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PERSPECTIVE

Effects of solar ultraviolet radiation on terrestrial ecosystems. Patterns, mechanisms, and interactions with climate change

C. L. Ballaré,*[a] M. M. Caldwell,[b] S. D. Flint,[b] S. A. Robinson[c] and J. F. Bornman[d]

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Ultraviolet radiation (UV) is a minor fraction of the solar spectrum reaching the ground surface. In this assessment we summarize the results of previous work on the effects of the UV-B component (280–315 nm) on terrestrial ecosystems, and draw attention to important knowledge gaps in our understanding of the interactive effects of UV radiation and climate change. We highlight the following points: (i) The effects of UV-B on the growth of terrestrial plants are relatively small and, because the Montreal Protocol has been successful in limiting ozone depletion, the reduction in plant growth caused by increased UV-B radiation in areas affected by ozone decline since 1980 is unlikely to have exceeded 6%. (ii) Solar UV-B radiation has large direct and indirect (plant-mediated) effects on canopy arthropods and microorganisms. Therefore, trophic interactions (herbivory, decomposition) in terrestrial ecosystems appear to be sensitive to variations in UV-B irradiance. (iii) Future variations in UV radiation resulting from changes in climate and land-use may have more important consequences on terrestrial ecosystems than the changes in UV caused by ozone depletion. This is because the resulting changes in UV radiation may affect a greater range of ecosystems, and will not be restricted solely to the UV-B component. (iv) Several ecosystem processes that are not particularly sensitive to UV-B radiation can be strongly affected by UV-A (315–400 nm) radiation. One example is the physical degradation of plant litter. Increased photodegradation (in response to reduced cloudiness or canopy cover) will lead to increased carbon release to the atmosphere *via* direct and indirect mechanisms.

Introduction

Terrestrial ecosystems represent the largest store of active organic carbon in the biosphere,[1] and include biomes of widely variable climate regimes with a diverse set of organisms adapted to this range of conditions.[2] Key ecosystem services include food and fibre production, as well as protection of watersheds and water quality and regulation of atmospheric composition.[3]

Terrestrial ecosystems are being perturbed directly and indirectly by anthropogenic activity. Increased temperature and atmospheric CO_2, and altered precipitation patterns, are generally considered to be the most important climate change factors affecting terrestrial ecosystems. Superimposed on those drivers are changes in the levels of solar UV-B radiation resulting from stratospheric ozone depletion and other atmospheric factors.[4] Model calculations that incorporate satellite measurements of ozone, and cloud and aerosol reflectivity, show a significant increase in UV-B radiation reaching the Earth's surface between 1979 and 2008; this increase occurred at all latitudes except the equatorial zone, with the largest increments taking place at mid to high latitudes in the Southern Hemisphere[5] (see also McKenzie *et al.*[4]).

Recovery of stratospheric ozone, due to the successful implementation of the Montreal Protocol, is predicted over the decades ahead.[4,6] However, the additional effects of climate change on ozone chemistry and UV transmission through the atmosphere make future UV levels at the Earth's surface much more difficult to predict.[4] Changes in UV-B radiation also occur in response to environmental and anthropogenic factors other than ozone depletion. For example, changes in cloudiness (associated with climate change) and aerosol concentrations may also affect UV irradiance at regional, or even global scales.[4,7] Reduced cloud cover and conditions of increased aridity, predicted by current climate models for some regions,[8–10] are likely to have strong effects on the UV irradiance received at ground level. Furthermore, deforestation or changes in agricultural practices that alter plant canopy cover or structure may have important effects on UV levels received by vegetation, canopy arthropods, and microbes in terrestrial ecosystems. These changes in UV radiation are predicted to occur over a greater geographic area than that affected

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[a] *IFEVA and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Buenos Aires (C1417DSE), Argentina. E-mail: ballare@ifeva.edu.ar*

[b] *Department of Wildland Resources and the Ecology Center, 5230 Old Main Hill, Utah State University, Logan, UT, 84322-5230, USA*

[c] *Institute for Conservation Biology and Environmental Management, University of Wollongong, Northfields Avenue, NSW, 2522, Australia*

[d] *International Global Change Centre, University of Waikato, Private Bag 3105, Hamilton, 3240, New Zealand*

by ozone depletion,[4] and may therefore affect a much more diverse range of terrestrial ecosystems.

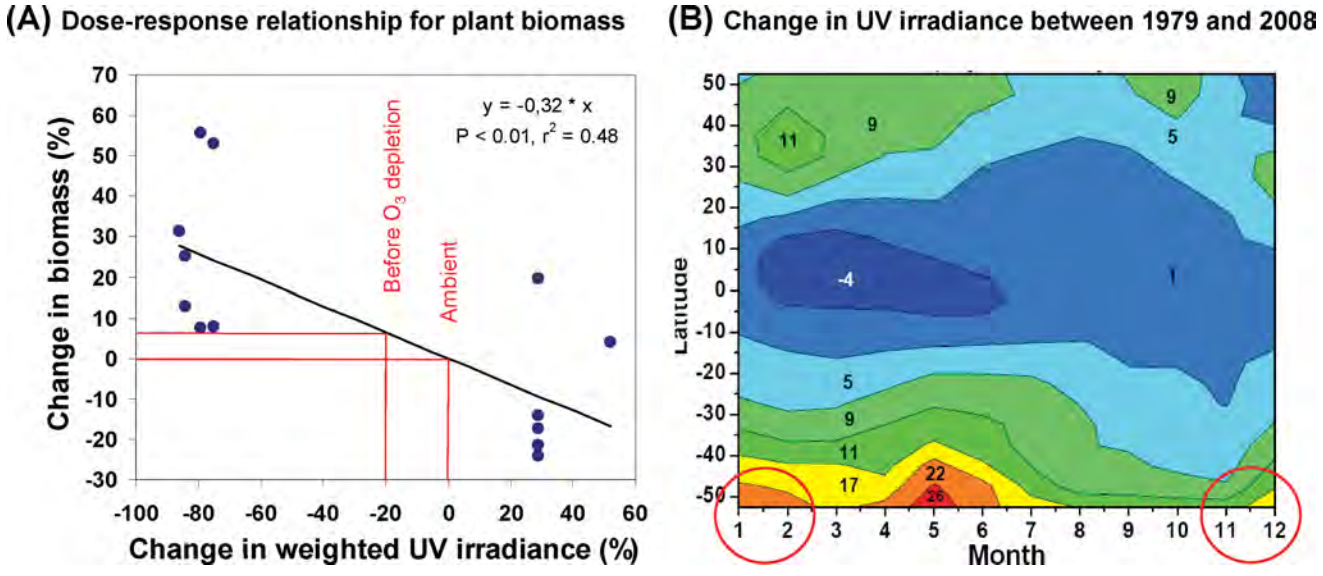
In this report, we consider recent advances in our understanding of the effects of UV radiation on terrestrial ecosystems, and assess the biological consequences of changes in UV radiation resulting from ozone depletion and other climate change factors. In the first part, we build upon our latest report[11] and yearly updates[7,12,13] and present an analysis of the responses to UV-B radiation of the various components (trophic levels) and processes (trophic-level interactions; biogeochemical cycles) of terrestrial ecosystems. Next, we highlight recent progress in the understanding of the basic mechanisms of plant responses to UV-B radiation. Finally, we briefly address technical issues associated with the design and interpretation of experiments intended to evaluate biological effects of UV-B radiation. This assessment is mainly concerned with UV-B radiation effects, but because climate change may also result in significant variation in UV-A levels (for example, due to changes in clouds[4]), the effects of this spectral region will be considered in those cases where there is sufficient information to anticipate possible ecological consequences.

Effects of UV radiation on organisms at different trophic levels

Primary producers

Growth responses. The general conclusion that has emerged from studies with terrestrial plants is that photosynthesis (CO_2 fixation per unit leaf area) is not significantly affected by changes in UV-B radiation when plants are grown under natural conditions. However, UV-B radiation may have subtle inhibitory effects on biomass accumulation, often correlated with a reduction in the rate of leaf area expansion. The primary literature reporting on these effects has been discussed in previous reports[11] and in several reviews.[14–17]

In this report, we have focused on a selected number of reviews and meta-analyses of published information that permit a quantitative assessment of the sensitivity of plant growth to ozone-induced variations in UV-B levels under field conditions. One such study is a meta-analysis of experiments carried out in polar regions in both hemispheres.[15] This analysis considered results from both UV-B attenuation (reduction through filtering or screening) and supplementation (addition of UV-B radiation using lamps) studies, and provides rough estimates of dose-response functions, where parameters such as leaf area and biomass are plotted against the dose of UV-B radiation received by plants (Fig. 1A). The authors of this analysis concluded that the effects of UV-B radiation on plants (mosses and angiosperms) of Arctic and Antarctic ecosystems are similar to those reported for higher plants of lower latitudes (Ballaré *et al.*;[14] Searles *et al.*[16]). The response is characterized by small reductions in leaf area and growth rate (biomass accumulation) as UV-B radiation increases (Fig. 1A), and is accompanied by responses at the biochemical and physiological levels (see following section on Protection and acclimation).


(A) Dose-response relationship for plant biomass

(B) Change in UV irradiance between 1979 and 2008

Fig. 1 A quantitative estimate of the reduction in the growth of the primary producers that may have occurred as a consequence of increased UV-B radiation between 1979 and 2008. (A) Change in above-ground biomass as a function of experimentally-imposed changes in weighted UV irradiance. The growth data are derived from a meta-analysis of field studies in high-latitude ecosystems (which involved experimental attenuation or supplementation of ambient solar UV-B radiation), and are expressed as percentage change in relation to the growth of the plants receiving ambient solar radiation.[15] The UV doses are weighted using the generalised plant function,[162] and expressed as % change relative to the ambient level (note that, for this function, a 10% increase in UV corresponds to a 5% reduction in ozone; *i.e.*, a RAF of 2 (see McKenzie *et al.*[4]). The red lines focus on the example discussed in the text. For areas where ozone depletion over the last three decades has led to a 20% increase in the summertime levels of weighted UV radiation (areas approximately designated by the red circles in panel B), the difference in plant growth between 1979 and the present would be 6% or less, given the slope of the dose-response relationship and assuming that all other factors are equal. (B) Percentage change in UV irradiance (numbers inside the coloured areas), weighted using the generalised plant function,[162] as a function of time of the year and latitude (between 55°S and 55°N), between 1979 and 2008 (data from Herman[18]). Note that the relative changes in weighted UV irradiance at 50–55°S are much greater near the winter solstice, but the absolute irradiance levels are very low during the winter and vegetation is less physiologically active and possibly snow-covered at that time of year.

The slope of the plant biomass response to UV-B irradiance derived from this meta-analysis (–0.32; Fig. 1A) indicates an approximate 1% reduction in growth for each 3% increase in weighted UV-B irradiance. If this slope is considered in the context of the changes in weighted UV-B irradiance that occurred over the last 30 years (Fig. 1B),[18] it is possible to produce an estimate of the magnitude of the changes in the growth of the primary producers that may have occurred as a consequence of ozone depletion. Thus, for example, in areas such as the southern tip of South America (at 55°S), where ozone depletion has led to a 20% increase in the summertime levels of UV-B radiation (the areas approximately designated by the red circles in Fig. 1B), the estimated difference in plant growth rate between the present and 1979 would be 6% or less (see red lines in Fig. 1A).

This analysis has several strengths, which are summarized below.

(1) The analysis produces a quantitative estimate of the effects of changes in UV-B radiation on the growth of terrestrial primary producers.

(2) The estimate agrees well with quantitative data produced by other analyses of field experiments. For example, the UV-B attenuation experiments carried out in southern South America in the late 1990s (the peak in ozone depletion), indicated that the negative effect of the enhanced UV-B radiation on plant growth was ~3–4% (Ballaré *et al.*[14]). Furthermore, a comprehensive meta-analysis of UV-B supplementation studies[16] concluded that the average response to treatments that simulated 10 to 20% depletion of ozone was a 6% reduction in plant biomass. A more recent meta-analysis[19] yielded results that were quantitatively consistent with those of Searles and co-workers,[16] and suggested that the average sensitivity to UV-B radiation would be lower in woody perennials than in herbaceous plants.

(3) Combining results from several studies reduces effects of random variation in individual experiments. The coefficient of variation in individual field studies in natural ecosystems is frequently >10%. Because the number of replicates in these studies is normally low, due to cost and logistic limitations, it is clear that responses of the magnitude predicted by the analysis presented in this report are unlikely to be detected as statistically significant in individual studies.

At the same time, the analysis presented here has some limitations. First, it assumes a linear dose-response relationship, which is not necessarily the case. Second, it assumes that the growth responses measured in experiments where the UV-B radiation levels are abruptly increased or decreased (by supplementation or filtering techniques) would hold true for conditions where the UV-B irradiance received by the ecosystems changes gradually over a period of several years.

Protection and acclimation. Terrestrial plants have highly efficient protective mechanisms against the damaging effects of solar radiation, and this is one of the reasons why increased UV-B radiation resulting from ozone reduction has only modest consequences on plant growth (Fig. 1A). As sessile photosynthetic organisms, they are continuously exposed to extreme variations in the levels of solar radiation, including the UV-B component. Plants acclimate to changes in UV-B levels through several defence responses, including morphological changes, accumulation of effective UV-screening compounds, production of increased amounts of antioxidants, stimulation of DNA repair, as well as other regulatory adjustments. Plant acclimation is mediated by UV-B-induced changes in gene expression *via* UV-B-specific and non-specific signaling pathways.[20] Numerous mechanisms of acclimation and adaptation have been detailed in previous reports.[7,11–13]

Depending on the degree of stress, acclimation responses are likely to involve an energy cost with consequent redistribution of resources for production of protective compounds or structures. As an example, the metabolic cost of accumulating increased levels of UV-absorbing compounds in response to abrupt increases in UV-B radiation was calculated for an Antarctic leafy liverwort. That cost represented only 2% of the carbon fixed by photosynthesis, but such a cost could have cumulative effects on plants growing in polar regions that are already constrained by short growing seasons.[21] In an experiment with a native Patagonian shrub (*Grindelia chiloensis*), plants responded to attenuation of solar UV-B radiation with more plant biomass, greater height and increased leaf area, which correlated with a reduction of 10% in the glucose equivalent used in the synthesis of UV-B protective resin.[22] From these experiments, it may be inferred that energy is allocated from growth to protection when plants are exposed to natural sunlight with its UV-B component. The magnitude of the energy cost is likely to be species-specific and dependent on environmental conditions. Protective responses other than production of secondary metabolites are also likely to incur a cost to the plant.

Genotypes within a given species of plant can differ in their tolerance to UV-B radiation.[23–25] Genotypic differences in acclimation to UV-B radiation may contribute to the variation in growth responses that has been documented in field studies (see, for example, scattering in Fig. 1A), and may allow for directional selection for UV-B tolerance within plant populations in response to long-term changes in UV-B levels. A recent short-term study[26] assessed the natural variation in constitutive (inherent) and induced protection of the photosynthetic function from UV-induced damage using over 200 lines (varieties) of *Arabidopsis thaliana*, a member of the mustard family (Brassicaceae). Constitutive protection did not correlate with the latitudinal distribution (and presumed gradation in natural UV-B radiation) of the populations tested. Also, among lines from high altitudes, both constitutively highly tolerant and moderately tolerant populations were found. However, lines from lower latitudes were found to activate UV defences more readily than those of higher latitudes. Correlation between acclimative/adaptive response to UV-B radiation and habitat origin has also been reported in studies with other species.[27] Jansen *et al.*[26] point out that some of the differences reported in the literature may be explained by the selection of parameters used to measure plant resistance to UV-B radiation, as well as confounding effects of environmental variation in factors other than UV-B radiation (see also Torabinejad and Caldwell[24]).

UV-B radiation and other variables of the biotic and abiotic environment can interact to produce cross-tolerance (*i.e.*, tolerance to one stress induced by another stress), as well as resilience to subsequent stress due to the establishment of a level of protection.[28] Cross-tolerance has been documented for a number of environmental stressors (examples in Izaguirre *et al.*[29] and Mittler *et al.*[30]) and has, in some instances, been attributed to the activation of common signaling pathways. For example, in an analysis of gene-expression responses to pulses of drought, cold, and high UV-B radiation under laboratory conditions, plants were found to exhibit commonalities in their reactions to the various stressors, involving a core set of stress-related genes.[31] A well-documented case of UV-induced protection against other stress factors is the effect of solar UV-B radiation increasing plant resistance to insect herbivory.[32] UV-B radiation induces the synthesis of several secondary metabolites, including those of the phenylpropanoid pathway, which act as effective UV-absorbing sunscreens.[20] The response usually involves an increase in the concentration of these compounds as well as differential regulation and shifts in their relative abundance.[33–37] Studies that combined detailed analyses of plant tissue chemistry and herbivory bioassays suggest the effect of UV-B radiation increasing plant resistance against herbivorous insects may be at least partially mediated by changes in phenolic metabolites, which may have toxic effects on plant consumers[38] (see also section on Consumers and decomposers).

From the point of view of modeling the quantitative impacts of changes in UV radiation on plant growth (Fig. 1), an important implication of acclimation/adaptation responses is that the slope of the dose-response relationship may change depending on the duration of the experiment. Thus, in a short-term experiment (days), where plants have little time to acclimate to changes in the light environment, changes in UV-B radiation may trigger larger effects on growth than those produced by gradual increases in UV-B irradiance over a period of several years.

Consumers and decomposers

Canopy arthropods. Some of the most prominent and best characterized effects of solar UV-B radiation in terrestrial ecosystems have been documented at the interface between plants and plant-eating (herbivorous) insects.[14,17,39–41] Generally, the intensity of herbivory on plants grown under field conditions increases if the UV-B in the solar spectrum is attenuated using filters.[17]

The "anti-herbivore" effect of UV-B radiation can be considerable. The dose-response relationship published in our last report,[11] and reproduced here in Fig. 2, indicates a doubling in the intensity of herbivory by insects with an attenuation of 25% in the level of solar UV-B radiation. This strong effect of attenuation of solar UV-B radiation on levels of herbivory has been confirmed in more recent studies.[38] Importantly, the slope of this response is substantially steeper than the one shown in Fig. 1A for the effects of UV-B radiation on plant growth. Hence, there is reason to suspect that the increases in UV-B that occurred as a consequence of ozone depletion and other environmental factors (Fig. 1B) may have caused larger effects on levels of herbivory than directly on primary productivity. Similarly, herbivory is likely an important determinant of the impacts of future variations in UV-B levels (increases or decreases) on biomass production and losses of biomass to herbivory.

The conclusion regarding quantitative impacts has several caveats. First, it is difficult to estimate the biological effects (quantitative changes in herbivory levels) that may have occurred over a time span of three decades from responses obtained in short-term experiments, where the UV-B levels are instantaneously manipulated with filters. In the long-term, plants may have adjusted to the enhanced doses of UV-B caused by ozone reduction and the insects adapted to the gradual changes in plant tissue quality elicited by the higher UV-B levels. Second, although the effect of UV-B radiation increasing plant resistance to herbivory has been extensively documented, cases have been reported where an increase in UV-B radiation resulted in increased levels of insect herbivory or differences in the responses between species of insects.[17,42,43] Therefore, in any given ecosystem, different species of insects may have a range of responses to the changes in plant tissue quality caused by enhanced UV-B radiation. An implication of this variation in the response is that changes in UV-B radiation resulting from ozone depletion (or recovery), clouds and aerosols,[4] or from other sources, such as changes in canopy cover and architecture, have great potential to alter the species composition and diversity of the community of canopy insects.

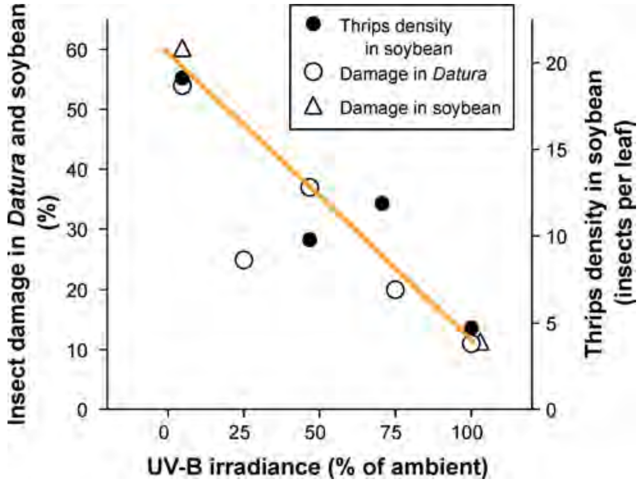


Fig. 2 Changes in insect herbivory in response to experimental attenuation of the UV-B irradiance received by the plant canopy. The graph shows the effect of attenuating the UV-B component of solar radiation on the intensity of insect herbivory by thrips (a piercing-sucking insect) in soybean crops,[46] and leaf beetles (chewing insects) in plants of the common annual weed *Datura ferox*.[32]

The mechanisms that mediate the effects of solar UV-B radiation on insect herbivory have been studied in some detail. The conclusion emerging from that body of work is that some of these effects are a consequence of a direct action of UV-B radiation on the insects, whereas others are indirect, *i.e.* mediated by changes in the quality of plant tissues.

Direct deleterious effects of UV-B radiation on insect performance (*e.g.*, increased mortality of larvae) were documented some time ago.[44,45] Recent research has demonstrated that UV-B radiation may also serve as a signal to canopy arthropods (insects, spiders, *etc.*) that elicits changes in behaviour.[46–49] Direct perception of solar UV-B radiation has been demonstrated in field studies with thrips, *Caliothrips phaseoli*, a common crop pest.[46,47] Presumably, specific UV-B sensitivity plays a role in the mechanisms that allow canopy arthropods to locate favourable feeding positions or areas of low UV-B exposure within the plant canopy.[50–52] Although not directly connected with herbivory studies, Li and co-workers demonstrated that females of a jumping spider species (*Phintella vittata*) choose a mate based on sex-specific UV-B reflectance patterns,[48,49] and observational studies with hornets showed that flight activity correlated better with solar UV-B irradiance than with other environmental variables.[53] Mazza and co-workers proposed that specific perception of UV-B in thrips is achieved by a combination of broad-band UV receptors and filtering compounds in the insect's visual system.[51] Studies in vertebrates also suggested perception of UV-B in poison dart frogs.[54] The finding that some animals can react specifically to UV-B under natural conditions has important implications for our understanding of the ecological roles of UV-B radiation, and suggests that changes in the UV-B environment in plant communities may have complex effects on the behaviour of animals in the canopy. However, the quantitative significance of direct behavioural responses of animals to UV-B radiation in defining response patterns at the ecosystem level (*e.g.* changes in rates of herbivory) has yet to be established.

Indirect effects of solar radiation on animals (*i.e.*, effects mediated by changes in the plant host) have been extensively documented in bioassays where the insects themselves are not exposed to the UV-B radiation treatments. Thus, "choice" and "no-choice" bioassays with herbivorous insects have shown that ambient solar UV-B radiation can produce changes in the plant tissues that affect choice of sites for insect feeding[32,55] and oviposition (egg-laying),[56,57] as well as insect growth and survival.[29,43,58–60] The increase in plant resistance to herbivory by insects has been correlated with UV-B-induced variations in a number of tissue quality traits, such as nitrogen content,[61] leaf phenolics,[37,43,45,60,62] cyanogenic compounds,[63] and defence-related proteins such as inhibitors of insect proteinases.[29,64,65] Increased accumulation of phenolic compounds in plant tissues is one of the most consistently reported responses to UV-B radiation. These phenolic compounds contribute to filtering out UV-B photons before they reach sensitive molecules in the interior tissues (mesophyll). However, they are also thought to play a role in direct defence against herbivores.[38,66–71] In fact, UV-B radiation and insect damage trigger partially overlapping patterns of phenolic compounds in some plant species.[37] A partial convergence in response also has been evidenced in studies that measured changes in gene expression elicited by herbivory/wounding treatments and exposure to UV-B radiation.[29,72]

These observations have lent support to the idea that the effects of solar UV-B radiation on interactions between plants and insects may be mediated by stimulation of the hormonal signaling cascades that plants activate to defend themselves against herbivore attack.[11,29,37,64] Recent studies in a species of wild tobacco (*Nicotiana attenuata*) have indicated that some effects of solar UV-B radiation on plant defence against insects require biosynthesis of jasmonates (which are the principal hormones that orchestrate plant defence responses against insects), while others do not. Among the responses to UV-B radiation that do not depend on jasmonate signaling are the accumulation of flavonoids and other phenolic compounds with potential anti-herbivore activity. On the other hand, the UV-B-induced accumulation of several polyamine conjugates is totally dependent on jasmonate production, and UV-B strongly enhances the expression of defence-related proteins (proteinase inhibitors) triggered by herbivory through a jasmonate-dependent pathway.[38] Solar UV-B radiation does not increase accumulation of jasmonates in *N. attenuata*, but increases sensitivity to jasmonates, presumably *via* regulation of some of the downstream components involved in jasmonate signaling. The increased sensitivity to jasmonate thus leads to stronger defence responses in plants exposed to UV-B radiation compared to those grown under attenuated levels of UV-B.[38] Bioassays carried out in the field have indicated that those effects of UV-B radiation on plant chemistry that require jasmonate signaling play a quantitatively important role in the mechanisms whereby solar UV-B increases plant resistance to herbivorous insects.[38,56] Detection of significant effects of solar UV-B on jasmonate signaling is important, because recent field studies have shown that the impacts of elevated concentrations of atmospheric CO_2 on the intensity of herbivory (more herbivory under elevated CO_2) may be caused by a reduced activation of the jasmonate pathway of plant defence.[73] Thus, improved understanding of the effects of UV-B radiation on the mechanisms of defence may be useful for analyzing the impacts of multiple environmental factors (such as UV-B, CO_2, *etc.*), as well as for the design or selection of crop varieties with increased resistance to herbivory.

Microbial communities. Solar UV-B radiation is one of several environmental factors that influence the biodiversity of microbes growing on a range of materials, including the surfaces of leaves and dead plant material (plant litter). By altering the microbial communities that are present, UV-B radiation can thus affect microbial decomposition, which is globally an important process, since it affects the potential for carbon sequestration in terrestrial ecosystems and the flux of CO_2 to the atmosphere. For example, experimental attenuation of UV-B radiation reaching the surface of plant litter in a field study carried out in Tierra del Fuego (southern Patagonia) changed the species composition of fungal communities on the litter, and increased the rate of microbial decomposition.[74] Another recent study reporting changes in plant litter following exposure of branches of alder and birch trees to solar UV radiation indicated changes in tissue chemistry that subsequently influenced the microbial release of CO_2 as the litter was decomposing.[75] While it is difficult to generalize from such studies, they do indicate that UV radiation can have complex effects on microbial decomposition.

Live foliage can provide a habitat for a diverse set of microbes,[76] and the composition of these microbial communities can be influenced by solar UV-B radiation striking the leaf surfaces.[77] Furthermore, studies in maize have shown that the effects of UV-B radiation on bacterial diversity depend on the plant genotype, suggesting that at least some of the effects of UV-B are indirect (*i.e.*, mediated by changes in the plant, such as changes in plant surface chemistry).[78] In parallel with these studies that focused on microbial diversity on the leaf surface, other researchers have shown that solar UV-B radiation can also alter plant resistance to leaf pathogens. When ambient UV-B radiation was filtered out from areas of tea crops during the wet season in Sri Lanka, the relative abundance of *Xanthomonas* spp. (a phyllosphere bacterium) increased, and this correlated with an increase in the incidence of the fungus that causes blister blight, the major leaf disease of tea plants.[79] A recent study in maize[80] found a genetic correlation between low bacterial diversity on leaf surfaces and resistance to fungal blight. This suggests that some dominant bacteria may suppress other bacteria and, at the same time, increase resistance of plants to fungal infection. These studies are beginning to reveal the nature of the interactions between microbial organisms that take place on living foliage. Progress in this direction will increase understanding of the biological implications of the effects of UV-B radiation on microbial diversity.

As in the case of plant-herbivore interactions, the effects of UV-B radiation on plant-associated microbes may be direct (*i.e.*, UV-B acting directly on the microorganisms) or indirect (mediated by UV-B-induced changes in the plant tissues). Indirect effects have not been studied to the same level of detail as plant-insect interactions. However, given the evidence showing that solar UV-B can interact with jasmonate signaling,[38] and the well established fact that jasmonates play a central role in plant defence responses against certain types of pathogens,[81] it seems likely that changes in UV-B levels will result in variations in plant resistance to pathogen attack.

Finally, experimentally imposed changes in UV radiation above-ground can alter the quantity and diversity of microbes in the soil[82] or microfauna below the surface in peatlands.[83,84] Unlike the leaf surface, this is an environment devoid of UV radiation. Consequently, shifts in microbial species composition are indirect UV effects, which may be mediated by processes such as changes in root exudates,[85,86] or in the case of peat, through changes in the plant tissues or exudates of the peat.[84] Although alterations in the populations of microorganisms and microfauna below the surface have been demonstrated, the broader significance of these changes for ecosystem function is still unclear.

Effects of UV radiation on biogeochemical cycles

In this section we highlight recent advances in the understanding of UV effects on biogeochemical cycles and their implications for predicting the responses of terrestrial ecosystems to variations in UV resulting from ozone and climate change. For further discussion of the subject, the reader is referred to Zepp *et al.*[87]

Carbon cycle

Of particular importance for the changing carbon balance of terrestrial ecosystems is net ecosystem exchange (NEE), the balance between gross photosynthesis of the vegetation and the total efflux of CO_2 from the ecosystem. As discussed previously (see Growth responses), manipulative field studies did not reveal general effects of UV-B radiation on net photosynthesis (carbon assimilation per unit leaf area), even though shoot biomass can show some sensitivity to variations in UV-B irradiance (Fig. 1A).[15,16] Another pathway whereby changes in UV-B radiation may affect ecosystems is through below-ground processes. Alterations in plant roots and associated microorganisms (mycorrhizae),[88] soil microbial communities[85] and microfauna[89] have been reported in response to above-ground manipulations of UV radiation. However, a general perspective of the chain of events causing these below-ground responses, and their significance for ecosystem function is still lacking. Therefore, at this point, there is little evidence to show how NEE will respond to variations in UV-B radiation.

A component of NEE that appears to be influenced by solar UV radiation is the photodegradation of plant litter. Although litter decomposition is largely a biological process involving microbes, purely physical photodegradation (degradation under the action of light) can play a prominent role in arid and semiarid ecosystems,[90] which represent *ca.* 40% of the Earth's land surface. Recent studies demonstrate a sizable effect of solar radiation in driving mass loss from above-ground organic matter in a range of terrestrial environments.[90–95] The activity spectrum for photodegradation indicates that effective wavelengths extend beyond the UV-B region, and even include part of the visible spectrum[93,96] (Fig. 3). Therefore, because the irradiances in the UV-A and visible regions are much higher than in the UV-B, the rate of photodegradation is unlikely to have increased significantly in response to changes in the solar spectrum resulting from ozone depletion.

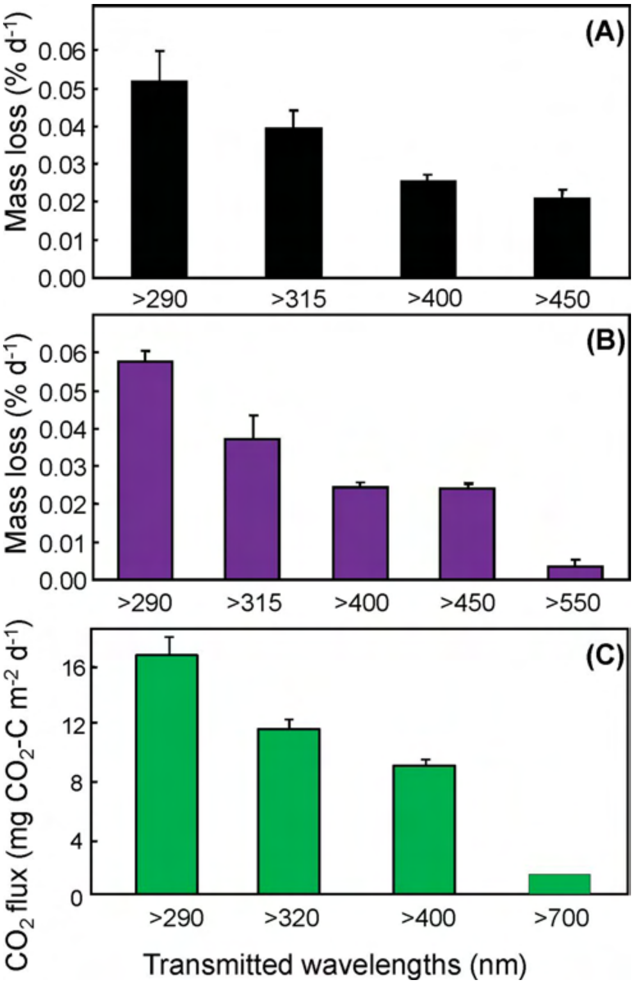


Fig. 3 Experimental attenuation of specific regions of the solar spectrum demonstrates that both UV (<400 nm) and visible (400–700 nm) radiation can drive photodegradation in the field. (A) Mass loss of grass litter exposed to solar radiation transmitted through different cut-off filters in a semi-arid grassland. (B) Mass loss of artificial cellulose-lignin substrates with 10% lignin concentration exposed to solar radiation transmitted through different cut-off filters. Adapted from Austin and Ballaré.[93] (C) CO_2 evolution from leaves exposed to solar radiation transmitted through different cut-off filters. Adapted from Brandt *et al.*[96]

However, because the effects of UV-A and short-wave visible radiation can be quite large, photodegradation could be strongly enhanced by increases in the amount of radiation resulting from decreased cloud cover or conditions of increased aridity.[93] Photodegradation affects predominantly the lignin fraction of plant litter, reducing its abundance when the material is exposed to sunlight (Fig. 4). Because lignin is known to play a key role in retarding biological (microbial) decomposition,[97] increases in

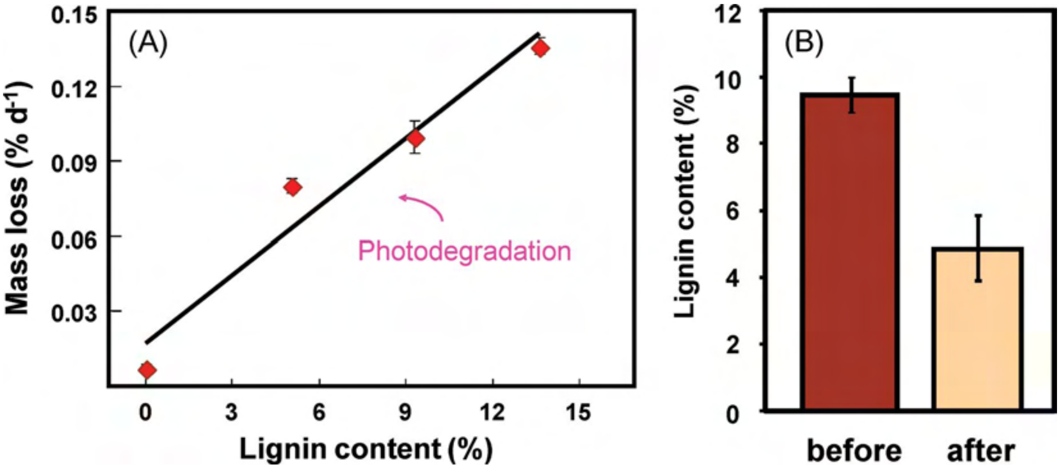


Fig. 4 Photodegradation reduces the lignin (biologically recalcitrant) fraction of plant litter. (A) When artificial cellulose-lignin substrates were exposed to sunlight for a period of one month during the summer in Buenos Aires (34°S), the rate of photodegradation increased with original lignin content in the exposed material. This is explained by the fact that lignin is an effective absorber of solar radiation over a wide range of wavelengths. (B) Lignin content decreased after photodegradation, which is predicted to render the material more labile to biological degradation catalyzed by microbial enzymes. The bars indicate lignin content before and after a period of exposure to sunlight. Adapted from Austin and Ballaré.[93]

photodegradation as a result of climate change may have important consequences, accelerating microbial respiration and hence carbon release to the atmosphere.[93] This indirect effect of increased photodegradation may be particularly important in scenarios of greater variability in climate, with increased alternation between dry periods (which may favour photodegradation) and periods of abundant precipitation (which favour microbial activity).

Nitrogen oxides

Trace gases of nitrogen, NO_x (NO and NO_2), are present in small quantities in the atmosphere, but are very important in a variety of chemical reactions.[98] These and other oxides of nitrogen, NO_y, can play important roles in atmospheric chemistry. One of those, nitrous oxide, N_2O, is now considered to be the single most important ozone-depleting emission, exceeding the contribution of chlorofluorocarbons.[99] Plant shoots have been shown to emit NO_x when exposed to solar UV radiation,[100] with NO_x likely originating from leaf tissues. Other nitrogen oxides (NO_y) from conifers appear to emanate from the surfaces of foliage when exposed to UV-B radiation.[101] There is a suggestion that global NO_x emissions from boreal forests might be roughly equivalent to those from industrial and traffic sources.[100] Although several uncertainties remain, this suggests an important role for solar UV-B radiation interacting with plant tissues in the production of reactive nitrogen.

Methane

Although the release of methane into the atmosphere had been generally considered to occur only under conditions of very low oxygen, measurable release of methane from vegetation in an atmosphere with normal oxygen levels has been reported.[102] This has led to considerable controversy.[103–108] Although interpretations vary, it appears that methane can be produced from plant pectins through a photochemical process driven by solar UV radiation.[104] Recent estimates suggest that the quantity of methane emitted from terrestrial ecosystems by this process is not relevant from the perspective of the global methane budget.[109] However, methane is the next most important greenhouse gas after water vapour and CO_2, and thus the potential importance of this process clearly deserves attention.[87]

Interactions with other climate change factors

Changes to incident UV radiation may occur in response to changes in climate and land use, as discussed earlier. Such changes could affect both UV-B and UV-A levels, and the effects are likely to be greater than those that have resulted from stratospheric ozone depletion.[4,110] For example, decreasing cloud cover in some regions (Fig. 5)[9] will increase transmittance of UV through the atmosphere,[4] and also through the plant canopy if the reduction in clouds is accompanied by conditions of increased aridity (as predicted by some models, Fig. 6)[8,10] and reduced vegetative cover. Similarly, in polar and alpine regions, vegetation is often protected for many months of the year by layers of

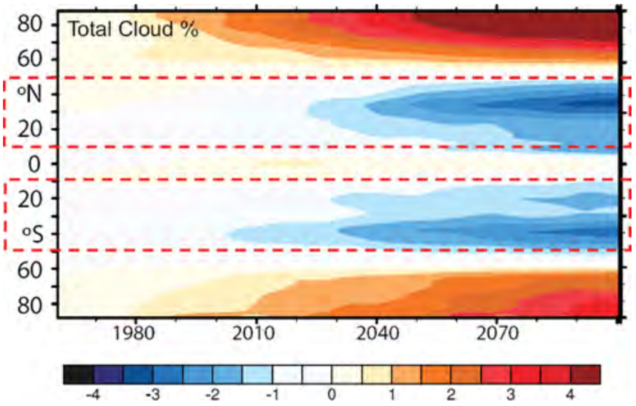


Fig. 5 Modeled trends for total cloud cover (percentage change 1960–2100; see colour scale at the bottom of the graph) as a function of latitude. Boxed areas highlight low and mid-latitudes, where models predict reduced cloud cover. Adapted from Trenberth and Fasullo.[9]

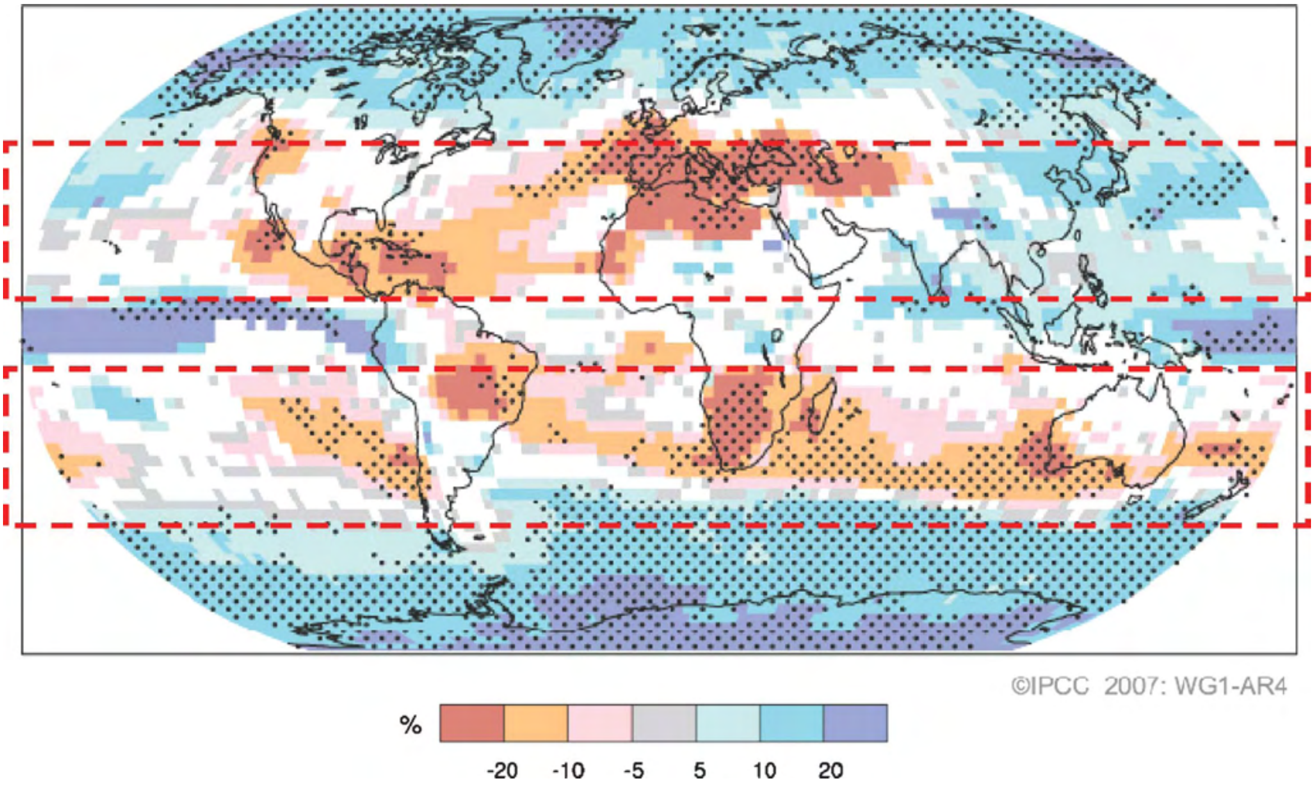


Fig. 6 Modeled trends for precipitation (percentage change between the periods 2090–2099 and 1980–1999; see colour scale at the bottom of the map). Values are multi-model averages based on the SRES A1B scenario for June to August. White areas are where less than 66% of the models agree in the sign of the change and stippled areas are where more than 90% of the models agree in the sign of the change. Boxed areas highlight mid-latitudes, where models predict reduced precipitation. Adapted from IPCC.[8]

snow and ice that effectively block solar radiation. Reductions in these protective layers due to climate warming will increase the duration of exposure to UV-B radiation and, particularly in the Southern Hemisphere, would coincide with ozone-depletion events.[111] This increased UV-B radiation is likely to be combined with changes in water availability and exposure to temperature extremes.[112–114]

Understanding how ecosystems will adapt to these changes requires identification of likely new combinations of stressors at a regional level, as well as studies that consider the biological effects of such combinations. Ideally, factorial studies should be used to evaluate the influences of simultaneous changes in various factors (*e.g.*, increased prevalence of drought, higher temperatures, more available nitrogen and increased UV radiation). Information from such studies is also required to apportion correctly the effects of combined factors. For example, increased incident UV-B radiation (as a result of ozone depletion) is correlated with the Southern Annular Mode, indicative of atmospheric variability, and with increasing wind at coastal Antarctic sites in the summer.[115,116] This can make it difficult to attribute changes in growth rate observed in Antarctic mosses specifically to the negative effects of UV-B radiation or to desiccation from drying winds, although the results clearly show an impact of the ozone hole on the dominant moss flora.[117,118]

The following examples from recent studies of factor combinations discuss how other changes in climate enhance or ameliorate effects of UV radiation. Given the paucity of such interaction studies, a comprehensive meta-analysis, as discussed earlier for plant growth, is not possible.

UV radiation and precipitation

Changes in precipitation patterns and increased evaporative loss due to increased temperature are likely to occur as a result of climate change in many regions.[8,10,119] Reduced water availability in terrestrial ecosystems is one of the few environmental factors that clearly interacts with UV-B radiation; past reports highlight numerous studies demonstrating reduced UV sensitivity in higher plants under water stress.[11] Recent studies of single plant species under controlled conditions have also shown some of the ways in which cross-tolerance to drought and UV-B radiation might occur. When grown under moderate UV-B levels, *Arabidopsis* plants were more tolerant to a 12-day drought treatment than plants grown without UV-B, as indicated by two-fold higher photosynthetic rates, and higher relative water contents.[120] In a study of poplar tree cuttings, exposure to enhanced UV-B radiation significantly decreased plant growth and photosynthesis under well-watered conditions, but these effects were obscured by drought, which by itself caused a more drastic growth reduction.[121] Two studies[122,123] which combined high doses of UV-B radiation and water deprivation showed that, overall, UV-B and water stress reduced growth considerably, but less than would be predicted from the additive effects of both stressors. While these results could reflect increased resilience to UV-B in higher plants pre-treated by water deprivation, the apparent interaction may simply indicate that the comparatively subtle effects of UV-B radiation are overwhelmed by those of reduced water availability (*e.g.*, reduced growth, or leaf expansion).

Most of these interaction studies have focused on higher plants (especially cultivated species) that were grown under well-watered conditions and then subsequently exposed to drought treatments. At the other end of the scale, in regions where water severely limits primary production, such as in arid lands, any reduction in availability of water could compromise the ability of the organisms to tolerate UV radiation. Cryptogamic communities (comprising lower plants such as mosses, lichens and algae) are common in these ecosystems. Such communities can be highly tolerant of desiccation. However, if precipitation declines further as a result of region-specific climate change (Fig. 6), almost all the fixed carbon would be allocated to maintenance and repair, potentially reducing the resources available for UV protection. This could critically compromise the ability of many desert organisms to survive.[124,125]

Studies in Antarctic mosses that related the changes in UV-B-protective pigments and accumulation of DNA photoproducts (damage) to a range of environmental factors suggest that water availability strongly influences the effects of UV-B radiation.[126] Accumulation of both UV-B-protective pigments and damage to DNA were negatively correlated with plant water content in *Bryum pseudotriquetrum*.[117,126] Fully desiccated Antarctic moss species can exhibit considerable resilience to high UV-B radiation; however, when the mosses are hydrated, greater DNA damage occurs at lower relative water content than in fully hydrated plants, and this is likely due to reduced ability for repair. For organisms already existing at their physiological extreme, the biological cost of UV-B protection[21] or repair[125] could compromise survival, but this has yet to be shown.

Biological soil crusts, a consortium of cyanobacteria, lichens, and mosses, are an important component of many dryland ecosystems. Although they produce relatively little biomass, they can be critical in stabilizing arid land soils. Results from a study that augmented UV-B radiation over two years showed that negative effects occurred during the warmer year, when increased temperatures reduced moisture and thus the time available for active growth and carbon gain.[124] The longer periods of desiccation are presumed to have reduced the ability of these organisms to fix carbon and allocate energy to the production of UV-protective pigments and other defences. While desert organisms can survive naturally high levels of UV radiation under current moisture conditions in extremely harsh environments, even limited climate change could shift the balance from sufficient productivity to increased morbidity.[124,125]

Interactions between UV radiation, elevated CO_2 and temperature

Although increased atmospheric CO_2 and temperature are important variables in climate change studies, adequately controlling these factors while simulating natural radiation (especially UV-B), is technically very challenging. As reported previously,[11] several studies have used sunlit controlled environment chambers to manipulate UV-B radiation, temperature and CO_2 simultaneously.[127,128] While such chambers were very useful in controlling these factors, they frequently fail to reproduce field conditions due to the high UV levels employed and the omission of solar UV-A radiation from the controls. These studies report that high temperatures combined with increased UV-B radiation had detrimental effects on a range of production[128,129] and reproductive[127,130] characteristics in soybean and cotton. Higher CO_2 failed to ameliorate the negative effects in soybean.[127,128] In two-factor experiments using cotton, elevated CO_2 similarly failed to ameliorate the negative effects of very high doses of UV-B radiation on photosynthesis and growth.[131,132]

Experiments designed to evaluate simulated global warming and different UV-B levels have shown responses to both of these factors for individual species and plant communities (see, *e.g.*, Day *et al.*;[133] Zaller *et al.*[134]). However, there is little evidence of significant interactive effects between UV-B radiation and warming.[135–138] For example, in a 2-year field experiment in a South American fen ecosystem, which combined warming of 1.2 °C (air temperature) with near ambient- or reduced-solar UV-B treatments,[134] plant decomposition was generally faster under near ambient UV-B than under reduced UV-B, but was unaffected by temperature. In contrast, the number and biomass of earthworms were negatively affected by warming but unaffected by UV-B radiation. An interesting feature of that study was that the effects of both UV and warming treatments were minor compared to the effect of additional rainfall in one of the years, which doubled plant biomass compared to the drier year. This highlights both the importance of long-term studies, which can control inter-annual variation in weather conditions, as well as the difficulties associated with designing experiments that fully consider multiple and interacting climate factors. Some evidence for significant interactive effects comes from studies with plants from Antarctic Peninsula tundra communities. Day *et al.*[135] used plastic film coverings (to increase air temperatures by 1.2 °C) and this was combined with three UV treatments (near ambient UV-B and two reduced solar UV-B radiation levels using different filter combinations in this area of naturally elevated UV-B radiation). After two years, reproduction in the studied species (*Deschampsia antarctica* and *Colobanthus quitensis*) was accelerated by UV-B at ambient temperatures, but in the warming treatments, UV-B had no effect.

UV radiation and increased nitrogen levels

Deposition of biologically available nitrogen occurs in many locations, especially in temperate latitudes near nitrogen sources from industrial and agricultural activity. Several studies have investigated the effects of interactions between nitrogen and UV-B radiation on agricultural and forest species (see Caldwell *et al.*[11]), but there is little evidence of consistent interactive effects. The effects tended to be species-specific. The available agricultural studies investigated the effects of nitrogenous fertilizer rather than the deposition of nitrogen from anthropogenic sources (the amounts and timing of nitrogen availability in fertilization and deposition events are usually quite different). In the study of biological soil crusts discussed above, deposition of nitrogen only alleviated UV-induced inhibition of growth in a limited number of cases.[124]

Future approaches to predicting interactive responses

While we have addressed interactions of UV-B radiation with a number of other potential combinations of environmental factors in this short synopsis, most studies, for logistic reasons, were only able to address one interaction or two, or occasionally three factors at a time. In addition, because of difficulties in manipulating multiple factors at the field plot level, many studies are performed in controlled environments. Most interaction studies address the effects of changes in the mean levels of a certain factor, rather than the interactive effects of discrete events of extreme conditions. Thus, the challenges of predicting real-world responses with several interacting environmental factors are not trivial, especially at the ecosystem scale. While the need for this type of assessment is clear, the pathway to achieve it is not.

Mechanisms of plant responses to UV-B radiation

Elucidating the mechanisms that mediate plant responses to solar UV-B radiation is important for understanding the effects of UV-B radiation on ecological interactions (*e.g.*, plant-herbivore interactions), and for devising strategies for manipulating and possibly exploiting plant sensitivity to UV radiation in species of economic interest.

One of the major obstacles to our understanding of how UV-B radiation is perceived by plants is that the identity of the primary UV-B photoreceptor/s is not well defined. Data derived from a variety of sources, as well as work done on animals, indicate that damage to DNA and activation of receptors on the surface of the cell may trigger some of the responses to UV-B radiation in plant cells.[11,20,64] However, evidence derived from physiological, molecular, and genetic studies indicate that other mechanisms of UV-B perception are present in plant cells.[11,20,139] There are several lines of evidence suggesting that plants have specific photoreceptors for UV-B radiation, analogous to the photoreceptors involved in the perception of visible light and far-red radiation (phytochromes, cryptochromes and phototropins).[11,20,139]

Studies in the reference plant, *Arabidopsis thaliana*, have demonstrated that the protein encoded by *UV RESISTANT LOCUS 8* (*UVR8*) controls the expression of numerous genes involved in acclimation to and protection against UV-B radiation. The genes regulated by UVR8 include genes involved in the biosynthesis of flavonoids (protective phenolic sunscreens), the gene encoding a cyclobutane pyrimidine dimer (CPD) photolyase (*UVR2*, which is essential for repair of UV-B-induced DNA damage), and genes connected with protection against oxidative stress and photooxidative damage.[140] Significant advances have been made in the last few years in the identification of additional components involved in this UV-B-specific signaling pathway. These components include the E3 ligase CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1)[141] and the bZIP transcription factors ELONGATED HYPOCOTYL 5 (HY5),[140,142] and HY5 HOMOLOG (HYH).[143] The UVR8 protein accumulates in the nucleus in response to UV-B radiation where it binds to chromatin in the region of the *HY5* gene promoter, orchestrating the expression of UV-protective genes.[144,145] COP1 is required for UV-B-stimulated *HY5* gene activation in light-grown seedlings.[141] Furthermore, recent work has demonstrated that UV-B radiation promotes the direct interaction between the UVR8 and COP1 proteins in the nucleus, and that this interaction is a very early step in UV-B signaling.[146] In experiments carried out in solar simulators, mutants defective in UVR8 or COP1 show increased sensitivity to UV-B radiation which is consistent with the idea that the UVR8-COP1 pathway plays a key role in activating protective mechanisms under natural conditions.[146]

Whereas the importance of the UV-B-specific UVR8-COP1 pathway in acclimation to UV-B radiation is now well-recognized, the photobiological mechanisms that lead to its activation upon UV-B exposure are unclear. Based on kinetic considerations and the results of genetic screenings (which have failed to find signaling components acting upstream of UVR8), Brown *et al.*[147] and Favory *et al.*[146] have advanced the intriguing possibility that UVR8 itself could act as a UV-B photoreceptor. This interesting hypothesis warrants further investigation.

Neither of the responses that have received quantitative analysis in this assessment (namely growth and herbivory inhibition by solar UV-B radiation, Fig. 1A and 2), have so far been linked explicitly with the UVR8-COP1 pathway. Since the UVR8-COP1 pathway controls the activation of protection and acclimation responses, such as expression of genes involved in DNA repair, it could be predicted that variation among genotypes in the activation of this pathway may lead to differences in their sensitivity to changes in UV-B radiation (slope of Fig. 1A), because UV-B-induced inhibition of growth in the field is often correlated with accumulation of DNA damage.[148,149] In fact, recent work showed that the inhibitory effects of UV-B radiation on plant growth were more pronounced in mutants that fail to activate the UVR8-COP1 pathway, and also revealed that this pathway is involved in the control of several features that are important for leaf development.[150] The connections between UVR8-COP1 activation and the UV-B-induced changes in plant secondary chemistry that determine differences in herbivory patterns (Fig. 2, and see section on canopy arthropods) remain to be explored.

Improved understanding of the molecular mechanisms of plant responses to UV-B radiation can be useful in facilitating attempts to enhance UV-B tolerance in crops. Ambient levels of UV-B radiation can diminish crop yield in sensitive varieties;[151] even though these effects are relatively small, they can be economically significant. Recent work on *Arabidopsis* indicates that it is possible to increase the capacity to repair UV-B-induced DNA damage by manipulating the expression of *UVR2* using biotechnology.[152] This technology could be transferred to sensitive plants of economic interest in order to reduce the negative effects of solar UV-B radiation. In addition, as discussed in this assessment, solar UV-B radiation induces plants to accumulate secondary metabolites that play important roles as anti-herbivore defences (see section on Consumers and decomposers) and alters the levels of chemical compounds that are pharmacologically active or nutritionally valuable (as discussed by Jensen *et al.*).[153] Therefore, a better understanding of the mechanisms of UV-B perception and signaling may be useful for the production of crop varieties that are more resistant to insect pests (and therefore less dependent on the use of synthetic pesticides) or have improved nutritional value for human consumption.

Technical issues in conducting and evaluating UV-B radiation research

In this section we very briefly address some technical issues in the implementation of biological experiments with UV radiation. Obviously, researchers in the field must make compromises, but appreciation of the limitations of such research is important, as illustrated by the examples presented below.

The analysis of results of multiple experiments shows sizable variation in plant responses to UV-B-manipulation treatments. This is indicated by the scatter of data points in Fig. 1A and by the graphically displayed variance in the meta-analysis of Searles *et al.*[16] Similar broad ranges of responses are seen in experiments with exclusion and/or reduction in UV radiation.[15,154] While it is clear that different species (or even varieties) of plants have greatly different sensitivities to UV-B radiation, differences in experimental techniques, as described below, may also have contributed to the variation observed among experiments.

Methodological issues in UV supplementation and exclusion/reduction experiments require careful attention. Filtered UV-B lamps do not have a spectral output that matches that of sunlight, with or without ozone depletion.[155,156] Biological Spectral Weighting Functions (BSWF) are therefore used for calculating "biologically effective" UV and relating this to depletion of stratospheric ozone (see Fig. 7 in McKenzie *et al.*[4]). These BSWFs are dimensionless factors that represent the relative effectiveness of the different wavelengths in influencing a particular biological response.[156] There are many issues involved in choosing the appropriate BSWF for a particular experiment, and there are many potential sources of error.[155] These potential errors are much greater in greenhouse and controlled-environment studies than in experiments conducted outdoors.[155,157] There have been only a few attempts to evaluate the appropriateness of different BSWFs in field environments.[148,158,159]

Experiments employing the reduction or removal of solar UV with various filter materials would appear more straightforward than experiments with UV supplements from lamps, but there are still many complications that need to be addressed, especially to allow comparisons among experiments. Ideally, measurements of solar UV radiation should also be made in association with these experiments.[154]

Subtle effects caused by small differences in shading can also be problematic. To suspend filters and/or lamps above plants used in experiments, various structures have been devised which inevitably cast shade on the plants to various degrees. However, the effect of even small differences in shading among different UV radiation treatments can be appreciable.[160] Other issues can occur in UV exclusion/reduction experiments such as those due to small differences in visible radiation and alterations of other environmental conditions, such as precipitation and wind exposure.[161]

The measurement of UV radiation in field UV lamp supplementation experiments presents many challenges, and simple UV dosimeter measurements supply very limited information. Spectral irradiance data are necessary to calculate BSWF-weighted irradiance. Furthermore, measurements of UV spectral irradiance in experimental settings need to be well documented.

Our understanding of biological responses to UV radiation has improved greatly in the past 5 to 10 years. Similar advances in the physical measurements with appropriate instrumentation, calibration and measurement protocols are needed.

General conclusions

In the coming decades, terrestrial ecosystems will be exposed to further changes in UV irradiance resulting from changes in stratospheric ozone, climate (*e.g.*, altered cloud cover, snow cover, *etc.*), and land use and agricultural practices (*e.g.*, deforestation, afforestation, changes in crop density, *etc.*). Predicting the effects of these changes is challenging, given the diversity of ecosystems that are likely to be affected, the paucity of biological response studies, and the need for models that integrate biological knowledge to estimate changes in ecosystem functioning. Also, a number of uncertainties remain regarding the basic mechanisms of plant responses to UV radiation and the experimental approaches that are most suitable to evaluate plant and ecosystem responses under field conditions. However, based on the evidence discussed in this assessment, we can make some inferences on the processes that are more likely to be affected by changes in solar UV radiation.

(i) Current information derived from field studies indicates that the effects of UV-B radiation on the above-ground biomass of terrestrial plants are relatively small. A synthesis of results from a host of comparable studies suggests that, because the Montreal Protocol has been successful in limiting ozone depletion, the reduction in plant growth caused by increased UV-B radiation in areas affected by ozone decline since 1980 is unlikely to have exceeded 6% (Fig. 1).[14–16] However, caution must be taken with this generalization because variation in susceptibility to UV-B radiation among plant species has been documented in several studies. In addition, while effects on plant growth may be small, long-term effects of these reductions may be important, particularly for potential carbon sequestration. Below-ground changes as a result of UV exposure above the soil surface also may result in complex interactions for plants, the soil microenvironment and soil microorganisms.

(ii) Sizable effects of changes in UV-B radiation on plant consumption by herbivores and other organisms may have occurred during the last three decades, and are likely to occur in the future in response to predicted variation in the levels of UV radiation. This may be inferred from short-term studies showing large effects of UV-B manipulations on plant interactions with herbivores and microorganisms (see, for example, Fig. 2). However, the long-term consequences of these effects have not been explicitly investigated. From a practical point of view, the knowledge gained on the mechanisms that mediate the effects of UV-B radiation on plant secondary chemistry and plant-herbivore interactions may be used in the design of cropping systems that take advantage of natural plant defences against herbivores and deliver plant products of increased nutritional value.

(iii) Changes in UV radiation resulting from climate change (*e.g.*, reduced cloud cover and/or vegetative cover in response to increased aridity) or changes in land use patterns may have more important consequences for terrestrial ecosystems than those that have resulted from ozone depletion. This is because the variations in solar radiation caused by climate and land use change: (a) will affect a greater range of ecosystems than those affected by ozone depletion; and (b) will not be restricted solely to the UV-B component of solar radiation. There are several biological and physical processes in terrestrial ecosystems that are not particularly sensitive to UV-B but which are strongly affected by UV-A radiation. Moreover, as discussed in this assessment, interactions between multiple global change drivers and UV radiation are not well understood.

(iv) One example of a process that is effectively driven by solar UV-A radiation is the physical degradation of plant litter.

Increased photodegradation, in response to reduced cloudiness or reduced canopy cover, will lead to increased carbon release to the atmosphere. In addition, because photodegradation primarily affects the lignin fraction of plant litter, which usually limits microbial decomposition, more photodegradation is also predicted to facilitate biological degradation, thereby increasing carbon release to the atmosphere.

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