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Review

On the history of phyto-photo UV science (not to be left in skoto toto and silence)

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A R T I C L E I N F O

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A B S T R A C T

This review of the history of ultraviolet photobiology focuses on the effects of UV-B (280–315 nm) radiation on terrestrial plants. It describes the early history of ultraviolet photobiology, the discovery of DNA as a major ultraviolet target and the discovery of photoreactivation and photolyases, and the later identification of Photosystem II as another important target for damage to plants by UV-B radiation. Some experimental techniques are briefly outlined. The insight that the ozone layer was thinning spurred the interest in physiological and ecological effects of UV-B radiation and resulted in an exponential increase over time in the number of publications and citations until 1998, at which time it was realized by the research community that the Montreal Protocol regulating the pollution of the atmosphere with ozone depleting substances was effective. From then on, the publication and citation rate has continued to rise exponentially, but with an abrupt change to lower exponents. We have now entered a phase when more emphasis is put on the "positive" effects of UV-B radiation, and with more emphasis on regulation than on damage and inhibition.

1. Ultraviolet radiation and the ozone layer

Ultraviolet radiation was discovered in 1801, when Johann Wilhelm Ritter in Germany observed that invisible rays just beyond the violet end of the visible spectrum were especially effective at darkening silver chloride-soaked paper. Another important component in our science, the ozone layer, is usually said to have been discovered in 1913 by the French physicists Charles Fabry and Henri Buisson, but surprisingly, Elizabeth Griffin (2005, 2009) realized about ten years ago that astronomers had already started to collect data on the thickness of the ozone layer around 1900, without knowing it. To gain an understanding of the composition of stars they measured the ultraviolet emission spectra, and these spectra have been preserved on photographic plates to our time. Now people can measure the spectra of the same stars using instruments in orbit, and assuming that the stars have not changed their output during a century, the ozone thickness can be computed. In reality the procedure is a little more complex: the star's elevation above the horizon etc. must be taken into account.

2. 1905–1933: early ultraviolet photobiology

Ultraviolet photobiology in a sense started in ancient Egypt, where white spots on the skin were treated with sunlight, in combination with a furo-coumarin extract of the plant *Ammi majus*. But let us jump a couple of thousand years forward in time. More than a century ago Niels Finsen (1896, 1900) cured cutaneous tuberculosis using ultraviolet radiation. The effect was probably accomplished via singlet oxygen generated by the action of ultraviolet-A radiation on porphyrins present in the tuberculosis bacterium, *Mycobacterium tuberculosis* (Møller et al., 2005; see also http://www.nobelprize.org/nobel_prizes/medicine/laureates/1903/finsen-bio.html). Hertel (1904), in Jena, studied how microorganisms are affected by ultraviolet radiation. He determined crude action spectra for killing, but was not able to draw any conclusions regarding the mechanism of action of the radiation. Harris and Hoyt (1917) found that if ultraviolet radiation was passed through solutions of various proteins, such as gelatin, it lost its killing activity. They drew the conclusion that this was because the active rays were absorbed by aromatic amino acids in those

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proteins, and that the killing effect of unfiltered radiation was due to absorption of active rays by aromatic amino acids in proteins in the bacteria. Rivers and Gates (1928) published action spectra for the inactivation of "vaccine virus" (smallpox virus) and of two strains of *Staphylococcus aureus* and found that the most efficient radiation was of wavelengths between 260 and 270 nm, but in this first publication they still mention proteins as the most likely radiation target. Later in the same year Gates (1928) (Fig. 1) pointed out that "other biochemical entities essential to life may also show a selective absorption over the toxic range, and it may be that the lethal action is due to some, or some one of these other substances". He further wrote: "Since the nucleus is recognized as the structural element in the cell on which growth and reproduction depend, attention was naturally directed to nuclear derivatives, and it was found that the reciprocal of the bactericidal curve matches certain derivatives of the nucleoproteins – cytosine, thymine and uracil – better than it does those for various aromatic amino acids, such as tyrosine, tryptophane, or phenylalanine, suggested by Harris and Hoyt". In a series of following papers he investigated this further and refined the action spectra (Gates, 1930, Fig. 2). He found (Gates, 1933) that cell division was much more sensitive to ultraviolet radiation than was cell growth, and concluded that "further studies are in progress." Unfortunately he died before he could publish the results of these studies.

Gates' experiments were done with viruses and bacteria, but have relevance also for plants; DNA is also a major target for ultraviolet radiation in plants. The experiments on inhibition of cell division have been followed up for plants in more refined ways up to the present; mechanisms are being explored, and the most sensitive states of the cell division cycle are being pinpointed (e.g., Jiang et al., 2011). In the following discussion I shall concentrate on the ultraviolet photobiology of higher plants, with side views on related topics. (A review dealing with the history of the photobiology of humans, animals, and microorganisms has been provided by Hockberger (2002).)

3. 1933–1970: photoreactivation

The next great step in ultraviolet photobiology was the discovery of photoreactivation, and in this case the first observation was made on plants (more specifically fruit peel) by Hausser and von Oehmcke (1933). They noticed that if unripe bananas were irradiated with ultraviolet radiation, they would turn brown rather than yellow during maturation, but that the browning could be prevented by irradiation with visible light immediately after the exposure to ultraviolet radiation. I show a repeat of this first photoreactivation experiment in Fig. 2. Hausser died the year after

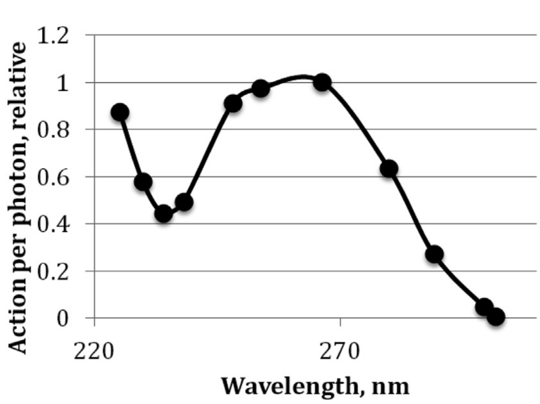

Fig. 1. The action spectrum for killing of *Eschericia coli* determined by Gates (1930). Note the similarity, also noticed by Gates, to the absorption spectrum of DNA (Fig. 3).

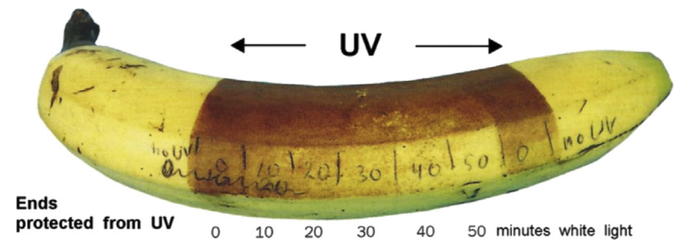

Fig. 2. A banana that at the unripe green stage was first irradiated with short-wave UV radiation, then for the indicated number of minutes with photoreactivating visible light, and finally left to ripen in darkness.

this first work on photoreactivation, but in 1938 his widow Isolde (Hausser 1938) continued the banana work and showed that there were two kinds of photo-induced browning effects, one caused exclusively by ultraviolet radiation, and one caused by light absorption in chlorophyll and, as we understand now, mediated by reactive oxygen species. She also studied action spectra for erythema and pigment formation in human skin. After this work, there was a long pause until, in 1949, there was a flush of papers on photoreactivation, and it was realized that photoreactivation involves repair of DNA. There soon followed additional papers on photoreactivation in higher plants (e.g., Bawden and Kleczkowski, 1952).

Rupert et al. (1958) succeeded in achieving photoreactivation of DNA *in vitro*, and soon after (Rupert (1960)) proved that the process is catalyzed by an enzyme, which can be isolated from yeast cells, and was later also isolated from plant cells (Saito and Werbin, 1969a,b). The enzyme, first called photoreactivating enzyme and later renamed photolyase, was found to repair cyclobutane pyrimidine dimers (CPDs) in DNA. Soon after, another type of enzyme that photorepaired (6-4) photoproducts was found in various organisms including plants (see Sancar, 1996 for a review).

4. 1970–1995: ozone depletion and the Montreal Protocol

In 1970 Paul Crutzen (Crutzen, 1970) realized that nitrogen oxides, which are emitted into the atmosphere by natural processes as well as by human activities, are able to decompose the stratospheric ozone which protects us from ultraviolet radiation. Soon after, Molina and Rowland (Molina and Rowland, 1974; Rowland and Molina, 1974) announced that chlorofluoromethanes (or

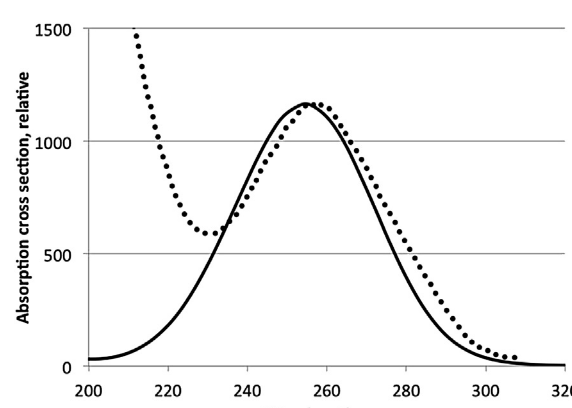

Fig. 3. Comparison of the absorption spectra of ozone and DNA. The absorption scale for ozone is in units of 10^{-10} cm^2 $molecule^{-1}$, and the curve for DNA (dotted line) is normalized to the same height at the maximum. The data for ozone (continuous line) are from Molina and Molina (1986) and those for DNA (from *Escherichia coli*) from Basu and Dasgupta (1967). Below 230 nm the O_2 form of oxygen blocks solar radiation completely.

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