# Contents

**From the Series Editors** v

**Series Editors** xiii

**Preface** xxvii

**The Editors** xxxi

**Contributors** xxxv

1  **The Non-Photochemical Quenching of the Electronically Excited State of Chlorophyll a in Plants: Definitions, Timelines, Viewpoints, Open Questions** 1–44
*George C. Papageorgiou and Govindjee*

<table>
<thead>
<tr>
<th>Summary</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Introduction</td>
<td>3</td>
</tr>
<tr>
<td>II. The Reign of Photochemical Quenching</td>
<td>7</td>
</tr>
<tr>
<td>III. The Emergence of the Non-Photochemical Quenching (NPQ) Concept</td>
<td>8</td>
</tr>
<tr>
<td>IV. NPQ Mechanisms and Atmospheric Oxygen Content</td>
<td>13</td>
</tr>
<tr>
<td>V. Timeline of Discoveries Relating to the Major NPQ Processes</td>
<td>15</td>
</tr>
<tr>
<td>VI. Concluding Remarks</td>
<td>32</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>33</td>
</tr>
<tr>
<td>References</td>
<td>33</td>
</tr>
</tbody>
</table>

2  **Lessons from Nature: A Personal Perspective** 45–72
*William W. Adams III and Barbara Demmig-Adams*

<table>
<thead>
<tr>
<th>Summary</th>
<th>45</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Introduction</td>
<td>46</td>
</tr>
<tr>
<td>II. Standing on the Shoulders of Giants</td>
<td>46</td>
</tr>
<tr>
<td>III. Contributions of Comparative Ecophysiology to the Initial Linking of Non-Photochemical Quenching of Chlorophyll Fluorescence and Zeaxanthin</td>
<td>51</td>
</tr>
<tr>
<td>IV. Additional Contributions of Ecophysiology and Evolutionary Biology to the Understanding of Photoprotection via Thermal Energy Dissipation</td>
<td>57</td>
</tr>
<tr>
<td>V. Concluding Remarks</td>
<td>64</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>65</td>
</tr>
<tr>
<td>References</td>
<td>65</td>
</tr>
</tbody>
</table>
3 Developments in Research on Non-Photochemical Fluorescence Quenching: Emergence of Key Ideas, Theories and Experimental Approaches 73–95

Peter Horton

Summary 73
I. Introduction 74
II. The Bioenergetics Era 75
III. The Importance of the Thylakoid Membrane 76
IV. A Return to Phenomenology: Probing the Physiology of Leaf Photosynthesis 77
V. Biochemical Approaches to Discovering the Mechanism of Quenching 78
VI. Biophysical Approaches to Discovering the Mechanism of Quenching 82
VII. Molecular Genetics: The Rise of Arabidopsis 85
VIII. The Key to NPQ: Understanding the Organization of the Thylakoid Membrane 86
IX. Integration: The State of the Art 88
X. Addendum: Ecology and Agriculture 89
XI. Concluding Remarks 91
Acknowledgments 91
References 92

4 Photophysics of Photosynthetic Pigment-Protein Complexes 97–128

Evgeny E. Ostroumov, Yaser R. Khan, Gregory D. Scholes, and Govindjee

Summary 98
I. Introduction 99
II. Chromophores in Photosynthesis and Their Electronic Properties 100
III. Radiative Transitions 104
IV. Nonradiative Transitions 106
V. Radiative Versus Nonradiative Processes in Chlorophyll 107
VI. Excitation Energy Transfer, Förster Theory 109
VII. Considerations Beyond Förster Theory 113
VIII. Delocalization of Excitation, Molecular Excitons 114
IX. Excited State Complexes 117
X. Basic Photophysics of Non-Photochemical Quenching of Chlorophyll Fluorescence 118
XI. Concluding Remarks 120
Acknowledgments 120
References 120

5 Non-Photochemical Quenching Mechanisms in Intact Organisms as Derived from Ultrafast-Fluorescence Kinetic Studies 129–156

Alfred R. Holzwarth and Peter Jahns

Summary 130
I. Introduction 130
II. The 4-State 2-Site Model of NPQ in Higher Plants 134
III. Similarity of the NPQ Quenching Sites and Mechanisms in Plants and Diatoms 139
IV. Emergence of a Third NPQ Quenching Mechanism/Site 140
V. In Vitro Models for the Q1 and the Q2 Quenching Sites 141
VI. Compartment Modeling of Fluorescence Kinetics for Distinguishing Between Various Possible Mechanisms 143
VII. The Importance of Target Analysis for Dissecting and Interpreting Intact Leaf Fluorescence and Differentiating Between Quenching Models 146
VIII. A Multitude of In Vivo Quenching Situations to be Distinguished 147
IX. Concluding Remarks 149
Acknowledgments 149
References 150

6 How Protein Disorder Controls Non-Photochemical Fluorescence Quenching 157–185
Tjaart P.J. Krüger, Cristian Ilioaia, Peter Horton, Maxime T.A. Alexandre, and Rienk van Grondelle
Summary 158
I. Introduction 159
II. Physical Descriptions of (Excitation) Energy Transfer 160
III. Protein Dynamics and Functionality 163
IV. Spectral Heterogeneity of Bulk LHCII In Vitro 164
V. Spectral Heterogeneity of Individually Probed LHCII Trimers 166
VI. qE: Regulation of a Conformational Nanoswitch 170
VII. Physical Model for qE: Controlled Disorder 173
VIII. Concluding Remarks 177
Acknowledgments 179
References 180

7 Context, Quantification, and Measurement Guide for Non-Photochemical Quenching of Chlorophyll Fluorescence 187–201
Barry A. Logan, Barbara Demmig-Adams, William W. Adams III, and Wolfgang Bilger
Summary 187
I. Introduction 188
II. Thermal Energy Dissipation in Context: Many Means of Adjustment for Optimal Utilization of Sunlight While Avoiding its Hazards 188
III. Methods of Quantifying Thermal Energy Dissipation 192
IV. Proper Measurement and Interpretation of NPQ 196
V. Concluding Remarks: Avoiding Pitfalls when Measuring Fluorescence 197
Acknowledgments 197
References 198
8 Spectroscopic Investigation of Carotenoids Involved in Non-Photochemical Fluorescence Quenching

Tomáš Polívka and Harry A. Frank

Summary 203
I. Introduction 204
II. NPQ Carotenoids in Solution 206
III. Changes in Molecular Structure and Excited-State Properties 216
IV. Spectroscopic Studies of Protein-Bound Carotenoids 220
V. Spectroscopic Properties of Carotenoid Radicals 221
VI. Conclusions 223
Acknowledgments 223
References 223

9 Electronic Carotenoid-Chlorophyll Interactions Regulating Photosynthetic Light Harvesting of Higher Plants and Green Algae

Peter Jomo Walla, Christoph-Peter Holleboom, and Graham R. Fleming

Summary 229
I. Introduction 230
II. Spectroscopic Observations 231
III. Mechanisms of Non-Photochemical Quenching 233
Acknowledgments 241
References 241

10 Antenna Protein Conformational Changes Revealed by Resonance Raman Spectroscopy

Andrew A. Pascal, Alexander V. Ruban, and Bruno Robert

Summary 245
I. Principles of Resonance Raman Spectroscopy 246
II. NPQ Mechanisms 247
III. Raman Studies on LHCII 248
IV. Crystallographic Structure of LHCII 251
V. Properties of LHCII in Crystals 252
VI. Measurements In Vivo 253
VII. Recent Developments and Perspectives 255
Acknowledgments 256
References 256

11 Fucoxanthin-Chlorophyll-Proteins and Non-Photochemical Fluorescence Quenching of Diatoms

Claudia Büchel

Summary 259
I. Introduction 260
II. Lhcx Proteins in Centric Versus Pennate Diatoms 261
III. Influence of Diadinoxanthin and Diatoxanthin Bound to FCP Complexes 265
IV. Influence of pH on the Fluorescence Yield of FCP Complexes 266
12 Involvement of a Second Xanthophyll Cycle in Non-Photochemical Quenching of Chlorophyll Fluoorescence: The Lutein Epoxide Story 277–295
Raquel Esteban and José I. García-Plazaola

Summary
I. Introduction 278
II. Discovery and Presence of Lutein Epoxide in Plant Tissues and Plastids 279
III. Lutein Epoxide Is Present in a Diversity of Species 280
IV. Lutein Epoxide Cycle Operation 283
V. Lutein Epoxide Function 284
VI. Why Two Xanthophyll Cycles? 286
VII. Ecological Significance of Two Xanthophyll Cycles 288
VIII. Perspectives 292
Acknowledgments 292
References 293

13 PsbS-Dependent Non-Photochemical Quenching 297–314
Matthew D. Brooks, Stefan Jansson, and Krishna K. Niyogi

Summary
I. Introduction 298
II. Discovery of PsbS and Involvement in qE 299
III. Biochemical Function of PsbS 301
IV. Does PsbS Affect the Organization of Photosynthetic Complexes? 303
V. Using Spectroscopic Measurements to Understand the Mechanism of qE 304
VI. Physiological Function of qE and PsbS 305
VII. Evolutionary Aspects of PsbS 308
VIII. Conclusions 308
Acknowledgments 309
References 309

14 Molecular Mechanisms for Activation of Non-Photochemical Fluorescence Quenching: From Unicellular Algae to Mosses and Higher Plants 315–331
Tomas Morosinotto and Roberto Bassi

Summary
I. Introduction: All Oxygenic Photosynthetic Organisms Exhibit NPQ Activity 316
II. LHCSR Is Responsible for NPQ Activity in Mosses and Many Algal Taxa 319
III. PsbS Is Responsible for NPQ Activity in Plants 320
IV. PsbS- vs. LHCSR-Dependent NPQ: Differences and Similarities 324
V. Concluding Remarks: Why NPQ Evolved from LHCSR to PsbS 326
Acknowledgments 327
References 327

15 Are Chlorophyll-Carotenoid Interactions Responsible for Rapidly Reversible Non-Photochemical Fluorescence Quenching? 333–342
Herbert van Amerongen

Summary 333
I. Introduction 334
II. Molecular Mechanism of qE 336
III. Conclusions 339
Acknowledgments 340
References 340

16 Structural Changes and Non-Photochemical Quenching of Chlorophyll a Fluorescence in Oxygenic Photosynthetic Organisms 343–371
Gyöző Garab

Summary 343
I. Introduction 344
II. The Macro-Organization of Thylakoid Membranes 345
III. Structural Flexibility of Thylakoid Membranes 349
IV. Structural and Functional Plasticity of Light-Harvesting Antennas 356
V. Conclusions and Outlook 364
Acknowledgments 365
References 365

17 Non-Photochemical Fluorescence Quenching and the Dynamics of Photosystem II Structure 373–386
Alexander V. Ruban and Conrad W. Mullineaux

Summary 373
I. Introduction 374
II. Reorganization of the PS II Antenna During NPQ Formation: Biochemical and Spectroscopic Evidence 375
III. Reorganization of the PS II Antenna During NPQ Formation: Structural Evidence 376
IV. Mobility of Chlorophyll-Protein Complexes Within Thylakoid Membranes 380
V. Induction of NPQ Correlates with Mobility of Protein Complexes 381
VI. An Integrated Model for NPQ Formation in Plants 383
Acknowledgments 384
References 384
18 Control of Non-Photochemical Exciton Quenching by the Proton Circuit of Photosynthesis 387–408
Deserah D. Strand and David M. Kramer

Summary 388
I. Introduction 388
II. Type I Flexibility Mechanisms: Non-Photochemical Quenching (NPQ) of Chlorophyll Fluorescence and Balancing of the Chloroplast Energy Budget 391
III. Type II Flexibility Mechanisms: Regulation of (pmf) Partitioning and ATP Synthase Activity and the Consequences for NPQ 399
IV. Concluding Remarks 402
Acknowledgments 402
References 402

19 Desiccation-Induced Quenching of Chlorophyll Fluorescence in Cryptogams 409–420
Wolfgang Bilger

Summary 409
I. Introduction 410
II. The Phenomenon of Desiccation-Induced Fluorescence Quenching 410
III. Occurrence Within the Plant Kingdom 412
IV. Photosystem Activity in the Dry State 413
V. The Mechanism of Desiccation-Induced Quenching 414
VI. Photoprotective Function of Thermal Dissipation Associated with Desiccation-Induced Quenching 417
VII. Conclusion 417
Acknowledgments 418
References 418

20 The Peculiar Features of Non-Photochemical Fluorescence Quenching in Diatoms and Brown Algae 421–443
Johann Lavaud and Reimund Goss

Summary 421
I. Introduction 422
II. Xanthophyll Cycle-Dependent NPQ 424
III. Importance of the Xanthophyll Cycle and NPQ in the Field 433
IV. Conclusion 436
Acknowledgments 437
References 437

21 High Light Acclimation in Green Microalgae 445–469
Giovanni Finazzi and Jun Minagawa

Summary 446
I. Introduction 447
II. ΔpH-Dependent Energy Quenching (qE) in Green Microalgae 448
22 Mechanisms Modulating Energy Arriving at Reaction Centers in Cyanobacteria 471–501
Diana Kirilovsky, Radek Kaňa, and Ondřej Prášil

Summary 472
I. Introduction 473
II. Phycobilisomes 473
III. Fluorescence Measurements 474
IV. Brief Description of Cyanobacterial Photoprotective Mechanisms Not Involving Phycobilisomes 478
V. The OCP-Related Photoprotective Mechanism 478
VI. State Transitions 485
VII. Phycobilisome Decoupling from Photosystems 491
VIII. Interaction Among Photoprotective Mechanisms in Cyanobacteria 493
IX. Conclusions 494
Acknowledgments 494
References 494

23 Photosystem II Efficiency and Non-Photochemical Fluorescence Quenching in the Context of Source-Sink Balance 503–529
William W. Adams III, Onno Muller, Christopher M. Cohu, and Barbara Demmig-Adams

Summary 504
I. Introduction 504
II. Non-Photochemical Quenching in Leaves Over Different Time Scales 505
III. Changes in Source-Sink Balance 507
IV. Manipulation of Carbohydrate Export from Source Leaves 511
V. Exposure to Excess Light 514
VI. Sustained NPQ, Photoinhibition, and Plant Productivity 516
VII. Concluding Remarks 520
Acknowledgments 522
References 522

24 Non-Photochemical Fluorescence Quenching in Contrasting Plant Species and Environments 531–552
Barbara Demmig-Adams, Seok-Chan Koh, Christopher M. Cohu, Onno Muller, Jared J. Stewart, and William W. Adams III

Summary 532
I. Introduction 533
II. Principal Differences in the Allocation of Absorbed Light to Photosynthesis Versus Thermal Dissipation Between Annuals and Evergreens 533

III. The Ability for Strong, Rapid Modulation of Light-Harvesting Efficiency Is Entrained by the Light Environment During Plant Development 536

IV. Lasting Maintenance of Thermal Dissipation and Arrested Xanthophyll Conversions in Nature 542

V. Thermal Dissipation and Photoinhibition 548

VI. Concluding Remarks 549

Acknowledgments 549

References 550

25 Non-Photochemical Fluorescence Quenching Across Scales: From Chloroplasts to Plants to Communities 553–582

Erik H. Murchie and Jeremy Harbinson

Summary 553

I. Introduction 555

II. The Basics of Chlorophyll Fluorescence and Excited States in Leaves 559

III. What Underlies the Diversity of NPQ? 566

IV. Conclusion 575

Acknowledgments 576

References 576

26 Beyond Non-Photochemical Fluorescence Quenching: The Overlapping Antioxidant Functions of Zeaxanthin and Tocopherols 583–603

Michel Havaux and José Ignacio García-Plazaola

Summary 584

I. Reactive Oxygen Species and Tocopherols 584

II. Interactions of VAZ-Cycle Pigments with Tocopherols 588

III. Environmental Regulation 591

IV. Evolutionary Considerations 595

V. Concluding Remarks 597

Acknowledgments 597

References 597

27 Thermal Energy Dissipation in Plants Under Unfavorable Soil Conditions 605–630

Fermín Morales, Javier Abadía, and Anunciación Abadía

Summary 605

I. Introduction 606

II. Drought 609

III. Salinity 611

IV. Macronutrient Deficiencies: N, P and K 612
28 Chloroplast Photoprotection and the Trade-Off Between Abiotic and Biotic Defense  
Barbara Demmig-Adams, Jared J. Stewart, and William W. Adams III

Summary 631
I. Introduction 632
II. Integration of Photoprotection into Whole-Plant Functioning 633
III. Lipid-Peroxidation-Derived Hormones as an Example for Redox Modulation of Plant Form and Function 634
IV. Feedback Loops Between Photoprotection and Whole-Plant Function Under Moderately Versus Highly Excessive Light 638
V. Conclusions 640
Acknowledgments 641
References 641

Subject Index 645–650
Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria
Demmig-Adams, B.; Garab, G.; Adams III, W.W.; Govindjee (Eds.)
2014, XXXVIII, 649 p. 170 illus., 88 illus. in color., Hardcover
ISBN: 978-94-017-9031-4