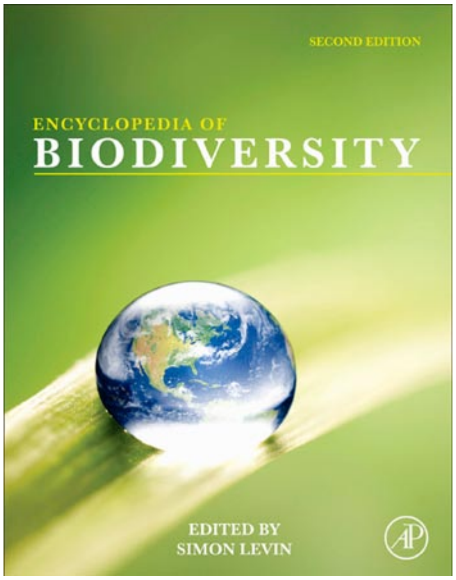

Blaustein Andrew R., and Searle Catherine (2013) Ultraviolet Radiation. In: Levin S.A. (ed.) Encyclopedia of Biodiversity, second edition, Volume 7, pp. 296-303. Waltham, MA: Academic Press.

U

Ultraviolet Radiation

Andrew R Blaustein, Oregon State University, Corvallis, OR, USA
Catherine Searle, Georgia Institute of Technology, Atlanta, GA, USA

This article is a revision of the previous edition article by Andrew R. Blaustein and Nareny Sengsavanh, volume 5, pp 723–732, © 2001, Elsevier Inc.

Glossary

Chlorofluorocarbon (CFC) A type of hydrocarbons that are nonreactive, nonflammable organic molecules in which both chlorine and fluorine atoms replace some of the hydrogen atoms. Use of CFCs is one of the primary causes of stratospheric ozone depletion.
Montreal Protocol A treaty signed by a number of nations to curtail CFC production.
Ozone A form of oxygen in which three atoms of oxygen occur together. Ozone forms a natural layer in the stratosphere that blocks living organisms from harmful ultraviolet radiation from the sun.
Photolyases DNA repair enzymes that repair damage caused by exposure to ultraviolet light.
Ultraviolet radiation Radiation with wavelengths shorter than violet light and with more energy.

Properties of Light

Light is a natural phenomenon that allows us to see objects, shapes, and colors. It radiates from the sun, the stars, a flame, or a light bulb. Light encompasses a broad spectrum of radiation that includes gamma rays, ultraviolet (UV) rays, infrared rays, microwaves, and radiowaves (Figure 1). These types of radiation are all classified as nonvisible light and consist of the longest and shortest wavelengths and frequencies. A small section of the spectrum is the visible light spectrum. The wavelengths of this region range from 380 to 750 nanometers (nm) and are the only part of the electromagnetic spectrum (Figure 1) that can be detected by the human eye. When light shines on an object, some of the light is absorbed and converted to heat; another percentage is scattered or dispersed in various directions; some are transmitted; and the rest may be reflected depending on the material on which the light strikes.

UV Radiation

The electromagnetic spectrum is continuous, but the types of electromagnetic radiation do not begin or end at precise points along the spectrum. For example, red light shades into invisible infrared (below red) radiation and violet light shades into invisible UV (beyond violet) radiation. The sun is the major source of UV radiation for the Earth. UV is responsible for producing suntans and vitamin D in the human body. In humans, overexposure to UV can lead to serious and sometimes irreparable harm. It can cause mutations in cellular DNA, which can ultimately lead to significant alterations in cells, the main cause of cancer. Other damaging effects of UV include premature aging, blindness, and sterilization. UV radiation also has the ability to kill microorganisms, plants, and animals.

UV can be divided into four wave bands. These are vacuum UV (<200 nm), UV-C (200–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm). At the earth's surface, vacuum UV and UV-C are not present because of their absorption by various gases such as oxygen and ozone. The formation of atmospheric oxygen and a stratospheric ozone layer was essential for the evolution of life on earth. The ozone layer shields the terrestrial surface from harmful UV radiation. Unfortunately, through anthropogenic emissions of chlorofluorocarbons (CFCs) and other gases, the ozone layer has been adversely affected. It has thinned and has developed "holes" in polar regions. Thus, there is potential for increased UV radiation hitting the earth's surface.

The ozone hole over Antarctica has dramatically increased since its discovery in the 1970s. At midlatitudes, ozone levels have also continued to decrease. Stratospheric ozone levels are at their lowest point since measurements began, so the current UV-B radiation levels are thought to be close to the maximum. Global ozone measurements from satellites from 1979 to 1993 show increases in UV-B radiation at high and midlatitudes of both hemispheres, but only small changes in the tropics. These estimates assume that cloud cover and pollution

 http://dx.doi.org/10.1016/B978-0-12-384719-5.00147-7

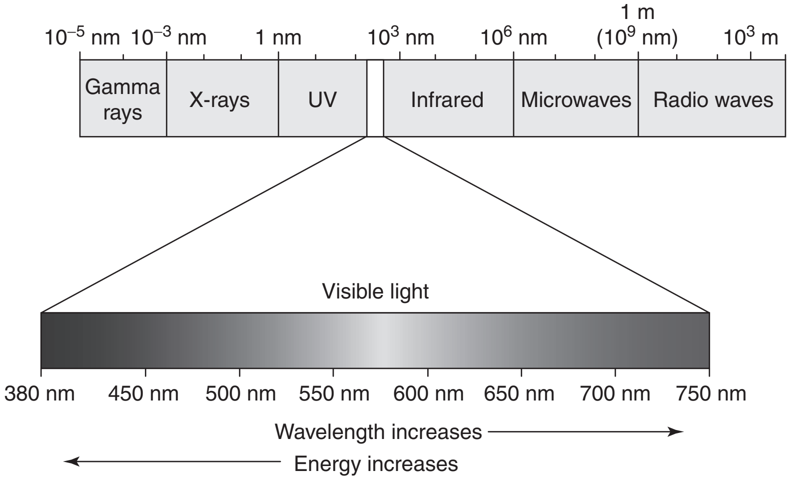

Figure 1 The electromagnetic spectrum. Visible light and other forms of electromagnetic energy radiate through space as waves of various lengths. Reprinted from figure 10.5 in Campbell NA (1996) Biology, 4th edn, with permission from Benjamin Cummings.

have remained constant over the years. Increases in surface erythemal (sunburning) UV radiation relative to values obtained in the 1970s are estimated to be about : 7% at Northern Hemisphere midlatitudes in winter and spring and 4% in summer and fall; 6% at Southern Hemisphere midlatitudes throughout the year; 130% in the Antarctic in spring; and 22% in the Arctic in spring. The resulting increases in UV radiation threaten humans, animals, plants, and microorganisms in both terrestrial and aquatic ecosystems.

The pioneering work of Rowland and Molina showing that CFCs were responsible for the decrease of stratospheric ozone caused considerable concern among atmospheric and environmental scientists. They reasoned that CFCs in the stratosphere would be subjected to intense UV radiation, which would break them apart, releasing free chlorine atoms.

All the chlorine of a CFC molecule would eventually be released due to further photochemical breakdown. The free chlorine atoms could then damage stratospheric ozone, forming chlorine monoxide (ClO) and molecular oxygen. Molecules of ClO can react to release more chlorine and an oxygen molecule.

These reactions are part of the chlorine cycle because of the continuous regeneration of chlorine as it reacts with ozone. Chlorine is the catalyst in the reaction because it promotes the chemical reaction without being used up. Because chlorine can last for 40–100 years, every chlorine atom in the atmosphere can potentially break down 100,000 molecules of ozone. CFCs are especially damaging because they are transport agents that constantly move chlorine atoms into the stratosphere and because chlorine atoms are removed from the stratosphere very slowly.

By 1978, most Scandinavian countries and the US banned the use of CFCs in spray cans. In 1983, most European countries proposed a voluntary reduction in the use of CFCs. As a result of increasing concern over the effects of ozone depletion, an international agreement was signed to reduce and eventually eliminate certain anthropogenic ozone-destroying substances. A treaty, known as ''The Montreal Protocol,'' was signed by a number of nations on 16 September 1987, in Montreal, Quebec. The protocol which consisted of a plan that would dramatically cut CFC production was recognized as the first worldwide effort to solve a massive environmental problem. Since 1987, more than 150 countries signed the agreement to phase out all the uses of CFCs by 2000. Despite this agreement, the worsening environmental news about CFCs and ozone depletion in the 1990s led certain nations to adopt stricter measures, limiting CFC production.

Several industrial companies have developed CFC substitutes. CFCs and several other chemicals that contribute to ozone depletion have been phased out in the US and several other countries. Nevertheless, existing stockpiles of these chemicals can be used until the deadline. Moreover, developing countries are on a different time course and will phase out CFCs by 2006. Unfortunately, CFCs are very stable and estimates suggest that those in use today will continue to deplete stratospheric ozone for 50–150 years. Atmospheric scientists believe that the Antarctic ozone hole will reappear each year until about 2050. However, because of the Montreal Protocol and other measures to limit ozone-depleting substances, there is some optimism about ozone depletion being curtailed.

Bromine (Br) is another important source of ozone depletion. Br is present in smaller quantities than chlorine but is more destructive on an atom-to-atom basis. The largest source of Br is methyl bromide, which comes naturally from the oceans and wildfires. However, a large portion of methyl bromide is human-made and is used as a fumigant. Another important source of bromine is fire extinguishers. Like CFCs, methyl bromide has a long atmospheric lifetime (approximately 72 years). Regulations on the use of methyl bromide are being debated.

Measurement of Environmental UV Radiation

Although significant advances have been made, measuring UV radiation is difficult. There are significant differences in how various devices measure UV radiation. Moreover, there are a number of factors that affect UV radiation. For example, there are geographical and seasonal variations in UV. Thus, recent studies have confirmed that there are generally higher UV-B levels at lower latitudes in the US. Other measurements confirm latitudinal differences in Europe, Asia, and New Zealand.

Spectral measurements show higher summer values of both UV-A and UV-B radiation in New Zealand and Australia compared with Germany due to the yearly cycle of the sun–Earth distance and due to the lower stratospheric ozone levels in the southern hemisphere and higher air pollution levels in Germany. Additional UV data are being accumulated for midlatitudes, and eventually, a more complete picture of the UV situation at these latitudes will emerge.

Cloud cover also affects UV-B radiation levels on the earth's surface. Data from several locations in the US suggest that the monthly average UV levels are reduced by 10–50% by cloud cover, depending on the location and season. Aerosols (small particles suspended in the air) may also reduce UV levels in polluted areas. The magnitude of this effect is highly variable and may depend on the number of particles and their chemical and physical composition.

UV levels are expected to increase with increasing surface elevation above sea level due to a thinner atmosphere overhead. Measurements in a remote area of Chile, for example, showed increases of 4–10% per km in elevation. Other locations showed larger vertical gradients of up to 40% per km near Santiago, Chile, and 9–23% per km in the Swiss Alps.

Because of the high spatial and temporal variability of surface UV radiation and the difficulty of maintaining calibration within instruments, it is difficult to provide global UV climatology and represent long-term UV trends based on ground monitoring stations alone. However, satellite-based measurements can provide global coverage and continuous long-term monitoring. Yet, it is difficult to use remote satellite data in an attempt to estimate UV levels from specific microhabitats on earth. The derivation of surface UV irradiance from satellites is indirect because satellites detect radiation reflected by the atmosphere and the surface of the earth. The use of radiative transfer models is necessary to relate transmission, reflection, and atmospheric absorption. These models have been useful in showing general changes in UV radiation reaching the surface, and are computed for clear skies using satellite ozone measurements.

Effects of UV Radiation on Biological Systems

DNA Repair

At the terrestrial surface, most UV radiation of biological concern is in the 280–315 nm (UV-B) band. UV light induces a variety of photoproducts in DNA. UV photoproducts impede gene expression by blocking transcription, and they can cause cell death or mutagenesis. There are a number of responses to DNA damage by living cells. The two fundamental processes for repairing UV-induced DNA damage are direct reversal of DNA damage or its excision. These processes can be explained by analogy. If we consider a rope with a knot, we can either undo the knot (direct reversal of damage) or cut the knot out and replace the rope with a new piece (excision of the knot). This descriptive analogy roughly represents how photoreactivating enzyme, photolyase, and excision repair, respectively, work to undo DNA damage.

Thus, harmful photoproducts can be removed by photoreactivating enzyme, photolyase. In some species, this is the most important mechanism for DNA repair. In excision repair, when DNA molecules are damaged, a segment of the strand of DNA containing the damage is cut out by one repair enzyme, and the resulting gap is filled in with nucleotides (building blocks of DNA) properly paired with nucleotides in the undamaged strand.

Effects of Increased Solar UV Radiation on Terrestrial Plants

Obviously, it is extremely important to understand the effects of increasing solar UV radiation on terrestrial plants. Plants comprise most of the living matter in terrestrial ecosystems. Damage to plants within natural ecosystems and in agricultural systems can have far-reaching consequences on other organisms, including humans.

Both the physiological and developmental processes of plants are affected by UV-B radiation. Several studies have shown that some plant species in greenhouses, growth chambers, and in the field have reduced growth and leaf area under close to ambient UV-B conditions compared with plants grown under reduced UV-B levels. Increased UV-B radiation may greatly affect photosynthesis. In certain species, such as soybean, sunflower, and corn seedlings, solar UV-B radiation reduced photosynthesis by about 15% when a 12% ozone depletion was simulated. UV-B radiation can also alter the time of flowering and the number of flowers in certain species. Alteration of flowering time can have a severe impact on plants because pollinator availability may be subsequently affected. Anther walls can absorb more than 98% of incident UV-B radiation, and pollen walls contain UV-B-absorbing compounds, providing some protection from the negative effects of UV-B. However, after the transfer to the stigma, pollen may be directly exposed to UV-B radiation. Several experimental studies using Mylar or glass filters that shielded plants from UV-B radiation showed that flowering was enhanced under these regimes. Different studies have shown the different effects of UV-B on flowering in various species. For example, flowering was inhibited in plants such as *Melilotus* and *Trifolium*, but *Zea mays* and *Sorghum* were not affected. In sexually reproducing populations of a desert plant, the effects of UV-B radiation on growth and biomass seemed to accumulate in subsequent generations that were exposed to UV-B radiation. Thus, the effects of exposure to UV-B radiation may be amplified. Even roots of plants can be affected by elevated UV-B radiation. For example, the microorganisms associated with the roots of sugar maple trees were altered when the shoots of the trees were exposed to UV-B radiation.

The yields of certain crop plants may be significantly affected by increases in UV-B radiation. The available data on the effects of UV-B radiation on yield illustrate significant interspecific variability and, also, variability among cultivars complicated by differences in how the experiments were performed. Nevertheless, some species and certain cultivars seem to be more tolerant to UV-B than others. For example, results from greenhouse and field tests suggest that the soybean cultivar "Forrest" was more tolerant to UV-B radiation than the cultivar "Shore." A study of 10 crop species in Florida showed that under UV-B radiation, yields were reduced by 5–90% in half of them, including wheat (5% reduction), potato (21% reduction), and squash (90% reduction). In this study, rice, peanut, and corn were not affected.

Several studies have shown that plant susceptibility to herbivores and pathogens is altered by UV-B radiation. For example, a number of studies have shown that ambient UV-B radiation can reduce insect herbivory of agricultural pests and native plants. Supplementation of solar UV-B radiation in field studies can reduce the population of herbivorous insects in certain systems. It is unclear why changes in herbivory occur. It is possible that the secondary compound plant defenses may be altered, or that UV-B directly affects the herbivores. However, most of these studies suggest that the changes in insect herbivory are due to changes in host plant tissues.

Experiments conducted in greenhouses and in the laboratory suggest that viral and fungal pathogens react differently to UV-B radiation. Some studies indicate that UV-B radiation promotes the severity of disease, whereas other studies indicate a reduction in infection severity. For example, cucumber plants first exposed to UV-B radiation were more susceptible to subsequent infection by fungal pathogens. However, if exposed to UV-B radiation after infection, there was no effect on the severity of the disease. Other studies have shown that when UV-B radiation is removed, there is increased incidence of fungal infection.

Because there are differences in tolerance to UV-B radiation in different species, it is suggested that a reduction of primary productivity in one plant species may lead to an increase in primary productivity in another more UV-B-tolerant species. Thus, it is possible that the overall productivity within an ecosystem may change, even if species composition is unaffected. Even if the plant species composition does not change, individual plant form may change, which could affect how these plants compete for sunlight, moisture, and nutrients. This could lead to significant changes in the overall characteristics of ecosystems.

Effects of Radiation on Aquatic Systems

The attenuation of solar radiation on the water column is dependent on a variety of factors. The transparency of the water to UV radiation is dependent on many characteristics of the water. For example, there can be highly turbid coastal waters that do not allow much UV-B to penetrate very deeply. In comparison, some ocean waters are clear enough so that the UV-B penetration can be for dozens of meters. In the Antarctic, 1% of the solar UV-B hitting the surface has been measured at a depth of 65 m. Solar UV-B has been shown to degrade dissolved organic carbon (DOC). Increased breakdown of DOC and subsequent consumption by bacteria increases the UV-B penetration in the water column.

Across life histories, trophic groups, habitats, and experimental venues, UV-B negatively affects the growth and survival of aquatic organisms. A meta-analysis investigating the effects of UV-B across life stages found that UV-B had a greater negative effect on embryonic growth compared with growth at the larval stages. However, in amphibians, the larval stage experiences greater mortality than the embryonic stage. Additionally, across taxonomic groups, protozoans appear to undergo the greatest reduction in growth rates compared with animals or plants.

Plankton

Globally, phytoplankton is the most important producer in aquatic ecosystems. Thus, damage to phytoplankton populations will affect higher trophic levels. A number of studies in a variety of aquatic ecosystems have shown that UV-B radiation affects the growth, survival, and distribution of phytoplankton. Phytoplankton exist on the top layers of the oceans and freshwater aquatic systems. The Antarctic is especially productive in phytoplankton, and the region is significantly impacted by UV-B because of the Antarctic ozone hole. Therefore, a number of studies on the effects of UV-B on phytoplankton have been conducted in that region. In certain experiments, productivity was two to four times higher in tanks where UV-A and UV-B were excluded. Pigmentation was also affected. *In situ* incubations of natural phytoplankton assemblages in the Antarctic waters indicated that photosynthesis was impaired by about 5% under the ozone hole. A similar result was found in the tropics. Screening of most UV <378 nm resulted in a 10–20% increase in photosynthesis. However, no significant decrease in stratospheric ozone have been observed in the tropics.

Many phytoplankton can actively move to different positions within a particular habitat. They may do this via flagella, cilia, or by utilizing buoyancy to adjust their position in the water column. Various chemical, magnetic, light, and gravity cues influence movement so that plankton can maintain specific positions within the water column. To cope with constantly changing environmental conditions, these organisms must constantly adjust their positions. If UV radiation affects motility, or the ability of phytoplankton to respond to external cues, this may negatively affect their growth and survival. There is growing evidence that many phytoplankton species are under stress from ambient levels of UV radiation.

Macroalgae and Seagrasses

In contrast to the motile phytoplankton, macroalgae and seagrasses are attached to their growing sites. Thus, they are restricted to certain depth zones. It is thought that this zonation is caused, at least in part, due to limits of visible light penetration at various depths. Some species may be more tolerant to solar radiation than others. Thus, increased levels of UV-B radiation may expose algae and seagrasses to levels that they have not encountered, perhaps affecting growth and photosynthesis. Several studies have shown that UV-B radiation inhibits photosynthesis in many of the red, brown, and green algae. Deep water algae were the most affected, whereas intertidal algae were the least sensitive.

The DNA of algae appears to be poorly shielded when compared to higher plants. For example, doses of UV-C radiation (at 254 nm) necessary to kill leaves of higher plants appear to be about four orders of magnitude greater than that necessary to kill highly resistant algae. Flavenoids, highly effective UV-screening compounds found in higher plants, have not been found in algae. In higher plants, flavenoids exist in high enough concentrations in the epidermis of leaves so that in combination with cuticle waxes and other cell-wall components, the incidence of UV radiation is reduced by one or two orders of magnitude. However, algae do produce other UV-absorbing substances, including a yellow protein–carotenoid complex in some species and other substances that afford some protection from UV radiation.

An experimental study conducted in Canada illustrates how ecosystems may have complex responses to increased solar UV-B radiation. Solar UV radiation can reduce photosynthesis and growth in bottom-dwelling algal communities in shallow freshwater. However, in this study, it was observed that greater amounts of algae were accumulated in UV-exposed habitats than in UV-protected environments. UV-A and UV-B radiation inhibited insects that feed on algae. Because larval algal consumers are more sensitive to UV radiation than algae, algal abundance increased.

Invertebrates

Sunlight can be lethal to a wide variety of marine and freshwater plankton exposed for just a few hours or a few days. Mortality rates are usually lower in zooplankton that contain photoprotective compounds including pigments derived from dietary plant carotenoids, melanin, and substances known as mycosporine-like amino acids that gets absorbed in the UV-A and UV-B range. The presence of these photoprotective compounds suggests that there is significant selection pressure associated with the harmful effects of UV radiation.

A number of experimental studies have shown that natural levels of UV radiation are lethal to zooplankton. For example, one study in Pennsylvania showed that zooplankton communities exposed to ambient levels of UV-B for 3 days experienced significant mortality when they were not shielded from UV-B radiation. However, mortality was significant only in an oligotrophic lake, not in an eutrophic lake where light penetration is not as high.

Marine invertebrates differ considerably in their sensitivity to UV-B radiation. For example, while one species of crustacean may suffer about 50% mortality at current levels of ambient UV-B radiation at the sea surface, some shrimp can tolerate irradiances higher than those predicted for a 16% ozone depletion. Bottom-dwelling invertebrates of the ocean may also be affected by UV-B radiation. For example, cleavage in sea urchins is impaired by UV radiation. Marine organisms associated with coral reefs, such as sponges, bryozoans, and tunicates, are also adversely affected by UV-B radiation.

Corals are affected by UV radiation in a number of ways. Depending on the species and the particular ecosystem, a number of studies illustrate that UV radiation can cause death, inhibit growth, and contribute to coral bleaching. Bleaching, a well-recognized phenomenon, occurs principally via the loss or expulsion of symbiotic algae from the coral host tissue. When the algae are lost, the coral loses its characteristic color and the remaining white polyp is most noticeable. Although a number of events, including elevated seawater temperature and heavy rains, can contribute to bleaching, there is some evidence that UV radiation may also play a role in certain bleaching events.

UV radiation can inhibit photosynthesis in symbiotic algae. UV radiation affects respiration among corals and their symbiotic algae, but not in a consistent way. In some species, respiration increases under UV radiation, whereas in other species it may decrease and in others respiration may be unaffected.

UV radiation inhibits the growth of symbiotic algae in culture. Reproduction in corals may be affected by UV-B radiation. Broadcast spawning at night, a nearly universal phenomenon among many reef invertebrates and corals, might be related to avoiding UV-induced DNA damage as well as to reducing predation. In at least one study, it was observed that the larvae of reef corals from shallow water were more resistant to UV-B radiation than those from deeper water.

In the Antarctic, a number of marine invertebrates sustain UV-induced DNA damage. These include worms and crustaceans. Krill, copepods, and gelatinous zooplankton generally have transparent eggs, larvae, or adult stages that are pelagic and planktonic, and are often found in surface water for several months. Thus, these species are especially vulnerable to DNA damage from elevated UV-B exposure. These species are important components of the ecosystem, and damage to them could have significant consequences on the ecosystem.

Fishes and Amphibians

A study of Antarctic zooplankton, including larval fish, showed that they sustain DNA damage during periods of increased UV-B flux. Fish larvae in Antarctic marine ecosystems sustained UV-B-induced DNA damage greater than the lethal limit determined for Antarctic diatoms, and comparable to the lethal limit of damage for cultured goldfish cells. DNA damage has been shown to be especially correlated with daily UV-B flux in icefish eggs. Icefish larvae, however, showed patterns of DNA damage that correlated less significantly with daily UV-B flux. Antarctic fish appear to primarily use photolyase to remove harmful UV-B-induced photoproducts.

Other fish species may also be affected by UV-B radiation. For example, in the Arctic ecosystem, many economically important fish species, including cod, pollock, herring, and salmon, spawn in open shallow water and are subjected to increased solar UV-B radiation. Because many of their eggs are found near the surface, it is possible that marine fish productivity could decline in this region due to increased UV-B radiation. At this point in time, however, it is difficult to assess the impact of UV-B radiation on Arctic fish productivity. However, a laboratory experiment demonstrated that salmon exposed to UV-B radiation are more prone to fungal infections and skin lesions.

Several laboratory studies have shown that UV radiation affects the growth, development, and hatching success of certain amphibian species. These studies have shown that under simulated UV light of various intensities, amphibians may develop skin lesions, edema, eye damage, curvature of the body, and behavioral abnormalities. Under relatively low-level but prolonged doses of UV radiation, the mortality of embryos increases compared with controls that are shielded from UV radiation.

Amphibian Declines and UV Radiation

Amphibian populations are undergoing a serious decline in various regions of the world. Unfortunately, the causes for amphibian population declines have been difficult to assess. Much of the information on amphibian declines comes from observational or anecdotal accounts. Hypothesized causes for the declines include habitat destruction (the most obvious cause), climate change, pathogens, introduced exotic species, pollution, and increased UV radiation. These agents may act alone or in combination to contribute to the decline of amphibian populations.

The diversity of locations where amphibian populations have declined prompted consideration of atmospheric factors such as increased UV irradiance associated with depletion of stratospheric ozone. Several investigators have used field experiments to examine the potential role of UV-B radiation in amphibian population declines by measuring the mortality of embryos that were shielded from UV radiation compared with the embryos that were unshielded. Continuous high mortality in early life stages may ultimately contribute to a decline in the population level.

Field experiments from North America, Europe, and Australia show that ambient UV-B damages the embryos of certain amphibian species but not others. Results of these experiments by several different investigators strongly indicate that the hatching success of at least nine species of amphibians, from widely separated locales, is reduced under ambient UV-B radiation. This includes a taxonomically diverse group of two frog species, one toad species, two salamander species, and a newt from North America; two frog species from Australia; and a toad species from Europe. Some of these species are found in montane areas, and others are found at sea level. A key characteristic shared by these species is that they often lay their eggs in shallow water, where they are exposed to solar radiation.

Hatching success of several other amphibian species in North America, Australia, and Europe was not affected by UV-B radiation. This is not surprising because several studies have demonstrated differential sensitivity of amphibians to various abiotic factors. There may be variation in response to UV-B radiation, perhaps even within a species, at different locations. For example, embryos of western toads in Oregon are sensitive to ambient levels of UV-B, while those of a different subspecies in Colorado are unaffected.

Based on a limited sample, there is a correlation between resistance to UV-B and the activity of photoreactivating enzyme, photolyase. Species with the highest photolyase activities seem to be more resistant to UV-B radiation. Furthermore, of the species examined, frogs and toads generally show more photolyase activity than salamanders. It is also possible that nuclear excision repair is also being used to counter UV-induced DNA damage, but this has not been measured in amphibian species taken from the wild.

In nature, more than one environmental agent may affect an animal as it develops. This also seems true for amphibians developing at their natural field sites. Field experiments have been conducted to examine at least three factors that seem to interact synergistically with UV-B: a pathogenic fungus, low pH, and fluoranthene, a polycyclic aromatic hydrocarbon that may pollute aquatic environments impacted by petroleum contamination. A meta-analysis investigating the combined effects of UV-B with pH, contaminants, and disease found that UV-B radiation interacted synergistically with other stressors, resulting in greater-than-additive effects on survival. In certain combinations with UV radiation, these three agents increase mortality to levels greater than that contributed by UV radiation alone.

Obviously, UV-B cannot be regarded as contributing to all amphibian population declines. For example, UV-B radiation is unlikely to contribute to mortality in amphibians that are primarily nocturnal, live under dense forest canopies and lay eggs hidden from solar radiation, or have high photolyase activities.

Amphibian Deformities and UV Radiation

Reports of deformed amphibians have been given wide media attention, with the most common reports of deformities being frogs and toads with extra or missing limbs. Three major agents are being examined: pesticides, UV radiation, and parasitic trematode infection. However, only limited data are available on this subject based on experimental work. One laboratory study of northern leopard frogs showed that on exposure to 24 h of simulated ambient UV light, frogs developed hindlimb malformations. It remains unclear as to whether UV radiation can cause extra limbs in wild amphibian species. However, other deformities in wild species have been observed. These include edema, curvature of the spine, and lesions in larvae and newly metamorphosed amphibians. One report showed severe retinal abnormalities consistent with UV damage in a basking frog species.

Effects of UV Radiation on Biogeochemical Cycles

The effects of increased UV-B radiation on biogeochemical processes may be complex. For example, increased UV-B radiation may affect the magnitude and direction of trace gas on emissions and mineral nutrient cycling in terrestrial systems. Moreover, the effects on these processes may be species specific and may vary in different ecosystems. Increased UV-B radiation may alter the chemical composition of plant tissue, the photodegredation (breakdown) of dead plant matter, the release of carbon monoxide, and the activity of microbial decomposers, and nitrogen-fixing organisms.

In aquatic ecosystems, increased UV-B radiation may affect the processes that produce organic matter and the processes that degrade organic matter. There may be photodegradation of dissolved organic matter, which may lead to the production of organic acids and ammonium. Photoinhibition of surface aquatic organisms may also affect biogeochemical processes.

The potential effects of increased UV-B radiation on terrestrial and aquatic carbon, nitrogen, sulfur, oxygen, and metal cycles have been explored in a number of studies. These effects and similar effects on biogeochemical cycles in the atmosphere may aid or help impede the buildup of greenhouse gases and aerosols in the atmosphere.

Effects of UV Radiation on Humans

UV-B radiation does not penetrate deep into the body because most of it is absorbed in the superficial tissue layers. Therefore, much of the UV radiation affects the skin and eyes. However, there are also systemic effects. UV-B is the main cause of sunburn and tanning and the formation of vitamin D_3 in the skin. UV-B also affects the immune system. UV-B can cause snowblindness and is a significant factor causing cataracts. It also contributes significantly to the aging of the skin and the eyes and is effective in causing skin cancer.

Eyes

Photokeratitis is the effect most attributable to exposure to UV radiation. It is similar in effect to a sunburn and often occurs after short-term exposure to UV radiation. The eyeball becomes inflamed and reddens, often accompanied by pain and photophobia (fear of light). This is frequently diagnosed in skiers as snowblindness.

Exposure of the eye to UV radiation can also have effects on the cornea, contributing to degeneration of its fibrous layer. Under certain conditions, exposure to UV radiation can cause an outgrowth of the outermost mucous layer over the cornea, resulting in the loss of transparency. Squamous cell carcinoma (SCC) of the cornea, a malignant neoplasm, can also be found after exposure to solar radiation. These diseases are associated with outdoor living or working near areas of high reflectance (e.g., near water, concrete, and sand).

Cataracts are the leading cause of blindness in the world. They are characterized by a gradual loss in the transparency of the lens of the eye due to oxidized lens proteins. This can lead to blindness unless the affected lens are removed. There is a correlation between certain types of cataracts and exposure to UV-B radiation. Several studies have suggested that the relative risk associated with increased exposure to sunlight and cortical cataracts (those that develop in the outer layer of lens protein) is between about one- and threefold. One model suggests that a sustained 10% loss of ozone worldwide would lead to an additional 30,000 blind people per year.

Sunburn

Sunburn is the most common effect of exposure to UV radiation. This results in the reddening of the skin and possibly blistering. Sensitivity to sunburn and tanning varies with pigmentation. Heavily pigmented individuals are less sensitive to sunburning than less heavily pigmented individuals. There are various categories with regard to sunburn and tanning sensitivity. The most sensitive individuals (skin type I) develop a moderate to severe burn and usually do not tan within an hour of exposure to the summer sun. These persons usually have very fair freckled skin, red or blond hair, and blue eyes. The most resistant individuals (skin type VI) are darkly pigmented and become more pigmented after exposure to the sun.

Photoaging

Exposure to sunlight ages the skin. This is known as photoaging and is characterized by wrinkles, altered skin pigmentation, and an overgrowth of abnormal elastic fibers in the dermis.

Skin Cancer

There are various types of skin cancers. These are basal cell carcinoma (BCC), SCC, and cutaneous melanoma (CM). The carcinomas of the skin are often referred to as the "non-melanoma skin cancers (NMSC)." The NMSCs are clearly correlated with sunlight. They occur primarily in light-skinned individuals, and usually on the areas of the body most exposed to sunlight.

BCC is the predominant form of NMSC in light-skinned individuals. Individuals most susceptible to BCC are those with the lightest skin and a poor tanning ability. The incidence of BCC in light-skinned populations has been increasing in certain regions. Although it was originally thought that cumulative lifetime exposure to sunlight was directly related to developing BCC, recent information suggests that this may not be the case.

SCC is much less common than BCC but is much more common than CM in the US. Epidemiological data suggest that cumulative lifetime exposure to UV is a critical risk factor for developing SCC compared to other types of skin cancers. Several studies found an increase in the risk of developing SCC with incidence of childhood sunburns. However, this may be related to a high level of childhood exposure to sunlight rather than the number of sunburns *per se*.

CM is relatively rare compared with BCC or SCC. It accounts for only about 2–3% of the skin cancers associated with solar radiation, but it also accounts for most of the mortality. Like BCC, there does not seem to be a clear relationship between developing CM and cumulative lifetime exposure to UV radiation. Furthermore, CM often appears on areas of the body that are not the most heavily sun exposed. Several epidemiological studies have shown that exposure to sun during childhood increases the risk of developing CM. An additional risk factor is the appearance of freckles or moles.

Effects on the Immune System

In humans, the skin is the first line of defense against foreign bodies that may threaten an individual's health. Thus, the skin in combination with the immune system helps maintain health against infectious diseases, cancers, and parasites. The skin incorporates a number of cells from the immune system that can mount or influence immune responses to foreign substances. Substances entering the body, such as viruses, have to be "recognized" by the immune system as either "self" or "nonself" (foreign) entities. UV radiation can induce photochemical changes in the skin and potentially alter cell surface proteins that are used to determine "self" from "non self" entities. Thus, UV radiation can be immunosuppressive. The immunosuppressive effects of UV-B radiation can influence the outcome of melanoma and NMSCs, certain infectious diseases, some forms of autoimmunity, and allergy. For example, implants of UV-induced tumors in genetically identical mice are rejected in unexposed hosts but fail to be rejected by UV-exposed mice. UV-B radiation can inhibit local inflammatory responses within UV-irradiated skin. Thus, the response elicited by injection of an antigen into the skin of sensitized individuals may be diminished in UV-irradiated skin.

Some infectious agents can directly be harmed by exposure to UV radiation, whereas others are unaffected. Immunosuppression may also decrease an individual's resistance to certain infectious diseases. In animal models, human infectious diseases have been shown to be influenced by exposure to UV-B radiation. These diseases include herpes, tuberculosis, trichinella, candidiasis, leshmaniasis, listeriosis, and Lyme disease. Effects include suppression of immune responses to the organisms or their antigens, reactivation of latent infections, increased body loads of infectious organisms, decreased resistance to reinfection, and reduced survival. The impact of UV-B exposure on antigen-presenting cells in the skin suggests the possibility that UV-B radiation may exacerbate or ameliorate autoimmune diseases such as Lupus or human immunodeficiency virus (HIV). At the very least, UV-induced immune suppression could affect the course of certain diseases within human populations.

Appendix

List of Courses

1. General Biology
2. General Chemistry
3. Environmental Science
4. Photobiology

See also: Biogeochemical Cycles. Endangered Amphibians. Endangered Reptiles. Greenhouse Effect. Plankton, Status and Role of. Seagrasses

References

AMBIO (1995) Environmental effects of ozone depletion: 1998 assessment, 24: 137–196.

Bancroft BA, Baker NJ, and Blaustein AR (2007) Effects of UVB radiation on marine and freshwater organisms: A synthesis through meta-analysis. *Ecology Letters* 10: 332–345.

Bancroft BA, Baker NJ, and Blaustein AR (2008) A meta-analysis of the effects of ultraviolet B radiation and its synergistic interactions with pH, contaminants, and disease on amphibian survival. *Conservation Biology* 22: 987–996.

Blaustein AR, Kiesecker JM, Chivers DP, *et al.* (1998) Effects of ultraviolet radiation on Amphibians: Field experiments. *American Zoologist* 38: 799–812.

Häder D-P (ed.) (1997) *The Effects of Ozone Depletion on Aquatic Ecosystems*. Georgetown, TX, USA: RG Landes Co.

Tevini M (ed.) (1993) *UV-B Radiation and Ozone Depletion*. Boca Raton, FL: Lewis Publishers.

UNEP (1998) *Environmental Effects of Ozone Depletion: 1998 Assessment*. Nairobi, Kenya: United Nations Environment Programme.