GENERAL PHOTOBIOLOGY

by

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and

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Preface

Photobiology is an interdisciplinary science which during the past few years has undergone a dramatic development. Despite its central role in biology, medicine, physics and chemistry, until now no modern introductory text has been available. Photobiology is rooted in quite diverse fields of science which makes it difficult for the beginner to comprehend. Therefore we have decided to introduce the photochemical and photophysical basics in the opening chapters rather than to assume a solid knowledge of the required background.

The first chapter describes the fundamental photophysics with a special emphasis on the terminology, using the internationally accepted Si system of units. Studying the current photobiological literature shows that many scientists have problems using the physical units in the energetic and visual systems. Therefore we include a table with the most important physical units. Since this book is not intended to present the theoretical background, but to supply the experimenter with practical clues, the following chapters describe the commonly used light sources, filters and monochromators, as well as instruments and methods to measure radiation. The emphasis is on practical usage, and therefore we discuss the limitations of the techniques and the possible sources of error, without assuming an intimate mathematical knowledge.

Teaching photobiology in class reveals that students without a solid background in chemistry have difficulties understanding the photochemical processes at the level of electrons, atoms and molecules. Therefore the introductory part contains a detailed description of the basic photochemical reactions and the energy transfer during excitation and relaxation of molecules.

The main part of the book covers the classical photochemical topics subdivided into processes in which energy is derived from light, such as photosynthesis, and those in which light is used as a sensory signal. This second group comprises the effects of light on development (photomorphogenesis), on orientation of plants and microorganisms (photomovement) and on sensory systems of animals and men. The final chapter describes the damaging effects of UV and the possible repair mechanisms.

This book is not intended to be an encylopedic collection of reviews but rather attempts to present the subject using relevant examples. The selection is naturally subjective. The most important goal is always to explain the underlying general principle.

The wide scope of this interdisciplinary subject prohibits any individual to completely master the whole field; therefore we have relied on critical and competent help from our colleagues, to whom we are indebted. We appreciate the constructive criticism and productive discussions with Dr Braslavsky, Prof. Hartmann, Prof. Haupt, Priv.-Doz. Jabben, Prof. Nultsch, Dr Pfister, Prof. Scheer, Prof. Stieve, Prof. Trebst and Prof. Wagner. We would like to thank Prof. Song, who critically read the translated version. We are also very grateful to Dipl. Biol. G. Traxler for her help with the translation and to Mr Bosch, who completed most of the line drawings.

Marburg and Karlsruhe
Spring 1986

D.-P. Häder
M. Tevini

Important Units in the SI System

Basic units

length	meter	[m]
mass	kilogram	[kg]
time	second	[s]
electric current	ampere	[A]
temperature	kelvin	[K]
luminous intensity	candela	[cd]
quantity	mol	[mol]

Derived units

frequency	Hertz	$[Hz]=[s^{-1}]$
force	Newton	$[N]=[kg\ m\ s^{-2}]$
energy	Joule	$[J]=[W\ s]=[kg\ m^2\ s^{-2}]$
power	Watt	$[W]=[kg\ m^2\ s^{-3}]$
pressure	Pascal	$[Pa]=[N\ m^{-2}]=[kg\ m^{-1}\ s^{-2}]$
electric potential	Volt	$[V]=[J\ A^{-1}\ s^{-1}]=[W\ A^{-1}]$
electric charge	Coulomb	$[C]=[A\ s]=[J\ V^{-1}]$
magnetic flux	Weber	$[Wb]=[W\ s\ A^{-1}]$
magnetic induction	Henry	$[H]=[V\ s\ A^{-1}]$

Photophysical units

(*a*) *Based on photons*

quantity of photons	[mol]
steric photon density	$[mol\ sr^{-1}]$
photon fluence	$[mol\ m^{-2}]$
photon flow	$[mol\ s^{-1}]$
photon fluence rate	$[mol\ s^{-1}\ m^{-2}]$

(*b*) *Based on energy*

radiant energy	$[J]=[W\ s]$
steric energy flux	$[J\ sr^{-1}]=[W\ s\ sr^{-1}]$

energy fluence	[J m^{-2}]
energy flow	[W]=[J s^{-1}]
energy fluence rate (=flux)	[W m^{-2}]=[J s^{-1} m^{-2}]

(*c*) *Photometrical units*

luminous intensity	[cd]
luminous flux	[lm]=[cd sr]
luminous energy (light quantity)	[talbot]=[lm s]
luminance	[nit]=[cd m^{-2}]
illumination = light flux	[lx]=[lm m^{-2}]=[cd sr m^{-2}]
photometric fluence	[lx s]=[lm s m^{-2}]

Decimal prefixes

tera- (T) 10^{12}	centi- (c) 10^{-2}
giga- (G) 10^{9}	milli- (m) 10^{-3}
mega- (M) 10^{6}	micro- (μ) 10^{-6}
kilo- (k) 10^{3}	nano- (n) 10^{-9}
hecto- (h) 10^{2}	pico- (p) 10^{-12}
deca- (da) 10^{1}	femto- (f)10^{-15}
deci- (d) 10^{-1}	atto- (a) 10^{-18}

Fundamental constants

Gas constant	8.314 J mol^{-1} K^{-1}
Avogadro's number	6.022×10^{23} mol^{-1}
Boltzmann's constant	1.381×10^{-23} J K^{-1}
Elementary electric charge	1.602×10^{-19} C
Gravitational acceleration	9.806 m s^{-2}
Faraday's constant	9.649×10^{4} C mol^{-2}
Velocity of light	2.998×10^{8} m s^{-1}
Planck's constant	6.626×10^{-34} J s

Introduction

... the sun is not only the author of visibility in all visible things, but of generation and nourishment and growth ...

Plato, *The Republic*

The radiation from the sun is the single most important source of energy for life on our planet. The sun supplies the total energy for the atmospheric and climatic phenomena which cause the physical and chemical changes on the earth's surface. In addition, solar radiation has played a key role during the evolution of organisms on earth. The solar radiation is the result of nuclear fusion and covers the wavelength range from about 200 to 3200 nm when measured outside our atmosphere. The basic unit for all calculations is the solar constant, which is the extraterrestrial radiant energy which passes through a unit area perpendicular to the incident rays during 1 minute (measured at the mean solar distance). In the stated wavelength range, the solar constant amounts to about 1350 W m^{-2}. Due to absorption by oxygen, ozone, carbon dioxide and water vapour in the atmosphere the global radiation which reaches the earth's surface is about 17% less than the solar constant. Ultraviolet radiation below 300 nm is selectively filtered out of the solar spectrum by ozone, which evolves from oxygen in a photochemical reaction in the stratosphere.

The evolution of life on this planet began at a time when no oxidizing atmosphere existed which allowed the short ultraviolet radiation to reach the surface. Among other factors, it was this radiation which induced chemical evolution and caused the important changes in the already existing molecules, such as the nucleic acids. In their experiments Miller and Ponnamperuma demonstrated the photochemical production of organic molecules such as amino acids in the presence of the reducing atmosphere which is believed to have covered the earth during the initial phase of evolution.

The effect of high-energy radiation on the genesis of self-reproducing nucleic acids as the basis for the reproduction of organisms is still obscure. After the chemical evolution of light-absorbing pigments such as chlorophylls and carotenoids, bacteria-like organisms succeeded in harvesting the solar energy and transforming it into chemical energy. This process, called photosynthesis, results in the production of high-energy organic compounds (biomass) from low-energy precursors. This development gave the phototrophic organisms an ecological advantage over the chemosynthetic organisms, since solar energy is available in a virtually unlimited supply. Fossil fuels such as oil and coal result from the photosynthetic biomass production of higher and lower plants. The first primitive photosynthetic pathways operated without oxygen production. Photosynthetic bacteria still exist as representatives for this anoxigenic photosynthesis. The next step in evolution was the development of a water-splitting system which generated the oxygen in our atmosphere. Evolution could then proceed sheltered from the damaging short-wavelength UV radiation by the stratospheric ozone layer.

In addition to energy fixation, microorganisms, plants and animals use light for a wide range of complex sensory processes. It is not only aminals that orient in light and search actively for a favorable range of light intensities in their environment. Microorganisms use light-dependent movement responses to find a suitable niche in their photoenvironment. Even rooted higher plants orient with respect to light, as can easily be observed in pot plants which turn their leaves toward the window. The necessity for photoorientation is obvious in photosynthetic organisms which depend on the availability of radiation, but non-photosynthetic organisms also use photoorientation, for example to escape extreme light intensities which might bleach their pigments and damage cellular components.

In addition, light triggers developmental rhythms in plants and animals. It would be awkward if birds used the ambient temperature as a signal to initiate their annual migrations, since a cool late summer or a warm autumn would disturb their time schedule. Instead they use the day length as a very precise timer. Likewise plants utilize this parameter as a signal for flower initiation or leaf abscission. Both plants and animals are capable of measuring the day length very exactly and compare it with their internal oscillator ('*Zeitgeber*'). The morphology of an organism is controlled by light. When a plantlet grows out of the soil it develops leaves only above the surface. Light induces leaf growth and stimulates chloroplast development since in darkness the photosynthetic apparatus would be useless.

The basic photochemical and photophysical reactions are the same in all organisms regardless of whether the absorbed radiation is used for energy fixation or to control development or movement. A quantum of light of a defined wavelength is absorbed by a photoreceptor molecule. This process excites an electron which undergoes a transition to an energetically higher state. This energy can be lost again when the molecule returns to its ground state by emission of a quantum or by losing the energy as heat. As an alternative the energy of the excited state can be utilized for chemical reactions.

The book is divided into three parts. First we introduce the photophysical and photochemical principles of excitation and relaxation of photoreceptor molecules. Then we discuss the energy-fixing processes in bacteria and higher plants. Finally we cover the sensory processes in microorganisms, plants, animals and men, controlled by light.

Contents

PART I

General Photophysics