Chapter 5

UV-B Effects

5.1 Introduction

The correlation between the characteristics of the world's biomes and climatic factors such as temperature and precipitation is well understood, but it is only recently that scientists have recognized a similar equilibrium between ecosystem characteristics and UV-B radiation. Studies have shown that both reductions and increases in incoming UV-B result in observable and significant changes in ecosystem characteristics, although in either case the system may continue to function well. As a consequence of the continuing depletion of the stratospheric ozone layer, the amount of UV-B radiation reaching the earth's surface has increased over the past two decades. In response to these increases, fundamental changes to the structures and processes of existing ecosystems, both aquatic and terrestrial, may now be occurring. These changes are subtle and could evolve for many years until a new equilibrium is established. Even if mitigating measures were to succeed immediately in halting further increases in ambient levels of UV-B, ecosystems would continue to adjust for another 30 to 40 years. Whether these fundamental ecological changes will be good, bad, or inconsequential from a human perspective is not yet known. Consequently, there is a need for ecologists to expand their understanding of the role of UV-B in ecological processes and improve their ability to predict and measure natural impacts arising from UV-B increases at the earth's surface as a result of stratospheric ozone depletion.

Concerns about higher levels of UV-B are related not only to absolute increases in ambient levels but also to UV-B peaks that may occur at critical stages in the life cycles of organisms. Although many organisms have developed defence mechanisms to protect themselves from such fluctuations, the egg and larval stages of some species can be particularly susceptible to harm from UV-B peaks.

In Canada, these concerns are compounded by the impact of other environmental stressors, such as global warming, acid rain, land use changes, and toxic chemicals. As a result, UV-B impacts cannot be considered in isolation from these other factors. In any given case, UV-B may be either a causal factor or one of several contributing factors that cumulatively result in undesirable effects. The distinction between the two possibilities is seldom clear. It is essential, therefore, that studies of UV-B impacts on Canadian ecosystems be integrated with existing ecological research, monitoring, and assessment programs.

This chapter discusses the results of recent research on the effects of increased levels of UV-B radiation resulting from stratospheric ozone depletion on human health and terrestrial and aquatic ecosystems. The studies referred to are primarily Canadian and cover not only short-term direct impacts of UV-B but also life processes (e.g., photosynthesis) where the full effects may be evident only after several years of monitoring. Cumulative effects resulting from interactions with other anthropogenic stressors are discussed wherever possible. Where data permit, the potential socioeconomic consequences to Canada are also highlighted.

5.2 HUMAN HEALTH

Concern over stratospheric ozone depletion has led to scientific speculation about the effects of increased exposure to UV on human disease and on the incidence of skin cancers in particular. This concern has led to an enhanced level of research on human UV effects. In this section, some of the major advances taking place between 1987 and 1996 are described briefly by disease categories.

5.2.1 Cutaneous Malignant Melanoma

As several studies published in the early 1980s have shown, the relationship between cumulative sun exposure and melanoma risk is neither simple nor direct. Canadian and Australian scientists have independently hypothesized that melanoma is caused by strong intermittent sun exposure on unacclimatized skin [Elwood and Hislop 1982; Elwood and Gallagher 1983; Holman et al. 1983]. The Western Canada Melanoma Study [Elwood et al. 1985a; Gallagher et al. 1986] and the West Australia Melanoma Study [Holman et al. 1986] both demonstrated associations with indicators of intermittent recreational solar exposure. Furthermore, previous studies had demonstrated a strong and unexpected association between socioeconomic status and risk of melanoma – that is, workers in lower socioeconomic occupations with substantial outdoor exposure paradoxically had lower melanoma risk than members of indoor professional, managerial, and technical occupations. The Western Canada Melanoma Study showed that this gradient of risk was due to greater intermittent recreational sun exposure in the higher socioeconomic groups [Gallagher et al. 1987]. This observation was confirmed a year later in an important study conducted in East Denmark [Østerlind et al. 1988].

A large number of investigations by researchers from Europe [Beitner et al. 1990; Nelemans et al. 1993; Autier et al. 1994], Australia [Green et al. 1986], and the U.S. [Weinstock et al. 1989b; White et al. 1994; Holly et al. 1995] have confirmed the importance of intermittent solar UV radiation as a risk factor for melanoma. Australian and American studies [Khlat et al. 1992; Weinstock et al. 1989b] have also demonstrated the importance of childhood and adolescent exposure to solar UV as factors in adult melanoma risk.

Because reported exposure is subject to substantial error due to faulty memory among study subjects, investigators have used sunburn history as an indicator of strong intermittent solar exposure. Numerous studies have shown sunburn to be related to melanoma risk [Green et al. 1985; Elwood et al. 1985b; Østerlind et al. 1988; MacKie et al. 1989].

5.2.2 Acquired Melanocytic Nevi

Recent epidemiological research indicates that the strongest and most consistent indicator of elevated risk of cutaneous malignant melanoma is the presence of large numbers of acquired melanocytic nevi (skin moles) [Holly et al. 1987; Grob et al. 1990; Garbe et al. 1989; Marrett et al. 1992; Weinstock et al. 1989a]. The finding that many melanomas have histologic evidence of pre-existing nevi has led to major interest in the causes and formation of benign nevi. Although slightly over 1% of the population have nevi present at birth, that is, congenital nevi [Rivers et al. 1990], most nevi develop in childhood. A number of investigations of nevi in children have been carried out to evaluate whether solar UV radiation is involved in the genesis of these lesions.

A study of acquired melanocytic nevi among Vancouver schoolchildren, ages 6–18, revealed that nevus density increased with age in both males and females. Nevus density (nevi per square metre of body surface area) reached a maximum by about age 15, suggesting that the full adult complement of moles is acquired quite early in life [Gallagher et al. 1990a]. Furthermore, among white children, those with the highest nevus density tended to have light skin, were inclined to burn rather than tan in the sun, and were likely to have a history of sunburn [Gallagher et al. 1990b]. These risk factors are similar to those seen in studies of adult melanoma and suggest that sunlight exposure is involved in the genesis of both nevi and melanoma [McLean et al. 1995].

Further research, conducted by Australian and Canadian investigators, showed a direct relationship between latitude of residence and nevus density in Australian schoolchildren [Kelly et al. 1994]. Another Australian study of nevi in preschool age children confirmed the relationship between solar UV exposure and nevus density [Harrison et al. 1994].

Current research in Canada, Europe, and especially Australia is evaluating the use of programs promoting solar avoidance and sunscreen use as a means of reducing the number of nevi that children develop between birth and the teenage years. This research presupposes that nevi are an intermediate step in a continuous spectrum of lesions ranging from normal melanocytes to malignant melanoma. If this assumption is correct, reduction of the nevus density in children should result in lower melanoma rates in adult life.

5.2.3 Non-melanocytic Skin Cancer

Traditionally, the incidence of non-melanocytic skin cancer in white populations was thought to bear a simple direct relationship to cumulative solar UV exposure [Scotto et al. 1983]. This assumption was based largely on studies demonstrating that the incidence of such cancers in white populations increased with proximity to the equator. However, until recently, relatively few analytic studies of basal cell carcinoma (BCC) and squamous cell carcinoma (SCC), the two principal types of non-melanocytic skin cancer, had been conducted.

Several recent studies have discussed the relationship of BCC and SCC to UV radiation. In Australia Kricker et al. [1995] demonstrated an increased risk of BCC with increased exposure to sunlight on weekends, a surrogate measure of intermittent solar exposure. This increase in risk was most pronounced for solar UV exposure in the late teenage years (15–19). Similar findings were seen in an Alberta study of non-melanocytic skin cancer [Gallagher et al. 1995a], with elevated risks for BCC in subjects with the highest solar exposure before the age of 20. Furthermore, the Canadian and Australian studies demonstrated a stronger effect of solar exposure in subjects with a propensity to burn rather than tan in the sun.

The Canadian study also showed an increased risk of SCC among people with chronic sunlight exposure obtained largely in occupational settings. The strongest effect was related to exposure in the 10 years prior to diagnosis [Gallagher et al. 1995b]. No difference in exposure effect was observed for SCC between those who burned and those who tanned easily in the sun.

Thus, the data for BCC, like those for melanoma, suggest that intermittent sun exposure, particularly in childhood, may be more important in accounting for risk than total cumulative dose. For SCC, in contrast, current evidence suggests that chronic cumulative dose is more important.

Finally, results from a study of non-melanocytic skin cancer conducted in high sunlight areas of Southern Europe [Rosso et al. 1996, Zanetti et al. 1996] confirm the elevated risk of non-melanocytic skin cancer in subjects with light skin colour, red hair, and a propensity to burn in the sun. Because of the greater range of solar UV exposure in this study than in the Canadian study, the investigators were able to produce dose-response curves relating BCC and SCC to accumulated solar exposure. The curves showed an increased risk of SCC occurring only after prolonged accumulated exposure (70,000+ hours), whereas the dose-response curve for BCC rose rapidly with relatively little exposure and then reached a plateau. These findings are consistent with the low-sunlight Canadian data and the Australian data.

5.2.4 Immune Suppression

Recent investigations indicate that UV radiation can suppress cellular components of the human immune system. Following exposure to 10–100 mJ cm^{-2} of UV-B, in the absence of sunscreen, the Langerhans cell population is depressed for more than two weeks [Miyagi et al. 1994]. This may be a marker for a potentially significant immunologic defect, particularly in relation to primary contact sensitization. Approximately 100 minutes of midday sun exposure in Italy could suppress resistance to *Listeria monocytogenese* (a bacterial agent that can produce meningitis and other diseases) to a medically significant degree [Garssen et al. 1996]. Other investigations have indicated that use of sunscreens likely does not prevent systemic immunosuppression by UV-B [Wolf et al. 1993]. However, it is difficult to assess the medical significance of studies that have shown immune suppression by UV radiation, as historically humans have spent a great deal of time in the sun and have moved to protect against overexposure only in recent years.

Recent studies have revealed an increase in skin cancers in medically immune-suppressed patients. In a follow-up of kidney transplant patients in Australia, 7% developed a skin cancer after 1 year, 45% after 11 years, and 70% after 20 years [Bouwes-Bavinck et al. 1996]. Other investigations have demonstrated that the increase in nevus counts in kidney transplant children receiving immunosuppressive treatment is greater than in children in control groups [Smith et al. 1993]. Furthermore, children receiving chemotherapy for hematological cancers demonstrated a median increase of 66 nevi per child three years after chemotherapy [Baird et al. 1992]. These data indicate that UV-B increases may be very important to medically immunosuppressed patients, even if the immune-suppressing effects of ultraviolet radiation in the normal healthy population are clinically insignificant.

A different line of investigation suggests that UV irradiation can stimulate synthesis of the interleukins IL-1, IL-6, and IL-8 (factors important in stimulating cell growth and proliferation) and that IL-1 and IL-8 can stimulate growth of subcutaneously injected melanoma B-16 cells in mice [McKenzie et al. 1994]. Furthermore, whole-body UV radiation also appears to stimulate increased IL-1 activity in humans [Granstein and Sauder 1987]. However, it is not clear that this has an effect on the ability in humans to resist tumour growth . Further research is required on basic mechanisms in humans in order to understand which UV effects are of concern in basic disease susceptibility. Currently, the clinical importance of this knowledge is not known.

5.2.5 Infectious Diseases

Adverse effects of UV on the course of a number of infectious diseases have been reported since the turn of the century, when Finsen [1901] showed that smallpox lesions were made larger by sun exposure. More recently, it was demonstrated that lesions from Herpes Simplex Virus I and II are reactivated by UV exposure [Spruance 1985]. There is also speculation that excessive UV exposure may have an adverse effect on patients who are HIV-positive, as UV activates HIV *in vitro* [Zmudzka and Beer 1990]. However, no alteration in CD4+ cell count levels was seen after treatment of HIV patients with 60% of their minimal erythemal dose of UV for dermatologic disease [Warfel et al. 1993].

Global climate change also appears to be affecting the distribution of infectious diseases, especially those normally confined to tropical areas [Patz et al. 1996]. It is possible that an increase in ground-level UV-B might act synergistically with climate change on the frequency and severity of infectious disease [Patz et al. 1996].

5.2.6 Eye Damage

The deleterious effects of sunlight on the eye have been recorded since antiquity. It has become apparent in recent years, however, that the effects of UV radiation are more insidious and detrimental to the eye and vision than had been suspected previously. The effects may be acute (usually after a latent period), long-term after acute exposure, or chronic following long-term exposure to levels of UV below those required for an acute response [Cullen and Perera 1994].

Research on animals and fish has shown that premature aging of the lens, or cataract, has long been associated with UV radiation [Doughty and Cullen 1990; Cullen and Monteith-McMaster 1993]. A study by Cullen and Perera [1994] suggests that adverse effects such as chemosis, damaged epithelial cells, and development of inflammatory cells would result to the conjunctiva of the eye within minutes of direct exposure to sunlight at ambient levels of solar UV-B. Bergmanson et al. [1996], in their review of the clinical implications of exposure to solar UV, summarize several signs and symptoms associated with UV-induced keratoconjunctivitis. Because of the amount of new information available supporting the notion that UV radiation can harm the skin and the eye, these researchers suggest that practitioners should not hesitate to prescribe UV filters for sun glasses.

5.3 TERRESTRIAL ECOSYSTEMS

The biological diversity of Canada, coupled with the latitude dependence of ozone layer thinning, creates a scenario for possible nutrient-driven and predator-driven disruptions to the stability of existing ecosystems. Such perturbations to population dynamics would be interwoven among terrestrial, aquatic, and wetland ecosystems.

Very little research exists on the effects of UV-B on terrestrial ecosystems within Canada. None exists for UV-B effects on flora and fauna, except for certain commercial agricultural and forest species, and these investigations have been skeletal and often conjectural. However, even this minimal research provides some insight into the potential implications of continuing increases in UV-B.

5.3.1 Agriculture

Approximately 7% of Canada's land area of 997 million hectares is arable. The agrifood sector produces 10% of Canada's gross domestic product and employs 15% of the country's 30 million people. The agro-ecosystem is unique in that most of it has been created and controlled by humans. The opportunities for mitigating the impacts of increased UV-B may be easier in such a system because it is likely to have fewer environmental variables to consider than natural systems and can be modified on an annual basis. Breeding crop varieties with increased resistance to UV-B, for instance, could be an effective mitigation strategy for agricultural systems.

In plants, UV-B radiation damages the membrane surrounding the cell, and the DNA within the cell nucleus. Other primary targets are the membrane-bound chloroplasts, which use sunlight to convert carbon dioxide and water into sugar. With damaged chloroplasts, the plant's capacity to produce energy is reduced and plant yields eventually decline. Plants do have the ability to repair damage caused by UV-B radiation; however, when the disruption exceeds the plant's ability to repair itself, permanent damage occurs.

UV-B radiation can affect a number of important plant processes and characteristics in the following ways.

- *Photosynthesis:* the ability of chloroplasts to produce sugars may be disrupted, resulting in reduced leaf productivity.
- *Growth:* leaf area, plant height, and fruit size can be altered.
- *Reproduction:* exposed pollen and eggs can be damaged, leading to reduced fertility and seed production.
- *Ecology:* differential tolerances may favour the growth of one plant type over others, an important consideration in weed-crop situations and in pasture mixtures.
- *Quality:* surface blemishes on vegetables or fruits reduce the quality of the produce. The production of pigments in response to UV-B may affect the taste of the crop. A reduction in crop quality may be far more damaging, in terms of dollars, than a reduction in yield.

5.3.1.1 Forage

Papadopoulos et al. [1996] tested the UV-B tolerance of different varieties of forage crops (alfalfa, red clover, birdsfoot, trefoil, white clover, timothy, orchard grass, bromegrass, and meadow fescue) and vegetables (carrots and broccoli). Tests were done under field conditions using filters to screen out ambient levels of UV-B. The removal of UV-B radiation from timothy grass resulted in increased rates of leaf elongation during the second regrowth and a greater number of tillers per plant [Belanger et al. 1996]. However, the vegetative yield of legume species from the spring growing period was lower in the first year of growth when ambient UV-B radiation was filtered out. UV-B radiation had an effect on the yield of grass species in only one of the two years.

A related study, this time under greenhouse conditions, assessed the effect of increased UV-B radiation on eight varieties from two forage legume and two forage grass species [Bush et al. 1995a]. Illumination was provided by grow lights, augmented by UV lamps which provided three UV-B levels: mid-summer ambient, 2x ambient, and 3x ambient. No significant differences in plant growth among the three UV-B levels were observed.

In yet another study, four broccoli varieties were grown under filter frames. Levels of UV-B–absorbing pigments were greater in plants grown under ambient sunlight than in those grown under the filters [Goodyear et al. 1996]. The response to UV-B radiation differed somewhat with the variety.

5.3.1.2 Soybean

In 1994, eight Ontario soybean (*Glycine max* [L] Merr.) varieties were grown in the field under lamps providing a UV-B radiation dose equivalent to a 25% decrease in the ozone layer (Table 5.1). As a control, a similar group of plants was grown under lamps with the UV-B radiation removed by filters. Six of the eight cultivars had their yield reduced as a result of increased UV-B radiation. The average yield loss from the simulated 25% decrease in the ozone layer was 7%. In 1995, with the soybean crop worth over $700 million at the farm gate (information from Ontario Ministry of Agriculture Food and Rural Affairs), a 7% yield loss would equate to $49 million in lost revenue.

Table 5.1: Effect of UV-B Radiation on the Seed Yield (kg ha^{-1}) of Eight Varieties of Soybean

Soybean variety	Yield of enhanced UV-B group	Yield of control group	Percentage difference from control
Mandarin	2570	2880	11
Crest	2520	2890	13
Maple Arrow	3103	2960	–5
9061	2710	3090	12
SOO-88	3070	3620	15
PS42	3320	2770	–20
AC Bravor	3050	3670	17
9071	3020	3290	8
Average	2920	3150	7

The function of the flavonol glycosides in plant cells is unclear, although they have been implicated in growth regulation, disease resistance, and protection of the leaf mesophyll from UV radiation. The plant's capacity to produce UV-absorbing pigments is likely the first line of resistance to the damaging effects of UV radiation. These pigments, located in the hairs of soybean plants, give the plants a grey or tawny appearance, depending on the type of flavonol glycosides present. When soybean plant hair is grey, kaempferol flavonol glycosides are present in the leaves. However, when soybeans appear tawny in colour, the plants contain both quercetin and kaempferol flavonol glycosides.

In experiments done in 1995, Agriculture Canada researchers exposed soybean plants, with either grey or tawny pubescence, to UV-B radiation in controlled environmental cabinets. Leaves from the exposed plants and a control group of non-exposed plants were sampled at regular intervals. When UV-B–absorbing pigments were extracted from the leaves and measured using a spectrophotometer, concentrations of these pigments were found to be greater in the exposure cabinet than in the control cabinet. The pigment concentrations also increased for three days following UV-B exposure, then levelled off.

In addition, leaf cross-sections were scanned for UV-B–absorbing pigments using a microspectrophotometer, an instrument combining a spectrophotometer and a microscope [Pietrzak et al. 1995]. Most of the protective pigmentation was located in the palisade layer of the leaf tissue, with relatively less pigmentation in the epidermis and mesophyll regions. Concentrations of UV-B–absorbing pigments were also greater in the upper surface of the leaf than in the lower surface, which may explain why sunburn symptoms are usually more severe on the lower surface of soybean leaves.

5.3.1.3 Tomatoes

In experiments at the University of Guelph, 37 varieties of processing tomato (*Lycopersicon esculentum* Mill.) were screened for tolerance to UV-B in controlled environmental chambers. The plants were subjected to ambient UV-B, as well as UV-B levels equivalent to a 20% reduction in the ozone layer. Reductions in plant height as a result of enhanced UV-B exposure varied from 10% to 32%, while plant leaf area was reduced by 10–28%. The response to UV-B was also characterized by genetic variability within species (S. Keelan, University of Guelph, personal communication, 1995).

5.3.1.4 Maize

Maize (*Zea mays* L.) hybrids exhibited no deleterious effects on dry matter production, even when grown in controlled environmental cabinets under UV-B radiation simulating a 40% decrease in the ozone layer. Therefore, there is sufficient genotypic tolerance in Canadian maize hybrids to minimize the effects of predicted increases in UV-B [Van Doren 1995].

5.3.1.5 Canola

Researchers at the University of Guelph have screened canola (*Brassica napus* and *B. rapa* L.) varieties for tolerance to UV-B radiation in controlled environmental chambers. The plants were grown under ambient UV-B levels and levels equivalent to those arising from a 20% decrease in the ozone layer. *B. rapa* varieties were more susceptible to UV-B radiation than the *B. napus* varieties. Varietal differences for the growth parameter measured indicate that UV-B tolerance is a characteristic that can be bred into new varieties (D.J. Home, University of Guelph, personal communication, 1996).

In a related field study, researchers at the University of Guelph grew the same varieties of canola and exposed them to UV-B radiation equivalent to a reduction in the ozone layer of about 25%. The plants were exposed to UV-B from the onset of flowering to maturity. Table 5.2 shows that within both *Brassica napus* and *B. rapa* types of canola tolerance to UV-B radiation is variable. The average yield reduction from UV-B radiation was 14%. In 1996, the Canadian canola crop was worth $2.2 billion at the farm gate (data supplied by the Canola Council of Canada); thus, a 14% yield loss would equate to $308 million in lost revenue.

Table 5.2: Seed Yield (kg ha^{-1}) of Spring Canola Varieties Exposed to 10-14 kJ m^{-2} d^{-1} UV-B, Corresponding to a Decrease in the Ozone Layer of 25%.

Cultivar	Enhanced UV-B	Control	Yield reduction from control (%)
B. napus			
Bounty	1765	2440	27.7
Cyclone	2255	3052	26.1
Garrison	6630	5546	–19.6
Hyola 401	6221	5978	–4.1
Shiralee	2141	3809	43.8
Average	**3802**	**4165**	**14.8**
B. rapa			
AC Parkland	3521	6450	45.4
Horizon	5591	7688	27.3
Tobin	4257	3283	–29.7
Average	**4457**	**5807**	**14.3**

Canola adjusts to UV-B stress by synthesizing UV-screening epidermal flavonoid pigments. The increased flavonoid levels protect photosynthesis from UV change. Other research at the University of Waterloo has shown that an essential enzyme of respiration (ribulose-bisphosphate carboxylase) is photomodified to a form with a higher molecular weight by UV-B. This photomodification process is being examined *in vitro* to probe the mechanism of UV-B damage to proteins [Wilson and Greenberg 1993a, 1993b].

5.3.1.6 Wheat Straw

The straw and chaff left behind by a combine are incorporated into the soil through light tillage or, in the case of minimal tillage, left on the soil surface to decompose. The rate at which this material decomposes is increased by exposure to higher levels of UV-B [Ellert et al. 1995]. As well as providing raw material for soil humus, plant litter is an energy source for soil organisms and a nutrient source for plants.

Two recent experiments have examined the effect of UV-B on the decomposition of plant litter. In one of these, wheat straw was exposed to UV-B radiation under laboratory conditions, and the soluble carbon was measured. In the other, UV-B filters were placed over wheat straw exposed to ambient solar radiation. Solubilized carbon was extracted and measured. In both experiments, the soluble carbon concentration of the straw was enhanced by exposure to UV-B radiation, and the amount solubilized was positively related to the intensity of the UV-B. UV-B may accelerate the rate of decomposition by causing an increase in the rate of release of carbon from plant litter. This effect is of significance in arid environments or in minimum-till situations [Ellert et al. 1995].

5.3.1.7 UV-B Effects on Yield

Many factors determine yield. If a plant cannot compensate for the physical damage caused by UV-B, its yield will decrease. Krupa and Kickert [1989] examined studies of the effects of UV-B on over 100 varieties of 12 important crop species and rated crop sensitivity to UV-B on the basis of changes in biomass production. Of the varieties examined, 40% were unaffected by UV-B radiation equivalent to a 20% decrease in the ozone layer, while 60% were affected in some way. In Canada, most crops are tolerant of or have intermediate sensitivity to moderate increases in UV-B radiation (Table 5.3).

Table 5.3: UV-B Sensitivity Rating, Based on the Work of Krupa and Kickert [1989]

UV-B Sensitivity Rating		
TOLERANT	**INTERMEDIATE**	**SUSCEPTIBLE**
wheat	barley	oat
sunflower	rye	pepper
corn	soybean	cucumber
tobacco	pea	mustard
red clover	tomato	canola
alfalfa	potato	
bluegrass		
orchard grass		
cabbage		

The following approach has been used to create a simple model for predicting the effect of increased UV-B radiation on future crop yield.

- The Krupa and Kickert [1989] UV-B sensitivity rating was used to classify the major Canadian crops into tolerant, intermediate, and susceptible categories. Tolerant crops were excluded from further calculation.
- Three levels of UV-B radiation increase above the ambient level were established: 5%, 10%, and 20%.
- Three levels of yield reduction, corresponding to the three UV-B scenarios were then established. Intermediate tolerant crops had yields reduced by 1%, 2.5%, and 5% with a 5%, 10% and 20% increase in UV-B respectively. Susceptible crops had yields reduced by 2%, 5%, and 10% respectively with similar increases in UV-B.
- A farm gate dollar value, based on the 1995 yield estimates, was established for intermediate and susceptible crops.
- Other associated stresses, such as drought, or potential mitigating factors, such as increased atmospheric CO$_2$, were not considered.

A 5% increase in UV-B radiation would result in losses to sensitive and intermediate crops of $89 million per year (Table 5.4). With a 20% increase in UV-B, farm gate receipts would be reduced by $387 million per year. It is, however, very difficult to substantiate the conclusion that yield reductions are the result of one specific stress such as UV-B. Nevertheless, given current information on the response of plants to UV-B, it is reasonable to assume that increased UV-B will result in some crop loss.

5.3.1.8 Research needs

UV-B impacts in several areas remain unexplored or underexplored. These include:

- the soil ecosystem, including its fauna and flora
- animal production and health
- the interaction of UV-B impacts with plant diseases, weeds, and pests
- agrochemical interactions and degradation

Understanding the ramifications of effects in these areas is essential to a full understanding of the implications of UV-B increases for Canadian agriculture.

5.3.2 Forests

Canadians are custodians of 10% of the world's forest lands. Spread across 417 million hectares and covering 42% of the national landscape [CCFM 1995], Canada's forests are of huge cultural, economic, and social importance. Because of their extent and diversity, they are also of considerable ecological significance, providing habitat for wildlife and playing a major role in the global climate system and related processes such as the carbon cycle.

Table 5.4: Predicted Canadian Crop Loss for a Predicted Increase in UV-B radiation (UV-B Tolerant Crops not Included)

Crop	UV-B sensitivity	Current yield (million $)	Predicted yield (million $) with a UV-B increase		
			5%	10%	20%
canola	susceptible	2100	2048	1995	1890
oat	susceptible	226	220	215	203
soybean	intermediate	700	693	683	665
barley	intermediate	796	788	776	756
tree fruit	intermediate	230	228	224	219
soft fruit	intermediate	204	202	199	194
potato	intermediate	506	501	493	481
vegetable	intermediate	652	645	636	619
TOTAL		5414	5325	5221	5027
DIFFERENCE (TOTAL $ LOSS)			89	192	387

Forests are dynamic and continuously subjected to a changing complex of natural and anthropogenic stresses. In 1994, approximately 750,000 ha of forest in Canada were lost to fire, 11.6 million ha were defoliated by insects, and 988,960 ha were harvested [CCFM 1995]. In addition, it is estimated that 35 million ha of forest are exposed to acidic deposition and tropospheric ozone on a routine basis. The impacts of these pollutants, however, are regional in scale. On a national scale, Canada's forests are threatened by two important components of global environmental change, climate change and increases in UV-B radiation.

Unlike agricultural crops, forests are long-lived and will be exposed to increased UV-B over many years and decades. While some short-term effects have been reported, there is evidence that effects induced at the tree level are cumulative over many years [Sullivan and Teramura 1992]. Generally, not much is known concerning UV-B effects on forests, a surprising situation when one considers that forests comprise nearly 80% of total terrestrial biomass [Whittaker 1975].

The overwhelming majority of the literature on UV-B effects on plants deals with crop species and cultivars. Relatively little is known about impacts on forest tree species, and much of the limited knowledge that is available is derived from UV-B simulation experiments using species not native to Canada. A report by Loucks [1994], which linked elevated UV-B levels in 1993 to "sun-scalding" of white pine foliage in Ohio and Ontario, is the only study so far to have documented UV-B effects in the field.

5.3.2.1 Effects of UV-B on Photosynthesis in Trees

The literature on forest trees indicates that photosystem (PS) II is more affected by UV-B than PS I [Bornman and Teramura 1993]. Because of differences in experimental protocols, stage of plant and leaf development, genotypic variability, and other factors, the direction and magnitude of these effects in plants have not been consistent throughout the various studies.

Two recent, non-Canadian studies serve to illustrate the kind of research now under way into the effects of UV-B on photosynthesis. In the first of these, Naidu et al. [1993] investigated cumulative damage potential by exposing three-year-old loblolly pine (*Pinus taeda* L.) seedlings in the field to ambient (8.5 kJ m^{-2} at summer solstice) or enhanced (13.5 kJ m^{-2}) levels of biologically effective UV-B (UV-B_{BE}). The most recently expanded needles showed a 6% decrease in the ratio of variable to maximum fluorescence following dark adaptation, but older needles did not. No effects of enhanced UV-B on other measures of photosynthesis were noted. However, the carbon isotope ratio, which is a common time-integrated measure of photosynthesis, was more negative in two of the four needle age classes of treated seedlings, and needle length in three age classes was reduced. Because of differences in the photosynthesis measures and in the foliar chemical composition of the youngest and oldest needle age classes, the authors speculated that the differences observed between needles exposed to enhanced UV-B and those exposed to ambient levels could also reflect adaptation to shaded conditions within the canopy.

In the second study, the influence of UV-B on photosynthesis in seedlings of Norway spruce (*Picea abies* (L.) Karst.) was investigated over a two-year period by Bavcon et al. [1996]. Enhanced UV-B irradiances were extremely high (17.7 or 28 kJ m^{-2} over 8 hours) compared to maxima that might be expected from ozone depletion.The experiments also included temperature as a co-factor, since treatment was continued year-round. Synergistic effects between low temperature and enhanced UV-B were observed in the second winter. Chlorophyll concentrations were lower in one- and two-year-old needles exposed to higher UV-B levels. As temperature decreased, photochemical efficiency, vitality index, and photosynthetic activity diminished in treated plants and led to premature needle senescence.

5.3.2.2 Effects of UV-B on Tree Growth and Biomass

Sullivan and Teramura [1988] examined the effect of UV-B on seedling growth in the Pinaceae. Seedlings were grown for 22 weeks under daily doses of 0, 12.4, or 19.1 kJ m^{-2} of biologically effective UV-B. Seedling height was reduced by enhanced UV-B in lodgepole pine (*Pinus contorta* Dougl.), red pine (*Pinus resinosa* Ait.), and loblolly pine. Biomass, however, increased in Engelmann spruce (*Picea engelmannii* Parry). Fraser fir (*Abies fraseri* (Pursh) Poir), pinyon pine (*Pinus edulis* Engelm.) and black pine (*Pinus nigra* Arnold) were unaffected. Biomass reductions occurred in all other species. Effects of UV-B were less for species native to higher elevations, implying natural adaptation to higher UV-B levels at high altitude. Visual symptoms were observed, including stunting and needle discolouration, but only in three of the ten species studied.

Using older seedling material (one-year-old) and longer exposure times (seven months), the same authors [Sullivan and Teramura 1989] simulated loblolly pine exposure to 16%, 25%, and 40% ozone depletions (11.5, 13.6, and 19.1 kJ m^{-2} UV-B_{BE}). They found that enhanced UV-B affected growth and suggested that the effects might be cumulative throughout the growing season.

To test the cumulative effects hypothesis, Sullivan and Teramura [1992] conducted a three-year field experiment with natural and supplemented UV-B irradiances and seed sources from seven latitudes in the U.S. (31°N to 39°N). After three seasons of exposure, cumulative biomass reductions were noted in three of the four sources, with the reductions split equally between root and shoot portions. Therefore, reductions in biomass were attributed to an overall decrease in biomass accumulation rather than a shift in carbon partitioning. The authors inferred that continued ozone depletion would affect the commercial productivity of the leading commercial species in the southeast. The inconsistencies in response between the one-year and three-year exposures highlight the need for multiyear experiments with long-lived, forest tree species.

It is well known from studies with trees [Caldwell et al. 1982] and with species from alpine areas in Europe [Rau and Hofman 1996] that plants adapted to grow at higher elevations are more resistant to UV-B than their counterparts from lower elevations. A similar relationship was seen in a study involving 38 plant species growing in natural systems along elevational gradients in Hawaii [Sullivan et al. 1992; Ziska et al. 1992]. Recent evidence also confirms that the UV-B tolerance of Canadian tree species shows a similar correlation with elevation (S. L'Hirondelle, B.C. Ministry of Forests, personal communication). Thus, not only latitude but elevation of seed source may need to be considered in any future adaptation strategy for intensively managed forest lands.

5.3.2.3 Interaction of Enhanced UV-B with Increased Atmospheric CO_2 Concentrations

Global environmental change, including increasing anthropogenic production of carbon dioxide and depletion of the stratospheric ozone layer, is altering the growth environment for forests. Some recent studies, therefore, have investigated the effects of interactions between enhanced UV-B and increased, usually doubled, CO_2 concentrations.

Stewart and Hoddinott [1993], for example, grew jack pine (*Pinus banksiana* Lamb.) seedlings for nine months in greenhouses with CO_2 concentrations of either 350 or 750 μmol mol^{-1} and low or high UV-B irradiances. High UV-B treatment decreased seedling dry weight, although dry weight was unaffected by CO_2. Carbon allocation to leaf production was favoured under high UV-B levels. High UV-B inhibited photosynthesis at 350 μmol mol^{-1} CO_2, but not at 750 μmol mol^{-1}. Interestingly, stomatal density was increased by high UV-B irradiance, but not by CO_2 enhancement.

In another study, Yakimchuck and Hoddinott [1994] examined the interactive effects of UV-B and CO_2 enrichment on the growth and physiology of seedlings of three species, jack pine, black spruce (*Picea mariana* (Mill.) B.S.P.), and white spruce (*Picea glauca* (Moench) Voss) that were grown from seed for 16 weeks. Biomass production in all species increased at high CO_2 concentrations (750 μmol mol^{-1}) but decreased at high UV-B irradiances.

A greater production of UV-B–absorbing pigments was measured in jack pine, a shade-intolerant species, than in the shade-tolerant spruces. The authors concluded that future conifer seedling growth and competitive ability will be altered by changes in ambient levels of UV-B and CO_2.

Sullivan and Teramura [1994] continued their studies with loblolly pine by investigating the effects of enhanced UV-B (13.8 kJ m^{-2} UV-B) in combination with increased CO_2 (650 μmol mol^{-1}). The higher UV-B irradiance reduced seedling biomass by 12% after 22 weeks treatment at both CO_2 levels (350 and 650 μmol mol^{-1}). However, dry matter partitioning was altered by the interaction between UV-B and CO_2, with dry matter being allocated more to shoot components by UV-B radiation when the CO_2 concentration was 350 μmol mol^{-1} and to roots when the concentration was 650 μmol mol^{-1}. The authors indicated that these subtle interactions could be important in the future to seedling establishment and competitive interactions.

These few studies indicate that UV-B impacts on forests should not be considered in isolation. Rather, the dominant components of global environmental change – UV-B and CO_2 – should be considered together as interactive stresses when considering the likely impacts of either on forests.

5.3.2.4 New Canadian Research

Currently, at least three centres are actively involved in research into UV-B effects on forest trees in Canada. Their programs are in various stages of development and are focused on different aspects of the problem.

Natural Resources Canada, Canadian Forest Service

The Fredericton-based Atlantic Forestry Centre of the Canadian Forest Service (CFS) has been conducting in-house and collaborative research into UV-B effects since 1993. In initial collaborative studies with colleagues in the UK, "model" crop species were used to provide a rapid means of determining the direction and magnitude of UV-B effects on cuticles. This information was then used to optimize experimental design for longer-term work with tree species. Responses of single crop species, transgenic mutants, and six varieties of pea (*Pisum sativum* L.) indicated that moderately enhanced UV-B had the potential to cause deleterious and specific alteration of both the surface properties of leaves and the chemical composition of the epicuticular wax [Barnes et al. 1994; Barnes et al. 1996; Gonzalez et al. 1996].

Since then, research supported by the CFS and the Natural Sciences and Engineering Research Council (NSERC) has been conducted into UV-B effects on the surface physico-chemical characteristics, surface properties, ultrastructure, and physiology of leaves. In one of these studies, two-year-old seedlings of four spruce species – white spruce, red spruce

(*Picea rubens* Sarg.), black spruce, and Norway spruce – were exposed to a gradient of biologically effective UV-B (0.81–6.61 kJ m^{-2} d^{-1}) over a period of 11 weeks from bud-break to bud-set. The chemical composition of the epicuticular wax was affected in all species as the dosage increased [Gordon et al. 1995]. Effects were often induced early in the 35-day experimental period. In particular, nonacosane diol and alkyl ester proportions increased in Norway spruce needles, while fatty acids increased on black spruce needles, and estolide proportions increased in red spruce needle wax [Gordon et al. 1997a]. Norway spruce was the only species, however, to show a reduction in internode extension due to UV-B. It should be noted that the highest UV-B enhancement in this study (6.6 kJ UV-B_{BE} m^{-2} d^{-1}) was low relative to other dosages at which significant effects on conifer species have been reported.

Preliminary indications of a direct effect of UV-B at the enzyme level in wax biosynthesis were confirmed in a native deciduous species, the sugar maple (*Acer saccharum* Marsh.). *De novo* wax synthesis was studied using radiotracer techniques and leaf discs irradiated by biologically effective UV-B during [1–^{14}C] acetate uptake. Maximum incorporation of [1–^{14}C] into epicuticular waxes occurred at 6.2 kJ m^{-2} d^{-1} and decreased significantly at greater UV-B doses [Gordon et al. 1997b]. Incorporation of [1–^{14}C] into alkyl esters decreased, while incorporation into alkanes increased with increasing UV-B dose. These initial results are being followed up using radio- and heavy-isotope labelling techniques to determine the effect of UV-B on enzyme activity at a critical stage in conifer wax biosynthesis.

In the first stage of a three-phase parallel study now in progress, the New Brunswick Department of Natural Resources and Energy and the British Columbia Ministry of Forests, in partnership with CFS, are investigating the sensitivity to UV-B of 20 Canadian tree species at the juvenile seedling stage. Simultaneously, physiological growth modelling experiments with a sensitive species are underway, using both UV-B and nitrogen as co-factors. The third phase includes genetic engineering research aimed at the production of plants for use as field biomonitors for UV-B effects.

British Columbia Ministry of Forests

Research into UV-B effects has been underway at the B.C. Ministry of Forests' Glyn Road Research Station in Victoria since 1995. Three studies have been completed and one is ongoing. In one of the completed studies, three-month-old Engelmann spruce seedlings from five elevations (850–1700 m) were exposed to 0, 4.75, 9.5, or 14.25 kJ m^{-2} UV-B for six hours daily. Measurements were made of seedling morphology, biomass, chlorophyll fluorescence, membrane leakage, pigment content, and frost hardiness. Strong effects due to elevation were noted. Seedlings from the lowest elevation manifested changes in morphology and physiology at the highest UV-B dose [Binder and L'Hirondelle 1996].

In a second study, L'Hirondelle and Binder [1996] exposed Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) from three elevations to UV-B dosages of 0, 4, 8, and 14 kJ m^{-2} d^{-1}. Sitka spruce seedlings were less sensitive than Douglas-fir seedlings. Within four days of exposure, Douglas-fir seedlings exposed to the highest doses were dead. At lower doses, there were strong UV-B effects on Douglas-fir height, root collar diameter, and dry weight. Dry weights of Douglas-fir seedlings decreased 34–37% as UV-B increased from 0 to 8 kJ m^{-2} d^{-1}, while the dry weight of Sitka spruce seedlings decreased 20% over the same range. There was no overall effect of elevation on response within the range studied.

Other species were investigated in a third study, similar in design to the preceding two. Frost hardiness was demonstrated to decrease with increasing UV-B dose in interior white spruce seedlings, but it increased in interior Douglas-fir seedlings (S. L'Hirondelle, B.C. Ministry of Forests, personal communication). A fourth study is underway using western red cedar (*Thuja plicata* Donn.).

Centre for Forest Biology, University of Victoria

Research work, under the leadership of Dr. D.P. Ormrod, is focused on molecular genetics, tree physiology, and anatomy and morphology. The goal is to ensure that the array of genotypes currently utilized in forest regeneration has the capability to thrive under increasing UV-B irradiation.

Short-term objectives are:

1. to compare Douglas-fir with other conifers and with model plant systems for their defence response to UV-B and other environmental stressors,
2. to define common elements of the responses among species, and
3. to make comparisons among genotypes within each species.

Growth chambers and a field simulation facility are being used. Species exposed include Douglas-fir, ponderosa pine (*Pinus ponderosa* Laws.), western red cedar, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and white spruce. Other stressors to be applied along with UV-B include drought, heat, cold, and high visible irradiance.

5.3.2.5 Research and Monitoring Needs

Estimation of long-term UV-B impacts on the growth of natural ecosystems, unmanaged or managed forests, biodiversity structure, and forest sustainability cannot be accurately predicted with the limited knowledge base now available. With the exception of several reports from multiyear field simulations, experimental scientific research with forest trees has been conducted in the laboratory at the seedling, leaf, and cellular levels. Extrapolation of these data to the field level is not possible at this time [Percy and Hall 1997].

In order to address knowledge gaps, effort should be focused on the following areas:

- screening and identification of sensitive species, genotypes, and growth stages
- identification of biochemical and physiological attributes contributing to sensitivity or resistance
- modelling of effects on seedling growth
- multiyear field simulations of UV-B enhancement
- instrumentation of selected forest health monitoring sites for continuous UV-B measurement
- consideration of UV-B in breeding/reforestation strategies
- investigation of effects on reproduction
- assessment of potential for UV-B to alter biodiversity in forest ecosystems

The 50-year window of significant ozone depletion has sufficient potential to affect Canadian forest productivity on a large scale. Chronic UV-B damage to our long-lived, slow-growing tree species could have far-reaching consequences which are not yet apparent.

5.4 FRESHWATER AND WETLAND ECOSYSTEMS

Freshwater ecosystems within Canada have been examined for effects from UV radiation more extensively than terrestrial, wetland, and marine ecosystems. Chemical and biological effects on shallow water ecosystems, in particular, can be extensive. In combination with other stressors, enhanced UV radiation affects a wide variety of ecosystem functions and processes. Examples are depressed primary productivity, disrupted nutrient cycles, altered community structures, and modified toxic chemical patterns in the food chain. Socioeconomic impacts may also occur. Scientists are far better at describing these effects than they are at quantifying, modelling, or predicting their relative significance. This is in large part a consequence of the non-linear nature of ecosystem responses to UV-B.

5.4.1 Inland Waters

The penetration of UV-B in boreal lakes is known to be a function of the concentration of dissolved organic carbon (DOC) [Scully and Lean 1994]. As levels of DOC decline, UV-B penetration into the water column increases exponentially. Schindler et al. [1996] showed that climate warming, acid deposition, and ultraviolet radiation are intimately linked through interactions with DOC. Data taken from 46 lakes over 20 years in northwestern Ontario showed a sharp decline in DOC in the water. The average DOC level dropped 15–20%, while UV-B penetration into the water increased by between 22% and 60%. The study concluded that both climatic warming and lake acidification had produced significant declines in the DOC content of boreal lakes. In essence, UV-induced chemical and biological reactions have been responsible for changes in the aquatic ecosystems that had previously been attributed solely to acidic intrusions. Similar conclusions come from Yan et al. [1996] in their analysis of DOC decline and overall terrestrial and aquatic impacts on carbon cycle dynamics in Swan Lake, Ontario, and its basin.

Additionally, in a comprehensive empirical modelling analysis of over 2000 lakes covering eastern North America and the western United States, Williamson et al. [1996] determined relationships between DOC content and UV-B depth penetration. Their study suggested that in lakes with a DOC content less than 2 mg L^{-1}, UV-B penetration depth was more sensitive to changes in DOC levels than to changes in stratospheric ozone.

By exposing zooplankton to various levels of solar UV-B radiation, Williamson et al. [1994] showed that UV-B, even at ambient levels, inhibits some species of zooplankton from frequenting their preferred ecotones.

Through experiments in shallow flumes shielded from various wavelengths of sunlight, Bothwell et al. [1994] demonstrated that, although enhanced levels of UV light diminished the primary production of phytoplankton as expected, they reduced the size of the chironomid community that fed on the phytoplankton to an even greater extent. As a result, the accumulated phytoplankton biomass actually increased with exposure to higher UV levels, even though primary production of phytoplankton biomass was reduced. This occurred because a vital link in the food chain had been weakened and less production was being transferred to higher levels. The implications for food chain integrity and the persistence of desirable species and attributes in aquatic ecosystems are disturbing.

Recently, within the western basin of Lake Erie, blooms of the toxic blue-green alga *Microcystis* have appeared. Prior to this algal growth, dramatic colonization by the exotic zebra mussel and concurrent disruptions to algal population dynamics had resulted in increased water clarity. This, in turn, has increased the depth of the UV-B photic zone.

Polycyclic aromatic hydrocarbons (PAHs) are a ubiquitous group of toxic and mutagenic pollutants. Greenberg and colleagues at the University of Waterloo have observed that ambient UV irradiation significantly increases the toxicity of PAHs to *Lemna gibba* (an aquatic higher plant), *Daphnia magna* (an aquatic invertebrate), and aquatic bacteria. Of greater concern is their finding that PAHs are rapidly photooxidized by solar radiation to compounds with dramatically enhanced toxicity. However, since PAH loads in the environment have been calculated solely on the basis of the intact chemicals, the impacts of these substances are likely to have been underestimated [Wilson and Greenberg 1993a; Huang et al. 1995; Ren et al. 1994].

5.4.2 Amphibians

The effects of increased UV-B radiation on amphibians could be widespread. Possible direct effects include mortality, abnormal embryonic and larval development, damage to exposed organs such as the eye and skin, and systemic effects through the suppression of the immune system [van der Leun and de Gruijl 1993]. Indirect effects include changes in the relative abundance of predators, parasites, and competitors as well as toxic effects from chemicals produced or released from sediments as a result of photochemical reactions [Ovaska and Pauli 1997].

Research on UV-B effects on amphibians (frogs, toads, salamanders, etc.) within North America has been minimal. Within Canada, Grant and Licht [1995] carried out laboratory experiments on the eggs and larvae of several frog and toad species common in Ontario to establish lethal and sublethal levels of UV-A and UV-B radiation.The eggs were either exposed directly or allowed to hatch. Following the hatching of the unexposed eggs, the subsequent larval and metamorphosed forms were tested. The study concluded that current ambient levels and fluctuations of UV radiation in Ontario do not appear to adversely affect any of the life stages of the tested native amphibian species. A combination of factors, such as a copious jelly covering the eggs, photorepair mechanisms in the embryos, melanin pigmentation, and physical protection in the environment, is sufficient to protect these amphibians at current levels of exposure.

Several studies of central and northern Ontario lakes, however, suggest a potential for deleterious effects as a result of interactions between UV-B, climate change, and lake acidification [Schindler et al. 1996, Yan et al. 1996]. In one such study Mallory and co-workers described patterns of UV-B irradiance across central Ontario. They then linked these patterns with existing lake chemistries and amphibian habitat preferences to develop a preliminary risk assessment. Their modelling of UV-B patterns since 1979 suggests that exposure of amphibian eggs and embryos to UV-B has increased due to direct increases of irradiance. They concluded that, although there are no studies that provide measurements of actual mortality due to the cumulative impact of acidity, climate change, and UV-B, there is nevertheless a high potential for destructive synergistic impacts on lake food webs, habitat structure and composition, and amphibian reproduction and physiology as a result of these and other anthropogenic stresses (M.L. Mallory, personal communication).

Ovaska and Pauli [1997] have provided a brief synopsis of UV-B and amphibian research over the past two decades which reinforces conclusions about the lack of data in this area. They and other researchers also point to the importance of considering the cumulative impacts of UV-B in association with pressures such as acid rain, global warming, fungal infections, and toxic chemicals [Grant and Licht 1993; Scully and Lean 1994; Blaustein et al. 1994]. To compensate for the paucity of data on the resistance of different species, Ovaska [Ovaska and Pauli 1997] developed UV vulnerability scores for amphibians based on potential exposure at the egg, larval, and adult stages. The resulting scores reveal that many amphibian species in Canada are vulnerable to increased solar UV-B, particularly at the egg and larval stages. Vulnerable species include the western toad (*Bufo boreas*), spotted frog *(Rana pretiosa*), and Canadian toad (*Bufo hemiophrys*). For salamanders, sensitive species include the northwestern salamander (*Ambystoma gracile*), roughskin newt (*Taricha granulosa*), and tiger salamander (*Ambystoma tigrinum*). However, about 50% of the salamander species in Canada are not exposed to solar radiation at early stages of development. Relative scores such as these serve as a key tool for setting reporting, research, and monitoring priorities.

5.4.3 Research Needs

Because of the complex association of UV-B impacts with other environmental factors, research needs are varied. Foremost among these is the requirement for an integrated approach to the study of ecosystem effects which would help to identify opportunities to minimize or adapt to these impacts. This research would concentrate initially on wetlands, since they are the ecosystems that are believed to be most sensitive to changes in UV-B.

Other research needs include

- development and application of action spectra (inhibition coefficients, biological weighting functions, etc.) covering the diverse flora and fauna of Canadian ecozones;
- studies of the impacts of land use activities (e.g., clearcutting) on UV-B effects on freshwater streams;
- determination of UV-induced genetic change in Canadian flora and fauna;
- assessments of the cumulative impacts of various ecological stressors, such as climate change, acid rain, UV-B, and toxic chemicals, and of the links among them.

5.5 MARINE ECOSYSTEMS

Covering 71% of the earth's surface and accounting for some 40% of the world's primary biological productivity, the marine environment is of fundamental importance to the planet's well-being. The growth of marine plants (principally phytoplankton) fuels food webs that support fish, birds, marine mammals, and humans. As well, marine primary production plays a crucial role in global climate change by maintaining, in conjunction with physical processes, a large and variable oceanic sink for atmospheric carbon dioxide [Sarmiento and Bender 1994]. Enhanced UV-B radiation reduces marine primary productivity and might influence food web structure. It is therefore critical to assess these impacts on marine ecosystems and to understand how any large-scale changes might interact with physical and chemical processes in the ocean to influence such things as fish stocks and global climate.

UV-B is harmful to many biological processes [Vincent and Roy 1993] and it penetrates ocean waters to ecologically significant depths [Jerlov 1950; Smith et al. 1992]. UV-B also causes photochemical transformations in surface waters that can increase the availability of organic matter [Kieber et al. 1989]) and essential nutrients [Bushaw et al. 1996]. But although enhanced UV-B influences many crucial ecological processes in the ocean, the net effects are difficult to predict on the ecosystem level. Impacts of UV-B must not only be described but also quantified and evaluated in the context of ecosystem response. This is a very difficult task that is generally addressed through a series of complementary approaches, namely

- demonstration of UV-B effects on specific physiological processes as well as on the growth and survival of organisms;
- quantification of these effects in nature, as a function of UV exposure, through experimentation in the field, extrapolation of laboratory results, or direct detection of UV-B effects in the field;
- prediction of complex ecological responses to enhanced UV-B through quantification of the relative sensitivity of key ecological links or experimental observation of ecosystem responses to altered UV-B;
- synthesis of responses to UV-B in a biogeochemical context as a means of understanding the potential impacts on ecosystems, fisheries, and global climate.

Substantial progress in research related to UV-B and marine ecosystems has been made, but responses of marine ecosystems to ozone depletion cannot yet be predicted with confidence.

5.5.1 Synopsis of Research

Recent research has reinforced the conclusion that changes in UV-B exposure alter the growth, survival, and biogeochemical activities of microbes, plants, and animals in the sea. Damage to DNA is a particularly important effect of UV-B that directly influences survival [Karentz et al. 1991]. However, UV-B has other direct effects: interference with orientation (and hence the vertical movements) of motile phytoplankton [Häder and Worrest 1991], alteration of nitrogen metabolism [Döhler 1992; Göes et al. 1995] and photosynthesis [Cullen and Neale 1994] in phytoplankton, increased mortality of larvae [Vetter 1996], and negative impacts on processes ranging from viral infection to hatching success in fish eggs [Hunter et al. 1979, 1982].

Because different methods have been used to generate and quantify experimental irradiance in key studies, it is difficult to determine which physiological processes are most sensitive to solar UV-B. Comparison of results requires a biological weighting function (BWF, also called an action spectrum) to quantify biologically effective irradiance [Caldwell et al. 1986; Cullen and Neale 1996]. BWFs have been determined for key processes such as damage to DNA as well as inhibition of photosynthesis and motility in phytoplankton. The natural variability of these functions and the determination of BWFs for other processes are topics of active research. For phytoplankton [Karentz et al. 1991a; Pelletier et al. 1996], zooplankton [Williamson et al. 1994], and fish larvae [Vetter 1996], there are strong differences between species in sensitivity to UV-B.

Important responses that tend to counter UV effects have also been discovered. These include the synthesis of UV-screening agents such as mycosporine-like amino acids [Karentz et al. 1991b] and of antioxidants such as carotenoids and specific enzymes (e.g., superoxide dismutase) that protect against forms of active oxygen produced under the influence of UV radiation [Lesser 1996]. Damage to DNA, induced by UV-B, can also undergo repair: photoreactivation [Weinbauer et al. 1996; Wilhelm et al. 1996] and dark excision repair are the two major mechanisms involved [Karentz et al. 1991; Buma et al. 1995; Jeffrey et al. 1996].

Many studies have demonstrated a direct influence of altered UV-B on ecologically important processes in natural waters [Wängberg et al. 1996], and biological effects of UV-B have been detected tens of metres into the water column [Smith et al. 1992]. Perhaps the best quantified biological effect is the inhibition of short-term (hours to a day) photosynthesis of phytoplankton in the Antarctic [Helbling et al. 1994; Neale et al. 1994; Prézelin et al. 1994]. As approaches are being refined and more observations accumulate, estimates of the inhibition of photosynthesis associated with ozone depletion, though variable, are converging. Daily water column productivity is significantly decreased by both UV-A and UV-B under normal ozone, and it might be reduced a few percent further under the Antarctic ozone hole or a similarly severe depletion. Most measurements of UV effects on plankton require containment of samples for an hour to a day or more under conditions simulating fixed depths. In nature, however, planktonic organisms are commonly mixed by winds near the surface, so results for fixed depths may not apply [Cullen and Neale 1994; Helbling et al. 1994]. Despite the uncertainties associated with vertical mixing, there is growing consensus that, even under normal ozone, UV plays a major ecological role in surface waters, affecting the productivity, survival, and distribution of both bacterioplankton and phytoplankton. It follows that enhanced UV-B, due to ozone depletion, will alter ecological processes in the ocean.

5.5.2 Prediction of Ecosystem Response

Responses of ecosystems to increased UV-B would occur over days to years and likely involve adaptive responses, species selection, and changes in food web interactions. For example, work by Bothwell et al. [1994], described earlier in the section on inland waters, showed how enhanced UV-B exposure could result in an increase in plant biomass as a result of changes to the food web. Similar experiments can be conducted to examine the influence of UV-B on coastal or estuarine systems [Ferreyra 1995], but UV-B cannot be altered experimentally in realistic open ocean ecosystems. Consequently, researchers studying natural marine ecosystems must rely on information about the relative sensitivities of different components in these systems. Confident prediction is impossible at this time because very little quantitative information exists on the effects of vertical mixing and on the sensitivities to UV of eggs, zooplankton, and larval fish found in surface layers. Further, the net effects on microbial activity cannot be resolved. UV-B induces photochemical processes that might enhance microbial activity, but it also directly harms microbes in surface layers [Herndl et al. 1993].

Some toxic dinoflagellates show UV-photoprotective mechanisms [Carreto et al. 1989] which might give them a competitive edge in an enhanced-UV environment. Such a response to changes in UV-B might lead to a greater dominance of toxic or nuisance algae in coastal or estuarine systems. Increases in UV-B could also favour species of phytoplankton that produce dimethyl sulphide (DMS), a reactive gas implicated in cloud formation and, hence, local climate and heat balance. Indeed, UV-B has direct effects on both the synthesis of DMSP (the precursor of DMS) in estuarine phytoplankton [Sakka et al. 1996] and on photolysis rates of DMS in seawater [Crocker et al. 1995]. The influence of UV-B on species composition, and hence on DMS production and food web interactions, has also been identified in the context of competition between diatoms and the prymnesiophyte *Phaeocystis* in Antarctic waters [Davidson and Marchant 1994; Karentz and Spero 1995].

At present there are no data to disprove the suggestion that enhanced UV-B from ozone depletion can alter the species composition of phytoplankton communities and the structure of the food web. However, no such changes have been documented in the ocean. This is not surprising, given the inherent variability of marine systems and our lack of baseline information.

5.5.3 Synthesis

Despite the large uncertainties about UV-B impacts on primary productivity and food web structure, it is important to evaluate the global implications of changes that might occur. For example, what are the potential consequences of a hypothetical decrease (e.g., 5%) in primary productivity associated with ozone depletion? To answer such a question, one could take an estimate of annual global carbon dioxide fixation by marine phytoplankton and assume that a 5% reduction in this sink would translate directly into an equivalent (or directly proportional) reduction in atmospheric carbon dioxide stored in the ocean. This would be an overestimate, however, because only a fraction of marine primary production influences the balance between atmospheric and oceanic carbon dioxide. This fraction is called new production and consists of the organic matter that can be transported to the deep ocean by the sinking of particles or by water motions [Eppley and Peterson 1979]. But because the export of organic matter from surface layers is largely balanced by upward mixing of carbon dioxide, new production also cannot serve as a straightforward measure of the flux of atmospheric carbon to the ocean [Platt et al. 1992; Cullen and Neale 1994]. Consequently, the potential impact of ozone depletion on atmospheric carbon dioxide, mediated through inhibition of marine primary production, is unknown. However, it is likely to be much smaller than the reduction of carbon fixation *per se* [Peng 1992].

General relationships between primary production and fish production [Nixon 1988] serve to illustrate what the impacts of enhanced UV-B on fisheries might be. However, a more thorough approach is needed to estimate the extent to which the inhibition of near-surface primary production influences the productivity of major fish stocks. Enhanced UV-B inhibits phytoplankton mostly near the surface in the spring and summer, away from coastal waters that have higher levels of UV-absorbing dissolved organic matter, and in higher latitudes. How inhibition of productivity at these times and places affects the flows of energy to higher trophic levels is not known [International Arctic Science Committee 1995]. Thus, we cannot predict if ozone-related reductions in primary productivity, as opposed to a general decrease in primary production, are more or less likely to influence fish stocks.

5.5.4 Future Directions for Canadian Research

Although much progress has been made, important questions about the effects of ozone depletion on marine systems remain unanswered. Information on the effects of UV on lower trophic levels and photochemical transformations is accumulating rapidly, and an appreciation of natural variability in these processes is developing. Instruments for measuring UV in the marine environment are commercially available, experimental procedures for quantitative assessment of UV effects have been established, and techniques for detecting the physiological impacts of UV in nature have been tested.

The time has come to apply these capabilities to a comprehensive, ecosystem-based, quantitative assessment of UV effects. For productive coastal areas and estuaries, impacts of UV-B need to be evaluated in the light of UV-B–induced photochemical reactions with dissolved organic matter [Schindler et al. 1996], substrate availability for bacterioplankton and phytoplankton, and toxicity (UV-produced oxidants and metal complexes).

It is also important to determine the responses of higher trophic levels to UV. Work is progressing, and experiments on zooplankton (*Calanus*) and fish (Atlantic cod) reveal strong negative impacts as a result of near-surface exposures (Kouwenberg, Beland, Browman, and Runge, personal communication).

Predicting ecosystem response to increasing UV is linked inherently to understanding the ability of organisms and ecosystems to adapt to and ameliorate the effects of damaging radiation over short (hours to days) and long (weeks to years) time scales. In a Canadian context, this implies greater research emphasis on key ecological and economic species that may be affected by increases in UV, while recognizing that many of the effects will be global as well as regional. Part of this effort should be directed towards the identification of indicator organisms or bioassays that are sensitive to UV and may herald ecosystemic responses to increases in UV.

Information on responses to UV-B is useful for assessment only if exposures in nature are known. Thus, it is necessary to describe the climatology of UV as well as its penetration in surface waters. Presently, very few measurements of UV in Canadian marine waters exist, but this situation is changing. Interpretations of UV effects in Canadian waters require recognition of the fundamental differences that exist between the Antarctic and waters of the northern hemisphere, including the Arctic [International Arctic Science Committee 1995; Wängberg et al. 1996]. Consequently, basic research on the function of marine ecosystems in Canadian waters is essential, if immediate questions on the potential ecological effects of ozone depletion are to be answered.

5.6 MATERIALS

Degradation of materials exposed to sunlight has received considerable attention in the scientific community, particularly since the advent of synthetic polymers for outdoor use. To date, most of the research has been on these polymers, although much is also known about the nature and extent of solar damage to several other materials. Available data indicate that shorter wavelength radiation, largely within the UV-B spectrum, is mainly responsible for these effects [Andrady et al. 1995; Searle 1994].

Recent scientific reviews of the effects of photodegradation, however, indicate that the body of international knowledge, although extensive, is neither comprehensive nor adequate, even for a particular material [Andrady et al. 1991, 1995]. The mechanisms and kinetics of the degradation processes, for example, are not well understood, particularly at the molecular level. Combining photodegradation in the UV-B range with photoinduced processes at longer wavelengths and with other environmental variables adds further complexity to the issue.

In Canada, direct research into the effects of increased levels of UV-B radiation on materials has been limited, except for materials used in equipment designed for applications in space. However, several researchers are working either in areas that are specifically concerned with UV-B effects on materials or in related areas in which UV-B is a non-measured component or one of a number of specified and monitored environmental variables.

5.6.1 Polymers

Researchers at Lakehead University are studying the photodecomposition of several polymers, including poly(o-acetylstyrene) (POAS), poly(parapropionylstyrene) (PPPS), poly(alpha-methylvinylacetophene) (PMVAP), and poly(vinylacetophene)(PVAP) among others. The more photostable polymers tend to be POAS and PMVAP. These polymers, along with poly(o-butyrylstyrene) (POBS) and poly(o-isobutyrylstyrene) (POIS), have potential for solar energy conversion and various other outdoor applications [Weir and Whiting 1990, 1992; Weir et al. 1993, 1996a]. Researchers at the Institute for Environmental Chemistry of the National Research Council in Ottawa have been instrumental in uncovering the mechanisms of the photoinitiated oxidation of polyolefins [Lacoste and Carlsson 1992; Lacoste et al. 1993]. Photodegradation experiments with polyethylene and polypropylene films showed that, although these polymers produce different proportions of products during photooxidation, the overall oxidation occurs early and rapidly at the exposed film surface and advances into the films as exposure levels increase. Analysis of the obverse surface of polypropylene showed that this surface also oxidized rapidly [Lacoste et al. 1995].

5.6.2 Wood and Paper

Pulp production using relatively inexpensive thermomechanical and chemithermomechanical techniques in Canada tripled from 1982 to 1992 [Heitner 1993], primarily for the production of short-life products such as newsprint. One of the limitations to wider use of paper made from these processes is that it turns yellow on exposure to sunlight. This light-induced yellowing is due to photooxidative discolouration of lignin I in the fibre wall [Heitner 1993; Weir et al. 1994]. However, if the light-induced yellowing could be slowed by 3–36 months, the market for chemithermomechanical pulp alone would increase significantly. If the yellowing were stopped altogether, both pulps would be used in the manufacture of high brightness papers, increasing the global market for these pulps by 2.6 million tonnes [Cockram 1989].

Weir and co-workers at Lakehead University extended their earlier photodegradation work with polymers to include biopolymers such as lignin. They exposed several lignin polymers to UV light of wavelengths 300 nm and higher. The polymers underwent yellowing, which was attributed to the formation of quinonoid entities, and subsequent research defined further plausible reaction mechanisms [Weir et al. 1994a, 1994b, 1995, 1996a, 1996b]. Their work demonstrates that lignin-type compounds can undergo colouration reactions that are both totally photoinduced and independent of oxidation [Weir et al. 1996b], implying that discolouration of lignin-based pulps cannot be totally inhibited by conventional antioxidants [Weir et al. 1995].

Researchers from Paprican in Pointe Claire, Quebec, have focused on the functional groups in lignin that play a role in light-induced yellowing [Schmidt and Heitner 1991] and on lignin compounds [Schmidt et al. 1991, 1993]. Results of their experiments, in which reduced and methylated bleached thermomechanical pulp was exposed to UV radiation for two hours, show that discolouration reflects the presence of functional groups in lignin that produce coloured chromophores that are dissociated from aromatic carbonyl and phenolic hydroxyl groups [Schmidt and Heitner 1992]. Through this research, reaction pathways causing the yellowing of bleached mechanical and high-yield pulps have been identified.

Researchers at the Pulp and Paper Research Centre at McGill University in Montreal are now working with Paprican scientists and members of the Mechanical and Chemimechanical Woodpulps group of the Canadian Network of Centres of Excellence to improve the light-aging qualities of pulp and paper products. One particular study is looking into the rebound in brightness of paper that has been exposed to accelerated UV irradiation and then removed to a UV-free location [Ek et al. 1993].

Wan and co-workers at Queen's University first discovered the phototriplet mechanism in chemically induced dynamic electron polarization (CIDEP) systems in 1972. Since that time they have continued their research on the phenomenon and developed a popular technique for use in photophysical and photochemical studies. More recently, their research has examined the nature of free radical–induced photooxidation of phenols and benzenes, since both phenolic groups and methoxy-substituted phenoxy radicals play a key role in the light-induced yellowing of thermomechanical pulp. Several experiments have outlined the roles of peroxy and alkoxy radicals in initiating photooxidation processes [Wan et al. 1993].

5.6.3 Building Materials

Canadian research on the effects of UV-B radiation on building materials other than plastics is limited. In one of the studies currently under way, researchers at the National Research Council in Ottawa have been investigating the degradation of various building materials, such as roofing membranes and outdoor sealants, as a result of exposure to ultraviolet radiation. They are not, however, examining the potential effects of an increase in ambient levels of UV-B radiation (M. Lacasse and R. Peroli, NRC Building Materials Laboratory, personal communication). In another study, Feldman and co-workers at Concordia University are using both accelerated and ambient weathering tests to improve the mechanical characteristics and durability of various building materials. These tests, which were carried out both with and without UV radiation and which also included temperature cycling to failure, revealed no durability differences between modified and original epoxies [Feldman and Khoury 1988; Feldman et al. 1998]. Recent studies aimed at decreasing the weather sensitivity of PVC construction materials have attempted to replace titanium dioxide with less expensive kraft lignin, both of which serve to absorb some of the incoming UV radiation [Feldman et al. 1994].

5.6.4 Paints and Coatings

Very little Canadian effort has been directed towards the effects of UV-B radiation on paints and other coatings, although Ortech International does routine testing on behalf of commercial clients to assess conformance to provincial and national standards. Typically, these are weatherability and exposure time tests for such items as automotive coatings, solar collector coatings, and other paints. These tests do not focus on UV-B impacts specifically; however, UV-B is monitored as part of the weathering studies (D. Hacker, Ortech International, personal communication). Other research laboratories across the country, for example, the Composite Materials Centre in St-Jérôme, Quebec, the Alberta Research Council in Edmonton, and the BC Institute of Technology in Vancouver, do similar client-oriented studies. However, details of these studies and their results are not available to the public.

5.6.5 Textiles and Clothing

Researchers at the University of Alberta in Edmonton have been studying the effect of light on silk. Aging studies using a xenon arc weatherometer reveal that the range of light from UV-B through to visible fades dyed silk and turns undyed silk yellow. It also decreases fibre tensile strength and extensibility and increases fabric stiffness [Halvorson and Kerr 1994].

The effectiveness of UV-B protection offered by commercially available clothing is another important area that has received recent attention. Using spectrophotometry, Capjack et al. [1994] and Davis et al. [1997] measured UV transmission through a variety of clothing materials as a function of wavelength over the 250–400 nm range. Protection generally increased with fabric weight, with closer weaves, and with darker colours. Their work demonstrates that careful selection of fabrics is necessary if a sun protection factor (SPF) of at least 15 is to be achieved. For best protection from UV radiation, dark clothing made from polyester or blends of polyester and another fibre are recommended.

5.6.6 Economic Implications

When the UNEP report on Environmental Effects of Ozone Depletion was published in 1994, understanding of the wavelength sensitivities and thus, service lifetimes of key polymeric components used in outdoor applications was incomplete, and data about other materials was even more limited. These deficiencies remain. Since the resistance of current photostabilizers and protective coatings to increased levels of UV-B radiation has still not been adequately tested, the economic implications of any strategy to counteract future potential UV-B damage to exposed materials remain speculative. However, there are economic concerns that deserve comment.

One implication of the limited level of Canadian research into the effects of UV-B radiation on materials is that Canadians will receive little direct scientific recognition and economic advantage from developments arising in this area. It is therefore legitimate to ask: Is the cost of doing nothing to offset enhanced levels of UV-B radiation higher than the cost of developing more resistant materials, paints, and coatings? However, a further question also arises, because if the Montreal Protocol is fully implemented, UV-B levels could begin to stabilize and decrease by early next century and possibly return to 1990 levels as early as the year 2020. If that were to happen, would the damage to materials inflicted by two decades of increased spring and summer exposure to UV-B radiation warrant the increased efforts and costs of developing and marketing new products that would be redundant within 30 years?

It is not obvious, however, that product research and development for these new materials would be any more expensive than current efforts to make existing polymers and other materials more photoresistant to present UV-B levels. Indeed, some product formulation costs may go down as less expensive substitutes are found. The protection of existing materials and the development of new photoresistant materials and stabilizers can, in fact, be seen as an opportunity for new business and employment generation.

If levels of UV-B radiation increase, the degradation of existing materials will be accelerated and the potential for damage hazards resulting from product failure will increase. It is impossible to make an assessment of the costs of these potential hazards with current available information, but such an assessment would need to involve safety considerations, replacement costs, and potential liability costs.

5.6.7 Data Gaps

There are several areas in which further information is needed by the international scientific community. Major priorities include:

- improved understanding of the way in which materials respond to different wavelength regions of both natural and artificial ultraviolet light sources and to simulated UV-B–enriched sunlight;
- improved and more widely distributed measurements of ambient UV radiation in the wavelength bands most responsible for the deterioration of synthetic and natural materials;
- more complete and up-to-date databases on the UV spectral response characteristics of all exposed materials, as determined by activation spectra;
- consistent quantitative relationships between field and laboratory exposure results for polymeric materials;
- more data on UV-B transmission through window glass in typical user applications.

Thus, in materials science, as in most other areas of research, much still has to be done before many of the details of UV effects can be adequately understood.

REFERENCES

Andrady, A.L., M.B. Amin, S.H. Hamid, X. Hu, K. Fueki, and A. Torikai, 1991. Materials damage. Pages 45–50 in *Environmental Effects of Ozone Depletion: 1991 Update.* Nairobi: United Nations Environment Programme.

Andrady, A.L., M.B. Amin, S.H. Hamid, X. Hu, and A. Torikai, 1995. Effects of increased solar ultraviolet radiation on materials. *Ambio*, **24**(3), 191–196.

Autier, P., J.F. Dore, F. Lejeune, K.F. Koelmel, O. Geffeler, P. Hille, J.P. Cesarini, et al., 1994. Recreational exposure to sunlight and lack of information as risk factors for cutaneous malignant melanoma. *Mel. Res.*, **4,** 79–85.

Baird, E.A., P.M. McHenry, and R.M. MacKie, 1992. Effect of maintenance chemotherapy in childhood on numbers of melanocytic nevi. *Br. Med. J.*, **305,** 799–801.

Barnes, P.W., S.D. Flint, and M.M. Caldwell, 1990. Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. *Am. J. Bot.*, **77,** 1354–1360.

Barnes, J. D., N.D. Paul, K.E. Percy, P. Broadbent, C.K. McLaughlin, and A.R. Wellburn, 1994. Effects of UV-B radiation on wax biosynthesis. Pages 196–204 in *Air Pollutants and the Leaf Cuticle* . K.E. Percy, J.N. Cape, R. Jagels, and C. Simpson, eds. NATO ASI Series G, vol. 36. Heidelberg: Springer-Verlag.

Barnes, J.D., K.E. Percy, N.D. Paul, P. Broadbent, C.K. McLaughlin, P.M. Mullineaux, G. Creissen, and A.R. Wellburn, 1996. The influence of UV-B radiation on the physico-chemical nature of tobacco (*Nicotinia tabacum L.*) leaf surfaces. *J. Exp. Bot.*, **47,** 99–109.

Bavcon, J., A. Gaberscik, and F. Batic, 1996. Influence of UV-B radiation on photosynthetic activity and chlorophyll fluorescence kinetics in Norway spruce (*Picea abies (L.) Karst*.) seedlings. *Trees,* **10**, 172–176.

Beitner, H., S.E. Norell, U. Ringborg, G. Wennerstin, and B. Matson, 1990. Malignant melanoma: aetiological importance of individual pigmentation and sun exposure. *Br. J. Dermatol*., **122**, 43–51.

Belanger, G., Y.A. Papadopoulos, R. Gordon, N. Goodyear, K.B. McRae, R.S. Bush, E.A. Butler, and S.A.E. Fillmore, 1996. Effects of UV-B radiation on grass morphogenesis. Abstract. *Can. J. Plant Sci*., **76**, 359.

Bergmanson, J., T. Sheldon, and A.P. Cullen, 1996. A sting in the rays. *Optician,* **212**(5560), 17–22.

Berinstain, A.B., M.K. Whittlesey, and J.C. Scaiano, 1993. Laser techniques in the study of the photochemistry of carbonyl compounds containing ligninlike moieties. Pages 111–121 in *Photochemistry of Lignocellulosic Materials*. Amer. Chem. Soc. Symposium Series 531. C. Heitner and J.C. Scaiano, eds. Washington D.C.: American Chemical Society.

Berwick, M., C. Begg, J. Fine, G. Roush, and R. Barnhill, 1996. Screening for cutaneous melanoma by skin self-examination. *J. Natl. Cancer Inst*., **88**, 17–23.

Binder, W.D., and S.J. L'Hirondelle, 1996. Ultraviolet-B radiation effects on some British Columbia conifers: (1) Engelmann spruce from five elevations. Paper presented at The International IUFRO Meeting For Population, Ecological and Conservation Genetics, University of British Columbia, Vancouver, August 5-9, 1996.

Blaustein, A.R., P.D. Hoffman, D.G. Hokit, J.M. Kiesbecker, S.C. Walls, and J.B. Hays, 1994. UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proc. Nat. Acad. Sci,*. **91**, 1791–1795.

Bornman, J.F., and A.H. Teramura, 1993. Effects of ultraviolet-B radiation on terrestrial plants. Pages 427–471 in *Environmental UV Photobiology*. A.R. Young et al., eds. New York: Plenum Press.

Bornman, J.F., and T.C. Vogelmann, 1988. Penetration of blue and UV radiation measured by fiber optics in spruce and fir needles. *Physiol. Plant*., **72**, 699–705.

Bothwell, M.L., D.M.J. Sherbot, and C.M. Pollock, 1994. Ecosytem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science,* **265**, 97–100.

Bouwes-Bavinck, J., D. Hardie, A. Green, S. Cutmore, A. MacNaught, B. O'Sullivan, V. Siskind, F. van der Wonde, and I.R. Hardie, 1996. The risk of skin cancer in renal transplant recipients in Queensland, Australia: a follow-up study. *Transplantation,* **61**, 715–721.

Buma, A.G.J., E.J. Van Hannen, L. Roza, M.J.W. Veldhuis, and W.W.C. Gieskes, 1995. Monitoring ultraviolet-B-induced DNA damage in individual diatom cells by immunofluorescent thymine dimer detection. *J. Phycol*., **31**, 314–321.

Bush, R.S., Y.A. Papadopoulos, E.A. Gallant, N. Goodyear, R. Gordon, K.B. McRae, and R. Martin, 1995a. Preliminary evidence of intolerance to UV light by alfalfa cultivars. Paper presented at the annual meeting of the Atlantic Advisory Committee on Forage Crops, October 27–28, Halifax, N.S.

Bush, R.S., Y.A. Papadopoulos, R. Gordon, G. Belanger, N. Goodyear, K.B. McRae, E.A. Butler, and S.A.E. Fillmore. 1995b. Evidence of tolerance to UV-B radiation among currently cultivated alfalfa varieties. Pages 37–38 in *Proceedings of the 11th Eastern Forage Improvement Conference*, Ottawa, Ontario.

Bushaw, K.L., R.G. Zepp, M.A. Tarr, D. Schulz-Janders, R.A. Bourbonniere, R.E. Hodson, W.L. Miller, D.A. Bronk, and M.A. Moran. 1996. Photochemical release of biologically available nitrogen from aquatic dissolved organic matter. *Nature,* **381**, 404–407

Caldwell, M.M., R. Robberecht, R.S. Nowak, and W.D. Billings, 1982. Differential photosynthetic inhibition by ultraviolet radiation in species from the arctic-alpine life zone. *Arctic and Alpine Res*., **14**, 195–202.

Caldwell, M.M., L.B. Camp, C.W. Warner, and S.D. Flint, 1986. Action spectra and their key role in assessing biological consequences of solar UV-B radiation change. Pages 87–111 in *Stratospheric Ozone Reduction, Solar Ultraviolet Radiation, and Plant Life*. R.C. Worrest and M.M. Caldwell, eds. Berlin: Springer-Verlag.

Caldwell, M.M., A.H. Teramura, and M. Tevini, 1989. The changing solar ultraviolet climate and the ecological consequences for higher plants. *Trends in Ecol. and Evol*., **4**, 363–367.

Capjack, L., N. Kerr, S. Davis, R. Fedosejevs, K.L. Hatch, and N.L. Markee, 1994. Protection of humans from ultraviolet radiation through the use of textiles: a review. *Family and Consumer Sciences Res. J*., **23**(2), 198–218.

Carreto, J.I., S.G. DeMarco, and V.A. Lutz, 1989. UV-absorbing pigments in the dinoflagellates *Alexandrium excavatum* and *Prorocentrum micans*. Effects of light intensity. Pages 333–336 in *Red Tides: Biology, Environmental Science, and Toxicology*. T. Okaichi, T.M. Anderson, and T. Nemoto, eds. Elsevier.

CCFM (Canadian Council of Forest Ministers), 1995. *Compendium of Canadian Forestry Statistics*. Ottawa: Canadian Council of Forest Ministers.

Clark, J.B., and G.R. Lister, 1975. Photosynthetic action spectra of trees. II: The relatiobship of cuticle structure to the visible and ultraviolet spectral properties of needles from coniferous species. *Plant Physiol*., **55**, 407–413.

Cockram, R.A. 1989. CTMP in fine papers. *Proceedings of the International Mechanical Pulping Conference*. Helsinki: Finnish Pulp and Paper Research Institute.

Crocker, K.M., M.E. Ondrusek, R.L. Petty, and R.C. Smith, 1995. Dimethylsulfide, algal pigments, and light in an Antarctic *Phaeocystis* sp. *Mar. Biol*., **124**, 335–340.

Cullen, A.P., and S. Monteith-McMaster, 1993. Damage to the rainbow trout (*Oncorhyncus mykiss*) lens following acute dose of UVB. *Curr. Eye Res*., **12**, 97–106.

Cullen, A.P., and S.C. Perera, 1994. Sunlight and human conjunctival action spectrum. Ultraviolet radiation hazards. *SPIE Proceedings,* **2134**, 24–30.

Cullen, J.J., and P.J. Neale, 1994. Ultraviolet radiation, ozone depletion, and marine photosynthesis. *Photosyn. Res*., **39**, 303–320.

Cullen, J.J., and P.J. Neale, 1996. Biological weighting functions for describing the effects of ultraviolet radiation on aquatic systems. In *Effects of Ozone Depletion on Aquatic Ecosystems.* D-P. Häder, ed. R.G. Landes.

Davidson, A.T., and H.J. Marchant, 1994. The impact of ultraviolet radiation on *Phaeocystis* and selected species of Antarctic marine diatoms. Pages 187–205 in *Ultraviolet Radiation in Antarctica: measurements and biological effects*. C.S. Weiler and P.A. Penhale, eds. Washington, D.C.: American Geophysical Union.

Davis, S., L. Capjack, N. Kerr, and R. Fedosejevs, 1997. Clothing as protection from ultraviolet radiation: which fabric is most effective? *International J. Dermatology,* in press.

Day, T.A., T.C. Vogelmann, and E.H. DeLucia, 1992. Are some plant life forms more effective than others in screening out ultraviolet-B radiation? *Oecologia,* **92**, 513–519.

Day, T.A., G. Martin, and T.C. Vogelmann, 1993. Penetration of UV-B radiation in foliage: evidence that the epidermis behaves as a non-uniform filter. *Plant Cell Environ*., **16**, 735–741.

Day, T.A., B.W. Howells, and W.J. Rice, 1994. Ultraviolet absorption and epidermal-transmittance spectra in foliage. *Physiol. Plant*., **92**, 207–218.

DeLucia, E.H., T.A. Day, and T.C. Vogelmann, 1992. Ultraviolet-B and visible light penetration into needles of two species of subalpine conifers during foliar development. *Plant Cell Environ*., **15**, 921–929.

DeLucia, E.H., S.L. Naidu, and J. Chen, 1994. Effects of simulated stratospheric ozonr depletion on seedling growth of several species of hardwood trees. *Erigenia,* **13**, 132–140.

Dillenberg, L.R., J.H. Sullivan, and A.H. Teramura, 1995. Leaf expansion and development of photosynthetic capacity and pigments in *Liquidambar styraciflua (Hamamelidaceae)* – Effects of UV-B radiation. *Am. J. Bot*., **82**, 878–885.

Döhler, G., 1992. Impact of UV-B radiation on uptake of 15N-nitrate by phytoplankton of the Wadden Sea. *Mar. Biol*., **112**, 485–489.

Doughty, M.J., and A.P. Cullen, 1990. Long-term effects of a single dose of ultraviolet-B on albino rabbit cornea – II. Deturgescence and fluid pump assessed *in vitro*. *Photochem. and Photobiol*., **51**, 439–449.

Dunning, C.A., L. Chalker-Scott, and J.D. Scott, 1994. Exposure to ultraviolet-B radiation increases cold hardiness in Rhododendron. *Physiol. Plant*., **92**, 516–520.

Ek, M., H. Lennholm, G. Linblad, T. Iverson, and D.G. Gray, 1993. Photochromic behaviour of UV-irradiated mechanical pulps. Pages 147–155 in *Photochemistry of Lignocellulosic Materials*. Amer. Chem. Soc. Symp. Series 531. C. Heitner and J.C. Scaiano, eds. Washington, D.C.: Amer. Chem. Soc.

Ellert, B.H., H.H. Janzen, and E.G. Gregorich, 1995. Environmental driving variables and plant litter decomposition in Canada. Page 74 in *Driven by Nature: Plant Litter Quality and Decomposition*. Proceedings of an international conference held at Wye College, U. of London, England. September 17–20, 1995.

Elwood J.M., and R.P. Gallagher, 1983. Site distribution of malignant melanoma. *Can. Med. Assoc. J*., **128**, 1400–1404.

Elwood J.M., and T.G. Hislop, 1982. Solar radiation in the etiology of cutaneous malignant melanoma in Caucasians. *Natl. Cancer Inst. Monograph,* **62**, 167–171.

Elwood J.M., R.P. Gallagher, G.B. Hill, and J. Pearson, 1985a. Cutaneous melanoma in relation to intermittent and constant sun exposure: the Western Canada Melanoma Study. *Int. J. Cancer* **35**, 427–433.

Elwood, J.M., R.P. Gallagher, J. Davison, and G.B. Hill, 1985b. Sunburn, suntan, and risk of cutaneous malignant melanoma: the Western Canada Melanoma Study. *Br. J. Cancer,* **51**, 543–549.

Eppley, R.W., and B.J. Peterson, 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature,* **282**, 677–680.

Falkowski, P.G., 1994. The role of phytoplankton photosynthesis in global biogeochemical cycles. *Photosyn. Res*., **39**, 235–258.

Feldman, D., and M. Khoury, 1988. Epoxy-lignin polyblends. Part II: Adhesive behaviour and weathering. *J. Adhesion Sci. Technology,* **2**(2), 107–116.

Feldman, D., M. Lacasse, and D. Banu, 1988. Contribution to the modification of an acrylic sealant with lignin. *J. Polymeric Materials,* **5**, 131–139.

Feldman, D., D. Banu, and S. El-Raghi, 1994. Poly(vinyl chloride)-lignin blends for outdoor application in building. *J. Macromolecular Sci. Part A: Pure and Applied Chem.,* **A31**(5), 555–571.

Fernbach, E., and H. Mohr, 1990. Coaction of blue/ultraviolet-A light and light absorbed by phytochrome in controlling growth of pine (*Pinus sylvestris*). *Planta,* **180**, 212–216.

Fernbach, E., and H. Mohr, 1992. Photoreactivation of the UV light effects on growth of Scots pine (*Pinus sylvestris* L.) seedlings. *Trees,* **6**, 232–235.

Ferreyra, G. A., 1995. Effets du rayonnement ultraviolet sur le plancton des régions froides tempérées et polaires. Dept. of Oceanography, Laval University.

Finsen, N.R., 1901. The treatment of *lupus vulgaris* by concentrated chemical rays. Pages 73–75 in *Phototherapy*. London: Edward Arnold.

Gallagher, R.P., J.M. Elwood, and G.B. Hill, 1986. Risk factors for cutaneous malignant melanoma: the Western Canada Melanoma Study. *Rec. Results Cancer Res.*, **102**, 38–55.

Gallagher, R.P., J.M. Elwood, W.J. Threlfall, J.J. Spinelli, S. Fincham, and G.B. Hill, 1987. Socioeconomic status, sunlight exposure, and risk of malignant melanoma: the Western Canada Melanoma Study. *J. Nat. Cancer Inst.*, **79**, 647–652.

Gallagher, R.P., D.I. McLean, C.P. Yang, A.J. Coldman, H.K.B. Silver, J.J. Spinelli, and M. Beagrie, 1990a. Anatomic distribution of acquired melanocytic nevi in white children. *Arch. Dermatol.*, **126**, 466–471.

Gallagher, R.P., D.I. McLean, C.P. Yang, A.J. Coldman, H.K.B. Silver, J.J. Spinelli, and M. Beagrie, 1990b. Suntan, sunburn, and pigmentation factors and the frequency of acquired melanocytic nevi in children. *Arch. Dermatol.*, **126**, 770–776.

Gallagher, R.P., G.B. Hill, C.D. Bajdik, S. Fincham, A.J. Coldman, and D.I. McLean, 1995a. Sunlight exposure, pigmentation factors, and risk of non-melanocytic skin cancer: I – basal cell carcinoma. *Arch. Dermatol.*, **131**, 157–163

Gallagher, R.P., G.B. Hill, C.D. Bajdik, S. Fincham, A.J. Coldman, and D.I. McLean, 1995b. Sunlight exposure, pigmentation factors, and risk of non-melanocytic skin cancer: II – squamous cell carcinoma. *Arch. Dermatol.*, **131**, 164–169.

Garbe, C., S. Kruger, R. Stadler, I. Guggenmoss-Holzmann, and C.E. Orfanos, 1989. Markers and relative risk in a German population for developing malignant melanoma. *Int. J. Dermatol.*, **28**, 517–523.

Garssen, J., W. Goettsch, F. de Gruize, W. Slob, and H. Van Loveren, 1996. Risk assessment of UVB effects on resistance to infectious diseases. *Photochem. Photobiol.*, **64**, 269–294.

Göes, J. I., N. Handa, S. Taguchi, T. Hama, and H. Saito, 1995. Impact of UV radiation on the production patterns and composition of dissolved free and combined amino acids in marine phytoplankton. *J. Plankton Res.*, **17**, 1337–1362.

Gonzalez, R., N.D. Paul, K. Percy, M. Ambrose, C.K. McLaughlin, J.D. Barnes, M. Areses, and A.R. Wellburn, 1996. Responses to ultraviolet-B radiation (280–315 nm) of pea (*Pisum sativum*) lines differing in leaf surface wax. *Physiol. Plant.*, **98**, 852–860.

Goodyear, N., R.R. Bush, R. Gordon, Y.A. Papadopoulos, G. Belanger, K.B. McRae, E.A. Butler, and S.A.E. Fillmore, 1996. Growth and physiological responses of four broccoli cultivars to ambient and reduced levels of UV-B radiation during two seasons. *Abstract. Can. J. Plant Sci.*, **76**, 358.

Gordon, D.C., K.E. Percy, and R.T. Riding, 1995. Effect of UV-B radiation on cuticular characteristics in four spruce species. Abstract. In *Solar Ultraviolet Radiation: Modeling and Measurement*. Proceedings of a NATO Advanced Study Institute workshop, Halkidiki, Greece, October 2–11, 1995.

Gordon, D.C., K.E. Percy, and R.T. Riding, 1997a. Effect of enhanced UV-B radiation on four *Picea* species. *New Phytol.*, forthcoming.

Gordon, D.C., K.E. Percy, and R.T. Riding, 1997b. Effect of enhanced UV-B radiation on adaxial leaf surface micromorphology and epicuticular wax biosynthesis of sugar maple. *Chemosphere,* in press.

Granstein, R.D., and D.N. Sauder, 1987. Whole body exposure to ultraviolet radiation results in increased serum interleuken-1 activity in humans. *Lymphokine Res.*, **6**, 187–193.

Grant, K.P., and L.E. Licht, 1993. Acid tolerance of anuran embryos and larvae from central Ontario. *J. Herpetol.*, **27**, 1–6.

Grant, K. P., and L.E. Licht, 1995. Effects of ultraviolet radiation on life-history stages of anurans from Ontario, Canada. *Can. J. Zool.*, **73**, 2292–2301.

Green, A., V. Siskind, C. Bain, and J. Alexander, 1985. Sunburn and malignant melanoma. *Br. J. Cancer,* **51**, 393–397.

Green, A., C. Bain, R. MacLennan, and V. Siskind, 1986. Risk factors for cutaneous melanoma in Queensland. *Rec. Results Cancer Res.*, **102**, 76–97.

Grob, J.J., J. Gouvernet, D. Aymer, A. Mostaque, M.H. Romano, A.M. Collet, M.C. Noe, M.P. Dicostanzo, and J.J. Bonerandi, 1990. Count of benign melanocytic nevi as a major indicator of risk for non-familial nodular and superficial spreading melanoma. *Cancer,* **66**, 387–395.

Häder, D-P. and R.C. Worrest, 1991. Effects of enhanced solar ultraviolet radiation on aquatic ecosystems. *Photochem. Photobiol.*, **53**, 717–725.

Halvorson, B.G., and N. Kerr, 1994. Effect of light on the properties of silk fabrics coated with Parlene-C. *Studies in Conservation*, **39**, 45–56.

Harrison, S.L., R. McLennan, R. Speare, and I. Wrongski, 1994. Sun exposure and melanocytic nevi in young Australian children. *Lancet*, **344**, 1529–1532.

Heitner, C., 1993. Light-induced yellowing of wood-containing papers. Pages 2–25 in *Photochemistry of Lignocellulosic Materials*, Amer. Chem. Soc. Symposium Series 531. C. Heitner and J.C. Scaiano, eds. Washington, D.C.: American Chemical Society.

Helbling, E. W., V. Villafañe, and O. Holm-Hansen, 1994. Effects of ultraviolet radiation on Antarctic marine phytoplankton photosynthesis with particular attention to the influence of mixing. Pages 207–227 in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*. C.S. Weiler and P.A. Penhale, eds. Washington, D.C.: American Geophysical Union.

Herndl, G. J., G. Müller-Niklas, and J. Frick, 1993. Major role of ultraviolet-B in controlling bacterioplankton growth in the surface layer of the ocean. *Nature,* **361**, 717–719.

Hoddinott, J, 1994. Impacts of UV-B and CO_2 on boreal forest seedlings. Pages 23–27 in *International conference on ozone depletion and ultraviolet radiation: preparing for the impacts*, April 27–29, 1994, Victoria, B.C. Proceedings. K. Heidorn and B. Torrie, eds. Victoria: The Skies Above Foundation.

Holly, E.A., J.W. Kelly, S.N. Shpall, and S-H Chiu, 1987. Number of melanocytic nevi as a major risk factor for malignant melanoma. *J. Amer. Acad. Dermatol.*, **17**, 459–468.

Holly, E.A., D.A. Aston, R.D. Cress, D. Ahn, and J. Kristiansen, 1995. Cutaneous melanoma in women. I: Exposure to sunlight, ability to tan and other risk factors related to ultraviolet light. *Amer. J. Epidemiol.*, **141**, 923–933.

Holman, C.D.J., B.K. Armstrong, and P.J. Heenan, 1983. A theory of the etiology and pathogenesis of human cutaneous malignant melanoma. *J. Natl. Cancer Inst.*, **71**, 651–656.

Holman, C.D.J., B.K. Armstrong, and P.J. Heenan, 1986. Relationship of cutaneous malignant melanoma to individual sunlight exposure habits. *J. Natl. Cancer Inst.*, **76**, 403–414.

Huang, X-D., D.G. Dixon, and B.M. Greenberg, 1995. Toxicity of polycyclic aromatic hydrocarbons to the duckweed *Lemna gibba* L. G-3 in natural sunlight. *Ecotoxicol. Environ. Safety,* **32**, 194–200.

Hunter, J. R., J.H. Taylor, and H.G. Moser, 1979. Effect of ultraviolet radiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, during the embryonic stage. *Photochem. Photobiol.*, **29**, 325–338.

Hunter, J. R., S.E. Kaupp, and J.H. Taylor, 1982. Assessment of effects of UV radiation on marine fish larvae. Pages 459-497 in *The Role of Solar Ultraviolet Radiation in Marine Ecosystems*. J. Calkins, ed. London: Plenum.

International Arctic Science Committee. 1995. *Effects of Increased Ultraviolet Radiation in the Arctic*. IASC Secretariat.

Jeffrey, W. H., R.J. Pledger, P. Aas, S. Hager, R.B. Coffin, R. Von Haven, and D.L. Mitchell, 1996. Diel and depth profiles of DNA photodamage in bacterioplankton exposed to ambient solar ultraviolet radiation. *Mar. Ecol. Prog. Ser.*, **137**, 293–304.

Jenkins, G.I., J.M. Christie, G. Fuglevand, J.C. Long, and J. Jackson, 1995. Plant responses to UV and blue light: biochemical and genetic approaches. *Plant Sci.*, **112**, 117–138.

Jerlov, N.G., 1950. Ultraviolet radiation in the sea. *Nature* **166**, 111–112.

Jungblut, T.P., J-P. Schnitzler, W. Heller, N. Hertkorn, J.W. Metzger, W. Szymczak, and H. Sandermann, Jr., 1995. Structures of UV-B induced sunscreen pigments of the Scots Pine (*Pinus sylvestris* L.). *Angew. Chem.*, Int. Ed. Engl., **34**, 312–314.

Karentz, D., and H.J. Spero, 1995. Response of natural *Phaeocystis* population to ambient fluctuations of UVB radiation cased by Antarctic ozone depletion. *J. Plankton Res.*, **17**, 1771–1789.

Karentz, D., J.E. Cleaver, and D.L. Mitchell, 1991a. Cell survival characteristics and molecular responses of Antarctic phytoplankton to ultraviolet-B radiation. *J. Phycol.*, **27**, 326–341.

Karentz, D., F.S. McKuen, M.C. Land, and W.C. Dunlap, 1991b. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Mar. Biol.*, **108**, 157–166.

Kelly, J.W., J.K. Rivers, R. MacLennan, S. Harrison, A.E. Lewis, and B.J. Tate, 1994. Sunlight: a major risk factor associated with development of melanocytic nevi in Australian school children. *J. Amer. Acad. Dermatol.*, **30**, 40–48.

Kerr, J.B. and C.T. McElroy, 1993. Evidence for large upward trends of ultraviolet radiation linked to ozone depletion. *Science,* **262**, 1032–1034.

Khlat, M., A. Vail, M. Parkin, and A. Green, 1992. Mortality from melanoma in migrants to Australia: variation by age at arrival and duration of stay. *Amer. J. Epidemiol.*, **135**, 1103–1113.

Kieber, D.J., J. McDaniel, and K. Mopper, 1989. Photochemical source of biological substrates in sea water: implications for carbon cycling. *Nature,* **341**, 637–639.

Kossuth, S.V., and R.H. Biggs, 1981. Ultraviolet-B radiation effects on early seedling growth of Pinaceae species. *Can. J. For. Res.*, **11**, 243–248.

Kricker, A., B.K. Armstrong, D.R. English, and P.J. Heenan, 1995. Does intermittent sun exposure cause basal cell carcinoma? A case-control study in Western Australia. *Int. J. Cancer* **60**, 589–494.

Krupa, S.V., and R.N. Kickert, 1989. The greenhouse effects: impact of UV-B, CO_2, and O_3 on vegetation. *Env. Pollut.*, **61**, 263–393.

Lacoste, J., and D.J. Carlsson, 1992. Gamma-, photo- and thermally-initiated oxidation of linear low density polyethylene: a quantitative comparison of oxidation products. *J. Polymer Sci. Part A: Polymer Chem.*, **30**, 493–500.

Lacoste, J., D. Vaillant, and D.J. Carlsson, 1993. Gamma-, photo-, and thermally-initiated oxidation of isotactic polypropylene. *J. Polymer Sci. Part A: Polymer Chem.*, **31**, 715–722.

Lacoste, J., Y. Deslandes, P. Black, and D.J. Carlsson, 1995. Surface and bulk analyses of the oxidation of polyolefins. *Polymer Degradation and Stability* **49**, 21–28.

Lesser, M. P., 1996. Acclimation of phytoplankton to UV-B radiation: oxidative stress and photoinhibition of photosynthesis are not prevented by UV-absorbing compounds in the dinoflagellate *Prorocentrum micans*. *Mar. Ecol. Prog. Ser.*, **132**, 287–297.

L'Hirondelle, S.J. and W.D. Binder, 1996. Ultraviolet-B radiation effects on some British Columbia conifers. 2: Sitka spruce and coastal Douglas-fir from three elevations. Paper presented at the International IUFRO Meeting for Population, Ecological, and Conservation Genetics, University of British Columbia, Vancouver, August 5–9, 1996.

Loucks, O.L., 1994. Sun-scald on 1993 foliage of white pine (*Pinus strobus*) linked to UV-B radiation in Ohio and Ontario. Pages 39–47 in *International conference on ozone depletion and ultraviolet radiation: preparing for the impacts*, April 27–29, 1994, Victoria, B.C. Proceedings. K. Heidorn and B. Torrie, eds. Victoria: The Skies Above Foundation.

MacKie, R.M., T. Freudenberger, and T.C. Aitcheson. 1989. Personal risk factor chart for cutaneous melanoma. *Lancet II,* 487–490.

Madronich, S., R.L. McKenzie, M.M. Caldwell, and L.O. Bjorn, 1995. Changes in ultraviolet radiation reaching the earth's surface. *Ambio,* **24**, 143–164.

Marrett, L.D., W.D. King, S.D. Walter, and L. From, 1992. Use of host factors to identify people at high risk for cutaneous malignant melanoma. *Can. Med. Assoc. J.*, **147**, 445–453.

McKenzie, R.C., E.S. Park, E.S. Brown, W.R. Brown, G.S. Shivji, and D.N. Sauder, 1994. Effect of ultraviolet inducible cytokines on melanoma growth *in vivo*: stimulation of melanoma growth by interleukin 1 and 6. *Photoderm., Photoimmunol. Photomed.*, **10**, 74–79.

McLean, D.I., R.P. Gallagher, A.J. Coldman, and V.C. Ho., 1995. The Vancouver Mole Study: nevi in children. *Ann. RCPSC,* **28**, 297–300.

Miyagi, T., A. Bhutto, and S. Nonaka, 1994. The effects of sunscreens on UVB erythema and Langerhans cell depression. *J. Invest. Dermatol.*, **21**, 645–651.

Naidu, S.L., J.H. Sullivan, A.H. Teramura, and E.H. DeLucia, 1993. The effects of ultraviolet-B radiation on photosynthesis of different aged needles in field-grown loblolly pine. *Tree Physiol.*, **12**, 151–162.

Neale, P. J., M.P. Lesser, and J.J. Cullen, 1994. Effects of ultraviolet radiation on the photosynthesis of phytoplankton in the vicinity of McMurdo Station, Antarctica. Pages 125–142 in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*. C.S. Weiler and P. Penhale, eds. Washington, D.C.: American Geophysical Union.

Nelemans, P., H. Groenendal, L. Kiemoney, F.H.J. Rampen, D.J. Ruiter, and A.L.M. Verbeek, 1993. Effect of intermittent exposure to sunlight on melanoma risk among indoor workers and sun-sensitive individuals. *Environ. Health Persp.*, **101**, 252–255.

Nixon, S.W., 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnol. Oceanogr.*, **33**, 1005–1025.

Østerlind. A., M.A. Tucker, B.J. Stone, and O.M. Jensen, 1988. The Danish case-control study of cutaneous malignant melanoma. Importance of UV light exposure. *Int. J. Cancer,* **42**, 319–324.

Ovaska, K., and B. Pauli, 1997. *Vulnerability of Amphibians in Canada to Climate Warming and Increased UV-B Radiation*. Canadian Wildlife Service Report. Hull: Environment Canada, forthcoming.

Papadopoulos, Y.A., N. Goodyear, R. Belanger, G. McRae, K.B. Bush, R.R. Butler, E.A. Butler, and S.A.E. Fillmore, 1996. Impact of current UV-B radiation on forage grass and legume production in northern latitudes. Abstract. *Can. J. Plant. Sci.*, **76**, 358–359.

Patz, J.A., P.R. Epstein, T.A. Burke, and J.M. Balbus, 1996. Global climate change and emerging infectious diseases. *J. Amer. Med. Assoc.*, **275**, 217–223.

Pelletier, H., W.W.C. Gieskes, and A.G.J. Buma, 1996. Ultraviolet-B radiation resistance of benthic diatoms isolated from tidal flats in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.*, **135**, 163–168.

Peng, T-H., 1992. Possible effects of ozone depletion on the global carbon cycle. *Radiocarbon*, **34**, 772–779.

Percy, K.E., and J.P. Hall, 1997. Enhanced UV-B: A threat to Canada's forests? In *Proceedings of the Ontario Climate Advisory Committee workshop on atmospheric ozone: issues, science, impacts, policy and programs*, September 30–October 1, 1996, Toronto. In press.

Pietrzak, L.N., J. Dorell, M.J. Morrison, and J. Fregeau-Reid, 1995. In situ microspectral characterization of flavonoids in soybean leaves. Abstract. Page 172 in *Proceedings of the 80th annual meeting of Am. Ass. Cereal Chemists*, San Antonio, Texas, November 5–9, 1995.

Platt, T., P. Jauhari, and S. Sathyendranath, 1992. The importance and measurement of new production. Pages 273–284 in *Primary Productivity and Biogeochemical Cycles in the Sea*. P.G. Falkowski and A. Woodhead, eds. London: Plenum.

Prézelin, B.B., N.P. Boucher, and R.C. Smith, 1994. Marine primary production under the influence of the Antarctic ozone hole: Icecolors '90. Pages 159–186 in *Ultraviolet Radiation in Antarctica: Measurements and Biological Effects*. C.S. Weiler and P.A. Penhale, eds. Washington, D.C.: American Geophysical Union.

Rau, W., and H. Hofman, 1996. Sensitivity to UV-B of plants growing in different altitudes in the Alps. *J. Plant Physiol.*, *148*, 21–25.

Ren, L., X-D. Huang, B.J. McConkey, D.G. Dixon, and B.M. Greenberg, 1994. Photoinduced toxicity of three polycyclic aromatic hydrocarbons (fluoranthene, pyrene, and naphthalene) to the duckweed *Lemna gibba* L. G-3. *Ecotoxicol. Environ. Safety*, **28**, 160–171.

Rivers, J.K., P.C. Frederiksen, and C. Dibdin, 1990. A prevalence survey of dermatoses in the Australian neonate. *J. Amer. Acad. Dermatol.*, **23**, 77–81.

Robberecht, R., and M.M. Caldwell, 1978. Leaf epidermal transmittance of ultraviolet radiation and its implications for plant sensitivity to ultraviolet-radiation induced injury. *Oecologia*, **32**, 277–287.

Rosso, S., R. Zanetti, C. Martinez, M. Tormo, S. Schraub, H. Sancho-Garnier, S. Franceschi, L. Gafa, et al., 1996. The multicentre South European Study "Helios" II: different sun exposure patterns in the aetiology of basal cell and squamous cell carcinomas of the skin. *Br. J. Cancer,* **73**, 1447–1454.

Runeckles, V.C., and S. Krupa, 1994. The impact of UV-B radiation and ozone on terrestrial vegetation. *Environ. Pollut.*, **83**, 191–213.

Sakka, A., M. Gosselin, M. Levasseur, S. Michaud, and S. Demers, 1996. Effects of reduced ultraviolet radiation on concentrations of dimethylsulfoniopropionate and dimethylsulfide during a microcosm study in the lower St. Lawrence estuary. *Mar. Ecol. Prog. Ser.*, in press.

Sarmiento, J.L., and M. Bender, 1994. Carbon biogeochemistry and climate change. *Photosyn. Res.*, **39**, 209–234.

Scaiano, J.C., J.C. Netto-Ferreira, and V. Wintgens, 1991. Fragmentation of ketyl radicals derived from alfa-phenoxyacetophenone: an important mode of the decay for lignin-related radicals. *J. Photochem. and Photobiol.*, **59**, 265.

Schindler, D.W., P.J. Curtis, B.R. Parker, and M.P. Stainton, 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature,* **379**, 705–708.

Schmidt, J.A., and C. Heitner, 1991. Light-induced yellowing of mechanical and ultra-high yield pulps: Part 1, effects of methylation, $NaBH_4$ reduction, and ascorbic acid on chromophore formation. *J. Wood Chem. Tech.*, **11**(4), 397.

Schmidt, J.A., and C. Heitner. 1992. Light-induced yellowing of mechanical and ultra-high yield pulps; Part 2, the role of etherified guaiacylglycerol-beta-arylether groups. *Proceedings of the Second European Workshop on Lignicellulosics and Pulp*, Grenoble.

Schmidt, J.A., A.B. Berinstain, F. de Rege, C. Heitner, C. Johnston, and J.C. Scaiano, 1991. Photodegradation of the lignin model alfa-guaiacoxyacetoveratrone: unusual effects of solvent, oxygen, and singlet state participation. *Can. J. Chem.*, **69**, 104.

Schmidt, J.A., E. Goldszmidt, C. Heitner, J.C. Scaiano, A.B. Berinstain, and L.J. Johnston, 1993. Photodegradation of alfa-guaiacoxyacetoveratrone. Pages 122–128 in *Photochemistry of Lignocellulosic Materials*. Amer. Chem. Soc. Symposium Series 531. C. Heitner and J.C. Scaiano eds. Washington, D.C.: American Chemical Society.

Schnitzler, J-P., T.P. Jungblut, W. Heller, C. Langbartels, M. Kofferlein, and H. Sandermann. 1994. Effects of ozone and UV-B radiation on Scots pine. *Acta Hort.*, **381**, 463–469.

Schnitzler, J-P., T.P. Jungblut, W. Heller, M. Kösterlein, P. Hutzler, U. Heinzmann, E. Schmezler, D. Ernst, C. Langbartels, and H. Sandermann, 1996. Tissue localization of UV-B–screening pigments and of chalcone synthase mRNA in needles of Scots pine seedlings. *New Phytol.*, **132**, 247–258.

Scotto, J., T.R. Fears, and J.F. Fraumeni Jr., 1983. *Incidence of Non-melanoma Skin Cancer in the United States*. NIH Publ. No. 82-2433. Washington, D.C.: U.S. Public Health Service, National Institutes of Health.

Scully, N.M., and D.R.S. Lean, 1994. The attenuation of the ultraviolet radiation in temperate lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 135–144.

Searle, N.D., 1994. Effect of light source emission on durability testing. Pages 52–67 in *ASTM STP 1202: Accelerated and Outdoor Durability testing of Organic Materials*. W.D. Ketola and D. Grossman eds. Philadelphia: American Society for Testing Materials.

Smith, C., J.M. McGregor, J.N.W. Barker, R.W. Morris, S.P.A. Rigden, D.M. MacDonald, 1993. Excess melanocytic nevi in children with renal allografts. *J. Amer. Acad. Dermatol.*, **28**, 51–55.

Smith, R.C., B.B. Prézelin, K.S. Baker, R.R. Bidigare, N.P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H.A. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K.J. Waters, 1992. Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science,* **255**, 952–959.

Spruance, S.L., 1985. Pathogenesis of herpes simplex labialis: experimental induction of lesions with UV light. *J. Clin. Microbiol.*, **22**, 366–368.

Stewart, J.D., and J. Hoddinott, 1993. Photosynthetic acclimation to elevated atmospheric carbon dioxide and UV irradiation in *Pinus banksiana*. *Physiol. Plant.*, **88**, 493–500.

Sullivan, J.H., and A.H. Teramura, 1988. Effects of ultraviolet-B radiation on seedling growth in the Pinaceae. *Amer. J. Bot.*, **75**, 225–230.

Sullivan, J.H., and A.H. Teramura, 1989. The effects of ultraviolet-B radiation on loblolly pines. 1: Growth, photosynthesis, and pigment production in greenhouse grown saplings. *Physiol. Plant.*, **77**, 202–207.

Sullivan, J.H., and A.H. Teramura, 1992. The effects of ultraviolet-B radiation on loblolly pine. 2: Growth of field seedlings. *Trees,* **6**, 115–120.

Sullivan, J.H., and A.H. Teramura, 1994. The effects of UV-B radiation on loblolly pine. 3: Interaction with CO_2 enrichment. *Plant Cell Environ.*, **17**, 311–317.

Sullivan, J.H., A.H. Teramura, and L.H. Ziska, 1992. Variation in UV-B sensitivity in plants from a 3,000-m elevation gradient in Hawaii. *Am. J. Bot.*, **79**, 737–743.

Sullivan, J.H., B.W. Howells, C.T. Ruhland, and T.A. Day, 1996. Changes in leaf expansion and epidermal screening effectiveness in *Liquidambar stryaciflua* and *Pinus taeda* in response to UV-B. *Physiol. Plant*. **98**, 349–357.

van der Leun, J.C., and F.R. de Gruijl, 1993. Influences of ozone depletion on human and animal health. Pages 95–123 in *UV-B Radiation and Ozone Depletion: Effects on Humans, Animals, Plants, Microorganisms, and Materials*. M. Tevini, ed. Boca Raton: Lewis.

Van Doren, K.S., 1995. Effect of enhanced UV-B radiation on Ontario soybean cultivars and maize hybrids. M.Sc. Thesis, U. of Guelph.

Vetter, R. D., 1996. UV-B irradiance and DNA damage in pelagic fish eggs and larvae: temperate and polar habitats. *Eos,* **76**, OS164.

Vincent, W. F., and S. Roy, 1993. Solar ultraviolet-B radiation and aquatic primary production: damage, protection, and recovery. *Environ. Rev.*, **1**, 1–12.

Wan, J.K.S., I.A. Shkrob, and M.C. Depew, 1993. Primary photophysical and photochemical processes of alpha-guaiacoxyacetoveratrone. Pages 99-110 in *Photochemistry of Lignocellulosic Materials*. Amer. Chem. Soc. Symposium Series 531. C. Heitner and J.C. Scaiano eds. Washington, D.C.: American Chemical Society.

Wängberg, S-A., J-S. Selmer, N.G.A. Eklund, and K. Gustavson, 1996. UV-B effects on Nordic marine ecosystems – a literature review. *TemaNord*, **515**, 1–45.

Warfel, A.H., J.A. Moy, T. Meola, M. Sanchez, N.A. Soter, and D.V. Belsito, 1993. Effect of ultraviolet B (UVB) on the expression of human immunodeficiency virus (HIV) in mice and humans. *Photochem. Photobiol.*, **57**, 755–759.

Weinbauer, M. G., S.W. Wilhelm, and C.A. Suttle, 1996. Significance of photoreactivation for maintaining high concentrations of infectious viruses in the sea. Abstr. Amer. Soc. Microbiol. New Orleans, LA, May 1996.

Weinstock, M.A., G.A. Colditz, W.C. Willett, M.J. Stampfer, B.R. Bronstein, M.C. Mihm, and F.E. Speizer, 1989a. Moles and site specific risk of non-familial cutaneous malignant melanoma in women. *J. Natl. Cancer Inst.*, **81**, 948–952.

Weinstock, M.A., G.A. Colditz, W.C. Willett, M.J. Stampfer, B.R. Bronstein, M.C. Mihm, and F.E. Speizer, 1989b. Non-familial cutaneous melanoma incidence in women associated with sun exposure before 20 years of age. *Pediatrics,* **84**, 199–204.

Weir, N.A., and K. Whiting, 1990. Studies of poly(ortho-acetylstyrene)s II: Photoreactions of poly(o-acetylstrene), *J. Polymer Sci. Part A: Polymer Chem.*, *28*, 1935–1945.

Weir, N.A., and K. Whiting, 1992. Photolysis of poly(o-acetylstyrene) in solution. *J. Polymer Sci. Part A: Polymer Chem.*, **30**, 1601–1608.

Weir, N.A., J. Arct, and A. Ceccarelli, 1993. Photoreactions of poly(o-butyrylstyrene) in the long wave region. *J. Photochem. and Photobiol. Part A: Chem.*, **72**, 87–93.

Weir, N.A., J. Arct, and A. Ceccarelli, 1994a. Photodecomposition of lignin model compounds. Part I. *Polymer Degradation and Stability,* **43**(3), 409-414.

Weir, N.A., J. Arct, A. Ceccarelli, and A. Siren, 1994b. Some photoreactions of substituted poly(acrylophenomes). *European Polymer J.*, **30**(6), 701–706.

Weir, N.A., J. Arct, and A. Ceccarelli, 1995. Chromophore production in lignin model compounds – anaerobic reactions. *Research Chemistry Intermediate,* **21**(3–5), 353–371.

Weir, N.A., J. Arct, A. Ceccarelli, and K. Whiting, 1996a. Polymers with enhanced photostability: photoreactions of poly(o-isobutylstyrene) in the long wave region. *J. Photochem. and Photobiol. Part A: Chem.*, **96**, 203–209.

Weir, N.A., J. Arct, and A. Ceccarelli, 1996b. Long-wave photodegradation of poly(3,5-dimethooxyacrylophenone) in the solid state. *European Polymer J.*, **32**(7), 805–810.

Weir, N.A., J. Arct, A. Ceccarelli, and D. Puumala, 1996c. Long-wave photochemistry of dimethoxylated compounds related to lignin. *Polymer Degradation and Stability,* **52**, 119–129.

Wellburn, A., 1994. Effects of UV-B radiation on wax biosynthesis. Pages 195–204 in *Air Pollutants and the Leaf Cuticle*. NATO ASI Series G, vol. 36. K.E. Percy, J.N. Cape, R. Jagels, and C. Simpson, eds. Heidelberg: Springer-Verlag.

White, E., C.S. Kirkpatrick, and J.A.H. Lee, 1994. Case-control study of malignant melanoma in Washington State. I: Constitutional factors and sun exposure. *Amer. J. Epidemiol.*, 139, 857–868.

Whittaker, R.H., 1975. *Communities and Ecosystems*. 2nd ed. New York: Macmillan.

Wilhelm, S. W., M.G. Weinbauer, D.R. Garza, K.M. Rodda, and C.S. Suttle, 1996. In situ light-mediated destruction and repair of marine virus communities and isolates. *Eos,* **76**, OS208.

Williamson, C.E., P.C. Schulze, B.R. Hargreaves, and J. Seva, 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in northern temperate lakes. *J. Plankton Res.*, **16**, 205–218.

Williamson, C.E., R.S. Stemberger, D.P. Morris, T.M. Frost, and S.G. Paulsen, 1996. Ultraviolet radiation in a North American lake: attenuation estimates from DOC measurements and implications for plankton communities. *Limnol. Oceanogr.*, **41**, 1024.

Wilson, M.I., and B.M. Greenberg, 1993a. Protection of the DI photosystem II reaction center protein from degradation in ultraviolet radiation following adaptation of *Brassica napus* L. to growth in UV-B. *J. Photochem. and Photobiol.*, **57**, 556–563.

Wilson, M.I., and B.M. Greenberg, 1993b. Specificity and photomorphogenic nature of UV-B induced cotyledon curling in *Brassica napus* L. *Plant Physiol.*, **102**, 671.

Wolf, P., C. Donawho, and M. Kripke, 1993. Analysis of the protective effect of different sunscreens on ultraviolet radiation induced local and systemic suppression of contact hypersensitivity and inflammatory responses in mice. *J. Invest. Dermatol.*, **100**, 254–259.

Yakimchuck, R., and J. Hoddinott, 1994. The influence of ultraviolet-B light and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species. *Can. J. For. Res.*, **24**, 1–8.

Yan, N.D., W. Keller, N.M. Scully, D.R.S. Lean, and P.J. Dillon, 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature,* **381**, 141–143.

Zanett, R., S. Rosso, C. Martinez, C. Navarro, S, Schraub, H. Sancho-Garnier, S. Fraceschi, L. Gafa, et al., 1996. The multicentre South European Study “Helios” I: skin characteristics and sunburns in basal cell and squamous cell carcinomas of the skin. *Br. J. Cancer,* **73**, 1440–1446.

Ziska, L.H., A.H. Teramura, and J.H. Sullivan, 1992. Physiological sensitivity of plants along an elevational gradient to UV-B radiation. *Am. J. Bot.*, **79**, 863–871.

Zmudzka, B.Z., and J.Z. Beer, 1990. Activation of human immunodeficiency virus by ultraviolet radiation. *Photochem. Photobiol.*, **52**, 1153–1162.