Preface

Public awareness of the dangers to health of exposure to ultraviolet (UV) light has increased in recent years. Although exposure to UV can have positive effects on humans – sunbathing generally induces a feeling of well-being, partly due to production of natural endorphins, and stimulation of synthesis of vitamin D – the dangers far outweigh the benefits. The most noticeable effect of exposure is sunburn, or erythema; more serious is the increase in risk of skin cancer, and of damage to the eyes, and these symptoms may not surface for several years. At the same time, the public has also become aware that protection from solar UV is provided by ozone in the upper atmosphere, the stratosphere, but that, over recent years, the ozone layer has suffered depletion due to the action of man-made chemicals. The predicted result of this is that more UV radiation from the sun will reach the earth's surface.

Energy from the sun covers the whole electromagnetic spectrum, from short gamma rays (10^{-5} nm) to long radio waves (10^{3} m). UV light is that region of the spectrum with shorter wavelengths than blue light, between about 400 nm and 250 nm, and this is divided still further into UV-A (400–320 nm); UV-B (320–280 nm) and UV-C (280–250 nm). UV-A does not interact with ozone, since individual photons do not carry enough energy to carry out the necessary photochemical reactions; the energy in UV-B is used in breaking the bonds between oxygen atoms in molecules of ozone, which effectively results in absorption of the UV-B; UV-C is effectively absorbed by ozone/oxygen, and would still be so even under high depletions of ozone. Any reduction in the ozone layer will therefore mean that less UV-B is absorbed, and will lead to more UV-B reaching the earth's surface.

Until the early 1980s there was no evidence that the ozone in the stratosphere was actually being depleted; the first recorded evidence for a thinning in the ozone layer came in 1984 from a British team in Antarctica, led by Joe Farman. Since then, comprehensive and continuous data have come from the total ozone mapping spectrometer (TOMS) carried on the Nimbus 7 satellite; together with other instruments, this has detected thinning of ozone not just over Antarctica, but over the entire globe (see chapter by Pyle). By 1987 it was recognised that the threat to the ozone layer from various gases, particularly man-made chlorofluorocarbons (CFCs) was real, and as a result, the Montreal Protocol on Substances that Deplete the Ozone Layer was agreed by representatives of 27 of the technologically developed countries. Specified limits for a number of gases were agreed at Montreal; however, CFCs are very long-lived, so that, despite limitations being agreed, these were probably not sufficient to allow recovery of depleted ozone before well into the twenty-first century.

Although changes in stratospheric ozone would suggest that incident UV-B will increase, it is clearly vital to have accurate information as to whether increases in UV-B can actually be detected at ground level, against a background of other climate variation (see chapter by Webb). The most recent analyses show that ozone has declined globally by about 4–5% since 1979, leading to a fairly general assumption that, over the next three decades, there will be a depletion of the ozone layer of about 15%, which may result in an increase in effective UV-B of 30% over the current level. It should be noted, however, that within this range there are significant latitudinal variations in incident UV-B. For example, the amount of UV-B experienced at tropical latitudes is much greater than in temperate regions because the angle of the sun is such that there is less absorption by the atmosphere. In addition, the ozone layer itself is thinner in equatorial regions. Thus even with substantial reductions in ozone in temperate regions the effective UV-B would still not exceed that currently experienced in the tropics. However, if there were thinning of ozone in tropical regions, the levels of UV-B would exceed those previously recorded. Conversely, in regions of very high latitude, the amount of UV-B radiation is relatively low, but since it is here that thinning of the ozone layer is most marked, the *relative* increase in UV-B is potentially greatest.

Over the past few years, research has been carried out to investigate whether increases in UV-B radiation resulting from ozone depletion would have a significant impact on plants, in particular, on aspects of physiology and crop yield, and this volume of the Cambridge University Press seminar series is intended to provide a comprehensive review of our current knowledge in this area. It arose partly from a session entitled *UV-B and Plants* held at the annual meeting of the Society for Experimental Biology (SEB), Lancaster University, 1996, to which researchers from the UK, funded by the Biological Sciences and Biotechnology Research Council (BBSRC), Natural Environment Research Council (NERC), Department of the Environment (DOE) and Ministry of Agriculture Fisheries and Food (MAFF), and researchers from abroad were invited. All have contributed to the volume. Some chapters provide a fairly broad review, while others give a more detailed account of recent experimental work. Some of the current issues relating to research into UV radiation which were discussed at the meeting are summarised below, along with some detail of the contents of the chapters.

Experimental work has been carried out in laboratory growth chambers, where plants are grown under artificial white light to which is added different levels of UV-B, or outdoors, using artificial UV-B to supplement the UV-B in natural sunlight. From these studies it is now recognised that there are both *direct* and *indirect* effects of UV-B on plants. Direct effects include radiation-induced changes in photosynthesis, cell division, or other life processes of direct importance to growth and development. These effects are observed after relatively short periods of irradiation, hours or days. Damage to DNA has long been recognised as an important consequence of exposure to UV; this is discussed in the chapter by Taylor, Tobin and Bray, who describe the products formed as a result of damage to DNA, and the activity of the photolyase enzyme(s) involved in repair. Britt then describes a genetic approach of screening for mutants defective in DNA repair as a way of isolating the genes involved in the repair process. Effects of UV on photosynthesis are discussed by Baker, Nogués and Allen, the conclusion being that the primary damaging effect of UV is not on photosystem II reaction centres, but on some component of the Calvin cycle. This is demonstrated in more detail by Mackerness, Jordan and Thomas, who describe the effects of UV on the expression of photosynthetic genes and the levels of photosynthetic proteins. Clearly some of the UV-B induced down-regulation of photosynthetic genes is not simply a consequence of non-specific damage to DNA, since other defence-related genes are up-regulated, and there is developmental variation in the response to UV-B. Furthermore, protection under high light appears to be due to some component of photosynthetic activity rather than to photolyase activity. Direct responses, then, include not only *damage reactions*, but also *adaptive responses*, including the switching on of a range of defence mechanisms to afford protection against UV radiation. The best studied is the production of pigments, especially flavanoids, which will act to screen out the UV-B. Bornman *et al.* describe how the production of polyphenols is stimulated, with differential production of certain types, and that the largest concentration of pigments is located in the epidermis, effectively reducing the penetration of UV-B deeper into the mesophyll cells of the leaf. This type of response involves the stimulation of expression of particular genes, implying specific UV-B light detection systems and signal transduction processes which lead to the regulation of transcription. The question of perception of UV, and the relationship between perception of UV-A, UV-B and blue light is discussed by Jenkins, Fuglevand and Christie.

For these sorts of studies, essentially at the molecular and cellular level, the absolute amount of UV radiation does not need to equate closely to ambient levels, since the aim is to investigate the individual mechanisms associated with response to UV. It appears that responses to UV-B represent a new area of photomorphogenesis that has, to date, received little attention, and where new questions are consequently arising. For example, is there a 'simple' UV-B receptor, or are there several types of receptor, as appears to be the case with blue light responses? Is it possible to determine whether a response is a consequence of a 'damage' reaction, or is an adaptive response following specific perception? (Britt suggests that this discrimination might be achieved by treating a mutant which is defective in recovery; if there is still a response, then the effect is one of damage, and is not a function of a 'receptor'.) Understanding the molecular basis of perception and signal transduction is likely to be of direct relevance to a scenario of global climate change.

Effects seen at the whole-plant level, especially under natural conditions, are likely to involve both direct effects and *indirect* effects. Indirect effects are those mediated by radiation-induced changes in the plant environment, or changes in the plant which are of importance mainly in relation to other organisms. Examples include effects on other plants which compete with the plant under consideration (see chapter by Caldwell), effects on nutrient mobilisation, effects on herbivores and micro-organisms of importance to the plant. To understand these effects of UV requires the study of several components of natural ecosystems, and only recently have such studies been started. Unlike studies of direct effects, where responses occur quite rapidly, studies of indirect effects need to be carried out over a long period of time, since effects are likely to be of a slow, cumulative nature. To date, more effort has been given to understanding the direct effects, and indeed these are probably the most important ones in crops, growing as they do in a partly human-controlled environment, and mostly in monoculture. Indirect effects, however, may be more important for wild plants in a natural environment.

Outdoor studies require the construction of suitable irradiation facilities; the UK now has four sites with such facilities, at Lancaster University, Sheffield University, Monks Wood (Institute of Terrestrial Ecology) and Wellesbourne (Horticulture Research International). At these sites, supplementary UV irradiation is provided in a modulated form; most researchers carrying out experiments in the field recognise that modulated systems, where lamp outputs are adjusted to give a supplement which is a constant value above ambient (changing with cloud cover, for example) are preferable to square wave additions (where lamps are simply on or off). These outdoor facilities in the UK currently surpass those elsewhere in the world.

For outdoor studies, supplementary radiation should be related to realistic ozone depletion scenarios. To achieve this, it is crucial to have accurate information about the *action spectrum* of the response being studied. An action spectrum indicates the relative effectiveness of different wavelengths of radiation in bringing about a particular response; the relative effectiveness, derived from the action spectrum, can then be multiplied by the irradiance at each wavelength, and summed over the appropriate wavelength range to give the important function, *biologically effective radiation*. This term is most important in calculating predicted doses of UV resulting from different ozone depletion scenarios, but is also important in determining the dose provided by supplementary lamps, the spectrum of which is quite different from that of sunlight (see chapter by Paul). Throughout this volume the action spectrum used to calculate the biologically effective dose of supplementary UV will be quoted. There are several that can be used, the most common being derived from the Caldwell generalised plant action spectrum, normalised at 300 nm (PAS300). However, this spectrum is a composite from those available in the early 1970s, and it is quite likely that particular responses will have action spectra which are slightly or substantially different from this. The implications of this are discussed in the chapter by Holmes, where evidence is also presented that, when UV is given over an extended period of time, the action spectrum for overall growth has a significant 'tail' in the UV-A region. The reason for this is that, whereas short-term exposures will give spectra characteristic of absorption by a particular molecule (for example DNA), over an extended period, a number of processes may be involved, each with a slightly different action spectrum, added to which the plants will produce screening pigments which may alter the action spectrum.

The use of appropriate controls for outdoor arrays is a further issue also now receiving some attention. Tubes used to provide supplementary UV-B emit some energy at wavelengths below 280 nm, in the UV-C region. To exclude this, tubes are wrapped with cellulose acetate, which does not transmit below 290 nm. Control treatments have usually been unenergised tubes, providing the same shade as operational tubes. However, the UV-B tubes do emit a certain amount of UV-A, so that treatments with supplementary UV-B will also have a certain supplementation of UV-A above ambient. This can be overcome by an additional control treatment in which tubes are covered with polyester foil, which excludes wavelengths < 315 nm, thus providing a treatment which allows the effects of UV-B and UV-A to be separated. Since there is some evidence that UV-A has biological activity (see chapter by McLeod & Newsham), such an additional treatment is desirable. Since there is good evidence that responses to UV-B continue into the UV-A part of the spectrum, meters used should cover the UV-A as well. Detailed measurements, calibration of meters against standardised spectroradiometers and characterisation of the radiometric information, allowing comparisons to be made between different experimental systems, are also crucial.

Effects on growth and interactions between ecosystem components are reviewed in this volume for a range of species and habitats. Aquatic ecosystems, which are responsible for half of the biomass production of the planet, are reviewed by Häder, who discusses the penetration of solar UV radiation into the water column, the biological sensitivity of aquatic organisms, and the effectiveness of mitigating and protective measures in aquatic organisms. It is suggested that aquatic systems are already under UV stress, and that further depletion may result in changes in species composition, with significant consequences for productivity.

Effects on crops are reviewed in the chapter by Corlett *et al.*; although glasshouse and controlled environment experiments suggest that UV causes significant damage, evidence from field studies suggests that, even with a large ozone depletion, the impact on commercial monocultures may be limted, changes in morphology and pigment concentrations being more likely than large changes in productivity. Rozema, van de Staaij & Tosserams draw similar conclusions with respect to natural ecosystems, namely that effects on canopy architecture, competitive relationships and litter decomposition are as important as direct effects on productivity. A detailed description of how changes in species balance may come about, owing to slight changes in morphology, is given in the chapter by Caldwell.

Less research has been carried out into effects on more remote systems, such as upland moors and Arctic ecosystems. In Arctic regions, radiation levels are less than at temperate latitudes, but changes in the ozone layer are greater, giving the possibility of greater relative increases in UV. Moorlands and Arctic ecosystems are characterised by vegetation that is slow growing and perennial in nature, allowing effects to accumulate. Particularly in the Arctic, the low temperature may also impair repair processes. The chapters by Björn *et al.* and by Moody, Coop and Paul review effects on plant growth and on other components of these ecosystems, such as microbial activity, decomposition and herbivory. Moody *et al.* show that, in UK upland moorlands, the effects of UV-B on plant growth are generally small in comparison with the effects of CO_2, and that their opposing effects tend to cancel each other. As a result, biomass under high CO_2 plus high UV-B treatments is almost the same as that for ambient UV-B plus ambient CO_2. Effects of UV-B on microbial–plant interactions are complex; changes in plant chemical composition can reduce microbial activity, while a direct effect of UV-B during decomposition is to decrease colonisation by fungal decomposers. Increased UV-B may therefore lead to a slowing down of nutrient recycling.

Impacts on forest ecosystems are thoroughly reviewed by McLeod and Newsham, who consider the distribution of UV through forest canopies, direct effects on growth and physiology, where there is more evidence for stimulation of pigment accumulation than reductions in growth, and also impacts on leaf decomposition, micro-organisms, insects and nutrient recycling. Interestingly, it appears that increases in leaf thickness are due to UV-B, while an increase in lammas shoot length and some aspects of herbivory may be specifically due to elevated UV-A.

Finally, some specific examples of pathogen/plant interactions are reviewed in the chapter by Paul. Again, there is significant variation between species: *Septoria tritici* appears to be sensitive to UV-B, in that spore germination is inhibited by elevated UV-B, although strains from lower latitudes (where ambient UV-B is higher than in the UK) are more resistant. In other cases, the interaction is more complex; changes in plant chemical composition may alter the activity of fungal pathogens. Paul also considers in detail the consequences of using different action spectra in determining the UV-B doses supplied from supplementation with artificial lights, highlighting the very large differences in biologically effective dose that can be derived.

Despite the significant progress made in recent years, or perhaps more accurately, because of the progress made, a number of questions arise. At the climate level, is the thinning of the ozone layer having a real effect on terrestrial levels of UV-B? At the biological level, is it possible to separate damage and adaptive responses, and further, is it possible to link responses at the molecular level with those occurring at the eco-system level? Plant responses to UV-B is an exciting area; new insights into fundamental mechanisms are being gained, while the subject has very real significance in the light of changes in climate. However, many of the studies need to be carried out over longer time period to provide definitive answers to questions such as cumulative effects of UV-B, effects of UV-B at the ecosystem level, and interactions of elevated UV-B with other stress factors. Further information on UV-B, and other aspects of plant photobiology can be found across the Worldwide Web. A good starting point is the Plant Photobiology page, the address for which is http://cc.joensuu.fi/photobio/photobio.html

Peter J. Lumsden
HRI Wellesbourne
Warwick
1996