

Biological Impacts of
**INCREASED
INTENSITIES
OF SOLAR
ULTRAVIOLET
RADIATION**

A Report of the
AD HOC PANEL ON THE BIOLOGICAL IMPACTS
OF INCREASED INTENSITIES
OF SOLAR ULTRAVIOLET RADIATION
to the
ENVIRONMENTAL STUDIES BOARD
of the
NATIONAL ACADEMY OF SCIENCES
NATIONAL ACADEMY OF ENGINEERING

NATIONAL ACADEMY OF SCIENCES
NATIONAL ACADEMY OF ENGINEERING
WASHINGTON, D.C. 1973

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The members of the study committee were selected for their individual scholarly competence and judgment with due consideration for the balance and breadth of disciplines. Responsibility for all aspects of this report rests with the study committee, to whom sincere appreciation is hereby expressed.

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LIBRARY OF CONGRESS CATALOGING IN PUBLICATION DATA

Environmental Studies Board. Ad hoc Panel on the Biological Impacts of Ultraviolet Radiation.

Biological impacts of increased intensities of solar ultraviolet radiation.

Includes bibliographical references.

1. Ultra-violet rays—Physiological effect. I. Title. [DNLM: 1. Radiobiology. 2. Sunlight. 3. Ultraviolet rays—Therapeutic use. 4. Ultraviolet rays—Adverse effects WN 610 A189b 1973]

QH652.E57 574.1'9154 72-13835

Available from

Environmental Studies Board, National Academy of Sciences
2101 Constitution Avenue, N.W., Washington, D.C. 20418

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Preface

In the spring of 1971 the possible environmental impacts of a future fleet of supersonic transport (SST) aircraft had become a topic of intense national interest. Knowledge of SST effects on the atmosphere and consequences thereof was quite limited. One of the possibilities discussed was that emissions from SST aircraft might reduce the amount of ozone in the upper atmosphere and thereby lead to an increase in solar ultraviolet (UV) radiation reaching the surface of the earth. While the likelihood of this possibility is still a topic of scientific debate, it is important to explore the implications of such changes. Thus, the Environmental Studies Board was receptive to a suggestion from Professor Kendrick Smith of Stanford University for a study of the biological consequences of an increase in terrestrial UV radiation. A committee of 9 knowledgeable people was assembled, and they met and deliberated for three days in November 1971. A draft report resulted that was circulated for comment among the attendees and other qualified scientists and was reviewed by the ESB.

The Environmental Studies Board is publishing *Biological Impacts of Increased Intensities of Solar Ultraviolet Radiation* in the interest of making information on the subject accessible. The Board gratefully acknowledges the financial support of the study by the Department of Transportation and the Scaife Family Charitable Trusts Foundation.

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I Introduction

Solar radiation is a very important element in our environment, yet, perhaps because of its ubiquity, the wide scope of its chemical and biological effects is often not fully appreciated. The sun is necessary for life: We are warmed by its rays, and we are able to see because our eyes respond to that portion of the solar spectrum known as visible light. More important, visible light is required for photosynthesis—the process by which plants obtain the energy needed for their growth and for man's sustenance.

Nevertheless, many of the effects of solar radiation are detrimental. Most people are aware that a painful sunburn can be caused by excessive exposure to the sun and that sunlight causes colors to fade and materials to age. Skin cancer is also produced by excessive exposure to sunlight. There are many other effects of solar radiation on cells, including the production of chemical changes (mutations) in their hereditary (genetic) material. Recent study has shown that plant and animal cells are able, to varying extents, to repair radiation-induced genetic damage. Evidently, plants and animals have evolved such repair systems in order to help protect themselves from the detrimental radiations of the sun and thereby allow themselves to receive the benefit of other wavelengths of solar radiation. The situation is one of balance: Sunlight is necessary for life, yet in excess it can be harmful.

It is the ultraviolet (UV) portion of sunlight that is most detrimental to plant and animal cells. The small amount of ozone in the earth's stratosphere filters out these harmful wavelengths of ultraviolet light and thus prevents most such radiation from reaching the surface of the earth. The formation of this protective shield of ozone

in prehistoric time was most likely a prerequisite for the evolution of terrestrial life. Even in the presence of this ozone layer, however, a significant amount of biologically inactivating ultraviolet radiation does reach the surface of the earth.

Recent testimony in the *Congressional Record** and an article in *Science*† suggest that water and especially the oxides of nitrogen emitted as combustion products in the operation of numerous commercial supersonic transport (SST) aircraft may partially destroy the protective shield of stratospheric ozone. This would allow an increased amount of ultraviolet radiation to reach the surface of the earth. Other human activities that lead to the large-scale emission of particulate matter into the atmosphere may decrease the amount of solar radiation reaching the earth. It is important, therefore, to explore the consequences to man and his environment of changes in both the intensity and character of the solar UV radiation reaching the earth's surface.

The goals of this report are:

1. To review some of the known effects of ultraviolet radiation on man and other living organisms;
2. To assess, as far as possible, the consequences to man and other living organisms should the amount of solar ultraviolet radiation reaching the surface of the earth increase;
3. To identify those areas where knowledge is inadequate and where further research is urgently needed.

*McDonald, J. E. *Congressional Record*. 92nd Congr. 1st Sess. Mar. 19, 1971, Vol. 117, p. S3483-3499.

†Johnston, H. 1971. Reduction of stratospheric ozone by nitrogen oxide catalysts from supersonic transport exhaust. *Science* 173(Aug. 6, 1971): 517-522.

II Conclusions

The Committee's review and discussion of the currently available information concerning the effects of ultraviolet radiation on man and other living organisms have led to the following conclusions:

- Knowledge of the wavelength distribution and intensity of the solar radiation that reaches the surface of the earth is important for understanding the biological effects of sunlight. It is the ultraviolet portion of sunlight that, in excess, is most harmful to plants and animals. A small amount of ozone in the earth's atmosphere filters out most of the ultraviolet radiation from sunlight. The concentration of ozone in the stratosphere is lowest at the equator and increases toward the higher latitudes. There are also daily and seasonal fluctuations in the ozone concentration, but, on an annual basis, the amount of ozone is rather constant for a given location. Thus, any change in the average ozone concentration will probably be of biological significance even though such a change might be less than present daily or seasonal fluctuations.

Because of the radiation-absorbing properties of ozone, a small decrease in ozone concentration will result in a much larger increase in ultraviolet radiation reaching the earth. For example, it has been estimated that a 5 percent decrease in average ozone concentration over the midlatitude of the United States would cause a 26 percent increase in ultraviolet radiation at 297.5 nanometer [(nm) equals 10^{-9} meter]; a 50 percent decrease in ozone would yield a 10-fold increase in radiation at this wavelength (one of the most biologically detrimental wavelengths of solar radiation). The question then arises as to whether man and other living organisms could sustain such increases in exposure to solar ultraviolet radiation.

- The biological effects of light are the consequence of the absorption of specific wavelengths of light by specific chemical molecules and their resultant photochemical alteration. Deoxyribonucleic acid (DNA) is the most important molecule in a cell since it carries the genetic information of that cell. DNA is easily modified by exposure to ultraviolet radiation, and this is the principal reason why ultraviolet radiation is detrimental to living organisms.

Most living cells have a significant enzymatic capacity for repairing ultraviolet radiation damage to their DNA; however, living things are in a delicate balance between the continual photochemical destruction of cellular components by solar radiation and their biochemical repair. If this balance is upset by exposure to increased amounts of ultraviolet radiation or by interference with repair, the organism will be injured and may die, or mutations may appear in offspring.

- In addition to biochemical repair mechanisms, organisms employ a number of other means to resist the damaging effects of sunlight. These are mainly (1) avoiding exposure to sunlight by appropriate behavioral responses to environmental cues (e.g., heat, visible light, etc.) and (2) preventing sunlight from reaching the sensitive tissues and cells by development of light-absorbing and light-scattering coats of hair, feathers, shells, or superficial pigment.

- A significant amount of ultraviolet radiation is transmitted through the skin of man and causes various degrees of damage to living cells absorbing it. Melanin, a dark pigment, is the main absorber of ultraviolet radiation in human skin and is highly efficient in protecting deeper structures from exposure to ultraviolet radiation. Too little is known about the relative penetration of various wavelengths of solar radiation deeper than the skin, even though important body functions (e.g., sexual maturation, biological time clocks) are known to be light-dependent.

- The induction of the three most common malignant tumors of human skin—basal cell and squamous cell carcinomas and malignant melanomas—is correlated with exposure to sunlight. The incidence of each shows a marked increase with the lack of skin pigmentation, with the inability to tan, with increasing time spent out-of-doors, and with decreasing latitudes of residence. (The ozone layer becomes thinner, and the average intensity of ultraviolet radiation increases with decreasing latitudes.)

From the relationship between the concentration of ozone in the upper atmosphere, its transmission of ultraviolet radiation, and the relationship between current levels of solar ultraviolet radiation and neoplastic changes in human skin, it has been calculated that a 5 percent decline in ozone would produce at least 8,000 extra cases of skin carcinomas and melanomas per year in a population the size of the white population of the United States.

- Sunlight produces a variety of detrimental effects in man, of which sunburn is the most common. In addition, chronic skin changes leading to wrinkling, discoloration, and thinning of the skin, which the white population interpret as aging, are primarily the result of exposure to ultraviolet radiation and are slowed by the presence of melanin in the skin. Tanning, the production of new melanin, is a protective response to the radiation injury of skin. However, many light-skinned people, genetically incapable of tanning adequately, are liable to repeated injury and consequent premature development of skin changes. While some features of the processes leading to skin damage by ultraviolet radiation are reasonably well understood, the molecular bases for these effects are not adequately known.

- A variety of chemicals, some used in medicine and some found in the environment, sensitize human skin and increase the effectiveness of solar radiation in producing phototoxic and photoallergic reactions. As more and more chemical agents are introduced into our environment, either deliberately or accidentally, the number of patients with such disorders will continue to increase, particularly if solar ultraviolet radiation intensities also increase.

- Sunlight has long been believed to have prophylactic and healing powers for the promotion of health. This accounts for the behavior of millions of people who annually flock to beaches. Although the physiological, biochemical, and psychological mechanisms remain largely unstudied and unknown, there is evidence for two beneficial effects. First, ultraviolet radiation kills bacteria, of which some are beneficial to man and some are harmful. Prior to the discovery of antibiotics, ultraviolet radiation was used for the treatment of skin infected with tubercle bacilli and streptococci. Second, in man and all other animals with calcified internal skeletons, ultraviolet radiation converts provitamin D in the skin to vitamin D. A deficiency in vitamin D leads to rickets; an excessive amount of vitamin D, however, can be toxic.

Whether man and other animals would benefit or be harmed by an increased production of vitamin D from an increased amount of solar ultraviolet radiation cannot be predicted from available information.

- Solar ultraviolet radiation of the wavelengths reaching the surface of the earth is transmitted through pure water. Because of the great amount of life in the world's oceans and its importance to man, any deleterious effects of increased ultraviolet radiation in this environment could have serious ecological consequences. Present information on the depth to which ultraviolet radiation penetrates natural bodies of water, as well as the effect it has on the organisms therein, is fragmentary.

- Unlike man and other vertebrates, most insects see in a portion of the ultraviolet (near ultraviolet, at wavelengths from 300 to 400 nm), as well as in the portion of the solar spectrum that is visible to man. Moreover, near ultraviolet light is a distinct color for many species of insects and has special significance in influencing the behavior of members of this large and ecologically important group of animals. For example, because near ultraviolet light is the most effective light in attracting insects, insect traps are fitted with ultraviolet lamps. Conversely, because lamps that are poor in blue and ultraviolet light offer much less stimulation to insects, yellow bulbs are frequently used to illuminate porches and patios. There are other examples, less obvious but vastly more important ecologically: celestial navigation by insects using the blue and ultraviolet polarization pattern of skylight, recognition of flowers by their distinct colors and patterns of color generated by ultraviolet reflectance, and sex recognition in butterflies based on ultraviolet reflectance patterns from wings.

An increase in the intensity of ultraviolet radiation, at wavelengths shorter than 320 nm, would increase the relative brightness of objects reflecting in this spectral region. However, neither the effects on insect behavior nor possible deleterious consequences of increased chronic exposure of the receptor cells can be accurately predicted from available data.

- Under laboratory conditions, ultraviolet radiation is clearly detrimental to a wide variety of plant species ranging from bacteria to higher plants. Agricultural species are among the plants most sensitive to ultraviolet radiation. Although it is not possible to predict the

exact biological consequences of increased ultraviolet radiation at the earth's surface, sensitive plant species may well be endangered. Natural defenses against ultraviolet radiation and efficient repair systems exist in plants, but these may not be sufficient to cope with higher intensities of ultraviolet radiation.

III Recommendations

Sufficient knowledge is at hand to warrant utmost concern over the possible detrimental effects on our environment by the operation of large numbers of supersonic aircraft. In order to better analyze and predict the consequences to man and other living organisms of a significant reduction in the stratospheric ozone concentration by these aircraft, this Committee recommends that the following research be carried out in the very near future.

Monitoring the Quality and Quantity of Solar Radiation

A network of monitoring stations should be established to determine the spectral distribution and intensity of natural ultraviolet radiation reaching the surface of the earth. These stations should be located at various latitudes and altitudes and be capable of extended operation so that short-term and long-term changes in the intensity and spectral quality of solar ultraviolet radiation can be adequately recorded. This information is needed not only as a base line for monitoring possible environmental changes (e.g., from SST's) but is also critically necessary in order to evaluate numerous biological effects of sunlight (e.g., the regional incidence of skin cancer) that now are only correlated with changes in latitude (i.e., changes in ozone concentration) or altitude.

It is important that these measurements provide narrow-band spectral data rather than mean values of intensity for wide wavelength intervals.

Laboratory Use of Wavelengths of Light Found in Sunlight

Most of our information on the chemical and biological effects of ultraviolet radiation comes from experiments using so-called germicidal lamps that emit radiation at a wavelength (254 nm) not normally found in sunlight reaching the earth's surface. Several published studies on bacteria, plant viruses, and man show that the biological damage produced at 254 nm is different from that produced with ultraviolet radiation at wavelengths found in sunlight. Therefore, the chemical and biological effects of the wavelengths of ultraviolet radiation found in sunlight should be studied. This may require the development of lamps that match the output of the sun in the ultraviolet region measured at the surface of the earth.

The biological effects of ultraviolet radiation have usually been studied in the laboratory in the absence of visible radiation. There is growing evidence that visible light can, under different conditions, either help cells to repair ultraviolet-radiation-induced damage or can potentiate the detrimental biological effects of ultraviolet radiation. Thus, to better understand the effects of sunlight on man and his environment, experiments should be performed using natural sunlight or artificial lamps whose spectral output closely approximates that of sunlight.

Skin Cancer in Man

Studies are needed to describe and quantify the interactions between environment, behavior, and genetic background that lead to the development of the malignant skin tumors in man induced by ultraviolet radiation. Such studies should contribute to methods for the early recognition of individuals with a high risk of developing skin cancer, so that they can receive specific advice.

Studies in laboratory animals are urgently needed to establish the basic mechanisms for the induction, by ultraviolet radiation, of the various types of malignant skin tumors.

Phototoxicity and Photoallergy

Too little is known about the mechanism of photosensitization and photoallergy in animals and man. The rapid and unselective introduction of many potentially photoactive agents into our environment necessitates development of methods to predict the extent and type

of photoinjury by such agents. A national registry of cases of phototoxicity would speed the removal of such agents from commerce.

Beneficial Effects of Ultraviolet Radiation

Claims made in earlier literature, supported by few data, of beneficial effects of ultraviolet radiation on man, such as the lowering of blood pressure and blood cholesterol, the relief of asthma, and improvements in cardiovascular functions should be reinvestigated under carefully controlled conditions.

Photobiological Resistance of Plants and Animals

Do plants and animals have sufficient reserve capacity (natural defense shields plus repair capacity) to endure an intensity of ultraviolet radiation greater than that now reaching the earth? The sensitivity to natural ultraviolet radiation and the damage repair capacity of both animals and plants should be studied in order to answer this question. In addition to laboratory studies, it is imperative to carry out field experiments in which normal solar irradiation is supplemented with UV radiation at those wavelengths (i.e., 280–320 nm) where an increase in intensity is expected if there is a decrease in the concentration of stratospheric ozone.

Although artificial sources of ultraviolet radiation, particularly those emitting at 254 nm, are quite effective in producing mutations, too little is known about the effectiveness of natural sunlight in producing mutations. It is important that further research be directed toward the assessment of the mutagenic capacity of natural sunlight (with and without supplementation by artificial UV radiation) in a wide variety of plants and animals.

Effects of Ultraviolet Radiation on the Behavior of Insects

Since insects are so necessary to our ecology, and since their vision extends into the ultraviolet portion of sunlight, information is needed on the behavioral effects of different amounts and wavelengths of ultraviolet light on insects and other animals under realistic ecological conditions. Studies of behavioral ecology and sensory physiology on a much wider sample of animal species in both tropical and temperate environments are necessary.

Effects of Ultraviolet Radiation on Ecosystems

Environmental changes can have profound effects on ecosystems as well as individual organisms. Effects that are not immediately lethal to individuals may nevertheless endanger reproductive capacity and thus the future of whole species. (The possible deleterious effects of DDT on several species of birds provide a recent example.) The study of the biological effects of ultraviolet radiation should therefore include experiments on real and model ecosystems.

Education

This Committee was convened in response to a specific issue—the possibility that SST's will damage the earth's ozone shield, and its charge was correspondingly limited—to assess the effects of increased ultraviolet radiation on living organisms. We have nevertheless been unable to avoid the following observation:

In society where political decisions are influenced by the way people vote, it is imperative that both the public at large and their political leaders be sensitive to issues and arguments based on scientific criteria, in addition to more traditional political and economic concerns. Therefore, if the general public is to understand the profound importance of sunlight in our daily life, beyond the obvious of warmth and vision, photochemists and photobiologists should concern themselves with demonstrating the relevance of their expertise to national problems. The most important conceptual roadblocks that need to be overcome are: (1) the lack of respect for the importance of the biological effects of sunlight simply because sunlight is ubiquitous and (2) the concept that if something is natural it must be totally beneficial and safe. It must be made clear that life on earth is in a delicate balance between the beneficial and detrimental effects of sunlight.

Priorities

Of the recommended projects listed in this section, the following are the ones that the Committee feels are the most critical for an early assessment of the biological impact of a possible increase in solar ultraviolet radiation.

1. Ground-level stations should be established at various latitudes to monitor the intensity and wavelength distribution of solar ultraviolet radiation. This information is needed not only as a base line for monitoring possible environmental changes but also to properly evaluate data that are currently available on the latitudinal variations in the incidence of skin cancer in man.
2. The ability of important agricultural plants to grow and produce when exposed to additional amounts of ultraviolet radiation over the region of 280-320 nm (those wavelengths expected to be most affected by changes in stratospheric ozone concentration) should be determined. These experiments should include both laboratory and field studies.
3. Because of the unique importance of plankton in the ecological food chain, their sensitivity to solar ultraviolet radiation should be studied systematically, including both laboratory and field studies. An important adjunct to these studies would be the accurate measurement of the depth of penetration into natural waters of the various wavelengths of solar ultraviolet radiation.
4. Laboratory experiments using animals are urgently needed to gain more insight into the molecular bases and dose response characteristics of ultraviolet-radiation-induced skin cancer.
5. The public should be informed that, even today, excessive exposure to solar radiation should be avoided.

IV *Documentation*

I

SOLAR ULTRAVIOLET RADIATION-VARIATIONS IN SPECTRUM AND INTENSITY

Ultraviolet (UV) radiation is usually defined as electromagnetic radiation between the wavelengths of 40 and 400 nm. It occurs between the longest wavelength x rays and the shortest wavelength of light visible to the human eye (Figure 1).

The earth's atmosphere partially shields terrestrial organisms from exposure to short wavelength solar UV radiation. Measurements by early investigators¹⁻³ using spectrographic (photographic) techniques showed that the earth's atmosphere transmits no detectable amount of solar UV at wavelengths shorter than 286 nm as measured at the earth's surface. The absence of UV radiation below 286 nm is accounted for by its efficient absorption by atmospheric ozone and oxygen.

Atmospheric ozone is mainly distributed at altitudes between 15 and 35 km.⁴ In spite of its small total amount [2.4-4.6 mm at standard temperature and pressure (STP)] ozone is the principal absorber for wavelengths from 320 nm down to about 225 nm.

In evaluating the effects of damage to the ozone shield on living organisms, it is important to know the extent to which a given decrease in atmospheric ozone can shift the current detectable limit of 286 nm toward shorter wavelengths, as well as increase the intensity of UV flux between 286 and 320 nm (the most biologically detrimental

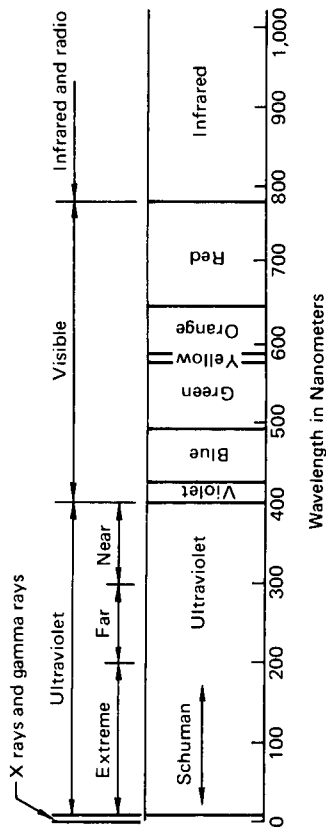


FIGURE 1 The electromagnetic spectrum.

tal wavelengths of sunlight). At present, the total amount of ozone in the atmosphere varies seasonally in thickness from 2.4 to 2.6 mm (at STP) at the equator and from 3.1 to 4.3 mm at 70° N latitude. At the equator, the noon sun plus sky intensity at 297.5 nm amounts to about $5 \times 10^{-7} \text{ W cm}^{-2} \text{ nm}^{-1} \text{ ster}^{-1}$ on clear days and for all seasons. The intensity decreases rapidly toward higher latitudes and in summer attains about $7 \times 10^{-9} \text{ W cm}^{-2} \text{ nm}^{-1} \text{ ster}^{-1}$, or 1.4 percent, at 70° N latitude. A gradually steeper decrease occurs in spring, fall, and winter, respectively.⁵ This trend is caused by the increase of ozone and the decrease of solar altitude toward higher latitudes.

The large seasonal and geographical variation of atmospheric ozone, which ranges from 2.4 mm at the equator to 4.6 mm at high latitudes, produces a 7.8 nm variation in the short wavelength limit of noon-intensity, direct solar UV radiation. A man-made reduction in ozone by 50 percent would be expected to shift the current short-wavelength limit of direct solar UV radiation to shorter wavelengths by 4.5–6.3 nm depending on latitude, solar altitude, and the detectable minimum intensity.⁵

Figure 2 shows the influence of various assumed man-made percentage decreases in mean ozone concentrations on the intensity of UV radiation at 297.5 nm at selected latitudes. For this wavelength, a 5 percent reduction in the average total amount of ozone would increase the sun plus sky intensity by 20 percent at the equator and 26 percent at a latitude (40° N) corresponding to the mid-United States. Similarly, a 50 percent reduction of the ozone content would yield a 10-fold increase in intensity at this wavelength at 40° N latitude. In general, small decreases in the amount of atmospheric ozone would be expected to cause a relatively large increase in those wavelengths of solar UV radiation that are most biologically detrimental.

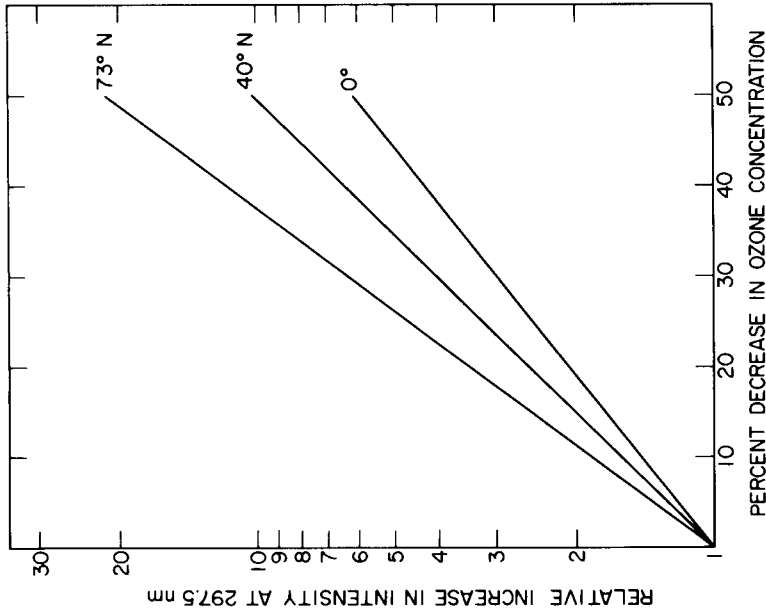


FIGURE 2 Influence of various percentage decreases in the mean total amount of stratospheric ozone on the sun plus sky intensity of ultraviolet radiation at 297.5 nm, for selected latitudes at sea level. The solar altitude is taken to be 60° for latitudes of 0° and 40° N, and 40° for 73° N latitude. The present average solar intensity has been normalized to a value of 1.0. Note that for a linear decrease in ozone concentration the intensity of the UV radiation increases exponentially (modified from Bener).⁵

This point is of utmost importance in considering the likely biological effects that might result from man-made changes in atmospheric ozone concentration.

A number of workers have monitored the transmitted solar UV flux in various wavelength regions longer than 286 nm, and much of the data has been useful for establishing trends and general relationships between observed intensities and environmental conditions or biological effects.^{4,6,7} However, a quantitative correlation

of the data of the various authors has been difficult because of the absence of common calibration standards and the lack of extended observations in most cases.

Photobiological and photochemical processes have a pronounced wavelength dependence. Many photobiological effects are produced by light in the region below 320 nm where the spectral distribution of natural UV radiation varies markedly with solar elevation and amount of ozone. It is evident that the spectral distribution must be known to compute the solar dose rate for each process.

Climatological measurements of natural UV radiation that are intended to meet the needs of scientists working in different fields should thus provide spectral data rather than mean values of intensity for wide wavelength intervals. In addition, these measurements should be made over extended periods of time and at several latitudes so that the type of data presented in Figure 2 can be confirmed.

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2

PENETRATION OF ULTRAVIOLET RADIATION INTO WATER AND BIOLOGICAL STRUCTURES

Water

There is a common feeling that water is a good shield for UV radiation; this is wrong. Although the transmission of UV radiation through long columns of water has been measured by only a few investigators, and the data are not fully consistent, they do demonstrate that UV radiation penetrates considerable distances through water. For example, Lenoble¹ reports the transmission of 1 m of distilled water at 360 nm to be 93 percent and at 310 nm to be 82 percent, while Sawyer² found 88 percent and 63 percent, respectively, for the same wavelengths. Measurements of natural waters have shown that the transmission at a depth of 1 m was 75 percent at 318.5 nm off the coast of Corsica and 43 percent at 321 nm off the coast of Brittany.¹ Furthermore, most clouds transmit more than 50 percent of solar UV radiation,³ thus explaining why man can sunburn even on cloudy days.

Oceans cover more than two thirds of the earth's surface. They provided the cradle in which life originated and currently support more than half of the biomass of the earth. Although UV radiation is known to have profound effects on all the biological systems that have been tested, including plankton and other marine organisms that are so vital to the natural food chain, we are largely ignorant of the effect of such radiation on these organisms in their natural habitat. An enhanced penetration of solar UV radiation through natural bodies of water as a consequence of stratospheric ozone destruction might well have a significant effect upon these important organisms.

Tissues

The skin of man and other vertebrates is the interface between the external and internal environments. Its response to sunlight radiation is fast, dramatic, and easily visible. Thus, its reactions have been studied extensively.⁴ The dissipation of the radiant energy impinging upon the skin can be by reflection, absorption, fluorescence,

scatter, and transmission, but it is difficult to assess all these factors adequately.⁵ The stratum corneum (the horny dead surface layer of skin) transmits about 20 percent of the UV radiation at 250 nm, 15 percent at 280 nm, 35 percent at 300 nm, and approximately 70 percent at 400 nm.⁶ Total transmission of whole epidermis (living epithelial cells and stratum corneum) is of the order of 2 percent at 250 nm, 3 percent at 280 nm, 18 percent at 300 nm, 40 percent at 350 nm, and 50 percent at 400 nm.

Studies taking into account direct transmission, as well as scattering, show that in Caucasians a physiologically significant proportion of incident UV radiation may penetrate through the stratum corneum and epidermis to the capillary blood vessels. In contrast to Caucasians, epidermis and stratum corneum of heavily pigmented Negroid or Oriental skin allows less than 1 percent of the UV radiation at 300 nm, and little or none at shorter wavelengths, to pass. Furthermore, transmission at 400 nm in Negroid skin is only 12 percent as compared to about 50 percent in Caucasian skin. The reduced transmission of heavily pigmented skin is primarily due to finely dispersed melanin in the stratum corneum and the upper epidermis.

Light of various wavelengths penetrates through skin, muscle, bone, brain, and other organs. For example, skull bones of rats transmit 5–30 percent visible light, and measurable amounts reach the depths of the brain.⁷ Similar findings were made in rabbits, dogs, and sheep.⁸ The body wall of small desert lizards even transmits significant amounts of radiation in the 350–400-nm range.⁹

Fabrics

From 25 to 75 percent of UV radiation below 320 nm can penetrate through woven fabrics, particularly certain of the newer synthetic fibers, and sunburn can be produced through such cloth.¹⁰

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3

BASIC CONCEPTS IN PHOTOCHEMISTRY AND PHOTOBIOLOGY

The biological effects of light are the consequence of the absorption of specific wavelengths of light by specific chemical molecules in cells and their resultant photochemical alteration. If the molecules absorbing the radiation are present in multiple copies in a cell and only a small proportion are altered, little biological effect may be noted. If the number of absorbing molecules is few and their biological significance is great, the effects of the radiation on a cell can be profound.

In all cells there is one compound, deoxyribonucleic acid (DNA), that is present in only one or a relatively few copies and that carries the genetic information of the cell. It is not surprising, therefore, that, if a DNA molecule is altered by radiation, the functioning of the cell is markedly affected, resulting in mutations or death. The electronic structure of DNA is such that it absorbs UV radiation but not visible light. This is the principal reason why UV radiation is so detrimental to cells and why visible light is much less harmful unless photosensitizing compounds are present.

Principles of Photochemistry¹⁻³

For radiation to have an effect it must first be absorbed. The electronic structure of each type of molecule is unique, and it is this uniqueness of structure that determines which wavelengths of radiation will be selectively absorbed. Once energy is absorbed, photochemical alterations can occur.

Molecules are normally in a stable (low-energy) ground state. When molecules absorb radiation, they are raised to a higher energy (excited) state that has a high chemical reactivity. Such absorbed energy cannot be "stored" within the molecule but must be quickly dissipated. While excited molecules may release their energy by undergoing chemical alteration, they can also return to the ground state by releasing their absorbed energy harmlessly in the form of heat or of light (fluorescence and phosphorescence).

The direct absorption of light is not always required to cause photochemical change. A molecule that has been raised to its excited state by the direct absorption of radiation can transfer its energy during a collision with a molecule of a different chemical type, thereby inducing a photochemical change in the second molecule. In another indirect mechanism, called *photodynamic action*, the excited molecule known as the photosensitizer transfers its energy to oxygen and the excited oxygen then oxidizes some target molecule. These reactions exemplify how cells, in the presence of photosensitizing compounds, can be damaged by radiation at wavelengths that normally would have little effect upon them (e.g., phototoxicity and photoallergy in man).

Repair of Radiation Damage to DNA³⁻⁷

Some cells and organisms are protected from the damaging effects of UV radiation by external shields such as shells, feathers, and pigments. For cells that are actually exposed to radiation, their sensitivity, measured in terms of lethality, depends mainly on their ability to repair radiation damage to their DNA. This point is dramatically exemplified in Figure 1: The ease with which bacterial strains, genetically deficient in repair capacity, are killed by UV radiation is compared with the resistance to UV radiation of a repair proficient strain.

Currently, three major enzymatic pathways under different genetic control are known for the repair of UV-induced damage to DNA.

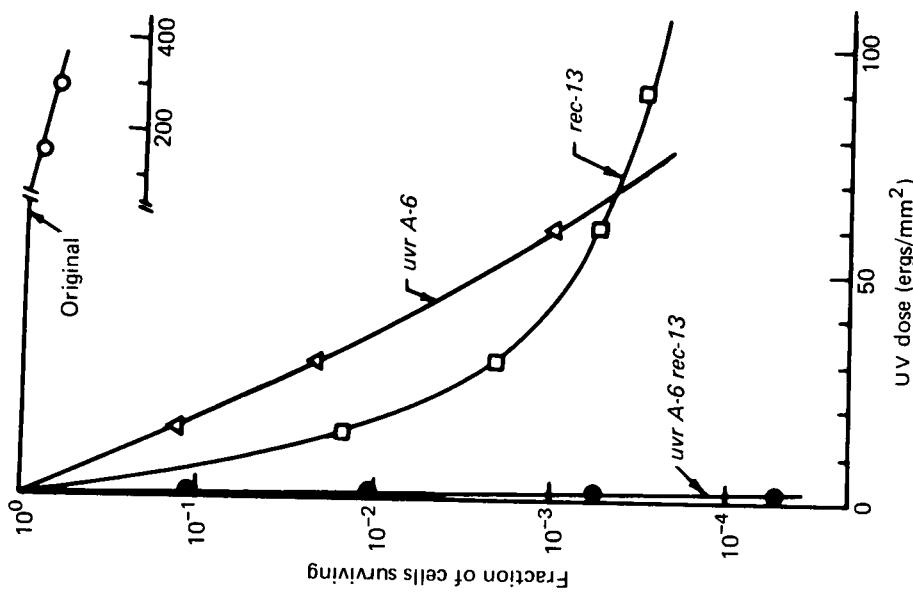


FIGURE 1 The sensitivity of different strains of *Escherichia coli* K-12 to UV radiation (254 nm). The survival curve marked "original" is the "wild type" parent strain from which the other strains were derived. The *uvr-A6* mutant is deficient in the excision repair of radiation damage. The *rec-13* mutant is defective in the postreplication repair of radiation damage. The double mutant *uvr-A6 rec-13* is deficient in both repair systems and is much more UV sensitive than either of the single mutants, which, in turn, are more sensitive than is the wild type strain. (Adapted from Howard-Flanders and Boyce).⁵

1. *The damaged part of the DNA molecule is restored to its functional state in place.* A large percentage of a culture of bacterial cells that have been inactivated by UV radiation (254 nm) can be reactivated by a second irradiation with visible light around 400 nm. This enzymatic process is called *photoreactivation* and is a striking example of how a considerably different wavelength of radiation can modify—in this case beneficially—the effects of the first radiation.

2. *The damaged section of a DNA strand is excised and replaced with undamaged nucleotides to restore the normal function of the DNA.* This process, sometimes called the “cut and patch” system, requires several enzymatic steps that proceed in the absence of light. This “dark repair” system, so called to distinguish it from photoreactivation, has been shown to repair a variety of structural defects in DNA induced by radiation and chemicals.

3. *The damaged section of DNA is not directly repaired but is bypassed during replication.* When the damage in the parental strands of DNA are bypassed during normal replication, gaps are produced in the newly synthesized daughter strands of DNA. These gaps are subsequently repaired, yielding normal DNA, by enzymatic processes that are still not well understood. This postreplication repair process is also a dark repair system.

X rays and certain types of sensitized reactions mediated by near UV and visible light produce damage in DNA that differs chemically from that produced by UV radiation. At present, there is evidence for the existence in bacteria of at least three separate processes for the repair of this type of damage (chain breaks).

Thus, six distinct repair systems are currently known by which cells can repair radiation damage to their genetic material. This multiplicity of repair systems suggests that the repair of radiation-damaged DNA is of critical importance to the survival of cells. Several of these repair systems have now been identified in mammalian cells.⁶

Conclusions

Since the absorption of UV radiation means that photochemical change will probably occur, how can plants and animals survive this continual photochemical alteration of their constituent molecules? If their cells did not possess a multitude of systems for repairing

damage to their DNA, they could not survive the onslaught of solar and man-made radiation.

A dramatic example of this fact are patients with the hereditary disease xeroderma pigmentosum. Upon exposure to light these patients usually develop multiple skin cancers and die. Skin cells from these patients have been shown to be deficient in an enzyme required for the excision repair (dark repair) of radiation-damaged DNA. These results suggest a probable causal relationship between light-induced carcinogenesis and the defective repair of DNA.

Thus, in living things there is a delicate balance between the continual photochemical alteration of cellular components and their biochemical repair. If the amount of UV radiation damage exceeds the cell's capacity to repair this damage or if its repair systems are inactivated by mutation or by drugs, then the cell will die.

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PROTECTION OF ORGANISMS FROM ULTRAVIOLET RADIATION BY SHIELDING AND AVOIDANCE

In maintaining the delicate balance that is life, organisms are not only able to repair radiation damage to their genetic material but many have also evolved mechanisms to prevent such radiation damage in the first place. Two such preventative devices are (a) movement out of sunlight and (b) development of coverings that are opaque to light.

Behavioral Responses to Sunlight

Some simple motile organisms respond by reversing direction whenever light intensity increases, thus moving and remaining out of sunlight.¹ Growth of plant plankton in bodies of water usually occurs at depths where, at the present levels of sunlight, the UV component is greatly attenuated (e.g., maximal growth for many diatoms occurs 15 m down in clear water and higher in murky water). Animal plankton swim down as deep as 70 m by day and rise during the night and perhaps thereby escape danger from UV radiation shorter than 300 nm. Other single-celled organisms have been shown to sense and respond to UV radiation of short wavelengths.²

Some plants respond to intense sunlight by moving their leaves to positions of minimal exposure to sunlight.³ Although primarily a means of avoiding overheating, the role of sunlight UV in this response has not been determined.

Few animals remain in full sunlight, with the notable exception of humans, unless they possess some means for preventing free entry of light into their tissues. Thus, many sea animals hide by day in crevices in rocks, burrows, or deep water and come out to browse by night. Land animals also generally avoid sunlight, becoming most active at dusk and inactive again at dawn, except in the shade of a forest where some may be active by day. Whether the cue for these responses is the UV component of sunlight, heat, or visible light is not known.⁴

Thus, if UV radiation were increased without a corresponding change in day length, intensity of visible radiation, or heat, many organisms would probably be injured because the environmental

information to which they normally respond would give them no warning of the increased UV radiation hazard. For example, few people would lie down on a tennis court in a swimming suit at noon on a summer day because the heat would tell them to behave otherwise; however, at the beach on hazy or cloudy days the heat cue is reduced, but the intensity of the UV radiation is not greatly reduced, accounting for much sunburn in man.

Light-Impervious Coverings

Pigments that effectively absorb sunlight appear in all types of organisms, even the simplest ones. Some single-celled animals like the black brine ciliates have a pigment that absorbs light so completely that they persist and grow in salt pools in which there is no place to hide from the sun. Pigment also occurs in many animals that can hide by day, although it is generally absent in cave animals. Pigment, therefore, may serve purposes other than protection against solar UV radiation (e.g., camouflage). However, in Hereford cattle the high incidence of eye cancer appears to be correlated with the absence of skin pigment around the eye.⁵

Pigments occur in both marine and land plants, but their protective value against solar UV radiation has not been assessed.

Man also develops pigment (suntan) after exposure to sunlight. This melanin pigment not only absorbs but also scatters incident sunlight, conferring some protection from additional exposure. The capacity for tanning in man is genetically controlled, and those who burn instead of tan develop a slight degree of protection against sunlight by thickening of the skin.⁶

Hair, feathers, scales, and shells protect various animals from solar UV, scattering the incident radiation even in the absence of absorbing pigment. Many plants, especially in the desert, possess hairlike outgrowths of the epidermis that, like the hair of mammals, absorb and scatter the incident sunlight. Such coatings, however, may serve primarily for regulation of temperature.

Summary

A number of adaptations, other than repair mechanisms, exist that enable animals, plants, and microorganisms to resist exposure to UV radiant energy from sunlight. To what extent these would serve if the UV component in sunlight were increased is conjectural. Perhaps

some behavioral responses would fail because increases in solar UV radiation may not be sensed, inasmuch as the cue for response to sunlight may well be either the visible light or the heat component. However, for organisms that have them, pigments and other shields for preventing entry of UV radiation into tissues might possibly afford adequate protection.

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GENETIC EFFECTS OF SUNLIGHT

Although DNA absorbs UV light maximally at 260 nm, wavelengths in the band 280-320 nm can produce mutations if the intensity is high enough. Tumors can result from UV damage to somatic cells, but mutations in eggs and sperm are passed on to successive generations. The persistence of these mutations in the population is controlled by natural selection. In nature, the germ cells of higher organisms are ordinarily protected from normal fluxes of mutagenic UV radiation by pigments or other absorbing structures, but lower organisms may have less effective screens or more vulnerable stages in their life cycle.^{1,2} For example, pollen of the wandering jew plant (*Tradescantia*) is about 10 times more susceptible to UV-induced mutagenesis than the germ cells of the fruit fly (*Drosophila*).¹

Another point concerns the nature of the dose-response relationships for mutagenesis and cell death. In bacteria with efficient

mechanisms for DNA repair, low fluxes of UV radiation delivered over long times are less effective in killing than the same total energy given in a short time. On the other hand, for protozoans the effect appears to be greater at lower dose rates.² The effects of chronic exposure to relatively low fluxes are not known for many organisms. Having this knowledge is important because the current daily total flux density of UV radiation at the surface of the earth at wavelengths shorter than 320 nm is significant. Indeed, an hour's exposure to sunlight near noon on a clear day in Washington, D.C., has been shown to produce mutations in the molds *Aspergillus* and *Penicillium*.³ Just one minute of exposure to noon sunlight in Texas is sufficient to kill 99.9 percent of a population of a strain of bacteria (*Escherichia coli K-12 uvrA recA*) that is deficient in two repair systems.⁴

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6

SUNLIGHT AND THE COMMON MALIGNANT TUMORS OF SKIN

The role of sunlight in the production of human skin cancer has been inferred largely from epidemiological and anatomical distribution studies. However, the production of skin cancer in laboratory animals by exposing them to wavelengths of UV radiation found in sunlight strongly supports the hypothesis that excessive exposure to sunlight can be carcinogenic in man.

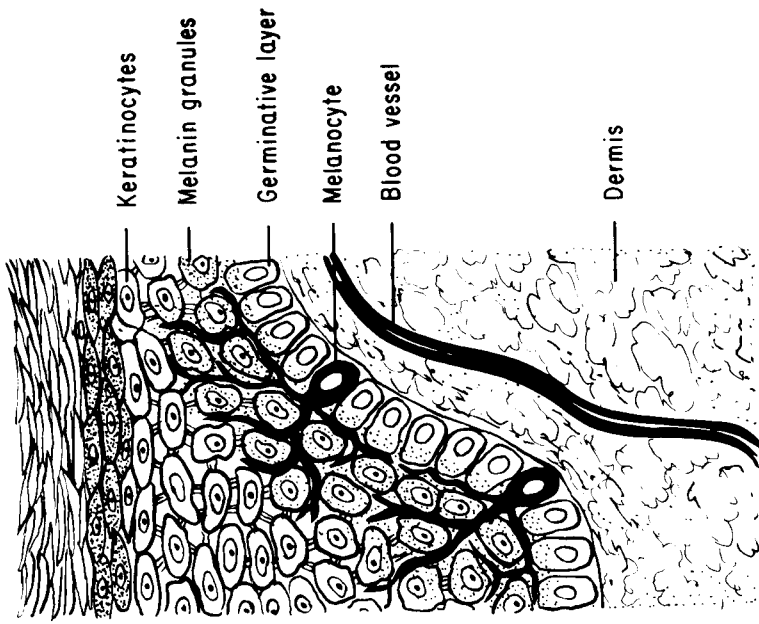


FIGURE 1 Diagrammatic section of human skin.

cases are fatal, and most of these deaths could have been avoided by earlier treatment. Basal cell carcinomas are very common, with a yearly incidence rate varying from 380 per million white males in the north to 2,000 per million in the southern United States. They usually occur on the face and, if untreated, are capable of producing tragic disfigurement. Rarely do they give rise to secondary tumors, and present treatment is almost totally effective. In contrast, malignant melanomas are rare, with incidence rates of 20–30 per million in white populations living in temperate climates,⁶ while the maximum rate reported from a similar population in tropical Queensland, Australia, is 160 per million.⁷ However, malignant melanomas readily produce secondary tumors that spread to other parts of the body, and treatment is much less effective than for the localized squamous

Laboratory Studies on Mice

Many of our ideas about the causation of human skin cancer have come from rather extensive studies of the effect of UV irradiation on laboratory mice. The main conclusions resulting from these studies can be summarized as follows^{1,2}:

1. Wavelengths between 230 and 320 nm are effective in inducing the development of skin tumors. UV radiation between 280 and 320 nm, the wavelengths in sunlight that are regulated by atmospheric ozone, are the most effective in producing skin cancer. Wavelengths less than 280 nm and greater than 320 nm are very much less effective.
2. The presence of skin pigmentation, hair, and greater skin thickness serve to make an individual mouse less susceptible to the UV-induction of tumors.
3. The time required to cause the formation of a skin tumor is inversely related to the dose of UV radiation. From these and other studies it has been suggested that the UV-induction of malignant tumors is a cumulative process that begins with the initial exposure to UV radiation.
4. Certain chemicals have been shown to interact synergistically with UV radiation to accelerate the formation of malignant skin tumors in laboratory animals.² These findings suggest that chemicals in the environment may well affect the incidence of sunlight-induced skin cancer in man.

Epidemiological Studies on Man

The common malignant tumors of skin are (a) *squamous cell carcinoma*, derived from a malignant change in normal keratinocytes (Figure 1), (b) *basal cell carcinoma*, from cells of the germinative layer at the base of the epidermis, and (c) *malignant melanoma*, from melanocytes that provide the brown or black pigments of normal skin. Squamous cell carcinomas occur with an average yearly incidence of about 120 per million white U.S. males,³ concentrated in the oldest section of the population with a mean age of about 70. White populations exposed to strong sunlight, for example, in Arizona or Queensland, Australia,^{4,5} may have much higher rates of the order of 1,000 per million. Squamous cell carcinomas can almost always be treated effectively—only about 1 percent of the

cell or basal cell carcinomas. About 40 percent of patients with malignant melanomas are dead within 5 years, a rate comparable with that for breast cancer.⁸ Patients who die of malignant melanoma are about 20 years younger, on the average, than those who die of other kinds of skin cancer. Thus, while the incidence of both squamous cell and basal cell carcinomas is 10 and 30 times that of malignant melanomas in most developed countries with white populations, the number of deaths from these tumors and melanomas is of the same order of magnitude.⁹

Both the incidence and the death rates from squamous cell carcinomas and melanomas increase from high latitudes toward the equator within Australia, Britain, Japan, and the United States.¹⁰ (The concentration of stratospheric ozone decreases and the intensity of solar UV radiation increases on going from the higher latitudes toward the equator.) Because of the high incidence of squamous and basal cell carcinomas, the proportion of people in a community, who in a lifetime will need treatment is as much as 10 percent of white populations.¹¹

While both squamous cell and basal cell carcinomas are concentrated in areas of the body exposed to sunlight, this correlation is not as marked for malignant melanomas. The susceptibility to both squamous cell carcinoma and basal cell carcinoma is related to lightness of skin color and the inability to tan¹²; susceptibility to malignant melanoma has thus far only been correlated with lightness of skin color.¹³ Light-complexioned people living on the northern fringes of Europe (Irish, Scots, Swedes) have high rates for both squamous and basal cell carcinomas¹¹ and malignant melanoma.¹⁴ People of Irish extraction living in Australia have higher rates for malignant melanoma than other white Australians.

The genetic character of people, as expressed in their skin color and ability to tan; their total exposure to solar radiation on their jobs and in their leisure hours; the amount and type of clothing they wear; and the value they place on a suntan all profoundly modify the basic relationship between malignant skin tumors and the environment. Nevertheless, the variations in the death rates from malignant skin tumors, which are related to quite small variations in the environment, suggest that a 5 percent reduction in the ozone shield by a fleet of commercial SST aircraft would account for at least 8,000 extra cases of skin cancer a year in the white population of the United States leading with current treat-

ment to about 300 extra deaths.* Apart from any consideration of the individual people involved, this potential loss to society should be incorporated into any consideration of the cost per benefit relationship of these aircraft.

*Calculated from the data of Bener¹⁵ on the relationship between changes in ozone concentration and changes in ultraviolet light (see Figure 2, p. 15), the relationship between current levels of solar UV radiation and neoplastic changes in human skin,¹⁰ on the conservative assumption by the Committee that 80 percent of the squamous and basal cell carcinomas and 40 percent of the melanomas are caused by ultraviolet light,^{3-7,10,16} and for a population of the size of that of the U.S. whites living at 40° N latitude (that of Philadelphia). The deaths are similarly derived from the current U.S. experience, making allowance for the deaths certified to squamous cell carcinomas that are really due to other causes.¹⁷

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7

DETRIMENTAL EFFECTS OF ULTRAVIOLET RADIATION TO MAN OTHER THAN SKIN CANCER

Natural and artificial UV radiation has a variety of effects on man and animals, many of which are detrimental. The best known of these is sunburn, due to acute overexposure to wavelengths of UV radiation below 320 nm. Less well known, but equally detrimental, is the repeated long-term exposure to the sun, leading to skin changes interpreted by western Caucasian culture as signs of "aging."¹

In addition, a number of heritable diseases predispose the skin to sensitivity to UV radiation.² In one of these, xeroderma pigmentosum, the defect has been traced to the absence of one of the DNA repair enzymes (see p. 20). This is of considerable interest, because even in early childhood most of the skin of these patients shows changes normally found only in the aged. Furthermore, multiple skin cancers form early in life and are usually fatal. This disease is a prime example of the extreme importance that repair mechanisms play in the survival of UV-irradiated cells and further supports other

experimental and epidemiological data that aging and skin cancer in human skin are mainly a consequence of UV radiation injury.

Sunburn

It is now clear that the portion of the UV spectrum below 320 nm has a direct destructive effect on human skin that eventually results in a variety of chronic tissue changes appearing later in life. Although a good deal is known about the sunburn and pigment-producing effects of various wavelengths of UV radiation, the location and nature of the photochemical lesion produced have not been adequately defined. Also, it is clear that the different wavelengths of UV radiation have significantly different effects. This may be due to a difference in depth of penetration into the skin, or the type of photochemical reaction produced by the various wavelengths of radiation. Much more information is needed on the reason for these differences and the photochemical events involved.

Until very recently there was little evidence for wavelengths of radiation longer than 320 nm participating in any of the adverse reactions following exposure to intense solar radiation, except for the process of pigment darkening. It has now been shown, however, that UV radiation of wavelengths between 320 and 400 nm significantly augments the sunburn erythema response and the histological evidence of damage induced by UV radiation below 320 nm.³

"Aging" of the Skin

The criteria accepted as visible evidence of aging in white populations (excluding graying of the hair) are changes in the skin such as wrinkling, mottling, dilation of blood vessels, dryness, flaccidity, and growth of various excrescences. Sunlight is far more important than the passage of time in destroying the visage of youth. Such changes are most striking in fair individuals who are easily sunburned. These changes are correlated with the degree of exposure to sunlight and begin in the second decade of life, although they usually do not become clinically evident until later. Melanin in the upper layers of skin of most humans effectively protects against such changes.^{4,5} It is important to point out here that single overdoses of UV radiation can cause permanent destruction of melanocytes, leading to depigmented areas that henceforth are more susceptible to the UV-induced

chronic changes listed above.⁶ Very likely the mottling usually observed in the aged represents, in part, a destruction of the effective melanin screen by UV radiation. Thus, exposure in advancing years may also contribute considerably to the late changes, including carcinogenesis.

Suntan

The production of a suntan is the result of injury of the skin by UV radiation. Individuals with an effective pigment-producing system in their skin are thereby partially protected from further damage after an initial exposure to sunlight. Because they lack the hereditary factors for tanning, a significant number of northern Caucasians freckle and sunburn easily and repeatedly, but do not tan evenly (typically the Celts of Irish, Scot, and Welsh descent). They are thus highly vulnerable to UV-radiation-induced skin injury and they must protect themselves from sunlight or suffer the consequences.⁷ Thus, an increase in UV radiation would increase the frequency of severe sunburn and advance the onset of the "aging" of skin in such sensitive individuals and possibly in others, both because of increased cumulative dose and the increased probability of the destruction of melanocytes, which, by producing melanin, help protect against UV radiation damage.

Phototoxicity and Photoallergy

A variety of chemical agents, whether administered internally or externally can cause serious, abnormal reactions of the skin to UV radiation. Some of these are medically useful drugs (e.g., certain antibiotics, diuretics, tranquilizers) while some are used as surface antibacterial agents in soaps, cosmetics, or detergents. Still other compounds come from atmospheric pollution. These compounds either enhance sunburn reactions or result in allergy to UV radiation. Most known sunburn enhancers (phototoxic agents) absorb wavelengths of UV radiation that normally cause little or no discernible biologic effect. However, these compounds are capable of transferring their absorbed solar energy to biologically important molecules, with the consequent development of a demonstrable skin reaction.⁸

In photoallergy, the chemical is changed by the absorption of radiation into another compound that stimulates the development of antibodies. Patients with such light allergies may be almost totally

disabled, since they cannot venture into sunlight and may even be adversely affected by light from fluorescent lamps.^{9,10}

Eye Injury

The eyes may also be injured by UV radiation. While most such "burns" follow inappropriate exposure to artificial light sources (welder's arcs, sunlamps, etc.), inflammation of the outer covers of the eye can occur naturally. This happens mainly in snowy and arctic areas, where the UV radiation is highly reflected and the days are long. An increase in total terrestrial UV radiation intensity could make this unpleasant injury more common in the absence of adequate shielding. In addition, UV radiation has been implicated in the etiology of cataracts of the eye.

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BENEFICIAL EFFECTS OF ULTRAVIOLET RADIATION ON MAN

In 1945, Blum¹ stated that:

There exists a widespread belief in the beneficial effects of sunlight, which finds expression in the current fad of sun-bathing. This belief stems in part from false analogies that have been drawn. For example, the idea that since sunlight is beneficial and necessary to plants, it must be beneficial and necessary to man, which—however absurd—is found frequently in scientific literature, sometimes directly stated, sometimes implied. The detrimental effects of sunlight have received much less consideration and publicity, yet when one sets about the preparation of a critical review he is struck by the fact that the balance is weighted heavily on the side of effects which appear injurious rather than beneficial. Perhaps if some of the many claims were supported by better experimental evidence this would not be true.

The same situation applies today.

The sun has been worshipped in many ways in many cultures and places, and deliberate exposure of patients to sunlight as a therapeutic measure goes back to at least Roman and Greek times. It is an almost universal personal experience that time spent in the sun at the beach or under a sunlamp short of a sunburn is pleasant.² The winter vacation in the Mediterranean or Caribbean is eagerly sought by most light-skinned people. The recent musical *Hair* ends with a chorus that repeatedly pleads "Let the sunshine in." Basking behavior is familiar in many animals and is assumed to spare metabolic heat production and to kill surface parasites. The history of ultraviolet therapy has recently been reviewed.^{3,4} The use of heliotherapy at the height of its popularity (1926) is described by Mayer.⁵ However, even with this long experience, the physiological and biochemical mechanisms of the assumed beneficial effects of sunbathing are not well understood.

The one certain biochemical effect in the human body from UV radiation is the photochemical conversion in the skin of 7-dehydrocholesterol to vitamin D₃.⁶ A deficiency of vitamin D results in rickets, in which bones fail to calcify and become deformed.⁷ With the addition of vitamin D to the diet, rickets has become greatly reduced in Europe and North America. However, dietary supplement-

tation has also created the problem of toxicity from an excess of vitamin D.

Vitamin D excess produces calcification in the kidney and other tissues. The idiopathic hypercalcemia syndrome of infancy is a result of excess vitamin D ingestion. The fact that light-skinned children are more susceptible to this syndrome than dark-skinned children has been interpreted as indicating that the vitamin D synthesized more efficiently in the light skin is additive with the ingested vitamin D; in the darker skin there is less vitamin D synthesis from sunlight.⁸ Patients with a certain type of skin disease (sarcoidosis) have a higher calcium level in the summer⁹ than in the winter, and this is also believed to be due to an excess synthesis of vitamin D in the skin. The importance of the observation in these two diseases is that regulatory mechanisms—if they exist—for limiting the effect of dietary plus skin synthesized vitamin D appear to be inadequate to prevent vitamin D toxicity.

All bony animals require vitamin D, and most of it is synthesized in the skin, on feathers, or on fur by the action of UV radiation. There is no information on whether birds, mammals, reptiles, amphibians, and bony fishes could regulate a sudden increase in the vitamin D synthesized in or on their skin. This is an important area for study. Lower animals, including protozoans, require sterols in their diets but none are known to require vitamin D.

A well-known effect of UV radiation is the killing of microorganisms, of which some are beneficial to man and others are pathogenic. Germicidal UV lamps are used in many operating rooms to inactivate pathogenic bacteria and viruses. The relationship of the germicidal effect of solar UV radiation to the decreased rate of respiratory illness in the summer and in tropical areas has not been adequately studied.

Niels R. Finsen received the Nobel Prize in 1903 for demonstrating the cure of skin tuberculosis with UV lamps. Generalized irradiation of the body for bone tuberculosis and the UV radiation treatment of streptococcal infections of the skin were discontinued with the advent of chemotherapy and antibiotics. Therefore, most research on the beneficial effects of UV was done between 1893 and the early 1940's.

Several skin diseases are still treated with UV lamps: Acne and boils involve bacteria; psoriasis and eczema do not. The list of formerly treated diseases occupies over a page in the review by Licht.³

Other possible medical and physiological benefits from solar radiation or sunlamp treatment include claims of lower blood pressure,

lower blood cholesterol, increased blood hemoglobin, improvement in asthma, improved cardiovascular work capacity, and generalized increase in physical fitness. Some are believed to result from increased vitamin D synthesis, some from redistribution of blood, some from stimulation of nerve endings in the skin, and some through inactivation of viruses and bacteria.

There are several reports on the benefits of irradiating people in classrooms or factories and in some countries miners are given UV "baths" by law. Investigators in Russia, Sweden, and other far northern countries have had particular interests in such treatments.¹⁰⁻¹⁴ Some of these studies show statistically significant benefits of UV treatment on an exercise tolerance test, immunological responsiveness as defined by injecting certain antigens, and in reducing the number of upper respiratory infections compared to control groups. While Berven¹⁵ was unable to confirm some of the earlier findings, the many reports from different places call for repetition of the tests under carefully controlled conditions.

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9

EFFECTS OF ULTRAVIOLET RADIATION ON THE VISION AND BEHAVIOR OF INSECTS

Most of the species of animals are insects, and insects play a large role in terrestrial ecological systems. Some species are agricultural pests, but many others are important links in food chains or essential to the pollination of plants. Consequently, any environmental change that affects insects is ecologically important. An increase in natural UV radiation would probably be such a change.

Vision in the Near Ultraviolet (300-400 nm)

For man, the visible spectrum ends at 400 nm in the violet, but for many insect species vision extends to 300 nm in the UV. An increase in radiation at wavelengths shorter than 320 nm caused by damage to the atmospheric ozone shield would therefore be perceived by insects.

Color vision is probably widely distributed among insects, but the best behavioral evidence is based on work with honeybees (*Apis mellifera*).¹ Bees can also make discriminations between patterns of color.²

In bees, and probably other species as well, UV light is a distinct color, distinguished from all other spectral regions. Moreover, for light to be white for bees, it must include energy in the region of 300–400 nm; white light lacking near UV wavelengths is confused with blue-green by bees. Mixtures of UV and yellow light produce for bees distinct colors known as “bee-purples.” Only a small proportion of near UV light, about 1 percent on an energy basis, is sufficient to make a yellow light appear bee-purple.²

Factors Affecting the UV Sensitivity of Arthropods

Visual sensitivity to UV radiation is common among insects. It is present also in spiders, but it seems to be much less common among aquatic arthropods such as crustacea,³ perhaps owing to the fact that UV light does not penetrate deeply into naturally turbid water.

UV Light Plays Several Special Roles in Insect Behavior

1. *Phototaxis.* In several orders of insects, near UV light has been shown to be the most effective region of the spectrum in directing phototaxis, i.e., movements toward or away from a source of light.⁴ This is true for nocturnal as well as diurnal species and is the basis for using UV lamps in insect traps.

Mazokhin-Porshnyakov² has suggested that UV light is a sign of open space to insects. Most objects in nature absorb rather than reflect UV radiation. Since the light of the sky is the only extensive natural source of UV radiation, these wavelengths can signify room for free flight and maneuvering.

2. *Celestial Navigation and the Sun Compass Reaction.* Many arthropods are able to select a compass direction from knowledge of the sun's position and their intrinsic biological clock. As studied most extensively in bees, the sun's position can be inferred even when the sun itself is obscured by clouds if the insects are able to view an area of blue sky. The relevant cue is the pattern of linearly polarized light that varies in a systematic way with the position of the sun. As the polarization pattern is caused by light scattering and is more pronounced at short wavelengths, it is specifically the blue and UV regions of the spectrum that are effective in directing this behavioral response. Moreover, the position of the sun can also be determined through solid cloud cover, and this too is based on the near UV.⁵

3. *Recognition of Flowers.* Although olfaction and floral shape can also play significant roles, the colors of flowers are important to insect pollinators. Moreover, the colors and patterns of colors that are relevant to insects frequently depend on UV reflectance.

For example, many flowers that are yellow to the human eye are in fact bee-purple due to variable amounts of UV reflectance. White flowers frequently absorb UV light and are therefore colored for bees.

In addition, many flowers that have no pattern to the eye of man display to insects characteristic patterns known as “nectar guides.”

These generally take the form of high UV reflectance at the periphery of the blossom and a region of UV absorption in the center.

Such nectar guides are “sign stimuli” that release characteristic feeding behavior such as extension of the proboscis in honeybees.^{2,5}

4. *Communication and Sex Recognition.* The wings of butterflies sometimes show regions of high UV reflectance. In many species the sexes are different in this regard, with the upper surfaces of the forewings of the males possessing bright patches of UV reflectance.² These patterns can be viewed with a television camera fitted with a quartz lens and a UV filter, where they appear as bright flashes when the insect flies. Such signals are, of course, invisible to vertebrate predators but are presumed to be of importance in communication and mating between members of a species.

There is only one published case that has been analyzed in any detail, the oriental variant of the white cabbage butterfly *Pieris rapae crucivora*.⁶ The males are attracted to the females at rest. The undersides of the females' wings have a characteristic UV reflectance, and this has been shown by appropriate experiments to be the relevant cue. Inanimate models with the right UV brightness attracted males, but models with either too much or too little UV reflectance failed. Thus, the intensity of natural UV radiation plays an important role in the mating behavior of these butterflies. Behavioral analyses of other species, particularly where the males show bright patches, are lacking.

Conclusions

Although it is abundantly clear that the behavior of insects is markedly affected by their ability to perceive the near UV region of the solar spectrum, very few situations have been analyzed in sufficient detail so that one can rank the relative importance of vision, olfaction, and the other senses on behavior. The importance of the bright-

ness of UV reflecting objects relative to other features of the visual field is also unknown. Consequently, it is difficult to predict the effects on insect behavior of an increase in the amount of natural UV light. Obara's observation⁶ that the attractiveness of female cabbage butterflies for males depends on a critical amount of UV reflectance is a fragmentary piece of data, but it points up the necessity of using great caution in any enterprise that might disturb the present ecological balance.

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10

EFFECTS OF ULTRAVIOLET RADIATION ON PLANTS

Although intense UV radiation is clearly detrimental to plants and is usually lethal,^{1,2} a wide variety of physiological reactions have been observed when plants are irradiated with sublethal doses at various wavelengths of UV radiation. These include the cessation of cytoplasmic streaming,³ inhibition of photosynthesis,⁴ severe damage to outer leaf cells,⁵ induction of tumors,⁶ enhanced mutation in a variety of plant species ranging from bacteria to higher plants,⁷ and stunting of plant growth. Unfortunately, many of these conclusions, though now legendary, are confounded by the use of questionable techniques to simulate solar UV radiation and the lack of control of other environmental factors, especially leaf temperature.^{8,9}

Protective Mechanisms of Plants against Solar Radiation

Both higher and lower plants seem to have evolved defense mechanisms to cope with the solar UV radiation currently reaching the earth's surface. Two primary mechanisms by which plants protect themselves are: (1) the absorption of UV radiation in outer tissue layers by waxes and pigments and (2) repair processes such as photoreactivation, i.e., the photoreversal of UV-induced lesions in genetic material by concomitant or subsequent exposure to radiation of longer wavelengths.

Although photoreactivation and other repair processes may be efficient in the current radiation environment of the earth, it is not known whether such repair capacity is sufficient to deal with possible increased solar UV radiation intensities. For example, if the inactivating UV radiation is too intense, photoreactivation does not occur.^{1,10} Also, the effectiveness of photoreactivation is somewhat dependent upon the wavelength of the inactivating UV radiation.¹⁰

Variations in UV Sensitivity among Species

Species of higher plants vary considerably in sensitivity to UV radiation. Grasses, succulent species, and conifers are much more resistant than broad leaf species, and agricultural species are some of the most sensitive (e.g., tomato, sugar beets, clover, onions, lettuce, and watermelon). These differences in sensitivity have been attributed to differences in orientation and optical properties of the outer tissue layers of various plant organs.^{1,2} It is also possible that plants may differ considerably in their inherent repair capacities.

Except for a limited amount of evidence suggesting that plants from higher elevations may have more effective shields to absorb UV radiation in outer tissue layers than plants from lower elevations,^{11,12} there is little other information available to suggest that plants originating from different latitudes, altitudes, or geographical areas may differ in sensitivity to UV radiation.

Conclusions

Although there exists considerable literature depicting a wide range of physiological and morphological phenomena (mostly detrimental) resulting from the UV irradiation of plants, most of this research was performed a number of years ago before repair systems were appreciated and under conditions far removed from an ecological context.

These data, therefore, provide little help in the quantitative prediction of what would happen in the event that increased UV radiation intensities reached the earth's surface.

Because of the supreme importance of plants in our ecology and our economy, it is essential that information be gathered on the capacity of plants to sustain additional fluxes of UV radiation that might occur if the stratospheric ozone layer is partially destroyed.

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