area	310
2.3.2	Coordination of Molecules of Biogenic Silica	311
2.3.3	X-Ray Diffraction and Wide-Angle X-Ray Scattering	313
2.3.4	Small-Angle X-Ray Scattering	313
3	In Situ Silica Synthesis	321
3.1	The Application of Templates	321
3.2	Synthesis of PEG-Templated Silicas	322
4	A New Concept: Mesophases in Structure-Directing Processes in Diatom Silica Biomineralization	326
5	Conclusions and Future Perspectives	329
	References	330
	Subject Index	335

Silicon Biomineralization

Biology — Biochemistry — Molecular Biology —
Biotechnology

Müller, W.E.G. (Ed.)

2003, XIII, 340 p., Hardcover

ISBN: 978-3-540-00537-7