# Chlorophyll a Fluorescence

A Signature of Photosynthesis

#### Edited by

### George C. Papageorgiou

National Center for Scientific Research Demokritos, Athens, Greece

and

#### Govindjee

University of Illinois, Urbana, Illinois, U.S.A.



## Contents

Ed	itorial	V
Со	ntents	<b>x</b> i
Pre	eface	xxi
Со	lor Plates	CP-1
1	Chlorophyll a Fluorescence: A Bit of Basics and History  Govindiee	1–42
	Summary I. Introduction II. The Two-Light Reaction and Two-Pigment System Concept III. Photosynthetic Unit and Excitation Energy Transfer IV. The Fluorescence Transient V. The Photosystem II Reactions and Chlorophyll Fluorescence VI. Non-photochemical Quenching of Chl Fluorescence VII. Concluding Remarks Acknowledgments References	2 12 18 22 24 28 31 32
2	Fluorescence of Photosynthetic Pigments in Vitro and in Vivo George Christos Papageorgiou	43–63
	Summary I. Introduction II. Origin and Evolution of Oxyphototrophic Organisms III. Chromophores for Light Harvesting and Excitation Handling IV. Intramembranous Pigment Holochromes V. Extramembranous Light Harvesting Antennae—Phycobiliproteins and Phycobilisomes VI. Concluding Remarks Acknowledgments References	43 44 44 46 50 57 58 58 58
3	Chlorophyll Fluorescence as a Probe of Photosynthetic Productivity Neil R. Baker and Kevin Oxborough	65–82
	Summary  I. Introduction  II. Fluorescence Terminology  III. Fluorescence Parameters	66 66 67 68
	IV. Relationship between the Operating Efficiencies of PS I and PS II Electron Transport	71

	<ul><li>V. Factors Associated with Changes in PS II Operating Efficiency</li><li>VI. The Relationship between PS II Operating Efficiency and the Quantum</li></ul>	71
	Yield of CO <sub>2</sub> Assimilation	75
	VII. Can Rates of Electron Transport and CO <sub>2</sub> Assimilation be Calculated	
	Accurately from PS II Operating Efficiencies?	77
	VIII. Concluding Remarks	78
	Acknowledgments References	79 79
	1 telefolioes	13
4	Nuts and Bolts of Excitation Energy Migration and Energy	
	Transfer 83-	105
	Robert M. Clegg	
	Summary	84
	I. Introduction	84
	II. Historical Background	84
	III. Why Fluorescence Resonance Energy Transfer (FRET) Is Such a Popular Method of Measurement	87
	IV. FRET Basics: A Short Description	88
	V. What Can We Learn from Energy Transfer?	90
	VI. Simple Portrayal of the FRET Process that Explicates the Different Ways	
	of Measuring Energy Transfer Efficiency	91
	VIII. Transfer between Identical Molecules Detected by Fluorescence Anisotropy	100
	<ul><li>IX. Models of Energy Transfer through Photosynthesis Antennae Systems</li><li>X. Energy Transfer by Electron Exchange</li></ul>	100 101
	XI. Assumption of Non-coherent Mechanisms. Cooling Off to the Equilibrium	101
	Position of the Nuclei Positions	102
	XII. Cascade Mechanism of Transfer—Emission and Reabsorption of a Photon	102
	Acknowledgments	102
	References	102
5	Transfer and Trapping of Excitations in Plant Photosystems 107–	132
	Rienk van Grondelle and Bas Gobets	
	Summary	107
	I. Introduction	108
	II. Transfer and Trapping of Excitations in Photosystem (PS) I	112
	III. Transfer and Trapping of Excitations in PS II	118
	IV. Concluding Remarks	127
	Note Added in Proof References	127 128
	neielences	120
6	System Analysis and Photoelectrochemical Control of Chlorophyll	
	Fluorescence in Terms of Trapping Models of Photosystem II:	
	A Challenging View 133-	172
	Wim J. Vredenberg	
	Summary	134
	I. Introduction	134
	II. The 'Classic' Two-state Trapping Model Of Photosystem II	137
	III. Photoelectrochemical Control of PS II Chlorophyll Fluorescence	148

	<ul> <li>IV. A Three-state Energy Trapping Model of Photosystem II</li> <li>V. Concluding Remarks, Controversies and Perspectives Acknowledgments</li> <li>References</li> </ul>	153 163 168 168
7	Photon Capture, Exciton Migration and Trapping and Fluorescend	
	Emission in Cyanobacteria and Red Algae  Mamoru Mimuro	173–195
	Summary I. Introduction II. Antenna Systems in Cyanobacteria and Red Algae III. Excitation Energy Transfer and Trapping IV. Energy Transfer Mechanisms V. Diversity of Pigments and Antenna Systems in Cyanobacteria VI. Concluding Remarks Acknowledgments References	174 174 175 183 188 189 191 191
8	Photosystem II: Oxygen Evolution and Chlorophyll a Fluorescenc Induced by Multiple Flashes  Vladimir Shinkarev	e 197–229
	Summary I. Introduction to Photosystem II II. Biochemical Organization of Photosystem II III. Electron Transport IV. The Kok Model for the Flash-induced Oxygen Evolution V. Binary Oscillations of the Plastosemiquinone on the Acceptor Side of Photosystem II VI. Chlorophyll a Fluorescence VII. Conclusions Acknowledgments References	198 199 199 204 208 213 214 223 224 225
9	Fluorescence of Photosystem I Shigeru Itoh and Kana Sugiura	231–250
	Summary I. Introduction II. Fluorescence of Photosystem I in Vivo III. Fluorescence in Isolated Photosystem I Reaction Centers IV. Fluorescence in the Chlorophyll-depleted Reaction Center of Photosys V. Photosystem I with Chlorophylls Other than Chlorophyll a VI. Concluding Remarks Acknowledgments References	231 232 234 238 stem   241 244 246 247 247

10	The Relationship between Photosynthetic Electron Transfer	
	and its Regulation 2	251–278
	David M. Kramer, Thomas J. Avenson, Atsuko Kanazawa,	
	Jeffrey A. Cruz, Boris Ivanov and Gerald E. Edwards	
	Summary	252
	I. Introduction	252
	II. A 'Static' Model for Photosynthesis and Down-regulation	253
	III. Possible Mechanisms of Short-term Variation in Down-regulatory Sensi	tivity 255
	IV. Conclusions and Working Model	270
	Note Added in Proof	270
	Acknowledgments	271
	References	271
11	Pulse-Amplitude-Modulation (PAM) Fluorometry and Saturation	
	Pulse Method: An Overview 2	79–319
	Ulrich Schreiber	
	Summary	280
	I. Introduction	280
	II. Principle of Pulse-Amplitude-Modulation	282
	III. Information Carried by Chlorophyll Fluorescence Yield	284
	IV. Saturation Pulse Method of Quenching Analysis	287
	V. Assessment of Quantum Yield and Relative Electron Transport Rate	294
	VI. Intrinsic Heterogeneity of Variable Chlorophyll Fluorescence	297
	VII. Pulse Amplitude Modulation (PAM) Fluorometry for Special Applications	
	Acknowledgments References	312 312
40	Analysis of the Ohlavenhyll a Flyerencence Translant	04 000
12		21–362
	Reto J. Strasser, Merope Tsimilli-Michael and Alaka Srivastava	
	Summary	322
	I. Introduction	323
	II. Theoretical Background	325
	III. Fluorescence Transients in the Presence of Diuron at Room Temperatu	
	<ul><li>IV. Fluorescence Transients at Low Temperature (77K)</li><li>V. Polyphasic Fluorescence Transients in Vivo</li></ul>	337 339
	VI. Concluding Remarks and Future Perspectives	356
	Acknowledgments	358
	References	358
13	Light Emission as a Probe of Charge Separation and Recombination	n
. •	in the Photosynthetic Apparatus: Relation of Prompt Fluorescence	•
	to Delayed Light Emission and Thermoluminescence 3	63–388
	Esa Tyystjärvi and Imre Vass	
	Summary	364
	I. Introduction	364
	II. Thermodynamics of Reaction Kinetics	364

	<ul> <li>III. Variable Chlorophyll Fluorescence</li> <li>IV. Delayed Light Emission (DLE) from Photosynthetic Systems</li> <li>V. Thermoluminescence (TL)</li> <li>VI. Concluding Remarks</li> <li>Acknowledgments</li> <li>References</li> </ul>	372 374 379 381 382
14	Chlorophyll Fluorescence Imaging of Leaves and Fruits Ladislav Nedbal and John Whitmarsh	389–407
	Summary	390
	I. Introduction	390
	II. Imaging Technology and Techniques	394
	III. Sources of Heterogeneity in Fluorescence Images	401
	IV. Future Applications	403
	Acknowledgments	404
	References	404
15	Using Chlorophyll a Fluorescence Imaging to Monitor	
	Photosynthetic Performance  Kevin Oxborough	409–428
	Summary	410
	I. Introduction	410
	II. Theoretical Background	412
	III. Technical issues	412
	IV. High Resolution Examples	419
	<ul><li>V. Low Resolution Examples</li><li>VI. The Immediate Future and Concluding Remarks</li></ul>	422 425
	Acknowledgments	425 427
	References	427
16	Remote Sensing of Chlorophyll Fluorescence: Instrumentation	
	and Analysis	429-445
	(Ismaël Moya and Zoran G. Cerovic	
	Summary	429
	I. Introduction	430
	II. Ground Based Measurements	431
	III. Long Distance Fluorosensing	440
	IV. Concluding Remarks	443
	Acknowledgments References	443 443
	rielelelices	440
17	Probing the Mechanism of State Transitions in Oxygenic Photosynthesis by Chlorophyll Fluorescence Spectroscopy,	
	Kinetics and Imaging  John F. Allen and Conrad W. Mullineaux	447–461
	Summary	447
	I. Introduction to State Transitions	448

	<ul> <li>II. Studying State Transitions using Continuous Measurements of Fluorescence</li> <li>III. Studying State Transitions using Picosecond Fluorescence Kinetics</li> <li>IV. Using Fluorescence Recovery after Photobleaching (FRAP) to Study Protein Mobility</li> <li>V. Screening for State Transition Mutants</li> <li>VI. Concluding Remarks</li> <li>Acknowledgments</li> <li>References</li> </ul>	45° 45° 45° 45° 46° 46° 46°
18	Non-photochemical Energy Dissipation Determined by Chlorophy Fluorescence Quenching: Characterization and Function  G. Heinrich Krause and Peter Jahns	II 463–495
	Summary I. Introduction II. Definition of Quenching Parameters III. Characterization and Mechanisms of Non-photochemical Quenching IV. Function of Thermal Energy Dissipation V. Conclusions Acknowledgments References	464 464 465 467 481 485 485
19	Excess Light Stress: Multiple Dissipative Processes of Excess Excitation  Doug Bruce and Sergej Vasil'ev	497–523
	Summary I. Introduction II. Origins, Measurements and Interpretations of Variable Chlorophyll Fluorescence III. Fluorescence Quenching, Multiple Mechanisms for the Dissipation of Energy IV. Concluding Remarks Acknowledgments  / References	498 498 500 509 518 519 519
20	Using Mutants to Understand Light Stress Acclimation in Plants Talila Golan, Xiao-Ping Li, Patricia Müller-Moulé, and Krishna K. N	
	Summary I. Introduction II. Biochemical and Physiological Aspects of Light Stress III. Genetic Methods to Study Abiotic Stress IV. Insights into Light Stress Acclimation V. Genomics and the Future Acknowledgments References	526 526 527 531 538 546 547

21	Excess Light Stress: Probing Excitation Dissipation Mechanisms through Global Analysis of Time- and Wavelength-Resolved Chlorophyll a Fluorescence 555	-581
	Adam M. Gilmore	
	Summary I. Introduction II. Time- and Wavelength-Resolved Fluorescence Instrumentation III. Overview of Global Analysis IV. Applications of Global Statistical Analysis V. Conclusions and Future Research Acknowledgments References	556 556 560 564 569 577 578 578
22	Chlorophyll Fluorescence as a Tool to Monitor Plant Response	
	to the Environment 583 William W. Adams III and Barbara Demmig-Adams	-604
	Summary  I. Introduction  II. Regulation of Excitation Energy Transfer within Photosystem II Complexes	584 584 585
	III. Photoinhibition, Zeaxanthin Retention, and Sustained Decreases in F <sub>v</sub> /F <sub>m</sub> IV. Using Chlorophyll Fluorescence to Assess Photosynthetic Performance V. Strategies of Adjustment to Excess Light: Light Harvesting Capacity,	592 595
	Photosynthetic Electron Flow, and Excitation Energy Transfer Efficiency VI. Concluding Remarks: What Chlorophyll Fluorescence Can and Cannot	597
	Reveal about Stress in Plants	598 500
	Acknowledgments References	599 599
23	Plant Responses to Ultraviolet Radiation Stress  Manfred Tevini  605	-621
	Summary	605
	I. Introduction: Ozone Reduction and UV Radiation Stress	606 607
	General Responses to UV Radiation     Responses in Photosynthesis	609
	IV. Photosynthesis Under Ecological Conditions	614
	V. Conclusions	615
	Acknowledgments References	615 615
24	Effects of Water Stress on the Photosynthetic Efficiency	
		-635
	Nikolai G Bukhov and Robert Carpentier	
	Summary	623
	Introduction     Mater Deficit in Deciseption televant or Beildishydria Lewer Blants	624
	II. Water Deficit in Desiccation-tolerant or Poikilohydric Lower Plants III. Water Deficit in Desiccation-tolerant Vascular Plants	624 626
	IV. Water Deficit in Desiccation-sensitive Higher Plants	627

	<ul> <li>V. Photosystem II Function in Crassulacean Acid Metabolism Species under Drought Conditions</li> <li>VI. Conclusions</li> <li>References</li> </ul>	63 63 63
25	· · ·	37–661
	<ul> <li>Summary</li> <li>Introduction</li> <li>Dynamics of Chlorophyll a Fluorescence Changes and Their Relationsh to the Structure-Function of Photosynthetic Membranes</li> <li>Role of Chlorophyll a Fluorescence Imaging in Detection/Understanding of Metal Ion Stress</li> <li>Commonality in Metal Ion Action</li> <li>Amelioration of Metal Ion Action by Other Metal Ions</li> <li>Action of Selected Heavy Metal Ions on Plants</li> <li>Conclusions and Perspectives</li> <li>Acknowledgments</li> <li>References</li> </ul>	639
26	Water and Solute Transport in Cyanobacteria as Probed by Chlorop Fluorescence 666  George C. Papageorgiou and Kostas Stamatakis  Summary  I. Introduction  II. Light-induced and Osmotically-induced Changes of Chlorophyll a Fluorescence in Cyanobacteria  III. Applications  IV. Do Osmotically-induced Changes in Chlorophyll a Fluorescence and State Transitions Share a Common Mechanism in Cyanobacteria?  V. Conclusions  Acknowledgments  References	664 664 664 664 669 675 675
27	Assembly of Light-Harvesting Complexes of Photosystem II and the Role of Chlorophyll b  J. Kenneth Hoober and Joan H. Argyroudi-Akoyunoglou  Summary  I. Introduction II. Biological Context for Considering LHC II Assembly III. The Role of Chlorophyll (Chl) b IV. Identification of Chls within Native and Reconstituted LHC II Note Added in Proof Acknowledgment References	<b>79–712</b> 680 680 683 690 698 703 704

28	Light Adaptation and Senescence of the Photosynthetic Apparatu Changes in Pigment Composition, Chlorophyll Fluorescence	s.
	Parameters and Photosynthetic Activity	713-736
	Hartmut K. Lichtenthaler and Fatbardha Babani	
	Summary  I. Introduction: Occurrence and Function of Photosynthetic Pigments  II. Light Adaptation of Pigment Composition and Chloroplast Function  III. Chlorophyll Fluorescence Parameters as Indicators of Photosynthetic Function	713 714 716 721
	IV. Chlorophyll Fluorescence and Pigment Changes During Autumnal	
	Senescence V. Chlorophyll Fluorescence Imaging of Photosynthetic Activity VI. Conclusions Acknowledgments References	724 730 733 733 734
29	From Leaves to Ecosystems: Using Chlorophyll Fluorescence to Assess Photosynthesis and Plant Function in Ecological Studies Jeannine Cavender-Bares and Fakhri A. Bazzaz	737–755
	Summary	737
	I. The Role of Photosynthesis in Ecological Research	738
	<ol> <li>Definition and Explanation of Fluorescence Parameters</li> </ol>	739
	III. Detecting Stress in Plants at the Leaf and Whole Plant Level	741
	<ul> <li>IV. Measuring Productivity at the Ecosystem Level</li> <li>V. Scaling from the Bottom Up — The Role of Species Composition in</li> </ul>	747
	Ecosystem Dynamics VI. Concluding Remarks	750 752
	Acknowledgments	752 752
	References	752 752
30	Development and Application of Variable Chlorophyll	
	Fluorescence Techniques in Marine Ecosystems Paul G. Falkowski, Michal Koblížek, Maxim Gorbunov and Zbigniew Kolber	757–778
	Summary	757
	I. Introduction	758
	II. Fluorescence-based Estimation of Photosynthetic Electron Transport	762
	III. The Functional Absorption Cross Section of Photosystem (PS) II	764
	<ul><li>IV. Measuring Variable Chlorophyll Fluorescence in Marine Environment</li><li>V. Variations in the Maximum Quantum Yield of Fluorescence in Marine</li></ul>	766
	Environments	768
	VI. Fluorescence-based Estimates of Primary Production	771
	VII. Applications of Variable Fluorescence in Benthic Ecosystems	773
	VIII. Aerobic Anoxygenic Phototrophs	774 776
	IX. Concluding Remarks Acknowledgments	776 776
	References	776 776

Plant Productivity of Inland Waters  John A. Raven and Stephen C. Maberly	779–793
Summary	780
l. Introduction	780
II. The Habitat	781
III. The Organisms	785
IV. Primary Production and Biomass	787
V. Conclusions and Future Prospects	791
Acknowledgments	791
References	791
ıdex	795

.