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COMPREHENSIVE SOVIET ENCYCLOPEDIA
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EDITED TRANSLATION

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U. S. BOARD ON GEOGRAPHIC NAMES TRANSLITERATION SYSTEM

Block	Italic	Transliteration	Block	Italic	Transliteration
А а	А а	A, a	Р р	Р р	R, r
Б б	Б б	B, b	С с	С с	S, s
В в	В в	V, v	Т т	Т т	T, t
Г г	Г г	G, g	У у	У у	U, u
Д д	Д д	D, d	Ф ф	Ф ф	F, f
Е е	Е е	Ye, ye; E, e*	Х х	Х х	Kh, kh
Ж ж	Ж ж	Zh, zh	Ц ц	Ц ц	Ts, ts
З з	З з	Z, z	Ч ч	Ч ч	Ch, ch
И и	И и	I, i	Ш ш	Ш ш	Sh, sh
Й й	Й й	Y, y	Щ щ	Щ щ	Shch, shch
К к	К к	K, k	Ъ ъ	Ъ ъ	"
Л л	Л л	L, l	Ы ы	Ы ы	Y, y
М м	М м	M, m	Ь ь	Ь ь	'
Н н	Н н	N, n	Э э	Э э	E, e
О о	О о	O, o	Ю ю	Ю ю	Yu, yu
П п	П п	P, p	Я я	Я я	Ya, ya

*ye initially, after vowels, and after ъ, ь; e elsewhere.
 When written as ё in Russian, transliterate as yë or ë.
 The use of diacritical marks is preferred, but such marks may be omitted when expediency dictates.

GREEK ALPHABET

Alpha	A α α	Nu	N ν
Beta	B β	Xi	Ξ ξ
Gamma	Γ γ	Omicron	Ο ο
Delta	Δ δ	Pi	Π π
Epsilon	Ε ε ε	Rho	Ρ ρ ϱ
Zeta	Ζ ζ	Sigma	Σ σ ς
Eta	Η η	Tau	Τ τ
Theta	Θ θ ϑ	Upsilon	Υ υ
Iota	Ι ι	Phi	Φ φ ϕ
Kappa	Κ κ κ	Chi	Χ χ
Lambda	Λ λ	Psi	Ψ ψ
Mu	Μ μ	Omega	Ω ω

RUSSIAN AND ENGLISH TRIGONOMETRIC FUNCTIONS

Russian	English
---------	---------

sin	sin
cos	cos
tg	tan
ctg	cot
sec	sec
cosec	csc
sh	sinh
ch	cosh
th	tanh
cth	coth
sch	sech
csch	csch
arc sin	\sin^{-1}
arc cos	\cos^{-1}
arc tg	\tan^{-1}
arc ctg	\cot^{-1}
arc sec	\sec^{-1}
arc cosec	\csc^{-1}
arc sh	\sinh^{-1}
arc ch	\cosh^{-1}
arc th	\tanh^{-1}
arc cth	\coth^{-1}
arc sch	sech^{-1}
arc csch	csch^{-1}

rot	curl
lg	log

GRAPHICS DISCLAIMER

All figures, graphics, tables, equations, etc. merged into this translation were extracted from the best quality copy available.

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"Bol'shaya Sovetskaya Entsiklopediya" [Comprehensive Soviet Encyclopedia], Third Edition, Vol 3, "Bari" to "Braslet," A.M. Prokhorov, editor in chief

Biological Rhythms

Cyclical fluctuations in the intensity and character of biological processes and phenomena. Biological rhythms are observed in almost all animals and plants, both unicellular and multicellular, in several isolated organs, and in individual cells. Some biological rhythms (heart beat, respiratory rate, etc.) are relatively self-sustaining (cf. Physiological Rhythms), and others--biological rhythms per se--make it possible for organisms to adapt to cyclical variations in the surrounding environment (24-hour, seasonal, etc.).

Solar Circadian Cycle--This (24-hour) rhythm is characteristic of the majority of physiological processes (cell division rate, variations in body temperature and intensity of metabolism and energy metabolism in animals and man, etc.). It is manifested in the condition and behavior of living organisms (cf. Activities Cycle); through it appear variations in the motor activity of animals, the position of leaves and flower petals on plants, the consumption of glycogen in the liver of mammals, and other biochemical processes (Figs. 1 and 2). In animals have been found neurohumoral centers which coordinate the 24-hour recurrence of physiological processes. Depending on the number of periods of activity in the course of 24 hours, monophasic and polyphasic circadian cycles are distinguished. In the course of individual development (ontogenesis) of many animals and man, a transition takes place from a polyphasic cycle to a monophasic (thus, for infants multiple shifting between sleep and being awake within a 24-hour period is characteristic).



Fig. 1. Twenty-Four-Hour Variations in the Position of Leaves on Leguminous Plants with Normal Alternation Between Night and Day (A) and with Constant Darkness (B). (Diagram 1) Twenty-Four-Hour Cycle of Variation in the Coloration of the Luring Crab under Normal Conditions (A) and with Constant Darkness (B). (Diagram 2)

Key:

- | | |
|------------------|-------------|
| 1. Number of day | 4. B |
| 2. Noon | 5. Midnight |
| 3. A | |

Lunar Circadian Cycle (24.8-hour)--Also called the tidal cycle, this rhythm is characteristic for the majority of coastal and marine animals and plants and is manifested in conjunction with the solar circadian cycle in variations in motor activity, in the cycle during which mollusks open their valves, in the vertical distribution of tiny marine animals in the ocean depths, etc. The solar and lunar circadian cycles as well as the stellar circadian cycle (23.9-hour) are of great importance in animal navigation (e.g., of migratory birds and many insects) for animals which "utilize" celestial references.

Lunar Monthly Cycle (29.4-24-hour-period)--This rhythm corresponds to the cycle of variation in the level of ocean tides and is manifested in the rhythmic cycle observed by insects hatched in coastal areas when they emerge from pupas, in the reproduction cycle of the palolo worm, of several types of algae, and of many other animals and plants. It is close to the lunar monthly rhythm and menstrual cycle of women.

Annual (Seasonal) Cycle--This rhythm in the variation in the number and activity of animals and in the growth and development of plants is widely known. Annual rhythms in plants and animals are regulated in many instances by variations in the duration of daylight (cf. Photoperiodism), temperature, and other climatic factors.

A biological rhythm is not only a direct reaction to variations in external conditions. It is maintained under artificial conditions--with constant illumination, temperature, humidity, and atmospheric pressure; and the length of each period as well. Biological rhythms under such conditions almost do not depend on the intensity of metabolic processes. For example, chemical substances which retard metabolic processes have no influence on the circadian cycle for sporulation in several types of algae; mass hatching of fruit flies recurs in darkness every 24 hours and does not depend on temperature (when it varies from 16 to 26°C); sea mollusks continue to maintain their valve-opening cycle, which is lunar, for an extended period in an aquarium; the germination of seeds kept in darkness at a constant temperature (from -22 to +45°C) varies distinctly according to the season. Under steady conditions the solar circadian cycle is usually transformed into a so-called "circadian rhythm" with a period characteristic of each subject and differing somewhat from 24 hours. Circadian recurrence occurs in organisms grown under steady conditions after a short-term change in these conditions, which proves a congenital predisposition to

this type of rhythm. Thus, rhythmic activity close to normal takes place in fruit flies grown in darkness after a single flash of light lasting 0.5 microseconds.

There are currently two points of view on the nature of biological rhythms: 1) Biological rhythms are based on strictly periodic physiochemical processes taking place in the organism--on a "biological clock." Variations in external conditions act as timing signals which can shift rhythmic phases. When conditions are steady the periodic cycle is totally spontaneous, as proven by lack of conformity of the circadian rhythm to fluctuations in geophysical factors. 2) The organism is sensitive to cycles in permeating geophysical factors (the geomagnetic field, cosmic rays, etc.). The internal system for measuring time, if there is one, plays a secondary role. Changes in light and temperature can shift the phase of a biological rhythm relative to the geophysical cycle. A regular shift in the phase of the biological rhythm can take place under the influence of conditions which are constant but unnatural for the organism.

Bibliography: Byunning, E. "Rhythms of Physiological Processes," translated from German, Moscow, 1961; "The Biological Clock," collection of articles translated from English, Moscow, 1964.

V.B. Chernyshev

Biological Cycles

This term refers to the rhythmic recurrence of biological phenomena in communities of organisms (populations and biocoenosis) which acts as an adaptation to cyclical changes in the conditions of their existence. Biological cycles come under the more general concept of biological

rhythms, which includes all rhythmically recurring biological phenomena. Biological cycles can be daily, seasonal (annual), or perennial.

Daily Biological Cycles--These are expressed by regular variations in physiological phenomena and in animal behavior in the course of a 24-hour period (cf. Activity Cycle). They are based on automatic mechanisms which are modified by the effect of external factors--24-hour variations in light, temperature, humidity, etc.

Seasonal Biological Cycles--These are based on changes in metabolism which are controlled in animals by means of hormones. At different seasons there are variations in the condition and behavior of organisms within the population or biocoenosis: Reserve substances are stored (consumed), the integument is replaced (moulting), and reproduction, migration, dormancy, and other seasonal phenomena begin (end). Being automated to a considerable extent, these phenomena are modified by external influences (the weather, supply of food, and the like).

Perennial Biological Cycles--These are caused by cyclical fluctuations in climate and other conditions of existence (associated with changes in solar activity and other cosmic or planetary factors); such biological cycles take place on the level of the population or biocoenosis and are expressed by fluctuations in reproduction and number of various species (cf. Dynamics of Animal Population, and Life Waves), in resettlement of a population in new areas, or in extinction of part of it. These phenomena are the end result of cyclical changes in populations and biocoenosis and of fluctuations in the conditions of their existence, in climate, mainly.

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translated from English, Moscow, 1967; Emme, A.M., "The Biological Clock," Novosibirsk, 1967.

N.P. Naumov

Biological Effect of Ionizing Radiation

Changes brought about in the vital activity and structure of living organisms under the influence of shortwave electromagnetic waves (x-rays and gamma rays) or a stream of charged particles (alpha particles, beta rays, protons) and neutrons.

Studies of the biological effect of ionizing radiation were begun immediately after the discovery of x-rays (1895) and radioactivity (1896). In 1896 the Russian physiologist I.R. Tarkhanov demonstrated that x-rays passing through living organisms impair their vital activity. Studies of the biological effect of ionizing radiation received special impetus with the beginning of the use of atomic weapons (1945), and subsequently with the worldwide use of atomic energy (cf. Radiology).

There are a number of general patterns characteristic of the biological effect of ionizing radiation: 1) Intense impairment of vital activity is caused by negligible quantities of absorbed energy. Thus, the energy absorbed by the body of a mammal or of a human being when irradiated with a lethal dose, when converted into heat, would result in heating the body a total of 0.001°C. An attempt to explain the "lack of agreement" between the quantity of energy and the results of the effect has resulted in creation of the target theory (cf. Target Theory), according to which radiation injury develops when the energy strikes an especially radiation-sensitive section of the cell--the "target." 2) The biological effect of ionizing radiation is not restricted to the organism subjected to irradiation but can spread to succeeding generations, which is explained by its influence on the

organism's hereditary apparatus. It is precisely this characteristic which confronts mankind with urgent questions relating to radiation, the biological effect of ionizing radiation, and protection of the organism from radiation. 3) Characteristic of the biological effect of ionizing radiation is a dormant (latent) period, i.e., the development of radiation injury is not observed immediately. The extent of the latent period can vary from several minutes to scores of years, depending on the radiation dose, the sensitivity of the organism to radiation, and a function which is under study (Figs. 1 and 3). Thus, with irradiation in very large doses (scores of thousands of rads) it is possible to cause "radiation death," and long-term irradiation in small doses results in a change in the condition of the nervous and other systems, and to the appearance of tumors years after irradiation.

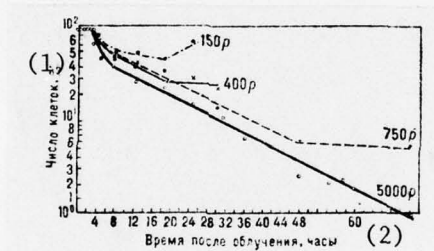


Fig. 1. Influence of Irradiation Dose on the Survival Rate (%) and Length of Survival of Bone Marrow Cells in Rats

Key:

1. Number of cells, %
2. Time after irradiation, in hours

The sensitivity of different kinds of organisms to radiation is different. Death is caused in one half of the following animals subjected to irradiation (total irradiation) within 30 24-hour periods after irradiation (lethal dose--LD 50/30), by the following x-ray doses: Guinea pigs, 250 rads; dogs, 335 rads; monkeys, 600 rads; mice, 550 to

650 rads; crucian carp (at 18°C), 1800 rads; and snakes, 8000 to 20,000 rads. More resistant unicellular organisms: Yeast dies with a dose of 30,000 rads; amoebae with 100,000 rads; and infusorians withstand radiation in a dose of 300,000 rads. The sensitivity to radiation of the higher plants is also different: Lily seeds lose their ability to germinate completely with an irradiation dose of 2000 rads, and a dose of 64,000 rads has no influence on cabbage seeds.

Age also has a great influence (Fig. 2), as well as the physiological condition and intensity of the metabolic processes of the organism, and irradiation conditions also. Furthermore, in addition to the dose with which the organism is irradiated, the following play a role: The exposure rate, the radiation cycle, and the nature of the irradiation (one-time, multiple, intermittent, chronic, external, total or partial, internal), its physical features, determining the depth of penetration of energy into the organism (x-rays and gamma rays penetrate to a great depth, alpha particles as much as 40 microns, and beta particles several millimeters), and the density of ionization brought about by the rays (under the influence of alpha particles it is greater than under the influence of other types of irradiation). All these features of the active radiating agent determine the relative biological effectiveness of the radiation. If the radiation source is radioactive isotopes striking the organism, then of immense importance to the biological effect of the ionizing radiation emitted by these isotopes are their chemical characteristics, which determine participation of the isotope in metabolism, its concentration in one organ or another, and, consequently, the nature of the irradiation the organism is subjected to.

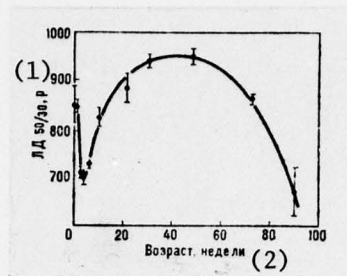


Fig. 2. Survival Rate of Irradiated Mice (LD 50/30) vs. Age

Key:

1. LD 50/30, rads

2. Age, weeks

The primary effect of any type of radiation on any biological subject begins with the absorption of radiation energy, which is accompanied by excitation of molecules and their ionization. When molecules of water ionize (indirect effect of radiation) in the presence of oxygen active radicals (OH^- , etc.), hydrated electrons, and molecules of hydrogen peroxide appear, which are then included in the chain of chemical reactions in the cell. When organic molecules ionize (direct effect of radiation), free radicals arise (cf. Free Radicals), which, being included in the chemical reactions which take place in the organism, disturb the process of metabolism, and, bringing about the appearance of compounds foreign to the organism, disturb the processes of vital activity. During irradiation with a dose of 1000 rads in a cell of average size (10^{-9}g) about one million of these radicals arise, each of which, in the presence of the oxygen in the air, can cause the beginning of chain reactions of oxidation which increase the number of mutated molecules in the cell by a great factor and which cause an extreme alteration of supermolecular (submicroscopic) structures. Understanding of the great role of free oxygen in chain reactions resulting in radiation injury, the so-called oxygen effect, has been conducive to the development of a number of effective radio-protective substances, which cause artificial hypoxia in the organism's

tissues. Of great significance also is the migration of energy through molecules of biopolymers, as the result of which the absorption of energy taking place at any place in the macromolecule results in damage to its active center (e.g., to inactivation of an enzyme-protein). The physical and physical-chemical processes which underly the biological effect of ionizing radiation, i.e., the absorption of energy and the ionization of molecules, take fractions of a second (Fig. 3).

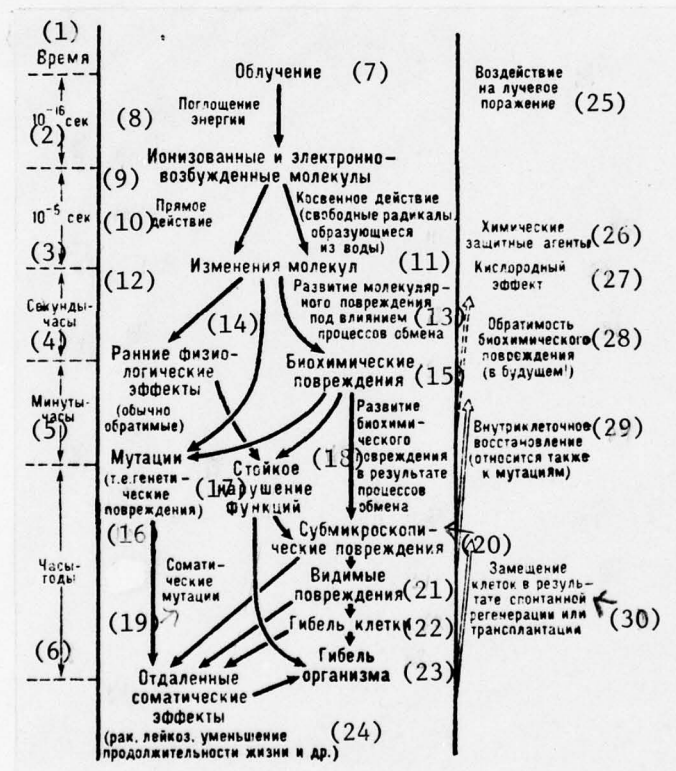


Fig. 3. Diagram of the Development of Radiation Injury (in center), and Methods of Influencing It (at right)
[key on following page]

Key:

- | | |
|--|--|
| 1. Time | 16. Mutations (i.e., genetic damage) |
| 2. 10^{-16} s | 17. Persistent functional impairment |
| 3. 10^{-5} s | 18. Development of biochemical damage as the result of metabolic processes |
| 4. Seconds to hours | 19. Somatic mutations |
| 5. Minutes to hours | 20. Submicroscopic damage |
| 6. Hours to years | 21. Visible damage |
| 7. Irradiation | 22. Cell destruction |
| 8. Absorption of energy | 23. Destruction of organism |
| 9. Ionized and electronically excited molecules | 24. Remote somatic effects (cancer, leukemia, shortening of life span, etc.) |
| 10. Direct effect | 25. Influencing radiation injury |
| 11. Indirect effect (free radicals formed from H_2O) | 26. Chemical protective agents |
| 12. Molecular changes | 27. Oxygen effect |
| 13. Development of molecular damage under the influence of metabolic processes | 28. Reversibility of biochemical damage (in future!) |
| 14. Early physiological effects (usually reversible) | 29. Intracellular regeneration (refers also to mutations) |
| 15. Biochemical damage | 30. Replacement of cells through spontaneous regeneration or transplantation |

The following biochemical processes of radiation injury develop more slowly: The active radicals formed disrupt normal enzymatic processes in the cell, leading to a reduction in the quantity of energy-rich (macroergic) compounds. Especially sensitive to irradiation is the synthesis of deoxyribonucleic acids (DNA) in intensively dividing cells. Also, as the result of chain reactions taking place during the absorption

of radiation energy, many cell components are altered, including macromolecules (DNA, enzymes, etc.) and comparatively small molecules (adenosine triphosphoric acid, coenzymes, etc.). This results in impairment of enzymatic reactions, physiological processes, and cellular structures.

The effect of ionizing radiation brings about cell damage. The most important is the impairment of cell division--mitosis. With irradiation in comparatively small doses temporary cessation of mitosis is observed. Large doses can cause total cessation of division or destruction of cells. Impairment of the normal process of mitosis is accompanied by chromosomal rearrangement and the appearance of mutations resulting in shifts in the cell's genetic apparatus and, consequently, in alteration of subsequent cell generations (the cytogenetic effect). With irradiation of the sex cells of multicellular organisms impairment of the genetic apparatus results in alteration of hereditary properties of organisms developing from them (cf. Genetic Effect of Radiation). With irradiation in large doses swelling and pyknosis of the nucleus (chromatin consolidation) take place, and then the structure of the nucleus disappears. In the cytoplasm, with irradiation in doses of 10,000 to 20,000 rads, are observed alteration of viscosity, swelling of protoplasmic structures, formation of vacuoles, and increased permeability. All this drastically impairs the vital activity of the cell.

A comparative study of the radiation sensitivity of the nucleus and cytoplasm has demonstrated that the nucleus is sensitive to irradiation in the majority of cases (e.g., irradiation of nuclei of the cardiac muscle of a newt with a dose of several protons brought about typical destructive changes in the nuclei; a dose several thousand times greater did not harm the cytoplasm). Numerous data demonstrate that the cells are most sensitive to radiation in the

period of division and differentiation; growing tissues are injured first and foremost during irradiation. This makes irradiation most dangerous for children and pregnant women. This is also the basis for radiotherapy of tumors--the growing tissue of the tumor is destroyed during irradiation with doses which do less harm to the surrounding normal tissue.

The changes which take place in irradiated cells result in impairments in tissues and organs and in the vital activity of the entire organism. Especially pronounced is the reaction of tissues in which individual cells live a comparatively not-too-long time. An example is the mucous membrane of the stomach and intestine, which after irradiation becomes inflamed and covered with ulcers, resulting in impairment of digestion and absorption, and then to malnutrition of the organism, intoxication with products of cell degeneration (toxemia), and penetration of bacteria living in the intestine into the blood (bacteriemia). The hematogenic system undergoes intense damage, resulting in a drastic decline in the number of leukocytes in the peripheral blood and to lowering of its protective properties. The production of antibodies drops at the same time, weakening the protective power of the organism even more. (Reduction in the ability of an irradiated organism to produce antibodies and at the same time to resist introduction of a foreign protein is utilized in transplanting tissues and organs--the patient is irradiated before the operation.) The number of erythrocytes is also reduced, with which is associated impairment of the blood's respiratory function. The biological effect of ionizing radiation causes impairment of sexual functioning and of the formation of sex cells right up to the point of total infertility (sterility) in irradiated organisms. The nervous system plays an important role in the development of radiation injury in animals and man. Thus, in rabbits a lethal outcome with irradiation using a dose of 1000

rads is frequently determined by disturbances in the central nervous system which cause cessation of cardiac activity and respiratory paralysis. Studies of bioelectric potentials of the brain of irradiated animals and people subjected to radiotherapy have demonstrated that the nervous system reacts to the influence of radiation earlier than other systems of the organism. Irradiation of dogs using a dose of five to 20 rads and chronic irradiation using an 0.05-rad dose to achieve a dose of three rads result in alteration of conditioned reflexes. A major role in the development of radiation sickness is also played by disturbances in the activity of endocrine glands.

Characteristic of the biological effect of ionizing radiation is a result which can be of a very long-term nature, since upon the termination of irradiation the chain of biochemical and physiological reactions, which begin with the absorption of radiation energy, continues for a long time. Some of the remote effects of irradiation are blood changes (reduction in number of leukocytes and erythrocytes), nephrosclerosis, cirrhosis of the liver, changes in the muscular layers of vessels, early ageing, and the appearance of tumors (cf. Blastogenic Effect of Irradiation). These processes are associated with disturbance of metabolism and the neuroendocrinal system, and also with damage to the genetic apparatus of the body's cells (somatic mutations).

Plants are more sensitive to radiation than animals. Exposure in not-too-large doses can stimulate the vital activity of plants (Fig. 4)--seed germination, intensity of root growth, accumulation of green mass, etc. Large doses (20,000 to 40,000 rads) cause a reduction in the survival rate of plants, the appearance of malformations and mutations, and the occurrence of tumors. Disturbances in the growth and development of plants subjected to irradiation are associated to a considerable extent with changes in metabolism and with the appearance of primary radiotoxins, which stimulate vital activity in small amounts but suppress and impair it in large. Thus, irrigation of irradiated

seeds in the course of a 24-hour period after exposure reduces the depressing effect 50 to 70 percent.

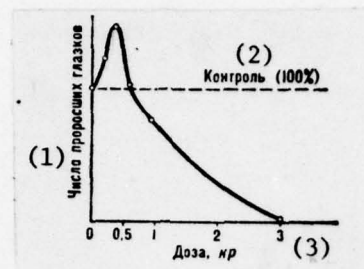


Fig. 4. Relationship between the Number of "Lorkh" Variety Potato Eyes Germinated and the Exposure Dose

Key:

1. Number of eyes germinated
2. Control
3. Dose, in kilorads

Radiation injury to the organism is accompanied simultaneously by the ongoing process of regeneration, which involves normalization of metabolism and cell regeneration. Therefore, divided exposure or exposure with doses of a low level cause less damage than a massive effect. Study of the processes of regeneration is important for the search for radioprotective substances and for methods and means of protecting the organism from radiation. All inhabitants of the Earth are constantly subjected to the effect of ionizing radiation in small doses--to cosmic rays in radioactive isotopes which make up organisms themselves and the surrounding environment (cf. Radioactivity of the Atmosphere, and Radioactive Contamination of the biosphere). Testing of atomic weapons and the worldwide use of nuclear energy are increasing the radioactive background. This makes the study of the biological effect of ionizing radiation and the search for protective means all the more important.

The biological effect of ionizing radiation is being utilized in biological research and in medical and agricultural practice. Radio-therapy, radiodiagnosis, and radio isotope therapy are all based on the biological effect of ionizing radiation.

In agriculture, radiation effects are being used to derive new forms of plants, for treatment of seeds prior to sowing, for combating blight (by producing and deriving males sterilized through irradiation for infested plantations), for preserving fruit and vegetables through radiation, for protecting crop-growing products from pests (doses which destroy insects are harmless for grain), etc.

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S.I. Landau-Tylkina, edited by A.M. Kuzin

Bioluminescence

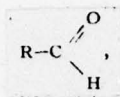
(From bio- and luminescence), visible luminescence of organisms associated with processes of their vital activity; observed in several scores of species of bacteria and lower plants (mushrooms), in some invertebrates (from the simplest to and including insects), and in fish (cf. insertion, Table XXII). Bioluminescence is more widespread among inhabitants of seas and oceans. Here luminescent organisms sometimes reproduce to such an extent that they cause a sea glow. In many organisms

(bacteria, very simple organisms, crustaceans, fungi, etc.) luminescence occurs steadily and continuously if there is oxygen in the surrounding environment. In others bioluminescence occurs in individual flashes and is associated with the conditions of their vital activity (hunger, reproduction period, etc.). The biological significance of bioluminescence varies. Thus, in luminescent insects outbursts of bioluminescence act as a signal making it possible for males and females to find one another; in a number of deepwater fish, for lighting up and luring a catch; in cuttlefish, for protection from predators (by ejecting illuminating fluids), etc. Many animals have complexly arranged phosphorescence organs. In some instances the source of an animal's bioluminescence is symbiote bacteria (e.g., the so-called non-independent phosphorescence of a number of fish).

Bioluminescence is related in mechanism to chemoluminescence. Phosphorescence occurs during enzymatic oxidation of specific substances called luciferins by the air's oxygen. Owing to the chemical energy released in the process, a portion of the luciferin's molecules go into the excited state, and when they return to the principal state they emit light. Luciferins, like the enzymes (luciferases) which catalyze their oxidation, are different in organisms of different types. Thus, for example, in bacteria the luciferin is flavin mononucleotide (riboflavin-5-phosphate)--a coenzyme of a number of redox enzymes. The common property of all luciferins is their ability to yield intense fluorescence. A luciferin derived in crystalline form can be oxidized chemically, but in this case, unlike enzymatic oxidation in the organism, the energy is released in the form of heat, and not of light quanta.

Three systems of bioluminescence in organisms are differentiated with regard to degree of complexity. The simplest, consisting only of a luciferin and luciferase, is present in Cypridina (this crayfish emits a blue-green light with a maximum wavelength of 440 to 460 nm),

in the Argon fish, and others. The phosphorescing system of bacteria is more complex. Here, in addition to a luciferin and luciferase, there is also a long-chain aldehyde, i.e., a compound of the type



where R is a straight hydrocarbon chain containing from seven to 14 atoms of carbon. A simplified picture of the bioluminescence reaction in this instance is as follows: $\text{FMN} \cdot \text{H}_2 + \frac{1}{2} \text{O}_2 + \text{E} + \text{R} \cdot \text{CHO} \rightarrow \text{FMN} + \text{H}_2\text{O} + \text{reaction products} + \text{light}$. (Here FMN is the oxidized form of flavin mononucleotide, and $\text{FMN} \cdot \text{H}_2$ is its reduced form, and E is the luciferase enzyme.) Bacteria emits a green light with a maximum wavelength of about 560 nm. Insects, e.g., glowworms, have a more complicated bioluminescence system. Their bioluminescence organs emit flashes of yellow-green light (about 560 nm) brought about by nerve pulses. For a bioluminescence reaction in insects ATP (cf. Adenosine Phosphoric Acids) and magnesium are necessary in addition to the luciferin and luciferase. The energy released in the hydrolysis of ATP (cf. Bioenergetics) apparently activates the luciferin-luciferase system and makes possible oxidation of the luciferin with the emission of light. This system does not function in the absence of ATP.

It has been suggested (the American scientist U.D. MacElroy, et al., 1962) that bioluminescence originated at the stage of transition from anaerobic forms of life to aerobic, i.e., when oxygen began to accumulate in the initial atmosphere of Earth. Probably, oxygen was toxic for the anaerobic organisms then in existence and organisms capable of reducing it rapidly received preference. Furthermore, the release of energy in the form of light was more advantageous than in the form of heat in a number of instances. In the most simple bioluminescing forms the energy released in the oxidation of substrates was let out in the form of light or heat, i.e., it was released without benefit to the organism.

Therefore, in the course of further evolution organisms in whom an energy accumulation mechanism arose (cf. Phosphorylation, oxidative) received preference. With the appearance of these forms oxidative luminescent reactions began not to yield advantages in natural selection and even became injurious. But as the result of secondary evolutionary processes bioluminescence could be preserved as a rudimentary trait in individual groups of organisms not related to one another, in which it acquired other functions, e.g., the function of a mating signal in glowworms.

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Bioenergetics

Biological energetics studies the mechanisms of energy conversion in the vital activity processes of organisms. In other words, bioenergetics deals with vital activity phenomena in their energy aspect. The methods and approaches to phenomena studied which are used in bioenergetics are physical chemical, and the subjects and problems biological. Thus, bioenergetics represents the meeting point of these sciences and is in part molecular biology, biophysics, and biochemistry.

The beginning of bioenergetics can be considered the studies of the German physician J.R. Mayer, who discovered the law for the conservation and conversion of energy (1841) based on research on the energetic

processes in the human organism. A comprehensive study of processes which are sources of energy for living organisms (cf. Respiration, and Fermentation) and of the energy balance of the organism, and of its changes under different conditions (rest, work of varying intensity, ambient temperature) has for a long time been the major content of bioenergetics (cf. Basal Metabolism, Heat Emission, and Heat Production). In the middle of the 20th century, in line with the general trend in the development of the biological sciences, a central spot in bioenergetics was occupied by studies of the mechanism of energy conversion in living organisms.

All research in the field of bioenergetics has been based on a uniquely scientific viewpoint, according to which the laws of physics and chemistry are totally applicable to vital phenomena, with the fundamentals of thermodynamics providing the basis for explaining energy conversion in an organism. But the complexity and specific nature of biological structures and of the processes taking place in them bring about a number of sharp differences between bioenergetics and the energetics of the inorganic world, industrial energetics, in particular. The primary fundamental feature of bioenergetics consists in the fact that organisms are open-ended systems which function only under conditions of steady exchange of matter and energy with the surrounding environment. The thermodynamics of such systems differs essentially from classical thermodynamics. The concept of equilibrium states, which is an axiom for classical thermodynamics, is replaced by the notion of stationary states; the second principle of thermodynamics (the principle of growth in entropy) receives a different formulation in the form of the Prigogine theorem. The second most important feature of bioenergetics involves the fact that processes in cells take place under conditions of the absence of differentials in temperature, pressure, and volume; for this reason the conversion of heat into work is impossible in an organism and heat release represents an irreversible loss of energy.

Therefore, in the course of evolution organisms have developed a number of specific mechanisms for direct conversion of one form of free energy into another, bypassing its conversion into heat. In an organism only a moderate portion of released energy is converted into heat and lost. The greater part of it is converted into the form of the free chemical energy of particular compounds in which it is extremely mobile, i.e., it can be converted into other forms even at a steady temperature; in particular, it can carry out work or be used for biosynthesis with very high efficiency levels, reaching 30 percent in the case of muscle work, for example.

One of the major results of advances in bioenergetics in recent decades has been proof of the uniformity of energetic processes in the entire living world--from microorganisms to man. Substances in which energy is stored in a mobile biologically assimilable form and the processes by means of which this storage is accomplished have been shown to be uniform for the entire world of plants and animals. The same uniformity has been established also for processes of utilization of the energy stored in these substances. For example, the structure of contractile proteins and the mechanism of the mechanical-chemical effect (i.e., conversion of chemical energy into work) are basically the same in the movement of cilia in protozoans, lowering of leaves in mimosa, or in the complicated movements of birds, mammals, and man. This uniformity is characteristic not only of phenomena studied in bioenergetics, but also of other functions present in all of life, such as the storage and transmission of hereditary information, the major means of biosynthesis, and the mechanism of enzymatic reactions.

The substances through which energy processes in organisms occur are macroergic compounds, which are characterized by the presence of phosphate groups. The role of these compounds in energy conversion processes in the organism was first established by the Soviet

biochemist, V.A. Engel'gard, when he was studying muscle contraction. Later it was demonstrated by the studies of many researchers that these compounds participate in the storage and conversion of energy in all vital processes. The energy released in separation of phosphate groups can be used to synthesize biologically important substances with a high margin of free energy, and for processes of vital activity associated with conversion of free chemical energy into work (mechanical, active transfer of matter, electrical, etc.). The most important of these compounds is a substance which plays, for the entire living world, the role of almost the only converter and transmitter of energy--adenosine triphosphoric acid, or ATP (cf. Adenosine Phosphoric Acids), which splits up into adenosine diphosphoric acid (ADP) or adenosine monophosphoric acid (AMP). Hydrolysis of ATP, i.e., separation of the endmost phosphate group from it, takes place as follows: $\text{ATP} + \text{H}_2\text{O} \rightarrow \text{ADP} + \text{phosphate}$, and is accompanied by a decrease in free energy equal to ΔF . If this reaction proceeds with an 0.1 mole concentration of all reactants and products at 25°C and pH 7.0, the free energy of the ADP will be 29.3 kJ (7000 cal) less than the free energy of the ATP. This change in free energy is greater in a cell: $\Delta F = 50 \text{ kJ/mole}$ (12,000 cal/mole). The value of ΔF for the $\text{ATP} \rightarrow \text{ADP}$ reaction is higher than in the majority of hydrolysis reactions. Also called macroergic are the bonds of the third (final) and second phosphate groups in the ATP molecule and similar bonds in other macroergic compounds. These bonds are symbolized by this sign: ~ (a tilde); e.g., the formula for ATP can be written thus: adenine ~ - ribose - phosphate ~ phosphate ~ phosphate. In speaking of the energy of macroergic bonds in bioenergetics, what is meant is not the actual energy of the covalent bond between atoms of phosphorus and oxygen (or nitrogen), as is understood in physical chemistry, but only the difference between the values of the free energy (ΔF) of the parent reactants and products of reactions for hydrolysis of ATP or other similar reactions. The "bond energy" in this sense, strictly speaking,

is not localized in a specific bond but is characterized by the reaction as a whole.

The energy of the macroergic bonds of ATP is the universal form of free energy storage for the entire living world: All conversion of energy in processes of vital activity is accomplished through storage of energy in these bonds and through its utilization when they are broken. The value of ΔF for these reactions represents, as it were, a "biological quantum" of energy, since all conversion of energy in organisms takes place in portions approximately equal to ΔF . In enzymatic hydrolysis of ATP in a cell the phosphate group which is split off is always transferred to the substrate, whose energy reserve, as a result, turns out to be greater than in the initial compound.

Exchange of matter (metabolism) in a cell consists of continuously occurring decomposition of complex substances to simpler ones (catabolic processes) and of synthesis of more complex substances (anabolic processes). Catabolic processes are exergonic, i.e., they take place with a reduction in free energy ($\Delta F < 0$); anabolic processes are endergonic, and they take place with an increase in free energy ($\Delta F > 0$). According to the general laws of thermodynamics, exergonic processes can occur spontaneously, of their own accord, and endergonic processes require an inflow of free energy from outside. This is accomplished in a cell by combining both processes: They utilize the energy released while others are taking place. This combination, which underlies all metabolism in the vital activity of the cell, is made possible by the ATP-ADP system, which creates intermediate energy-rich compounds.

For example, synthesis of saccharose from glucose and fructose takes place owing to the energy released in the ATP hydrolysis reaction,

by forming an intermediate activated compound--glucose-1-phosphate:

1) $\text{ATP} + \text{glucose} \rightarrow \text{ADP} + \text{glucose-1-phosphate}$; 2) $\text{glucose-1-phosphate} + \text{fructose} \rightarrow \text{saccharose} + \text{phosphate}$. Total reaction: $\text{ATP} + \text{glucose} + \text{fructose} \rightarrow \text{ADP} + \text{saccharose} + \text{phosphate}$.

Energy balance of the process:

$\text{ATP} \rightarrow \text{ADP} + \text{phosphate}$, -29.3 kJ/mole (-7000 cal/mole) (reduction of free energy); $\text{glucose} + \text{fructose} \rightarrow \text{saccharose}$, $+23 \text{ kJ/mole}$ ($+5500 \text{ cal/mole}$) (increase in free energy). Loss of energy to heat, 6.3 kJ/mole (1500 cal/mole), i.e., the efficiency of the process is 79%.

A combination of reactions of the same sort is accomplished in the synthesis of other complex compounds (lipids, polysaccharides, proteins, and nucleic acids). In these processes, in addition to ATP other similar compounds take part which include, instead of adenine, other nitrogen bases (guanine, cytosine, uridine, and thymidine trisphosphates, or creatine phosphates). In synthesis of proteins and nucleic acids from ATP, one final phosphate group is not split off, but the last two (pyrophosphate). Thus, all energy storage (accumulation) processes in organisms must boil down to processes for formation of ATP, i.e., for phosphorylation (including phosphate groups in ADP or AMP).

The energetics of metabolic processes, in which energy maintains the form of chemical energy, is clear as far as its basic features are concerned, but this cannot be said about processes in which the energy is converted from chemical form into mechanical work or some other form of energy (e.g., electrical). Thus, it is known, for example, that the work performed by a contracting muscle is produced on account of the energy released in the hydrolysis of ATP, but the mechanism for this conversion of energy is still not clear. Explanation of the

intimate mechanisms of the mechanical-chemical effect and of other types of conversion of chemical energy is an important and urgent problem facing bioenergetics, the solution to which can open the way to direct conversion of chemical energy into mechanical and electrical without the intermediate "destructive" conversion of it into heat.

The major and practically sole source of energy for life on Earth is the energy of the Sun's radiation, a portion of which is absorbed by pigments of plants and some bacteria and in the process of photosynthesis is stored by autotrophic organisms in the form of chemical energy, partly in the form of ATP (processes of photosynthetic phosphorylation), and partly in the form of the energy of several specific compounds (reduced nicotinic-amide-adenine dinucleotides), which are the most important intermediate accumulators of energy. The entire further process of synthesis of carbohydrates and then of lipids, proteins, and other cell components is accomplished in the cycle of dark enzymatic reactions owing to the energy of the forementioned compounds.

In the reaction for synthesis of carbohydrates [overall: $6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$], the increase in free energy, $\Delta F = 2.87$ MJ/mole (686,000 cal/mole), and the heat content of the products (molar enthalpy) is altered by an amount of $\Delta H = 2.82$ MJ/mole (673,000 cal/mole). Thus, carbohydrates, lipids, proteins, and other food products represent a form of long-term storage of radiation energy absorbed by plants.

In heterotrophic organisms ATP forms in the process of respiration at intermediate stages in oxidation of food substances into CO_2 and H_2O . In this process about 40 to 50 percent of the free energy is converted into the energy of macroergic bonds of ATP, and the remainder is lost in the form of heat. The total amount of energy stored by plants in a

year (with the simplified assumption that all the carbon is fixed in the form of glucose) equals approximately 10^{18} to 10^{21} J, which amounts to only 0.001 times the total flow of solar energy striking Earth (10^{24} J per year).

A certain amount of energy is stored in processes of chemosynthesis owing to oxidation of reduced inorganic compounds, but the contribution of these processes to the energetics of the biosphere is not great.

The above describes only the total energy balance in processes of storing and using energy. Study of the primary mechanisms of energy migration at the cellular and molecular level has demonstrated that a decisive role in these mechanisms is played by transport of electrons through a chain of transmitters. In individual links of this chain of redox reactions release of small portions of free energy takes place corresponding approximately to the values of ΔF for macroergic bonds of ATP.

Further study of the problems of bioenergetics, in particular of mechanisms for converting chemical energy into work, requires entering a discussion of these processes on the submolecular level, at which the laws of quantum physics and chemistry enter into the picture.

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