

## Effects of increased solar ultraviolet radiation on terrestrial ecosystems

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### Abstract

Elevated solar UV-B radiation associated with stratospheric ozone reduction may exert effects on terrestrial ecosystems through actions on plants, microbes, and perhaps on some animals. At the ecosystem level, the effects are less well understood than at the molecular and organismal levels. Many of the most important, yet less predictable, consequences will be indirect effects of elevated UV-B acting through changes in the chemical composition and form of plants and through changes in the abiotic environment. These indirect effects include changes in the susceptibility of plants to attack by insects and pathogens in both agricultural and natural ecosystems; the direction of these changes can result in either a decrease or an increase in susceptibility. Other indirect effects of elevated UV-B include changes in competitive balance of plants and nutrient cycling. The direct UV-B action on plants that results in changes in form or function of plants appears to occur more often through altered gene activity rather than damage. The yield of some crop varieties can be decreased by elevated UV-B, but other varieties are not affected. Plant breeding and genetic engineering efforts should be able to cope with the potential threats to crop productivity due to elevated UV-B. For forest trees, this may be more difficult if effects of elevated UV-B accumulate over several years. All effects of elevated UV-B radiation must be considered in the context of other climate changes such as increased temperature and levels of carbon dioxide, which may alter the UV-B responses, especially for plants. The actions of elevated carbon dioxide and UV-B appear to be largely independent, but interactions occur between changes in UV-B and other factors. Other ecosystem-level consequences of elevated UV-B radiation are emerging and their magnitude and direction will not be easily predicted. © 1998 UNEP. Published by Elsevier Science S.A. All rights reserved.

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### 1. Introduction

Terrestrial ecosystems include agricultural lands, agro-ecosystems, and less intensively managed lands such as forests, grasslands, savannahs, deserts, tundra, etc. In any of these environments, ecosystem function includes many attributes that could potentially be affected by increased solar UV-B radiation, including plant biomass production, seed production, plant consumption by herbivores including insects, disease incidence of plants and animals, population fluctuations of plants and animals, and changes in species composition and mineral nutrient cycling. Treatment of some aspects of ecosystem function, e.g., nutrient cycling, overlap with Ref. [1], and effects on amphibians in aquatic components of terrestrial systems overlap with Ref. [2].

Study of the effects of solar UV-B increase at ecosystem level has only been undertaken in the past few years. However, much attention has been directed to the effects of UV-B radiation on higher plants since the first reports of potential stratospheric ozone reduction over 25 years ago (e.g., [3,4]). Approximately 600 papers have appeared, but the majority of these deal with herbaceous, agricultural plants under laboratory or glasshouse conditions. Fewer than 5% of the studies have been conducted under field conditions, and fewer still with plants from forests and other nonagricultural systems.

Numerous reviews of this literature dealing primarily with effects on terrestrial plants have appeared in the last decade [5–26]. Rather than a review of the literature, this paper provides an overview with interpretation of the results for both agriculture and other ecosystems such as forests, grasslands, etc.

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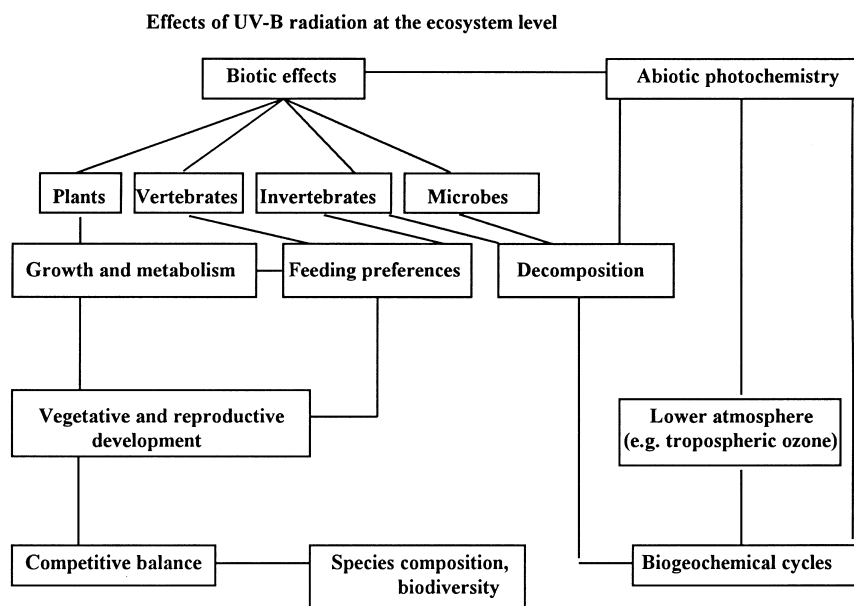


Fig. 1. Scheme of direct photochemical effects of elevated solar UV-B radiation on plants, microbes, and animals and indirect ecosystem effects mediated through changes in plant competition, microbial population changes, secondary chemistry, plant litter decomposition, and air quality. The lines indicate some of the potential interactions and consequences of UV-B radiation. See also Fig. 2 for related ecosystem-level effects and processes.

In terrestrial ecosystems, organisms apart from higher plants have received comparatively little attention with respect to the direct effects of solar UV-B radiation increases. Some direct effects on microbes and animal life have been demonstrated (e.g., [27,28]; see also Refs. [2,29]). Microbes perform many important ecosystem functions including litter decomposition, cycling of mineral nutrients, pathogenic action, and symbiotic interaction with both plants and animals. Direct UV-B effects on microbes have been extensively studied [30], but the ecological relevance is not well understood. Animals are often thought to be generally well shielded from solar UV-B radiation by pigments such as melanin, and body coverings such as feathers, fur, etc. In some animals, the eyes may be at risk if there is prolonged UV-B exposure (see Ref. [29]). However, microbes exposed to sunlight are usually not so well shielded.

The major anticipated effects of increased solar UV-B on agricultural and nonagricultural ecosystems (such as forests, grasslands, savannahs, deserts, tundra, etc.) may result from direct UV-B radiation effects on plants, insects, and microbes, or indirect effects of UV-B on these organisms that mediate other effects (Fig. 1). Nonbiological UV-B effects such as direct photochemical reactions in plant litter during decay [1] or effects on the ambient air quality [31] can influence other processes in ecosystems. Although the principal processes may be the same in highly managed agroecosystems (e.g., agronomic crops) and in nonagricultural ecosystems, their importance may differ. For example, effects on litter decomposition or plant competitive balance may be less important in annually cultivated crop fields.

For individual organisms, there are several potential pathways of UV-B action in damage and regulatory processes

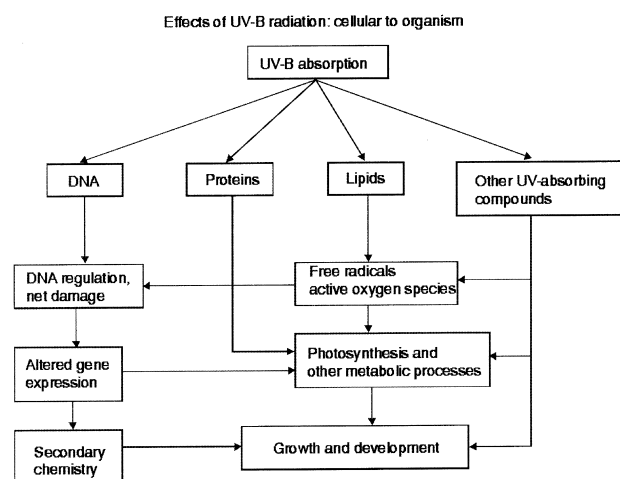


Fig. 2. The influence of UV-B radiation on several damage and regulatory processes in organisms. Much of the initial damage can be repaired (e.g., DNA damage). Damage and regulatory changes in plants and other organisms alter metabolism and ultimately growth, reproduction, and survival. The arrows indicate some of the potential interactions and consequences of UV-B radiation.

that affect whole organism performance, such as growth and reproduction (Fig. 2).

## 2. General effects on organisms

### 2.1. Basic effects of UV-B radiation on organisms and their protective responses

Enhanced UV-B radiation can have many direct and indirect effects on organisms. However, organisms have devel-

oped mechanisms of protection and mitigation of UV-B radiation damage. General deleterious effects include production of active oxygen species and free radicals, DNA damage and, for plants, partial inhibition of photosynthesis. Protective responses include radiation shielding due to structural or pigment changes and specific damage-repair systems. Although photochemical lesions of DNA and proteins and damage as a result of active oxygen species and free radicals may occur, many of the effects of UV-B radiation may be expressed through increased regulation rather than sustained damage.

In order for UV radiation to be effective in most organisms, it must effectively penetrate into the tissues and be absorbed. Structural and biochemical changes induced by enhanced levels of UV-B radiation ultimately modify the penetration of UV radiation into plants and other organisms. The UV shielding in most animals is thought to be quite effective in minimizing UV-B damage, but this should be further examined (see Ref. [29]). For example, different stages of insect larvae may be less well protected by UV-absorbing pigments. In plants, a certain amount of UV-screening pigments may be constitutive, and additional UV-absorbing compounds (usually phenolic compounds) can be synthesized when plants are exposed to increased levels of UV radiation. This will naturally be important in reducing the penetration of UV-B radiation to underlying tissues. Experimental mutant plants that lack these pigments are very sensitive to natural sunlight UV-B [32,33]. Other adjustments in plant leaves after exposure to increased UV-B radiation may also contribute to a heightened UV defense. At the structural level, increased leaf thickness is often induced by UV-B radiation and reduces UV-B penetration to internal leaf tissues [34]. Ultraviolet radiation penetration varies among different plant species and this may be reflected in the sensitivity of these species. Penetration of UV-B was found to be greatest in herbaceous dicotyledons (broad-leaved plants) and was progressively less in woody dicotyledons, grasses, and conifers [35]. The UV penetration also changes with leaf age; younger leaves attenuate UV-B radiation less than do the more mature leaves, as was shown for some conifers [36,37].

Of the different kinds of molecular damage, radiation damage to DNA is potentially dangerous to cells, because a single photon hit in a single molecule may have dramatic, and sometimes even lethal, effects. Many different types of DNA damage are known that result from free radicals and reactive oxygen species formed in various photochemical processes. The two most common UV-B-induced DNA lesions are the cyclobutane pyrimidine dimers and (6–4) photoproducts which are pyrimidine adducts. These two types of lesions differ from other DNA lesions in that many organisms living in sunlit habitats possess special enzymes (photolyases) that can effectively repair many of these lesions in the presence of visible light and favorable temperatures. Some DNA-repair systems can also operate without light [38,39]. Much of the research in this area has been conducted under laboratory conditions, but the level of DNA lesions in intact plants

has also been measured under field conditions (e.g., [40–42]). While these studies indicate effective repair of DNA damage [42], the UV component of sunlight is still sufficient to result in some level of persistent damage. Low temperature can slow this enzymatic repair of DNA damage [38,43]. Therefore, plants, cold-blooded animals, and microbes in cold environments may suffer from a less favorable balance between damage and repair than others. Unfortunately, these environments overlap with those exposed to the greatest ozone depletion.

When exposure to increased UV radiation leads to stimulation of UV-absorbing compounds in plant tissues, another protective effect can result from the antioxidant properties that certain of the compounds confer. Enhanced levels of UV-B radiation appear to stimulate selectively those flavonoids (a type of phenolic) with potential antioxidant properties [33,44–46]. This selective enhancement can be up to 500% [33]. At present, it is not known how extensive this selective induction is within the plant kingdom.

Many genes in plants, animals, and microorganisms are regulated by UV-B, and changes in UV-B may have important consequences by altered gene action [14,22,47]. The mechanisms of how the organism perceives UV-B radiation and how signals are transduced are not yet well understood. Active oxygen can be one trigger for altered gene activity [48]. No matter what the triggering agent, altered gene activity is important, since UV-B radiation is involved in changes of gene expression which are reflected in many aspects of plant function. For example, an increased amount of UV-B radiation results in enhanced synthesis of UV-screening pigments and is due to the expression of particular genes [49]. It appears that the effects of UV-B radiation on photosynthesis, growth, and development of plants are caused by altered gene action. This is currently a topic of intensive research.

Decreased elongation may also be due to UV-induced destruction of the plant hormone auxin, which absorbs in the UV-B range and could be photodegraded by high levels of UV-B radiation. Oxidative enzymes, such as the peroxidases, the activity of which is increased by enhanced UV-B radiation, may also be involved in plant hormone-regulated growth responses, as shown in sunflower and rice plants [50,51]. The levels of another plant hormone, ethylene, which causes greater radial growth and less elongation, are increased after UV-B irradiation in sunflower seedlings [50] and cultured shoots of pear seedlings [52]. Changes in hormone levels ultimately may be due to UV-B-induced gene expression, but this remains to be demonstrated.

## 2.2. *The biological effectiveness of changes in sunlight*

As explained in Ref. [53], the biological effectiveness of solar UV-B radiation needs to be taken into account in assessing what ozone reduction, and the resulting changes in solar radiation, may mean for biological systems and processes. The biological weighting functions used for this purpose often come from action spectra. Action spectra assumed to

be relevant for organisms, especially plants (Fig. 3), all indicate that the shorter UV-B wavelengths are the most important. However, the relative importance of shorter versus longer UV-B wavelengths (the slopes in Fig. 3) varies considerably. Depending on these slopes and the tails of the spectra extending into the UV-A range, the radiation amplification factors (RAFs) (discussed in Ref. [53]) vary enormously. Only the weighting functions with steep slopes result in RAF values suggesting that ozone reduction is potentially important. Thus, the evaluation of weighting functions (and therefore action spectra) is critical. Although there is evidence that action spectra for some plant functions are steep, indicating that ozone reduction translates into large increases

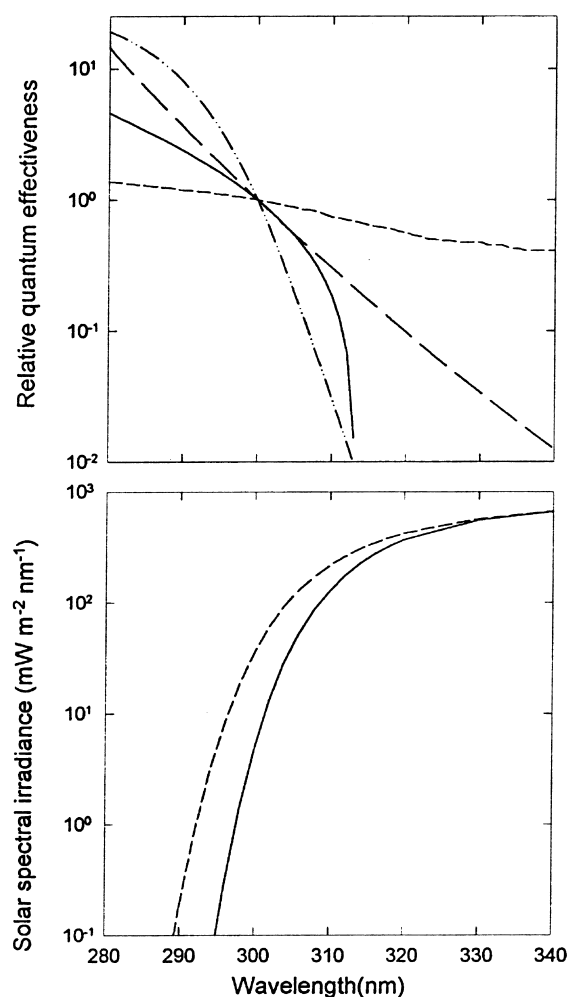


Fig. 3. Upper panel: action spectra for 'naked' DNA damage [54] (lines with dashes and dots), DNA dimer formation (a type of DNA damage) in intact alfalfa seedlings [55] (line with long dashes), a generalized plant action spectrum compiled from various plant spectra [56] (continuous line), and a spectrum for putative lipid damage based on a luminescence indicator [57] (line with short dashes). The lower panel shows solar spectral irradiance at 360 (continuous line) and 180 (dashed line) Dobson Units (DU) of total atmospheric ozone. (Dobson Units are used for describing the thickness of the ozone layer at standard temperature and pressure ( $0^\circ$  and 101.3 Pa). 1 mm ozone layer thickness is equivalent to 100 DU.) The solar irradiation is calculated for latitude  $49^\circ\text{N}$  at solar noon at the summer solstice (June 21) using the model of Green et al. [58].

in effective solar UV-B [54,56], some more recent spectra developed specifically for evaluating the ozone reduction problem show somewhat flatter slopes (and therefore somewhat lower RAF values) than the earlier work [55,57,59,60]. Still, many of these spectra are sufficiently steep that ozone reduction must be taken seriously [61,62]. Biological weighting functions also are needed to relate solar UV radiation to the UV light from lamps used in many experiments.

### 2.3. Plant growth responses

In many plant species reduced leaf area and/or stem growth have been found in studies carried out in growth chambers, greenhouses, and in the field [8,17,25,63,64]. These studies have traditionally been conducted with specially filtered UV lamps. It is important in such experiments to maintain a realistic balance between different spectral regions, since both UV-A (315–400 nm) and visible (400–700 nm) radiation can have strong ameliorating effects on responses of plants to UV-B [65]. In growth chambers and greenhouses, the radiation conditions are usually quite different from those in nature. For example, the visible radiation that is used in photosynthesis (400 to 700 nm, photosynthetically active radiation, PAR) and the UV-B/UV-A/PAR ratios are different from those in the field. If UV-A and PAR are low, the effects of UV-B may be much more severe. Thus, even if realistic levels of UV-B are used in simulating ozone reduction, the plant response may be exaggerated relative to that in the field. In addition, other factors, such as temperature, water, and nutrients, differ from conditions in the field and this can alter the response to UV-B radiation. It is, however, important that these studies conducted under controlled conditions be verified as much as possible under field conditions. Even under field conditions, if applied UV-B is not adjusted downward during cloudy periods, the UV-B sensitivity may be unduly pronounced [66]. Unfortunately, the most expensive and difficult experiments, i.e., those conducted in the field with UV-B supplements adjusted for cloudiness and other atmospheric conditions, are seldom undertaken. In the last few years more field experiments have been conducted and many of these employ lamp systems with controls to make continual adjustments according to prevailing sunlight conditions.

Also, there are several studies in which the UV component of existing sunlight has been altered by special filters in the field or in special small greenhouses or growth chambers located outdoors. The filters have involved special glass, plastics, or in one series of studies, ozone gas in a UV-transparent Plexiglas envelope [67,68]. Many of these studies involving filtered sunlight have shown that normal ambient solar UV-B can cause somewhat reduced leaf area, smaller seedlings, etc. [41,69–71].

Plant species vary considerably in their response to UV-B in both controlled-environment and field studies. Also, varieties of the same species can vary in their response. For example, in the field, sizeable differences in response to UV-

B were found among varieties of soybean [72] and rice [73–75]. Experiments in greenhouses covered by different materials that transmitted different amounts of UV indicated that varieties of bean (*Phaseolus vulgaris*) from lower latitudes were less affected than those from higher latitudes under higher UV-B radiation [71].

#### 2.4. Plant reproductive processes

UV-B radiation can alter both the timing of flowering [17,70,76–78] as well as the number of flowers in certain species [71,79,80]. Differences in timing of flowering may have important consequences for the availability of pollinators. Such effects may be due to regulatory alterations in the plant rather than damage per se. Poorly protected reproductive organs might, however, be susceptible to damaging effects. Most of the reproductive parts of plants, such as pollen and ovules, are rather well shielded from solar UV-B radiation. For example, anther walls can absorb more than 98% of incident UV-B radiation [81]. In addition, the pollen wall contains UV-B-absorbing compounds affording protection during pollination, as do the other flower parts such as sepals, petals, and walls of the ovaries [82]. Only after transfer to the stigma might pollen be susceptible to solar UV-B radiation. In vitro experiments have shown that germinating pollen can be sensitive at this time to UV-B radiation in some cases [83]. However, often pollen germination itself is not affected, but pollen tube growth of many species can be retarded, as shown in a survey of 34 plant species or varieties [84].

#### 2.5. Carry-over effects of UV-B irradiation in subsequent generations

In sexually reproducing populations of an annual desert plant, effects of UV-B irradiation on growth and allocation of biomass appeared to accumulate as subsequent generations were exposed to UV-B irradiation [85]. Furthermore, after four generations of UV-B irradiation, the effects persisted in a fifth generation that was not exposed to UV-B treatment [86]. If this phenomenon is common, it could amplify the effects of UV-B radiation changes. This is somewhat analogous to apparent accumulated effects of UV-B irradiation over several growing seasons in long-lived woody plants discussed later.

### 3. Ecosystem-level UV-B radiation effects involving higher plants

#### 3.1. Competitive balance

In forests, grasslands, etc., overall primary plant productivity may not be greatly affected by ozone reduction even if the growth of some plants is diminished. However, since plant species differ greatly in growth responsivity to UV-B, it is

anticipated that a productivity reduction of one species will probably lead to increased productivity of another more UV-tolerant species. This is likely because more resources (e.g., light, moisture, and nutrients) will be available to the tolerant species. Thus, the overall productivity of the system may well remain about the same while species composition may change. However, a change in the balance of species could have far-reaching consequences for the character of many ecosystems.

Another mechanism whereby the competitive balance of plant species can be changed by increased UV-B is through changes in plant form. Even if plant production per se is not affected by increased UV-B, changes in plant form can result in changes in which species can more effectively compete for sunlight. This phenomenon has been demonstrated in several experiments. For example, in a six-year field study using modulated UV-B lamp systems, the competitive balance of two species (wheat and a common weed, wild oat) could be changed even though the increased UV-B radiation had no effect on production and growth of these species if grown by themselves [87]. A quantitative analysis of competition for sunlight in the mixed stands with and without supplemental UV-B showed that subtle changes in plant form of the two species were sufficient to change the balance of competition for sunlight that is necessary for photosynthesis [88]. Therefore, one species can achieve some advantage over the other because one captures more sunlight for photosynthesis. In these experiments, the wheat benefited from increased UV-B and the weed suffered. However, in other mixtures of crop and weeds, the situation might be reversed. Also, other changes in plant form, such as greater allocation of biomass to roots, might change competitive effectiveness of individual species for soil moisture and nutrients. In grasslands and forests that are not managed intensively, similar changes in species composition may be experienced.

Ecosystem-level experiments with nonagricultural systems are only beginning. Early reports of one experiment in a subarctic heath ecosystem suggest that species composition changes may result from UV-B supplementation [63].

#### 3.2. Plant susceptibility to pathogens and insects

The extent to which plant tissues are consumed by insects or the degree to which pathogens attack plants is regulated by several properties of the plant host tissues. Experiments in which solar UV-B radiation has been modified by selective filters show that present-day solar UV-B radiation can substantially reduce insect herbivory of agricultural and native plant foliage [41,89,90]. Field studies involving supplementation of solar UV-B radiation with lamp systems indicated a substantial reduction in populations of a herbivorous insect on a heathland plant [91]. The reasons for these changes are not always clear, but they may be mediated through changes in plant secondary chemistry or alterations in plant nitrogen or sugar content. Studies involving UV lamps indicated decreased herbivory by a moth caterpillar under elevated UV-

B radiation and this was attributed to increases nitrogen content of the host pea plant tissue [92]. Mulberry plants previously irradiated with UV from lamps suffered less herbivory by silkworms (*Bombyx mori*) and the lower consumption was attributed to lower sucrose content of the foliage [93]. McCloud and Berenbaum [94] have shown in laboratory studies that UV-B radiation can increase furanocoumarin content of plant tissue, which, in turn, results in slower development of certain insect larvae during early life stages of the larvae. Although the foregoing would suggest that insect herbivory may always be decreased by UV-B radiation, another study shows that herbivory can be increased three-fold (e.g., [95]).

The results of most of these studies indicate that the effects on insect herbivory are all due to changes in the host plant tissues. However, there are some indications that some insects may respond directly to solar UV-B radiation. Thrips on soybeans were found to consume less foliage if the foliage had been previously exposed to ambient solar UV-B. Furthermore, the thrips appeared to sense and avoid solar UV-B radiation directly even though they were mildly attracted to UV-A radiation [89].

Plant fungal and viral diseases react in a number of different ways to UV-B radiation in several experiments, conducted primarily in laboratory and greenhouse conditions. In four out of ten studies, UV-B was found to counteract disease severity, and in the other six studies, it promoted disease development [19]. The direction of the UV-B radiation effect on disease severity can also vary with the variety of the host. In a rust-resistant variety of wheat, additional UV-B radiation had little effect, but it promoted the rust infection in a rust-sensitive wheat variety [19]. It is not clear in many of these experiments whether the changes in disease severity were due simply to changes caused by UV-B radiation in the host plant, or whether direct UV-B radiation effects on the fungal or viral pathogens were involved. Cucumber plants first exposed to UV-B radiation were more susceptible to subsequent infection by two fungal pathogens if the host plants were exposed to UV-B radiation prior to infection; but UV-B irradiation after infection had no effect on disease severity [96]. Such an experiment suggests the effect of UV-B radiation was mediated through changes in the host plant tissues. There is also evidence from solar UV-B exclusion studies showing increased incidence of fungal disease when UV-B is removed [97].

These changes in insect herbivory and disease severity caused by alterations of solar UV-B can be sizeable; they can operate in different directions and have very important implications for both agricultural and nonagricultural ecosystems. They may be much more important than known influences of UV-B radiation on plant production based on realistic field studies.

Even roots of plants whose shoots are exposed to elevated UV-B radiation can be affected, as indicated by root interactions with microorganisms. For example, the nature of microorganism assemblages that were associated with roots

of sugar maple trees (*Acer saccharum*) was altered by exposure of the tree shoots to elevated UV-B radiation [98]. This was obviously a systemic effect of UV-B expressed in the roots of the host plant.

### 3.3. Timing of life phases

The timing of life phases of plants is a combination of response to environmental factors and the genetic constitution of the plant. For example, as mentioned earlier, UV-B exposure can alter the timing of flowering. This timing of events such as flowering, entering and breaking of dormancy, and even senescence is important not only to the individual plant, but also in how plants interact with other plants and animals. For example, a shift in the timing of flowering can mean that a plant species might not have sufficient insect pollinators available at the new time of flowering, either because the insects are not present or because other plant species are attracting these pollinators. Such changes could also conceivably be important in agricultural systems, but intervention with management options may make these changes less important. As indicated earlier, increased UV-B has been shown to advance or delay (depending on species) the time of flowering in plants. There is little work at present on flowering responses and virtually nothing on other potential effects of UV-B on life phase timing of plants or other terrestrial organisms.

### 3.4. Other effects due to changes in higher plant tissues

In higher plants, secondary compounds, such as lignin, are important as structural materials. These are related to phenolic compounds and may change in composition with elevated UV-B radiation (e.g., [28]). If the ratio of lignin to cellulose in plant tissues changes, it can alter the rate of decomposition. This has very important implications for biogeochemical cycles as discussed fully in Ref. [1].

## 4. Ecosystem effects of solar UV-B not mediated by higher plants

Although the considerable emphasis on UV-B effects on plants and plant-mediated ecosystem effects is deserved, elevated solar UV-B radiation may affect ecosystem function through other mechanisms (Fig. 1). Direct effects of solar UV-B on terrestrial animal life, microbes, and the lower atmosphere [31] can all have important ecosystem-level implications. Comparatively little study has been directed to effects on animal life apart from humans [29].

It has been experimentally established that animals, from fish to mammals, can acquire skin cancer under laboratory conditions and some domestic animals exhibit such symptoms in poorly pigmented body areas [29]. However, in nature, protection by fur and plumage or behavioral patterns make it unlikely that there will be sufficient UV-B radiation

exposure for skin cancer to be a hazard for most animals. There is a possibility of eye damage in animals, but that has not been investigated under field conditions.

Microbes exposed to sunlight play important roles in many ecosystem functions, including decomposition of plant litter, diseases of plants and animals, biogeochemical transformations [1], etc. Microbes in several habitats are exposed to sunlight, including those that are airborne, or live on soil, litter, and foliage surfaces. Gehrke et al. [28] found that among fungi in plant litter, *Mucor hiemalis* and *Truncatella truncata* were reduced in abundance by UV-B radiation corresponding to pronounced ozone depletion, while *Penicillium brevicompactum* was unaffected by increased UV-B radiation exposure. Cyanobacteria growing on soil surfaces may be important for nitrogen fixation from the air. It is known that their sensitivity to UV-B radiation also varies considerably among species (see Refs. [1,2]). Leaf surface microorganism assemblages have also been shown to be altered by increased UV-B radiation [99].

When the stratospheric ozone is depleted, solar UV-B penetrates more effectively into the lower atmosphere and can alter local air pollution [31], which in turn can influence terrestrial ecosystems. For example, under conditions of substantial ambient NO<sub>x</sub> more ozone can be formed in the lower atmosphere due to ozone reduction in the stratosphere [31]. It is well known that ambient ozone can adversely affect higher plants [19]. Other nonbiological effects of elevated solar UV-B radiation include accelerated photodestruction of plant litter exposed to sunlight [1].

### 5. Which terrestrial ecosystems might be most affected by increased UV-B radiation?

Much of the experimentation has been designed to simulate UV-B levels expected on clear days with unobstructed sunlight, whereas many areas have persistent cloud cover and, correspondingly, lower UV-B flux rates. However, there is some suggestion that plant responsiveness to UV-B may be influenced by the ratio of UV-B light to visible sunlight as much as by the absolute level of UV-B radiation [100,101]. Certain clouds tend to transmit more radiation at shorter wavelengths than at longer wavelengths [102]; therefore, the UV-B:PAR ratio would be greater than under clear-sky conditions. Yet, this has not been documented over extended time periods in different environments. The potential importance of plant responsiveness to greater UV-B:PAR ratios during cloudy periods deserves further attention and ecosystems that occur in cloudy environments should not necessarily be dismissed from consideration for the ozone-reduction problem.

Overall, the consequences of increased solar UV-B in forests, grasslands, and other nonagricultural ecosystems may involve several complex pathways (Fig. 1) rather than simply a reduction in overall ecosystem primary productivity. However, the effects of these more involved pathways are

difficult to predict without conducting experiments with assemblages of plant species and long-term study of ecosystem responses. This has, thus far, received very little attention in experimental research.

Where ecosystem-level studies of terrestrial responses to increased solar UV-B have been initiated, high-latitude ecosystems have been emphasized, since the relative ozone reduction is more pronounced at high latitudes. However, the absolute UV-B flux is greater at low latitudes where ozone reduction is not very pronounced.

Further discussion of the implications for specific types of ecosystems follows later in this paper.

### 6. Interaction of UV-B and other factors

Plants and other organisms in nature are seldom affected by only a single stress factor, such as UV-B radiation. Instead, they typically respond to several factors acting in concert, such as water stress, increased atmospheric CO<sub>2</sub>, mineral nutrient availability, heavy metals, tropospheric air pollutants, and temperature. Therefore, it is important to keep in mind that the effectiveness of UV-B radiation can be greatly increased or decreased by such factors. Visible radiation is an important ameliorating factor and, thus, as natural levels as possible should be applied in laboratory experiments for attaining more realistic results, as discussed earlier.

Among the most common factors in nature is water stress. In a field study, Sullivan and Teramura [103] demonstrated that UV-B-mediated reductions in photosynthesis and growth were observed only in well-watered soybeans. When soybeans were water stressed, there was no significant effect of the UV-B radiation on either photosynthesis or growth. The interpretation was that water stress resulted in a large reduction in photosynthesis and growth that masked the UV-B effect. Furthermore, water-stressed plants resulted in a higher concentration of leaf flavonoids, which in turn, provided greater UV-B protection. Other interactions between UV-B radiation and water status of plants also occur. Elevated UV-B radiation in field experiments tended to alleviate drought symptoms in two Mediterranean pine species [104,105]. In a moss species, UV-B radiation inhibited growth when the moss was under water stress, but stimulated growth when the moss was well hydrated [106].

Increases of atmospheric CO<sub>2</sub> are a certain element of global climate change and the atmospheric CO<sub>2</sub> concentration will likely double by the middle of the next century [107]. Many experiments with elevated CO<sub>2</sub> employ a twice-ambient CO<sub>2</sub> concentration as a treatment condition. Such a doubling often results in more pronounced plant responses than are evident in many elevated UV-B radiation lamp experiments designed to simulate up to 20% ozone column reduction under field conditions. However, responses to CO<sub>2</sub> are small in semi-natural ecosystems where nutrient or water availability may strongly constrain plant growth. For example, Gwynn-Jones et al. [108] showed that growth responses

to elevated CO<sub>2</sub> and enhanced UV-B (both alone and in combination) were small during the first three years of experimentation in a sub-arctic heath. Also, most ecosystem-level effects of elevated CO<sub>2</sub> are mediated through changes in plant tissues. When studied independently, plant growth responses to changes in UV-B radiation and atmospheric CO<sub>2</sub> concentration generally are thought to be in opposite directions. Usually, however, in most experiments employing both elevated CO<sub>2</sub> and UV-B radiation, these factors do not yield interactions, with some exceptions (see Refs. [24,109]). Elevated CO<sub>2</sub> sometimes appears to provide some protection against elevated UV-B radiation for some species; yet, elevated UV-B radiation can limit the ability of some species to take advantage of elevated CO<sub>2</sub> in photosynthesis. Allocation of biomass in plants can also change in a complicated fashion with the combination of CO<sub>2</sub> and UV-B radiation treatments (reviewed by Sullivan [24]). Increased temperature is also a predicted element of global climate change. In a study combining two levels of UV-B radiation with two levels of CO<sub>2</sub> and two temperatures, the results indicated that either elevated CO<sub>2</sub> or somewhat higher temperature had similar effects in reducing the growth-inhibiting effects of elevated UV-B radiation on sunflower and maize seedlings [68].

Plant uptake and translocation of mineral nutrients within the plant can be affected by elevated UV-B radiation, but the mineral nutrient status of plants also can affect plant responsiveness to UV-B radiation [110–112]. Nitrogen concentration in plant tissues can increase under elevated UV-B, which has been linked with reduced insect herbivory [90,92]. The uptake of certain nutrients may also be modified by UV-B radiation and cadmium. In oilseed rape (*Brassica napus*) plants grown under additional enhanced UV-B radiation and simultaneously exposed to different concentrations of cadmium, the manganese content in the shoots decreased in plants exposed to cadmium and UV-B radiation, while significant increases in magnesium, calcium, phosphate, copper, and potassium occurred only in those plants exposed to cadmium and UV-B radiation. Cadmium uptake was not affected by UV-B radiation. The UV-B had no additional influence on the nutrient content of the roots [113]. An earlier study showed that both cadmium and UV-B radiation negatively influenced photosynthetic efficiency in spruce seedlings [114].

Interaction of UV-B radiation with tropospheric air pollutants is also of concern, although little work thus far has been conducted in this area. One field study of soybean plants showed them to be sensitive to ozone in the air, but not sensitive to UV-B supplements from lamps under the particular test conditions. There were no significant interactions of supplemental UV-B and ozone [115]. However, in pine seedlings grown in a growth cabinet with simulated solar UV radiation, increasing the ozone concentration increased the sensitivity of the pine seedlings to UV-B radiation, since the ozone reduced the levels of UV-B-absorbing pigments in the plant tissues. In another experiment with tobacco, UV-B radi-

ation increased the level of ozone-induced foliage lesions [116].

## 7. Implications for agriculture, forests, and other ecosystems

### 7.1. Crops

One of the primary concerns about future increases in solar UV-B radiation is its potential effect on global agriculture. Despite the obvious potential consequences of the issue, we cannot make quantitative predictions of anticipated effects resulting from stratospheric ozone depletion. This is due to the limitation in controlled-environment studies as discussed earlier and the overall paucity of well-replicated experiments performed in the field. Even in comparisons of field studies, there are large differences in temperature, precipitation, soil types, etc., from year to year and in different locations. This adds to the difficulty in making generalizations about the effects. Also, a common finding is that different varieties of the same crop species often react differently to elevated UV-B radiation (Fig. 4).

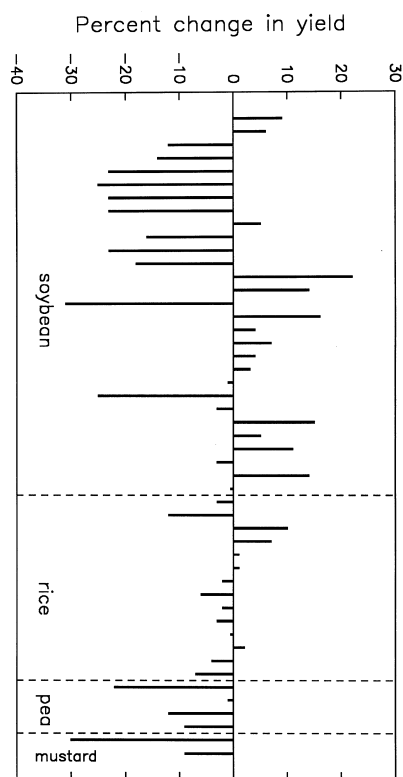


Fig. 4. Relative changes in yield (seed production) of four crops evaluated for UV-B radiation responsiveness in 49 field trials with UV-B supplementation from lamps. Each bar represents results obtained with one variety in one field experiment in which ozone depletion was simulated (usually  $\approx 20\%$  depletion). Soybean data from Refs. [72,115,117–119]; rice data from Refs. [120,121]; pea data from Ref. [64]; and mustard data from Ref. [122]. Most effects smaller than 10% were not statistically significant, but small sample sizes and other environmental factors may have obscured differences.

The general procedure in such field experiments is to supplement ambient sunlight with special fluorescent UV lamps filtered to supply either extra UV-B radiation (treatment) or with the UV-B removed (control). The methodology has continuously been improved, e.g., by introduction of automatic systems that change the lamp output to simulate more realistically the UV-B supplement with proper balance with the existing sunlight. Therefore, older experiments, and especially those performed in glasshouse or growth-chamber conditions, are presently considered to be less reliable.

The compilation of harvestable yield in field experiments in Fig. 4 indicates how variably different varieties responded and also that many varieties did not respond in a significant manner (statistically speaking) and a very few were even stimulated in production. From the entire population of studies, there is a tendency toward more negative effects.

In addition to quantitative changes in crop yield, evidence exists for qualitative changes as well. For instance, in the study mentioned above, UV-B radiation also resulted in small changes in the order of 1 to 5% in the protein and oil content of the soybean seed [72].

Because of the broad range of response patterns in crop species, plant breeding and genetic engineering for UV tolerance is an important aspect to be considered in order to avoid significant crop production losses. There may, however, be some qualitative changes in seed or foliage characteristics that accompany the development or use of more UV-B-tolerant varieties. This remains to be explored. Other agroecosystem consequences of elevated UV-B radiation are likely to be more important, such as changes in insect or pathogen susceptibility of crops.

## 7.2. Forests

Relatively little information exists on the effects of UV-B radiation on forest tree species. Tropical forests, though representing nearly one half of global productivity and much of the total tree species diversity, have received very little attention with respect to the ozone reduction problem. Although little, or no, ozone reduction has thus far occurred in the tropics, only a small decrease of ozone at these latitudes would result in a very sizeable absolute increase of UV-B radiation, since solar UV-B radiation is already very intense in these regions (see Ref. [53]). One study has shown that excluding existing solar UV-B radiation with filters can result in increased growth of some tropical tree species [69]. Otherwise, the effects of UV-B radiation on tropical tree species have not received much attention.

Fortunately, there is some information for mid-temperate-latitude tree species. Because they are long-lived, trees present the opportunity to observe the longer-term cumulative effects of UV-B exposure over several years for the same individuals. These effects cannot be explored in annual crop species. In a field study using loblolly pine [123], seedlings from several different geographic regions were grown for three consecutive years under UV-B lamps in a field experiment. Seedlings were exposed to either ambient solar UV-B or ambient levels supplemented with the UV-B from lamps, similar to studies with soybean yield [72]. After the first year of UV-B exposure, reductions were observed in the biomass of seedlings derived from several geographic areas. By the end of the third year, these biomass reductions were several-



One of the two field sites with a UV-B radiation enhancement system in Adventdalen, Svalbard (78°N). The site vegetation is dominated by *Salix polaris*, graminoids and mosses. Open-top chambers for increasing air temperature also can be seen. (Photograph: Ulf Johanson)

fold larger in one variety. These overall growth reductions were generally associated with small decreases in both roots and shoots, but not necessarily accompanied by reductions in photosynthesis. This may be due to changes in needle growth or shifts in allocation of biomass, as has been found for some crop species. These results suggested that the effects of UV-B radiation may accumulate in long-lived plants such as trees.

The fact that decreases in conifer needle biomass and needle length and leaf area of broadleaf trees were not accompanied by sizeable reductions of photosynthesis [123–125] may be due to the very low penetration of UV-B radiation into older foliage. It appears that the decreased growth of leaves and conifer needles upon exposure to enhanced levels of UV-B radiation may be due, in part, to epidermal cell-wall thickening. This might prevent cell-wall extension and, thereby, growth of these cells [125,126]. Thus, changes at the level of the epidermis, the first leaf cell layer to receive the incident radiation, can have other important consequences.

### 7.3. Other ecosystems at mid and high latitudes

Although absolute UV-B irradiance is naturally very low in high-latitude ecosystems, such as tundra and subarctic areas, there is experimental evidence that the plants in such systems react to increases in UV-B associated with realistic levels of ozone depletion. Some plant species exhibit growth inhibitions and others do not, thus, eventually altered community composition may be expected [63,90,127]. Longer-term observations of species composition are being pursued in high-latitude subarctic systems in Sweden, a high arctic site on Spitzbergen Island, and in southernmost Argentina (Tierra del Fuego). In the last system, attenuating the naturally occurring solar UV-B radiation increased insect herbivory, decreased plant tissue nitrogen concentrations, and increased populations of some microfauna (amoeba and rotifers) that inhabit peat bogs [90,127]. The subarctic studies in Sweden have been underway for several years and these show several effects including decreased litter decomposition [28], increased fruit formation, and greatly increased insect herbivory [95,108]. Similar ecosystem studies are underway in a mid-latitude site in The Netherlands where dune grasslands are important [25].

Although terrestrial ecosystems at high latitudes are not highly productive for grazing, timber production, etc., the influence of ozone reduction on these systems may be important for several reasons. Carbon sequestration is generally quite high in these ecosystems, including the extensive peat formations which are also being studied in the Swedish subarctic and southern Argentinian systems. Compared with other locations, these ecosystems are under the greatest ozone depletion, especially in the Southern Hemisphere, and they also experience the greatest warming as the global greenhouse effect intensifies. Thus, they are sensitive indicators of several features of climate change. These high-latitude eco-

systems are also very important for the survival of indigenous ethnic groups in the Northern Hemisphere.

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