

All you wanted to know about UV radiation and plants

by

Alenka Gabersčik, Alan Jones and Marcel Jansen

Sunlight, in its many guises, is force that has shaped and driven the miraculous living fabric of this planet for billions years. It embodies the best engineering, the widest safety margins, and the greatest design we experience now. It provides amply for our needs, yet limits our greed... It is safe, eternal, universal and free.

Theodore B. Taylor, Sceptic (1977)

This quotation summarises the essence of the importance of sunlight for our planet. Part of sunlight is radiation in the UV range which has been one of “engineering tools” that significantly contributed to the diversity of the present Earth biocenosis, the community of all interacting organisms. In spite of this, the attitude of the public towards UV radiation is usually one of negativity. The majority of people associate UV radiation with sun burns and skin cancer, while little awareness exists of the positive role of UV radiation in our lives. On this web page you can find descriptions of the effects of UV radiation that enhance our lives.



UV radiation ends where the colours of the rainbow begin

The nature of light on the Earth

Sunlight is electromagnetic radiation coming from the sun. It consists of a spectrum of visible and non-visible energy with different wavelengths. The most important parts of sunlight for life on Earth are ultraviolet radiation, visible light and infrared radiation. Packages of light (photons) coming from the sun travel directly through space, as long as nothing obstructs them. The amount of solar radiation just outside the Earth's atmosphere is therefore more or less constant (about 1.36 kW/m^2). Different particles in the atmosphere affect the quantity and quality of incoming radiation. Photons are absorbed, scattered, and reflected by the ozone layer in the stratosphere as well as by gasses, aerosols, clouds and other particles (i.e. dust or different pollutants) in the troposphere. As a result only about half of the total solar radiation reaches the Earth's surface.

Different wavelengths of light are affected differently by dust particles or water droplets. Thus, different wavelengths of light that hit water droplets are reflected into different directions, resulting in a rainbow.

What is UV radiation?

Ultraviolet radiation (UVR) is a type of solar radiation with wavelengths between 100 and 400 nm. It ends where the colours of rainbow start. The atmosphere absorbs all UV-C ($< 280 \text{ nm}$), a significant part of UV-B (280 – 315 nm) but transmits most of the UV-A radiation (315 – 400 nm). UVR represents only about 7-9 % of total solar radiation reaching the biosphere, but unlike other types of solar radiation, UVR is highly energetic radiation. This means that UVR can cause reactions between molecules that are hit by such radiation.



Visible light consists of different colours which can be seen as a rainbow when shone through a prism, or when sunlight shines through raindrops.



Reflected light from water vapour (clouds) appears white because it contains all colours. Blue light is of shorter wavelengths. It is scattered by gas molecules and is why the sky appears blue.

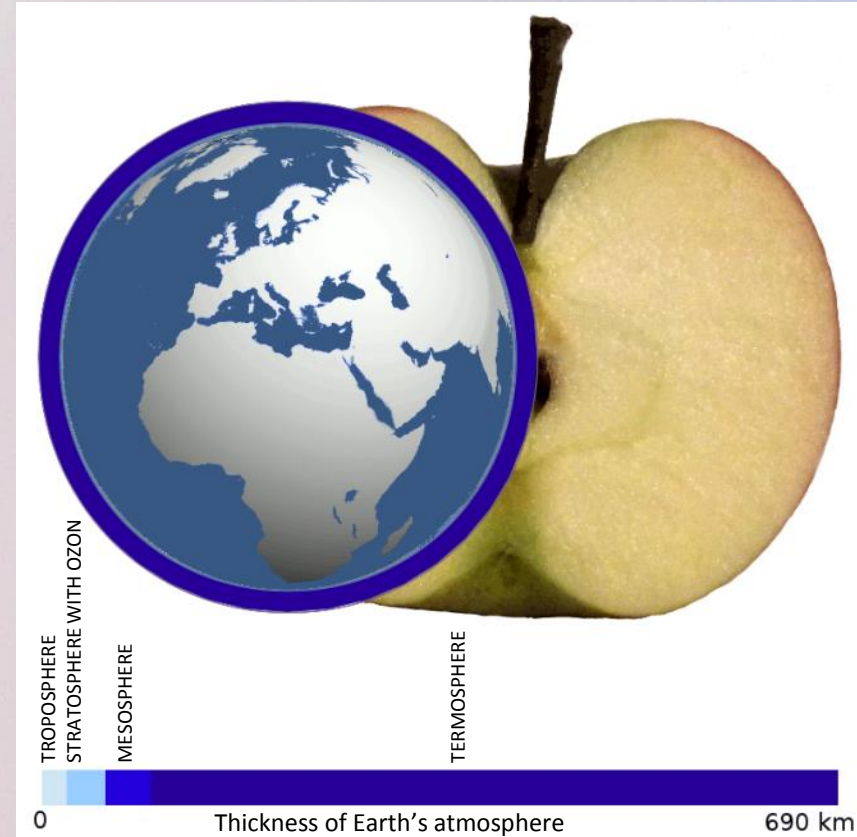
UV radiation and plant photosynthesis enable the existence of protective ozone layer

UV radiation and plant photosynthesis enable the existence of protective ozone layer

The Earth's biosphere is protected from short-wave UVR by an ozone layer in the stratosphere. The formation of this ozone layer has been possible due to photosynthesis, in which plants take up carbon dioxide and release oxygen (O_2). When UV photons (especially UV-C) hit O_2 molecules these fall apart to atoms of oxygen, which in turn, react with remaining O_2 to form ozone (O_3). The ozone layer extends from 10 km to 50 km above the Earth's surface, however, the total amount of ozone is small since the average concentration is only about 8 parts per million (ppm). If condensed to a liquid and spread evenly over the Earth, the ozone layer would be only about 4 micrometers (0.000004 m) thick. The amount of ozone is expressed as Dobson units (DU). Normal amount is around 300 DU, which corresponds to 3 mm of pure ozone at a pressure of 1 atmosphere and at 0 °C. Worryingly, the ozone layer is very delicate and some chemicals cause its destruction. Reductions in the ozone column, primarily due to the anthropogenic (i.e. by humans) discharge of chlorofluorocarbons used in fridges and spray cans have led to substantial increase in UV-B radiation on the Earth's surface. Climate change might additionally affect UVR through changes in cloud formation and albedo.



Concern about ozone layer depletion by chlorofluorocarbons led to a very successful international treaty. All major countries in the world jointly agreed to restrict the use of chlorofluorocarbons in order to save the ozone layer. This is the so-called Montreal treaty which was agreed in 1987, and has been hailed as an example of exceptional international co-operation, and an inspiration for the international community in its battle against climate change and loss of biodiversity.



The atmosphere is rather thin. The thickness of troposphere and stratosphere which are crucial for the life on Earth is shown in light blue colours. If we compare the Earth with an apple, the thickness of the troposphere corresponds to the apple's skin.

Light shaped the life on the Earth

Plants are well 'equipped' to use solar radiation efficiently

Plants, as primary producers, are fully dependent on solar radiation. Light is their source of energy, driving photosynthesis and directing plant development from germination to flowering. However, light is not just beneficial, but it can also exert warming and destructive effects. Therefore proper 'equipment' to exploit solar radiation efficiently without suffering the damage is crucial for plants. This holds especially true for radiation in the UV range.

DNA damage and repair

The targets of UVR in any living cell are DNA, lipids and proteins (which form enzymes and hormones). DNA is the genetic material in all living organisms, that is passed on from generation to generation. DNA damage will occur whenever the organism is exposed to UVR. Yet, DNA damage is not simply bad news. UVR has been an important evolutionary force, generating mutations, leading to new traits, and driving the development of species diversity. Mutations are, however, mostly negative, inhibiting vital cellular processes (DNA transcription and replication) and resulting in disturbed cellular function, sometimes even cell death. Fascinatingly, plants exploit blue and UV-A wavelengths to drive DNA repair processes. Researchers have showed that DNA damage due to UVR is mostly repaired by subsequent exposure to light in the blue or UV-A range of the spectrum. This is because blue light and/or UV-A exposure activate an enzyme (photolyase) that repairs damaged DNA sequences. The beauty of this system is that when plants are exposed to UVR, there is always a lot of blue light present. The involvement of blue or UV-A light in this process is known as photoreactivation. Photoreactivation is the major defence against UV-induced damage in plants. Apart from photoreactivation, plants have gained many other adaptations to cope with UVR during their evolutionary history.



Humans, and many animals, withdraw in to the shadows on a hot day. However, sessile plants can't do that, and can therefore be exposed to very intense radiation.



Exposure to low UVR doses is unlikely to have negative impacts on most organisms. Exceptions are for poorly adapted (unhardened) plants (e.g. intensively bred cultivated plants) and plants that are subject to additional environmental constraints (i.e. plants in deserts, or arctic regions).

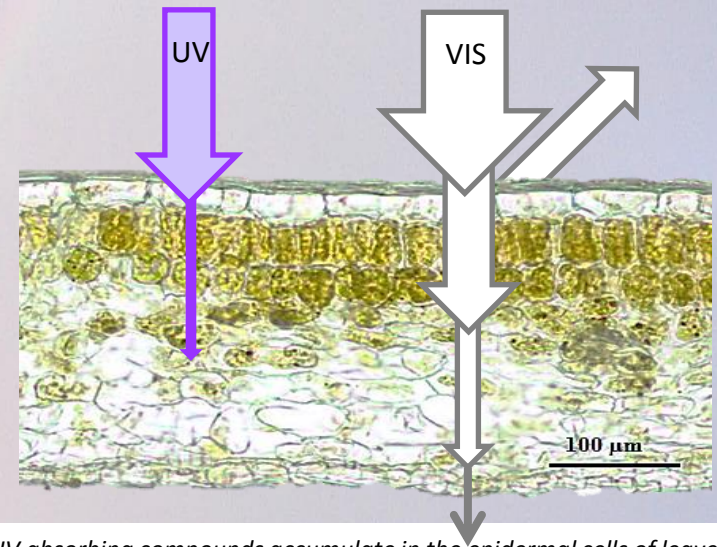
Plants respond when exposed to UVR

Plants 'see' light

Solar UVR is unlikely to cause serious damage to most plants. Rather, plants have learned how to perceive (see) UVR and to use that information to control their own growth. Plants have evolved to sense the quality, intensity, duration and direction of light. Besides sensing visible light such as blue and red light, plants also use “sensors” for UV-B radiation. Perception of UVR enables plants, not only to switch on protection against excessive UVR exposure, but also to physiologically adjust to it. For example, studies have shown that UVR induces morphogenic responses (i.e. altered plant shape and chemical make-up), which are mediated by a specific UV-B sensor, the UVR8 photoreceptor protein.

UVR triggers production of UV-absorbing filters in plants

One of the most consistent morphogenic responses of plants to solar UVR is synthesis and accumulation of UV absorbing compounds. The diversity and complexity of these substances in plants has increased through evolution. UV-protective compounds in plants include mycosporine-like amino acids (MAAs), which are found in algae and variety of phenolic substances synthesised in vascular plants. Phenolic substances (phenolics) are plant secondary metabolites comprising around 8000 naturally occurring compounds, possessing one common structural feature, a phenolic (aromatic) ring. The concentration and type of these compounds generally depends on the group of organisms and the level of UV-B radiation. Besides photoprotection, phenolics have many other functions: they provide defence against injury, infection and stress (frost, high temperatures, drought), protect plants against herbivory and the improve the survival of plants in soils rich with toxic metals. Since UV absorbing compounds accumulate in the surface layers of plant tissue, they may significantly change optical properties of plant organs including fruits, flowers and leaves. The presence of these substances in plant tissue is also one of the reasons that soil is a dark brown colour, because phenolics in dead plant material eventually form the soil.



UV absorbing compounds accumulate in the epidermal cells of leaves and act as selective sunscreens to reduce the penetration of UVR into the leaf tissue. At the same time, they do not affect the penetration of visible light, which is essential for photosynthesis. They work similarly to the sunscreens which humans use to protect our skin from UVR.



In many cases the production of UV-B absorbing compounds is not only dependent on the UV-B dose. Plants growing in open places, tropical and high altitude environments already contain high levels of these phenolics, and enhanced UV doses do not contribute to increased production.

UVR may affect plant growth

Different studies have shown that UVR induces diverse growth responses in plants. Many of these responses are found in alpine plant species. Scientists presume that alpine flora have adapted in this way partly due to enhanced UVR at high elevations. It has been argued that each of these architectural changes allows plants to efficiently scatter and reflect UVR, protecting their cells for damage. However, researchers are still debating whether this is really the case. Indeed, some scientists have even argued that these UV-induced changes in plant shape are only to help the plant survive heat and drought. The reason for increased drought tolerance of UVR treated plants is morphogenetic changes (especially smaller leaves) which increase water use efficiency in plants, while phenolic compounds also protect tissues from damage.

Exposure of plants to UVR might alleviate negative impacts of other environmental constraints

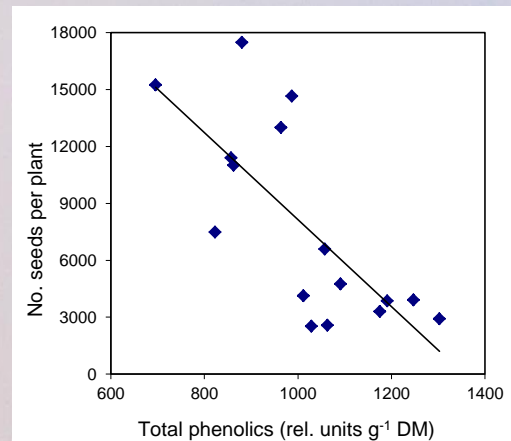
Several studies have shown that plant treatment with UVR may increase the plant's tolerance to drought and *vice versa*, plants that are more tolerant to drought are also likely to be more tolerant to UVR. UVR may also reduce plant infections with pathogens, since fungi and bacteria are generally more sensitive to damage by UVR than are higher plants. Moreover, many of UV-induced phenolic substances also have an antimicrobial activity.

Everything in nature is a question of cost and benefit

Everybody knows that efficient equipment costs a lot. It also holds true for plant traits that are needed to cope with UVR. Plants as sessile organisms that live in constantly changing environment, are subjected to permanent 'trade off' between investments in growth and in secondary functions, such as UV protection. Thus, the environmental trigger for production of phenolic screening compounds is not only a sufficient UVR dose, but a high level of visible (photosynthetic active radiation). This combination of cues ensures a high photosynthetic rate is available to provide energy for both processes.



Plants growing in high level UVR environment remain shorter and have denser branching, compared with plants exposed at lower doses. Leaves become smaller, but thicker and have different epidermal and cuticular structures, and other leaf properties such as waxy layer, leaf hairs and leaf bladders.



The production of protective UV absorbing compounds (phenolic screening compounds) is costly since it needs additional input of energy which lowers energy available for growth, tissue development and seed production as was the case in St. John's wort (above)

UV-B and the co-evolution of plants and pollinators

The vision of pollinators and optical properties of flowers are a result of long lasting co-evolution

Perception of light by humans reveals a very colourful world. But the colour of the world for some other organisms is not like it seems to us. The vision of bees, butterflies and some other insects, for example, extends into the ultraviolet range. Therefore, many insects can see the accumulation of UV-absorbing pigments by plants. It appears that plants exploit animal vision in the UV range for advertising their flowers and *vice versa*, insects gained further adaptations to see flower patterns which are visible in UV range only. In many flowers ultraviolet light uncovers secret paths and "landing strips" that lead to delicious food. These markings are visible only to selected insects, while they are hidden from majority of other animals and humans. Thus, on the evolutionary scale the colour vision of some insects and the spectral properties of flowers have developed in to mutual plant – pollinator relationships. The benefits of plant -pollinator coevolution are efficient reproduction for plants and availability of high energy food for pollinators. Some carnivorous plants, however, use these ultraviolet markings for a more sinister reason. They attract pollinators to their insect traps, by imitating the UV-visible patterns of flowers.



The colour of many flowers may significantly differ for humans and insects, since insects see in UV range.



The colour vision of some insects and the spectral properties of flowers have developed in to mutual plant – pollinator relationships.

Plants grown under UVR are beneficial for humans

Plants provide protective substances for humans

Plants are an essential resource for humans in many ways. Each atom of carbon, that builds our body, is first taken up by plants and fixed in the process of photosynthesis and only then can we use it. The same holds true for minerals that come from soil and become available to humans with the assistance of plants. Beside this, plants also produce many important protective substances and vitamins that are indispensable for them, but also benefit us, since our bodies are not able to synthesise them. You probably know vitamin C and antioxidants are important components of healthy food. We have already learned that the production of many beneficial compounds is triggered by UVR. The most important group of chemicals are the phenolics that exhibit a wide variety of beneficial biological roles, including antiviral, antibacterial, immune-stimulating, anti-allergic, anti-inflammatory, anti-carcinogenic and others. They are also powerful antioxidants scavenging reactive oxygen species and free radicals and can bind (chelate) with metal ions such as iron and copper, enabling our bodies to use these important micro-nutrients. Important sources of phenolics are different herbs (i.e. medical plants), fruits, vegetables, grains (i.e. buckwheat, wild rice), tea, coffee beans, bee pollen (propolis), and red wine.

UV might increase the amount of active substances in medical plants

Many studies have shown that enhanced UVR, especially UV-B radiation, increases the amount of active substances in many plant species. We have already mentioned the importance of different phenolics (i.e. flavonoids, stilbenes) and vitamin D, production of which is stimulated by UV-B. Vitamin D is also synthesised in plankton, which is then ingested by fish and can eventually become human food rich with vitamin D and beneficial to health. UVR stimulation has also been shown to increase plant production of different (phenolic) alkaloids, essential oils and terpenoids, that have known medicinal properties.



Grapes are rich in phenolics. It is important fruit that can be used for making wine, jam, raisins, vinegar or eaten raw.



UV increases the amount of active substances in medical plants.

UVR enhances plant food quality

Human efforts to increase food production and to control plant production have changed basic environmental conditions for plant growth. Plant breeding has increased the yield of plant cultivars, which require irrigation and fertilisation during the entire growth season to ensure favourable harvests. Plants are also cultured in greenhouses to avoid different pests and weeds and to prolong the growing season. Because of long distance food transportation we often consume unripe fruits that are usually poor in phenolics and vitamins. The race for more food that is grown faster has neglected some basic things; (1) Everything in nature is question of cost and benefit. Thus, if plants invest more in yield it is likely that less energy will be left for investment in secondary chemicals for plant protection; (2) If plants are bred to grow in a favourable environment they will lose the natural genetic adaptations needed to cope with adverse environmental conditions. Therefore, it may happen during drought that poorly 'equipped' plants will be more susceptible compared with plants growing under natural conditions; (3) plants subjected to intensive breeding might have lower potential to produce beneficial phenolic substances following exposure to UV-B; (4) many studies show a negative effect on food quality when the natural UVR dose is reduced in greenhouses. Culturing plants in greenhouses might have two adverse consequences: less radiation at visible wavelengths for photosynthesis and less or no UVR (due to glass or plastic covers that block UVR). This latter reduces the production of UV-induced phenolic substances.



Picking unripe fruit before long distance transportation negatively affects the amount of phenolics and vitamins.



In greenhouses there is less or no UVR, reducing the production of UV-induced phenolic substances, which are an important component of healthy food.

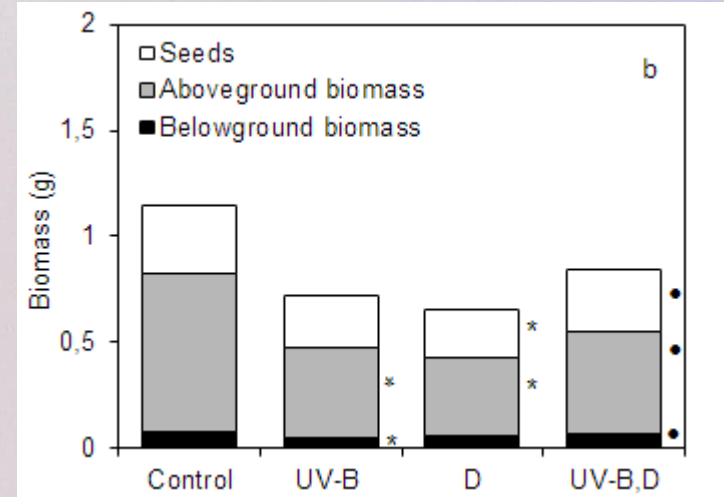
How 'burning' is the issue of increased UV-B radiation today?

The stratospheric ozone layer is expected to recover by 2050

The stratospheric ozone layer protects life from damaging UV radiation. Depletion of the stratospheric ozone layer has occurred mainly as a consequence of emissions of chlorofluorocarbons (CFCs), methyl bromide (CH_3Br), nitrogen oxides (NO_x) and some other substances released by human activities. Continuous observations since the 1980s have shown that ozone amounts have decreased by 3 to 6 %, resulting in a 6 to 14 % increase of UV-B radiation at Earth's surface. The stratospheric ozone depletion in high latitudes of the Northern Hemisphere is less pronounced and more erratic than in the Southern Hemisphere, where an annual reduction in ozone density occurs each spring. The half-life of chlorofluorocarbons (CFCs) ranges from 50 to 150 years and each CFC molecule may cause the destruction of many molecules of ozone. Therefore CFCs will remain in the upper atmosphere for a long time and it is expected that decreased ozone levels will only recover to pre-1970 levels after several decades. The generally accepted forecast is that the stratospheric ozone layer will recover by 2050, even though this is uncertain due to the interactive effects of global climate change.

Negative effects of enhanced UV-B on productivity are found in many agricultural plants, but rarely in plants from natural environments

The effects of enhanced UVR, especially UV-B radiation on plants, have been widely studied. The negative effects depend on the species and on the balance between potential damage and the induction of protective and repair mechanisms. As already mentioned, the most common response of field-grown plants to elevated level of UV-B is an increase in levels of different UV-absorbing phenolics. Changes in metabolism affect the timing of seasonal changes in plant activity (phenology), together with biomass and seed production. Studies have also shown that UV-B radiation can cause damage to DNA and affect photosynthesis, respiration, water management, growth and development.



Distribution and amount of biomass in different parts of Tartary buckwheat subjected to UV-B radiation and drought (D) .



Crops, which have been selectively bred for maximum yield are more sensitive to the detrimental effects of UV-B. Studies have shown crop yield to be decreased by enhanced UV-B radiation. However, this is not the case in all crops (e.g. buckwheat).

Conclusion

There is a comprehensive range of benefits and threats from UVR, ranging from decreased yields of some crops to enhanced quality (phenolics) and drought and pest and disease tolerance of others. It is up to us to take proper measures to avoid possible damaging effects to humans and the plants and animals we deal with. We need to ensure the advantages of UVR are also used, similar to how many organisms have benefited from this radiation during evolution.



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Check what did you learn about UV radiation and plants?

1. Why do we see different colours?
2. Are the wavelengths of UVR long, or short compared to visible light?
3. What components of the biosphere are necessary to create ozone?
4. Why are plants particularly vulnerable to UVR exposure?
5. Some bands of UV light are less destructive than others, name a less destructive one?
6. Besides sensing UV light in order to protect themselves from it, what other uses do plants have for their light senses?
7. Phenolics are effective sunscreens for UVR, what essential leaf process do they not interfere with and how?
8. How might plant adaptations to UVR also provide protection to other conditions in extreme environments?
9. How might UVR help plants adapt to climate change?
10. Why do plants not synthesise UVR screening compounds in their leaves all the time?
11. How do plants use UVR to communicate with insects?
12. Why is it difficult to tell whether the ecosystem level effect of UVR is detrimental or beneficial?
13. Why is it important to eat food plants that have been exposed to UVR?
14. Which group of mammals would find it difficult to synthesise vitamin D from sunlight alone?
15. Because they are not exposed to significant doses of UVR, how do dolphins and whales obtain their vitamin D?
16. CFCs were used as a relatively safe and stable gas in refrigerators, how does this quality mean they are such a long-term threat to the ozone layer?
17. How might UVR affect the yield of crop plants?

Photos: Alenka Gabersčik, Archiv of Notranjska Regional park