

# Current Research in Photosynthesis

Volume IV

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Stockholm, Sweden, August 6–11, 1989*

*edited by*

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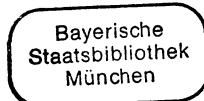
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## GENERAL CONTENTS

### Volume I

1. Reaction Centers From Purple Bacteria	1
2. Photosystem II	209
3. O <sub>2</sub> Evolution	675

### Volume II

4. Prokaryotic Antennae Systems	1
5. Eukaryotic Antennae Systems	209
6. Photoinhibition	349
7. Photosystem I	523
8. Structure, Function and Dynamics of the Thylakoid Membrane	715

### Volume III

9. H <sup>+</sup> ATPases	1
10. Cytochrome B/C <sub>1</sub> and B/F Complexes	221
11. Rubisco	323
12. Structure, Function and Regulation of Photosynthetic Genes	423
13. Biosynthesis and Assembly of the Photosynthetic Apparatus	653
14. Chloroplast Differentiation	827

### Volume IV

15. Respiration and Photosynthesis	1
16. Regulation of Chloroplast Metabolism	111
17. Adaptation Mechanisms	291
18. CO <sub>2</sub> Concentrating Mechanisms	433
19. Stress and Photosynthesis	549
20. Photosynthesis in Nature	821



## CONTENTS TO VOLUME IV

General Contents	V
Contents Volume IV	VII
Preface	XXI
Acknowledgements	XXIII
Organizing Committees	XXV
Opening Speech	XXVII
15. Respiration and Photosynthesis	
Transfer of Redox Equivalents Between Subcellular Compartments of a Leaf Cell H.W. Heldt, D. Heineke, R. Heupel, S. Krömer, B. Riens	1
Photorespiratory Dependent Leaf Mitochondrial ATP Production P. Gardeström, B. Wigge	9
Photorespiratory Metabolism and Pigment Changes in Photorespiration Mutants P.J. Lea, R.D. Blackwell, K.J. Lewis, A.J. Young, G. Britton	15
The pH Stat of Chloroplasts in Relation to Ribulose Bisphosphate Carboxylase Activity and Inorganic Nitrogen and Sulphate Assimilation I.R. Kennedy	23
The Light Response of CO <sub>2</sub> Gas Exchange and Internal CO <sub>2</sub> Concentration Separated for the Upper and Lower Side of a Maize Leaf W. Postl, H.R. Bolhar-Nordenkampf	31
Using Whole Plant Net CO <sub>2</sub> Exchange Data for Predicting Productivity of Greenhouse Roses J. Jiao, M.J. Tsujita, B. Grodzinski	35
Photosynthesis Dark Respiration and Plant Production in <i>Nicotiana tabacum</i> Genotypes Derived from Haploids Selected by Low CO <sub>2</sub> Survival E. Delgado, J. Azcon-Bieto, H. Medrano	39
ATP Deprivation Induces State I to State II Transition in the Dark in <i>Chlamydomonas reinhardtii</i> P. Gans, L. Bulte, F. Rebeille, F.-A. Wollman	43
Effect of the Salinity on the ATPase Activity (CF1, F1) Electron Transport in Photosystems I, II and Respiratory Chain in <i>Medicago sativa</i> and <i>Amaranthus hypochondriacus</i> M.S. González, M.J. Vázquez, Z.R. Quintanar, G.R. Velasco	47
Interaction of the Photosynthetic and Respiratory Electron Transport Chains of <i>Rhodobacter sphaeroides</i> S. Brown, J.P. Armitage	51

## VIII

The Effect of Low Intensity Blue Light on the Rates of Respiration and Photosynthesis, Composition and Growth of <i>Lemna gibba</i> J. Gale, G. Granot, M. Zeroni, J. Reubeni	55
Glycine Oxidation in Green and Etiolated Tissue P. Gardeström, D. Henricson, B. Wigge	59
Upshift of Light Intensity on Synechocystis 6714 Causes Increases in Glycogen, Respiration, and P700 Reduction J. Myers	63
Does NADH Availability Limit Nitrate Reduction in Wheat Genotypes? M.Z. Abdin, P.A. Kumar, Y.P. Abrol	67
The Effect of H <sub>2</sub> O <sub>2</sub> on the Photosynthetic Biochemistry of <i>Pisum sativum</i> L. Ford, N.W. Pammenter, A.M. Amory, C.F. Cresswell	71
Use of Computer Simulation and Non-Linear Regression in Photosynthetic Studies A.M. Amory, N.W. Pammenter, C.F. Cresswell	75
Photosynthesis, Photorespiration and Partitioning in Leaflets, Stipules and Tendrils of <i>Pisum sativum</i> R. Côté, B. Grodzinski	79
Effects of Glucose Feeding on Photoautotrophic Cell Suspension of <i>Dianthus caryophyllus</i> M.H. Avelange, F. Sarrey, F. Rebeille	83
Affinity Labeling of Phosphoribulokinase by Adenosine Polyphosphopyridoxals H.M. Mizjorko, C.A. Brodt	87
Catalase in an Aerobic Photosynthetic Bacterium, <i>Erythrobacter</i> sp. OCH 114 M. Morita, K.-I. Takamiya	91
Immunocytochemical Localization of the Electron Carrier Proteins Ferredoxin-NADP <sup>+</sup> Oxidoreductase and Cytochrome c 553 in the N <sub>2</sub> -Fixing Cyanobacterium <i>Anabaena variabilis</i> A. Serrano, P. Gimenez, S. Scherer, P. Böger	95
A Soluble Polysaccharide Fraction from Higher Plants: A Possible Physiological Substrate of the Cytosolic Phosphorylase Isozyme Y. Yang, B. Greve, M. Steup, E.W. Weiler	99
The Effect of Photosynthesis on Different Steps of Dark Respiration N. Mamushina, H. Zubkova, L. Filippova	103
Photosynthesis as a Thermal Process G.G. Komissarov	107
16. Regulation of Chloroplast Metabolism	
Regulation of Light Harvesting by Metabolic Events P. Horton	111
Regulation of Ribulose Bisphosphate Carboxylase Activity by Rubisco Activase: Aspects of the Mechanism A.R. Portis, Jr., S.P. Robinson, R. McC. Lilley	119
Redox-Regulation of Chloroplast Enzymes: Mechanism and Physiological Significance R. Scheibe	127
Light/Dark-Regulation of C <sub>4</sub> -Photosynthesis Enzymes by Reversible Phosphorylation R. Chollet, R.J.A. Budde, J.-A. Jiao, C.A. Roeske	135

Purification and Characterization of Phosphoribulokinase from N <sub>2</sub> Fixing Cyanobacterium <i>Nostoc muscorum</i>	143
D.V. Amla	
Molecular Models of 3-Dimensional Structures of Chloroplast and Cytoplasmic Phosphoglycerate Kinase from Wheat	147
E.M. McMorrow, B.J. Sutton, J.W. Bradbeer	
The Regulation of Synthesis of Chloroplastic and Cytosolic Isoenzymes of Phosphoglycerate Kinase in Barley	151
N. Shah, J.W. Bradbeer	
A Comparison of the Regulation of Yeast Phosphoglycerate Kinase with the Isoenzymes of Barley Chloroplast and Cytosol	155
E.M. McMorrow, J.W. Bradbeer, P.O. Montiel-Canobra, M. Larsson-Raźnikiewicz	
Relationship Between the Primary Structure of Ferredoxin and Thioredoxin and Their Reactivity	159
J.P. Jacquot, F. de Lamotte, M. Miginiac-Maslow, R. Peyronnet, J.B. Peyre, E. Wollman, P. Decottignies	
<i>In Vivo</i> Synthesis and Immunological Relationship of Thioredoxin f from Pea and Spinach	163
A. Chueca, M. Sahrawy, J.L. Carrasco, J.L. Ramos, J.J. Lázaro, R. Hermoso, J. López Gorgé	
Primary Structures of Regulatory Proteins of the Ferredoxin-Thioredoxin System of Spinach Chloroplasts	167
R. Schürmann, L. Gardet-Salvi, M. Kamo, K. Yano, A. Tsugita	
Regulation of Photosynthesis: Photosynthetic Control and Thioredoxin-Dependent Enzyme Regulation	171
D. Lechtenberg, B. Voss, E. Weis	
Function of Two Dissimilar Thioredoxins in the Cyanobacterium, <i>Anabaena</i> sp. 7120	175
F.K. Gleason	
Effect of Heterotrophic Growth on the Thioredoxins of Wild Type and y-1 <i>Chlamydomonas reinhardtii</i>	179
H.C. Huppe, B.B. Buchanan, J.-P. Jacquot	
Regulation of Pyruvate-Orthophosphate Dikinase from Maize Leaves. Magnesium-Dependent Dimer-Tetramer Interconversion	183
H. Nakamoto	
Separation and Characterization of Fructose-1,6-Bisphosphatases and Sedoheptulose-1,7-Bisphosphatases from Leaves of <i>Pisum sativum</i> L.	187
D. Nothnagel, J. Hoffstäd, E. Latzko	
Control of Stromal Fructose 1,6 Bisphosphatase and Sedoheptulose 1,7 Bisphosphatase by Metabolite Levels	191
D. Schimkat, D. Heineke, H.W. Heldt	
Interaction of Chloroplast Fructose-1,6-Bisphosphatase with Micelles of Triton X-114	195
G. Prat-Gay, R. Rodriguez-Suarez, R.A. Wolosiuk	
The <i>in vivo</i> Functioning Forms of Ribulose 1,5-Bisphosphate Carboxylase/Oxygenase in Plants	199
A. Yokota, T. Taira, H. Usuda, S. Kitaoka	
Structural Analysis of the Triose Phosphate-3-Phosphoglycerate-Phosphate Translocator from Spinach Chloroplasts	203
U.I. Flügge, K. Fischer, A. Gross	

**X**

Binding of the Lipophilic Tertiary Amine and 'Selective' Uncoupler Dibucaine to Thylakoid Membranes G. Günther, H. Laasch	207
Localized Proton Domains in pH-Dependent Control of Photosynthetic Electron Transport under the Influence of Lipophilic Tertiary Amines A. Janowitz, G. Günther, H. Laasch	211
Oscillations of Photosynthesis in Intact Isolated Pea Chloroplasts in the Presence of DCMU and Antimycin A S. Veljović, Z.G. Cerović, M. Plesničar	215
Photosynthetic Metabolism in Barley Leaves Infected with Powdery Mildew J. Scholes, P. Lee, P. Horton, D. Lewis	219
The Relationship Between the Development of Haustoria of <i>Erysiphe graminis</i> and the Energy Status of Leaves D.P. Wright, J.D. Scholes, P. Horton, B.C. Baldwin, M.C. Shephard	223
Synthesis of Alanine from 3-Phosphoglycerate by Intact Bundle Sheath Cells of Zea Mays E.M. Valle, H.W. Heldt	227
The Principal Scheme of Photosynthetic Carbon Conversion in Cells of Isoprenereleasing Plants G.A. Sanadze	231
The Enhancement Effect of Isoprene Evolution by Poplar Leaves D.I. Baazov, G.A. Sanadze	239
Regulation of NADP-Malate Dehydrogenase Light-Activation by the Reducing Power. I. Functional Studies M. Miginiac-Maslow, P. Decottignies, J.-P. Jacquot, P. Gadal	243
Regulation of NADP-Malate Dehydrogenase Light-Activation by the Reducing Power. II. Structural Studies P. Decottignies, J.-M. Schmittner, M. Miginiac-Maslow, P. Le Maréchal, J.-P. Jacquot, P. Gadal	247
Light Activation of Membrane-Bound Fructose-1,6-Bisphosphatase from Pea Leaf Chloroplasts J.J. Lázaro, A.R. Andrés, A. Chueca, R. Hermoso, J. López Gorgé	251
How Can the C <sub>4</sub> Stromal System Sense Differences in Light Intensity to Adjust Its Activities to the Overall Flux? H. Usuda	255
The Relationship Between the Efficiencies of Photosystems I and II and the Control of Electron Transport J. Harbinson, B. Genty, C.H. Foyer, N.R. Baker	259
Differential Diurnal Carbon Exchange and Photoinhibition in a psbA Plastid Gene Chronomutant of <i>Brassica napus</i> J. Dekker, R. Burmester	263
Photosynthesis and Chlorophyll Fluorescence Quenching in Aging Leaves of Three Sunflower ( <i>Helianthus annuus</i> L.) Genotypes D. Saftić, M. Plesničar	267
Developmental Variation in Aspartate-Family Amino Acid Biosynthesis by Isolated Chloroplasts W.R. Mills, S.F. Capo, S.A. Bergh, C.B. Lassiter	271

Activities of Carbondioxide Fixing Enzymes in Maize Tissue Cultures in Comparison to Young Seedlings A. Kumar, S. Roy, K.-H. Neumann	275
Measurement of Photochemical and Non-Photochemical Quenching: Correction for Turn-over of PS2 During Steady-State Photosynthesis T. Markgraf, J. Berry	279
Regulation of CO <sub>2</sub> Assimilation During Photoinhibition M. Dujardyn, C.H. Foyer	283
Intermediates, Catalytic Components and Light and Dark Regulation of ALA and Chlorophyll Formation in the Green Alga <i>Scenedesmus</i> D. Dörnemann, V. Breu, K. Kotzabasis, P. Richter, H. Senger	287
<b>17. Adaptation Mechanisms</b>	
Adaptation of Photosystem Stoichiometry in Oxygen-Evolving Thylakoid Membranes A. Melis	291
Factors Determining Light Response Characteristics of Leaf Photosynthesis I. Terashima, A. Takenaka	299
Physiological Control of Primary Photochemical Energy Conversion in Higher Plants E. Weis, D. Lechtenberg, A. Krieger	307
Trans-Δ <sup>3</sup> -Hexadecenoic Acid, LHC II and Low Temperature Development in Herbaceous Plants N.P.A. Huner, M. Krol, S. Boese, V. Hurry, J.P. Williams, G. Oquist	313
Chromatic Adaptation in <i>Porphyridium cruentum</i> Expressed in the Distribution of Excitation Energy and in the Thylakoid High-Energy Fluorescence Quenching O. Canaani, S. Driesenaar, S. Malkin, E. Gantt	321
The Involvement of LHC 2 Phosphorylation in the Adaptation of Higher Plants to Changing Light Intensities and Some Results on the Regulation of LHC 2 Phosphorylation <i>in vivo</i> H. Dau, O. Canaani	325
Thylakoid Protein Phosphorylation in an Algae with Chlorophyll A/C/Fucoxanthin Light Harvesting Antenna P. Gibbs, J. Biggins	329
Characterisation and Purification of Polypeptides Undergoing Light-Dependent Phosphorylation in the Cyanobacterium <i>Synechococcus</i> 6301 M. Harrison, J.F. Allen	333
Functional Analysis of the Photosynthetic Apparatus in a Chlorophyll-Deficient Mutant of Cowpea D. Habash, B. Genty, N.R. Baker	337
Slow Fluorescence Transients in Photosynthetic Bacteria I. Šetlik, M. Waldburger-Schlapp, R. Bachofen	341
The Influence of Light Itensity on the Organization of the Photosynthetic Apparatus Rhodopseudomonas Palustris Strain AB Y.E. Erokhin, Z.K. Makhneva, I.R. Prokhorenko	345
Effects of Growth Irradiance on the Photosynthetic Apparatus of the Red Alga <i>Porphyridium cruentum</i> F.X. Cunningham, Jr., R.J. Dennenberg, L. Mustardy, P.A. Jursinic, E. Gantt	349

## XII

Red Light Enhances Q <sub>A</sub> Relative to P <sub>700</sub> and Phycobilisomes in the Red Alga <i>Porphyridium cruentum</i>	353
F.X. Cunningham, Jr., R.J. Dennenberg, L. Mustardy, P.A. Jursinic, E. Gantt	
Regulation of LHC II mRNA Levels During Photoadaptation in <i>Dunaliella tertiolecta</i> (Chlorophyceae)	357
J. LaRoche, A. Mortain-Bertrand, J. Bennett, P.G. Falkowski	
Fluorescence Responses on Step Changes in Irradiance by Plants from Different Light Habitats	361
G. Johnson, P. Horton, J. Scholes, P. Grime	
The Relationship Between the Relative Quantum Efficiencies of Photosystems in Leaves. Efficiency of PS2 in Relation to Non-Photochemical Fluorescence Quenching	365
B. Genty, J. Harbinson, J.M. Briantais, N.R. Baker	
Adaptation of the Light Harvesting Apparatus to Shade in <i>Silene dioica</i> (L.): Relationship Between PSI and PSII Efficiencies	369
M. McKiernan, B. Genty, N.R. Baker	
Different Amino Acid Exchanges in the D1 Protein Cause Different Degrees of Shade Type Appearance in Herbicide Tolerant <i>Anacystis</i>	373
F. Koenig	
Characterization of the Light Dependent Regulation of the Apparent Quantum Yield of PSI	377
A.M. Rehm, A. Ried	
Alteration in Thylakoid Composition and Structure of <i>Brassica rapa</i> Ssp. <i>Oleifera</i> During Ageing in High and Low Light	381
A. Nurmi	
Changes in Thylakoid Surface Area When Shade Acclimated <i>Helianthus annuus</i> L. Chloroplasts Are Exposed to High P.F.D.	385
W.R. Fagerberg	
Effect of Cold-Hardening on the Quantum Yield of Spinach Leaves	389
K.J. van Wijk, P.R. van Hasselt	
Environmental and Hormonal Dependence of Induction of Crassulacean Acid Metabolism in <i>Mesembryanthemum crystallinum</i>	393
G. Edwards, S.-H. Cheng, C. Chu, M. Ku	
Control of Oxidative Phosphorylation in the Adaptation of <i>Medicago sativa</i> , <i>Phaseolus aureus</i> and <i>Phaseolus vulgaris</i> to Salinity	397
M.S. González, Z.R. Quintanar, M.J. Vázquez, G.R. Velasco	
Salinity and the Regulation of Pyruvate Pi Dikinase	401
D. Moualem-Beno, A. Shomer-Ilan	
Nitrogen Deprivation and the Photosynthetic Apparatus of the Green Alga <i>Chlorella fusca</i>	405
M.H. Rieß, I. Damm, L.H. Grimme	
Gas Exchange, Chlorophyll a Fluorescence, and Metabolite Levels in Leaves of <i>Trifolium Subterraneum</i> During Long-Term Exposure to Elevated CO <sub>2</sub>	409
T. Betsche, F. Morin, F. Cote, F. Gaugain, M. Andre	
Chlorophyllous <i>Calli</i> from <i>Psoralea bituminosa</i> L. – Adaptation to Photomixotrophism	413
J. Diamond, A. Casimiro, M.S. Pais	
Photosynthesis in Flowers of Petunia Hybrida: Low Co <sub>2</sub> Flow and Coordinated Reduction Between Photosynthetic Systems	417
D. Weiss, A. Shomer-Ilan, A.H. Halevy	

The Reversible Photochemistry of Phycoerythrocyanin S. Siebzehnrübl, G. Lipp, R. Fischer, H. Scheer	421
Quantitative Analysis of the Chlorophyll Fluorescence Induction Curve: Facts and Artefacts S. Mauro, R. Lannoye	425
Physiologically Active Products of Chloroplast Components Degradation I.A. Tarchevsky, A.N. Grechkin, S.I. Pankratova, A.U. Yarin, J.E. Andrianova	429
<b>18. CO<sub>2</sub> Concentration Mechanisms</b>	
Photosynthetic Inorganic Carbon Transport and Accumulation in Macroalgae F. Brechinac	433
Photosynthetic Acclimation to Low Carbon Concentrations in <i>Chlamydomonas reinhardtii</i> G. Samuelsson, K. Palmqvist, Z. Ramazanov, L.-G. Sundblad	441
Proteins Synthesized During Induction of the CO <sub>2</sub> Concentrating Mechanism in <i>Chlamydomonas reinhardtii</i> J.V. Moroney	449
The Molecular Biology of Carbonic Anhydrase Expression in <i>Chlamydomonas reinhardtii</i> J.R. Coleman	455
Mutations in the 5' Flanking Region of <i>rbcL</i> Inhibit the Growth of <i>Synechococcus</i> PCC7942 in Air-Level of CO <sub>2</sub> and Alter the Carboxysome Structure D. Friedberg, A. Kaplan, R. Ariel, R. Schwarz, E. Sadovnick, M. Kessel, J. Seijffers	463
Identification of the Genomic Region Which Complements a Temperature-Sensitive High-CO <sub>2</sub> Requiring Mutant of the Cyanobacterium, <i>Synechococcus</i> PCC7942 E. Suzuki, H. Fukuzawa, T. Abe, S. Miyachi	467
Molecular Analysis of Mutants of <i>Synechocystis</i> PCC6803 Defective in Inorganic Carbon Transport T. Ogawa, J.G.K. Williams, T. Omata	471
Is Carbonic Anhydrase Required for Photosynthesis? C.A. Roeske, J.M. Widholm, W.L. Orgen	475
Carbonic Anhydrase Activity in Barley Leaves After Treatment with Abscisic Acid and Jasmonic Acid L.P. Popova, G.N. Lazova	479
Isolation of Carbonic Anhydrase from the Higher Plant <i>Pisum sativum</i> N. Majeu, J.R. Coleman	485
Membrane-Bound Carbonic Anhydrase Takes Part in CO <sub>2</sub> Concentration in Algae Cells N.A. Pronina, V.E. Semenenko	489
Chemical Cross-Linking of Periplasmic Carbonic Anhydrase from <i>Chlamydomonas reinhardtii</i> H.D. Husic	493
The Role of Carbonic Anhydrase in Regulating Photosynthetic CO <sub>2</sub> Fixation in Higher Plants G. Yuzhu, Z. Zhenlin, G. Minliang, W. Zhong	497
Expression of a Cyanobacterial Gene Regulated by CO <sub>2</sub> Concentration D. Chamot, J.R. Coleman	501
Adaptation of <i>Chlamydomonas reinhardtii</i> High CO <sub>2</sub> -Requiring Mutants to Limiting CO <sub>2</sub> M.H. Spalding, K. Suzuki, A.M. Geraghty	505

## XIV

A Phosphoglycolate Phosphatase Mutant of <i>Chlamydomonas reinhardtii</i> K. Suzuki, L.F. Marek, M.H. Spalding	509
Selective Inhibition of CO <sub>2</sub> Transport in a Cyanobacterium G.S. Espie, A.G. Miller, D.T. Canvin	513
CO <sub>2</sub> Storage and CO <sub>2</sub> Concentrating in Brown Seaweeds. I. Occurrence and Ultrastructure H. Ryberg, L. Axelsson, S. Carlberg, C. Larsson, J. Uusitalo	517
CO <sub>2</sub> Storage and CO <sub>2</sub> Concentrating in Brown Seaweeds. II. Function in Gas Phase J. Uusitalo, L. Axelsson, S. Carlberg, C. Larsson, H. Ryberg	521
CO <sub>2</sub> Storage and CO <sub>2</sub> Concentrating in Brown Seaweeds. III. A Tentative Working Model L. Axelsson, S. Carlberg, C. Larsson, H. Ryberg, J. Uusitalo	525
Inducible CO <sub>2</sub> Concentrating Mechanisms in Green Seaweeds. I. Taxinomical and Physiological Aspects S. Carlberg, L. Axelsson, C. Larsson, H. Ryberg, J. Uusitalo	529
Inducible CO <sub>2</sub> Concentrating Mechanisms in Green Seaweeds. II. Ecology and Field Observations C. Larsson, L. Axelsson, S. Carlberg, H. Ryberg, J. Uusitalo	533
Substrate Binding to NADP-Malic Enzyme from Maize Leaves as Determined by Intrinsic Fluorescence Quenching C.S. Andreo, F.E. Podesta, A.A. Iglesias	537
The CO <sub>2</sub> Concentrating Function of C <sub>4</sub> Photosynthesis R.T. Furbank, C.L.D. Jenkins, M.D. Hatch	541
Regulation of CO <sub>2</sub> Fixation in the CAM Plant <i>Kalanchoe pinnata</i> (L.) Pers. by Cellular Nitrate T. Balakumar, M. Sivaguru, P. Moorthy, M.R. James, P.R. Anburudurai	545
19. Stress and Photosynthesis	
Effects of Stress on Photosynthesis T.D. Sharkey, F. Loreto, T.L. Vassey	549
Nitrate Reduction in Leaves is Coupled to Net Photosynthesis W.M. Kaiser	557
Analysis of Chill-Induced Depressions of Photosynthesis in Maize N.R. Baker, G.Y. Nie, A. Ortiz-Lopez, D.R. Ort, S.P. Long	565
Spatial and Temporal Heterogeneities of Photosynthesis Detected Through Analysis of Chlorophyll-Fluorescence Images of Leaves K. Raschke, J. Patzke, P.F. Daley, J.A. Berry	573
Structure and Possible Function of Chloroplast Heat-Shock Proteins and the Effect of Cyclic Heat-Shock on Plant Morphogenesis and Circadian Rhythmicity G. Knack, B. Otto, P. Ottersbach, R. Alexander, Z. Liu, K. Kloppstech	579
Carotenoids and Oxidative Stress A.J. Young, G. Britton	587
Analysis of the Mechanisms of Ozone Damage to Photosynthesis <i>in vivo</i> P.K. Farage, S.P. Long, E. Lechner, N.R. Baker	591
The Effect of Ozone on Plant Pigments A. Price, A. Young, P. Beckett, G. Britton, P. Lea	595

Effects of SO <sub>2</sub> on Photosynthetic Carbon Metabolism in Leaves of Winter Barley ( <i>Hordeum vulgare</i> CV. IGRI)	599
P.O. Montiel-Canobra, J.W. Bradbeer, N.M. Darrall	
Influence of Photosynthetic Capacity, Irradiance and SO <sub>2</sub> Fumigation on Shoot Growth of Azalea ( <i>Rhododendron</i> ) Cultivars	603
D.J. Ballantyne	
Simultaneous Measurements of Chlorophyll Fluorescence and CO <sub>2</sub> -Gas Exchange on Spruce under Fumigation with Peroxides	607
S. Drenkard, J. Maguhn, A. Ziegler-Jöns, D. Knoppik	
The Effect of Prolonged Exposure to Air-Borne Pollutants on the Photosynthesis of Douglas Fir ( <i>Pseudotsuga menziesii</i> ) Studied with <i>in vivo</i> Chlorophyll Fluorescence	611
O. van Kooten, L.W.A. van Hove, W.J. Vredenberg	
Properties of Selenium-Induced Glutathione Peroxidase in Low-CO <sub>2</sub> -Grown <i>Chlamydomonas reinhardtii</i>	615
S. Shigeoka, T. Takeda, T. Hanaoka, A. Yokota, S. Kitaoka, Y. Iizuka	
Molecular Properties of Ascorbate Peroxidase from Tea Leaves	619
G.-X. Chen, K. Asada	
Recovery of Photosynthesis in Winter Stressed Scots Pine	623
C. Ottander, G. Öquist	
Chilling-Induced Alterations in the Photosynthetic Capacity of Chilling-Tolerant and Chilling-Sensitive Cultivars of Zea Mays	627
C.S. Ting, T.G. Owens, D.W. Wolfe	
Photoinhibition and Recovery in Isolated Mesophyll Cells of Hardened and Non-Hardened Rye	631
L. Lapointe, N. Huner	
Photoinhibition and Recovery of Photosynthesis in Antarctic Bryophytes under Field Conditions	635
A. Post, E. Adamson, H. Adamson	
Photosynthesis in <i>Grimmia antarctica</i> , An Endemic Antarctic Bryophyte, is Limited by Carbon Dioxide	639
E. Adamson, A. Post, H. Adamson	
Photosynthetic Characterization of Spinach Developed at Cold Hardening and Non Hardening Temperatures	643
S.R. Boese, N.P.A. Huner	
Frost Resistance of Wheat and CHL a <i>in vivo</i> Fluorescence Induction Kinetics	647
L. Shiqing, Y. Dianan, Z. Jide, L. Tongzhu, T. Chongqing, L. Shiqing, K. Tingyun	
Changes of Photosynthetic Membrane and Cell Resistance of a Leaf of Wheat Seedlings During Temperature Acclimation	651
A.A. Filimonov, A.A. Virolainen, E.G. Sherudilo, A.F. Titov	
Effect of Heat Stress on Intact Wheat Leaves and Its Recovery Studied by Fluorescence Induction Kinetics	655
R.K. Mishra, G.S. Singhal	
Synthesis of Sucrose and Fructans in Wheat Leaves: The Effects of Temperature	659
C. Paulino, M.C. Arrabaça	
The Effect of Temperature on Photosynthesis and Amounts and Transport of Assimilate in Sunflower and Rape	663
M.J. Paul, D.W. Lawlor	

## XVI

Effects of Low Temperature on Chlorophyll Protein Complexes and Regulation Capacity of Excitation Energy Distribution in Chloroplast Membrane of Cucumber C.H. Xu, F.H. Zhao, K.B. Wang, D.H. Yang, Y.L. Dai	667
Genetic Variation and Diversity of Low Temperature Induced Damages in Maize Seedlings as Assessed by Chlorophyll Fluorescence Induction Curves M.-F. Scharll, R. Lannoye, S. Mauro	671
The Effects of Low Temperature on Activities of Carbon Metabolism Enzymes in <i>Zea mays</i> L. Seedlings M.R. Hull, S.P. Long, C.R. Raines	675
Chill-Induced Modifications to the Relationship Between Thylakoid Protein Phosphorylation and Energy Distribution of Photosystem 2 in Maize J. Val, N.R. Baker	679
Chilling Stress and Active-Oxygen Enzymes in <i>Zea mays</i> and <i>Zea diploperennis</i> L.S. Jahnke, M.R. Hull, S.P. Long	683
Low Temperature Perturbation of Thylakoid Protein Metabolism During Maize Leaf Development G.Y. Nie, N.R. Baker	687
Perturbation of the Maize Light-Harvesting Apparatus by Chilling D.A. Campbell, D.B. Hayden, L.B. Johnson, N.R. Baker	691
Effects of Fire on Photosynthesis and Transpiration in a Mediterranean Ecosystem I. Fleck, F.J. Iñiguez, C. Diaz, M. Pascual	695
Protective Effect of Putrescine and Spermidine on the Thylakoid Membrane Activity After High Temperature Treatment I.T. Yordanov, V. Goltsev, L. Kruleva	699
Two Sites of Heat-Induced Damage to Photosystem II D.W. Becker, G. Bain, J. Norman, M. Moholt-Siebert	705
Light Regulation of the 22 kd Heat-Shock Protein in <i>Chlamydomonas reinhardtii</i> D. Ish-Shalom, A. Post, K. Kloppstech, I. Ohad	709
Responses of Some Photosynthetic Parameters in C <sub>3</sub> and C <sub>4</sub> Crop Plants under Water Deficit M. Castrillo, D. Fernández, A.M. Calcagno, I. Trujillo	713
A Gas Exchange Procedure to Evaluate Non Uniform Stomatal Closure Effects in Single Mesophyte Evergreen Leaves Under High VPD G. Bongi	717
Does Air Relative Humidity During Growth Condition Photosynthetic Characteristics of Coffee Leaf? M.A. Nunes, P.S. Rijo	721
The Effect of Drought on Chlorophyll Fluorescence in Two Maize Lines L. Jovanović, V. Janjić, S. Veljović	725
Drought Effect on Photosynthesis and Plant Production of Two Contrasting <i>Trifolium</i> Cultivars J. Vadell, C. Cabot, H. Medrano	729
Water Stress Effects on Canopy Photosynthesis, Temperature, Transpiration and Shedding of Leaves and Fruit in Cotton A. Ben-Porath, D.N. Baker, A. Marani	733

Water Use Efficiency in Field-Grown Maize: Effects of Soil Structure O. Béthenod, F. Tardieu	737
An Evaluation of the Effect of Salinity of Photosynthesis E. Brugnoli, M. Lauteri	741
Salinity Induced Changes in Leaf Expansion, Photosynthesis and K <sup>+</sup> Accumulation in Sunflower J.M. Cheeseman, S. Basu	745
Effect of Environmental Stress on Photosynthesis of Isolated Mesophyll Cells from Cowpea Leaves Z. Plaut, C.M. Grieve, E. Federman	749
Assimilatory Force in Illuminated Leaves Grown in Sun or Shade or Under Mineral Deficiency K. Siebke, K.-J. Dietz, U. Heber	753
Iron Deficiency-Induced Mechanisms of Dissipation of Excess Energy in Higher Plants A. Abadia, F. Morales, J. Abadia	757
Low-Iron Stress in the Cyanobacterium <i>Anabaena variabilis</i> B. Michelsen, M. Miller, R.P. Cox	761
Violaxanthin Cycle and Fluorescence in Iron-Deficient Maize Leaves J. Val, E. Monge	765
Acid Resistance and the CO <sub>2</sub> – Conductance of the Plasma Membrane of <i>Dunaliella Acidophila</i> C. Weiss, U. Weis, H. Kugel, H. Gimmier	769
The H <sup>+</sup> -Export Capacity of <i>Dunaliella acidophila</i> and the Permeability of the Plasma Membrane for H <sup>+</sup> and Weak Acids H. Gimmier, M. Bental, H. Degani, M. Avron, U. Pick	773
Variable Fluorescence for Monitoring Algal Activity in a High Rate Photosynthetic Pond B. El Hamouri, R. Moundib, R. Berrada	777
The Effects of Diclofop-Methyl and Methabenzthiazuron on Photosynthetic Parameters in <i>Vicia faba</i> D. Vidal, M.A. Miranda, F. Rodriguez, E. Simon	781
Influence of Environmental Stresses on the Photosynthetic Capacity of S-Triazine Susceptible and Resistant Biotype of <i>Solanum nigrum</i> A. Winterberg, P. Panneels, R. Lannoye	785
Inhibition of Photosynthesis in Barley ( <i>Hordeum vulgare</i> L.) Leaves by Phosphinothricin (Glufosinate). Short and Long-Term Effects M. Lacuesta, C. González-Murua, A. Muñoz-Rueda, M. Sivak	789
Effect of the Herbicide SAN 6706 on Pigment Composition in Barley: Measurements Using HPLC R. Juhler, R.P. Cox	793
Changes in Photosynthesis of Wheat Plants Infected by Stem Rust G. Schmittmann, B. Moerschbacher, H.J. Reisener	797
Drought Effect on the Structural and Functional Characteristics of Photosynthetic Apparatus I.A. Tarchevsky, Y.E. Andrianova, N.I. Safina, E.A. Philippova, D.I. Babuzhina	801
Isolation and Characterization of Two Isozymes of Superoxide Dismutase from Scots Pine G. Wingsle, P. Gardeström, J.-E. Häggren	805

## XVIII

An Assessment of Ethylene and Carbon Dioxide Exchange in Plants B. Grodzinski, L. Woodrow	809
Response of Aging Chloroplasts to UV Radiation B. Biswal, G. Kulandaivelu	813
Estimating SO <sub>2</sub> Stress by Chlorophyll Fluorescence Measurements with an Active System Used in the Remote Sensing Mode C. Kliffen	817
<b>20. Photosynthesis in Nature</b>	
Photosynthesis and Field Environmental Productivity Indices P.S. Nobel	821
Photosynthesis of Plants in Relation to Resource Availability in the Field E.-D. Schulze	827
Damage to Photosynthesis During Chilling and Freezing, and Its Significance to the Photosynthetic Productivity of Field Crops S.P. Long, P.K. Farage, Q. Groome, J.M.N. Macharia, N.R. Baker	835
Some Factors Limiting Photosynthesis in Nature Y.-K. Shen	843
Photosynthetic Capacity to Solve the Carbon Dioxide Problem S. Leu, A. Michaels	851
Water Use Efficiency in Potato: Model and Experimental Test of Crop Photosynthesis O. Bethenod, J.-P. Lhomme, N. Katerji	855
Photosynthetic Characteristics of the Mangrove, <i>Bruguiera parviflora</i> , (Roxb.) Wright & Am., Under Natural Conditions D.R. Carter, J.M. Cheeseman, B.F. Clough, C. Lovelock, R.G. Sim, J.E. Ong	859
Some Physiological Aspects of <i>Paspalum dilatatum</i> Grown Under Field Conditions J. Marques da Silve, A. Bernardes da Silva, D. Coelho Rebelo, M.C. Arrabaça	863
Immunogold Localization of Ribulose 1,5-Bisphosphate Carboxylase in Amphibious <i>Eleocharis</i> Species in Relation to C <sub>3</sub> and C <sub>4</sub> Photosynthesis O. Ueno, M. Samejima	867
Relationships Between Source Leaf Photosynthesis, Export and Grain Filling in Maize J.-L. Prioul, A. Reyss, N. Schwobel-Dugue, A. Lecharny	871
The Dependence of Some Photosynthetic Parameters on the Phosphorus Concentration in a Nutrition Solution and Wheat Genotype S. Zatezalo, Ž. Stanković, M.R. Sarić	875
Influence of Mineral Nutrition on the Content of Photosynthetic Pigments in Various Wheat Cultivars M.R. Sarić, Ž. Stanković, B. Krstić, S. Zatezalo	879
Dorsiventrality of the Photosynthetic-Light Response in Naturally Occurring C <sub>3</sub> Dicots T.A. Day, E.H. DeLucia, W.K. Smith	883
The Effect of Cultivar and Leaf Age on the Content of Photosynthetic Pigments in Wheat Ž. Stanković, M.R. Sarić, B. Krstić, S. Zatezalo	887
Effect on Net Carbon Assimilation and Allocation of Assimilates under Elevated CO <sub>2</sub> in Mungbean U.K. Sengupta, A. Sharma	891

$\delta^{13}\text{C}$ Analysis to Approach the Mechanism of Varietal Difference of Photosynthetic Rate in Rice Plants H. Sasaki, M. Samejima, R. Ishii	895
A New Open Gas-Flow System Configuration for Measurement of Photosynthetic $\text{CO}_2$ Response Curve L. Nátr, R. Hák, V. Kotvalt	899
Impairment of Chloroplast Development and Sink Strength by Blockade of Light in Chlороembryos of <i>Cyamopsis tetragonoloba</i> (L.) Taub P. Kaladharan, M. Vivekanandan	903
Estimation of the Light Limitation of Photosynthesis H.G. Jones, A. Massacci	907
The Efficiency of Utilization of Photosynthetically Active Radiation and Distribution of Assimilates in Sunflow ( <i>Helianthus annuus</i> L.) Z. Sakać, T. Čupina	911
The Relation of Chlorophyll Delayed Fluorescence of Plant with Photosynthesis: Light Dependence V. Morgan, N. Znak, S. Doldjikov	915
Intercepted Irradiance Limits Carbon Assimilation of a Coastal Dune Plant N.W. Pammenter, V.R. Smith	919
Phytoplankton Photosynthesis in the Atlantic Ocean as Measured from a Submersible Pump and Probe Fluorometer <i>in situ</i> P.G. Falkowski, Z. Kolber	923
Comparison of Growth of Micro-Algae <i>Nostoc Linckia</i> & <i>Chlorella</i> sp. in Dilute Culture N. Sen	927
Effects of Suboptimal Temperature and Light Conditions During Growth on Temperature Dependent Chlorophyll Fluorescence of Tomato L.H.J. Janssen, P.R. van Hasselt	931
Phototrophic Bacteria that form Heat Resistant Endospores J. Ormerod, T. Nesbakken, Y. Torgersen	935
Index of Names	939

## THE REVERSIBLE PHOTOCHEMISTRY OF PHYCOERYTHROCYANIN

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### 1. INTRODUCTION

Plant and algal biliproteins have two major functions: The phycobiliproteins are light-harvesting pigments for photosynthesis (1); the phytochromes are the photoreceptors of plant photomorphogenesis. Many cyanobacteria also show responses suggesting photoreversibly photochromic pigments as photoreceptors (see 2,3,4,5). The putative pigments have been termed adaptochromes and phycomorphochromes. Isolation attempts (review in 2) resulted in the spectral characterization of at least four different fractions termed phycochromes a-d; but in no case has there been conclusive evidence, that these are the putative photoreceptors.

The absorption spectra of all phycochromes suggest that they are biliproteins, too. These pigments may then combine both functions of light harvesting and photomorphogenesis induction in one molecule. Phycochrome b has indeed been shown to be most likely the  $\alpha$ -subunit of the antenna pigment phycoerythrocyanin (PEC) (6). PEC is present in several species of cyanobacteria (7). It carries an unusual phycobilin chromophore on its  $\alpha$ -subunit (Fig. 1) (8), which is responsible for its photochromic response. Here we want to give further (9) results on the photochemistry of PEC from two cyanobacteria, e.g. *Mastigocladus (M.) laminosus* and *Chroococcidiopsis (Ch.) spec.*. We have characterized the photochemistry of the pigment in different states of aggregation, and the mutual interdependence of its phototransformation and aggregation.

### 2. MATERIALS AND METHODS

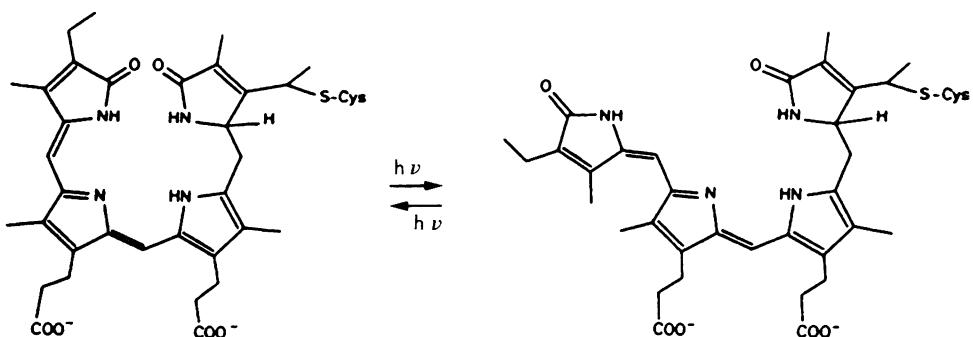
Phycoerythrocyanin (PEC) of *M. laminosus* and *Ch. spec.* were prepared by the method of Füglistaller et al. (10). The subunits of PEC were obtained by isoelectric focusing (11) under anaerobic conditions. Absorption and absorption difference spectra were measured in split beam mode with thermostated cell holders. Irradiation was done in the photometer (150 W, light guide and suitable interference filters). The aggregation state of PEC was studied by sucrose-density gradient centrifugation at 238,000 x g (12). In the reactions relating irradiation with aggregation, a PEC (*M. laminosus*) stock solution ( $A_{570} = 0.6 \text{ cm}^{-1}$ ) was irradiated alternately with green and orange light. Before the first and after each subsequent illumination an aliquot (0.2 ml) was applied to the sucrose gradient (5 ml, 7 to 17 % w/w).

### 3. RESULTS AND DISCUSSION

#### 3.1. Characterization of photochemistry

When PEC or its  $\alpha$ -subunit isolated from the blue-green algae *M. laminosus* or *Ch. spec.* were irradiated either with orange (600 nm; 575

nm for *Ch. spec.*- $\alpha$ -subunit) or green light (500 nm), a typical photochemistry was observed. Irradiation with orange light leads to an absorption difference spectrum with a maximum at 502-504 nm and a negative extremum at 565-570 nm. Illuminating the sample with green light reverts the spectrum fully to the original. The amplitudes of the difference spectra are strongly dependent on the state of the pigment (Table 1). It is maximum in the presence of 4 M urea, whereas it is lower in the fully denatured pigment (8 M urea) and very small in high aggregates and phycobilisomes. Upon addition of increasing amounts of urea, the difference extrema of the reversible reaction remain stationary up to denaturant concentrations of 4 M (Table 1). At the same time, the amplitudes increase. At higher urea concentrations, the amplitudes decrease again, and the extrema shift gradually to 510 and 600 nm. Reversible photochemistry is retained up to 8 M urea, when the polypeptide chains are fully unfolded. The photochemistry is very similar in PEC isolated from the two different organisms, e.g. *M. laminosus* and *Ch. spec.*. Reversible photochemistry is also retained in denatured PEC at low pH.



**Fig. 1:** Structures of phycoviolobilin chromophores in their 10Z,15Z (left) and 10Z,15E-configuration (right). Schematic, native chromophores have extended geometries.

The  $\beta$ -subunit of PEC shows no reversible photochemical effects. However the two phycocyanobilin chromophors of this subunit are very sensitive against irradiation, and bleach rapidly to colorless product(s) (viz. by 60 - 70 % within 12 min). This rapid bleaching contrasts with the relative stability of the phycocyanin  $\beta$ -subunit (11).

The reversible photochemistry of PEC and its  $\alpha$ -subunit is probably related to a Z=E isomerisation of the phycoviolobilin chromophore (Fig.1). Of the different chromophore types of phycobiliproteins, it is the only one which shows a reversible photochemistry in its native and denatured state. We suggest that isomerization takes place in the  $\alpha$ -subunit of PEC at the  $\Delta 15$ -double bond, similar to the phytochrome primary reaction.

### 3.2. Interrelations of photochemistry and aggregation

Aggregation not only strongly influences the photochemical activity of PEC (Table 1), but the inverse is also true, e.g. pre-irradiation

**Table 1** : Absorption difference extrema and amplitudes of different PEC samples or samples subjected to different pre-treatments.

Sample	C <sub>buffer</sub> [mM] <sup>a)</sup>	C <sub>urea</sub> [M] <sup>a)</sup>	pH	Difference extrema [nm] orange green	ΔΔA <sup>b)</sup> [%]
PEC	100	0	7.0	570 503	18
PEC	100	1	7.1	569 503	32
PEC	100	4	7.3	567 502	35
PEC	100	6	7.5	600 510	12
PEC	100	8	7.0	599 515	6
PEC	100	8	3.0	598 507	13
PEC-monomer	100	c)	7.0	565 504	36
α-Subunit	100	0	7.0	569 504	50

a) Buffer - potassium phosphate buffer.

b) Amplitude (Min-max) of difference spectra.

c) 1 M KSCN, no urea.

**Table 2** : Comparison of photochemistry of PEC between *Mastigocladus laminosus* and *Chroococcidiopsis* spec.

Pigment	<i>Mastigocladus laminosus</i>	<i>Chroococcidiopsis</i> spec.
<b>native Pigment<sup>a)</sup></b>		
λ <sub>max</sub>	573	574
ΔΔA <sub>max</sub>	(+) 503 / (-) 570 <sup>b)</sup>	(+) 507 / (-) 576 <sup>b)</sup>
ΔΔA [%]	18 %	26 %
<b>denatured Pigment<sup>c)</sup></b>		
λ <sub>max</sub>	603 / 661 <sup>e)</sup>	604 / 661 <sup>e)</sup>
ΔΔA <sub>max</sub>	(+) 507 / (-) 598 <sup>b)</sup>	(+) 506 / (-) 597 <sup>b)</sup>
ΔΔA [%]	13 %	10.4 %
<b>denatured Pigment<sup>d)</sup></b>		
λ <sub>max</sub>	587	597
ΔΔA <sub>max</sub>	(+) 515 / (-) 600 <sup>b)</sup>	(+) 507 / (-) 595 <sup>b)</sup>
ΔΔA [%]	6 %	2.4 %
<b>α-Subunit (native)<sup>a)</sup></b>		
λ <sub>max</sub>	562	561
ΔΔA <sub>max</sub>	(+) 504 / (-) 569 <sup>b)</sup>	(+) 501 / (-) 563 <sup>b)</sup>
ΔΔA [%]	50 %	15 %

a) Green irradiated form in 100 mM phosphate buffer, pH 7.

b) Difference extrema (orange irradiated vs. green irradiated sample),  
(+)-positive, (-)-negative.

c) Green irradiated form in 8 M urea, 100 mM phosphate buffer acidified with HCl to pH 2.

d) Green irradiated form in 8 M urea + 100 mM phosphate buffer, pH 7.4.

e) Double maximum in the acidified state.

with different light qualities influences the aggregation of PEC (9). A sample of PEC was irradiated alternately with orange and green light. Aliquots of the original sample were then analyzed for aggregate distribution by ultracentrifugation. In every case, the sample is a mixture of mono- and trimeric PEC, but the amount of higher aggregates is always increased after irradiation with green light, and decreased after irradiation with orange light. A reversible dissociation as response to different light qualities would principally offer indirect routes for signal transduction, since a direct effect of the phycobiliproteins may be questioned on the basis of the small size of the PEC molecule primarily(?) optimized for light-harvesting.

An indirect route could be based on e.g. photodynamic effects of free biliproteins (13) or the release of linker peptides (14-16).

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## Index of Names

- Aartsma, T.J., II.4.161, II.4.185  
 Aasa, R., I.3.777  
 Abad, M.S., II.5.231, III.13.731  
 Abadia, A., IV.19.757  
 Abadia, J., IV.19.757  
 Abdin, M.Z., IV.15.67  
 Abe, T., IV.18.467  
 Abramchik, L.M., III.13.819  
 Abresch, E., I.1.77,  
 Abrol, Y.P., I.3.941, III.12.597, IV.15.67  
 Abu-Much, E., III.9.193  
 Abuja, P.M., III.11.373  
 Adamson, E., IV.19.635, IV.19.639  
 Adamson, H., III.13.687, IV.19.635,  
     IV.19.639  
 Adir, N., II.6.409  
 Ajlani, G., I.2.543, II.6.427  
 Åkerlund, H.-E., I.3.897, I.3.901  
 Albertsson, P.-Å., II.5.301, II.8.831, II.8.835,  
     II.8.839, II.8.843, II.8.923,  
 Albrecht, A.C., II.5.289, II.5.293  
 Alexander, R., IV.19.579  
 Allakhverdiev, S.I., I.2.379,  
 Alldrick, S., III.13.671  
 Allen, J.F., II.4.81, II.8.915, II.8.919,  
     IV.17.333  
 Allen, J.P., I.1.61,  
 Allen, Jr., L.H., III.11.399  
 Allen, K.D., II.5.269, II.8.903  
 Allakhverdiev, S.I., I.2.247  
 Althoff, G., III.9.81, III.9.133  
 Amesz, J., II.4.25, II.4.145, II.4.161,  
     II.4.185, II.4.189  
 Amla, D.V., IV.16.143  
 Amory, A.M., II.6.443, IV.15.71, IV.15.75  
 Ampe, F., III.12.521  
 Anandan, S., II.5.285  
 Ananyev, G., I.2.247  
 Anburdurai, P.R., III.13.699, IV.18.545  
 Andersen, B., II.7.523, II.7.671, II.7.679,  
     III.12.613  
 Anderson, J.M., II.8.803, II.8.935  
 Andersson, B., I.2.299, II.5.253, II.5.265,  
     II.5.273, II.6.349, II.6.423, II.7.583,  
     II.8.763, II.8.799, III.9.201  
 Andersson, P.-O., II.4.11, II.4.117  
 Andre, M., II.6.511, IV.17.409  
 Andreasson, E., II.8.831, II.8.839, II.8.843,  
     II.8.923  
 Andréasson, L.-E., I.2.527, I.3.785,  
     III.10.319  
 Andreo, C.S., IV.18.537  
 Andrés, A.R., IV.16.251  
 Andrews, T.J., III.11.331  
 Andrianambinintsoa, S., I.2.463  
 Andrianova, J.E., IV.17.429, IV.19.801  
 Andriesse, X., III.12.533  
 Angerhofer, A., I.1.109, I.1.145  
 Apley, E., III.9.81  
 Apley, E.C., III.9.53, III.9.81, III.9.93  
 Arata, H., III.10.315  
 Argyroudi-Akoyunoglu, J.H., III.13.803  
 Ariel, R., IV.18.463  
 Armitage, J.P., IV.15.51  
 Aro, E.-M., II.6.439, II.6.459  
 Arrabaça, M.C., IV.19.659, IV.20.863  
 Asada, K., I.2.491, I.2.495, I.3.889,  
     IV.19.619  
 Astier, C., I.2.543  
 Aula Dei, E.E., II.8.907  
 Aumeier, W., I.1.133, I.1.153  
 Avelange, M.H., IV.15.83  
 Avital, S., III.9.45  
 Avron, M., IV.19.773  
 Axelsson, L., IV.18.517, IV.18.521,  
     IV.18.525, IV.18.529, IV.18.533  
 Azcon-Bieto, J., IV.15.39  
 Baake, E., I.2.567  
 Baaazov, D.I., IV.16.239  
 Babcock, G.T., I.2.239, I.2.263, I.2.483,  
     I.2.539, I.2.643, III.12.499  
 Babuzhina, D.I., IV.19.801  
 Bachofen, R., II.4.77, IV.17.341  
 Bader, K.P., I.3.861, I.3.865  
 Badger, M.R., III.11.331  
 Baggoo, A.K., III.13.695  
 Bagley, K.A., I.1.77, I.1.81  
 Bahnsen, K., III.14.885  
 Bain, G., IV.19.705  
 Baker, D.N., IV.19.733  
 Baker, N.R., II.6.463, IV.16.259, IV.17.337,  
     IV.17.365, IV.17.369, IV.19.565,  
     IV.19.591, IV.19.679, IV.19.687,  
     IV.19.691, IV.20.835  
 Bakker, H., III.12.533

- Balakumar, T., **III**.13.699, **IV**.18.545  
 Balangé, A.P., **III**.14.873  
 Baldwin, B.C., **IV**.16.223  
 Ballantyne, D.J., **IV**.19.603  
 Baltscheffsky, H., **II**.8.763, **III**.9.197, **III**.9.201,  
**III**.9.205  
 Baltschaffsky, M., **II**.8.763, **III**.9.197, **III**.9.205  
 Bansal, K.C., **I**.3.941, **III**.12.597  
 Bao, J.-S., **III**.11.347  
 Bar-Zvi, D., **III**.9.193  
 Barbato, R., **I**.2.339, **II**.6.419  
 Barber, J., **I**.2.223, **I**.2.279, **I**.2.307, **I**.2.327, **I**.2.415, **I**.2.419, **I**.2.431, **I**.2.435, **I**.2.455, **I**.2.611, **II**.6.415, **II**.6.515, **II**.6.519, **II**.8.715, **III**.12.617, **III**.12.637  
 Barends, J.P.F., **I**.3.693  
 Barillot, E., **I**.2.463  
 Barón, M., **I**.2.303  
 Barry, B.A., **I**.2.239, **I**.2.483  
 Bartling, D., **II**.5.253  
 Bass, W.J., **II**.4.73,  
 Bassi, R., **II**.5.209, **II**.5.249  
 Basu, S., **IV**.19.745  
 Baumgart, F., **I**.3.749,  
 Baumgarten, M., **I**.3.953  
 Baumgartner, B.J., **III**.12.423  
 Baur, P., **II**.8.827  
 Bauscher, M., **I**.1.77, **I**.1.81, **I**.1.85  
 Bayburt, T.H., **I**.3.821  
 Beachy, R.N., **I**.2.323  
 Béal, D., **II**.8.879  
 Beatty, J.T., **III**.12.453  
 Beauregard, M., **I**.2.331  
 Bechtel, C., **I**.2.355  
 Beck, W.F., **I**.3.721, **I**.3.817  
 Becker, D.W., **IV**.19.705  
 Becker, M., **I**.1.101, **I**.1.121  
 Beckett, P., **IV**.19.595  
 Bednárová, L., **II**.8.821  
 Beer, S., **III**.11.411  
 Beinsberger, S., **III**.13.775  
 Ben-Porath, A., **IV**.19.733  
 Bender, C., **I**.3.709,  
 Bennett, A., **II**.5.269  
 Bennett, J., **II**.8.747, **IV**.17.357  
 Bennoun, P., **III**.12.437  
 Bental, M., **IV**.19.773  
 Berg, S.P., **I**.2.671  
 Berger, G., **I**.1.89, **I**.2.463, **III**. 9.65  
 Bergh, S.A., **IV**.16.271  
 Bergström, H., **II**.4.153, **II**.4.173  
 Berliner, M.A., **I**.2.569,  
 Bernardes da Silva, A., **IV**.20.863  
 Bernarding, J., **II**.6.373  
 Bernier, F., **I**.3.945  
 Berrada, R., **IV**.19.777  
 Berry, J.A., **IV**.16.279, **IV**.19.573  
 Bertrand, M., **III**.13.787  
 Berzborn, R.J., **III**.9.57, **III**. 9.61  
 Bethenod, O., **IV**.19.737, **IV**.20.855  
 Betsche, T., **II**.6.511, **IV**.17.409  
 Betts, S.D., **I**.2.267, **I**.3.797  
 Betzel, Ch., **II**.7.547  
 Beuttenmüller, M., **III**.11.381  
 Bhattacharjee, R.C., **III**.13.695  
 Biaudet, P., **III**.9.141  
 Bickel-Sandkötter, S., **III**.9.77  
 Biggins, J., **II**.7.639, **IV**.17.329  
 Bingsmark, S., **II**.8.763, **II**.8.799  
 Biro, A.J., **III**.13.695  
 Bishop, N.I., **I**.2.507, **I**.3.929  
 Biswal, B., **IV**.19.813  
 Biswal, U.C., **I**.2.651  
 Bittersmann, E., **I**.2.667, **II**.4.165, **II**.4.169, **II**.5.297, **II**.7.611  
 Bixon, M., **I**.1.11,  
 Bizouarn, T., **III**.9.153  
 Blackwell, R.D., **IV**.15.15  
 Blankenship, R.E., **I**.1.121, **II**.4.17, **II**.4.37, **II**.4.169  
 Blättler, R., **III**.13.791  
 Blondel, J.D., **III**.14.873  
 Blubaugh, D.J., **I**.2.503  
 Blumenstein, S., **III**.9.193  
 Bock, C.H., **II**.7.619, **II**.7.623  
 Böddi, B., **III**.14.835  
 Boekema, E.J., **I**.2.267, **I**.2.375, **III**.9.33  
 Boese, S.R., **IV**.17.313, **IV**.19.643  
 Bogatyrenko, V.R., **I**.2.379,  
 Bogdanoff, P., **III**.9.217  
 Bogdanović, M., **III**.13.683  
 Böger, P., **IV**.15.95  
 Bogorad, L., **III**.12.557  
 Bolhar-Nordenkampf, H.R., **IV**.15.31  
 Bonadies, J.A., **I**.3.709,  
 Bongi, G., **IV**.19.717  
 Bönigk, B., **I**.1.141  
 Booth, P.J., **I**.2.455, **I**.2.611, **II**.6.519  
 Borchard, A., **III**.9.97  
 Boschetti, A., **I**.2.315, **II**.5.257, **III**.13.791  
 Böttcher, B., **III**. 9.33  
 Bottin, H., **II**.7.539, **II**.7.631  
 Boucher, N., **III**.10.295

- Boussac, A., I.3.713  
 Bowden, S.J., I.2.603, I.2.411, I.2.519,  
   I.2.551, I.3.717  
 Bowes, G., III.11.399  
 Bowlby, N.R., I.2.539, I.2.239, I.2.263,  
   I.2.643, I.3.797  
 Bowyer, J., I.2.603, III.12.561, III.13.759,  
 Boxer, S.G., I.1.113, III.12.529  
 Boynton, J.E., III.12.509  
 Bradbeer, J.W., III.12.601, IV.16.147,  
   IV.16.151, IV.16.155, IV.19.599  
 Brand, J.J., II.6.401  
 Brändén, R., III.11.351, III.11.371  
 Brandt, P., III.13.783  
 Brechignac, F., IV.18.433  
 Breidenbach, E., III.13.791  
 Brentel, I., III.14.843  
 Breton, A.M., III.12.521  
 Breton, J., I.1.77, I.1.81, I.1.85, I.1.89,  
   I.2.463, I.2.467, II.4.125, II.5.305,  
   II.5.329, II.7.599  
 Brettel, K., I.2.447, I.3.837, II.7.539,  
   II.7.623, II.7.627  
 Breu, V., III.13.807, IV.16.287  
 Briantais, J.M., IV.17.365  
 Bricker, T.M., I.2.639, I.3.825  
 Britt, R.D., I.3.769,  
 Britton, G., II.4.53, III.14.827, IV.15.15,  
   IV.19.587, IV.19.595  
 Brodt, C.A., IV.15.87  
 Brown, R.G., II.7.615  
 Brown, S., IV.15.51  
 Brudvig, G.W., I.3.721, I.3.817  
 Brugnoli, E., IV.19.741  
 Brune, D.C., II.4.17, II.4.37  
 Brunisholz, R.A., II.4.61  
 Bryant, D.A., II.4.1  
 Buchanan, B.B., IV.16.179  
 Büchel, C., II.8.943  
 Buchholz, C., III.12.621  
 Budde, R.J.A., IV.16.135  
 Buetow, D.E., III.12.549  
 Bukhov, N.G., I.2.559,  
 Bull, A.D., III.13.807  
 Bulté, L., III.13.715, IV.15.43  
 Burmester, R., IV.16.263  
 Burnap, R., I.2.255  
 Bustos, S.A., II.8.863, III.12.445  
 Buurmeijer, W.F., II.8.891  
 Buvinger, M.E., II.8.747  
 Bylina, E.J., I.1.53, I.1.109, I.1.149  
 Cabot, C., IV.19.729  
 Cai, X., III.13.739  
 Calcagno, A.M., IV.19.713  
 Calie, P.J., III.12.475  
 Callahan, F.E., II.8.733  
 Camilleri, P., I.2.603  
 Camm, E.L., I.2.659,  
 Cammarata, K., II.5.341  
 Campbell, D.A., IV.19.691  
 Canaani, O., IV.17.321, IV.17.325  
 Canvin, D.T., IV.18.513  
 Cao, J., I.2.515  
 Capo, S.F., IV.16.271  
 Capuano, V., II.4.101  
 Carlberg, S., IV.18.517, IV.18.521,  
   IV.18.525, IV.18.529, IV.18.533  
 Carlson, T.J., III.12.525  
 Carmeli, C., III.9.29  
 Carnot, L., III.12.437  
 Carpenter, S.D., I.2.359  
 Carpentier, R., I.2.343, I.2.595, II.7.691,  
   III.10.295  
 Carrasco, J.L., IV.16.163  
 Carrillo, N., III.14.865  
 Carter, D.R., IV.20.859  
 Cashmore, A.R., III.13.779  
 Casimiro, A., IV.17.413  
 Castrillo, M., IV.19.713  
 Causgrove, T.P., II.4.17, II.4.37, II.5.325  
 Cerović, Z.G., I.2.607, IV.16.215  
 Chaika, M.T., III.13.819  
 Chaloub, R.M., II.8.847  
 Chamot, D., IV.18.501  
 Chan, R.L., II.8.871  
 Chang, M.C., II.4.65, II.4.73, II.4.133  
 Chao, S., III.12.601  
 Chapados, C., I.2.343  
 Chapman, D.J., I.2.223, I.2.327, II.6.515  
 Charité, J., I.2.231, I.2.359  
 Chaturvedi, R., II.6.393  
 Cheeseman, J.M., IV.19.745, IV.20.859  
 Chen, G.-X., I.2.491, IV.19.619  
 Chen, H.-B., III.11.347  
 Chen, H.-Q., III.12.549  
 Chen, Y., III.10.287  
 Cheng, S.-H., IV.17.393  
 Cheniae, G.M., I.2.503, I.3.721  
 Chirino, A., I.1.61  
 Chittock, R., II.7.615  
 Cho, D.-S.C., III.12.445  
 Chollet, R., IV.16.135  
 Chong, C.L., II.5.281

- Chongqing, T., IV.19.647  
 Choquet, Y., III.12.437  
 Chow, W.S., II.8.935  
 Christopher, D.A., III.12.491  
 Chu, C., IV.17.393  
 Chu, Z.-T., I.1.31,  
 Chueca, A., I.2.303, IV.16.163, IV.16.251  
 Chyaen, K., II.8.927  
 Chylla, R.A., I.2.383  
 Clark, S.E., II.5.231, III.13.731  
 Clarkson, J., II.8.787  
 Cleland, R.E., II.6.507  
 Clément-Métral, J.D., III.12.521  
 Clijsters, H., III.13.775  
 Clough, B.F., IV.20.859  
 Cmiel, E., III.13.691  
 Cobb, A.H., II.6.451, II.6.455  
 Coelho Rebelo, D., IV.20.863  
 Cogdell, R.J., II.4.11, II.4.61, II.4.117,  
     II.4.121, II.4.137  
 Coleman, J.R., III.12.581, IV.18.455,  
     IV.18.485, IV.18.501  
 Coleman, W.J., I.1.137, I.1.149, I.1.153  
 Connor, A.E., II.4.53,  
 Conrads-Strauch, J., III.12.605  
 Conway, A.B., I.3.829,  
 Cook, K.M., III.12.617  
 Cook, W., III.12.589  
 Copertino, D.W., III.12.491  
 Corrie, A.R., I.2.523, I.2.551, I.3.793  
 Cote, F., IV.17.409  
 Côté, R., IV.15.79  
 Cotton, T.M., II.8.907  
 Coughlan, S.J., II.7.667  
 Cox, A., II.4.81,  
 Cox, R.P., II.4.181, IV.19.761, IV.19.793  
 Cramer, S.P., I.3.685  
 Cramer, W.A., III.10.221, III.10.255,  
     III.10.271, III.13.799  
 Creighton, S., I.1.31,  
 Cresswell, C.F., II.6.443, IV.15.71, IV.15.75  
 Critchley, C., II.8.899  
 Crofts, A.R., I.2.547, II.6.381, III.9.89,  
     III.10.263, III.10.283, III.10.287,  
     III.10.291  
 Crofts, J., I.2.391  
 Cronshagen, U., III.14.869  
 Crystall, B., I.2.455, I.2.611, II.6.519  
 Cunningham, Jr., F.X., IV.17.349, IV.17.353  
 Cupina, T., IV.20.911  
 Curtiss, A., III.10.307  
 Czernuszewicz, R., I.3.773  
 Dahlin, C., II.8.813  
 Dai, Y.-L., II.5.281, IV.19.667  
 Dainese, P., II.5.209, II.5.249, II.6.419  
 Daldal, F., III.10.231  
 Daley, P.F., IV.19.573  
 Damm, I., II.7.607, II.8.855, IV.17.405  
 Darrall, N.M., IV.19.599  
 Dau, H., IV.17.325  
 Dauter, Z., II.7.547  
 Davies, T.G.E., III.13.747  
 Davis, D.J., III.10.303  
 Day, T.A., IV.20.883  
 De Ciechi, P., I.2.363  
 De Kouchkovsky, Y., III.9.153  
 De Lamotte, F., IV.16.159  
 De Lorimer, R., II.4.1  
 De Paula, J.C., I.2.239, I.2.643  
 Déák, Z., I.3.809,  
 Debus, R.J., I.2.239, I.2.483, I.3.829,  
     III.12.499  
 Decottignies, P., IV.16.159, IV.16.243,  
     IV.16.247  
 Degani, H., IV.19.773  
 Deinum, G., II.4.161  
 Dekker, J.P., I.2.239, I.2.263, I.2.267,  
     I.2.643, IV.16.263  
 Delgado, E., IV.15.39  
 Delrieu, M.J., I.3.833  
 Delucia, E.H., IV.20.883  
 Demeter, S., I.3.809,  
 Demetriou, C., I.2.411, I.2.519, I.2.551,  
     I.3.717  
 Demmig-Adams, B., II.6.357  
 Dennenberg, R.J., IV.17.349, IV.17.353  
 DePamphilis, C.W., III.12.475  
 Depka, B., I.2.217  
 Deprez, J., II.5.305, II.5.329  
 Derose, V.J., I.3.769, I.3.789  
 Dexheimer, S.L., I.3.761  
 Di Paolo, M.L., II.5.249  
 Diamond, J., IV.17.413  
 Dian, J., II.4.205  
 Dianan, Y., IV.19.647  
 Diaz, C., IV.19.695  
 Dibbayawan, T., II.5.333  
 Dietz, K.-J., IV.19.753  
 Dikanov, S.A., I.2.487  
 Dimagno, T., I.1.109,  
 Diner, B., III.12.561  
 Diner, B.A., I.2.259, I.2.471  
 Ding, H.G., II.8.817  
 Dismukes, G.C., I.3.773, I.3.953

- Dobek, A., II.5.329  
 Doi, M., III.14.853  
 Dolan, E., I.3.781  
 Doldjikov, S., IV.20.915  
 Donner, A., I.2.591  
 Dörnemann, D., IV.16.287  
 Downie, S.R., III.12.475  
 Drachev, A.L. I.1.185  
 Dracheva, S.M., I.1.185  
 Drager, R.G., III.12.491  
 Drake, A., I.2.431  
 Drenkard, S., IV.19.607  
 Drews, G., II.4.121  
 Driesenaar, S., IV.17.321  
 Dubbs, J.M., II.4.1  
 Ducamp, M., II.6.511  
 Ducruet, J.-M., I.2.543  
 Dujardin, E., I.3.921, III.13.787  
 Dujardyn, M., II.6.491, IV.16.283  
 Dumont, N., III.14.849  
 Dupree, P., III.12.625  
 Durell, S., III.10.311  
 Durrant, J.R., I.2.415, II.6.519  
 Dutton, P.L., I.1.157  
 Dyer, T.A., III.12.461, III.12.601
- Eaton-Rye, J.J., I.3.937  
 Eberl, U., I.1.133, I.1.153  
 Eckert, H.-J., II.6.373  
 Edelman, M., I.2.209, II.8.733  
 Edmondson, D.L., III.11.331  
 Edwards, G., IV.17.393  
 Eggengerger, A.L., I.2.363  
 Eggers, B., I.2.231, I.2.359  
 Ehara, T., III.12.629  
 Ehrenberg, A., II.6.349  
 Eichelmann, H., I.2.663  
 Eicher, S., II.4.77,  
 Eilenberg, H., III.11.411  
 Eilers, R.J., I.2.599  
 Eisenberg, Y., III.12.641  
 El Deeb, M., I.2.239,  
 El Hamouri, B., IV.19.777  
 El-Deeb, M., I.2.483  
 El-Shintinawy, F., I.2.511  
 Elanskaya, I.V., III.12.645  
 Elderfield, P., III.13.665  
 Elich, T.D., II.8.733  
 Ellis, R.J., III.13.671  
 Enami, I., I.2.319,  
 Erdös, G., III.12.549  
 Erokhin, Yu.E., II.4.81, IV.17.345
- Espie, G.S., IV.18.513  
 Esteban, A., II.4.93,  
 Etienne, A.-L., I.2.543, II.6.427  
 Evans, E.H., II.7.615  
 Evans, M.B., II.4.61,  
 Evans, M.C.W., I.1.189, I.2.523, I.2.551,  
 I.2.619, I.3.793, II.7.615, II.8.919  
 Evelo, R.G., I.2.487
- Fagerberg, W.R., IV.17.385  
 Fajer, J., II.4.149  
 Falbel, T.G., II.5.269  
 Falk, G., III.9.189  
 Falkowski, P.G., IV.17.357, IV.20.923  
 Fan, L., I.1.205  
 Farage, P.K., IV.19.591, IV.20.835  
 Farchaus, J.W., I.1.161, I.1.197, I.1.201  
 Federman, E., IV.19.749  
 Feezel, L.L., I.1.181  
 Feher, G., I.1.39, I.1.61, I.1.77, I.1.81,  
 I.1.141, I.1.161  
 Feick, R., I.1.133, I.1.137  
 Fenton, J.M., II.6.381  
 Ferguson, L., II.4.117  
 Fernández, D., IV.19.713  
 Filimonov, A.A, IV.19.651  
 Filippova, L., IV.15.103  
 Fillat, M.F., II.7.663  
 Findlay, J.B.C., II.8.767  
 Fine, P.L., I.3.905  
 Finke, W., III.9.57  
 Finkele, U., I.1.27,  
 Fischer, K., IV.16.203  
 Fischer, M.R., I.1.177, II.4.45, II.7.711,  
 IV.17.421  
 Fleck, I., IV.19.695  
 Flügge, U.I., IV.16.203  
 Ford, L., IV.15.71  
 Forti, G., II.8.775  
 Fotinou, C., I.2.275  
 Foyer, C.H., II.6.483, II.6.491, IV.16.259,  
 IV.16.283  
 Fragata, M., I.3.945  
 Frame, M., III.10.303  
 France, L.L., I.2.467  
 Franck, F., I.3.921, III.13.751, III.13.755,  
 III.13.787  
 Frank, G., II.4.61, II.4.89, II.4.93, II.7.591  
 Frank, H.A., I.1.105, II.7.639  
 Frankel, L.K., I.2.639, I.3.825  
 Franzén, L.-G., II.7.591, III.12.437  
 Frasch, W.D., I.3.725, I.3.781, I.3.905,

- III.9.9**
- Freiberg, A., **II.4.157**  
 Friedberg, D., **IV.18.463**  
 Friesner, R.A., **I.1.93**  
 Fromme, P., **III.9.15**  
 Fronko, R.M., **I.3.797**  
 Füglstaller, P., **II.4.93**  
 Fujii, T., **II.7.655**  
 Fujimura, Y., **I.2.403, I.3.957**  
 Fujita, S., **III.13.763**  
 Fukuzawa, H., **IV.18.467**  
 Furbacher, P.N., **III.10.221, III.10.271, III.13.799**  
 Furbank, R.T., **IV.18.541**
- Gaba, V., **I.2.209**  
 Gabai, C., **III.13.823**  
 Gad'on, N., **II.4.121**  
 Gadal, P., **IV.16.243, IV.16.247**  
 Gal, A., **II.8.779, II.8.783**  
 Gale, J., **IV.15.55**  
 Gale, M.D., **III.12.601**  
 Galmiche, J.-M., **III.9.65**  
 Gamble, P.E., **III.12.423**  
 Ganago, A.O., **I.1.117**  
 Gans, P., **IV.15.43**  
 Gantt, E., **IV.17.321, IV.17.349, IV.17.353**  
 Garab, G., **II.7.667**  
 Garbisu, C., **II.7.699**  
 Garcia-Vescovi, E., **II.8.895**  
 Gardeström, P., **IV.15.9, IV.15.59, IV.19.805**  
 Gardet-Salvi, L., **IV.16.167**  
 Garlaschi, F.M., **II.5.313, II.5.317**  
 Garnier, J., **II.5.277**  
 Gärtner, S., **I.2.295**  
 Gasparich, G.E., **II.4.1**  
 Gast, P., **I.3.953**  
 Gau, A.E., **I.2.295**  
 Gaugain, F., **IV.17.409**  
 Gaul, D., **I.1.113**  
 Geacintov, N.E., **I.2.467, II.4.125**  
 Geiken, B., **II.6.373**  
 Gennis, R.B., **III.10.263**  
 Genty, B., **IV.16.259, IV.17.337, IV.17.365, IV.17.369**  
 George, G.N., **I.3.685**  
 Georgi, S., **III.11.385**  
 Gepstein, S., **III.11.411**  
 Geraghty, A.M., **IV.18.505**  
 Gerhardt, V., **I.3.853, I.3.857**  
 Gerken, S., **I.3.837**  
 Gerrish, C., **III.13.759**
- Geva, N., **III.11.411**  
 Ghanatry, J.A., **II.4.73**,  
 Ghanotakis, D.F., **I.2.275, I.2.643**  
 Ghirardi, M.L., **II.8.733**  
 Ghosh, R., **II.4.77**  
 Giacometti, G.M., **I.2.339, II.6.419**  
 Giardi, M.T., **I.2.339, II.6.419**  
 Gibbs, P., **IV.17.329**  
 Gillbro, T., **II.4.11, II.4.117, II.4.181, II.5.301**  
 Gillham, N.W., **III.12.509**  
 Gilmore, A.M., **II.6.495**  
 Gimenez, P., **IV.15.95**  
 Gimmier, H., **IV.19.769, IV.19.773**  
 Gingras, G., **I.1.125**  
 Giorgi, L.B., **I.2.415, II.6.519**  
 Girard-Bascou, J., **III.12.437**  
 Girault, G., **III.9.65**  
 Girvin, M.E., **III.10.271**  
 Glaser, E., **III.13.815**  
 Glauser, M., **II.4.89,**  
 Gleason, F.K., **IV.16.175**  
 Gleiter, H.M., **I.2.479, I.2.531**  
 Gnanam, A., **III.12.633**  
 Godik, V.I., **II.4.157**  
 Goetze, D.C., **II.7.691**  
 Golbeck, J.H., **II.6.401, II.7.531**  
 Golden, S.S., **II.6.431, II.8.863, III.12.445**  
 Goldfeld, M.G., **III.9.105, III.9.111**  
 Goldschmidt-Clermont, M., **III.12.437**  
 Goltsev, V., **IV.19.699**  
 Gomez-Moreno, C., **II.7.663**  
 Gong, H., **II.6.397**  
 González, M.S., **IV.15.47, IV.17.397**  
 González-Murua, C., **IV.19.789**  
 Goodchild, D.J., **II.8.803**  
 Gorgé, J.L., **IV.16.163, IV.16.251**  
 Görlach, J., **III.14.857**  
 Gornicka, O., **II.8.887**  
 Gottstein, J., **II.4.45,**  
 Gough, S.P., **III.12.585**  
 Gounaris, K., **I.2.223, I.2.327**  
 Govindjee, I.2.451, I.2.459, I.2.511, I.2.515  
 Gräber, P., **III.9.15, III.9.33, III.9.37, III.9.217**  
 Grandoni, P.A., **III.9.145**  
 Granok, H., **I.2.367**  
 Granot, G., **IV.15.55**  
 Gratton, E., **I.2.459,**  
 Grätzel, M., **I.2.619,**  
 Gravett, A.E., **II.6.475**  
 Gray, J.C., **III.10.267, III.12.461, III.12.625**

- Gray, K.A., I.1.201  
 Grechkin, A.N., IV.17.429  
 Green, B.R., I.2.659, III.12.553  
 Green, J.P., I.3.725, I.3.781, III.9.9  
 Greenberg, B.M., I.2.209,  
 Greer, D.H., II.6.365  
 Greis, J., I.1.145  
 Greve, B., IV.15.99  
 Gribenow, K., II.4.141, II.4.177  
 Grieve, C.M., IV.19.749  
 Grime, P., IV.17.361  
 Grimm, B., III.12.585  
 Grimme, L.H., II.7.607, II.8.855, IV.17.405  
 Grodzinski, B., IV.15.35, IV.15.79,  
     IV.19.809  
 Gromet-Elhanan, Z., III. 9.45  
 Groom, Q.J., II.6.463  
 Groome, Q., IV.20.835  
 Gross, A., IV.16.203  
 Gross, E.L., III.10.299, III.10.307,  
     III.10.311  
 Gross, R., I.2.315  
 Grossman, A.R., III.12.541  
 Gruenberg, H., I.1.201  
 Gu, W., III.11.339  
 Gudowska-Nowak, E., II.4.149  
 Guikema, J.A., II.7.563, III.13.739  
 Guiles, R.D., I.3.789,  
 Gulyaev, B.A., I.2.427  
 Gunner, M.R., I.1.47,  
 Günther, G., IV.16.207, IV.16.211  
 Guo, Y.-S., II.7.695  
 Gustafsson, P., II.6.431, III.12.537  
 Guyon, D., II.5.277  
 Haag, E., I.2.375, I.2.479, I.3.869  
 Habash, D., IV.17.337  
 Hachtel, W., III.12.621  
 Haddy, A., I.3.753, I.3.777  
 Haehnel, W., II.7.611, II.7.675, II.8.739  
 Hagelstein, P., III.14.857  
 Hagemann, R., III.12.429  
 Haining, R.L., III.11.355  
 Hák, R., IV.20.899  
 Hala, J., II.4.205  
 Halevy, A.H., IV.17.417  
 Haley, B.E., III.11.363  
 Halford, N., III.11.351, III.11.371  
 Halkier, B.A., II.7.523  
 Hall, D.O., I.2.619, II.6.487, II.7.699  
 Hällgren, J.-E., IV.19.805  
 Hallick, R.B., III.12.491  
 Hammes, S., I.1.113  
 Hanaoka, T., IV.19.615  
 Hanke, W., III.9.83  
 Hansson, Ö., I.1.97, I.2.439, I.2.475, I.3.777  
 Hanssum, B., I.3.845  
 Haraux, F., III.9.141, III.9.153  
 Harbinson, J., IV.16.259, IV.17.365  
 Harmey, M.A., III.13.815  
 Harnett, T., I.2.291,  
 Harnois, J., III.10.295  
 Harris, D.A., III. 9.41  
 Harris, E.H., III.12.509  
 Harrison, M., IV.17.333  
 Hartman, F.C., III.11.343  
 Hase, E., III.11.391, III.12.629, III.13.735  
 Hatch, M.D., IV.18.541  
 Hauska, G., II.8.783  
 Hawthornthwaite, A.M., II.4.137  
 Hayashi, H., I.1.73,  
 Hayashida, N., III.13.767  
 Hayden, D.B., IV.19.691  
 He, W.-Z., I.2.431  
 Heber, U., IV.19.753  
 Heckmann, R., I.1.153  
 Hedrich, R., III.9.137  
 Hegde, U., I.2.247  
 Heineke, D., IV.15.1, IV.16.191  
 Heintze, A., III.14.857  
 Heldt, H.W., IV.15.1, IV.16.191, IV.16.227  
 Heller, B.A., II.4.65, II.4.73  
 Henricson, D., IV.15.59  
 Henry, R.L., II.7.567, III.13.739  
 Henrysson, T., II.8.759  
 Heras, L., II.6.499  
 Hermann, R., II.8.783  
 Hermoso, R., IV.16.163, IV.16.251  
 Hermann, R.G., II.5.253  
 Herzfeld, F., III.14.869  
 Heupel, R., IV.15.1  
 Hibino, T., III.13.719  
 Hideg, E., I.2.623, I.3.809  
 Hienerwadel, R., I.1.85, I.3.841  
 Higashi, S.-I., I.2.403  
 Hiller, R.G., III.12.545  
 Hind, G., II.7.667  
 Hinrichs, W., II.7.547  
 Hinsch, K.-D., II.8.787  
 Hioki, Y., II.5.241  
 Hippler, M., II.7.675  
 Hiramatsu, H., III.13.771  
 Hird, S.M., III.12.461  
 Hirschberg, J., III.12.641

- Hisabori, T., III.9.73, III.9.169  
 Hiyama, T., I.2.351, II.7.587  
 Hladik, J., II.7.579  
 Hoadley, J., I.2.431  
 Hodges, M., II.8.875  
 Hodgson, R.A.J., I.2.323  
 Hoff, A.J., I.1.177, I.2.487, II.7.711  
 Hoffmann, D., I.3.853, I.3.857  
 Hoffmann, P., III.14.885  
 Hoffstädt, J., IV.16.187  
 Hoganson, C.W., III.10.319  
 Høj, P.B., II.7.523  
 Holt, R.E., II.8.907  
 Holten, D., I.1.113  
 Holzapfel, W., I.1.27,  
 Holzwarth, A.R., I.2.387, I.2.443, II.4.141,  
     II.4.177, II.5.223, II.5.297, II.7.611  
 Hong, L., III.12.491  
 Hong, Y., II.7.667  
 Honig, B., I.1.47,  
 Hooyer, J.K., III.13.723  
 Hopkins, R.M., II.6.451  
 Hoppe, P., III.14.857  
 Horio, T., I.2.319, III.12.517  
 Horovitz, A., III.12.641  
 Horton, P., I.2.391, I.2.399, I.2.627, I.2.631,  
     II.6.507, IV.16.111, IV.16.219, IV.16.223,  
     IV.17.361  
 Hory, F.E., III.13.695  
 Hoshina, S., II.7.571  
 Hosoda, T., III.9.73  
 Houmard, J., II.4.101  
 Howard, R., III.11.419  
 Howe, G., III.13.711  
 Høyier-Hansen, G., III.13.783  
 Huault, C., III.14.873  
 Hubbard, J.A.M., I.1.189, I.2.523, I.2.551,  
     I.3.793, II.8.919  
 Hull, M.R., IV.19.675, IV.19.683  
 Humbeck, K., I.2.655  
 Hundal, T., II.6.423  
 Huner, N.P.A., II.6.467, II.6.471, III.14.861,  
     IV.17.313, IV.19.631, IV.19.643  
 Hunter, C.N., II.4.153, II.4.173  
 Huppe, H.C., IV.16.179  
 Hurry, V., II.6.467, IV.17.313  
 Husic, H.D., IV.18.493  
 Ichimura, N., III.12.517  
 Ichimura, T., I.2.583  
 Ideguchi, T., III.12.517  
 Iglesias, A.A., IV.18.537  
 Iizuka, Y., IV.19.615  
 Ikegami, I., II.7.643  
 Ikeuchi, M., I.2.347, I.2.351, I.2.507  
 Inaba, H., I.2.623  
 Inagaki, J., I.2.287  
 Inagaki, N., III.13.763  
 Ifíñiguez, F.J., IV.19.695  
 Innes, J.B., I.3.817  
 Inoué, H., I.3.917  
 Inoue, K., II.7.655  
 Inoue, Y., I.2.347, I.2.351, I.2.507, I.3.701,  
     I.3.741, I.3.801, I.3.909, II.6.409  
 Inui, T., I.3.765  
 Irrgang, K.-D., I.2.355, I.2.375  
 Isaacson, R.A., I.1.141  
 Ish-Shalom, D., III.13.823, IV.19.709  
 Ishidsu, J.-I., II.4.49  
 Ishii, R., IV.20.895  
 Ishikawa, H., III.13.719  
 Ishimaru, T., II.5.309  
 Isogai, Y., I.3.813  
 Israels, R., II.4.97,  
 Itoh, S., I.3.813, II.7.571, II.7.643, II.7.647,  
     II.7.651  
 Iwaki, M., II.7.647, II.7.651  
 Iwata, N., II.8.927  
 Jacquot, J.-P., IV.16.159, IV.16.179,  
     IV.16.243, IV.16.247  
 Jagendorf, A.T., III.9.29  
 Jahnke, L.S., IV.19.683  
 Jahns, P., I.3.881  
 James, M.R., III.13.699, IV.18.545  
 Janjic, V., IV.19.725  
 Janowitz, A., IV.16.211  
 Janssen, L.H.J., IV.20.931  
 Jansson, C., I.2.299, III.12.565, III.12.649  
 Jansson, S., III.12.537  
 Jawali, N., III.11.407  
 Jeggerschöld, C., II.6.349, II.6.405  
 Jelić, G., III.13.683  
 Jenkins, C.L.D., IV.18.541  
 Jennings, R.C., II.5.313, II.5.317  
 Jensen, M.T., II.8.939  
 Jepsen, L.B., III.12.609, III.12.613  
 Jewell, C.J., I.2.569  
 Jewess, P., I.2.603  
 Jiao, J.-A., IV.15.35, IV.16.135  
 Jide, Z., IV.19.647  
 Jie, T., I.1.205  
 Johnson, A.M., III.12.509  
 Johnson, D.G., I.2.451, IV.17.361

- Johnson, L.B., IV.19.691  
 Joliot, A., III.10.247  
 Joliot, P., II.8.879, III.10.247  
 Jones, A.R., III.12.509  
 Jones, H.G., IV.20.907  
 Jortner, J., I.1.11,  
 Joshi, P.N., I.2.651  
 Jovanovic, L., IV.19.725  
 Juhler, R., IV.19.793  
 Junesch U., III. 9.15  
 Junge, W., I.3.877, I.3.881, III.9.81, III.9.97,  
     III.9.133, III.9.137,  
 Jursinic, P.A., IV.17.349, IV.17.353  
 Juszczak, L.J., II.4.125
- Kaino, N., III.12.517  
 Kaiser, W.M., I.1.27, IV.19.557  
 Kakuno, T., I.2.319, III.12.517  
 Kaladharan, P., IV.20.903  
 Källbring, B., I.1.97  
 Kalosaka, K., I.3.721  
 Kamachi, H., I.3.917  
 Kamo, M., IV.16.167  
 Kamoh, K., I.2.499  
 Kane, H.J., III.11.331  
 Kaneko, M., I.2.319,  
 Kannangara, C.G., III.12.585, III.13.807  
 Kaplan, A., IV.18.463  
 Kapsa, V., II.8.825  
 Karapetyan, N.V., I.2.559,  
 Karukstis, K.K., I.2.569,  
 Katerji, N., IV.20.855  
 Katoh, S., I.2.319, I.2.583, I.3.737, II.7.595,  
     II.7.643, II.8.859  
 Katz-Downie, D.S., III.12.475  
 Kawamori, A., I.3.765  
 Kawamoto, K., I.3.889,  
 Kebire, M.S., III.13.695  
 Keegstra, K., III.13.799  
 Kellogg, E.C., I.1.129,  
 Kennedy, I.R., IV.15.23  
 Kessel, M., IV.18.463  
 Kessissoglou, D., I.3.709,  
 Kettleborough, C.A., III.11.351  
 Keys, A.J., III.11.371, III.11.395, III.11.351  
 Kim, B.-H., III.12.517  
 Kim, D.H., I.3.769,  
 Kingston-Smith, A.H., III.11.395  
 Kipper, M., I.2.217  
 Kirilovsky, D., I.2.543, II.6.427  
 Kirmaier, C., I.1.113  
 Kitamura, T., I.3.917
- Kitaoka, S., IV.16.199, IV.19.615  
 Kitatani, Y., I.2.583  
 Kittsteiner, U., III.13.679  
 Klein, M.P., I.3.761, I.3.769, I.3.789,  
 Kleinherenbrink, F.A.M., II.4.145, II.4.189  
 Klevanik, A.V., I.1.117  
 Kliffen, C., IV.19.817  
 Klimov, V.V., I.2.247, I.2.379  
 Kloppstech, K., IV.19.579, IV.19.709  
 Klug, D.R., I.2.415, I.2.455, I.2.611, II.6.519  
 Klyuchareva, E.A., III.13.819  
 Knack, G., IV.19.579  
 Knobloch, K., III.9.185  
 Knoetzel, J., II.8.867  
 Knoppik, D., IV.19.607  
 Knorpp, C., III.13.815  
 Knudsen, J., II.8.939  
 Ko, K., III.13.779  
 Kobayashi, M., I.3.885, II.4.109  
 Kobayashi, T., I.3.913  
 Kobayashi, Y., II.8.927  
 Koch, B., II.7.523, II.7.671  
 Kochubey, S.M., II.8.791, II.8.795  
 Koenig, F., IV.17.373  
 Koepke, J., I.1.173  
 Koike, H., I.2.347, I.2.351, I.2.507  
 Kolaczkowski, S., I.1.129,  
 Kolber, Z., IV.20.923  
 Komenda, J., II.6.389  
 Komissarov, G.G., IV.15.107  
 Komiya, H., I.1.61,  
 Korstanje, L.J., II.8.755  
 Kotvalt, V., IV.20.899  
 Kotzabasis, K., III.14.881, IV.16.287  
 Kramer, D.M., II.6.381, III.9.89, III.10.283  
 Krause, G.H., II.6.479, II.6.483  
 Kretschmann, H., I.3.837  
 Kreutz, W., I.3.841  
 Krieger, A., I.2.563, IV.17.307  
 Krishnaswamy, S., III.12.633  
 Krogmann, D.W., II.7.687, III.10.303  
 Krol, M., III.14.861, IV.17.313  
 Krömer, S., IV.15.1  
 Krstic, B., IV.20.879, IV.20.887  
 Kruleva, L., IV.19.699  
 Krupa, Z., II.6.431  
 Ku, M., IV.17.393  
 Kuang, T.-Y., I.2.335  
 Kugel, H., IV.19.769  
 Kühlbrandt, W., II.5.217  
 Kuhlmann, M., I.2.295  
 Kühne, U., III.14.869

- Kulandaivelu, G., IV.19.813  
 Kulikov, A.V., I.2.379,  
 Kumar, A., III.14.877, IV.16.275  
 Kumar, P.A., IV.15.67  
 Kunishima, N., II.7.571  
 Kusumoto, N., II.7.655  
 Kusunoki, M., I.3.801  
 Kutsunai, S., III.13.711  
 Kuwabara, T., III.13.743  
 Kuwata, K.T., I.2.569,  
 Kuznetsova, N.Yu., I.2.283  
 Kwa, S.L.S., I.2.279,
- Laasch, H., III.9.161, IV.16.207, IV.16.211  
 Labahn, A., III. 9.37  
 Labanowski, J., III.10.311  
 Lachica, M., I.2.303  
 Lacuesta, M., IV.19.789  
 Lagenfelt, G., I.2.527, III.10.319  
 Lah, M.S., I.3.709,  
 Laing, W.A., II.6.365  
 Laisk, A., I.2.663  
 Lamppa, G.K., II.5.231, III.13.731  
 Lang, E., I.1.137, I.1.153  
 Lange, W., II.4.105  
 Lannoye, R., IV.17.425, IV.19.671, IV.19.785  
 Lapointe, L., IV.19.631  
 Larkum, A.W.D., II.5.333, II.6.385  
 LaRoche, J., IV.17.357  
 Larson, E., I.3.709,  
 Larsson, C., IV.18.517, IV.18.521, IV.18.525, IV.18.529, IV.18.533  
 Larsson, S., I.1.97  
 Larsson, U.K., II.5.253, II.8.759, II.8.799, II.8.835, II.8.839  
 Larsson-Raźnikiewicz, M., IV.16.155  
 Lassiter, C.B., IV.16.271  
 Latzko, E., IV.16.187  
 Lauteri, M., IV.19.741  
 Lavergne, J., I.3.873, I.3.893, II.8.879  
 Lawlor, D.W., IV.19.663  
 Lázaro, J.J., IV.16.163, IV.16.251  
 Lazova, G.N., IV.18.479  
 Le Marechal, P., II.8.875, IV.16.247  
 Lea, P.J., IV.15.15, IV.19.595  
 Lebedeva, N.V., III.12.645  
 Lecharny, A., IV.20.871  
 Lechner, E., IV.19.591  
 Lechtenberg, D., IV.16.171, IV.17.307  
 Lee, C.-H., I.2.387  
 Lee, E.H., III.11.343  
 Lee, P., IV.16.219  
 Leibl, W., II.5.305, II.5.329  
 Lelandais, M., II.6.483  
 Lemieux, S., I.2.343  
 Lemoine, Y., II.6.491  
 Lempert, U., III.13.703  
 Lennon, M., III.13.687  
 Leonhard, M., I.1.85, I.1.89, I.2.463, II.7.599  
 Lersch, W., I.1.137, I.1.153  
 Leu, S., III.12.569, III.13.811, III.13.823, III.9.193, IV.20.851  
 Levine, Y.K., II.5.337, II.5.345, II.8.755  
 Lewis, A., III. 9.29  
 Lewis, D., IV.16.219  
 Lewis, K.J., IV.15.15  
 Lhomme, J.-P., IV.20.855  
 Li, L.-R., III.11.377  
 Li, M., II.7.563, III.13.739  
 Li, S.-J., II.7.695  
 Li, T.-Z., I.2.335  
 Li, X., I.3.709,  
 Liese, F., III.10.279  
 Likhtenstein, G.I., I.2.379,  
 Lill, H., III. 9.1, III.9.133  
 Lin, C.P., I.3.953  
 Lin, S.-Q., I.2.335  
 Lindberg-Møller, B., III.12.609  
 Lindblom, G., III.14.843  
 Lindqvist, Y., III.11.323  
 Lingberg-Møller, B., III.12.613  
 Lipp, G., IV.17.421  
 Liu, B.-L., I.1.177  
 Liu, Z., IV.19.579  
 Ljungberg, U., II.5.253  
 Lloyd, J.C., III.12.601  
 Loach, P.A., II.4.65, II.4.69, II.4.73, II.4.133  
 Lobysheva, I.I., III.9.111  
 Lockett, C.J., I.2.411, I.2.519, I.2.551, I.3.717  
 Lockhart, D.J., I.1.113  
 Logsdon, Jr., J.M., III.12.475  
 Lohse, D., III.9.121  
 Long, S.P., II.6.463, II.6.475, IV.19.565, IV.19.591, IV.19.675, IV.19.683, IV.20.835  
 Longstaff, M., III.12.601  
 Loreto, F., IV.19.549  
 Lorimer, G., III.11.419  
 Los, D.A., III.12.593, III.12.645  
 Lou, S.-Q., I.2.335  
 Lous, E.J., I.1.61,  
 Lovelock, C., IV.20.859

- Lu, T., II.8.907  
 Lübbers, K., I.3.877  
 Lubitz, W., I.1.141, II.2.531  
 Lucero, H.A., II.8.895  
 Lücken, U., III. 9.33  
 Lühring, H., III.9.81  
 Luinenburg, I., III.12.581  
 Lundin, M., III.9.197, III.9.201  
 Lundqvist, T., III.11.323, III.11.419  
 Lutz, M., I.2.423  
  
 Møller, B.L., II.7.523, II.7.671, II.7.679  
 Møller, I.M., II.8.813  
 Macharia, J.M.N., IV.20.835  
 Macmillan, F., I.2.531, I.3.749  
 Madden, M., III.11.419  
 Mäenpää, P., II.5.273  
 Maggard, S., I.3.929,  
 Maguhn, J., IV.19.607  
 Mahajan, S., II.4.197  
 Mahalingham, S., III.10.263  
 Majeu, N., IV.18.485  
 Makhneva, Z.K., IV.17.345  
 Malinowski, H., III.13.679  
 Malkin, R., II.7.575, IV.17.321  
 Maloney, M.A., III.13.723  
 Malyan, A.N., III. 9.69  
 Mamada, K., I.2.347, I.2.351  
 Mamushina, N., IV.15.103  
 Manodori, A., III.12.541  
 Mantele, W., I.1.77, I.1.81, I.1.85, I.1.89,  
     I.2.463, I.3.841, II.4.121, II.7.599  
 Mar, T., I.1.125  
 Marani, A., IV.19.733  
 Marano, M.R., III.14.865  
 Marcus, R.A., I.1.1,  
 Marder, J.B., I.2.307, II.6.415  
 Marek, L.F., IV.18.509  
 Marino, J., I.3.953  
 Markgraf, T., IV.16.279  
 Marks, D.B., III.13.723  
 Maroc, J., II.5.277  
 Maróti, P., I.1.165, I.1.169  
 Marques da Silve, J., IV.20.863  
 Marts, B.L., III.13.707  
 Martin, J.E., I.1.121  
 Maruthi Sai, P.S., II.4.197  
 Masojídek, J., II.6.389  
 Massacci, A., IV.20.907  
 Mathis, P., I.1.173, I.1.197, I.2.439, I.2.475,  
     I.2.535  
 Mathur, P., I.3.773  
  
 Matsuoka, M., III.12.577  
 Matsushita, T., I.3.801  
 Matsuura, K., I.1.193  
 Matthijs, H.C.P., II.4.201, II.7.667  
 Mattoo, A.A., II.8.733  
 Mattoo, A.K., I.2.209,  
 Mauro, S., II.7.683, IV.17.425, IV.19.671  
 Mayes, S.R., III.12.617, III.12.637  
 Mazzola, L., I.1.113  
 McCauley, S.W., II.5.297  
 McDermott, A.E., I.3.789,  
 McFadden, B.A., III.11.355, III.11.359  
 McIntosh, L., I.2.239, I.2.483, III.12.499,  
     III.12.649  
 McKiernan, M., IV.17.369  
 McLilley, R., IV.16.119  
 McMorrow, E.M., III.12.601, IV.16.147,  
     IV.16.155  
 McPherson, P.H., I.1.39,  
 Medrano, H., IV.15.39, IV.19.729  
 Mei, R., I.3.729,  
 Melandri, B.A., III.9.85  
 Melis, A., II.6.435, IV.17.291  
 Merchant, S., III.13.711  
 Messinger, J., I.3.845, I.3.849  
 Mets, L.J., II.8.779  
 Metz, J.G., I.2.471  
 Meunier, P.C., I.2.331  
 Michaeli, D., II.7.555  
 Michaels, A., III.9.193, III.12.573,  
     III.13.811, III.13.823, IV.20.851  
 Michalski, T., II.4.69,  
 Michel, H., I.1.173, I.3.933  
 Michel, H.P., II.8.747  
 Michel-Beyerle, M.E., I.1.11, I.1.19, I.1.133,  
     I.1.153, I.1.137  
 Michelsen, B., IV.19.761  
 Middendorf, D., I.1.101, I.1.121  
 Miginiac-Maslow, M., II.8.875, IV.16.159,  
     IV.16.243, IV.16.247  
 Mikami, K., III.13.767  
 Mikoyan, V.D., III.9.105, III.9.111  
 Miles, D., III.12.589  
 Miller, A.G., IV.18.513  
 Miller, M., II.4.181, IV.19.761  
 Millner, P.A., II.8.767, II.8.787  
 Mills, D., III. 9.49  
 Mills, W.R., IV.16.271  
 Mimuro, M., II.4.193, II.5.241, II.5.309  
 Minliang, G., IV.18.497  
 Miranda, M.A., IV.19.781  
 Mishra, R.K., IV.19.655

- Mitchell, R., **II.8.739**  
 Miyachi, S., **IV.18.467**  
 Miyao-Tokutomi, M., **I.3.909**,  
 Miziorko, H.M., **IV.15.87**  
 Mizobuchi, A., **I.2.287**, **III.13.771**  
 Mochizuki, Y., **I.2.319**,  
 Moenne-Loccoz, P., **I.1.65**, **I.2.423**  
 Moerschbacher, B., **IV.19.797**  
 Mogel, S.N., **III.11.359**  
 Mohamed, A., **III.12.565**  
 Moholt-Siebert, M., **IV.19.705**  
 Molnar, S.A., **III.10.299**  
 Monge, E., **II.6.499**, **IV.19.765**  
 Montañes, L., **II.6.499**  
 Montiel-Canobra, P.O., **IV.16.155**, **IV.19.599**  
 Moormans, R., **II.8.755**  
 Moorthy, P., **III.13.699**, **IV.18.545**  
 Mor, T.S., **II.8.783**  
 Morales, F., **IV.19.757**  
 Morand, L.Z., **III.10.303**  
 Morell, M.K., **III.11.331**  
 Morgun, V., **IV.20.915**  
 Morin, F., **IV.17.409**  
 Morisette, J.-C., **I.2.635**, **I.2.647**  
 Morishige, D.T., **II.5.261**  
 Morita, E.H., **I.1.73**,  
 Morita, M., **III.10.315**, **IV.15.91**  
 Morita, Y., **I.3.913**  
 Moroney, J.V., **IV.18.449**  
 Morris, A.L., **I.1.181**  
 Mörschel, E., **II.4.105**  
 Mortain-Bertrand, A., **IV.17.357**  
 Moskalenko, A.A., **I.2.283**, **II.4.81**  
 Moss, D.A., **I.1.85**  
 Mostowska, A., **III.13.679**  
 Moualem-Beno, D., **IV.17.401**  
 Mould, R., **III.13.665**  
 Moundib, R., **IV.19.777**  
 Mueller, M., **II.5.297**  
 Mühlenhoff, U., **II.7.547**  
 Mukerji, I., **II.5.321**  
 Mulay, M., **I.2.247**  
 Müller, H., **III.9.185**  
 Müller, M.G., **II.4.177**  
 Mullet, J.E., **III.12.423**  
 Muñoz-Rueda, A., **IV.19.789**  
 Mur, L.R., **II.4.201**  
 Murata, N., **I.2.403**, **I.3.937**, **I.3.957**  
 Mustardy, L., **IV.17.349**, **IV.17.353**  
 Myers, J., **IV.15.63**  
 Nabedryk, E., **I.1.77**, **I.1.81**, **I.1.85**, **I.1.89**,  
**I.2.463**, **II.7.599**  
 Nadanaciva, S., **III. 9.41**  
 Nagarajan, V., **I.1.101**, **I.1.121**  
 Nakamoto, H., **IV.16.183**  
 Nakane, H., **I.2.271**, **I.2.311**  
 Nalty, M.S., **III.12.445**  
 Namikawa, H., **III.12.517**  
 Napiwotzki, II.6.373  
 Nátr, L., **IV.20.899**  
 Neale, P.J., **II.6.435**  
 Nechushtai, R., **II.7.555**, **III.13.661**  
 Nedbal, L., **II.6.389**  
 Nelson, K.P., **III.12.491**  
 Nelson, N., **III. 9.1**  
 Nemoto, H., **III.9.169**  
 Nénonéné, E.K., **I.3.945**  
 Nesbakken, T., **IV.20.935**  
 Nespolous, C., **III.11.381**  
 Neumann, K.-H., **IV.16.275**  
 Newell, W.R., **I.2.279**,  
 Newman, S.M., **III.12.509**  
 Newton, M.D., **II.4.149**  
 Nguyen, A.P., **I.3.829**,  
 Nie, G.Y., **IV.19.565**, **IV.19.687**  
 Niederman, R.A., **II.4.33**, **II.4.57**, **II.4.129**,  
**III.10.259**  
 Nielsen, H.L., **II.7.523**  
 Nilsen, S., **II.6.397**  
 Nilsson, F., **I.2.299**,  
 Nishimura, M., **I.3.813**  
 Nishise, H., **III.12.517**  
 Nitschke, W., **I.2.535**  
 Nixon, P.J., **I.2.259**, **I.2.471**  
 Nobel, P.S., **IV.20.821**  
 Noctor, G., **I.2.627**  
 Nore, B.F., **III.9.23**, **III.9.205**  
 Norling, B., **III.9.173**  
 Norman, J., **IV.19.705**  
 Norris, J.R., **I.1.109**, **I.1.181**  
 Nothnagel, D., **IV.16.187**  
 Nugent, J.H.A., **I.2.411**, **I.2.603**, **I.2.519**,  
**I.2.523**, **I.2.551**, **I.3.717**  
 Nunes, M.A., **IV.19.721**  
 Nurmi, A., **II.6.439**, **III.13.795**, **IV.17.381**  
 Nyhus, K.J., **I.2.367**  
 Nyrén, P., **III.9.23**, **III.9.173**, **III.9.177**,  
**III.9.181**, **III.9.197**, **III.9.209**  
 Obokata, J., **III.13.767**  
 Oelze, J., **II.4.41**,  
 Oesterhelt, D., **I.1.27**, **I.1.197**, **I.1.201**  
 Oettmeier, W., **I.2.591**

- Offermann, K., III.12.483  
 Ogasawara, Y., III.12.629  
 Ogawa, T., III.12.525, IV.18.471  
 Ogiso, H., II.7.587  
 Ögren, E., I.3.949  
 Ogrodnik, A., I.1.19, I.1.133, I.1.153  
 Ohad, I., II.6.409, II.8.779, II.8.783,  
     III.13.823, IV.19.709  
 Ohad, N., III.12.641  
 Ohta, Y., III.9.169  
 Okamura, M.Y., I.1.39, I.1.77, I.1.141,  
     I.1.161  
 Okkels, J.S., II.7.523, II.7.671, II.7.679,  
     III.12.609, III.12.613  
 Oku, T., II.8.927  
 Olivera, L.M., II.4.33  
 Olsen, I., II.7.523  
 Olson, J.M., II.4.37, II.8.939  
 Omata, T., III.12.525, IV.18.471  
 Ong, J.E., IV.20.859  
 Ono, T., I.3.801  
 Ono, T.-A., I.2.507, I.3.701, I.3.741, I.3.909  
 Ooms, J.J.J., II.8.883, III.9.213  
 Öquist, G., II.6.431, II.6.471, IV.17.313,  
     IV.19.623  
 Orgen, W.L., IV.18.475  
 Ormerod, J., IV.20.935  
 Ort, D.R., III.9.145, IV.19.565  
 Ortiz-Lopez, A., IV.19.565  
 Osafune, T., III.11.391, III.12.629,  
     III.13.735  
 Oswald, A., III.12.483  
 Ottander, C., IV.19.623  
 Ottersbach, P., IV.19.579  
 Otto, B., IV.19.579  
 Otto, J., III. 9.61  
 Ottosen, C.-O., I.3.949  
 Ou, K.-L., III.13.687  
 Ougham, H.J., III.13.747  
 Owens, T.G., II.5.289, II.5.293, IV.19.627  
 Oxborough, K., III.9.145  
 Oyanagi, H., I.3.801  
 Packer, J., III.13.759  
 Packer, N., III.13.687  
 Paddock, M.L., I.1.39, I.1.161  
 Padhye, S., I.2.247  
 Pailletin, G., II.5.329  
 Pais, M.S., IV.17.413  
 Pakrasi, H.B., I.2.291, I.2.323, I.2.363,  
     I.2.367  
 Paliwal, R., I.2.371, I.2.407  
 Palmer, J.D., III.12.475  
 Palmqvist, K., IV.18.441  
 Pammenter, N.W., II.6.443, IV.15.71,  
     IV.15.75, IV.20.919  
 Pančoška, P., II.8.821  
 Pankratova, S.I., IV.17.429  
 Panneels, P., IV.19.785  
 Papageorgiou, G.C., I.3.957  
 Parkes-Loach, P.S., II.4.65, II.4.69, II.4.73,  
 Pärnik, T., III.11.415  
 Parry, M.A.J., III.11.351, III.11.371,  
     III.11.395, III.13.795  
 Parson, W.W., I.1.101, I.1.121, I.1.31,  
 Pascual, M., IV.19.695  
 Patzke, J., IV.19.573  
 Paul, K., III.11.331  
 Paul, M.J., IV.19.663  
 Paulino, C., IV.19.659  
 Paulsen, H., III.13.727  
 Pauly, S., I.3.745, I.3.837  
 Pecoraro, V.L., I.3.709  
 Pedersen, J.P., II.4.37  
 Pehu, E., III.13.795  
 Peine, G., III.14.885  
 Peng, D.-C., I.2.335  
 Penner-Hahn, J.E., I.3.797  
 Persson, A., II.8.923  
 Petersen, J., I.2.239, I.2.263, I.2.539  
 Peterson, R.B., I.2.395  
 Peyre, J.B., IV.16.159  
 Peyronnet, R., IV.16.159  
 Pfündel, E., II.6.503  
 Philippova, E.A., IV.19.801  
 Phillips, A.L., III.11.351  
 Phillips, J., I.2.587  
 Philo, J.S., I.3.953  
 Picaud, M., II.6.427  
 Pichersky, E., III.12.553  
 Pick, U., IV.19.773  
 Picorel, R., I.2.575, II.8.907  
 Pierce, J., III.12.525  
 Pille, S., III.12.521  
 Pilz, I., III.11.373  
 Pirner, B., III.9.185  
 Pistorius, E.K., I.2.295  
 Plato, M., I.1.133, I.1.141  
 Plaut, Z., IV.19.749  
 Plesničar, M., IV.16.215, IV.16.267  
 Plumley, F.G., II.5.341  
 Podesta, F.E., IV.18.537  
 Popova, L.P., IV.18.479  
 Popovic, R., I.2.331, I.2.635, I.2.647

- Porra, R.J., II.5.237  
 Porter, G., I.2.415, I.2.455, I.2.611, II.6.519  
 Portis, Jr., A.R., IV.16.119  
 Pospíšilová, L., II.7.579  
 Post, A., IV.19.635, IV.19.639, IV.19.709  
 Postl, W., IV.15.31  
 Pramanik, A., II.8.763, III.9.197, III.9.201  
 Prášil, O., II.6.389  
 Prasil, O., II.4.205  
 Prat-Gay, G., IV.16.195  
 Preston, C., I.2.451, I.2.459, I.3.925  
 Priatel, J.J., III.12.453  
 Price, A., IV.19.595  
 Prince, R.C., I.3.685  
 Prioul, J.-L., IV.20.871  
 Prokhortenko, I.R., IV.17.345  
 Pronina, N.A., IV.18.489  
 Pruijzen, G., II.8.755  
 Pullerits, T., II.4.157  
 Purvis, D.J., III.10.259  
 Putzger, J., I.3.853, I.3.857  
 Pålsson, L.O., II.5.301  
  
 Quensel, J., I.3.897  
 Quintanar, Z.R., IV.15.47, IV.17.397  
  
 Radebaugh, C., III.12.491  
 Radunz, A., III.11.381, III.11.385  
 Raines, C.A., III.12.601  
 Raines, C.R., IV.19.675  
 Rakhamberdieva, M.G., I.2.559,  
 Ramazanov, Z., IV.18.441  
 Ramos, J.L., IV.16.163  
 Randolph-Anderson, B.L., III.12.509  
 Rantz, B., III.11.419  
 Rao, K.K., I.2.619,  
 Rapp, J.C., III.12.423  
 Rappaport, F., I.3.873  
 Raschke, K., III.9.137, IV.19.573  
 Rashid, A., I.2.595  
 Ratajczak, R., II.7.611, II.7.675, II.8.739  
 Raval, M.K., I.2.651  
 Ravnikar, P., III.12.499  
 Rawal, R.K., I.2.651  
 Rebeille, F., IV.15.43, IV.15.83  
 Rees, D.C., I.1.61, I.2.399, I.2.627, II.6.507  
 Rehm, A.M., IV.17.377  
 Reisener, H.J., IV.19.797  
 Reiss, T., III.12.649  
 Reith, H., II.4.201  
 Remy, R., II.8.875  
 Ren, L., III.11.373  
  
 Renger, G., I.2.355, I.2.375, I.2.479, I.2.531,  
     I.3.749, I.3.845, I.3.849, I.3.869, II.6.373  
 Resta, C., II.8.775  
 Reuben, J., IV.15.55  
 Reuter, R.A., I.2.671  
 Reyss, A., IV.20.871  
 Rhiel, E., II.4.1  
 Rich, P.R., III.10.239  
 Richards, W.R., III.13.695  
 Richter, M.L., II.6.377, III.9.49  
 Richter, P., IV.16.287  
 Rieß, M.H., IV.17.405  
 Ried, A., IV.17.377  
 Riens, B., IV.15.1  
 Rigoni, F., I.2.339, II.6.419  
 Rijo, P.S., IV.19.721  
 Rintamäki, E., III.11.367  
 Ripley, B.S., II.6.443  
 Robenek, H., II.8.739  
 Robert, B., I.1.65, I.2.423  
 Robinson, C., III.13.665  
 Robinson, S.P., IV.16.119  
 Rochaix, J.D., III.12.437  
 Rodrigues, M.A., II.8.851  
 Rodriguez, F., IV.19.781  
 Rodriguez-Suarez, R., IV.16.195  
 Roegner, M., I.2.471  
 Roelofs, T.A., I.2.387, I.2.443  
 Roepstorff, P., III.12.609  
 Roeske, C.A., IV.16.135, IV.18.475  
 Rögner, M., I.2.259, II.7.547  
 Römer, S., I.2.655  
 Rongey, S.H., I.1.161, I.1.39,  
 Rosengard, F., I.3.833  
 Rosenqvist, E., I.3.949  
 Rowland-Bamford, A.J., III.11.399  
 Roy, S., III.14.877, IV.16.275  
 Rubin, A.B., I.2.427  
 Rüdiger, W., III.13.679, III.13.703,  
     III.13.727  
 Rühle, W., II.6.377, II.8.827  
 Rümbeli, R., II.4.93,  
 Rumberg, B., III.9.157, III.9.125, III.10.275,  
     III.10.279  
 Rutherford, A.W., I.1.173, I.2.535, I.3.713  
 Ryberg, H., II.8.813, IV.18.517, IV.18.521,  
     IV.18.525, IV.18.529, IV.18.533,  
 Ryberg, M., II.5.253  
  
 Šetlisk, I., II.6.389, II.7.563, IV.17.341  
 Šetlisková, E., II.7.563  
 Saadeh, S., I.3.709,

- Sadovnick, E., IV.18.463  
 Saenger, W., II.7.547  
 Safina, N.I., IV.19.801  
 Saftić, D., IV.16.267  
 Sagara, T., I.3.885  
 Sahrawy, M., IV.16.163  
 Sainis, J.K., III.11.407  
 Sakac, Z., IV.20.911  
 Sakai, Y., III.9.205  
 Sakurai, H., II.7.655, II.7.707, III.9.73, III.9.169  
 Salih, G.F., III.9.23, III.9.209  
 Salnikow, J., III.11.373  
 Salter, A.H., III.10.267  
 Salvucci, M.E., III.11.363  
 Samejima, M., III.12.577, IV.20.867, IV.20.895  
 Samson, G., I.2.635, I.2.647  
 Samuelsson, G., IV.18.441  
 Sanadze, G.A., IV.16.231, IV.16.239  
 Sandelius, A.S., II.8.813  
 Sandmann, G., I.2.303  
 Sane, P.V., II.6.393, II.6.447  
 Sangalli, A., II.8.775  
 Sano, S., I.2.495  
 Santhanam, R., III.13.699  
 Santos, C.P., II.8.851  
 Saric, M.R., IV.20.875, IV.20.879, IV.20.887  
 Sarrey, F., IV.15.83  
 Sasaki, H., IV.20.895  
 Satoh, K., I.2.271, I.2.319, I.2.439, I.2.475, I.2.499, I.2.583, III.13.763  
 Sauer, K., I.3.675, I.3.761, I.3.769, I.3.789, II.5.321  
 Savchenko, G.E., III.13.819  
 Saygin, Ö., I.3.837  
 Scaramuzzi, C.D., III.12.545  
 Schaafsma, T., I.2.419,  
 Schaefer, M.R., II.8.863, III.12.445  
 Schafheutle, M.E., II.7.563  
 Scharll, M.-F., IV.19.671  
 Schatz, G.H., II.4.105, II.7.611  
 Scheer, H., I.1.27, II.4.45, III.13.691, IV.17.421  
 Scheibe, R., IV.16.127  
 Scheidel, G., I.1.133  
 Scheller, H.V., II.7.523, II.7.671, III.12.609, III.12.613, II.7.679  
 Schenck, C., I.1.113  
 Scherer, S., IV.15.95  
 Schiff, J.A., III.13.735  
 Schiller, B., I.1.173  
 Schimkat, D., IV.16.191  
 Schmittmann, G., IV.19.797  
 Schlodder, E., I.2.447, I.3.745, I.3.837  
 Schmid, G.H., I.3.865, III.11.381, III.11.385  
 Schmidt, G.W., II.5.341  
 Schmitter, J.-M., IV.16.247  
 Schneider, G., III.11.323, III.11.419  
 Schneider, S., III.13.691  
 Schober, M., III.13.703  
 Schoch, S., III.13.703  
 Schoefs, B., III.13.755  
 Scholes, J.D., IV.16.219, IV.16.223, IV.17.361  
 Schöner, S., II.6.483  
 Schönfeld, M., I.1.39,  
 Schöcknacht, G., III.9.81, III.9.137  
 Schröder, W.P., I.3.901  
 Schrubar, H., III.12.483  
 Schubert, K., III.10.279, III.9.125  
 Schultz, G., III.14.857  
 Schulze, E.-D., IV.20.827  
 Schumann, J., III.9.129, III.9.161  
 Schürmann, R., IV.16.167  
 Schwarz, B., I.2.555  
 Schwarz, R., IV.18.463  
 Schwebel-Dugue, N., IV.20.871  
 Scott, R.Q., I.2.623  
 Sealey, R.V., II.6.451, II.6.455  
 Searle, G., I.2.419  
 Seibert, M., I.2.427, I.2.451, I.2.459, I.2.507, I.2.575, I.2.619, I.3.925, II.8.907  
 Seidler, A., I.3.933  
 Seijffers, J., IV.18.463  
 Selman, B.R., III.9.165  
 Selman-Reimer, S., III.9.165  
 Selstam, E., III.14.843  
 Semenenko, V.E., III.12.593, III.12.645, IV.18.489  
 Sen, N., IV.20.927  
 Senger, H., I.2.655, III.14.881, IV.16.287  
 Sengupta, U.K., IV.20.891  
 Serra, J.L., II.7.699  
 Serrano, A., IV.15.95  
 Sesták, Z., II.8.931  
 Sétif, P., II.7.539, II.7.631  
 Sexton, T.B., III.12.423  
 Shackleton, J., III.13.665  
 Shah, N., IV.16.151  
 Shaolong, W., III.9.101  
 Sharkey, T.D., IV.19.549  
 Sharma, A., IV.20.891  
 Sharma, P.K., II.6.487

- Sharp, P.J., III.12.601  
 Sharp, R.R., I.3.821  
 Shavit, N., III.9.193  
 Shaw, S.L., II.5.269  
 Sheats, J.E., I.3.773, I.3.953  
 Shen, J.-R., I.3.737  
 Shen, Y.-K., II.8.817, IV.20.843  
 Shephard, M.C., IV.16.223  
 Sherman, L.A. 255  
 Sherudilo, E.G., IV.19.651  
 Shestakov, S.V., III.12.645  
 Shield, M.A., I.1.101  
 Shigeoka, S., IV.19.615  
 Shimada, K., I.1.193, II.4.49, II.4.193  
 Shimizu, M., III.10.315  
 Shin, M., II.7.659  
 Shinkarev, V.P., I.1.185  
 Shinohara, K., III.9.169, III.13.743  
 Shioi, Y., III.14.853  
 Shipton, C.A., II.6.415  
 Shiqing, L., IV.19.647  
 Shirasawa, S.-I., II.7.707  
 Shiver, J.W., III.13.799  
 Shkuropatov, A.Ya., I.1.117  
 Shochat, S., II.6.409  
 Shoham, G., II.7.555  
 Shoji, T., I.3.913  
 Shomer-Ilan, A., IV.17.401, IV.17.417  
 Shreve, A.P., II.5.289, II.5.293  
 Shuvalov, V.A., I.1.117  
 Shyam, R., II.6.447  
 Sidler, W., II.4.93, II.4.97  
 Siebke, K., IV.19.753  
 Siebzehnrübl, S., II.4.45, IV.17.421  
 Sieckmann, I., II.7.623  
 Siefermann-Harms, D., II.5.245  
 Siegenthaler, P.-A., III.14.849  
 Siegl, J., I.1.153  
 Siemeister, G., III.12.621  
 Sigrist, M., II.5.257  
 Silva, C.B.C., II.8.847  
 Silvestri, M., II.5.249  
 Sim, R.G., IV.20.859  
 Simoes, H.A., II.8.847  
 Simon, E., IV.19.781  
 Simpson, D.J., I.2.299, II.8.725, II.8.867  
 Sinclair, J., I.2.571  
 Singh, D., III.12.597  
 Singh, M., II.6.393  
 Singhal, G.S., I.2.371, I.2.407, IV.19.655  
 Sinnig, I., I.1.173  
 Sithole, I., I.2.239, I.2.483, III.12.499  
 Sivaguru, M., III.13.699, IV.18.545  
 Sivak, M., IV.19.789  
 Sivaraja, M., I.3.953  
 Skála, L., II.8.825  
 Sleator, N.J., III.12.491  
 Slooten, L., III.9.149  
 Small, C.L., III.11.355  
 Smeekens, S., III.12.573  
 Smith, A.J., III.13.807  
 Smith, H.B., III.11.343  
 Smith, S., II.7.687  
 Smith, U., I.1.181  
 Smith, V.R., IV.20.919  
 Smith, W.K., IV.20.883  
 Snel, J.F.H., II.8.911  
 Snyder, W., II.4.1  
 Sofrova, D., II.7.579  
 Somersalo, S., II.6.479  
 Soncini, F.C., II.8.871  
 Sonoike, K., II.7.595  
 Sopory, S.K., I.2.209, II.8.733  
 Spalding, M.H., IV.18.505, IV.18.509  
 Spangfort, M., II.5.253, II.5.265  
 Sparrow, R., II.7.615  
 Specht, S., I.2.295  
 Speer, R., I.1.145  
 Speirs, J., III.12.545  
 Spence, S.M., I.2.571  
 Spillmann, A., II.8.739  
 Staehelin, L.A., II.5.269, II.8.903  
 Stankovic, Z., IV.20.875, IV.20.879,  
     IV.20.887  
 Steck, K., II.4.121  
 Stehlik, D., II.7.619, II.7.623  
 Steinmetz, D., II.7.607, II.8.855  
 Steinmüller, K., III.12.557  
 Steup, M., III.12.605, IV.15.99  
 Stevenson, J.K., III.12.491  
 Stilz, H.U., I.27,  
 Stirewalt, V.L., II.4.1  
 Stocker, J.W., III.12.529  
 Stolz, B., II.8.809  
 Strasser, R.J., I.2.555, I.2.567, I.2.61:5,  
     II.6.503  
 Streelow, F., III.9.125, III.9.157  
 Streubel, M., III.12.483  
 Streusand, V.J., I.2.599,  
 Strid, Å., III.9.23, III.9.173, III.9.177,  
     III.9.181  
 Strotmann, H., III.9.121, III.9.141  
 Struck, A., III.13.691  
 Strümper, P., III.9.77

- Struve, W.S., II.5.325  
 Strzałka, K., II.8.887  
 Sturgis, J.N., II.4.57  
 Styring, S., II.6.349, II.6.405, II.6.423  
 Sugiura, M., III.12.469, III.13.767  
 Sumida, S., III.11.391  
 Sundblad, L.-G., IV.18.441  
 Sundby, C., II.8.759  
 Sundström, V., II.4.153, II.4.173  
 Suter, F., II.4.97  
 Sutton, B.J., IV.16.147  
 Suzuki, E., IV.18.467  
 Suzuki, K., II.7.587, IV.18.505, IV.18.509  
 Suzuki, M., I.3.801  
 Svendsen, I., II.7.679  
 Svensson, P., II.5.301, II.8.831, II.8.839, II.8.923  
 Szczepaniak, A., III.10.221, III.10.255  
 Tae, G.-S., III.10.221  
 Taguchi, A.K., III.12.529  
 Taira, T., IV.16.199  
 Takabe, T., III.13.719  
 Takahashi, E., I.1.169  
 Takahashi, M., I.2.495, I.3.757  
 Takahashi, Y., I.2.311, I.2.499  
 Takaichi, S., II.4.49,  
 Takamiya, K.-I., III.10.315, IV.15.91  
 Takano, Y., II.7.587  
 Takeda, T., IV.19.615  
 Takenaka, A., IV.17.299  
 Takio, K., I.2.347  
 Tamai, N., II.4.193, II.5.309  
 Tamura, N., I.3.917  
 Tandeau de Marsac, N., II.4.101  
 Tang, C.-Q., I.2.335  
 Tanguay, N.A., II.7.639  
 Taoka, S., I.2.547  
 Tappermann, P., I.1.137  
 Tarchevsky, I.A., IV.17.429, IV.19.801  
 Tardieu, F., IV.19.737  
 Tasumi, M., I.1.73,  
 Taylor, M., III.13.759  
 Tchuinmogne, S.J., III.14.873  
 Telfer, A., I.2.419, I.2.431, I.2.435  
 Terakado, K., II.7.587  
 Terao, T., II.8.859  
 Terashima, I., IV.17.299  
 Tetenkin, V.L., I.2.427  
 Theiler, R., II.4.129, III.10.259  
 Thibodeau, D., I.1.85  
 Thiel, T., I.2.291  
 Thomson, W.W., II.8.803  
 Thornber, J.P., II.5.261, II.5.285  
 Thurnauer, M.C., I.1.181  
 Tiede, D.M., I.1.129,  
 Timmerhaus, M., II.8.771  
 Timmins, P.A., II.7.563  
 Timpmann, K., II.4.157  
 Ting, C.S., IV.19.627  
 Tingyun, K., IV.19.647  
 Titov, A.F., IV.19.651  
 Tjus, S., II.7.583  
 Todd, C., III.12.561  
 Tokito, M.K., III.10.231  
 Toner, W., II.7.615  
 Tongzhu, L., IV.19.647  
 Torgersen, Y., IV.20.935  
 Toropygina, O.A., II.4.81  
 Tourikas, C., III.9.173  
 Tran-Anh, T., III.9.125, III.9.157  
 Trautman, J.K., II.5.289, II.5.293  
 Trebst, A., I.2.217  
 Tremolieres, A., II.5.277  
 Trissl, H.-W., II.5.305, II.5.329  
 Trujillo, I., IV.19.713  
 Tschopp, P., II.4.77,  
 Tsinoremas, N.F., II.8.919  
 Tso, J., I.3.953  
 Tsugita, A., IV.16.167  
 Tsujita, M.J., IV.15.35  
 Turina, M.P., III.9.85  
 Tyystjärvi, E., II.6.439, II.6.459  
 Tzinias, G., III.13.803  
 Uehara, A., I.3.801  
 Uehara, K., II.5.241  
 Ueno, O., IV.20.867  
 Ullrich, J., I.1.145  
 Urbanová, M., II.8.821  
 Usuda, H., IV.16.199, IV.16.255  
 Uusitalo, J., IV.18.517, IV.18.521, IV.18.525, IV.18.529, IV.18.533  
 Vacek, K., II.4.205, II.8.821, II.8.825  
 Vacha, M., II.4.205  
 Vadell, J., IV.19.729  
 Val, J., II.6.499, IV.19.679, IV.19.765  
 Valcke, R., III.13.775  
 Valle, E.M., IV.16.227  
 Vallejos, R.H., II.8.871  
 Van 't Veld, A.A., II.8.755  
 Van Amerongen, H., I.2.279, II.4.113  
 Van Arkel, G., III.12.533

- Van Berkel, J., **III.12.605**  
 Van de Meent, E.J., **II.4.145**  
 Van de Ven, M., **I.2.459**,  
 Van der Est, A.J., **II.7.619, II.7.623**  
 Van der Staay, G.W.M., **II.4.201**  
 Van der Vies, S., **III.13.671**  
 Van Ginkel, G., **II.5.337, II.5.345, II.8.755**  
 Van Gorkom, H.J., **I.3.693, I.3.805**  
 Van Grondelle, R., **I.2.279, II.4.113, II.4.133, II.4.137, II.4.141, II.4.153, II.4.161, II.4.173**  
 Van Gurp, M., **II.4.113, II.5.337, II.5.345**  
 Van Haeringen, B., **II.4.113, II.4.141**  
 Van Hasselt, P.R., **IV.17.389, IV.20.931**  
 Van Hove, L.W.A., **IV.19.611**  
 Van Ieperen, W., **II.8.911**  
 Van Kan, P.J.M., **II.4.185**  
 Van Kooten, O., **IV.19.611**  
 Van Leeuwen, P.J., **I.3.693**  
 Van Loven, K., **III.13.775**  
 Van Mieghem, F.J.E., **I.2.535**  
 Van Mourik, F., **I.2.279, II.4.113, II.4.133, II.4.137, II.4.141**  
 Van Onckelen, H., **III.13.775**  
 Van Vliet, P.H., **III.9.213**  
 Van Wijk, K.J., **IV.17.389**  
 Van Zandvoort, M., **II.8.755**  
 Vandeloise, R., **II.7.683**  
 Vandenbranden, S., **III.9.149**  
 Vander Donckt, E., **II.7.683**  
 Vängård, T., **I.3.749, I.3.753, III.10.319**  
 Vass, I., **I.2.223, I.3.809**  
 Vassey, T.L., **IV.19.549**  
 Vater, J., **I.2.355, III.11.373**  
 Vázquez, M.J., **IV.15.47, IV.17.397**  
 Velasco, G.R., **IV.15.47, IV.17.397**  
 Veljović, S., **IV.16.215, IV.19.725**  
 Venturoli, G., **III.9.85**  
 Vermaas, W., **I.2.231, I.2.359, I.2.667**  
 Vermeglio, A., **III.10.247**  
 Vermotte, C., **I.2.543**  
 Versluis, W., **II.8.883**  
 Vesk, M., **II.5.333**  
 Vidal, D., **IV.19.781**  
 Viil, J., **III.11.415**  
 Violette, C.A., **I.1.105**  
 Virgin, I., **II.6.349, II.6.423, III.12.537**  
 Virolainen, A.A., **IV.19.651**  
 Visscher, K.J., **II.4.153**  
 Visschers, R.W., **II.4.133**  
 Vitseva, O.I., **III. 9.69**  
 Vivekanandan, M., **IV.20.903**  
 Volk, M., **I.1.133, I.1.153**  
 Volovik, O.I., **II.8.791, II.8.795**  
 Volz, E., **III.10.275**  
 Von Heijne, G., **III.13.653**  
 Von Schütz, J.U., **I.1.145**  
 Von Wettstein, D., **III.13.783**  
 Vonk, C.A., **II.4.137**  
 Vorst, O., **III.12.573**  
 Vos, M.H., **I.3.693, I.3.805**  
 Voss, B., **IV.16.171**  
 Vredenberg, W.J., **II.8.883, II.8.891, II.8.911, III.9.213, IV.19.611**  
 Wachtveitl, J., **I.1.197, I.1.201**  
 Wacker, T., **II.4.121**  
 Wacker, U., **I.3.869**,  
 Wada, K., **II.7.571**  
 Waggoner, C.M., **I.3.739**,  
 Wagner, R., **III. 9.53, III.9.81, III.9.93**  
 Waldburger-Schlapp, M., **IV.17.341**  
 Waldo, G.S., **I.3.797**  
 Walker, D.A., **II.6.507**  
 Walmsley, J., **III.13.687**  
 Walter, G., **III.14.885**  
 Walters, R.G., **I.2.631**  
 Walz, D., **II.8.809**  
 Wälzlein, G., **I.2.295**  
 Wan, J., **II.7.695**  
 Wang, J., **II.4.17**  
 Wang, K.-B., **II.5.281, IV.19.667**  
 Wang, W.Q., **II.6.515**  
 Wang, Z., **III.10.291**  
 Warden, J.T., **II.7.635**  
 Warncke, K., **I.1.157**  
 Warshel, A., **I.1.31**,  
 Wasielewski, M.R., **I.1.129, I.2.451**  
 Watanabe, T., **I.3.885, II.4.109**  
 Webb, R., **I.2.255**  
 Webber, A.N., **II.7.575, III.12.461**  
 Wedel, N., **II.5.253**  
 Weiler, E.W., **IV.15.99**  
 Weinberg, D., **III.13.811**  
 Weinzettel, A., **II.8.827**  
 Weis, E., **I.2.563, II.8.771, IV.16.171, IV.17.307**  
 Weisbeek, P., **III.12.533, III.12.573**  
 Weiss, C., **IV.19.769**  
 Weiss, D., **IV.17.417**  
 Weiss, E., **I.2.663**  
 Weiss, U., **IV.19.769**  
 Wellington, C.L., **III.12.453**  
 Welte, W., **II.4.121, II.7.563**

- Wen, H., II.7.699  
 Weng, J.-M., III.11.347  
 Westerhuis, W.H.J., II.4.129  
 Westhoff, P., III.12.483  
 Whelan, J., III.13.815  
 White, I.R., II.8.767  
 White, L.A., I.2.671  
 Whitelegge, J., I.2.603  
 Whitmarsh, J., I.2.383  
 Widholm, J.M., IV.18.475  
 Widler, W., II.4.89  
 Wigge, B., IV.15.9, IV.15.59  
 Wild, A., II.6.377, II.8.827  
 Wilhelm, C., II.4.105, II.8.943  
 Wilhelmová, N., II.8.931  
 Willey, D.L., III.12.461  
 Williams, J.G.K., IV.18.471  
 Williams, J.P., IV.17.313  
 Williams, M.L., II.6.451, II.6.455  
 Williamson, D.L., I.2.575  
 Wingsle, G., IV.19.805  
 Winterberg, A., IV.19.785  
 Witt, H.T., I.3.745, I.3.837, II.7.547  
 Witt, I., II.7.547  
 Wolf, H.C., I.1.145  
 Wolfe, D.W., IV.19.627  
 Wollman, E., IV.16.159  
 Wollman, F.-A., III.13.715, IV.15.43  
 Wolosiuk, R.A., IV.16.195  
 Won, Y., I.1.93  
 Wonders, J.H.A.M., II.8.891  
 Wood, W.F., II.6.385  
 Woodbury, N.W., II.4.165, II.4.169,  
     III.12.529  
 Woodrow, L., IV.19.809  
 Wraight, C.A., I.1.165, I.1.169  
 Wright, D.P., IV.16.223  
 Wu, B., II.5.277  
 Wu, G.-Y., III.11.339, III.11.403  
 Wu, X.-Y., III.11.339, III.11.403  
 Wünschmann, G., II.6.401  
 Wydrzynski, T., I.3.749  
 Wynn, R.M., II.7.575  
 Xu, C.-H., II.5.281, IV.19.667  
 Xu, R.-B., III.11.377  
 Xu, Y.-N., II.7.695, III.11.403  
 Yachandra, V.K., I.3.769, I.3.789  
 Yalovsky, S., III.13.661  
 Yamamoto, H.Y., II.6.495  
 Yamamoto, K., II.8.927  
 Yamamoto, Y., I.2.287, III.13.771  
 Yamashita, J., III.12.517  
 Yamashita, T., I.3.913  
 Yamazaki, I., II.4.193, II.5.309  
 Yanai, N., II.7.587  
 Yang, D.H., IV.19.667  
 Yang, L., I.1.177  
 Yang, S., II.5.325  
 Yang, Y., IV.15.99  
 Yano, K., IV.16.167  
 Yarin, A.U., IV.17.429  
 Yeh, S., I.3.821  
 Yepiz-Plascencia, G., III.12.491  
 Yerkes, C.T., II.6.381  
 Ying, W.-L., II.7.695  
 Yocum, C.F., I.2.239, I.2.263, I.2.267,  
     I.2.539, I.2.643, I.3.729, I.3.739, I.3.797  
 Yokota, A., III.11.391, IV.16.199, IV.19.615  
 Yokoyama, E.-I., II.7.655  
 Yordanov, I.T., IV.19.699  
 Yoshihira, T., II.8.927  
 Young, A.J., IV.15.15, IV.19.587, IV.19.595  
 Young, D.A., III.13.707  
 Youvan, D.C., I.1.53, I.1.137, I.1.149,,  
     I.1.153  
 Youze, L., III.9.101  
 Yu, S.-G., II.8.835, II.8.839, II.8.843  
 Yun, C.-H., III.10.263  
 Yushu, Z., I.1.205  
 Yuzhu, G., IV.18.497  
 Zatezalo, S., IV.20.875, IV.20.887,  
     IV.20.879  
 Zeroni, M., IV.15.55  
 Zhang, G.Z., II.5.281  
 Zhang, Q.-D., I.2.335  
 Zhang, Z.H., III.12.637  
 Zhao, F.H., IV.19.667  
 Zhao, J., II.6.401  
 Zharmukhamedov, S.K., I.2.247  
 Zhenglian, Z., I.1.205  
 Zhengping, M., III.9.101  
 Zhenlin, Z., IV.18.497  
 Zhong, W., IV.18.497  
 Zhou, F.-H., II.5.281  
 Zhou, J., II.4.1  
 Zhuravel, T.T., II.8.795  
 Ziegler-Jöns, A., IV.19.607  
 Zilber, A., II.7.575  
 Zilberstein, A., III.11.411  
 Zilinskas, B.A., II.4.125  
 Zimmermann, J.-L., I.3.713, I.3.789

Zinth, W., I.1.27,  
Znak, N., IV.20.915  
Zuber, H., II.4.61, II.4.89, II.4.93, II.4.97,  
II.7.591  
Zubkova, H., IV.15.103  
Zucchelli, G., II.5.313, II.5.317  
Zuo, B.-Y., I.2.335

