

Photosynthesis: Physiology and Metabolism

Cajumban, Alyssa A.

Photosynthesis: Physiology and Metabolism

Photosynthesis is the process used by plants, algae and certain bacteria to harness energy from sunlight into chemical energy. It is one example of how people and plants are dependent on each other in sustaining life. Photosynthesis happens when water is absorbed by the roots of green plants and is carried to the leaves by the xylem, and carbon dioxide is obtained from air that enters the leaves through the stomata and diffuses to the cells containing chlorophyll. The green pigment chlorophyll is uniquely capable of converting the active energy of light into a latent form that can be stored (in food) and used when needed. Photosynthesis provides us with most of the oxygen we need in order to breathe. We, in turn, exhale the carbon dioxide needed by plants. Plants are also crucial to human life because we rely on them as a source of food for ourselves and for the animals that we eat. There are two types of photosynthetic processes: oxygenic photosynthesis and anoxygenic photosynthesis. Oxygenic photosynthesis is the most common and is seen in plants, algae and cyanobacteria. On the other hand, anoxygenic photosynthesis uses electron donors other than water. The process typically occurs in bacteria such as purple bacteria and green sulfur bacteria. Plants make simple sugar by photosynthesis. It all happens in a fraction of a second. Water gets split into hydrogen and oxygen. The hydrogen is combined chemically with carbon dioxide to produce simple sugar. This dissolves easily in water and hence is transported to all parts of the plant. Oxygen is given off as a by-product. Thus, plants take in CO₂ and gives out oxygen during photosynthesis reaction. Sun shines each day and does not charge us any money for the light it gives us. The light falling on Earth is very clean and will be there for a very long time as long as the Sun lasts. In addition to the current applications, Photosynthesis-based technology could also include using the concept of efficient “energy capture” to our artificial systems just as plants have been doing: thousands of chlorophyll a molecules (antenna) serving one center where the process occurs efficiently; the use of compounds, produced by plants, in triggering reactions that kill cancer cells; and the use of photosynthetic organisms in cleaning of aqueous surface environments (lakes, etc). An excellent example is in the use of cyanobacteria that literally eat up the nitrates from ground water and clear it for us. The opportunities that photosynthesis-based technology provides us are enormous. This process is extremely important for life on earth as it provides the oxygen that all other life depends on.



Alyssa Cajumban graduated with a degree in Biology at the University of the Philippines - Manila. In the broad field of biological sciences, her interests focus on microbiology and plant pathology. Some of her works include researching and writing scientific papers regarding fungi, diseases of agricultural crops, and post-harvest techniques. She also works as an editorial assistant and writer for a scientific journal and textbook publication.



Alyssa A.

Photosynthesis: Physiology and Metabolism

a

ArclerPress

PHOTOSYNTHESIS: PHYSIOLOGY AND METABOLISM

Edited by
Cajumban, Alyssa A.

a
ArclerPress

Photosynthesis: Physiology and Metabolism

Edited by Cajumban, Alyssa A.

© 2017



Published by

Arcler Press LLC

708 3rd Avenue, 6th Floor

New York

NY 10017

United States of America

www.arclepress.com

ISBN: 978-1-68094-541-6 (Hardback)

Library of Congress Control Number: 2017933112

This book contains information obtained from highly regarded resources. Some content has been published with permission under Creative Commons License or similar. A Wide variety of references are listed. Reasonable efforts have been made to publish reliable data and views articulated in the chapters are those of the individual contributors, and not necessarily those of the editors or publishers. Editors or publishers are not responsible for the accuracy of the information in the published chapters or consequences of their use. The publisher believes no responsibility for any damage or grievance to the persons or property arising out of the use of any materials, instructions, methods or thoughts in the book. The editors and the publisher have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission has not been obtained. If any copyright holder has not been acknowledged, please write to us so we may rectify.

Notice: Registered trademark of products or corporate names are used only for explanation and identification without intent of infringement. Although care has been taken to check accuracy of formulas and procedures, the detailed methods should be tested further on a small scale before being adopted commercially.

Arcler Press publishes wide variety of books and eBooks. For more information about Arcler Press and its products, visit our website at www.arclepress.com.



About the Editor

Cajumban, Alyssa A.

Alyssa Cajumban graduated with a degree in Biology at the University of the Philippines - Manila. In the broad field of biological sciences, her interests focus on microbiology and plant pathology. Some of her works include researching and writing scientific papers regarding fungi, diseases of agricultural crops, and post-harvest techniques. She also works as an editorial assistant and writer for a scientific journal and textbook publication.

List of Abbreviations

ADP	Adenosine Diphosphate
ATP	Adenosine Triphosphate
ALA	Aminolevulinic Acid
BASF	Badische Anilin- & Soda-Fabrik
BIRD	Blackbody Infrared Radiative Dissociation
EET	Electronic Energy Transfer
EPR	Electron Paramagnetic Resonance
ETC	Electron Transport Chain
EPGase	Enolase-Phosphoglycerase
CCM	Carbon-Concentrating Mechanism
CO ₂	Carbon Dioxide
CAM	Crassulacean acid metabolism
DCA	Dichloroacetic Acid
LSC	Long Single Copy Section
MODIS	Moderate Resolution Imaging Spectroradiometer
MPD	Multiple photon dissociation
OEC	Oxygen Evolving Complex
PEPC	Phosphoenolpyruvate Carboxylase
PEP	Phosphoenolpyruvate
PGAL	Phosphoglyceraldehyde
SSC	Short Single Copy Section
SWCNT	Single Wall Carbon Nanotube

Preface

Photosynthesis is the process used by plants, algae and certain bacteria to harness energy from sunlight into chemical energy. It is one example of how people and plants are dependent on each other in sustaining life. Photosynthesis happens when water is absorbed by the roots of green plants and is carried to the leaves by the xylem, and carbon dioxide is obtained from air that enters the leaves through the stomata and diffuses to the cells containing chlorophyll. The green pigment chlorophyll is uniquely capable of converting the active energy of light into a latent form that can be stored (in food) and used when needed. Photosynthesis provides us with most of the oxygen we need in order to breathe. We, in turn, exhale the carbon dioxide needed by plants. Plants are also crucial to human life because we rely on them as a source of food for ourselves and for the animals that we eat. There are two types of photosynthetic processes: oxygenic photosynthesis and anoxygenic photosynthesis. Oxygenic photosynthesis is the most common and is seen in plants, algae and cyanobacteria. On the other hand, anoxygenic photosynthesis uses electron donors other than water. The process typically occurs in bacteria such as purple bacteria and green sulfur bacteria. Plants make simple sugar by photosynthesis. It all happens in a fraction of a second. Water gets split into hydrogen and oxygen. The hydrogen is combined chemically with carbon dioxide to produce simple sugar. This dissolves easily in water and hence is transported to all parts of the plant. Oxygen is given off as a by-product. Thus, plants take in CO₂ and gives out oxygen during photosynthesis reaction. Sun shines each day and does not charge us any money for the light it gives us. The light falling on Earth is very clean and will be there for a very long time as long as the Sun lasts. In addition to the current applications, Photosynthesis-based technology could also include using the concept of efficient “energy capture” to our artificial systems just as plants have been doing: thousands of chlorophyll a molecules (antenna) serving one center where the process occurs efficiently; the use of compounds, produced by plants, in triggering reactions that kill cancer cells; and the use of photosynthetic organisms in cleaning of aqueous surface environments (lakes, etc). An excellent example is in the use of cyanobacteria that literally eat up the nitrates from ground water and clear it for us. The opportunities that photosynthesis-based technology provides us are enormous. This process is extremely important for life on earth as it provides the oxygen that all other life depends on.

Content Coverage

Chapters One and Two introduce about photosynthesis process and chlorophyll, correspondingly. Chlorophyll is a complex organic molecule that enables plants,

and some other organisms, to carry out photosynthesis — the conversion of carbon dioxide and water to glucose and oxygen using sunlight.

Chapters Three and Four present the role of chloroplast and light-dependent reactions, respectively. In photosynthesis, the light-dependent reactions take place on the thylakoid membranes. The inside of the thylakoid membrane is called the lumen, and outside the thylakoid membrane is the stroma, where the light-independent reactions take place.

Chapter Five gives an overview of photodissociation, photolysis, or photodecomposition. Photolysis is part of the light-dependent reactions of photosynthesis. The effectiveness of photons of different wavelengths depends on the absorption spectra of the photosynthetic pigments in the organism. Chlorophylls absorb light in the violet-blue and red parts of the spectrum, while accessory pigments capture other wavelengths as well.

Chapter Six focuses on carbon fixation or carbon assimilation, which is the conversion process of inorganic carbon (carbon dioxide) to organic compounds by living organisms. The most prominent example is photosynthesis, although chemosynthesis is another form of carbon fixation that can take place in the absence of sunlight.

Chapters Seven and Eight present the process of CAM photosynthesis and RuBisCO, separately. Crassulacean acid metabolism (CAM) is a photosynthetic CO₂ fixation pathway that maximizes water use efficiency (WUE) many times relative to C₃ species by using a temporal CO₂ pump. RuBisCO, however, is an enzyme involved in the first major step of carbon fixation, a process by which atmospheric carbon dioxide is converted by plants and other photosynthetic organisms to energy-rich molecules such as glucose.

Chapters Nine and Ten introduces about the Emerson and Warberg Effect. The Emerson effect is the increase in the rate of photosynthesis after chloroplasts are exposed to light of wavelength 670 nm (red light) and 700 nm (far red light). However, the Warburg's effect is the decrease in the rate of photosynthesis by high oxygen concentrations.

Table of Contents

List of Abbreviations	xv
<i>Preface</i>	xvii

1 PHOTOSYNTHESIS: INTRODUCTION AND EVOLUTION

Introduction	1
Overview	4
Photosynthetic Membranes and Organelles	6
Chloroplast ultrastructure	6
Light-Dependent Reactions	7
Z scheme.....	8
Water Photolysis.....	9
Light-Independent Reactions	10
In Water	12
Order and Kinetics.....	13
Efficiency	13
Evolution	15
Symbiosis and the Origin of Chloroplasts.....	15
Cyanobacteria and the Evolution of Photosynthesis	16
Discovery.....	17
Development of the Concept.....	19
C3 : C4 Photosynthesis Research	19
Factors	20
Light Intensity (Irradiance), Wavelength and Temperature	21
Carbon Dioxide Levels and Photorespiration.....	22
References.....	23

2 CHLOROPHYLL FUNCTION AND CHEMISTRY

Introduction	29
Chlorophyll And Photosynthesis.....	30

Chemical Structure.....	32
Measurement of Chlorophyll Content.....	36
Biosynthesis	37
Complementary Light Absorbance of Anthocyanins with Chlorophylls.....	38
Distribution.....	38
Culinary Use	39
Chlorophyll Fluorescence	39
Measuring Fluorescence.....	40
Common Fluorescence Parameters	40
Calculated Parameters.....	40
Applications of the Theory	41
Measuring Stress and Stress Tolerance	42
Nitrogen Balance Index.....	42
Chlorophyll Fluorometers	43
Alternative Approaches	44
References.....	45

3 THE ROLE OF CHLOROPLAST

Introduction	51
Discovery	53
Chloroplast Lineages and Evolution.....	53
Cyanobacterial Ancestor	53
Primary Endosymbiosis.....	54
Primary Endosymbiosis.....	54
Rhodophyceae (Red Algae)	58
Chloroplastida (Green Algae and Plants).....	58
Helicosporidium	62
Secondary and Tertiary Endosymbiosis	62
Green algal Derived Chloroplasts	63
Euglenophytes.....	63
Chlorarachniophytes	64
Early Chromalveolates	64
Red algal Derived Chloroplasts (Chromalveolate Chloroplasts).....	65
Cryptophytes	65
Haptophytes	66
Heterokontophytes (Stramenopiles)	66
Apicomplexans.....	67
Dinophytes.....	68
Peridinin-Containing Dinophyte Chloroplast	69
Fucoxanthin-Containing Dinophyte Chloroplasts (Haptophyte Endosymbionts).....	70

Cryptophyte Derived Dinophyte Chloroplast.....	71
Diatom Derived Dinophyte Chloroplasts	71
Prasinophyte (Green Algal) Derived Dinophyte Chloroplast.....	72
Chromatophores	72
Kleptoplastidy	72
Chloroplast DNA.....	72
Molecular Structure	73
Inverted Repeats.....	73
DNA Replication	74
Deamination.....	76
Alternative Model of Replication	76
Gene Content and Protein Synthesis.....	76
Chloroplast Genome Reduction and Gene Transfer.....	76
Protein Synthesis.....	77
Protein Targeting and Import.....	77
Transport Proteins and Membrane Translocons.....	78
Structure	78
Outer Chloroplast Membrane	80
Intermembrane Space and Peptidoglycan Wall.....	81
Inner Chloroplast Membrane	81
Peripheral Reticulum.....	81
Stroma	82
Chloroplast Ribosomes	82
Plastoglobuli	83
Starch Granules	83
Rubisco ⁸⁴	
Pyrenoids.....	84
Thylakoid System.....	85
Granal Structure	85
Thylakoids.....	87
Pigments and Chloroplast Colors.....	87
Chlorophylls	87
Carotenoids.....	88
Phycobilins.....	89
Specialized Chloroplasts in C ₄ Plants.....	89
Location	91
Cellular Location.....	92
Function and Chemistry.....	93
Guard Cell Chloroplasts	93
Plant Innate Immunity	93
Photosynthesis.....	93
Light Reactions	94

Energy Carriers	94
Photophosphorylation.....	94
NADP ⁺ Reduction	95
Cyclic Photophosphorylation.....	95
Dark Reactions.....	95
Carbon Fixation and G3P Synthesis	95
Sugars and Starches	97
Photorespiration.....	97
pH.....	97
Amino Acid Synthesis.....	98
Other Nitrogen Compounds	98
Other Chemical Products.....	98
Differentiation, Replication, and Inheritance.....	98
Plastid Interconversion.....	100
Chloroplast Division.....	100
image · labels.....	102
Transplastomic Plants.....	103
Chloroplast Dna	103
Linear Structure.....	103
RNA Editing in Plastids	103
Cytoplasmic Translation and N-Terminal Transit Sequences.....	104
Phosphorylation, Chaperones, and Transport.....	105
The Translocon on the Outer Chloroplast Membrane (TOC).....	105
Toc34 and 33.....	105
Toc159.....	106
Toc75.....	107
The Translocon on the Inner Chloroplast Membrane (TIC)	108
Tic20.....	108
Tic214.....	108
Tic100.....	108
Tic56.....	109
References.....	109

4 LIGHT-DEPENDENT REACTIONS

Introduction	125
The Reaction Center.....	126
Photosynthetic Electron Transport Chains in Chloroplasts.....	127
Photosystem II	128
The Water-Splitting Complex	128
Structure	129

Oxygen-Evolving Complex (OEC)	130
Water Splitting	131
The Reaction Center.....	132
Link of Water-Splitting Complex and Chlorophyll Excitation.....	133
Summary	133
Cytochrome <i>b/6</i>	133
Photosystem I	133
Components and Action of Photosystem I.....	134
Ycf4 Protein Domain.....	136
Green Sulfur Bacteria and the Evolution of PS I	136
Photosynthetic Electron Transport Chains in Bacteria	138
Cyanobacteria	138
Purple Bacteria	138
Green Sulfur Bacteria.....	139
Light-Independent Reactions	140
Coupling to other Metabolic Pathways	140
Steps.....	141
Products.....	144
Light-Dependent Regulation.....	144
References.....	145

5 PHOTODISSOCIATION IN PHOTOSYNTHESIS

Introduction	147
Photolysis in Photosynthesis	148
Energy Transfer Models.....	148
Quantum Models	149
Photolysis in the Atmosphere	149
Astrophysics	150
Atmospheric Gamma-Ray Bursts	150
Multiple Photon Dissociation.....	151
Flash Photolysis.....	151
Photocatalysis	152
Types of Photocatalysis	152
Applications.....	154
Quantification of Photocatalytic Activity	156
Photohydrogen.....	156
Photochemistry	156
Basics of Photochemistry	157
Fluorescence and Phosphorescence	157
Experimental Set-Up.....	158

Photochemistry in Combination with Flow Chemistry	159
Photochemical Reactions	160
References.....	162

6 CARBON FIXATION: THE C₂, C₃, C₄ PATHWAYS

Introduction	165
Net Vs Gross CO ₂ Fixation.....	166
Overview of Pathways.....	167
Oxygenic Photosynthesis.....	167
Evolutionary Considerations.....	167
Carbon Concentrating Mechanisms.....	168
CAM Plants.....	168
C ₄ Plants.....	168
C ₃ Plants.....	169
Other Autotrophic Pathways.....	169
Reductive Citric Acid Cycle.....	169
Reductive Acetyl CoA Pathway	169
3-Hydroxypropionate and two Related Cycles	169
Chemosynthesis	170
Non-Autotrophic Pathways.....	170
Carbon Isotope Discrimination.....	170
PHOTORESPIRATION.....	170
Photorespiratory Reactions	171
Substrate Specificity of Rubisco	172
Conditions which Increase Photorespiration.....	173
Altered substrate availability: Lowered CO ₂ or Increased O ₂	173
Increased Temperature.....	173
Biological Adaptation to Minimize Photorespiration.....	173
Biochemical Carbon Concentrating Mechanisms	174
CAM (Crassulacean Acid Metabolism)	175
Algae.....	175
Biophysical Carbon-Concentrating Mechanisms	175
Eukaryotic Algae	175
Hornworts	176
Cyanobacteria	176
Possible Purpose of Photorespiration	176
References.....	177