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Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climatic change factors†

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Based on research to date, we can state some expectations about terrestrial ecosystem response as several elements of global climate change develop in coming decades. Higher plant species will vary considerably in their response to elevated UV-B radiation, but the most common general effects are reductions in height of plants, decreased shoot mass if ozone reduction is severe, increased quantities of some phenolics in plant tissues and, perhaps, reductions in foliage area. In some cases, the common growth responses may be lessened by increasing CO_2 concentrations. However, changes in chemistry of plant tissues will generally not be reversed by elevated CO_2. Among other things, changes in plant tissue chemistry induced by enhanced UV-B may reduce consumption of plant tissues by insects and other herbivores, although occasionally consumption may be increased. Pathogen attack on plants may be increased or decreased as a consequence of elevated UV-B, in combination with other climatic changes. This may be affected both by alterations in plant chemistry and direct damage to some pathogens. Water limitation may decrease the sensitivity of some agricultural plants to UV-B, but for vegetation in other habitats, this may not apply. With global warming, the repair of some types of UV damage may be improved, but several other interactions between warming and enhanced UV-B may occur. For example, even though warming may lead to fewer killing frosts, with enhanced UV-B and elevated CO_2 levels, some plant species may have increased sensitivity to frost damage.

Introduction

Several environmental changes are being imposed on terrestrial ecosystems, including increased solar ultraviolet-B radiation and warming at higher latitudes, increasing carbon dioxide levels globally, and regional tropospheric air pollution and atmospheric nitrogen deposition. Potentially significant changes in the frequency and nature of precipitation and storms are also predicted as the Earth warms. Depending on location, many of these factors will exert their influence on ecosystems more or less concurrently. Terrestrial ecosystems include agricultural lands (agroecosystems), less intensively managed lands such as forests, grasslands, and savannahs, and unmanaged lands such as deserts, tundra, *etc*. This overview addresses how increased UV-B radiation, interacting with other global change factors, may affect many of the important ecosystem processes and attributes, such as plant biomass production, plant consumption by herbivores including insects, disease incidence of plants and animals, changes in species abundance and composition, and mineral nutrient cycling. Some aspects of ecosystem function, *e.g.*, nutrient cycling, are treated in more detail in this volume.[1]

The present report consists of a brief update of our understanding of UV radiation effects, followed by coverage of factor interactions as much as they have been researched to date (Fig. 1). Ideally, these interactions should be considered across, as well as within, trophic levels. Trophic level refers to groups of organisms constituting different stages of the food chain in an ecosystem, *e.g.*, primary producers (plants), various levels of consumers (herbivores, carnivores, *etc.*), and decomposer organisms.

It is now some 30 years since the first suggestions of stratospheric ozone reduction appeared (*e.g.*, refs. 2 and 3). Within a few years of these early concerns about the atmosphere, several studies of UV-B effects on higher plants appeared and these continue to represent the emphasis of research in this area. Direct effects of UV-B on insects and other terrestrial animal life have traditionally received comparatively little attention as they are often assumed to be protected from damaging effects of solar UV either by their behavioral patterns or by largely UV-opaque body coverings (*e.g.*, fur, feathers, exoskeletons of insects, *etc.*). Terrestrial microbes have also received little attention though they are usually poorly shielded from penetrating solar UV. In recent years, more attention has been paid to UV-B influence on species interactions in an ecosystem context.

Biologically effective UV radiation for plants

The concept of biologically effective UV radiation has been discussed.[4] This involves weighting the radiation at different wavelengths with a factor to indicate its relative biological

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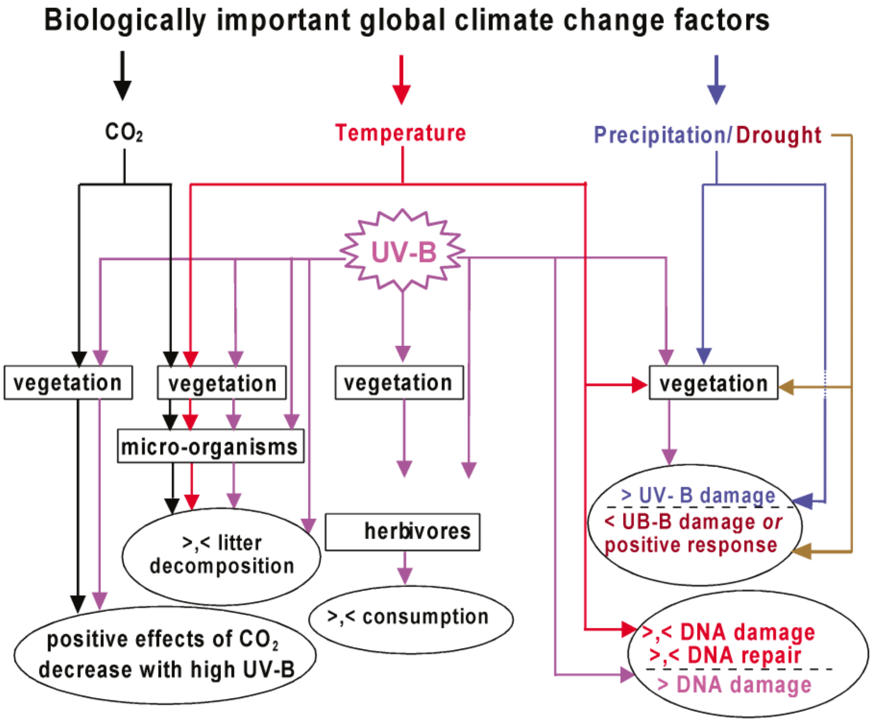


Fig. 1 Major interactions of elevated UV-B with other climate change factors in terrestrial ecosystems. Lines indicate influence of climate change factors on different trophic levels (in rectangles) that affect processes (in ovals). Colors of lines: black, elevated CO_2; red, elevated temperature; violet, enhanced UV-B; blue and brown, abundance and deficit of moisture, respectively. The symbols > and < refer to more and less, respectively.

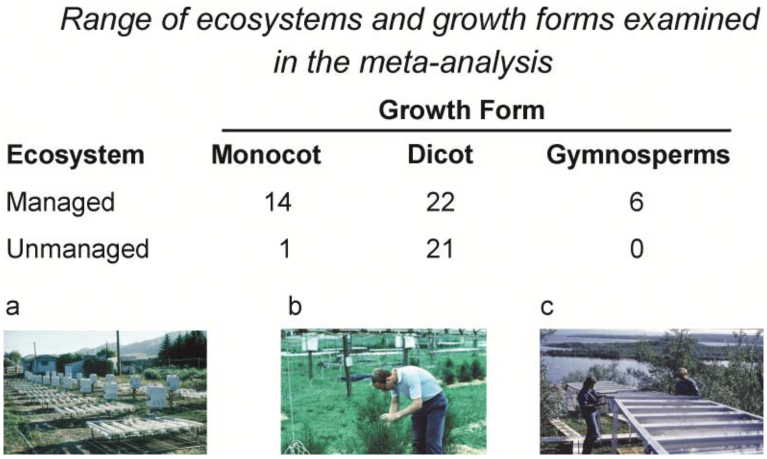
effectiveness. An example of erythemal (human sunburn) effectiveness is given in this volume.[4] For other biological effects, different weighting functions appear to be more appropriate. Earlier reports of this panel (*e.g.*, refs. 5 and 6) have portrayed the importance of different assumptions of the wavelength dependency of UV effects on plants and other organisms. These dependencies involve different degrees to which longer wavelength UV (UV-A) participates in various UV effects on plants. There are also important implications of this in calculating biologically effective UV based on different degrees of ozone reduction (see radiation amplification factors, this volume[4]) and in evaluating experiments with lamps to supplement the UV. A radiation amplification factor (RAF) refers to the relative increase of biologically effective UV radiation for each increment of ozone column change.[4] The greater the degree to which longer wavelengths in the UV-B and UV-A are effective in biological reactions, the smaller is the RAF, *i.e.*, less of an increase in biologically effective radiation for a given level of ozone reduction.[7,8] Biological weighting functions are also used to compare the biologically effective UV radiation from lamp systems with that from the Sun due to ozone reduction, since these UV lamps do not accurately simulate solar radiation.[7]

A new action spectrum for characteristics of higher plant growth and morphology indicates that UV-A participates in these effects more than originally assumed in earlier action spectra.[9] The new spectrum resembles the commonly used generalized plant response function[10] except that it indicates appreciable sensitivity into the UV-A. This spectrum was also tested by exposing plants in the field to different combinations of solar and artificial radiation and the indicated that the new spectrum is relevant under field conditions.[11] When used for the ozone reduction problem, this new spectrum predicts less of an increase of biologically effective radiation for a given decrease in ozone thickness (lower RAF) than the generalized plant spectrum. However, it also suggests that the levels of ozone reduction simulated in lamp experiments, often adjusted according to the generalized plant spectrum, results in less simulated ozone reduction than if computed using the new spectrum. For example, if one used the generalized plant spectrum to adjust lamps to result in a 30% simulated ozone reduction, this would only be an 8% ozone reduction if the resulting supplemental radiation is calculated according to the new plant growth spectrum.[11]

Plant growth is a complex response that integrates the influences of many environmental factors, including UV-B, on several physiological processes. It is worth pointing out that the new spectrum that describes the wavelength dependency of growth inhibition may not be appropriate to describe the spectral response of individual physiological processes. The shape of the spectra for individual processes will depend on the particular chromophores involved and, among other factors, the optical shielding imposed on these chromophores by surrounding molecules and cellular structures. Little work has been carried out to define appropriate weighting functions for individual responses under physiologically meaningful conditions. For DNA damage, various action spectra were tested in the field in southern Argentina as the Antarctic "ozone hole" passed over the experimental site and altered the wavelength composition of the solar radiation. The comparisons of plant DNA damage responses with different action spectra indicated an action spectrum with little participation of UV-A as the most appropriate[12] Similarly, Mazza *et al.*[13] found that the accumulation of phenolic sunscreens in field-grown soybeans was significantly enhanced by solar UV-B, whereas the UV-A component of sunlight had little effect. Therefore, for this particular response, a steep action spectrum also appeared to provide a good description of wavelength dependency.

A recent view of enhanced UV-B effects on plants: A synthesis using meta-analysis

Most UV-B research on terrestrial ecosystems continues to be focused on plants and emphasizes experiments addressing the sequence of events upon exposure to levels of UV-B radiation corresponding to stratospheric ozone reduction under outdoor conditions. It was recognized long ago, that if such experiments



Range of ecosystems and growth forms examined in the meta-analysis

	Growth Form		
Ecosystem	**Monocot**	**Dicot**	**Gymnosperms**
Managed	14	22	6
Unmanaged	1	21	0

Fig. 2 Types of vegetation examined in the meta-analysis. The numbers refer to studies for individual species. Photographs of three different systems are also shown (a. wheat and wild oat experiments in Logan, Utah, USA, W. Beyschlag; b. Loblolly pine in Maryland, USA, A. Teramura; c. Subarctic heath in Sweden, from ref. 5).

were conducted in glasshouse or growth-cabinet conditions, the effects of the added UV-B radiation were greatly exaggerated. Thus, over 20 years ago investigators began to conduct such experiments outdoors using special UV lamp systems. There are now well over 100 such studies on different species of plants. Meta-analysis is a technique to use quantitative and statistical information provided in a collection of individual studies in a combined analysis to assess how well the overall research predicts common trends and results. Of the *ca.* 100 studies reviewed, 62 provided enough quantitative information suitable for a meta-analysis[14] for several types of managed and unmanaged ecosystems (Fig. 2).

Of the 10 physiological and morphological traits examined, overall significance of elevated UV-B in the meta-analysis could only be concluded for shoot mass, plant height and leaf area and increased UV-B absorbing pigments (including flavonoids and other phenolic compounds). The other traits, including changes in chlorophyll and carotenoid pigments, reproductive yield, leaf mass per unit leaf area, net photosynthesis, and photosystem II activity of the photosynthetic system, might have been affected in some individual studies, but the overall effect was not sufficiently robust to be significant in the meta-analysis. For the four characteristics that were found to be significant, Fig. 3 shows the array of responses in individual studies to elevated UV-B relative to controls. For leaf area, the significant reduction was caused by the manner in which the experimental replicate was selected. When authors selected the individual plant as the replicate, the average response was significant. (These data are included in Fig. 3.) When they selected the plot as the replicate, the response was not significant.[14] For shoot biomass, there are two arrays of studies shown in Fig. 3 corresponding to the level of ozone reduction being simulated, 10–20% and >20%. Only the group of studies simulating >20% ozone reduction yielded a significant average response in the meta-analysis for shoot mass. (In these studies, the level of simulated ozone reduction was usually effected by adjusting the output of the UV lamps with the old generalized plant spectrum.[10] Had the new plant growth spectrum[9] been used, the levels of simulated ozone reduction would have been much smaller, as explained in the foregoing section.)

Although all these studies in the meta-analysis involved lamp systems under outdoor conditions in natural sunlight, the methods included different degrees of replication and control of the lamp intensities. Most of these studies employed an "on–off" system of lamp control, sometimes called "square-wave", while others used more elaborate control that gradually changed lamp output according to ambient solar UV-B, sometimes called "modulated" control. Thus, all studies are not of equivalent quality; they also do not have equal capability to

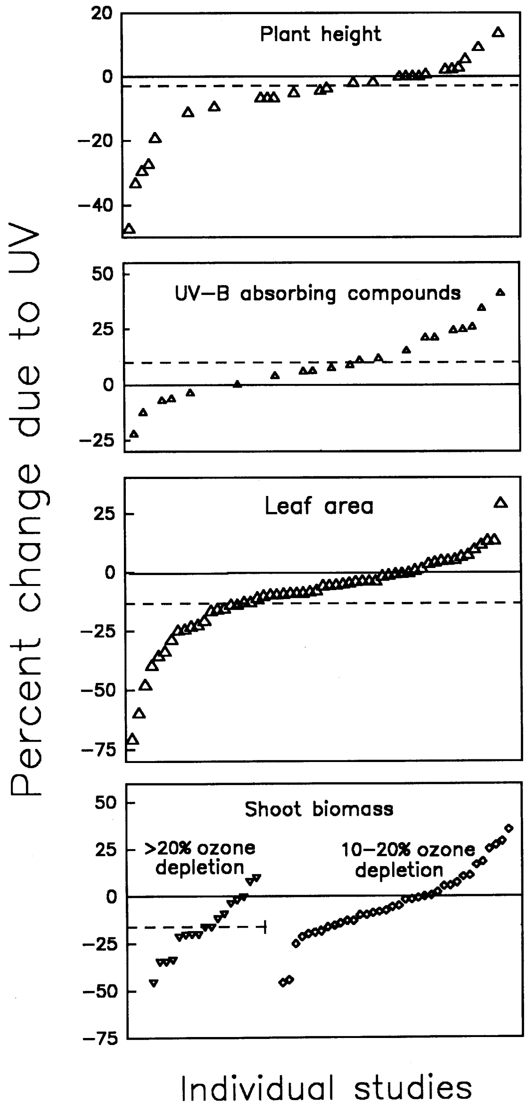


Fig. 3 The response of four plant characteristics in field studies in the order of increasing positive effects. These experiments all employed supplemental UV-B from lamp systems. Each symbol represents a different study. The dashed line in each represents the average response calculated by the meta-analysis over all studies shown. The average responses shown were significant at $P < 0.05$. For shoot mass, the studies are grouped into two arrays corresponding to studies in which the level of simulated stratospheric ozone reduction is between 10 and 20%, and those in which the simulated ozone reduction was greater than 20%.

discriminate plant responses. While this should be borne in mind, there is increased value in comparing a large number of such experiments through meta-analysis, since it affords a quantitative comparison.

Apart from experiments with UV-emitting lamps, there is a lesser number of experiments using special filters that remove, or attenuate the UV-B in normal sunlight (along with appropriate control filters that are largely transparent to UV-B). In the majority of cases, when sunlight UV-B was attenuated, plants exhibited better growth which indicates that normal sunlight UV-B reduces growth to some extent.[15–17] Attenuation experiments have been carried out in areas that are currently exposed to enhanced solar UV-B levels, such as the southern tip of South America (Tierra del Fuego, Argentina) and on the Antarctic Peninsula.[18,19] Herbaceous plants native to both regions were negatively affected by the ambient solar UV-B levels. A comparison between the growth inhibition data collected in these UV-B attenuation experiments carried out in Tierra del Fuego and the Antarctic Peninsula showed that a similar fractional level of UV-B attenuation by filters (approximately 80%) had effects on plant growth that increased with the level of ozone depletion (*i.e.*, from Tierra del Fuego to Antarctica).[18]

As can be seen in Fig. 3, some UV-B lamp studies reported enhancement in some plant characteristics (plant height, leaf area, and shoot mass), although most studies reported decreases in these characteristics. There are also a few recent reports of filter studies where solar UV-B promoted plant growth.[20,21] Mechanisms mediating this apparent enhancement of growth are not known and it is not clear that this would occur over the long term in a natural setting. Apart from higher plant responses, other effects of enhanced UV-B radiation on terrestrial ecosystems are represented by too few studies to allow for meta-analysis.

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Do small effects of UV-B accumulate through the years?

An intriguing, and potentially important, phenomenon suggested by some earlier research is that even small effects of UV-B radiation might accumulate to produce larger effects in subsequent years in perennial plants. The first suggestions of this were in seedlings of one of four seed sources of a conifer. In these plants, the effect of exposing the plants to elevated UV-B from lamps became progressively more expressed in subsequent years.[22] However, this did not appear to be significant in young trees tested from the other three seed sources. Indications of cumulative effects of elevated UV-B in Subarctic heath perennials were apparent for some traits of some species, but not for others (*e.g.*, ref. 23). Also, early indications of cumulative effects disappeared over a longer period of time.[24] Thus, while there may be some indications of this accumulation phenomenon in certain specific instances, there is no convincing evidence for it as a general trend. However, its potential significance should not be dismissed, since it might affect competitive persistence of some species through time.

Analogous to these putative cumulative effects, an apparent carry-over and accumulation of elevated UV-B effects on plant growth form, from generation to generation, have been reported for a desert annual plant species.[25,26] If this is a widespread phenomenon among species, an amplification of sorts might be effected. The mechanism for this is not understood.

Although suspected for some time, there are now a few new reports indicating that enhanced UV-B may affect the genetic stability of plants causing long-term heritable effects, with a high frequency of mutations which are generally considered to be deleterious to organisms. High UV-B exposure can activate what is known as "mutator transposons" in maize that amplify the mutation effect of the UV-B beyond the immediate DNA damage.[27] In *Arabidopsis*, increased UV-B was found not only to cause direct DNA damage; but also, errors in DNA repair leading to an increased tendency for mutations in subsequent generations.[28,29] In cyanobacteria, considerable genetic polymorphism was found in highly stressful environments, and was presumed to be caused by UV-B-induced genome instability and replication errors.[30] These instabilities could affect future generations, and result in an increased mutation rate even after the ozone layer has recovered.

Recent reports of UV-B effects on soil and soil surface processes such as nitrogen fixation and litter decomposition suggest that these changes are not transient phenomena. Elevated UV-B treatments applied over several years may become apparent years after the treatments had been initiated. This was the case for depression of nitrogen fixation in some species of cyanobacteria[31] that had been exposed to elevated UV-B for several years in both high Arctic and Subarctic locations. A one year exposure to elevated UV-B became apparent four years later as accelerated decomposition of oak leaf litter.[32] Both nitrogen fixation and litter decomposition are nutrient cycling processes that are important in ecosystem function.

Insect herbivory of plants

Insects have enormous potential to consume vegetation, but the degree to which they feed on different species is dependent not only on the species of plants, but also on a suite of other environmental factors, including UV-B radiation. There are now over 20 reports of various insect–plant species combinations that have been studied with respect to the influence of UV-B radiation (Table 1).

Generally, when there was an effect, a higher level of UV-B led to less insect herbivory and/or reduced insect growth compared to lower levels of UV-B. (Most of these experiments were conducted by filtering ambient solar radiation.) The magnitude of the effects can be sizeable, with potential ecosystem-level consequences for species composition, organic matter decomposition and nutrient cycling. In several cases, it was possible to show, using feeding bioassays, that the effects of the UV-B radiation were mediated through the host plant, *i.e.*, they were the result of UV-induced changes in the characteristics of the plant tissues. Two types of bioassays have been used: In the "no choice" bioassays (NC, in Table 1) insects were given either UV-B-exposed or control plant material (exposed to less, or no UV-B), whereas in the "choice" (C) bioassays the insects received both types of pretreated plant materials in the same feeding area. Of course, the interpretation of the response (altered herbivory or insect performance) in the context of projecting ecosystem-level consequences requires consideration of the type of experiment that was used to detect UV-B effects on plant–insect interactions. It is also important to point out that the nature of the UV-B-induced changes in plant characteristics that cause herbivory responses is not known for any system; the possible mechanisms listed in Table 1 are based on correlative, circumstantial evidence. Insects are generally thought to be blind to variations in the UV-B component of sunlight, since their visual systems are primarily sensitive to UV-A radiation. However, one field study showed that a species of thrips can perceive and avoid solar UV-B under natural daylight conditions[34], and laboratory study showed behavioral responses to artificial UV-B in a moth caterpillar.[39]

Bacteria and fungi

Fungi and bacteria play crucial roles in ecosystem function including decomposition of dead biological material, mineral nutrient cycling and as pathogens of plants and animals. In the last few years, more attention has been paid to direct UV-B effects on these microbes if they are exposed to sunlight (such as on foliage surfaces or litter). Changes in species composition and biodiversity of these microbes in response to UV-B have

Table 1 Effects of UV-B radiation on insect herbivory

Insect	Type of expt.[a]	Plant species	UV-B effect on herbivory/insects	Possible mechanism[e]	Study
Caliothrips phaseoli (thrips)	E	*Glycine max* (soybean)	Less herbivory[33]	Direct response of insects to solar UV-B	34
Diabrotica speciosa (leaf beetle), lepidopteran larvae, grasshoppers	E	*Glycine max* (soybean)	Less herbivory		35
Anticarsia gemmatilis (moth larva)	E[b]	*Glycine max* (soybean)	Slower growth, higher mortality	Indirect effect. (NC)[e] Increased phenolics but decreased lignin	
Schistocera gregaria (desert locust)	F[b]	*Lolium perenne, Festuca rubra, F. arundinaceae, F. pratensis*	No response in 3 species; in *Festuca pratensis*, preference for endophyte-infected plants changed	Indirect effect. (C)[e] Loline content changed, but this did not influence herbivory	36
Various chewing insects (not identified)	E	*Gunnera magellanica* (devil's strawberry)	Less herbivory	Not known	37
Spodoptera litura, Graphania mutans (moth larva)	C	*Trifolium repens* (white clover)	Tendency toward slight reduction in herbivory	Indirect effect. (NC) Slight N increase, larger carbohydrate decrease, population-specific changes in cyanogenesis	38
Epirrita antumnata (moth larva)	F	*Betula pubescens* (mountain birch)	More herbivory	Mechanism not known. (NC) Laboratory study indicated direct UV-B preference	39
Precis coenia, Trichoplusia ni (both lepidopteran larvae)	G	*Plantago lanceolata* (English plantain)	*Precis*—no effect *Trichoplusia*—more growth from eating treated material but direct UV-B growth inhibition	Direct inhibitory effect of UV-B on insect growth; indirect effects. (NC) Reduced crown and reproductive growth; some increase in leaf N and verbascosides	40
Various chewing insects (not identified)	F	*Quercus robur* (pedunculate oak)	No UV-B effect[c]		41
Caliothrips phaseoli (thrips)	E	*Glycine max* (soybean)	Less herbivory	Indirect effect (C) and direct UV-B avoidance	33,34
Lepidoptera: Noctuidae (moth larva)	E	*Gunnera magellanica* (devil's strawberry)	Less herbivory	Indirect effect. (C) Increase in leaf N	42
Strophingia ericae (psyllid)	F	*Calluna vulgaris* (heather)	Reduced insect populations	Not known. Reduced amino acid isoleucine	43
Operophtera brumata (moth larva)	G	*Betula pendula* (silver birch)	More herbivory	Indirect effect. (C) Leaf flavonoids increased, but flavonoids added to an artificial diet did not increase feeding.	44
Insects not identified	F	*Vaccinium myrtillus, V. uliginosum, V. vitis-idaea* (heathland shrubs)	More herbivory in *V. myrtillus*, less in *V. uliginosum*, no effect in *V. vitis-idaea*	Mechanism not known	45,46
Pieris rapae, (butterfly larva) *Trichoplusia ni* (moth larva)	C	*Arabidopsis thaliana*	*Pieris*: less herbivory and less insect weight gain	Indirect effect. (NC) Leaf flavonoids increased	47
Coleoptera (leaf beetles)	E	*Datura ferox* (summer annual)	Less herbivory	Indirect effect. (C) Mechanism not known	48
Acronicta, Nycteola, Orthosia, Ptiloden (moth larva)	F	*Quercus robur* (pedunculate oak)	No specific UV-B effect[c]		49
Autographa gamma (moth larva)	C	*Pisum sativum* (pea)	Less herbivory, but greater insect growth	Indirect effect. (NC) Higher phenolic and N contents	50
Ostrinia nubilalis (European corn borer)	E[d]	*Zea mays* (corn)	Less herbivory	Indirect effect. (NC) More cell-wall-bound truxillic and truxinic acids	51 [b]
Trichoplusia ni (moth larva)	G	*Citrus jambhiri* (rough lemon)	Decrease in survivorship and growth	UV-B increased furanocoumarin levels	52

[a] C = controlled environment chamber, G = greenhouse, F = field UV-B supplement from lamps, E = field UV-B exclusion. [b] Field-treated material used in laboratory feeding trials. [c] More herbivory under UV-A and UV-B lamps compared to controls, but no specific UV-B effect. [d] UV-A and UV-B responses cannot be separated. [e] "Indirect effect" implies that an UV-B effect mediated by changes in the plant was demonstrated in a bioassay, even if the nature of the changes was not identified. (C), "choice" bioassay, (NC) "no choice" bioassay.

been documented and many of these changes appear to be related to how well species and strains of these fungi and bacteria tolerate UV.[53–56] Beneficial fungi that infect plant roots and assist in absorption of nutrients (termed mycorrhizae), although not exposed to solar radiation, might be indirectly affected by UV-B exposure of the host plant shoots.[57,58] This would need to be mediated by systemic tissue changes in the roots caused by UV-B exposure of the shoots.

Bacteria and fungi can also be pathogenic for both plants and animals, although plant pathogens have received more attention than animal pathogens with respect to UV-B radiation. As compiled by Paul,[59] plant disease incidence can be increased or reduced by UV-B radiation. Increasing disease severity is thought to primarily involve modifications in the host plant tissues, while decreased severity appears due either to host plant changes or direct UV-B damage to the pathogen (Table 2).

Pathogens of insects and other animals may also be influenced by solar UV radiation. Studies involving biological control of insect pests using pathogens provide some indication of how solar UV may affect insect pathogens. For example, Braga *et al.*[77,78] showed that fungal strains of an insect pathogen were sensitive to solar UV-B radiation and to lamp UV-B in a range corresponding to that in sunlight. These particular fungi commonly used in biological control of insects such as grasshoppers were isolated from soil fungi that would not normally be exposed to sunlight. However, if strains isolated from locations at different latitudes were exposed to UV-B, their relative UV-B sensitivity corresponded to the respective latitudinal differences in solar UV-B at their sites of origin. Viral pathogens of insects are also inhibited by UV-B radiation[79] Thus, as used for biological control, attention to UV-B sensitivity is necessary and enhanced UV-B stemming from ozone reduction would further limit their usefulness.

Global environmental changes

The changing environment we are now witnessing and will likely experience in the coming decades involves both global climate change and broad regional changes. Both the predictability and the rate of these environmental changes vary widely. Solar UV-B has increased at higher latitudes, and CO_2 and temperature are continuing to increase globally. Regionally, nitrogen deposition and tropospheric ozone have increased. Changes in regional precipitation frequency and weather systems are driven by global climate change and are highly important, but less well understood and predicted.

Thus, all the foregoing changes need to be considered as acting in concert with stratospheric ozone reduction. Experimental work is progressing, usually with two-factor interactions, *e.g.*, elevated CO_2 and UV-B. However, the complications and costs of two- or multi-factor experiments clearly limit how representative and comprehensive such experiments can be.

Drawing on the existing experimental data base, we attempt to generalize how elevated UV-B might interact with each of the other factors with respect to vegetation and ecosystem responses. For example, some combinations of factors appear to have largely additive effects, although these can operate in opposite directions. There can also be significant interactions, *i.e.*, at different levels of one factor there is a non-additive response to a second factor (synergistic). The following sections contain such generalizations.

Elevated CO_2 and UV-B

Several studies are now available in which plants, and sometimes combinations of plants and insect herbivores, were subjected to combinations of two or more levels of CO_2 and UV-B. Typically, elevated CO_2 treatments involved a doubling of CO_2 and elevated UV-B treatments corresponded to a simulated 15 to 30% ozone depletion (assuming the generalized plant spectrum[10] as explained earlier). Generally, if either elevated CO_2 or UV-B exerted effects, the CO_2 influence was more pronounced than that of the enhanced UV-B. Also, the effects of elevated CO_2 and enhanced UV-B caused responses in opposite directions, *e.g.*, additional CO_2 stimulated plant growth and enhanced UV-B tended to depress growth.[46,69,80–89] In all these studies, the effects of the two factors were usually counteractive, as just described. Synergistic effects were rare.

Combined application of UV-B and elevated CO_2 followed by short exposures to ozone, as would be experienced from regional air pollution, resulted in interesting interactions. The stimulating effect of elevated CO_2 on plant growth was apparent when plants were exposed to ambient (normal) UV-B. If given both elevated UV-B and high CO_2, the stimulating effect of the high CO_2 was reduced. These patterns are typical of the combined effects of elevated UV-B and high CO_2. Application of a high ozone exposure following growth in the combinations of UV-B and CO_2 eliminated the stimulating effect of high CO_2 if the plants had been exposed to low UV-B, but did not if the plants had been given elevated UV-B along with the elevated CO_2.[86]

Apart from plant growth and related processes like photosynthesis, the attractiveness of plant foliage to insect herbivores may vary under a combination of elevated CO_2 and enhanced UV-B. Lavola *et al.*[90] found that insects preferred plants grown with enhanced UV-B, contrary to the general trend described above, and the combination of high CO_2 and enhanced UV-B led to even further tendency of the insects to consume foliage. In another study of this nature, enhanced UV-B either increased or reduced herbivory, depending on the plant species, but if the enhanced UV-B were combined with high CO_2, or if the plants were given just high CO_2 by itself, there was no effect on herbivory relative to controls (low UV-B and normal CO_2).[46]

UV-B, water and nitrogen supply

Climate change will likely result in modifications in the timing and amount of precipitation on a regional scale, although predicting these changes is difficult. Experiments to date largely suggest that if enhanced UV-B is applied to plants undergoing drought stress, the UV-B response seen with adequately watered plants is usually dampened (*e.g.*, refs. 91–93), at least where cultivated plants are concerned. However, some species native to the Mediterranean seemed to thrive during periods of water limitation if exposed to elevated UV-B.[94]

Atmospheric nitrogen (N) deposition in many regions leads to N fertilization of vegetation. Nitrogen supply to vegetation has received relatively little attention in relation to UV-B radiation. One study involving a combination of different levels of N supply and two levels of UV-B showed that as cucumber plants received more N, their growth was depressed to a greater degree by elevated UV-B.[95] If N deficient, these plants were not responsive to UV-B in that study.

Warming and UV-B

The Earth is warming and this is especially apparent in many regions at higher latitudes. These are also the latitudes where ozone depletion is more pronounced. Some responses to the combination of these factors might be rather predictable, such as increased repair (an enzymatic process) of DNA damage at higher temperatures. This has been experimentally demonstrated in terrestrial plants for DNA damage (manifest as DNA dimers). There was little repair of DNA damage at low temperatures and very adequate repair in a temperature range of 24–30 °C.[96,97] The effectiveness of DNA repair was low at relatively high temperature.[97,98]

Of course, temperatures that are above or below the optimum for a particular organism can limit performance and, in the extreme, cause direct damage. Interactions among factors can

Table 2 Effects of UV-B radiation on plant-microbe interactions for living plants and plant litter

A. Experiments on live plants

Microbe genus	Type of expt.[a]	Plant species	Fungal response to UV-B	Plant response to UV-B	Study
Aureobasidium (phylloplane yeast)	E	*Nothofagus antarctica (southern beech)*	Proportionately less on upper leaf surface, several other plant-microbe systems not affected	None	53
Bacteria (*e.g. Clavibacter*)	E	*Arachis hypogene* (peanut)	Altered species composition	None	55
Microsphaera (powdery mildew pathogen)	F	*Quercus robur* (pedunculate oak)	Increased infection	Photosynthesis decreased due to increased mildew	60
Neotyphodium (leaf endophyte)	F	*Lolium perenne* (rye grass)	No effect	Reduced yield in the presence of the leaf endophyte	61
Septoria (leaf blotch pathogen)	C	*Triticum aestivum* (wheat)	Fewer lesions on plant (a direct response to UV-B) or no effect depending on time of year	Not assessed. If changes occurred, they did not affect the pathogen	62
Exobasidium (blister blight pathogen)	E	*Camellia sinensis* (tea)	Reduced infection sites; no effect on sporulation	Not assessed	63
Aureobasidium, Sporobolomyces (phylloplane yeasts)	F	*Quercus robur* (pedunculate oak)	Abundance on the upper; but not lower leaf surface affected for some sampling dates. Several other fungi not affected	Not assessed	64
Fusarium (damping-off pathogen)	C	*Spinacia oleracea* (spinach)	More damping off evident	Decreased shoot growth	65
Bullera (phylloplane yeasts)	E	*Vicia faba* (faba bean), *Malus domestica* (apple), *Quercus robur* (pedunculate oak), *Pisum sativum* (pea)	Less colony forming units isolated from leaves	Not assessed	66
Pyricularia (also known as *Magnaporthe*) (rice blast pathogen)	G	*Oryza sativa* (rice)	Greater lesions on plant in a few cases (an indirect UV-B effect mediated through the plant)	Reduced plant height, leaf area, dry weight in a few cases	67
Cercospora (leaf spot pathogen)	C	*Beta vulgaris* (sugar beet)	Not assessed	Reduced dry weight of leaf laminae and other plant parts in the presence of the pathogen	68
Colletotrichum, Cladosporium (anthracnose and scab pathogens)	G	*Cucumis sativus* (cucumber)	Increased infection in some cases (an indirect UV-B effect mediated through the plant)	Reduced plant height, leaf area, dry weight; increased leaf mass per area	69
Puccinia (leaf rust pathogen)	F	*Triticum aestivum* (wheat)	Increased infection with results varying some by wheat cultivar	Little; if any, reduction in dry weight and seed yield	70
Diplocarpon (blackspot pathogen)	G	*Rosa* (rose)	Inhibition only when conidia were germinating	No response	71
Potato virus S	G	*Chenopodium quinoa*	Fewer lesions	No response	72

B. Experiments on plant litter

Fungal genus	Type of expt.[a]	Plant species	Fungal response to UV-B	Plant response to UV-B	Study
Cladosporium, Cystodendron, Phoma	F	*Betula pubescens* (mountain birch)	Changes in fungal community structure	Live plants received no treatments	73
Aspergillus, Cladosporium, Epicoccum	F[b]	*Brassica napus* (oil seed rape)	Direct and indirect effects on fungal competitive ability	Increased flavonoids	74
Cladosporium, Acremonium, and others (saprotrophs)	F	*Quercus robur* (pedunculate oak)	Reduced fungal colonization of decomposing leaves; change in fungal species composition	Some transitory UV-B effect on mass loss of decomposing litter	75
Mucor, Truncatella, Penicillium (saprotrophs)	F[b]	*Vaccinium uliginosum* (a heathland shrub)	Reduced fungal colonization of decomposing leaves; change in fungal species composition	Altered leaf litter quality	76

[a] C = controlled environment chamber, G = greenhouse, F = field UV-B supplement from lamps, E = field UV-B exclusion. [b] All or some decomposition conducted in laboratory.

occur such that the limits of temperature tolerance are altered. A study on Subarctic heath species showed that enhanced UV-B considerably increased the frost sensitivity in three of four species tested.[99] In one species, this meant that the lower temperature limit of frost tolerance for some plants was 5 °C higher than for plants not given elevated UV-B. Furthermore, elevated CO_2 led to an increase in frost sensitivity of these species and if both elevated CO_2 and enhanced UV-B were applied, there was a further increase in frost sensitivity. Thus, even with warming at high latitudes, the frost damage to some of the plant species may be increased at higher CO_2 and UV-B.[99]

When low temperatures are generally limiting growth or other processes, but not causing damage, warming should render a benefit to growth, but the degree to which this interacts with different levels of UV-B is not well understood. As appears to be the case with combinations of elevated CO_2 and enhanced UV-B, the effects of warming and UV-B usually exhibit few synergistic effects, based on the available experiments. This is the case for the response of Antarctic plants to combinations of warming and UV-B manipulations.[100,101] However, at high temperatures, some synergistic effects of enhanced UV-B and the elevated temperatures have been reported. In some tropical legumes, enhanced UV-B reduced growth of the plants at moderate temperatures (20 to 30 °C), but at 40 °C, chloroplasts in the leaves were modified and this masked UV-B depressions of growth (*e.g.*, refs. 102 and 103).

Interaction of global climate change factors across trophic levels

The interactions addressed above largely involve the effects of factor combinations on a single trophic level, usually higher plants. However, environmental factors may also interact by affecting different components of the same trophic chain (Fig. 1). For example, plant–insect interactions may be affected by the responses of both plants and insects to changes in UV-B, temperature, and precipitation patterns. Enhanced UV-B can affect the quality of plant foliage as a food source for insect herbivores and this has been shown in several studies (see earlier section). Of the climatic change factors, insects themselves are primarily affected by temperature[104] and changes in the frequency and patterns of precipitation.[105] These factors may exert a direct influence on the insect, and also indirect effects mediated through changes and seasonal timing of the vegetation. Thus, factor interactions across trophic levels might involve warming, altering plant and insect seasonal timing[104], and enhanced UV-B affecting the quality of plant tissue for insect consumption. The micro-organisms that are responsible for decomposing dead plant and animal materials constitute another trophic level. Warming may accelerate decomposition, given sufficient moisture, although UV-B exposure of vegetation when alive can change the decomposability of the plant material after senescence and death.[76] Furthermore, UV-B can also directly affect the microbes decomposing the plant litter if they are exposed to sunlight.[76,106] Thus, climatic change factors may affect or operate at different trophic levels, thereby complicating the analysis resulting from single trophic level studies.

Climate change over a longer span of time will also affect the geographic distribution of vegetation and animal populations.[107] Migration of different species in response to warming can involve shifts to higher latitudes and altitudes[108–110], which in turn would change their exposure to prevailing solar UV-B in these new locations.

Concluding remarks

This assessment emphasizes generalizations that can be made about the effects of enhanced UV-B on terrestrial ecosystems and those of UV-B when interacting with other climatic factors. Clearly, as with any generalization, exceptions are to be found and the generalizations necessarily involve simplifications. Also, when moving from effects of UV radiation and other factors at single trophic levels (such as higher plants) to whole-system function, numerous complications arise and experimentation becomes more difficult and costly. Nevertheless, progress is being made and we feel the conclusions drawn here are realistic.

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