5-2000

Responses of Sphagnum and Carex Peatlands to Ultraviolet-B Radiation, and a Meta-Analysis of UV-B Effects on Vascular Plants

Peter S. Searles
Utah State University

Recommended Citation

Searles, Peter S., "Responses of Sphagnum and Carex Peatlands to Ultraviolet-B Radiation, and a Meta-Analysis of UV-B Effects on Vascular Plants" (2000). *All Graduate Theses and Dissertations*. 6578.
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RESPONSES OF *SPHAGNUM* AND *CAREX* PEATLANDS TO ULTRAVIOLET-B RADIATION IN SOUTHERN SOUTH AMERICA, AND A META-ANALYSIS OF UV-B EFFECTS ON VASCULAR PLANTS

by

Peter S. Searles

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2000

ABSTRACT

Responses of *Sphagnum* and *Carex* Peatlands to Ultraviolet-B Radiation, and a Meta-Analysis of UV-B Effects on Vascular Plants

by

Peter S. Searles, Doctor of Philosophy

Utah State University, 2000

Major Professor: Dr. Martyn M. Caldwell
Department: Rangeland Resources

The severity of stratospheric ozone depletion in the temperate and polar latitudes has raised concerns about the sensitivity of terrestrial vegetation and ecosystems to solar ultraviolet (UV-B) radiation. This dissertation examined the responses of plants and microbes to solar UV-B for 3 years in Tierra del Fuego, Argentina (55° S). This region is under the influence of the Antarctic "ozone hole" during the austral spring. Additionally, a quantitative review of the UV-B literature was conducted using a set of statistical techniques known as meta-analysis.

For the field studies in Tierra del Fuego, plots were established in a *Sphagnum* moss peatland and a *Carex* sedge fen during the spring of 1996. These plots received either near-ambient solar UV-B (90% of ambient) or reduced UV-B (20% of ambient) using specially designed plastic films. At the end of the first field season, no effects of the solar UV-B treatments were apparent on the growth and pigmentation of the plant species in either community. The height growth of the moss *Sphagnum magellanicum* was less under near-ambient solar UV-B than reduced UV-B during the second and third growing seasons. In contrast, volumetric density of the moss was greater under near-ambient UV-B. The growth of the vascular plants did not respond to the solar UV-B treatments even after 3 years although UV-B-absorbing compounds were greater under near-ambient UV-B in some species. Populations of testate amoebae (i.e., shelled amoebae) inhabiting *S. magellanicum* had greater numbers under near-ambient UV-B than reduced UV-B throughout the 3 years. This response may be an indirect effect of solar UV-B mediated by the direct effect of UV-B on *S. magellanicum* height growth. Fungi on the leaf surfaces of the tree *Nothofagus antarctica* appeared to be directly inhibited by solar UV-B.

The quantitative literature review of plant field studies simulating stratospheric ozone depletion assessed the effects of elevated UV-B on 10 plant response variables from papers published between 1976 and mid-1999. Modest significant inhibitions of leaf area, aboveground biomass, and plant height were apparent due to increased UV-B using meta-analysis. An increase in UV-B-absorbing compounds appears to be the most robust general response to increased UV-B radiation.

(199 pages)

DEDICATION

The following poem is dedicated to the inspiring landscape and natural wonder around the city of Ushuaia in Tierra del Fuego, Argentina:

Una Oda a Ushuaia

Busquenme a la orilla del Beagle
donde el viento arranca mi pelo

Busquenme en la sombra de Olivia
donde el condor vola

Busquenme en el llano atardecido
donde los chulengos esconden en el pasto dorado

Busquenme los domingos en casa
cuando el primer churripan llega!

por Peter S. Searles, 1999

ACKNOWLEDGMENTS

I would like to offer my sincere appreciation to Martyn Caldwell and Steve Flint for their guidance and patience during the course of my study at Utah State University. Carlos Ballaré and Ana Scopel from the University of Buenos Aires provided extensive insights into the development of my dissertation in Tierra del Fuego, Argentina. Susana B. Díaz at the Centro Austral de Investigaciones Cientificas (CADIC) organized the ultraviolet-B radiation data from the U.S. National Science Foundation UV Monitoring Network and coauthored two chapters. Paul Barnes from Southwest Texas State University and Brad Kropp from USU graciously served as short-term collaborators in Tierra del Fuego as part of their sabbaticals. I would like to thank Nico Garibaldi, Nancy Lozano, Paco Escobar, Juan Rosales, Tim Hudelson, Ruben Ibarra, and Luis Pinedo for laboratory and field assistance. Maria Cecilia Rousseaux, Carla Giordano, Veronica Pancotto, Carlos Mazza, Osvaldo Sala, Oscar Bianciotto, Matt Robson, and Hans Zaller provided valuable support of the overall project in Tierra del Fuego. I would also like to thank Charles Ashurst for designing and building the device to create the louver matrix in the plastic film filters; Richard Mueller for extensive use of his compound microscope; and Susan Durham for helpful statistical advice. The research was supported through the NSF/DOE/NASA/USDA/EPA/NOAA Interagency Program on Terrestrial Ecology and Global Change (TECO) by the U.S. National Science Foundation (95-24144 and 98-14357). Partial support was provided by the United States Department of Agriculture (CSRS/NRICGP 95-37100-1612 and 98-35100-6107).

I thank my "original" committee members (Martyn Caldwell, Gene Schupp, Neil West, Keith Mott, and Helga Van Miegroet) for being outstanding educators and helping me through the doctorate program in Ecology at Utah State University. I am also appreciative of Richard Mueller and Brad Kropp for serving on the committee for purposes of the defense examination.

Peter S. Searles

FOREWORD

This project began in January of 1996 (i.e, summer) in the city of Ushuaia in Tierra del Fuego, Argentina, to assess the effects of solar ultraviolet-B radiation on terrestrial ecosystems in the region. Ushuaia is often under the influence of the Antarctic "ozone hole" in October and November (i.e., spring). Martyn Caldwell, Steve Flint, and I scouted potential field sites with Carlos Ballaré and Osvaldo Sala from the University of Buenos Aires. We decided on three sites including a *Sphagnum* peatland and a shrub-steppe community in the Parque Nacional Tierra del Fuego and a *Carex* fen on private property. We had concerns about disturbances from tourists in the national park, but stray horses at the private *Carex* fen site were surprisingly more troublesome. I returned to the United States around mid-March to continue with my classwork. M. Cecilia Rousseaux and Carlos Mazza from the University of Buenos Aires stayed until the end of April to finish installing an extensive boardwalk in the *Sphagnum* peatland. The only work stoppage involved an unfortunate disagreement with the Chilean border authorities as to whether our plots at the *Sphagnum* site might be impinging on Chilean soil.

I returned to Ushuaia in late September of 1996 along with Steve Flint to start the first season of UV-B treatments on the plots set up the previous summer. The beginning of the first season was marred by extensive damage to our plastic UV-B filters by high winds. Fortunately, we were able to obtain thicker material from Buenos Aires with the help of Carlos Ballaré and M. Cecilia Rousseaux. I returned to Logan in mid-March with enough data to write the first chapter of this dissertation.

The second and third seasons of experiments in Ushuaia were much smoother, and there was time for hiking through the wilds of the Andes Mountains or traveling north to Buenos Aires to vacation at the coastal resorts. The all-around foul weather in Tierra del Fuego was combated by consuming large amounts of a bitter Argentine tea known as maté. Highlights from the second season included a visit from Martyn Caldwell and Carlos Ballaré during November of 1997, and we were able to finish the first two manuscripts originating from the project. Paul Barnes from Southwest Texas State University was in Ushuaia in January of 1998 for three weeks to conduct a short-term study on UV-B transmittance through leaves. A paper is currently *in press* in *Physiologia Plantarum* from his visit. The third season was a bit of a transition as M. Cecilia Rousseaux and I started to phase-out of the project and new faces including Veronica Pancotto, Hans Zaller, and Matt Robson came on board after the grant renewal. Martyn treated us to his superb gourmet cooking in December just before the Christmas break. In January, Brad Kropp from USU helped me to start a new line of research involving the effects of solar UV-B radiation on fungi. This involved a Herculean effort on Brad's part considering the dated autoclave and other equipment that was available to us.

The results of each study will be discussed later, but I leave this project comfortable that stratospheric ozone depletion has not caused large changes in ecosystem functioning over the last two decades although subtle changes induced by solar UV-B may still be of importance.

Peter S. Searles (June 2000)

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CHAPTER 1

INTRODUCTION

Stratospheric ozone depletion leads to increased solar ultraviolet-B radiation (UV-B, 280-320 nm) in the temperate and polar latitudes. The chemical process of ozone depletion was first described by Molina and Rowland (1974), and reductions in ozone over Antarctica during the austral spring appear to have been occurring by the late 1970's (Farman *et al.* 1985). Ozone depletion associated with the edge of the "ozone hole" has been measured well into the Patagonian region of South America (e.g., Bojkov *et al.* 1995; Kirchhoff *et al.* 1997; Orce & Helbling 1997). In addition to the springtime depletion of ozone, substantial decreases in ozone and increases in UV-B are apparent through the summer months in southern South America and as far north as New Zealand (Frederick *et al.* 1994; McKenzie *et al.* 1999). This summertime ozone depletion is most likely related to the more general deterioration of the ozone layer throughout much of the Southern Hemisphere and not to the Antarctic ozone hole.

An international treaty, the Montreal Protocol, was signed in 1987 to initiate a phase-out of man-made substances that destroy ozone in the stratosphere. This treaty and its subsequent amendments have resulted in a large reduction in ozone-depleting chlorofluorocarbons (CFCs), and substitutes for CFCs used in aerosols and refrigeration are readily available. The abundance of stratospheric chlorine from CFCs is peaking and will reach its maximum around the year 2000 (World Meteorological Organization 1999). Recent predictions suggest that the ozone layer will recover over the next several decades although a number of uncertainties exist including interactions with other changes in global climate such as global warming (Schindell *et al.* 1998; Madronich *et al.* 1999).

The effects of increased solar UV-B on terrestrial vegetation and ecosystems have been reviewed recently by several authors (e.g., Fiscus & Booker 1995; Björn 1996; Allen *et al.* 1998; Caldwell *et al.* 1999; Rozema *et al.* 1999). Caldwell and Flint (1994) proposed that the frequency of UV-B effects in plants from most to least common is: Induction of UV-B-absorbing compounds (presumably flavonoids involved in UV-B protection) > morphological changes and reduced growth >> reduced photosynthesis. The productivity of agricultural crops in the temperate region is unlikely to be greatly affected by increasing UV-B radiation (Fiscus & Booker 1995; Björn 1996; Allen *et al.* 1998). Stratospheric ozone depletion in the temperate regions is not very severe, and the majority of cultivars from crop species do not appear to be sensitive to UV-B under field conditions. Rozema *et al.* (1997) suggested increasing solar UV-B may sometimes constitute a stress for terrestrial vegetation, but more importantly, it may regulate ecosystem processes such as nutrient cycling and herbivory through UV-induced changes in flavonoids, tannins, and lignin.

The UV-B responses of plants and ecosystems in the polar latitudes have received considerable attention in the last several years because of the often substantial ozone depletion at these latitudes. In Abisko, Sweden (66 ° N), some reductions in stem elongation as well as changes in herbivory, decomposition, and reproductive output were seen under supplemental UV-B for several dwarf shrub species in a heathland ecosystem after two to four growing seasons (Gehrke *et al.* 1995; Johanson *et al.* 1995; Gwynn-

Jones *et al.* 1997; Phoenix *et al.* 2000). The growth of potted mountain birch seedlings (*Betula pubescens*) that grow natively in these same Swedish heathlands was not affected by supplemental UV-B radiation in an outdoor study (Weih *et al.* 1998).

Bryophytes have also been shown to be sensitive to UV-B radiation in Sweden to some degree. The subarctic mosses *Hylocomium splendens* and *Polytrichum commune* showed reduced annual length increments in a 3-year study under supplemental UV-B and a natural water regime (Gehrke 1999). In contrast, supplemental UV-B increased some growth parameters under added water and elevated CO_2 (Gehrke *et al.* 1996). *Sphagnum fuscum*, a moss that commonly dominates peatbogs in the Northern Hemisphere, had decreased height growth under supplemental UV-B over 2 years (Gehrke 1998). However, production itself was not affected.

In Tierra del Fuego, Argentina (55° S) at the tip of South America, there are indications that some plant species and ecosystem processes are sensitive to solar UV-B. Midday DNA damage correlated well with ambient, solar UV-B in the native perennial herb *Gunnera magellanica* during the austral spring in Tierra del Fuego, Argentina (Rousseaux *et al.* 1999). Experimental manipulations of solar UV-B also indicated that solar UV-B reduces leaf expansion and increases insect herbivory in this same species (Rousseaux *et al.* 1998). Chapter 2 of this dissertation primarily assesses whether plants in a *Sphagnum* peatland and a *Carex* fen in Tierra del Fuego respond to solar UV-B radiation. Chapter 2 has been published previously and reports the findings from the first field season in these two ecosystems. Chapter 3 reports the UV-B responses of the vegetation in the *Sphagnum* peatland for a 3-year period.

On the Antarctic Peninsula, solar UV-B decreased the leaf growth of the tussock grass *Deschampsia antarctica* over two growing seasons, while the cushion-forming *Colobanthus quitensis* was little affected. Increased temperature simulating global warming appeared to be of greater overall importance than solar UV-B for the plant growth and reproduction of *D. antarctica* and *C. quitensis* (Day *et al.* 1999). Short-term studies have not suggested any photosynthetic damage due to UV-B in these Antarctic species under field conditions (Huiskes *et al.* 1999; Montiel *et al.* 1999).

The influence of solar UV-B on microbial communities inhabiting *Sphagnum* moss are examined in Chapter 4 (along with some results in Chapter 2). Communities of testate amoebae (i.e., shelled amoebae), rotifers, nematodes, microalgae, cyanobacteria, bacteria, and fungi can be found in *Sphagnum* moss. Due to the potential for differential UV-B effects on each of the microbial communities, both direct and indirect effects of UV-B are possible. For example, mesocosm experiments at Environment Canada's experimental river flume facility indicated less sensitivity to solar UV-B in algae than in its consumers (Bothwell *et al.*, 1994). This difference in sensitivity contributed to counterintuitive increases in algae when exposed to UV-B. In the *Sphagnum* peatland, changes in the *Sphagnum* moss itself under solar UV-B may also contribute to indirect UV-B effects on the microbial communities.

The last of the journal-style chapters, Chapter 5, is a quantitative review of plant field studies simulating stratospheric ozone depletion. This review synthesizes the results of 62 papers published between 1976 to mid-1999 using a set of statistical techniques known as "meta-analysis." The responses of 10 variables such as UV-B-absorbing compounds and aboveground biomass were assessed to determine if there was an overall effect of supplemental UV-B for each variable across the 62 papers. Meta-analysis has previously proven to be a useful tool in reviewing plant response to elevated CO_2 (e.g., Curtis 1996, Curtis and Wang 1998, Peterson et al. 1999). To the best of my knowledge, the only quantitative review of UV-B effects in field experiments is for the percentage change in yield of four crop plants (Caldwell et al. 1998).

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CHAPTER 2

SOLAR ULTRAVIOLET-B RADIATION INFLUENCE ON *SPHAGNUM* BOG AND *CAREX* FEN ECOSYSTEMS: FIRST SEASON FIELD SEASON FINDINGS IN TIERRA DEL FUEGO, ARGENTINA[1]

Abstract

Stratospheric ozone depletion occurs over Tierra del Fuego, southern Argentina and Chile, in the austral spring and summer due to the precession of the Antarctic "ozone hole" and the general erosion of the ozone layer. Plots receiving either near-ambient or reduced UV-B radiation were established using different louvered plastic film filters over *Sphagnum* bog and *Carex*-fen ecosystems in October 1996. In the *Sphagnum* bog system, growth measurements during the late spring and summer showed no significant differences in the moss *Sphagnum magellanicum*, or the vascular plants (*Empetrum rubrum*, *Nothofagus antarctica,* and *Tetroncium magellanicum*) between near-ambient and attenuated UV-B radiation treatments. In the *Carex* fen system, leaf length and spike height did not differ in the two dominant species, *Carex decidua* and *C. curta,* between UV-B radiation treatments. The length of individual spikelets of *C. curta* under near-ambient UV-B radiation was less than under the reduced UV-B radiation treatment, but this was not evident in *C. decidua*. No differences in seed number, seed mass, or

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[1] Coauthored by Peter S. Searles, Stephan D. Flint, Susana B. Díaz, M. Cecilia Rousseaux, Carlos L. Ballaré, and Martyn M. Caldwell; this chapter was published in Global Change Biology (5: 225-234). Blackwell Science Publishing retains full copyrights to the article. See Appendix A for their letter of consent to reprint the article in this dissertaion. Appendix A also includes release letters from the coauthors who are not on the supervisory committee.

viability were seen in either *Carex* species between the UV-B treatments. Two important constituents of the microfauna that inhabit the *Sphagnum* bog are testate amoebae and rotifers. These both appeared to be more numerous under near-ambient UV-B radiation than under reduced UV-B radiation. The subtle responses of the *Sphagnum* and *Carex* ecosystems may become more apparent in subsequent years as the treatments are continued. Trophic-level changes, such as the differences in number of amoebae and rotifers, may be more sensitive to solar UV-B radiation than growth and productivity of the vegetation.

Introduction

Ultraviolet-B radiation (UV-B, 280-320 nm) has increased since the early 1980's over southern South America during the austral spring with precession of the Antarctic Vortex and associated "ozone hole" over the continent (Frederick *et al.* 1993; Díaz *et al.* 1994; Kirchhoff *et al.* 1997). Low ozone levels and enhanced UV-B radiation often extend through the summer long after the ozone hole has broken up (Frederick *et al.* 1994). Calculations based on satellite data from the Total Ozone Mapping Spectrometer (TOMS) indicate a 10-20% increase in UV-B radiation during the growing season at 55° S latitude from 1979 to 1993, although interannual variations in UV-B radiation can be large due to variability in cloudiness (Frederick & Erlick 1995; Madronich *et al.* 1995). This area experiences much more ozone reduction than any other terrestrial region on the globe apart from the Antarctic continent.

Stratospheric ozone depletion is, and will be, more pronounced at high latitudes in both hemispheres, and thus, most of the ecosystem-level study is being conducted at these latitudes. Terrestrial ecosystem studies in northern Sweden have shown that growth, reproductive output, insect herbivory, and litter decomposition of heathland shrubs can be sensitive to augmented UV-B radiation from UV lamp systems (Gehrke *et al.* 1995; Johanson *et al.* 1995; Gwynn-Jones *et al.* 1997). Augmentation of solar UV-B radiation was employed in these studies since ozone reduction and associated solar UV-B radiation increases are much less pronounced in the Northern Hemisphere than in the Southern Hemisphere.

Ultraviolet-B radiation effects at different trophic levels, including direct and indirect effects on insect herbivory and litter decomposition, indicate the importance of extending study beyond higher plant responses, which has traditionally been the focus of much of the UV-B research (Caldwell & Flint 1994). At the ecosystem-level, UV-B radiation appears to function not only as an environmental stress, but also as a regulator of ecosystem processes (Rozema *et al.* 1997). For example, UV-B radiation may cause stress that results in reduced plant growth, but it may also regulate herbivory and decomposition rates principally through altered plant secondary chemistry. Both effects have been seen to some degree at high latitudes in a heathland in Sweden.

A few studies have investigated the responses of mosses and lichens to augmented UV-B radiation at high northern latitudes; these indicate mixed responses in that added UV-B radiation can either stimulate or depress cryptogam performance

(Sonesson *et al.* 1995; Gehrke *et al.* 1996; Sonesson *et al.* 1996). The response of non-vascular species may be of considerable importance in global environmental change because peatlands are estimated to store 450 Pg of carbon, which is one-third of the organic global soil pool (Gorham 1991). Gehrke *et al.* (1996) found *Sphagnum fuscum* height increment to decrease 20% in one field season under lamps that augmented solar UV-B radiation.

Southern South America provides an ideal opportunity to assess the effects of UV-B on terrestrial ecosystems because ozone reduction has already transpired in this region. Spectral, ground-level measurements of UV-B radiation have been made continuously since 1989 in Tierra del Fuego, Argentina, as part of the US National Science Foundation UV Radiation Monitoring Network (Booth *et al.* 1994). These measurements indicate that solar UV-B radiation is already substantially elevated in the southern high latitudes, as mentioned earlier. Therefore, we have chosen to attenuate, rather than augment the UV-B radiation in a series of long-term studies initiated in October, 1996.

The objectives of experiments described in this paper were to: 1) determine whether growth of plant species is affected by prevailing solar UV-B radiation in two communities, a *Sphagnum* bog and a *Carex* fen, 2) assess the role of solar UV-B radiation in seed production of *Carex* species, and 3) investigate the influence of UV-B radiation attenuation on other ecosystem characteristics such as testate amoebae (i.e., shelled amoebae) and rotifer populations in near-surface *Sphagnum*. Testate amoebae

(Protozoa: Rhizopoda) and rotifers (Rotatoria) are common, cosmopolitan microfauna in *Sphagnum* mosses; testate amoebae have previously provided a sensitive means of monitoring habitat changes in bogs (Buttler *et al.* 1996). The results reported here are for the first year of the planned multi-year study. The two communities were selected because of their regional importance in Tierra del Fuego and their role in global carbon sequestration.

Materials and methods

Experimental sites

Three experimental sites have been established on Isla Grande near the city of Ushuaia in the Argentine province of Tierra del Fuego (55° S latitude), two of which are described in this work. The general area is dominated by a deciduous *Nothofagus* forest, with extensive bogs in many Andean mountain valleys and some scattered shrub communities. The annual precipitation of 525 mm is fairly uniformly distributed over the year. Mean annual temperature is 5.5° C (FAO 1985). We selected a minerotrophic *Sphagnum magellanicum* bog 20 km west of Ushuaia adjacent to Laguna Negra in the Parque Nacional Tierra del Fuego as one site. There is nearly complete cover of *Sphagnum magellanicum*, but there are vascular plant species that emerge from the *Sphagnum*, including *Nothofagus antarctica* (a deciduous southern beech tree), *Empetrum rubrum* (an evergreen dwarf shrub), and *Tetroncium magellanicum* (a rhizomatous perennial monocot). Plant nomenclature follows Moore (1983). The plots were located in a part of the bog with fairly even microtopography rather than in areas where the bog takes on a pronounced hummock appearance.

Our *Carex* fen site is on private land close to the city of Ushuaia. The sedges, *Carex decidua* and *Carex curta* (also called *C. canescens*), comprise most of the plant cover; other *Carex* spp., *Juncus* spp., and *Caltha sagitata* are much less common. A third site (not reported here) is in a shrub-dominated community with vegetation similar to that found throughout the more northerly region of Patagonia.

Experimental setup and treatments

Potential experimental plots were assessed for the *Sphagnum* bog and *Carex* fen systems during February and March 1996. Twenty plots of 1.4 x 2.0 m and 18 plots of 1.4 x 1.5 m were selected in the bog and fen, respectively. A boardwalk was constructed in each community to avoid damaging the vegetation and altering the hydrology in and around the plots. During the early austral spring, the experimental UV-B manipulations were initiated on 15-16 October 1996 in the *Sphagnum* bog and on 26 October 1996 in the *Carex* fen. Half of the plots had near-ambient UV-B radiation and half had reduced UV-B radiation; plots of the two treatments were interspersed. The first significant precession of the ozone hole over Tierra del Fuego after plant growth began in early spring and the beginning of our experiments occurred on 17 October. Yet cloud cover kept UV-B levels moderate at this time (Fig. 1). The UV-B manipulation treatments were maintained in these plots until mid-March (Autumn) when leaf senescence was occurring in both communities and solar UV-B radiation had decreased to levels similar to early spring (Fig. 1).

Half of the plots were covered by clear 38-µm thick "Aclar" plastic film (type 22A, Allied Signal, Pottsville, PA) to provide near-ambient UV-B radiation and half by 100-µm polyester plastic (optically equivalent to "Mylar-D," DuPont Co., Wilmington, DE) to provide a reduced UV-B level. Our goal was to effect a partial, rather than complete, attenuation of UV-B radiation in the treatments and also to allow precipitation to penetrate through the filters to obviate the need for irrigation of the plots. Therefore, both filter types were perforated using an electric hot-wire melter that formed a perpendicular pattern of slits (slit size: 2 mm x 30 mm; slit spacing: 10 mm) in the plastic film. The slit edges created by the melting were resistant to tearing in this very windy environment, and the slits formed a matrix of louvers that allowed rainfall to pass through both plastic films.

Ultraviolet-B radiation transmittance of the films was determined using a SUV 100 scanning double monochromator (Biospherical Instruments, San Diego, CA) on the roof of the Centro Austral de Investigaciones Cientificas (CADIC). The instrument is part of the US National Science Foundation UV Radiation Monitoring Network (Booth *et al.* 1994). Unperforated polyester does not allow the transmission of any biologically effective UV-B radiation using the generalized plant action spectra (Caldwell 1971). Approximately 20% of the plant-weighted solar UV-B radiation passed through the perforated polyester. Transmission of solar radiation within the UV-A waveband increases to 60% at 330 nm and 80% at 380 nm. The perforated Aclar plastic (near-ambient control) allowed nearly 90% transmission in the UV-B and UV-A. Both plastics transmit nearly 90% of the photosynthetic photon flux density (PPFD, 400-700 nm) as measured by a quantum sensor (LiCor, Lincoln, NE). The plastic films were suspended horizontally 35 cm above the ground surface and 10 cm above the tallest vegetation.

Measurements of soil water content (by time-domain reflectometry) at 15 cm in the *Carex* plots and by gravimetric determinations for the upper 1 cm of the *Sphagnum* bog indicated no differences between filter types at either experimental site and did not appear to differ from that outside of the plots. Air temperatures under the plastic films were not substantially different than those in the ambient environment. This is based on the temperature measurements of portable UV sensors mounted inside and outside of the plots for several days with data recorded each minute by a Campbell Scientific 21X datalogger (Logan, UT). Monthly wind speed averages almost 5 m s^{-1} during the spring and summer which keeps the air under the filters very well mixed. A 25-µm polyester film was employed in reduced UV plots during the first four weeks of the experiment and then replaced with the 100-µm polyester due to considerable destruction of the thinner polyester plastic by the strong winds. Thereafter, the plastic films were replaced with new film only occasionally (but never used for more than two months) and measurements of UV transmission of the plastics revealed no photodegradation of either the polyester or the Aclar under these conditions.

Plant morphological and seed production measurements

Plant morphological measurements were taken in the late-spring and summer in both communities; a 35-cm border zone of each plot was not sampled. The cranked-wire method of Clymo (1970) was used to assess the height growth of *S. magellanicum*. This involves stainless steel wires (shaped like the handle of an old-fashioned car starting crank) as reference markers with one end of the wire pushed vertically into the *Sphagnum* carpet, a short horizontal section level with the *Sphagnum* surface, and the other end projecting vertically upward above the surface. Six cranked wires were installed in each plot on 31 October 1996, and height growth of the *S. magellanicum* was recorded on 13-15 January 1997, and 3-5 March 1997, as the moss grew up around the wires. For *E. rubrum*, the previous year's stem elongation was measured using a caliper on eight individual stems per plot on 18-22 November 1996 to ensure that there were no differences between the shrubs in the plots before the treatments were initiated. Measurement of the current year's stem elongation was done only on 13-15 January 1997, because little, if any, growth occurred later in the season for this species. A similar approach was used for *N. antarctica* with previous year's and current year's stem elongation growth recorded in mid-December and again in early March. Leaf blade elongation of *T. magellanicum* was measured in mid-January.

In the *Carex* fen, morphological parameters measured on 2-4 December 1996 were the leaf lengths of the second most recently produced leaves for *C. decidua* and the only new leaf produced during the current year for *C. curta*. All six of the plants measured in each plot were reproductive individuals and spike height was also recorded during the December measuring period. On 20-22 January 1997, leaf length was measured for an additional, younger leaf on *C. decidua* and spike height was again determined along with the length of two of the 5-6 spikelets per spike for both species. No new leaves appeared on either species after this second measurement period.

Measures of seed production were also made in the *Carex* community. Seed number and seed dry mass (oven-dried at 60°C for 48 h) were determined for one of the two spikelets measured on 20-22 January. Seeds from the second spikelet were used to assess seed viability after 6 h in a 0.5% tetrazolium chloride solution.

Pigmentation of S. magellanicum

Carotenoids, chlorophylls, and UV-B-absorbing compounds were determined for *S. magellanicum*. Five sections (3 x 3 cm of 4 cm depth) of *Sphagnum* "lawn" were taken from each plot on 3-5 March with pigment extractions performed on the uppermost 6 mm of the *Sphagnum* capitula (i.e., the compact hemispherical heads or apices of the moss). Six mm was equivalent to the depth for 99% light attenuation based on preliminary fibre-optic measurements in the *Sphagnum* carpet; this 6 mm was also composed entirely of material produced during the first growing season in our experiments. Five capitula per plot (one from each 3 x 3 cm section) were collected and pooled for carotenoid and chlorophyll extraction and analysis. The extraction was in 5 ml of 100% methanol heated at 60° C for 10 min similar to Day *et al.* (1996). The equations of Lichtenthaler (1987) and absorbance measurements at 470, 652, and 665 nm were used to estimate total carotenoids and chlorophyll a and b. In a separate extraction for UV-B-absorbing compounds, four capitula per plot were incubated in the dark in 5 ml of 1M NaOH at room temperature for 48 h and absorbance was measured at 305 nm. This is similar to the method of Schnitzler *et al.* (1996) designed to extract cell wall-bound pigments. Traditional ethanol and methanol solvents that only extract cell-content pigments yielded much lower absorbance values for the *Sphagnum,* suggesting a sizeable component of wall-bound pigments in this species.

Extraction and quantification of testate amoebae and rotifers

Testate amoebae and rotifers were extracted from the same 3 x 3 cm sections of *Sphagnum* carpet from each plot mentioned above; 15 *S. magellanicum* stems were separated into two segments corresponding to 0-6 mm and 6-15 mm depths. The extraction and counting followed Tolonen *et al.* (1992). Briefly, the *Sphagnum* was stirred in 15 ml water for 5 min along with two dissolved tablets each containing 12,500 spores of *Lycopodium* (Lund University Batch No. 124961) which is used as an exotic marker. After filtration through a 750-µm mesh sieve, the microfauna were concentrated by centrifugation (2000 rpm) for 2 min, stained with safranin, and stored in glycerine. A drop of the concentrate was viewed under a microscope at 100x and absolute numbers of testate amoebae and rotifers were calculated on the basis of fresh *Sphagnum* mass using the *Lycopodium* spores as a reference (Tolonen *et al.* 1992). Testate amoebae were identified at least to the genus level using Ogden and Hedley (1980); the rotifers were not identified other than noting they were predominantly of the order Bdelloidea.

Statistical analyses

To assess potential responses to differences between the near-ambient and reduced UV-B levels, plant morphological parameters, seed production, and pigmentation were analyzed with t-tests using the plot, rather than individual plants within plots, as the experimental unit (replicate). While plant growth and pigment characteristics were relatively uniform across the study sites, the number of amoebae in the *Sphagnum* bog increased by more than fivefold between the plots closer to the forest, compared to those nearer the lake. Thus, we used a blocked analysis of variance design (PROC MIXED; SAS Release 6.11, SAS Institute, Inc., Cary, NC) for the analysis of microfauna (Tables B.1 - B.3 of Appendix B). The plots were divided into three blocks based on spatial positioning. Neither moisture content nor *S. magellanicum* height increment varied much across the bog and when used as covariates did not explain the differences in microfauna across the bog. Results considered to be statistically significant are accompanied by their *P* values so the reader can assess the probability of significance.

Results

Solar UV-B radiation during the growing season

To compare the ambient solar UV-B radiation in the growing season of 1996-1997 with that of former years and also with theoretical calculations, Fig. 1 shows integrated daily total solar UV-B (direct beam+diffuse) radiation weighted with the generalized plant action spectrum (Caldwell 1971) normalized at 300 nm. Values during 1996-1997 are compared with the lowest and highest values ever recorded for each date in the period from 1989 to 1995. All measurements were conducted in Ushuaia, Argentina, by the US National Science Foundation UV Monitoring Network station. Theoretical values using the model of Frederick and Lubin (1988) for clear skies are also given. Validation of the model has shown strong agreement between measured and calculated irradiances over a full annual cycle when corrected for cloud cover (Díaz *et al.* 1996). The average monthly ozone column values for the period of 1980-1986 measured by the satellite-based Total Ozone Mapping Spectrometer (TOMS) were used in the model. This time period was chosen since it appears to have preceded most of the severe ozone depletion over southern South America. Therefore, the model values represent the normal daily radiation one would expect for clear skies before substantial ozone depletion in this region.

The daily solar UV-B radiation during the 1996-1997 growing season was similar to the lowest daily values for corresponding dates from the entire period 1989-1995 in the early spring (i.e., mid-October to mid-November). But, many of the days during the late spring were higher than the highest daily values previously measured for the 1989-1995 period on corresponding dates. These values were also greater than theoretical calculations of clear-sky UV-B radiation based on the 1980-1986 ozone column values. During the latter half of the growing season, the solar UV-B radiation in 1997 was low and seldom approached expected clear sky values (Fig. 1).

Plant morphology, seed production, and pigmentation

No differences were seen in the stem elongation of *S. magellanicum, E. rubrum,* and *N. antarctica* or leaf elongation of *T. magellanicum* between near-ambient solar UV-B (90% of ambient) and reduced UV-B (20% of ambient) levels (Fig. 2). For the stem elongation of *E. rubrum* and *N. antarctica* (Fig. 2), there were no treatment differences when relativized with respect to the previous year's elongation, as in Johanson *et al*. (1995) (data not shown). In the *Carex* fen, leaf length and spike height for *C. decidua* and *C. curta* did not respond to the differences in UV-B levels (Table 1). A reduction was seen in the spikelet length of *C. curta* under near-ambient UV-B radiation compared to the attenuated-UV-B treatment (*P* = 0.01), but not for *C. decidua*. The number of seeds, seed dry mass, and viability were not affected by the differences in UV-B radiation in either species (Table 2). *Sphagnum magellanicum* showed no differences in total chlorophyll, carotenoids, and UV-B absorbing compounds when sampled toward the end of the growing season (Fig. 3). The results for chl a, chl b, and chl *a*/b ratio were similar to total chlorophyll (data not shown).

Testate amoebae and rotifers

The vast majority of the testate amoebae were *Assulina muscorum* along with some individuals of *A. seminulum, Nebela, Heleopera* and *Euglypha* species. The numbers of *A. muscorum* (*P* = 0.08), total testaceans (*P* = 0.07), and total rotifers (*P* =

0.10) all tended to be higher under near-ambient UV-B radiation than under reduced UV-B radiation at the 0-6 mm (Fig. 4) sampling depth in *S. magellanicum.* Results at 6-15 mm depth were similar. The relative increase under near-ambient UV-B radiation was consistent among the three statistical blocks despite the much greater numbers of individuals in plots in the portion of the bog closer to the small lake than in plots closer to the forest.

Discussion

Essentially no differences were apparent in the plant morphological parameters between the near-ambient solar UV-B and reduced UV-B treatments in both the *Sphagnum* bog and the *Carex* fen during this first field season. In contrast, field studies in which the solar UV-B radiation was augmented with UV-B lamps in the heathlands and bogs of Abisko in northern Sweden (68° N) have indicated reduced stem elongation during the first growing season in species very similar to those in our study *(Empetrum hermaphroditum*, *Sphagnum fuscum*) (Johanson *et al.* 1995; Gehrke *et al.* 1996). However, *E. hermaphroditum* was not affected by supplemental UV-B radiation from lamps during a different 3-year study at a similar Abisko heathland site (Gwynn-Jones *et al.* 1997).

The reduction or exclusion of solar UV-B radiation and enhancement of ambient solar UV-B radiation with special fluorescent lamps are the two most common approaches to manipulating UV-B radiation in field studies. Reduction or exclusion of solar UV-B radiation is often used to explore the effectiveness of current UV-B levels on vegetation (Searles *et al.* 1995; Ballaré *et al.* 1996). It is also an ecologically relevant approach to assess the effects of stratospheric ozone layer reduction in regions that have already experienced this reduction and associated increases in solar UV-B radiation such as in Antarctica and southern South America. Supplementation of ambient solar UV-B radiation using lamps is an appropriate technique where ozone depletion has not substantially developed, as for most of the Northern Hemisphere.

The manipulation of UV-B dosage from lamps can be complicated by factors including clouds and inaccuracies in theoretical models which calculate ground-level solar UV-B radiation (Fiscus and Booker 1995). An intended enhancement of UV-B radiation to simulate a 15% ozone depletion under cloudless skies can actually represent a 23% depletion over the growing season when cloud cover is taken into account over Abisko, Sweden (Johanson *et al.* 1995), and an even greater effective ozone reduction would be simulated for a day of heavy cloud cover. Furthermore, there are difficulties in exactly simulating the spectral distribution of sunlight (Caldwell *et al.* 1986).

Another issue is whether the bog and fen system responses to UV manipulations will be more apparent in subsequent years of our study. There have been studies with the two higher plant species on the Antarctic Peninsula, *Deschampsia antarctica* (a tussock grass) and *Colobanthus quitensis* (a forb), in which solar UV attenuation experiments have been performed by Thomas.A. Day and colleagues (personal communication) with an emphasis on plant ecophysiological measurements. In the first field growing season, there were no differences for several vegetative growth characteristics between UV-B attenuation and near-ambient solar UV-B treatments. However, in the second growing season, one species, *D. antarctica*, did exhibit responses to the differences in UV-B treatments ($P < 0.05$). Because most of the species we examined in Tierra del Fuego either have foliage which persists for greater than one year or have leaves arising from buds formed prior to our imposition of the UV-B treatments, it is reasonable to expect some delay in the appearance of detectable treatment effects. Further, the growing season of 1996-1997 in Tierra del Fuego had periods of rather low UV-B radiation compared with previous years, except for the late spring when daily values often exceeded previously recorded highs (Fig. 1).

No differences were detected between the UV-B treatments in seed production of the two *Carex* species even though spikelet length was affected in *C. curta*. Ultraviolet-B radiation effects on seed production at high latitudes have been seldom examined. Gwynn-Jones *et al*. (1997) found that supplemental UV-B radiation stimulated fruit production in a *Vaccinium* dwarf shrub at Abisko, Sweden, by the second year of a 3-year field study. Similarly, there was a somewhat greater number of reproductive structures ($P < 0.10$) in the two Antarctic higher plant species under near-ambient UV-B radiation compared to substantially attenuated UV-B radiation in field studies (Thomas A. Day, personal communication). However, neither study monitored actual seed production.

The induction of flavonoids and related UV-B-absorbing compounds is a very common response to UV-B radiation supplementation in higher plants (Caldwell and

Flint 1994). The induction of UV-B-absorbing pigments in mosses by UV-B radiation is not well known. *Hylocomium splendens*, a heathland moss, showed no increase in UV-B-absorbing compounds after two years exposure to elevated UV-B radiation in northern Sweden (Gehrke *et al.* 1996). This is similar to our results reported here for *S. magellanicum* after one year in Tierra del Fuego. If phenolics in the *Sphagnum* bog are found to be increased in subsequent years of this study due to ambient solar UV-B radiation, this could have potential implications. For example, sphagnum acid (a cinnamic acid which is also a UV-B-absorbing compound) can play a role in inhibiting decomposition of peat and also in slowing growth of higher plants emergent in the *Sphagnum* (Verhoeven & Liefveld 1997).

Assessing terrestrial ecosystem-level responses to changes in the solar UV-B climate has received little attention thus far. The work of several years duration in northern Sweden, some new studies in grassland dune communities of the Netherlands and our work in Tierra del Fuego are, to our knowledge, the only studies of this kind. Most UV-B radiation research has been conducted on higher plants, and the majority of studies have been rather short-term experiments (i.e., days or weeks) in growth chambers or greenhouses using isolated plants grown in small pots (Caldwell and Flint 1994). A few studies were conducted in the field with UV-B lamp systems over several years duration (Barnes *et al.* 1988; Teramura *et al.* 1990; Sullivan & Teramura 1992), but these only considered the higher plant responses and (except for the loblolly pines of Sullivan and Teramura (1992) were confined to annual plants.

The potential role of trophic-level interactions as important components of ecosystem response to an altered UV-B climate has been stressed by Bothwell *et al.* (1994) and Paul *et al.* (1997). Laboratory and microcosm studies have indicated that the direction of these effects is not easily predicted. For example, UV-B radiation has been shown to have an indirect effect on larvae of a non-specialist moth herbivore, primarily due to elevated furanocoumarins in the leaves (McCloud & Berenbaum 1994). Elevated UV-B appeared to decrease natural populations of a sap-sucking insect on the ericaceous shrub *Calluna vulgaris* in England, yet, unlike the foregoing example, this decrease was not correlated with changes in parameters of host tissue quality the investigators chose to measure (Paul *et al.* 1997). A direct effect of UV-B radiation on the insects did not appear likely based on the behavior of the insects. Similarly, insect grazing on the perennial herb *Gunnera magellanica* was reduced under near-ambient solar UV-B radiation compared to UV-B radiation exclusion in field studies in Tierra del Fuego, Argentina (Rousseaux *et al.* 1998). Mesocosm experiments at Environment Canada's river flume facility have shown an increase in algal density when exposed to solar UV-B radiation; the reason for this increase was attributed to the reduced herbivory of the algae by larval chironomids which were much more sensitive to ambient solar UV-B radiation than were the algae (Bothwell *et al.* 1994).

There were apparent increases of testate amoebae and rotifers in the upper layers of the *Sphagnum magellanicum* in our study under near ambient UV-B radiation compared with the UV-B radiation attenuation treatment. This may have involved changes in the food sources of the testate amoebae which can include a diverse array of bacteria, microalgae, detritus, and other testate amoebae and naked amoebae (Ogden & Hedley 1980). Alternatively, changes in nematode predation on testate amoebae may be of importance. Little is known about the predator-prey relationships of rotifers in *Sphagnum* bogs (Pejler & Berzins 1993). Ephemeral changes in *Sphagnum* secondary chemistry may also have been involved even though this was not apparent in the pigment and phenolic measurements we conducted.

While the UV-B radiation manipulation treatments in this first year did not result in apparent changes in growth, morphology, seed production or productivity of either the higher plants or the *Sphagnum,* such effects may become apparent in subsequent field seasons as has occurred in some other studies. The apparent UV-B sensitivity of vegetation in northern Sweden (Johanson *et al.* 1995; Gehrke *et al.* 1996) contrasts our findings for this first year in Tierra del Fuego. Ultimately, trophic-level interactions, such as changes in herbivory or the invertebrate populations of the *Sphagnum,* may be the most important consequences of the changing solar UV-B climate in Tierra del Fuego.

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Table 1 Morphological parameters of *Carex decidua* and *Carex curta* under near-ambient solar UV-B radiation (90% of ambient) and reduced UV-B radiation (20% of ambient). The leaves and spikelets selected for measurement are described in the Materials and Methods. n= 9 plots per UV-B level with means ± SE. * indicates $P = 0.01$ using a t-test.

	UV-B level	Leaf length (cm) (early Dec)	Leaf length (cm) (late Jan)	Spike height (cm) (late Jan)	Spikelet length (cm) (Jan)
Carex decidua	Near-ambient	9.4 ± 0.3	10.0 ± 0.5	13.5 ± 0.6	1.67 ± 0.05
	Reduced	9.2 ± 0.6	9.7 ± 0.5	13.0 ± 0.4	1.65 ± 0.06
Carex curta	Near-ambient	14.6 ± 0.5	--	26.9 ± 1.1	0.76 ± 0.02 *
	Reduced	14.5 ± 0.7	--	26.7 ± 1.1	0.86 ± 0.02

Table 2 The number of seeds, seed mass, and seed viability of *Carex decidua* and *Carex curta* under near-ambient solar UV-B radiation (90% of ambient) and reduced UV-B radiation (20% of ambient). The results are shown for individual spikelets. n=9 plots per UV-B level with means ± SE. T-tests indicated no significant differences.

	UV-B level	Number of seeds	Dry mass (mg)	Viability (%)
Carex decidua	Near-ambient	60 ± 3	24.8 ± 1.6	66 ± 7
	Reduced	57 ± 3	26.0 ± 1.2	74 ± 4
Carex curta	Near-ambient	22 ± 1	9.3 ± 0.3	81 ± 2
	Reduced	22 ± 1	10.2 ± 1.0	79 ± 2

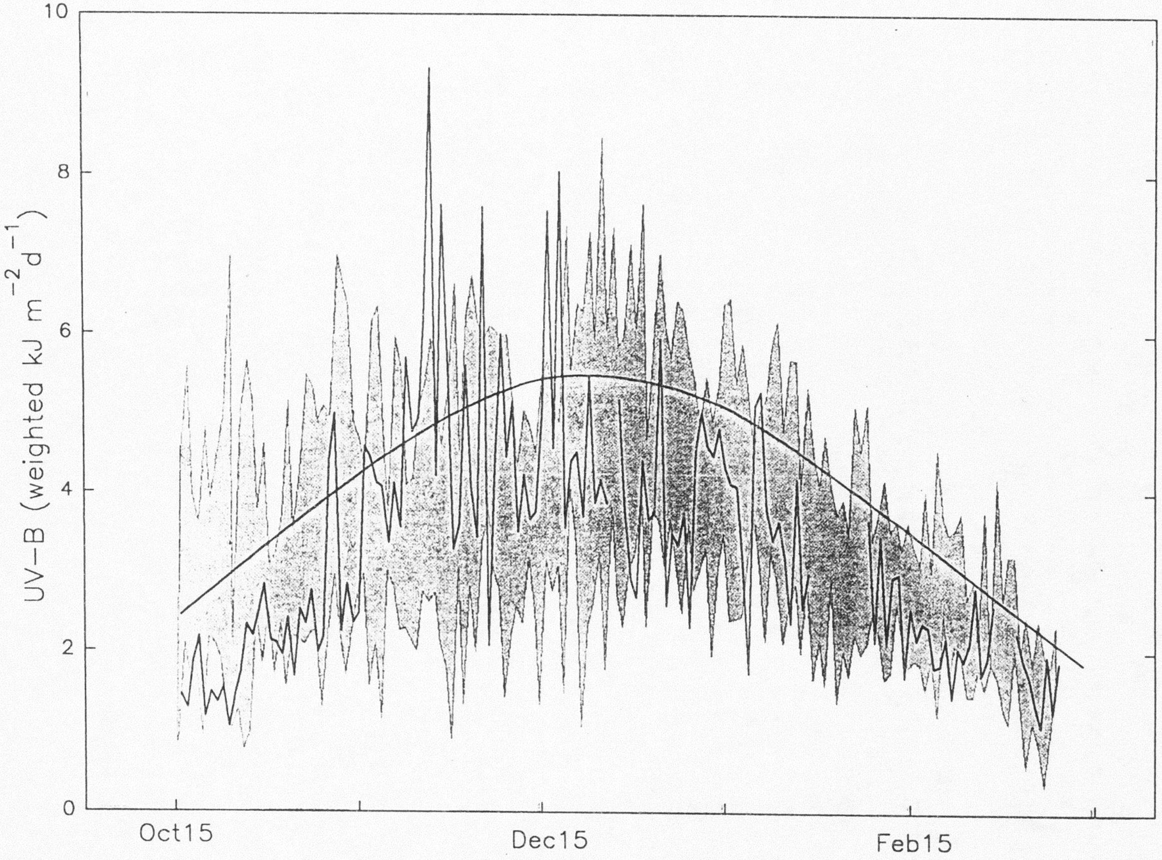

Fig. 1 Measured values and model calculations of integrated daily solar UV-B radiation (weighted by the generalized plant action spectrum) for Ushuaia, Tierra del Fuego, Argentina. The daily solar UV-B radiation for the 1996-1997 growing season is shown (erratic line) as well as the theoretical, clear-sky UV-B radiation (smooth curve). The shaded area reflects the range between the lowest and highest daily UV-B radiation measured for each day of the previous seven growing seasons.

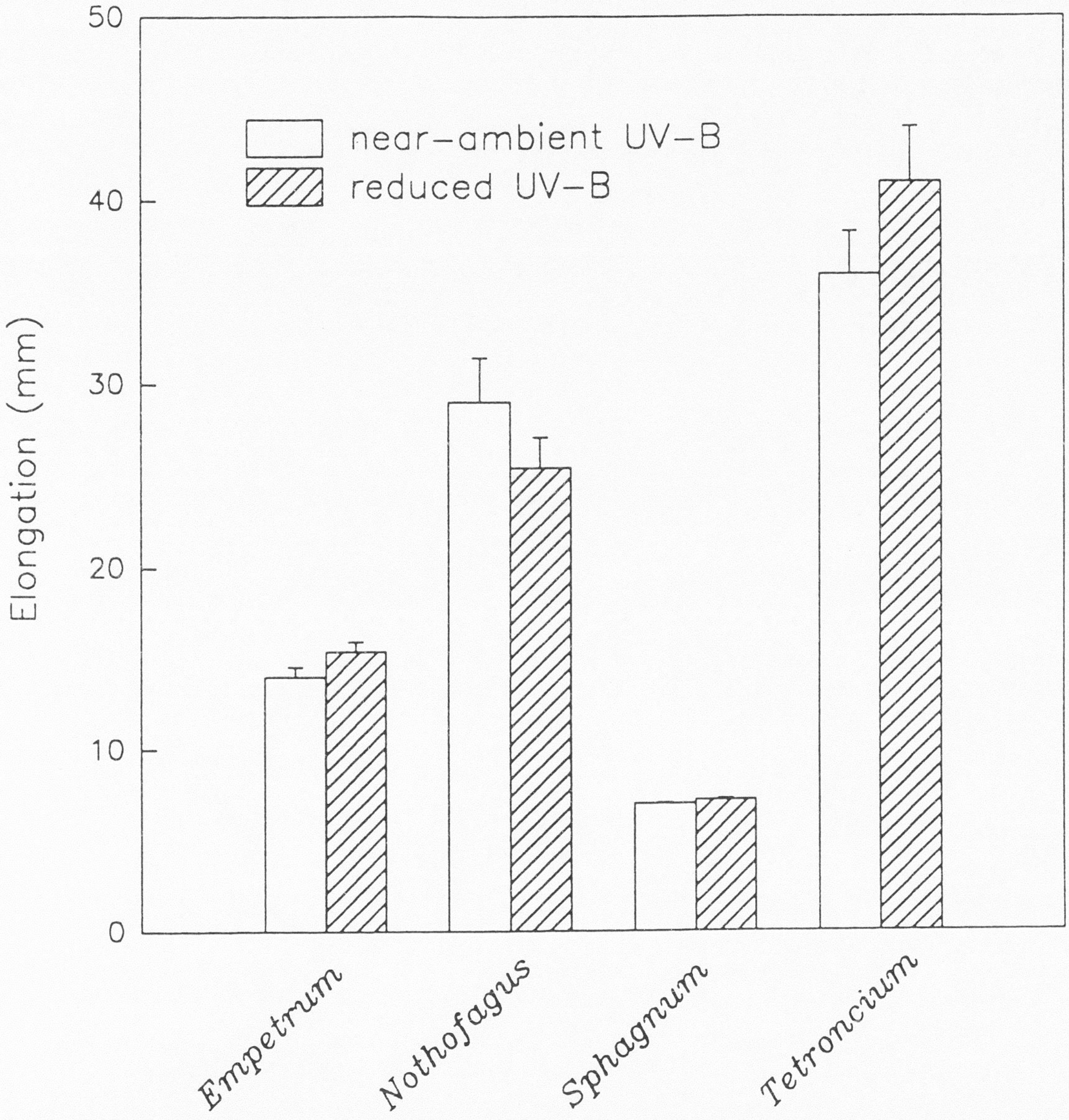

Fig. 2. Stem elongation of *E. rubrum*, *N. antarctica*, and *S. magellanicum*, and leaf elongation of *T. magellanicum* under near-ambient solar UV-B radiation (90% of ambient) and reduced UV-B radiation (20% of ambient). n=10 plots per UV-B level with means ± SE. *T*-tests showed no significant differences between treatments.

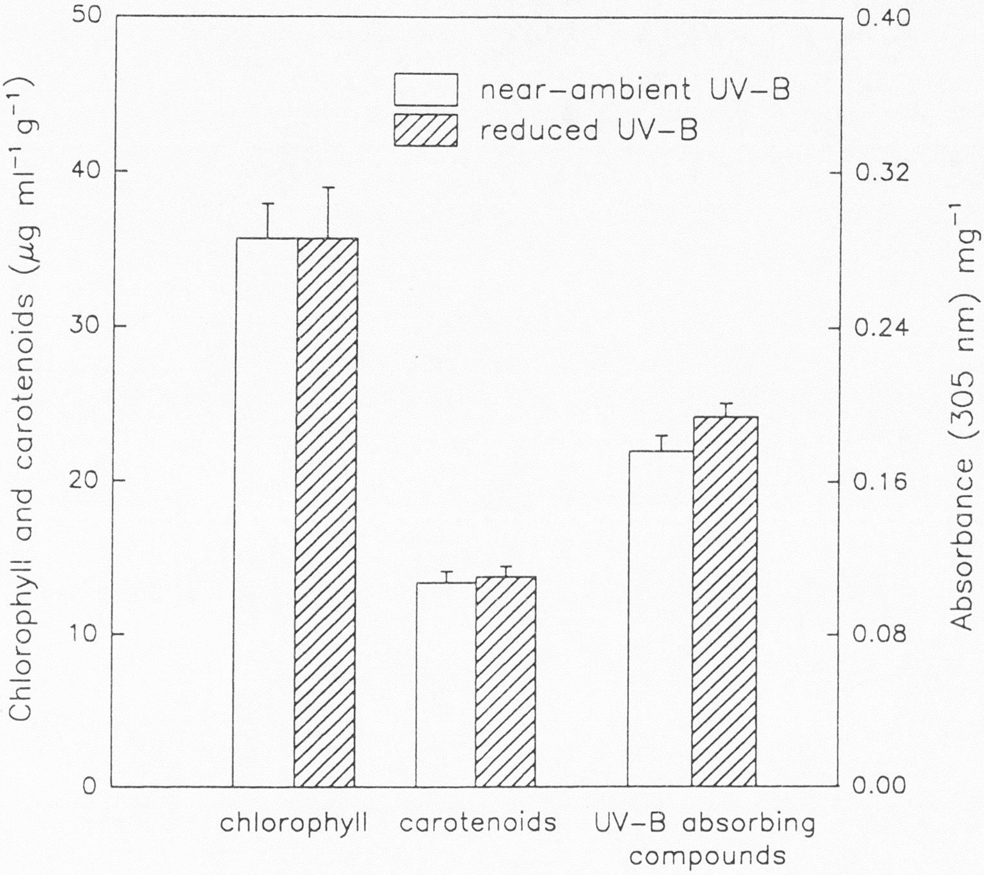

Fig. 3 Total chlorophyll, carotenoids, and UV-B-absorbing compounds in *S. magellanicum* under near-ambient solar UV-B radiation (90% of ambient) and reduced UV-B radiation (20% of ambient). Chlorophyll and carotenoids are expressed as mass per volume of plant solution extract per dry mass of *S. magellanicum*. The UV-B absorbing compounds are shown as absorbance per mg at 305 nm. n=10 plots per UV-B level with means ± SE. *T*-tests showed no significant differences between treatments.

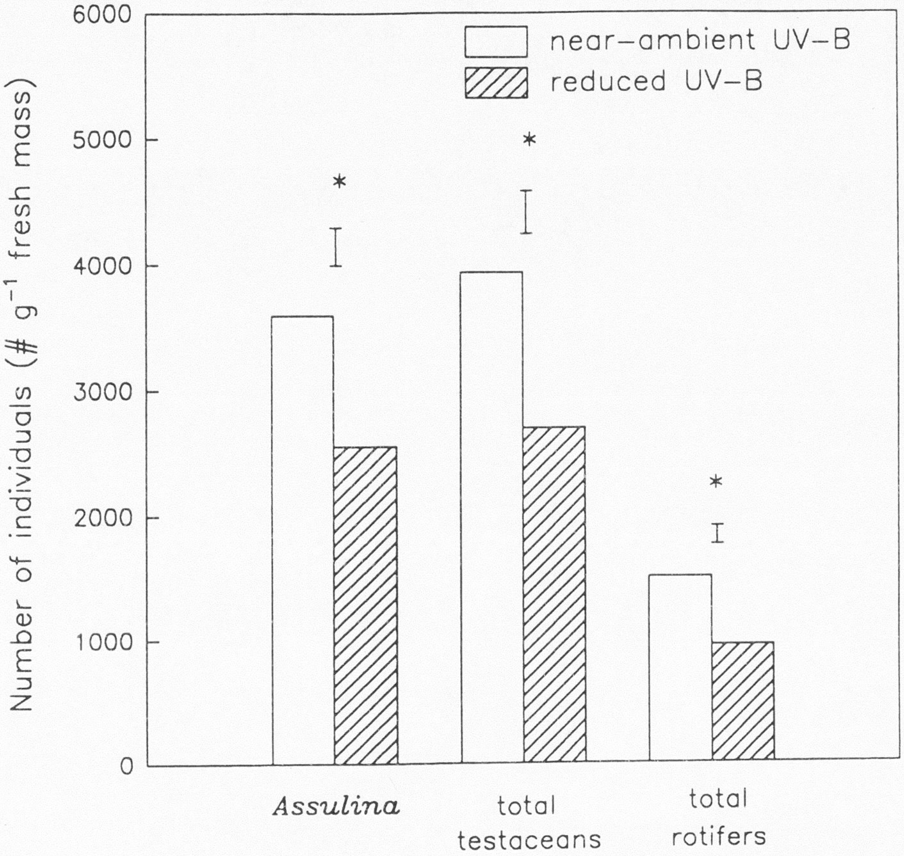

Fig. 4 The number of individuals of the testate amoebae *Assulina muscorum*, total testaceans including all testate amoebae species, and total rotifers in near-surface *S. magellanicum* under near-ambient solar UV-B radiation (90% of ambient) and reduced UV-B radiation (20% of ambient). The effect of the UV-B radiation level was assessed by using an analysis of variance design with the blocking of plots by spatial position in the *Sphagnum* bog. The results are shown for the 0-6 mm depth and were similar at 6-15 mm depth in the *Sphagnum*. The SE shown is the SE of the differences between treatments. The * indicates *P*-values of 0.08 for Assulina, 0.07 for total testaceans, and 0.10 for rotifers.

CHAPTER 3

PLANT RESPONSE TO SOLAR ULTRAVIOLET-B RADIATION IN A SOUTHERN SOUTH AMERICA *SPHAGNUM* PEATLAND[1]

Summary

1 Plant growth and pigmentation of the moss *Sphagnum magellanicum* and the vascular plants *Empetrum rubrum*, *Nothofagus antarctica*, and *Tetroncium magellanicum* were measured under near-ambient solar UV-B (90% of ambient) and reduced UV-B (20% of ambient) radiation for three growing seasons in a *Sphagnum* peatland in Tierra del Fuego, Argentina (55° S). Specially designed louvered plastic films were used to obtain the UV-B treatments in the experimental plots.

2 The climate-related growth of the dwarf shrub *E. rubrum* in *Sphagnum* peatlands was assessed retrospectively by correlating an 8-year record (1990-91 to 1997-98 growing seasons) of annual *E. rubrum* stem elongation with macroclimatic factors including UV-B radiation, visible light, precipitation, and temperature.

3 The reduction of solar UV-B in the experimental plots increased height growth and decreased volumetric density in *S. magellanicum* relative to near-ambient UV-B. These results tended to be offset such that biomass production was not influenced during the three years. The morphology of vascular plants only showed some modest effects of the UV-B reduction treatment.

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[1] Coauthored by Peter S. Searles, Stephan D. Flint, Susana B. Díaz, and Martyn M. Caldwell. Consent letters from Stephan Flint and Susana Díaz for use of this manuscript in the dissertation are given in Appendix A.

4 No main effects of solar UV-B reduction on pigmentation in *S. magellanicum* were apparent. An interaction between UV-B and year suggests that UV-B-absorbing compounds are starting to decrease due to the reduction of solar UV-B. A 10-20% decrease in UV-B-absorbing compounds occurred in *E. rubrum* and *T. magellanicum* relative to near-ambient UV-B.

5 No significant negative correlations with found between annual *E. rubrum* stem elongation and ambient solar UV-B, the ratio of UV-B/visible radiation, or the 305-nm-to-340-nm irradiance ratio; which is an indicator of changes in ozone, for an 8-year record (1990-91 to 1997-98). Stem elongation was positively correlated with visible radiation and negatively related to rainfall for the early summer.

6 The overall role of solar UV-B radiation in *Sphagnum* peatlands in Tierra del Fuego, Argentina, will likely depend on the severity of stratospheric ozone depletion over the next several decades. The increases in ambient solar UV-B associated with ozone depletion over the last 20 years are less than the difference between the near-ambient solar UV-B and reduced UV-B radiation treatments in our 3-year study. If the ozone layer substantially recovers by the middle of this century, only some modest effects of increased solar UV-B may be expected.

Introduction

Stratospheric ozone depletion leads to increased solar ultraviolet-B radiation (UV-B, 280-320 nm) over the tip of southern South America (55° S) with the passage of the Antarctic "ozone hole" for several day periods during the austral spring (Bojkov *et* *al.* 1995; Kirchhoff *et al.* 1997). Some reduction in ozone of Antarctic origin and associated with the broad edge of the polar vortex has been measured well into Patagonia north of 40° latitude (Orce & Helbling 1997; Perez *et al.* 1998). Upward trends in monthly solar UV-B reaching the Earth's surface are much more difficult to detect even over Antarctica in October than daily UV-B increases due to interannual variations in cloudiness (Booth *et al.* 1997). Nevertheless, the number of ozone-depleted days ($\leq$250 Dobson units) over Tierra del Fuego, Argentina, in October and November has increased greatly over the last two decades based on data from the Total Ozone Mapping Spectrometer (TOMS) satellite system (Rousseaux *et al.* 1999). Ground-based UV-B measurements in the austral spring are often higher than predicted solar UV-B levels prior to "ozone hole" formation in the early 1980's (Chapter 2). Substantial ozone depletion and increases in UV-B have also been demonstrated through the summer months of January and February in Tierra del Fuego (Frederick *et al.* 1994). Increases in ultraviolet intensities during the summer months have been measured as well in New Zealand (45° S) (McKenzie *et al.* 1999), and are likely due to the general year round deterioration of the stratospheric ozone layer in the Southern Hemisphere.

The greater severity of ozone depletion over high latitudes in the Southern Hemisphere than similar latitudes in the Northern Hemisphere has resulted in several recent field studies of plant responses to solar UV-B radiation. Midday DNA damage correlated well with ambient, solar UV-B in the native perennial herb *Gunnera magellanica* during the austral spring in Tierra del Fuego, Argentina (Rousseaux *et al.*

1999). Experimental manipulations of solar UV-B also indicated that solar UV-B reduces leaf expansion and increases insect herbivory in this same species (Rousseaux *et al.* 1998). Seedlings of the southern beech tree, *Nothofagus solandri*, have shown inhibition of photosystem II in younger leaves and changes in plant architecture due to solar UV-B in New Zealand (Hunt & McNeil 1999). *Nothofagus* species dominate the forests of Tierra del Fuego and much of southern Argentina and Chile along the Andes Mountains. On the Antarctic Peninsula, solar UV-B decreased the leaf growth of the tussock grass *Deschampsia antarctica* over two growing seasons. In contrast, the cushion-forming *Colobanthus quitensis* was little affected. Increased temperature simulating global warming appeared to be of greater overall importance than solar UV-B changes for the plant growth and reproduction of *D. antarctica* and *C. quitensis* (Day *et al.* 1999). Short-term studies have not suggested any photosynthetic damage due to UV-B in these Antarctic species under field conditions (Huiskes *et al.* 1999; Montiel *et al.* 1999). All of the above studies in the Southern Hemisphere have primarily used solar UV-B attenuation rather than UV-B supplementation because present-day UV-B is already increased over historic levels on many days.

In the Northern Hemisphere high latitudes, UV-B supplementation using special UV fluorescent lamps has been employed to simulate anticipated ozone depletion. Some reductions in stem elongation and changes in herbivory, decomposition, and reproductive output were seen under supplemental UV-B for several dwarf shrub species in a heathland ecosystem at Abisko, Sweden (66° N), after two to four growing seasons

(Gehrke *et al.* 1995; Johanson *et al.* 1995; Gwynn-Jones *et al.* 1997; Phoenix *et al.* 2000). No long-term oxidative stress could be measured after 7 years of UV-B treatment in the one dwarf shrub evaluated, *Vaccinium myrtillus* (Taulavuori *et al.* 1999). The growth of potted mountain birch seedlings (*Betula pubescens*) native to these same Swedish heathlands was not affected by supplemental UV-B radiation in an outdoor study (Weih *et al.* 1998).

The impact of UV-B radiation on bryophytes has been much less considered than on vascular plants. Bryophytes are critical components of many polar and subpolar ecosystems because of their ability to absorb nutrients and water, and their role in carbon accumulation in peatlands. The subarctic mosses *Hylocomium splendens* and *Polytrichum commune*, which form part of the understory in subartic heathlands, showed reduced annual length increments in a 3-year study under supplemental UV-B and normal moisture conditions (Gehrke 1999). With additional water and elevated CO_2, supplemental UV-B increased some growth parameters (Gehrke *et al.* 1996). *Sphagnum fuscum*, a hummock-forming *Sphagnum* species that commonly dominates ombrogenous peatbogs in the Northern Hemisphere, had reduced height growth under supplemental UV-B during two growing seasons (Gehrke 1998). However, *S. fuscum* biomass production itself was not affected. Attenuation of solar UV-B in a *Sphagnum* peatland in Tierra del Fuego, Argentina, did not affect height growth of the cosmopolitan *Sphagnum magellanicum* after the first field season nor were the vascular plant species affected in this peatland (Chapter 2). Pigments, including chlorophyll and carotenoids, tended to decrease with more UV-B in some of the studies mentioned above, while UV-B-absorbing compounds (i.e., phenolics) were seldom affected.

The complex ecological relationships between bryophytes and vascular plants have been recognized to be important in boreal forests and *Sphagnum* peatlands (Oechel & Van Cleve 1986; van Breeman 1995). *Sphagnum* growth and peat formation results in a feed-forward successional trajectory in which acidic, anoxic, and nutrient-poor conditions created by *Sphagnum,* favor its own growth and depress the growth of vascular plants. *Sphagnum* growing around and sometimes over vascular plant stems also results in a direct loss of photosynthetic leaf area and altered plant architecture in many vascular species (Luken *et al.* 1985). The slow growth of these long-lived perennial plants and of *Sphagnum* results in very slow changes in competitve balance due to environmental changes. Therefore, assessing effects of altered solar UV-B in 3 years is unlikely. The study will continue for at least another 2 years along with parallel *in situ* field studies in a Carex sedge fen and a shrub-steppe community in Tierra del Fuego, Argentina.

The objectives of this 3-year field study were to: (1) document the daily solar UV-B environment and its relation to long-term changes in ozone for each calendar month of the growing season, (2) assess the role of solar UV-B in the growth and pigmentation of *Sphagnum* moss and associated vascular plants in long-term field plots under two different UV-B levels in a *Sphagnum* peatland, and (3) investigate retrospectively whether the stem elongation of *Empetrum rubrum*, a dwarf shrub found in our long-term *Sphagnum* plots, shows any negative correlation with ambient solar UV-B or other macroclimatic variables over an 8-year period. Morphological indicators of annual growth have been used for other dwarf shrubs and mosses to evaluate growth related to historical climate records (Callaghan *et al.* 1989, 1997).

Materials and Methods

EXPERIMENTAL SITE

Our experimental site is located 20 km west of the city of Ushuaia (55° S) on Isla Grande in the Province of Tierra del Fuego, Argentina. The general vegetation types include deciduous *Nothofagus* (southern beech tree) forest with *Sphagnum* and *Carex* peatlands lying in the mountain valleys and along the coast and some shrub-steppe communities in disturbed habitats. Our field plots are adjacent to a small lake (Laguna Negra) in the Parque Nacional Tierra del Fuego. Cover of *Sphagnum magellanicum* is nearly 100% and the prominent emerging vascular plants from the *Sphagnum* peat are *Nothofagus antarctica* (a deciduous southern beech tree), *Empetrum rubrum* (an evergreen dwarf shrub), and *Tetroncium magellanicum* (a rhizomatous perennial monocot). The relatively high pH and the vascular plant vegetation of this peatland suggest that it is minerogenous and in an early successional stage towards becoming a raised, ombrogenous peatland (Mataloni 1999; Searles, personal observation). Annual precipitation and temperature are 525 mm and 5.5° C with precipitation being distributed fairly evenly throughout the year (FAO 1985).

EXPERIMENTAL SETUP AND TREATMENTS

Twenty experimental plots of 1.4 x 2.0 m were selected in February and March 1996, and a boardwalk was constructed to avoid damaging the vegetation and altering the hydrology around the plots. The experimental UV-B manipulations were initiated in October 1996 during the austral spring and maintained in the plots for three growing seasons from October until early- to mid-March (autumn). Solar UV-B had decreased to very low levels by mid-March and leaf senescence was occurring. The plots were covered by snow most of each winter, and the treatments were reinitiated in the spring 2-3 weeks before bud break of *N. antarctica*. Measurements of the moss *S. magellanicum* indicated that minimal or no growth occurred in the plots during the fall and winter. The three growing seasons discussed in this paper are 1996-97, 1997-98, and 1998-99.

Half of the plots were covered by clear 38-µm thick "Aclar" plastic film (type 22A, Honeywell; formerly Allied Signal, Pottsville, PA, USA) to provide near-ambient UV-B radiation and half by 100-µm clear polyester plastic (optically equivalent to "Mylar-D," DuPont Co., Wilmington, DE, USA) to provide a reduced solar UV-B level. Both filters were perforated using an electric hot-wire melter that formed a perpendicular pattern of slits (slit size: 2 x 30 mm) covering 8% of the plastic film to allow for a partial, rather than complete, attenuation of solar UV-B. The slits also formed a matrix of louvers that allowed rainfall to pass through the plastic filters.

Ultraviolet-B radiation transmittance of the perforated films was measured using the SUV 100 scanning double monochromator (Biospherical Instruments, San Diego, CA, USA) in Ushuaia, Argentina, and in Logan, Utah, using an Optronic 742 double-grating spectroradiometer (Optronic Labs, Orlando, FL, USA). The instrument in Ushuaia is part of the US National Science Foundation UV Radiation Monitoring Network (Booth *et al.* 1994) and the spectroradiometer in Logan has been previously described by Flint and Caldwell (1998). Measurements were taken on 12 February 1997 in Ushuaia under mostly cloudy skies and in Logan on both sunny and cloudy days at a midday solar elevation equivalent to that of Ushuaia at the summer solstice (21 December). Some measurements were done in Logan because the implementation of an increased scanning protocol at the Ushuaia monitoring station did not allow sufficient time for our scans. During measurements at both locations, instantaneous photon flux density (PFD, 400-700 nm) was monitored using a quantum sensor (LiCor, Lincoln, NE, USA) to assess the stability of cloud cover over the duration of the scan. The quantum sensor was also used to evaluate PFD transmission through the perforated filters. All of the above measurements were performed 15-20 cm below the plastic films. In the field plots, the films were horizontally suspended 35 cm above the ground surface and 10 cm above the tallest vegetation. Some longer-term UV-B transmittance measurements were attempted in the field plots using portable UV meters, but accurate measurements under the clear polyester filter were difficult due to somewhat different spectral characteristics of individual UV sensors. The plastic filters were inspected every 2-3 days and replaced if damaged by the wind. All filters were replaced during the middle of the season.

Measurements of UV absorbance in a spectrophotometer did not indicate any photodegradation of either the clear polyester or the Aclar.

Sphagnum moisture content and air temperature were periodically measured within the field plots. The moisture content of the *Sphagnum* capitula (the top centimeter of *Sphagnum* moss) inside the plots was over 1000% by gravimetric determination throughout the growing season with no apparent differences under the two types of plastic film. Moisture content of the *Sphagnum* outside of the plots was also greater than 1000%. No differences in air temperature could be detected inside and outside of the plots likely because of the persisent winds. Monthly wind speeds are near 5 m s^{-1}. Further details of the temperature measurements can be found in Chapter 2.

SOLAR RADIATION MONITORING AT LAGUNA NEGRA

Ambient solar UV and visible radiation were monitored every 15 min at the Laguna Negra field site using three erythemally weighted broadband UV sensors (Solar Light Co., Model PMA2102, Philadelphia, PA, USA) and a quantum sensor, respectively, with all of the instruments connected to a Campbell Scientific 21X datalogger (Logan, UT, USA). These measurements were conducted during the second and third growing seasons to assess if the radiation environment at the field site was similar to that of the UV monitoring station in Ushuaia. Using integrated daily values, both the broadband UV meters and the quantum sensor at Laguna Negra (20 km west of Ushuaia) showed regressions of approximately $r^2 = 0.70$ with the equivalent wavebands from the SUV 100 spectroradiometer in Ushuaia during the 1997-98 growing season. Differences are primarily related to daily levels of cloudiness at the two locations, and solar UV-B radiation over the entire season was calculated to differ by no more than 2% between the Laguna Negra field site and the UV monitoring station in Ushuaia. Results for the third growing season are similar.

PLANT GROWTH MEASUREMENTS

Plant morphological and growth measurements were taken for the *Sphagnum* moss and emergent vascular plants each of the three growth seasons during the late spring and summer. To measure the height growth of *S. magellanicum*, six stainless steel cranked-wires were installed in each plot in October 1996 using the method of Clymo (1970). Two more cranked-wires were added both inside and outside of each plot in October 1997. Height growth was measured each year during mid-January and in late-February to early-March. Six sections (5 x 5 cm) of *S. magellanicum* carpet from each plot were harvested at the exact locations of the original six cranked-wires near the end of the third growing season in late-February 1999. The number of *S. magellanicum* stems was counted in the 3 x 3 cm interior of each section and seven of these stems were cut into segments representing the biomass for the first season and for the second and third seasons combined. The second and third years were pooled due to concern about the error associated with the cutting of the moss. No capitulum correction factor was employed and some of the biomass in the capitula (i.e., the compact apices of the *Sphagnum* stem) may become a part of the fourth season's growth due to stem extension. The *S. magellanicum* segments were dried at 60-70° C for 72 h and weighed. Volumetric density (mg cm^{-3}) and biomass production (g m^{-2}) were calculated based on the number of *Sphagnum* stems in the 3 x 3 cm section interiors, the segment dry weights, and cranked-wire height growth.

For the vascular plants, the length of eight stems of *E. rubrum* was measured per plot for all three seasons during mid-January of the third year using innate yearly growth markers including a set of smaller leaves and a short space with no leaves that separate yearly growth increments. These stems were then harvested for yearly biomass determinations and a later counting of leaf number. Stem length in *N. antarctica* was assessed each season on six stems per plot in early- to mid-December and again at the end of each season. During the second and third seasons, leaf number and leaf length were also measured. No harvesting of *N. antarctica* stems was done due to the low number of actively growing stems in these stunted trees. For *T. magellanicum*, leaf elongation was measured for a set of marked leaves in November and another set in December during the second and third growing seasons when leaf growth rates are highest. The initial leaf blade length of young leaves was recorded and then remeasured after 2 weeks as the leaf was nearing its full length. Only one set of leaves was measured the first season. The leaves of *T. magellanicum* develop directly from rhizomes in the *Sphagnum* moss and no aboveground stem is present.

PIGMENTATION

Carotenoids, chlorophylls, and UV-B-absorbing compounds were determined for *S. magellanicum*, and UV-B-absorbing compounds were measured for the vascular plants. Three to five sections of *Sphagnum* carpet per plot were removed during mid-February or early-March of each year, and the pigments of the top 5-6 mm of five *Sphagnum* capitula from each plot were extracted. The extraction was in 5 ml of 100% methanol heated at 60° C for 10 min, similar to Day *et al.* (1996). Absorbance measurements were made at selected wavelengths throughout the UV waveband for the UV-B-absorbing compounds and at 470, 652, and 665 nm to estimate total carotenoids and chlorophyll using the equations of Lichtenthaler (1987). In a separate procedure, UV-B-absorbing compounds of *S. magellanicum* were extracted in 5 ml of 1 M NaOH in the dark at room temperature for 48 h based on the method of Schnitzler *et al.* (1996) due to the large component of wall-bound phenolics in this species.

For the vascular plants, several leaves from the current year's growth of each species were harvested per plot, extracted in a 99:1 MeOH:HCl solution for UV-B-absorbing compounds, and stored at -20° C until absorbance was measured in a spectrophotometer, similar to Beggs & Wellmann (1985). The samples were taken each year in mid-February to early-March such as with *S. magellanicum*. Mid-November (spring) samples were additionally used for the deciduous *N. antarctica* shortly after full expansion of the young leaves during the second and third growing seasons.

RETROSPECTIVE ASSESSMENT OF *E. RUBRUM* GROWTH

The growth of *E. rubrum* in *Sphagnum* peatlands was determined by correlating an 8-year record of *E. rubrum* stem elongation with macroclimatic factors including UV-B radiation, visible light, precipitation, and temperature. The irradiance ratios of solar UV-B-to-visible radiation and 305-nm-to-340-nm radiation were also compared to stem elongation. The 305/340 nm ratio provides an indicator of ozone depletion because the transmission of 305 and 340 nm to the Earth's surface is similarly affected by cloudiness, while the two wavelengths have markedly different coefficients of ozone absorption (Frederick *et al.* 1994).

The 8-year record of *E. rubrum* stem elongation included the growing seasons from 1990-91 to 1997-98. In total, 182 stems growing in *S. magellanicum* were collected in October and November 1999 from four *Sphagnum* peatlands with 40-50 stems collected from each of three peatlands in the Parque Nacional Tierra del Fuego and a peatland in the Valley of Andorra near the city of Ushuaia. The Laguna Negra site with the experimental field plots was not included as one of the locations due to the amount of standing water in the peatland at the time of sampling. Annual stem elongation was measured in the laboratory using calipers. The number of leaves produced annually could not be accurately determined due to the loss of some leaves from the older portion of the stems.

The average annual stem length was compared to the early spring (October), early summer (December), and overall growing season (October-February) values for each of the climatic factors and irradiance ratios. The early spring was chosen *a priori* because ozone fluctuations associated with the Antarctic "ozone hole" are the most pronounced and the early summer because solar radiation is greatest at this time. Both the current and the previous growing season's climate data were used in assessing climate-related growth. The solar radiation data were provided by the US National Science Foundation UV monitoring station and the temperature and precipitation data by the Centro Austral de Investigaciones Cientificas (CADIC) in Ushuaia.

STATISTICAL ANALYSIS

To assess potential differences in plant response between the near-ambient and reduced UV-B levels, growth and pigmentation parameters were analyzed separately using analyses of variance (Tables B.4 - B.13 of Appendix B). Repeated measures analyses of variance were employed with UV-B and year as fixed-effects factors, and with plots and repeated measurements on plots as the random-effects factors. A three-way factorial was incorporated as a split-plot-in-time design for *T. magellanicum* and *N. antarctica* growth parameters with UV-B, year, and season (or month) being the three fixed-effect factors, and with plots and repeated measurements on plots again being the random-effects factors. The effects of UV-B were also determined for each year in all analyses, and the plot was considered the experimental unit for the UV-B treatment rather than individual plants or stems within plots to avoid pseudoreplication. Computations were performed using PROC MIXED in SAS Release 6.12 (SAS Institute, Inc., Cary, NC).

For the retrospective assessment of *E. rubrum* growth, simple correlations were performed between annual *E. rubrum* stem length and climatic variables. Climatic data from both the same growing season and the previous season were used for the correlations. The *E. rubrum* data from all four peatlands was combined for analysis because we were not interested in specific site differences. Results considered to be statistically significant in this study are accompanied by their *P*-values so the reader can assess the probability of significance.

Results

SOLAR UV-B FILTER TRANSMITTANCE AND MODEL CALCULATIONS

Detailed measurements of solar UV-B transmittance through the plastic filters were done to assess the influence of the perforations (2 mm x 30 mm slits) in the filters under different sky conditions; especially for the UV-B-absorbing filter, clear polyester (Fig. 5). Measurements of the perforated clear polyester near midday under cloudy conditions in Ushuaia revealed transmission of about 17% at 300 nm using the generalized plant action spectrum (Caldwell 1971). UV-B transmittance of an unperforated plastic filter is near zero. UV-B transmission on cloudy and clear sky days in Logan, UT (USA) were similar to each other when integrated over the entire filter surface. The clear sky transmission of solar UV-B through the clear polyester was determined by the integration of UV-B levels for the projected area under the perforations (8%) and the unperforated portion of the filter (92%). Under cloudy skies, the perforations do not create very different levels of UV-B because the UV-B is more diffuse. Percentage transmittance of the polyester increases greatly with wavelength through the UV-A starting at 320 nm and is about 90% throughout the visible waveband (400-700 nm). The transmission of Aclar, the UV-B-transmitting filter, is around 90% for all solar wavelengths.

Our solar UV-B treatments can be compared to changes in the UV-B environment over the past 20 years. Approximately, a 10-15% increase in plant-weighted biologically effective UV-B radiation since the early 1980's was calculated throughout the growing season (Fig. 6). The calculations are for clear sky conditions using satellite-based ozone values from the Total Ozone Mapping Spectrometer and the atmospheric transmission model of Frederick & Lubin (1988). Ozone values from 1980-86 were used to provide a baseline for stratospheric ozone values over Tierra del Fuego similar to Frederick *et al.* (1994). These years appear to have preceded most of the severe ozone depletion over Tierra del Fuego. Our near-ambient UV-B treatment, which is calculated as 90% of the 1990's ambient UV-B, is similar to the normal daily radiation one would expect from 1980-86. The UV-B attenuation treatment greatly reduced the UV-B to approximately 20% of the solar UV-B during the 1990's and 30% of the 1980-86 value.

MEASURED SOLAR UV-B RADIATION

Ground-based measurements from the US National Science Foundation UV Monitoring Network station in Ushuaia, Argentina, also show an increase in the noon

305/340 nm irradiance ratio for the 1990's compared to calculated, model values for 1980-86 (Fig. 7). As mentioned earlier, the 305/340 nm ratio provides an indicator of ozone depletion because transmission through clouds is similar for these wavelengths, while 305 nm has a much greater coefficient of ozone absorption than 340 nm. Validation of the Frederick & Lubin (1988) model has shown strong agreement between measured and calculated irradiances over a full annual cycle (Díaz *et al.* 1996). Although the average increase in the noon 305/340 nm ratio compared to the 1980-86 value is similar throughout the growing season, ozone fluctuations are greater in the spring than the summer as indicated by the much greater standard deviation among days in the 305/340 nm ratio.

The measured, integrated daily UV-B levels for each month during the growing season of our 3-year study are shown in Fig. 8 along with the averaged values and their standard deviations for the seven growing seasons prior to our experiment (1989-90 to 1995-96). For the first field season (1996-97), all of the months are similar to the seven-year mean except for the low value in October, which is in part related to uncommonly high ozone levels during this month. In contrast, springtime UV-B values in November and summer values in February were higher than the average UV-B for the second season (1997-98). Based on preliminary data, the monthly averages for the third season (1998-99) were not too dissimilar from the 1989-96 means although the January value was more than one standard deviation above the longer-term mean.

PLANT MORPHOLOGY AND BIOMASS

The morphology of the moss *S. magellanicum* was affected by UV-B reduction with height growth increasing and volumetric density decreasing relative to values under near-ambient solar UV-B (Fig. 9 and 10). The effect on height growth was not apparent until the second growing season (1997-98; $P = 0.02$) and continued during the third growing season (1998-99; $P = 0.07$). Repeated measures analysis of variance indicated a *P*-value of 0.05 for height growth over the 3 years of the study. The decrease in volumetric density with UV-B reduction occurred during the second and third seasons ($P = 0.04$). The increase in height growth and decrease in volumetric density under reduced UV-B compared to near-ambient UV-B tended to offset such that biomass production was not influenced during the three years (Fig. 10). *S. magellanicum* stem density under reduced UV-B (32,200 ± 7,400 m^{-2}) and near-ambient UV-B (30,000 ± 5,800 m^{-2}) was not significantly different. Based on cranked-wires installed at the beginning of the second growing season, height growth inside and outside of the plots was similar (data not shown). Some inhibition of moss growth was apparent during the first few weeks after the cranked-wires were installed as the moss started to grow around the 1 cm bend in the wire at the *Sphagnum* surface.

In the vascular plants, leaf elongation of *T. magellanicum* (the perennial monocot) was somewhat increased with UV-B reduction during November of the second ($P = 0.09$) and third ($P = 0.06$) years, but not in December (Fig. 11). The *P*-value for the interaction between UV-B and month was 0.10. Leaf elongation for the first season was not sampled in the same manner although the results were similar (see Chapter 2). There were no UV-B effects on growth parameters in *N. antarctica* (the southern beech tree). An interaction between UV-B and season was apparent for leaf length in *N. Antarctica* with leaves being slightly longer under UV-B reduction through the late spring and then somewhat shorter in the late summer (Table 3; P =0.03). In *E. rubrum* (the dwarf shrub), there were no UV-B effects on number of leaves, stem length, or aboveground biomass (Table 4). A small increase in the number of leaves per stem length with solar UV-B reduction was seen during the first and second years (P = 0.06). The densely packed, small leaves could not be readily counted for the most recent (third) year.

PIGMENTATION

No effects of solar UV-B reduction on chlorophyll or carotenoids were found in *S. magellanicum* (Table 5). The absolute values of chlorophyll and carotenoids for 1996-97 were misreported in Searles *et al.* 1999, but are shown properly in Table 5. The moss did show an interaction between UV-B and year for UV-B-absorbing compounds. These compounds tended to be greater under UV-B reduction than near-ambient UV-B the first year and less during the second and third years (Table 6; P = 0.04). The UV-B-absorbing compounds were approximately six times greater using sodium hydroxide than an acidified methanol extraction, but the relative percentage differences between the treatments were the same regardless of the solvent used in the extraction.

For the vascular plants, the current year's leaves of the evergreen *E. rubrum* showed some decrease in UV-B-absorbing compounds measured at 305 nm ($P = 0.08$) under solar UV-B reduction during the 3 years of the study using repeated measures analysis of variance. UV-B effects on older leaves of *E. rubrum* were not determined. A decrease in UV-B-absorbing compounds at 305 nm ($P = 0.05$) under reduced UV-B was also seen during the study for *T. magellanicum*. Interestingly, a stronger response in absorbance at 360 nm ($P = 0.004$) and 400 nm ($P = 0.01$) was apparent in this species. UV-B-absorbing compounds were not affected in young leaves of *N. antarctica* in the spring or in older leaves in the summer. Measurements of anthocyanins in *N. antarctica* and *E. rubrum* during the third growing season also showed no effect (data not shown).

RETROSPECTIVE ASSESSMENT OF *E. RUBRUM* GROWTH

Annual *E. rubrum* stem length did not show a significant negative relationship with ambient solar UV-B, the ratio of UV-B/visible radiation, or the 305/340 nm irradiance ratio for the 8-year record (1990-91 to 1997-98) (Table 7). Stem length for a given year was positively correlated with visible radiation and negatively related to rainfall for the month of December (early summer). These significant correlations are for climatic values from the same year as the *E. rubrum* growth. Relationships between previous year's climate and *E. rubrum* stem length were not significant (data not shown).

Discussion

LONG-TERM CHANGES IN SOLAR UV-B RADIATION

Atmospheric model calculations using satellite-based ozone column measurements in combination with ground-based UV measurements in Tierra del Fuego, Argentina, indicate that solar UV-B radiation has increased 10-15% throughout the spring and summer since the early 1980's when variation due to cloud cover is removed. A similar increase of approximately 15% in plant-weighted UV-B has occurred over Lauder, New Zealand (45 ° S), in the summertime during the 1990's (McKenzie *et al.* 1999). The increase in solar UV-B radiation during the summer at both locations is most likely associated with the general decrease in stratospheric ozone in the Southern Hemisphere. The passage of the Antarctic "ozone hole" over the southern tip of South America is more influential during the spring when rapid increases in solar UV-B associated with the "ozone hole" have been demonstrated by many authors (Bojkov *et al.* 1995; Kirchhoff *et al.* 1997; Orce & Helbling 1997; Rousseaux *et al.* 1999). The greater variation in the measured 305/340 nm irradiance ratio over Ushuaia, Tierra del Fuego, Argentina, during the spring than the summer as reported in this study is also indicative of the passage of the "ozone hole."

PLANT PERFORMANCE UNDER REDUCED SOLAR UV-B

The morphological effects of reduced UV-B on the growth of the moss *S. magellanicum* in Tierra del Fuego are comparable to the effects of UV-B enhancement in *S. fuscum* in Abisko, Sweden (Gehrke 1998). Both studies showed UV-B effects on height and measures of volumetric density that offset such that no changes in biomass production were apparent. A further study at Abisko also has revealed no effect of UV-B on biomass in *S. fuscum* (L.O. Björn, personal communication). Given that *S. magellanicum* and *S. fuscum* are most often found in open, sunny environments and have densely packed growth forms with little penetration of potentially damaging UV-B radiation, it may not be surprising that UV-B effects on production could not be detected during 2 or 3 years of study in Abisko and Tierra del Fuego. The production values of *S. magellanicum* in this study are within the range expected for this latitude (Lindholm & Vasander 1990).

The effects of solar UV-B reduction on plant morphology in the three vascular species in this *Sphagnum* peatland tended to be very moderate. *T. magellanicum* showed some indication of increased leaf elongation under reduced UV-B relative to near-ambient UV-B conditions during the second and third growing seasons in November, but not in December. With solar UV-B exclusion, seedling height increased and number of leaves decreased for a *Nothofagus* species in New Zealand growing in fertilized, potted conditions (Hunt & McNeil 1999). In our study, *N. antarctica* may not have shown an overall response to UV-B reduction because *N. antarctica* is severely stunted in these peatlands by harsh conditions such as low pH and nutrient limitation. Other environmental stresses most often appear to dampen the response to UV-B radiation (Caldwell & Flint 1994). Similarly to Gwynn-Jones *et al.* (1997) with *Empetrum* *hermaphroditum* using enhanced UV-B enhancement, the stem elongation of *E. rubrum* did not respond to three growing seasons of UV-B reduction. A previous study at Abisko did find a large 33% reduction in *E. hermaphroditum* after only 2 years (Johanson *et al.* 1995). The differences between the two Abisko studies could possibly be explained by earlier snowmelt and slightly drier conditions for the first study (Gwynn-Jones *et al.* 1997). These results for *Nothofagus* and *Empetrum* indicate that UV-B effects may only occur under specific site conditions and for certain species.

UV-B-absorbing compounds (i.e., flavonoids and other phenolics) in plants are most often considered to be potentially important protective mechanisms against UV-B radiation. Cell wall-bound phenolics in the genus *Sphagnum* contribute greatly to the resistance of *Sphagnum* material to decomposition (Verhoeven & Liefveld 1997). In Tierra del Fuego peatlands, these phenolics may stay bound in the leaves of *S. magellanicum* for several years (Searles, unpublished data). The interaction in this study between UV-B and year for UV-B-absorbing compounds suggests that *S. magellanicum* is slowly responding to solar UV-B reduction. Any change in phenolics may be important for the decomposition of recalcitrant *Sphagnum* peat over decades. The 10-20% decrease in UV-B-absorbing compounds in *E. rubrum* and *T. magellanicum* under solar UV-B reduction is similar in magnitude to the response of vascular plant species from other systems to solar UV-B exclusion (Searles *et al.* 1995; Hunt & McNeil 1999). However, three dwarf shrub species of the genus *Vaccinium* did not respond to UV-B enhancement in Abisko, Sweden (Phoenix *et al.* 2000).

The possibility of a cumulative effect of UV-B on plant growth over several years has been suggested for perennial vegetation in polar systems (Johanson *et al.* 1995; Day *et al.* 1999). In our 3-year study, distinguishing between a cumulative treatment effect and a variable response to UV-B reduction associated with yearly differences in solar UV-B is difficult. For example; the increase in height growth of *S. magellanicum* under solar UV-B reduction during the second season might suggest a cumulative effect since no UV-B response was apparent the first season. However, ambient solar UV-B was also approximately 20% higher during the second growing season. This resulted in a larger absolute difference in solar UV-B between near-ambient UV-B and reduced UV-B plots in the second growing season than in the first season. For a truly cumulative effect, a larger UV-B effect would be expected during the third season, but the magnitude of the response was actually less than the second season. Similar to the *Sphagnum* peatland, cumulative effects were not apparent after three years in the perennial plants at our *Carex* fen and shrub-steppe sites in Tierra del Fuego (Searles & Rousseaux, unpublished data).

RETROSPECTIVE ASSESSMENT OF *E. RUBRUM* GROWTH

Ambient, solar UV-B radiation and irradiance ratios were not significantly correlated with the annual stem length of *E. rubrum* growing in *Spaghnum* peatlands for our 8-year record. For the entire growing season, there were nonsignificant, negative correlations of $r = -0.46$ for solar UV-B and $r = -0.60$ for the ratio of UV-B/visible radiation. A longer annual record of stem growth is likely needed to better assess UV-B effects on *E. rubrum* given the variation in absolute ambient UV-B among years due to differences in ozone and cloud cover. Alternatively, this species may not be sensitive to solar UV-B. Even a reduction of solar UV-B by 80% over three growing seasons did not appear to affect stem length compared to the near-ambient control (90% of ambient UV-B). In the circumpolar dwarf shrub *Cassiope tetragona*, the ratio of the UV-B-absorbing compounds, myricetin and quercetin, showed a modest significant increase near Abisko over the last 180 years based on extractions of herbarium material (Björn *et al.* 1998). While this increase cannot be related to changes in UV-B radiation, UV-B enhancement did increase myricetin and quercetin in experimental field studies.

Significant relationships were seen with other climatic variables including visible light and rainfall. The strong positive relationship between visible light (i.e., photosynthetic flux density) in the early summer and stem length coincides well with the period of maximum growth rate in *E. rubrum*. The negative correlation between rainfall and stem length in the early summer is likely a function of rainfall being low during years when visible light is high and the sky less cloudy.

POTENTIAL ECOSYSTEM CONSEQUENCES

After the first field season, essentially no effects of UV-B were apparent on plant morphology and biomass in either the *S. magellanicum* or the vascular plants (Chapter 2; and results reported here). Some effects of UV-B on growth are now apparent after 3 years especially in the *S. magellanicum*, but the ecosystem-level consequences are still uncertain. The negative impact of solar UV-B on height growth of the moss may be beneficial for the vascular plants over the long-term if the rate of moss overgrowth of vascular plant tissue is decreased. In this study, *E. rubrum* did show some indication of an increase in the number of leaves per stem length under reduced UV-B. This may be a response to the greater height growth of *S. magellanicum* under reduced UV-B. Overgrowth of vascular plants by hummock-forming *Sphagnum* mosses has been demonstrated to result in significantly higher leaf/stem ratios in shrub species in an Alaskan peatland (Luken *et al.* 1985). The response of height growth and volumetric density in *S. magellanicum* in this study may also affect hydrological conditions such as the level of the water table. As mentioned earlier, the indication that UV-B-absorbing compounds including cell wall-bound phenolics are slowly responding to the UV-B treatment could have very long-term effects on decomposition and peat formation.

In addition to the experimental plots in the *Sphagnum* peatland in Tierra del Fuego, field sites are also present in a *Carex* sedge peatland and a shrub-steppe community dominated by the shrub *Chiliotrichum diffusum*. In the shrub-steppe community, reduction of solar UV-B has shown consistent increases in leaf growth over 3 years in the herbaceous ground layer, but not in the *C. diffusum* (Rousseaux, unpublished data). Aboveground growth of *Carex* was not affected after 3 years, but there is some indication of increased root growth with UV-B reduction (Zaller and Searles, unpublished data). A limitation to the study of the *Sphagnum* peatland is that belowground stem and root biomass of the vascular plant species cannot be easily sampled without extensive damage to the plots. Thus, our measurements of *E. rubrum* stem and leaf biomass do not represent all of the yearly biomass production. A large proportion of living biomass in *E. hermaphroditum* was found at a depth of 2.5-7.5 cm due to overgrowth by *Sphagnum* in a subarctic peat bog (Wallén 1986).

The potential role of trophic interactions as important components of ecosystem response to an altered UV-B climate has been stressed by Bothwell *et al.* (1994) and Paul *et al.* (1997). The number of testate amoebae inhabiting the *S. magellanicum* capitulum were influenced by solar UV-B reduction after one year (Chapter 2), and this effect continued after three seasons (Searles, unpublished data). Insect herbivory on the perennial herb *Gunnera magellanica* in the shrub-steppe community was also affected during the austral spring when solar UV-B levels are most affected by the Antarctic "ozone hole" (Rousseaux *et al.* 1998). These kinds of UV-B effects at other trophic levels and their interaction with plants may be of greater importance in determining ecosystem-level effects of UV-B radiation than direct UV-B effects on vegetation.

The overall role of solar UV-B radiation in *Sphagnum* peatlands in Tierra del Fuego, Argentina, will likely depend on the severity of stratospheric ozone depletion over the next several decades. The increase in ambient solar UV-B over the last two decades associated with ozone depletion is much less than the difference between the near-ambient solar UV-B (90% of ambient) and reduced UV-B (15-20% of ambient) radiation treatments in our 3-year study. If the ozone layer substantially recovers by the middle of this century as predicted by the World Meteorological Organization (WMO

1999), only some minor effects of increased solar UV-B may be expected given the subtle nature of effects found in our study.

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Table 3 Morphological measurements of *N. antarctica* during the second and third growing seasons under near-ambient solar UV-B (+UV-B) and reduced UV-B (-UV-B) radiation treatments. n =10 plots per UV-B level with means ± SE. Number of leaves was not counted during the December sampling

		1997-1998		1998-1999	
Variable	Month	+UV-B	-UV-B	+UV-B	-UV-B
Number of leaves (#)	December	---	---	---	---
	February	5.8 ± 0.4	6.6 ± 0.3	6.1 ± 0.4	6.5 ± 0.4
Stem length (mm)	December	12.4 ± 0.7	13.6 ± 0.7	11.0 ± 0.7	12.1 ± 0.8
	February	21.6 ± 1.8	22.1 ± 1.9	24.8 ± 3.3	25.3 ± 2.6
Number of leaves per stem length (# per mm)	December	---	---	---	---
	February	0.31 ± 0.01	0.34 ± 0.02	0.32 ± 0.03	0.32 ± 0.02
Leaf length (mm)	December	8.9 ± 0.4	9.1 ± 0.4	9.1 ± 0.3	9.4 ± 0.5
	February	8.3 ± 0.4	7.8 ± 0.5	8.8 ± 0.3	8.2 ± 0.4

Table 4 Morphological measurements of *E. rubrum* during the three growing seasons under near-ambient solar UV-B (+UV-B) and reduced UV-B (-UV-B) radiation treatments. n =10 plots per UV-B level with means ± SE. Number of leaves was not counted for the third growing season

	1996-1997		1997-1998		1998-1999	
Variable	+UV-B	-UV-B	+UV-B	-UV-B	+UV-B	-UV-B
Number of leaves (#)	28.0 ± 1.3	31.5 ± 2.0	34.1 ± 2.2	38.0 ± 2.2	---	---
Stem length (mm)	19.2 ± 1.6	18.7 ± 0.8	23.9 ± 2.2	22.9 ± 1.1	17.2 ± 0.9	16.2 ± 0.8
Number of leaves per stem length (# per mm)	1.51 ± 0.09	1.71 ± 0.09 *	1.47 ± 0.08	1.65 ± 0.05 *	---	---
Leaf mass (mg)	23.7 ± 1.5	26.9 ± 1.6	27.3 ± 2.2	29.0 ± 1.4	---	---
Stem mass (mg)	10.5 ± 1.3	10.6 ± 0.9	11.1 ± 1.5	10.2 ± 0.8	---	---
Shoot mass (leaf + stem)	34.2 ± 2.7	35.7 ± 2.3	38.4 ± 3.6	39.2 ± 2.1	17.7 ± 1.0	17.8 ± 1.1

* $P = 0.08$ in each case

Table 5 Chlorophyll and carotenoids in *S. magellanicum* during the three growing seasons under near-ambient solar UV-B (+UV-B) and reduced UV-B (-UV-B) radiation treatments. n =10 plots per UV-B level with means ± SE

	1996-1997		1997-1998		1998-1999	
Variable	+UV-B	-UV-B	+UV-B	-UV-B	+UV-B	-UV-B
Chl $a + b$ (μg g^{-1})	892 ± 53	891 ± 77	818 ± 44	878 ± 64	720 ± 40	756 ± 62
Chl a/b	1.63 ± 0.08	1.80 ± 0.13	1.94 ± 0.05	2.01 ± 0.05	1.57 ± 0.06	1.64 ± 0.10
Carotenoids (μg g^{-1})	204 ± 13	220 ± 15	241 ± 6	255 ± 12	191 ± 11	206 ± 12
Carotenoids / Chl	0.23 ± 0.01	0.25 ± 0.01	0.30 ± 0.01	0.30 ± 0.01	0.27 ± 0.01	0.28 ± 0.02

Table 6 Absorbance (Abs. mg^{-1} at 305 nm for a 1 ml extract) of UV-B-absorbing compounds during the three growing seasons under near-ambient solar UV-B (+UV-B) and reduced UV-B (-UV-B) radiation treatments. The results shown are for acidified methanol extracts except for *S. magellanicum* where sodium hydroxide was used. n =10 plots per UV-B level with means ± SE

		1996-1997		1997-1998		1998-1999	
Species	Month	+UV-B	-UV-B	+UV-B	-UV-B	+UV-B	-UV-B
Empetrum	February	4.35 ± 0.20	3.96 ± 0.22	3.18 ± 0.17	2.67 ± 0.21 *	3.47 ± 0.14	3.07 ± 0.18
Nothofagus	November	---	---	7.89 ± 0.70	7.45 ± 0.48	7.43 ± 0.78	7.07 ± 0.55
	February	6.62 ± 0.53	6.79 ± 0.46	6.06 ± 0.38	6.04 ± 0.30	6.99 ± 0.44	6.48 ± 0.56
Sphagnum	February	0.88 ± 0.04	0.99 ± 0.07	0.97 ± 0.03	0.92 ± 0.03	0.94 ± 0.04	0.90 ± 0.04
Tetroncium	February	---	---	1.74 ± 0.07	1.54 ± 0.06 *	2.16 ± 0.08	2.03 ± 0.07

* $P = 0.07$ in each case

Table 7 The correlation coefficients between *E. rubrum* stem length and macroclimatic factors or irradiance ratios for the growing seasons 1990-91 to 1997-98. The months shown represent the spring, early summer, and the entire growing season

Months	UV-B	visible	UV-B/visible	305/340 nm	temperature	rainfall
Oct.	-0.07	-0.05	-0.05	-0.05	0.18	-0.25
Dec.	0.22	0.76**	-0.17	-0.18	0.44	-0.64*
Oct.-Feb.	-0.46	-0.15	-0.60	-0.15	0.24	-0.59

* $P = 0.09$, ** $P = 0.03$

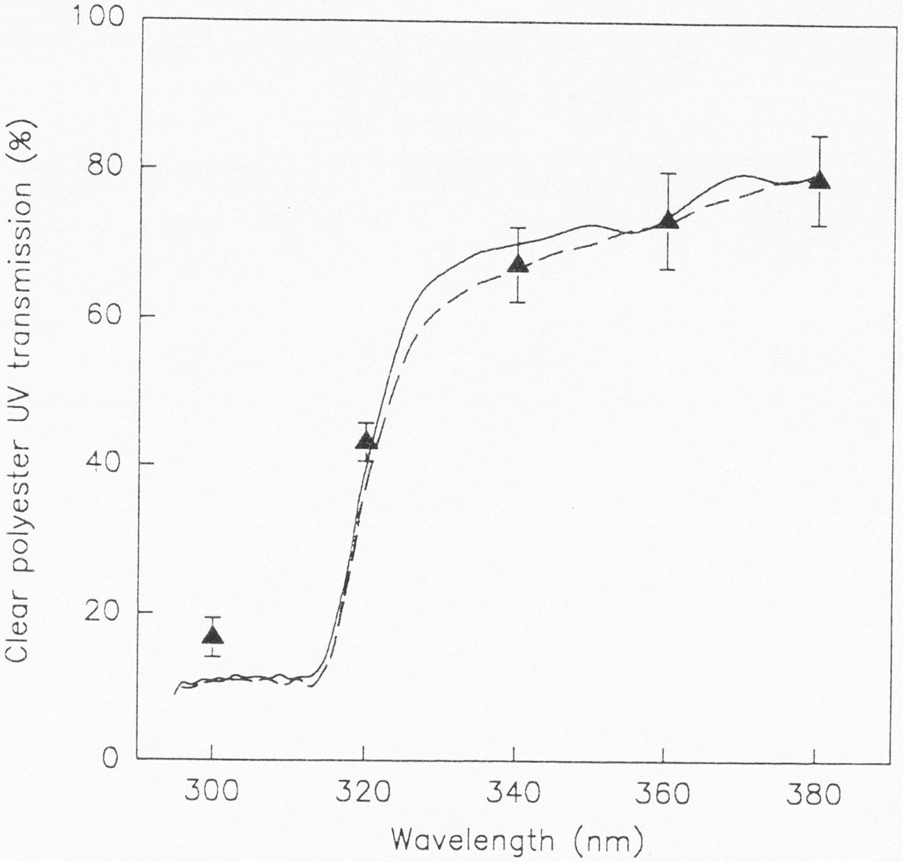

Fig. 5 Solar UV transmission (%) through perforated clear polyester filters under cloudy and clear sky conditions. Spectroradiometer scans were taken on 12 February 1997 in Ushuaia, Argentina, (triangles, mean ± standard deviation) under mostly cloudy skies and in Logan, Utah (USA), under both uniformly cloudy (solid line) and clear skies (dashed line) at a midday solar elevation equivalent to that of Ushuaia at the summer solstice (21 December). Measurements were only taken every 20 nm in Ushuaia.

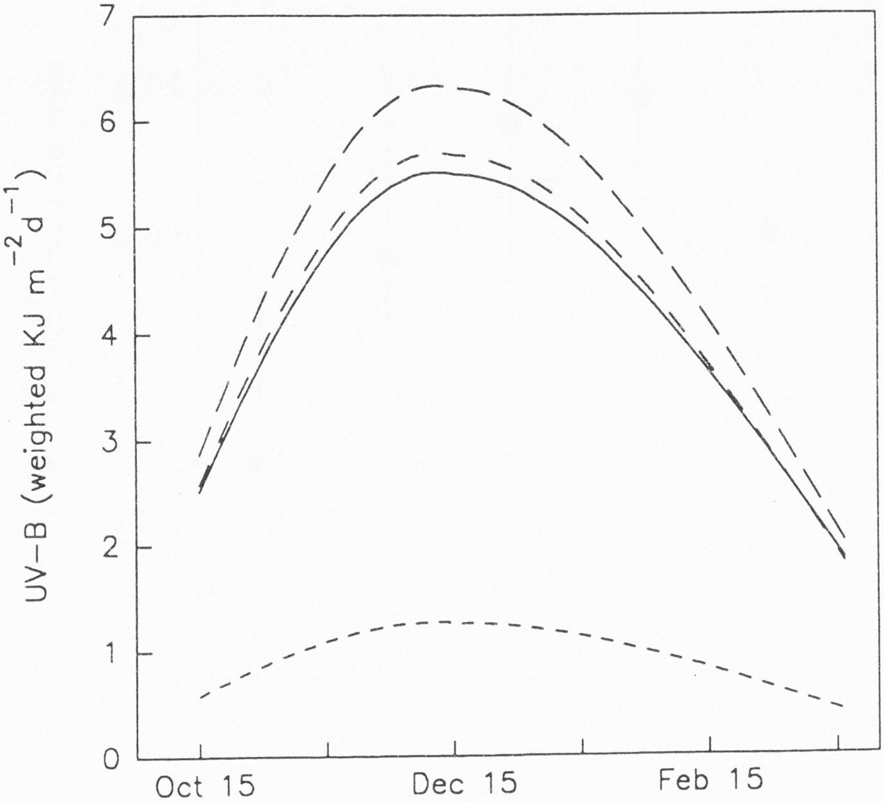

Fig. 6 Model calculations of daily, ambient solar UV-B radiation weighted by the generalized plant action spectrum in Ushuaia, Argentina, and the UV-B treatments. Calculated ambient solar UV-B levels are shown for the 1990's (top dashed line) and for 1980-1986 (solid line). The levels of solar UV-B in the near-ambient UV-B plots (second dashed line from top) and in the attenuated UV-B plots (bottom dashed line) are 90% and 20%; respectively, of the model-simulated UV-B for the 1990's. Only monthly ozone values from October, December, and March were used to calculate UV-B in order to generate a smooth curve.

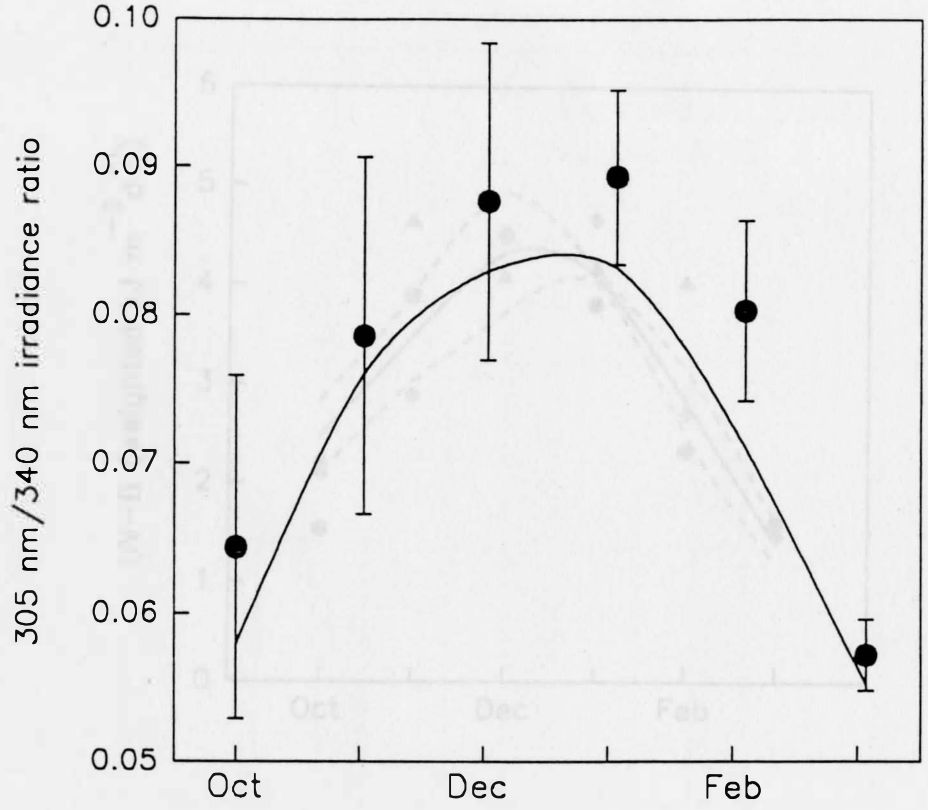

Fig. 7 Measured noon 305/340 nm irradiance ratios and model calculations for Ushuaia, Argentina. The solid line is the model-calculated 305/340 nm ratio at noon using monthly ozone values from 1980-86. The point for each month represents the measured monthly average at noon from the UV monitoring station in Ushuaia (1989-99). The error bars are the standard deviation among days for a given month. The narrow wavebands of 302.5-307.5 nm and 337.5-342.5 nm were used for all calculations. Data from the 1998-99 season are preliminary and subject to change by Biospherical Instruments, Inc. (San Diego, CA).

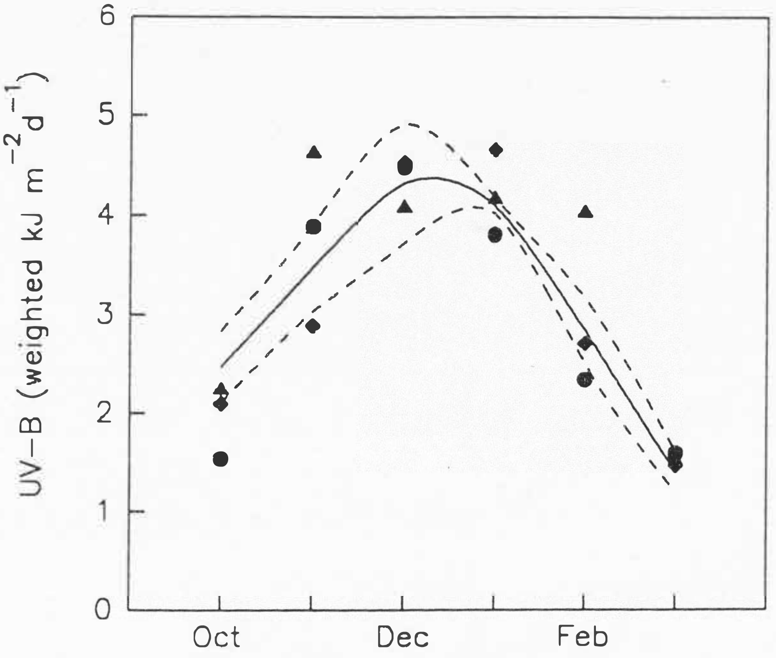

Fig. 8 Measured monthly averages of daily solar UV-B during the growing season weighted by the generalized plant action spectrum from 1989 to 1999 in Ushuaia, Argentina. The monthly average for all seven growing seasons (1989-90 to 1995-96) prior to our study is shown as the solid curve. The dashed curves are ± one standard deviation of the seven-year mean. The monthly averages of daily UV-B for each growing season of our study (1996-97, circles; 1997-98, triangles; 1998-99, diamonds) are also shown. Data from the 1998-99 season are preliminary and subject to change by Biospherical Instruments, Inc. (San Diego, CA).

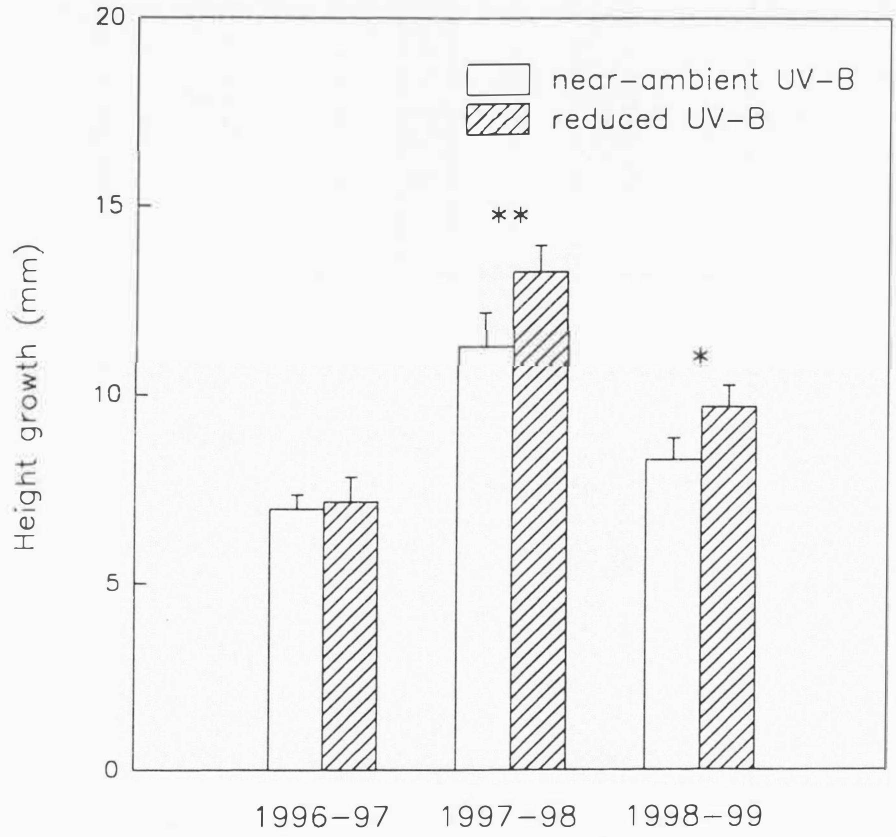

Fig. 9 The height growth of *S. magellanicum* during each of three growing seasons under near-ambient solar UV-B and reduced UV-B radiation treatments. n =10 plots per UV-B level with means ± the standard error. * $P = 0.07$, ** $P = 0.02$.

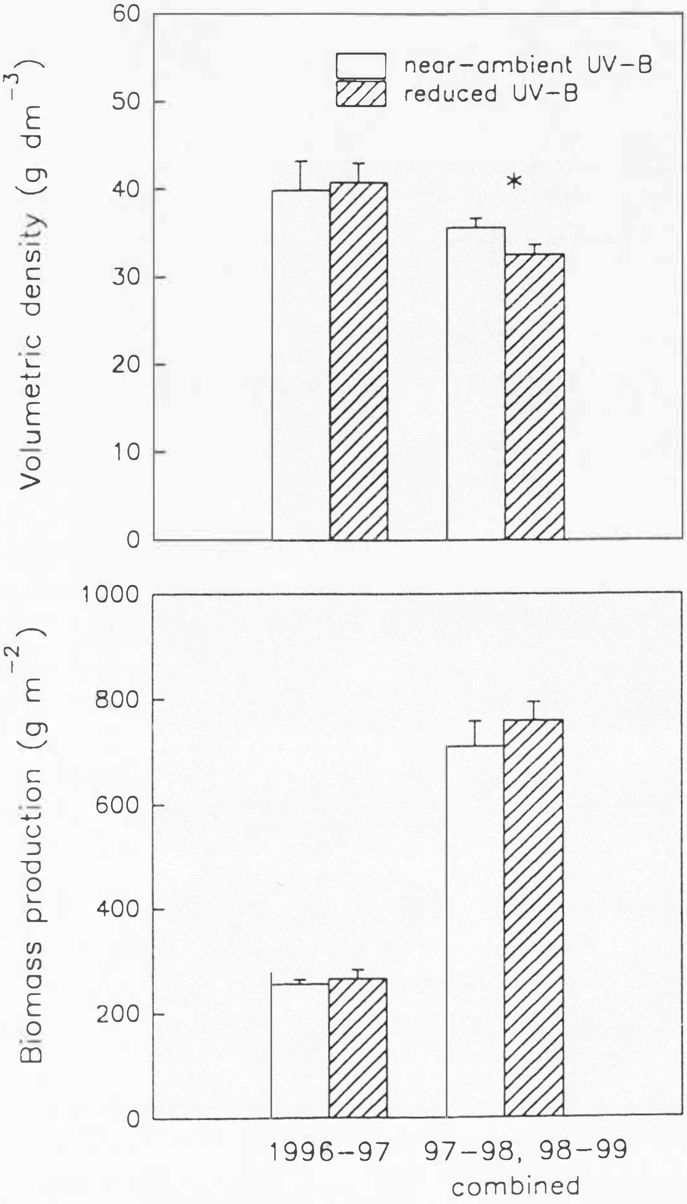

Fig. 10 The volumetric density and biomass production of *S. magellanicum* during the first growing season (1996-97) and the second and third growing seasons (1997-99) combined under near-ambient solar UV-B and reduced UV-B radiation treatments. The latter two seasons were harvested together to reduce error in cutting the yearly growth increments. n =10 plots per UV-B level with means ± the standard error. ** $P = 0.04$

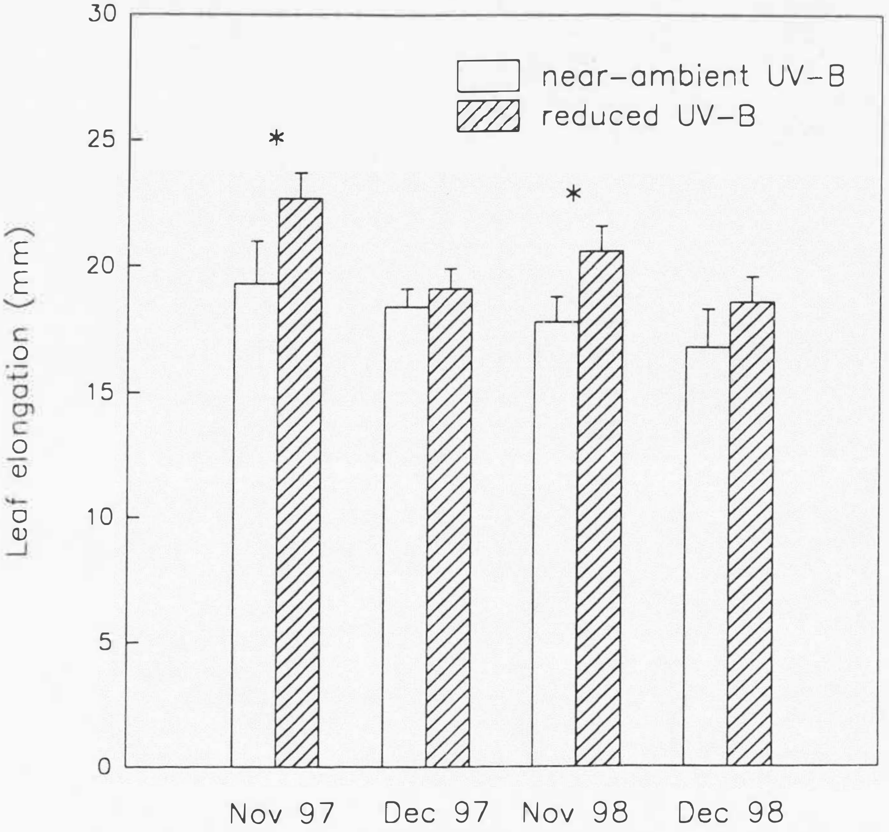

Fig. 11 The leaf elongation of *T. magellanicum* during November and December of the second and third growing seasons under near-ambient solar UV-B and reduced UV-B radiation treatments. Different sets of leaves were used each month. n =10 plots per UV-B level with means ± the standard error. * $P = 0.09$ in November 1997 and $P = 0.06$ in November 1998.

CHAPTER 4

THE INFLUENCE OF SOLAR ULTRAVIOLET-B RADIATION ON SOME MICROBIAL COMMUNITIES IN PEATLANDS OF TIERRA DEL FUEGO, ARGENTINA[1]

SUMMARY

Stratospheric ozone depletion occurs over Tierra del Fuego, Argentina, in the austral spring and summer due to the precession of the Antarctic "ozone hole" and the general erosion of the ozone layer. Field plots receiving either near-ambient or reduced solar ultraviolet-B radiation (UV-B) using specially louvered plastic filters were established in a *Sphagnum magellanicum*-dominated peatland and a *Carex* fen in the spring of 1996. The results reported here are for the effects of solar UV-B on microbial communities inhabiting *S. magellanicum* moss and the leaf surfaces of vascular plants during the second and third years of treatment under different UV-B conditions. The number of total testate amoebae (Protozoa, Rhizopoda) inhabiting *S. magellanicum* was greater under near-ambient solar UV-B than under reduced UV-B. The testate amoebae were mostly *Assulina muscorum*. The UV-B response for the testate amoebae occurred both for the 0-5 mm depth in the *S. magellanicum* moss where UV-B penetrates to some extent and the 5-10 mm depth where UV-B penetration is negligible. No response to UV-B was apparent for rotifers, nematodes, bacteria, microfungi, and a common

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[1] Coauthored by Peter S. Searles, Bradley R. Kropp, Stephan D. Flint, and Martyn M. Caldwell. Consent letters from Bradley Kropp and Stephan Flint for use of this manuscript in the dissertation are given in Appendix A.

microalga (*Euglena mutabilis*) in the *S. magellanicum*. The effect of solar UV-B was not statistically significant for the presence of fungi on the upper (adaxial) and lower (abaxial) leaf surfaces of the tree *Nothofagus antarctica* in the *S. magellanicum*-dominated peatland. However, the ratio of adaxial-to-abaxial yeast populations for the genus *Aureobasidium* and for total fungi was significantly lower under near-ambient solar UV-B than under reduced UV-B. Microfungi on foliage of the sedge *Carex decidua,* which has vertically oriented leaves, were not affected by the solar UV-B treatments. *Cladosporium* was the most common fungal genus on the *C. decidua*. The responses to UV-B manipulation in the *S. magellanicum*-dominated peatland are most likely direct effects of solar UV-B on the *N. antarctica* phylloplane fungi and indirect effects on the testate amoebae possibly mediated by UV-B-induced changes in the height growth of the *S. magellanicum*. These results emphasize the importance of examining the microbial response in a wide variety of organisms to assess the potential long-term effects of solar UV-B and stratospheric ozone depletion on peatland ecosystem function.

INTRODUCTION

Stratospheric ozone depletion leads to increased solar ultraviolet-B radiation (UV-B, 280-320 nm) over the tip of southern South America (55° S) with the passage of the Antarctic “ozone hole” (Bojkov *et al.*, 1995; Kirchhoff *et al.*, 1997). The more general deterioration of the ozone layer throughout much of the Southern Hemisphere also contributes to increased UV-B (Herman *et al.*, 1999). Over the last two decades, the number of ozone-depleted days associated with the "ozone hole" over Tierra del Fuego, Argentina, has increased greatly during the austral spring (Rousseaux *et al.*, 1999). Ground measurements of daily UV-B during both the spring and summer in Ushuaia, Tierra del Fuego, often exceed the predicted clear sky UV-B levels prior to significant ozone depletion in the early 1980's (Chapter 2). Even in New Zealand (45° S), the general deterioration of the ozone layer has led to increased peak ultraviolet intensities during the summer months (McKenzie *et al.*, 1999).

Direct effects of solar UV-B on organisms from terrestrial and aquatic ecosystems have been reported from southern South America and Antarctica. In Tierra del Fuego, midday DNA damage in the perennial herb *Gunnera magellanica* was well correlated with ambient UV-B levels during the austral spring (Rousseaux *et al.*, 1999). In this same species, leaf growth was consistently reduced by solar UV-B in a 3-year field study (Rousseaux, unpublished data). Similar effects of solar UV-B on the leaf growth of the grass *Deschampsia antarctica* have been found on the Antarctic peninsula over two growing seasons (Day *et al.*, 1999). The moss *Sphagnum magellanicum* did not show any changes in height growth or volumetric density during the first year of a 3-year study in Tierra del Fuego (Chapter 2). However, height growth decreased and volumetric density increased in response to solar UV-B to some extent during the second and third growing seasons (Searles, unpublished data). Direct effects of solar UV-B on aquatic organisms have included a reduction in the growth rate of a phytoflagellate population collected from the Beagle Channel in Tierra del Fuego (Hernando & San

Román, 1999), and reductions in phytoplankton productivity in Antarctic waters (Smith *et al.*, 1992; Helbling *et al.*, 1994).

The study of UV-B radiation on organisms is made more complicated if multiple trophic levels are considered. For example, mesocosm experiments at Environment Canada's experimental river flume facility indicated less sensitivity to solar UV-B in algae than in its consumers (Bothwell *et al.*, 1994). This difference in sensitivity contributed to counterintuitive increases in algae when exposed to UV-B. In terrestrial ecosystems, the effects of solar UV-B on phytophagous insects and plant fungal pathogens may be indirectly mediated by changes in the chemical or physical characteristics of plant leaves, or these organisms may be directly inhibited by UV-B (Mazza *et al.*, 1999; Paul, 2000). The herbivory of a nocturnal moth larvae on the herbaceous plant *G. magellanica* in Tierra del Fuego was indirectly reduced by UV-B apparently due to some change in the plant's leaf tissue when growing under solar UV-B radiation (Rousseaux *et al.*, 1998).

Sphagnum-dominated peatlands provide an opportunity to examine microbial responses at various trophic levels to solar UV-B. Protozoa, microalgae, rotifers, cyanobacteria, bacteria, microfungi, and nematodes all inhabit *Sphagnum* moss. They are often found living in the water film of *Sphagnum* leaves. The communities of these organisms are often dominated by a few species that can colonize even the upper 5 mm of the *Sphagnum* moss where solar UV-B penetrates. Gilbert *et al.* (1998a,b) recently reported changes in the structure of microbial communities in a French *Sphagnum* peatland due to nutrient additions. Some microalgae increased in relative biomass with nutrient inputs, while the proportion of testate amoebae (Protozoa, Rhizopoda) and other microalgae decreased. Testate amoebae represented as much as one-half of the microbial biomass in this peatland before nutrient addition. Testate amoebae have previously been used as bioindicators of the environmental impact of draining peatlands (Warner & Chmielewski, 1992) and for paleoenvironmental reconstructions because their shells remain well preserved in peat (Warner & Charman, 1994; Buttler *et al.*, 1996).

Many communities of microorganisms from natural ecosystems can be sensitive to UV-B. The first year of our field study in a *S. magellanicum*-dominated peatland in Tierra del Fuego, Argentina, indicated an increase in testate amoebae and rotifers under solar UV-B (Chapter 2). This may potentially be an indirect effect of solar UV-B mediated through another organism or through UV-B effects on the *Sphagnum* moss itself. Rotifers have been shown to be directly inhibited by UV-B in a high elevation lake in Chile (Cabrera *et al.*, 1997). Phylloplane fungi, particularly yeasts, growing on the upper surfaces of plant leaves seem to be directly affected by the UV-B radiation in sunlight, while the same fungal are most often not affected on the lower leaf surface (Ayres *et al.*, 1996; Newsham *et al.*, 1997). Leaf litter from a subartic dwarf shrub decomposed under UV-B in a laboratory incubation experiment was in general less colonized by fungi (Gehrke *et al.*, 1995). Different sensitivities of the individual fungal species to UV-B also led to a change in the structure of the decomposer community.

The objectives of the experiments described here were to: (1) assess the responses of microbial communities inhabiting *S. magellanicum* moss to solar UV-B radiation and (2) determine the sensitivity of phylloplane fungi living on *Nothofagus antarctica* (southern beech tree) and *Carex decidua* (a sedge) to UV-B. The experiments were conducted in long-term field plots in Tierra del Fuego, Argentina, receiving either near-ambient solar UV-B or attenuated UV-B radiation.

MATERIALS AND METHODS

Experimental sites

Our experimental sites include a *S. magellanicum*-dominated peatland and a *Carex* fen on Isla Grande in the Province of Tierra del Fuego, Argentina. The *S. magellanicum* site is 20 km to the west of the city of Ushuaia (55° S) and adjacent to a small lake (Laguna Negra) in the Parque Nacional Tierra del Fuego. Cover of *S. magellanicum* is nearly 100% and the prominent emerging vascular plants from the *Sphagnum* peat are *N. antarctica*, *Empetrum rubrum* (a dwarf shrub), and *Tetroncium magellanicum* (a rhizomatous perennial monocot). This peatland has previously been described as minerotrophic (Mataloni, 1999). The *Carex* fen site is located on private land in Andorra Valley just outside of Ushuaia. The sedges *Carex decidua* and *Carex curta* (also called *C. canescens*) dominate the plant community.

Experimental setup and treatments

The experimental UV-B manipulations were maintained from the early spring to early fall (October-March) for 3 years in 20 plots (1.4 x 2.0 m each) at the *S.*

magellanicum site and 18 plots (1.4 x 1.5 m each) at the *Carex* fen starting in 1996. In the late fall when the treatments were discontinued each year, solar UV-B is very low and biological activity at least of the plant species is minimal. The plots are covered by snow in the winter and the UV-B treatments were restored shortly after snow melt. Half of the plots received near-ambient solar UV-B below "Aclar" plastic film (Honeywell Co., Pottsville, PA, USA; formerly Allied Signal) and half received attenuated UV-B below clear polyester plastic (optically equivalent to "Mylar-D"; DuPont Co., Wilmington, DE, USA). Both films were perforated using an electric hot-wire melter to allow for a partial, rather than complete attenuation of solar UV-B and for rainfall to pass through the plastic. Ultraviolet-B radiation transmittance of the perforated clear polyester was 15-20% at 300 nm using the SUV 100 scanning double monochromator (Biospherical Instruments, San Diego, CA, USA). The instrument is part of the US National Science Foundation UV Radiation Monitoring Network and described by Booth *et al.* (1994). The perforated polyester has a sharp rise in transmittance around 320 nm similar to traditional unperforated clear polyester and transmitted about 90% of visible radiation (400-700 nm). Aclar transmits approximately 90% of all UV and visible wavelengths. Visible radiation was measured as photon flux density using a quantum sensor (LiCor, Lincoln, NE, USA). Measurements of air temperatures indicated that the temperatures in the plots under the plastic films were not substantially different from those in the ambient environment (Chapter 2). This is likely due to average wind speeds of almost 5 m s^{-1} in the spring and summer. Soil moisture content of the *Carex* plots to 15 cm soil depth and moisture content of the upper 1 cm of *S. magellanicum* stems were also similar inside and outside of plots and between filter types. Time-domain reflectometry was used for the measurements in the soil of the *Carex* fen, and gravimetric determination was used for the stems of *S. magellanicum*.

Field sampling

Three 3 x 3 cm sections of *S. magellanicum* from each plot were cut with a knife and placed in individual plastic bags on 4 March 1998 (early fall) at the *S. magellanicum* site for later extraction of testate amoebae, rotifers, nematodes, and microalgae. A second sampling was conducted the third week of February 1999 with five sections of the moss collected from each plot. Sections of *S. magellanicum* were similarly sampled on 27 January 1999 (mid-summer) for microfungi and bacteria. For the fungi sampling from the *N. antarctica* phylloplane, 10 leaves were excised from *N. antarctica* stems growing in each *S. magellanicum* plot using alcohol-cleansed forceps on 22 January 1999. The small leaves (about 1 cm in length) were placed into one humidified sterile Petri dish for each plot. At the *Carex* site, 10 leaves of *C. decidua* were collected from each plot on 3 February 1999 and stored in one 50-ml sterilized plastic tube per plot. All samples were transported to the laboratory facilities at the Centro Austral de Investigaciones Cientificas (CADIC) within 2-3 h. Microbial samples in the *S. magellanicum* moss were stored at 5° C and generally processed within 48 h. The phylloplane fungal samples were always processed the day of collection.

Extraction and quantification of microorganisms

To prepare the samples of testate amoebae, rotifers, nematodes, and microalgae for extraction, three to five stems of *S. magellanicum* were separated from each of the 3 x 3 cm sections collected in each plot. The top 1 cm of each *S. magellanicum* stem was then cut into two segments representing the 0-5 and 5-10 mm depths of the *S. magellanicum* carpet. Attenuation of solar UV-B was previously measured to be 99% at a depth of 6 mm in the *S. magellanicum* (Chapter 2). The stem segments from a given plot were combined for each depth and fresh mass of the moss was measured. The actual extraction and counting followed Tolonen *et al.* (1992). Briefly, the *S. magellanicum* stem segments were cut into smaller pieces with scissors and stirred in 15 ml water for 5 min along with two dissolved tablets each containing 12,500 spores of *Lycopodium* (Stockmarr, 1971; Lund University Batch no. 124961), which are used as an exotic marker. After filtration through a 750-µm sieve, the microfauna and flora were concentrated by centrifugation (2000 r.p.m) for 2 min, and stored in rose bengal stain and glycerine in 1 ml Eppendorf tubes. Testate amoebae, rotifers, and nematodes were counted in a drop of the concentrate under a microscope at 100x and a common microalgal *Euglena* species was counted at 250x. Other smaller and less common microalgae were not counted. Absolute numbers of the organisms were calculated on a *S. magellanicum* fresh mass basis using the *Lycopodium* spores as a reference. Testate amoebae were identified at least to the genus level using Ogden & Hedley (1980). The *Euglena* species was identified as *E. mutabilis* by Dr. Guillermo Tell at the University of

Buenos Aires using Tell & Conforti (1986). The nematodes and rotifers were not identified other than noting that the rotifers were predominately of the order Bdelloidea.

The fungal and bacterial samples from the *S. magellanicum* site were prepared similarly for extraction to the other microorganisms inhabiting *S. magellanicum* except that sterile conditions under a laminar flow hood were employed. Extraction from the *S. magellanicum* stem segments involved shaking the segments in a plastic tube with 30 ml of sterilized water for 45 s. There was one plastic tube for each depth and plot. To quantify colony-forming units (CFU) of fungi, a 250 μl volume from each tube was pipetted onto three Petri dishes containing potato dextrose agar medium (PDA; Difco, Detroit, MI) and streptomycin (1.0 g l^{-1} PDA) to inhibit bacterial growth. Three separate 1:10 and 1:100 serial dilutions from the shaken plastic tubes were performed to assess the number of bacteria CFU. From each of the 1:100 dilutions, 250 μl were pipetted onto three Petri dishes containing PDA. The bacteria and fungi CFU were counted 3 days after culturing.

For the phylloplane fungi, adaxial (upper leaf surface) and abaxial (lower leaf surface) leaf impressions of the 10 *N. antarctica* leaves from each plot were performed by gently pressing each leaf surface onto PDA medium using forceps under sterile conditions in a laminar flow hood. Three Petri dishes were used for each plot; the plates were stored at room temperature (20° C); and the fungal colonies were counted after 3 and 11 days. The leaves of the *N. antarctica* used for impressions were traced to determine if a correction for potential leaf area differences between the UV-B treatments was needed. Leaf impressions of *C. decidua* were made for 10 leaves from each plot using one 2-cm long section from each leaf blade. Only one leaf surface of the *C. decidua* leaves was used for the impressions because there was no apparent difference in UV-B environment between leaf surfaces for these vertically oriented sedge leaves. There were two Petri dishes per plot and CFU were counted after 2 days. Individual colonies could not be distinguished later for further counting. The microfungi in the *S. magellanicum* and on the leaves of *N. antarctica* and *C. decidua* were identified to genus according to Gams (1977), Carmichael *et al.* (1980), and Von Arx (1981).

Statistical analyses

To assess potential differences between near-ambient and reduced UV-B levels for each microorganism, microbial numbers were analyzed using mixed-model analysis of variance (Tables B.14 - B.19 of Appendix B). When sampling was performed both the second and third years (i.e., for testate amoebae, rotifers, nematodes, and *Euglena*), UV-B and year were the fixed-effects factors with plot and repeated measurements on plots as the random-effects factors. Effects of UV-B for each year were also tested in these analyses. UV-B and plot were the only factors in the analyses of bacteria and fungi, which were only sampled during the third year. The plot was considered the experimental unit for all analyses and log transformations of the data were used when the residuals from the statistical model were not normally distributed. All computations were performed in SAS Release 6.12 (PROC MIXED, SAS Institute, Inc., Cary, NC).

RESULTS

Identification of testate amoebae and fungi

The testate amoebae community in the upper centimeter of *S. magellanicum* was dominated by the genus *Assulina* with most individuals being *A. muscorum*. *Assulina* spp. represented 80-90% of all tests (i.e., shells) counted in both the 0-5 mm and 5-10 mm near-surface depths of the *S. magellanicum* moss. Tests from other genera including *Heleopera*, *Euglypha*, and *Nebela* were much less common. The fungi cultured from *S. magellanicum* were identified to genus as *Mortierella*, *Penicillium*, and *Mucor*. *Mortierella* comprised 75% of all colonies in the 0-5 mm depth and greater than 90% of all colonies for the 5-10 mm depth. *Penicillium* was generally more common than *Mucor* especially in the upper depth. Colonies of the yeast *Aureobasidium* were 55-65% of all colonies on both adaxial and abaxial leaf surfaces of *N. antarctica* with other genera including *Penicillium*, *Ulocladium*, and *Cladosporium*. *Cladosporium* comprised almost all of the colonies cultured from the leaves of *C. decidua* with a few colonies of *Penicillium*.

Effects of solar UV-B

The number of *Assulina* and total testate amoebae was greater under near-ambient solar UV-B than attenuated UV-B at the 0-5 mm sampling depth in the *S. magellanicum* moss when analyzing the UV-B effect over both years, 1998 and 1999 ($P \leq 0.05$; Fig. 12). The response to solar UV-B of the *Assulina* ($P = 0.07$) and total testate amoebae ($P = 0.06$) was similar at the 5-10 mm depth, but not as statistically significant. No interactions between solar UV-B and year were apparent although the effect of solar UV-B was somewhat more pronounced during the third year. The number of rotifers, nematodes, *E. mutabilis* (the microalga), microfungi, and bacteria inhabiting the upper centimeter of the *S. magellanicum* did not respond to solar UV-B (Table 8, Table 9). Solar UV-B did not affect the composition of genera in the testate amoebae and microfungi communities (data not shown). Identification was not done to the genus level for the other communities.

Correlations between total testate amoebae and various parameters of *S. magellanicum* growth and pigmentation were calculated to potentially explain the greater number of testate amoebae under near-ambient UV-B than under attenuated UV-B. Height growth, mass per unit of height growth, stem density, UV-B-absorbing compounds, chlorophyll, and carotenoids were measured in each of the plots as part of another study. The number of total testate amoebae was negatively correlated with *S. magellanicum* height growth during 1998 and 1999 (Fig. 13). Correlation coefficients between testate amoebae numbers and height growth were $r = -0.66$ under near-ambient UV-B and $r = -0.68$ under attenuated UV-B at the 0-5 mm sampling depth ($P \leq 0.05$). Similar correlation coefficients of $r = -0.64$ under near-ambient UV-B and $r = -0.76$ under reduced UV-B were calculated at the 5-10 mm depth ($P \leq 0.05$). The UV-B treatments did not affect the slopes of these correlations. The number of testate amoebae was not significantly correlated with any of the other *S. magellanicum* growth and pigmentation variables, nor did other microbes show any consistent relationships with these variables (data not shown). Of the *S. magellanicum* growth and pigmentation parameters, only height growth and mass per unit of height growth were affected by solar UV-B (Searles, unpublished data).

Solar UV-B did not have a statistically significantly affect on the presence of fungi on the adaxial and abaxial surfaces of *N. antarctica* leaves (Fig. 14a). However, the ratio of leaf adaxial-to-abaxial populations of the yeast *Aureobasidium* was lower under near-ambient UV-B than attenuated UV-B ($P \leq 0.05$; Fig. 14b). The adaxial-to-abaxial ratio of total fungi on the *N. antarctica* phylloplane was also somewhat lower under near-ambient UV-B ($P = 0.08$). The *Cladosporium*-dominated phylloplane of *Carex decidua,* which has vertically oriented leaves, was not affected by solar UV-B (Fig. 15).

DISCUSSION

Testate amoebae were consistently increased under solar UV-B throughout 3 years of study (Chapter 2; Fig. 12). This increase at first seems counterintuitive given that solar UV-B is generally detrimental to organisms. Indirect effects of UV-B on aquatic organisms have been suggested to be common and often complex (Williamson, 1995). For example, Herndl *et al.* (1997) found an indirect stimulation of bacterial activity under solar UV-B in the Adriatic Sea due to direct effects of UV-B on dissolved organic matter, which is consumed by the bacteria. However, this response was only seen when vertical mixing of the water column was properly considered.

The increase in testate amoebae inhabiting *S. magellanicum* was most likely an indirect response to solar UV-B. A strong negative correlation occurred between the number of testate amoebae and *S. magellanicum* height growth during the second (1998) and third (1999) years of the study. This correlation indicates that the number of testate amoebae was greater with less height growth, and that the relationship was similar for both near-ambient UV-B and reduced UV-B treatments. During these same years, the height growth of *S. magellanicum* was directly inhibited by near-ambient solar UV-B (Searles, unpublished data). Testate amoebae may potentially have had more time to colonize and reproduce on the moss capitula (i.e., the actively growing apices) of the more slower growing *S. magellanicum* plants receiving near-ambient solar UV-B. Alternatively, *S. magellanicum* height growth may merely be correlated with an unknown factor influenced by UV-B. Although a UV-B effect was seen for testate amoebae during the first year of the study and no effect was detected for the height growth of the moss, a subtle effect of UV-B on height growth may have been less easily detectable because the wires installed to measure the *S. magellanicum* caused some initial inhibition of height growth.

None of the microbial populations in *S. magellanicum* appeared to show a significant, direct response to solar UV-B in this study. The low transmittance of UV-B in the moss may explain the lack of direct responses. As mentioned earlier, attenuation of solar UV-B is approximately 99% at a depth of 6 mm in the *S. magellanicum*. A direct UV-B effect on the testate amoebae seems unlikely because the increases in testate amoebae occurred for both the 0-5 mm and 5-10 mm sampling depths. Among the fungi, *Mortierella* showed a nonsignificant 25% reduction in numbers at 0-5 mm in the moss under solar UV-B and no change at the 5-10 mm depth. This would suggest a direct effect on *Mortierella* at 0-5 mm, but the *P*-value for the decrease was not significant at $P = 0.12$. In high elevation alpine lakes where UV-B transmittance is great, populations of rotifers have been shown to be sensitive to UV-B (Cabrera *et al.*, 1997; Vinebrooke & Leavitt, 1999). Similarly, high solar UV-B in the summer in Portugal impaired the motility of the microalga *Euglena gracilis* although this was for laboratory-grown individuals (Häder, 1986).

All of the microbes in the *S. magellanicum* except for the rotifers had greater numbers at the 5-10 mm depth in the moss where UV-B and visible light are lower than at the 0-5 mm depth. This even included the photosynthetic *Euglena mutabilis*. Potential stresses such as periodic drying of the moss surface in the summer and visible light photoinhibition may be more important in determining the distribution of these microbes than avoidance of solar UV-B radiation. There is also the possibility that our sampling was not often enough or properly timed to detect UV-B effects in some of these organisms. The yearly samplings for the testate amoebae, rotifers, nematodes, and *E. mutabilis* were done in the late summer and early fall when UV-B levels were decreasing. For the testate amoebae, many potential difficulties associated with sampling frequency are likely alleviated because the tests (i.e., shells) do not deteriorate and an integrated measurement of testate amoebae number over time is possible.

A single cosmopolitan genus tended to dominate many of the microbial communities inhabiting the *S. magellanicum*. Individuals of *A. muscorum* represented the majority of the testate amoebae in the upper centimeter of the *S. magellanicum* moss. *A. muscorum* was previously found in every sample from seven different peatlands in southwestern Ontario, Canada (Warner, 1987) and is common across Europe (Mitchell *et al.*, 2000). Vucevitch (1974) previously identified 45 species of testate amoebae from *Sphagnum* peatlands in Tierra del Fuego, but most of these species appear to be uncommon even at lower depths in the *Sphagnum* peat. Similar to our findings in Tierra del Fuego, a *Mortierella* species dominated the microfungal community in the upper 2 cm of *S. magellanicum* in a peatland in England (Dickinson & Maggs, 1974) and was a common genus in a mixed mire in northern Sweden (Nilsson *et al.*, 1992). The presence of high frequencies of a few taxa is probably related to harsh conditions in these peatlands such as low pH.

The phylloplane fungi of the tree *N. antarctica* responded to solar UV-B in the *Sphagnum* peatland with a decrease in the ratio of fungi on the adaxial to the abaxial leaf surface. The most common genus on *N. antarctica* leaves was the yeast *Aureobasidium*. Leaf yeasts have also been affected by both solar UV-B and artificially enhanced UV-B in England under field conditions (Ayres *et al.*, 1996; Newsham *et al.*, 1997). Similar to our results with UV-B attenuation, Newsham *et al.* (1997) found a greater effect of enhanced UV-B on *Aureobasidium pullulans* on adaxial leaf surfaces of *Quercus robur* than on the abaxial surfaces. The fungus *Cladosporium* on the *Carex decidua* leaves was not affected by solar UV-B in the *Carex* fen. Similarly, no effect of UV-B on *Cladosporium* spp. was detected under enhanced UV-B in a field study in England or in a laboratory experiment, possibly due to the dark pigmentation of *Cladosporium* spp. (Newsham *et al.*, 1997; Moody *et al.*, 1999). In general, the reductions in leaf yeasts appear to be direct effects of UV-B because the number of colony-forming units is most often affected on the adaxial leaf surface where UV-B is high and not on the abaxial surface. Measurements of the leaf growth and crude phenolic compounds in *N. antarctica* growing under the UV-B treatments (Searles, unpublished data) did not indicate that the UV-B effects on the fungi were mediated through *N. antarctica*. However, data on tissue nitrogen, leaf surface properties, and phenolics with a specific role in inhibiting fungi were not measured as suggested by Paul (2000).

The changes in microbial population sizes and communities in the *S. magellanicum*-dominated peatland by solar UV-B radiation may have potential consequences for ecosystem functioning. Testate amoebae can represent up to 50% of microbial biomass in *Sphagnum* peatlands (Gilbert *et al.*, 1998a), and smaller testate amoebae such as *Assulina* spp. are likely important consumers of bacteria. If an increase in testate amoebae under solar UV-B ultimately affects bacterial numbers, this may affect decomposition of *Sphagnum* moss. UV-B-induced reductions of phylloplane fungi may also initially affect decomposition of leaves of the deciduous *N. antarctica*. The likelihood of such ecosystem effects has increased in Tierra del Fuego, Argentina, with the increasing levels of solar UV-B radiation over the last 20 years due to pronounced stratospheric ozone depletion at the southern tip of South America.

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Table 8 *Number of rotifers, nematodes, and a microalga* (Euglena mutabilis) *in* Sphagnum magellanicum *moss under near-ambient solar UV-B and attenuated UV-B radiation treatments*

		1997-1998		1998-1999	
Microorganism	Depth of *Sphagnum*	+UV-B	-UV-B	+UV-B	-UV-B
Rotifers	0-5 mm	2736 ± 326	2152 ± 287	1728 ± 133	1668 ± 168
	5-10 mm	1137 ± 252	1074 ± 256	814 ± 122	763 ± 165
Nematodes	0-5 mm	758 ± 140	572 ± 124	559 ± 72	564 ± 64
	5-10 mm	992 ± 178	784 ± 216	812 ± 128	744 ± 107
Euglena	0-5 mm	11531 ± 2801	10906 ± 4569	21889 ± 9452	23692 ± 7075
	5-10 mm	18681 ± 4632	16912 ± 5367	46647 ± 15130	50022 ± 10876

+UV-B, near-ambient UV-B radiation (90% of ambient); -UV-B, attenuated UV-B radiation (15-20% of ambient).
Data are shown as number of microorganisms per gram of *S. magellanicum* fresh mass for the near-surface depths of 0-5 mm and 5-10 mm in the *S. magellanicum* moss. n =10 plots per UV-B level with means ± SE. Analyses of variance showed no significant differences between treatments.

Table 9 *Colony-forming units of the dominant fungal genus* Mortierella, *total fungi, and bacteria in* S. magellanicum *moss under near-ambient solar UV-B and attenuated UV-B radiation treatments*

		1998-1999	
Microorganism	Depth of *Sphagnum*	+UV-B	-UV-B
Mortierella	0-5 mm	1211 ± 199	1608 ± 214
	5-10 mm	3340 ± 528	3396 ± 347
total fungi	0-5 mm	1841 ± 469	1913 ± 161
	5-10 mm	3402 ± 634	3690 ± 409
bacteria	0-5 mm	$3.8 \times 10^5 \pm 1.4 \times 10^5$	$4.0 \times 10^5 \pm 1.6 \times 10^5$
	5-10 mm	$7.4 \times 10^5 \pm 1.9 \times 10^5$	$7.3 \times 10^5 \pm 1.7 \times 10^5$

+UV-B, near-ambient UV-B radiation (90% of ambient); -UV-B, attenuated UV-B radiation (15-20% of ambient).

Data are shown as number of microorganisms per gram of *S. magellanicum* fresh mass for the near-surface depths of 0-5 mm and 5-10 mm in the *S. magellanicum* moss. n =10 plots per UV-B level with means ± SE. Analyses of variance showed no significant differences between treatments.

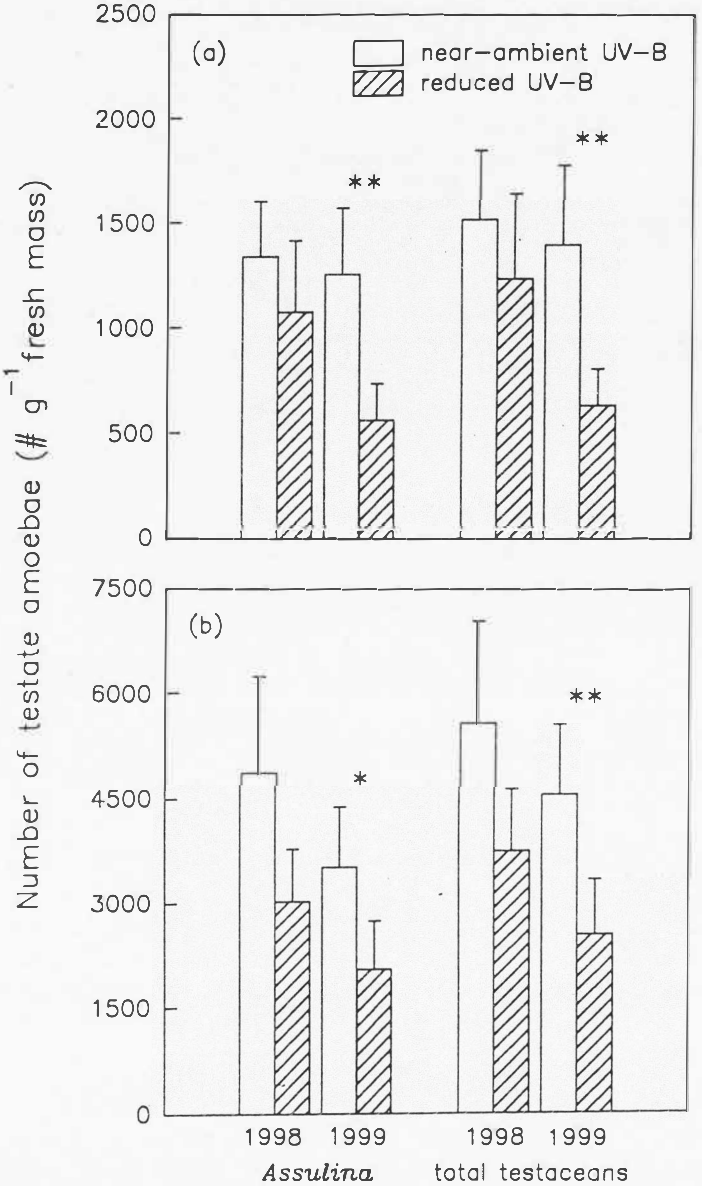

Fig. 12. The number of individuals of the testate amoebae *Assulina* and total testaceans under near-ambient solar UV-B (90% of ambient) and attenuated UV-B (15-20% of ambient) radiation treatments for the near-surface depths of (a) 0-5 mm and (b) 5-10 mm in the *Sphagnum magellanicum* moss. Data are shown as number of testaceans per gram of *S. magellanicum* fresh mass. n = 10 plots per UV-B level with means ± SE. ** $P \leq 0.05$; * $P \leq 0.10$

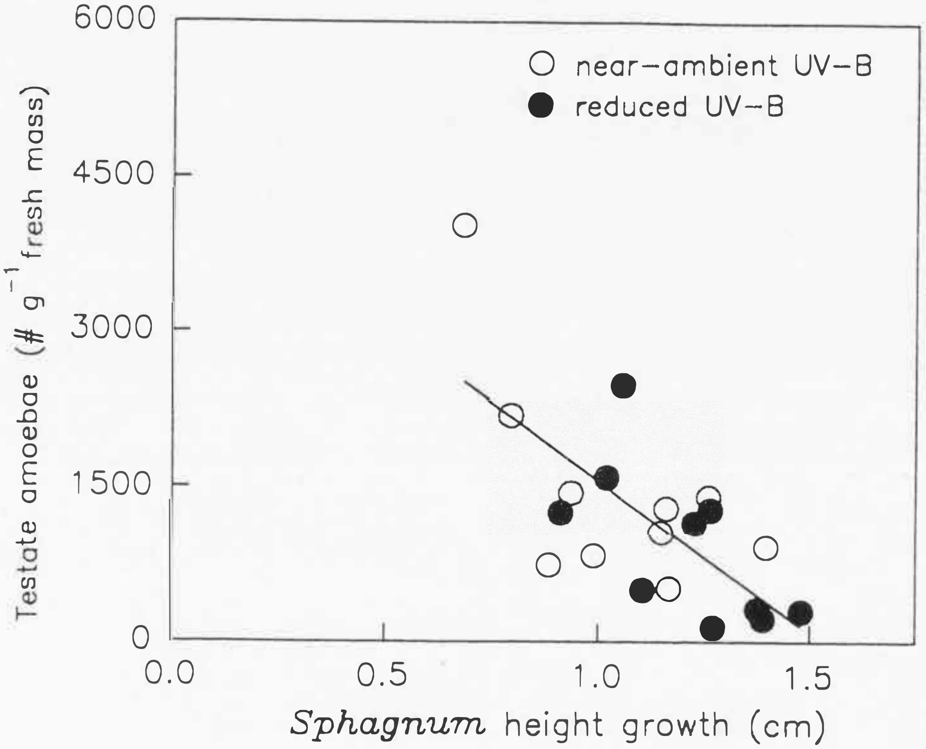

Fig. 13. The number of total testate amoebae as a function of *Sphagnum magellanicum* height growth under near-ambient solar UV-B (90% of ambient) and attenuated UV-B (15-20% of ambient) radiation treatments for the 0-5 mm testate amoebae sampling depth in the *S. magellanicum*. The values for number of testaceans and the moss height growth are averaged for the second and third years of the study. Only one line through the points is shown because the correlations are very similar for both UV-B levels (r = -0.66 for near-ambient UV-B, r = -0.68 for attenuated UV-B). n = 10 plots per UV-B level with $P \leq 0.05$ for both correlation values.

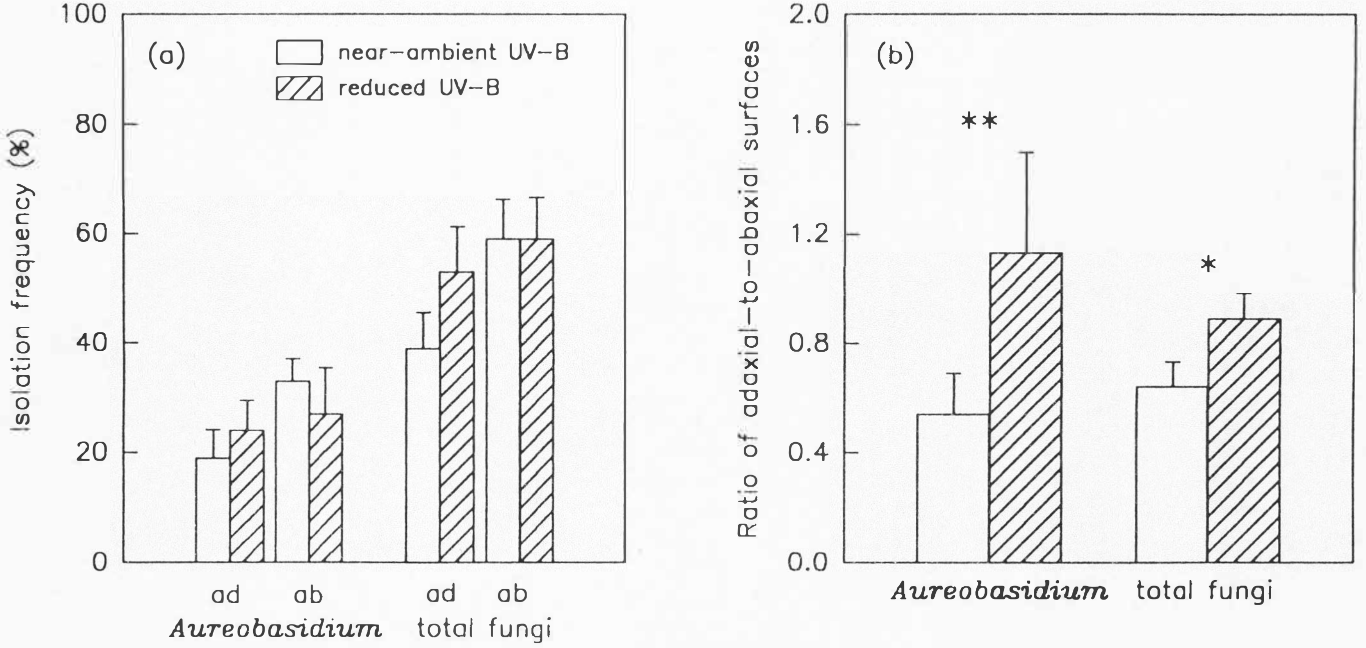

Fig. 14. The presence of *Aureobasidium* and total fungi from the phylloplane of *Nothofagus antarctica* under near-ambient solar UV-B (90% of ambient) and attenuated UV-B (15-20% of ambient) radiation treatments expressed as the (a) percentage frequency of isolation of fungi from the adaxial and abaxial leaf surfaces and (b) the ratio of fungi on the adaxial-to-abaxial leaf surfaces. Adaxial and abaxial are abbreviated as "ad" and "ab," respectively. n = 10 plots per UV-B level with means ± SE. ** $P \le 0.05$; * $P \le 0.10$

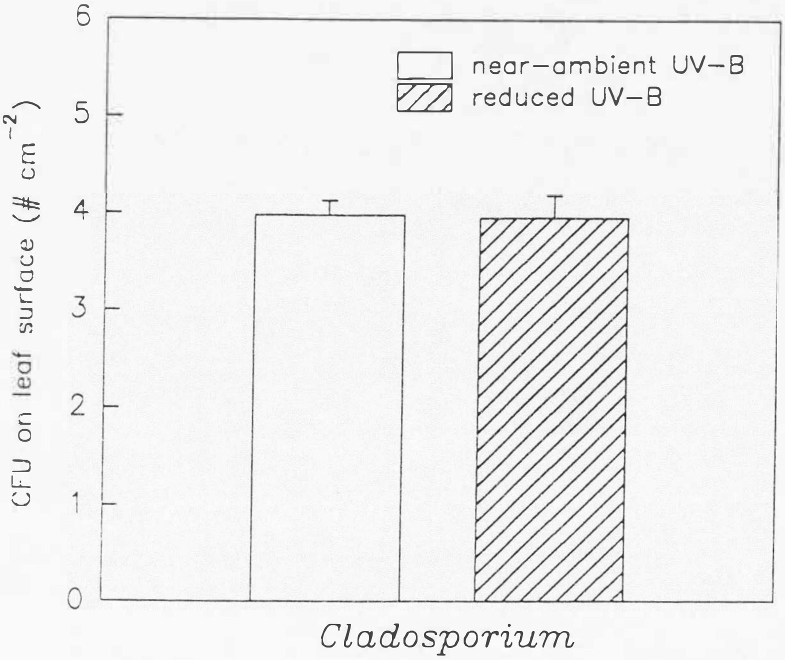

Fig. 15. The number of colony-forming units (CFU) of *Cladosporium* isolated from the *Carex decidua* phylloplane under near-ambient solar UV-B (90% of ambient) and attenuated UV-B (15-20% of ambient) radiation treatments. n = 9 plots per UV-B level with means ± SE.

CHAPTER 5

A META-ANALYSIS OF PLANT FIELD STUDIES SIMULATING STRATOSPHERIC OZONE DEPLETION[1]

Abstract The potential effects of increased ultraviolet-B radiation (UV-B, 280-320 nm) simulating stratospheric ozone depletion in field studies with vascular plants have previously been summarized only in narrative literature reviews. In this quantitative synthesis, we have assessed the significance of solar UV-B for 10 commonly measured variables involving leaf pigmentation, plant growth and morphology, and photosynthesis using meta-analytic statistical methods. Of 103 papers published between 1976 and mid-1999 from field studies, more than 450 reports from 62 papers were included in the database. Effects of UV-B were most apparent for UV-B-absorbing compounds with an average increase of approximately 10% across all studies when comparing the ambient solar UV-B control to the treatment (involving ambient UV-B plus a UV-B supplement from special UV lamps). Surprisingly, some morphological parameters such as plant height and leaf mass per area showed little or no response to enhanced UV-B. Measurements of leaf photosynthetic processes (leaf gas exchange and chlorophyll fluorescence) and photosynthetic pigments (total chlorophylls and carotenoids) were also not affected. Shoot biomass and leaf area showed modest decreases under UV-B enhancement. The reduction in shoot biomass occurred only under very high levels of

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[1] Coauthored by Peter S. Searles, Stephan D. Flint, and Martyn M. Caldwell. A consent letter from Stephan Flint for use of this manuscript in the dissertation is given in Appendix A.

simulated ozone depletion and leaf area was affected only when studies did not use the appropriate experimental replicate. To the best of our knowledge, this review provides the first quantitative estimates of UV-B effects in field-based studies using all suitable published studies as a database.

Introduction

The depletion of the stratospheric ozone layer over the last 25 years has been well documented. Besides the annual austral spring Antarctic "ozone hole," significant decadal trends (1979-1994) of total column ozone reduction are apparent in both the Northern and Southern Hemispheres at mid- and high-latitudes (McPeters et al. 1996; Herman et al. 1999). These satellite-based measurements from the Total Ozone Mapping Spectrometer agree well with much longer-term measurements from the Earth's surface (McPeters and Hollandsworth 1996). Present-day losses in stratospheric ozone relative to the 1970's are estimated to be 50% in the spring over Antarctica and around 5% for the mid-latitudes during the course of the year (World Meteorological Organization 1999; Madronich et al. 1999). Recent predictions suggest that ozone depletion due to man-made chlorofluorocarbons will reach its maximum around the year 2000 and recover over the next several decades although a number of uncertainties exist including interactions with other changes in global climate such as global warming (Madronich et al. 1998; Schindell et al. 1998; Madronich et al. 1999).

The increase in ultraviolet-B radiation (UV-B, 280-320 nm) accompanying ozone depletion may affect terrestrial vegetation and ecosystems. Long before ozone depletion was an issue, a screening study assessing the acute effects of germicidal UV radiation (UV-C at 254 nm) on the leaves of 67 plant species indicated a three orders-of-magnitude range in sensitivity with agricultural crop species being most affected (Cline and Salisbury 1966). Summaries of later studies indicated that elevated UV-B caused reductions in plant growth or reproductive yield in over 50% of 300 plant species or cultivars tested (Teramura 1983, 1990). However, most of these studies were conducted in growth chambers and greenhouses under unrealistic conditions using controls that entirely excluded UV-B and with low background UV-A and visible light (Tevini and Teramura 1989; Caldwell and Flint 1994). The UV-A and visible wavebands are often important in mitigating UV-B effects on plants (Caldwell et al. 1994).

Under more realistic field conditions, detectable effects of UV-B on vegetative growth, reproductive yield, and photosynthesis have long been suggested to be few (Caldwell et al. 1989). Between 1972 and the early 1990's, only 23 of 297 published papers assessed some aspect of terrestrial vegetation response to UV-B radiation in the field (Caldwell and Flint 1994). Thus, there were few data available to test this assertion. However, by mid-1999, 103 published studies addressed UV-B radiation effects in field studies. Based in part on this dramatic increase in field studies, several recent reviews have suggested that UV-B is unlikely to have much, if any, effect on productivity in agricultural and natural ecosystems (Fiscus and Booker 1995; Björn 1996; Corlett et al. 1998; Allen et al. 1998; Rozema et al. 1999). Caldwell and Flint (1994) proposed that the frequency of UV-B effects in plants from most to least common would be: Induction of UV-B-absorbing compounds (presumably flavonoids involved in UV-B protection) > morphological changes and reduced growth >> reduced photosynthesis. Under field conditions, Rozema et al. (1997) suggested increasing solar UV-B may sometimes constitute a stress for terrestrial vegetation, but more importantly, it may regulate ecosystem processes such as nutrient cycling and herbivory through UV-induced changes in the production of plant secondary metabolites including flavonoids, tannins, and lignin.

Reviews and commentaries concerning UV-B effects on vegetation in the field have been almost exclusively in the form of narrative opinions. This approach provides a qualitative summary and interpretation of the literature, and relates the collective judgments of experts. In contrast, meta-analysis allows a quantitative, statistical synthesis of results from numerous research studies and a determination of the combined magnitude of an effect (Gurevitch et al. 1992; Arnqvist and Wooster 1995). Meta-analysis has proven to be a useful tool in reviewing plant response to elevated CO_2 (e.g., Curtis 1996; Curtis and Wang 1998; Peterson et al. 1999). To the best of our knowledge, the only quantitative review of UV-B effects in field experiments is for the percentage change in yield of four crop plants (Caldwell et al. 1998). Plant studies of UV-B effects in the field seem well suited for meta-analysis because subtle effects of UV-B radiation cannot always be detected statistically in individual studies due to low sample sizes (Stephen et al. 1999). An aggregate test of numerous studies using meta-analysis can provide a more powerful test than the statistical tests of individual studies (Osenberg et al. 1999). Additionally, although details in methodology differ, the comparison in field studies is almost always between ambient solar UV-B and ambient UV-B plus a UV-B supplement using specially filtered UV-B fluorescent lamps.

The objectives of this meta-analysis are to: (1) quantitatively examine whether enhanced UV-B simulating stratospheric ozone depletion affects leaf pigmentation, plant growth and morphology, and photosynthesis, (2) estimate the magnitude of plant responses, and (3) assess whether the magnitude of the response is influenced by categorical variables including level of ozone depletion, the latitude of the study site, plant growth form, agricultural vs. nonagricultural ecosystem, and length of study. The results reported here are only intended to provide an approximate quantitative perspective on UV-B effects on vegetation under field conditions and to suggest what areas may be most fruitful for further research.

Methods

Data selection

The database of field studies was accumulated from literature of the past 25 years. Results from all journal articles and book chapters published between 1976 to mid-1999 were considered. Field studies prior to 1976 are unlikely to meet the criterion of simulating stratospheric ozone depletion since ozone destruction was first described only 2 years earlier (Molina and Rowland 1974). Ten common response variables were chosen for analysis in three categories: (1) leaf pigments -- chlorophyll, carotenoids, UV-B-absorbing compounds; (2) plant growth and morphology -- shoot biomass, reproductive yield, plant height, leaf mass per area, leaf area); and (3) photosynthesis --

gas exchange, variable-to-maximal chlorophyll fluorescence (Fv/Fm). Photosynthetic gas exchange was most often assessed as CO_2 uptake although O_2 evolution was measured in some instances. The UV-B-absorbing compounds were considered on both a leaf mass and area basis, while leaf chlorophyll and carotenoid data are on a leaf mass basis only because there were few reports on a leaf area basis. Other response variables such as root biomass and number of DNA lesions were not represented well enough in the literature for statistical analysis.

Of the 103 published field papers, one or more response variables from 62 papers were included in the database (Appendix C). As indicated above, papers for the database were limited to studies simulating the reduction of stratospheric ozone depletion by supplementing UV-B radiation. Only experimental designs comparing vegetation response under a solar, ambient UV-B control with a treatment of ambient UV-B plus a UV-B supplement were considered. The methodology in these experiments involves placing racks of specially filtered UV-B fluorescent lamps over treatment plots several square meters in area. Unenergized or energized lamps filtered to remove UV-B were placed over control plots to provide a microclimate similar to treatment plots. Experiments without some type of control lamps were not included in the database. Some studies were excluded because the experimental procedures were not clearly described and others because none of the 10 response variables we analyzed was reported. The minimal statistical information required for inclusion in the meta-analysis was the mean of the treatment and control groups and their sample sizes.

Many of the 62 papers included in the analysis contained more than one plant species, treatment level, growing season, or experimental factor. The entire database summed over all response variables consisted of more than 450 reports of UV-B effects (Appendix C). Multiple species or cultivars were considered to be separate reports for a given response variable within a paper. In the few cases where the number of species or cultivars was greater than eight in a paper, the values were averaged so that a few papers were not overly represented in the statistical analysis. Multiple treatment levels simulating two or more ozone depletion levels were included as separate reports. Individual growing seasons in a publication were considered to be separate observations for annual (primarily agricultural) species, while the last year of data was used for multi-year studies of perennials. More than one observation of a response variable within a growing season or multi-year study was used on the few occasions in which UV-B response was markedly different for two measurement periods. If the response to another environmental factor such as drought was being assessed along with UV-B effects, only data from the baseline control conditions for the second factor were used. Although many of the 450 reports are not statistically independent, loss of information by omitting multiple reports from a paper would have likely resulted in serious distortion of the results (Gurevitch et al. 1992).

Data categorization

Given the sometimes subtle nature of UV-B responses, we were first interested in whether overall UV-B effects for each response variable could be detected. We then assessed how different categorical variables influenced the magnitude of response. The categorical variables were: ozone depletion percentage (0-20%, >20%), latitude of the study (0-35°, 35-45°, >45°), plant growth form (monocot, dicot, gymnosperm), ecosystem (natural or agricultural), and length of study (0-60 d, >60 d). The experimental replicate chosen by the authors (i.e., the individual plant or plot) was later added to further explain some of the responses. The use of the individual plant, rather than the plot, as the statistical replicate is known as pseudoreplication (Hurlbert 1984). Unfortunately, the actual UV-B doses were not usually reported, so the latitude of the study site and the percentage of ozone depletion simulated were alternatively used as categorical variables in the analysis. Since there is a pronounced latitudinal gradient in ambient solar UV-B, latitude of the study site largely determined the ambient UV-B in the controls and the magnitude of the treatment UV-B dose for a given percentage reduction in ozone. Latitudinal categories did not distinguish between the Northern and Southern Hemispheres because only one study (Musil 1996) in the dataset was from the Southern Hemisphere. The numerical classes of a given categorical variable were created to allow for a sufficient number of reports in each class for statistical analysis. In addition to the above categorical variables, the UV-B responses of Fabaceae, a plant family recognized to be UV-B sensitive and commonly used in elevated UV-B studies, were compared to the response of all other plant families to avoid potentially misleading results.

Meta-analysis response ratio and statistics

The natural logarithm response ratio, ln(rr), was our metric of UV-B treatment effect (i.e., the effect size) in the meta-analysis. This ratio is merely the natural logarithm of the treatment mean (X_t) divided by the control mean (X_c) [$\ln(rr) = \ln(X_t/X_c)$]. This measure has been used successfully in an analogous meta-analysis of ecophysiological data comparing effects of ambient and elevated CO_2 for woody plants (Curtis and Wang 1998). Performing statistical analyses on the ln of X_t/X_c rather than on X_t/X_c is desirable because the distribution of the natural log values tends to be much more normal in small samples, and ln(rr) is much less affected by small changes in the denominator (Hedges et al. 1999). The ln response ratios were back-transformed using the anti-log for presentation.

Both parametric and nonparametric meta-analytic statistical techniques were performed using the calculated ln(rr) for the 450 reports in the database to test whether significant responses to UV-B occurred for the 10 response variables. Gurevitch and Hedges (1999) have recommended a weighted, parametric mixed-model analysis as the first choice of analysis and weighted, nonparametric resampling methods as a second approach. For parametric analysis, the studies must provide treatment and control means, standard deviations, and sample sizes. The parametric analysis was weighted to give greater weight to reports with smaller standard deviations using the reciprocal of the sampling variance of the ln(rr) as is traditional (Gurevitch and Hedges 1993; Curtis and Wang 1998). The nonparametric approach weights the ln(rr) to give reports with large sample sizes a greater weight than reports with small sample sizes. Although this weighting scheme does not estimate the inverse of the variance for the ln(rr) as would be desirable, it allowed us to approximately double the number of reports included for analysis because the standard deviations of the treatment and control are not required. This was crucial for variables such as carotenoids where the number of reports that could be used in the parametric analysis was very low. The UV-B response of a variable for either the parametric or nonparametric analysis was considered significant when the 95% confidence interval of the mean did not overlap zero. All statistical tests were performed in the MetaWin 1.0 statistical software package (Rosenberg et al. 1997).

Possible differences in the effect of UV-B for a response variable between classes of a categorical variable such as the latitude of the study were only assessed using nonparametric methods because of the small number of studies available in each class for parametric analysis. This nonparametric analysis uses a resampling method known as a randomization test where significance is determined by randomly reassigning the data to given classes and recalculating the statistic. This process is then repeated to generate a distribution of possible results that are compared to the actual statistic to determine the significance level.

Results

Of the 62 research papers in the database, 35 examined the response of agricultural plant species to supplemented UV-B, 26 assessed responses of plants from nonagricultural systems, and one study included both (Table 10). The family Fabaceae was represented in 19 of the 22 agricultural, dicot papers and 11 focused exclusively on

Glycine max (soybean). Statistical comparisons between Fabaceae and the rest of the dataset for UV-B effects for each of the 10 response variables did not show any differences between Fabaceae and the other plant families (data not shown). Nonagricultural monocots were underrepresented as only one paper examined the UV-B sensitivity of two species (Tosserams et al. 1997). Almost 50% of the agricultural studies were less than 60 d in length, while over 80% of the studies with nonagricultural plants were greater than 60 d and 40% exceeded one year duration. The amount of ozone depletion simulated was most often between 10 and 20% and one-fifth of all studies used two or more levels of supplementary UV-B. Sixty percent of all studies were conducted within the narrow latitudinal range of 35 to 45° N. Therefore, the UV-B doses employed in the majority of the studies should have been roughly comparable.

A difference in the average response to UV-B radiation across the published literature (i.e., the overall effect size) was seen between ambient and enhanced UV-B for UV-B-absorbing compounds, shoot biomass, leaf area, and plant height in either the parametric or nonparametric analysis at the 95% significance level (Fig. 16-18). The results using the two analysis methods were similar and there were only slight differences in the effect sizes since different published reports were included in the parametric and nonparametric analyses. The increase in UV-B-absorbing compounds due to elevated UV-B did not differ according to any of the categorical variables, but there was considerable variability in the magnitude of the responses. The expression of UV-B-absorbing compounds on a leaf mass or leaf area basis did not influence the results.

The overall responses of shoot biomass and leaf area to UV-B could be separated according to some of the categorical variables (Fig. 17). Shoot biomass was only reduced significantly when the simulated stratospheric ozone depletion was greater than 20%. The shoot biomass responses to UV-B for the two classes of simulated ozone depletion, 10 to 20% and greater than 20%, were significantly different from each other at $P = 0.003$ using a randomization test. The reduction of leaf area by enhanced UV-B was influenced by the experimental replicate chosen by the authors. Published reports using the individual plant (i.e., the subreplicate) as the experimental replicate showed a reduction in leaf area at $P < 0.05$, while reports using the plot did not show a significant response. When explicitly comparing the two classes of experimental replicate (plant and plot) using a randomization test, some tendency was found for a difference in response to UV-B between reports using the individual plant as the replicate and those using the plot ($P = 0.11$).

Of the seven remaining variables, only plant height indicated some response to elevated UV-B. A small but statistically significant reduction in plant height was seen for the parametric analysis using 26 published reports (Fig. 18). The nonparametric analysis did not indicate any significant UV-B effect on plant height for a larger sample size of 57 reports. Measures of photosynthesis including leaf gas exchange and chlorophyll fluorescence did not show any UV-B response nor did leaf pigments (chlorophyll and carotenoids) associated with photosynthesis (Fig. 16, Fig. 19). Reproductive yield and leaf mass per area also were not affected (Fig. 18).

Discussion

An increase in UV-B-absorbing compounds (presumably mostly flavonoids) has been perceived to be one of the most common responses to UV-B in field studies (Caldwell et al. 1994, 1999). In support of these expert-opinion reviews, UV-B-absorbing compounds were the only leaf pigments that were influenced by the supplemental UV-B radiation in this meta-analysis. The average 10% increase in UV-B-absorbing compounds in response to elevated UV-B may be a function of the action spectrum for the induction of UV-absorbing compounds. Leaves from soybean canopies grown in the field under several different plastic filters that cut off portions of the UV-B and UV-A wavebands had a sharp increase in UV-absorbing compounds below 325 nm (Mazza et al. 2000) resembling the generalized plant action spectrum (Caldwell 1971). Thus, even though the UV-B supplement represents an increase of less than 0.5% in the total solar radiation received by plants, these shorter wavelengths appear very biologically effective in stimulating the production of UV-B-absorbing compounds.

The average reduction in aboveground, vegetative biomass of 9-14% was largely driven by studies using high levels of ozone depletion. There was a significant decrease in shoot biomass of 16% for studies simulating greater than 20% ozone depletion, while only a nonsignificant 6% decrease in shoot biomass was apparent for studies simulating a 10-20% reduction in ozone. In contrast the response of UV-B-absorbing compounds to UV-B enhancement did not differ significantly according to the amount of ozone depletion simulated.

An 18% year-round depletion of the ozone column at the mid-latitudes has been calculated to be the worst-case scenario for the next century if the Montreal Protocol of 1987 and its subsequent amendments were not in effect (Fiscus and Booker 1995). These international agreements have resulted in a greatly reduced release of chlorofluorocarbons (CFCs) (WMO 1999). Due to these treaties, the abundance of stratospheric chlorine has peaked and substitutes for CFCs are readily available. Maximum ozone depletion is predicted to occur by the end of the 1990's or at least within the first two decades of the next century (WMO 1999). Relative to the 1970's, the current ozone depletion at mid-latitudes is only about 5% and recovery to levels of the 1970's is projected to occur as early as the middle of the next century although several uncertainties exist (Madronich et al. 1998, 1999). Given these projections of ozone recovery, the nonsignificant 6% decrease in vegetative shoot biomass from studies simulating a 10-20% ozone layer reduction is likely to be the more relevant than the 16% decrease in studies stimulating greater depletions of stratospheric ozone. No effect on reproductive yield was apparent in any of the analyses.

The average 15% decrease in leaf area is difficult to interpret because of concerns about the statistical rigor of many published papers. When papers were selected for inclusion into the dataset, no attempt was made to screen studies with regard to the appropriateness of experimental design and statistical analysis. This approach was taken to reduce the potential for subjectivity and bias as suggested by Gurevitch et al. (1992) and Englund et al. (1999). The preselected categorical variables including degree of ozone depletion simulated, latitude of study site, growth form, agricultural vs.

nonagricultural species, and duration of study could not explain the large amount of heterogeneity among studies for leaf area response to UV-B. Therefore, we chose to address whether pseudoreplication might explain some of the variability. Pseudoreplication is defined as the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated or replicates are not statistically independent (Hurlbert 1984). While most UV-B experiments use more than one plot of ambient UV-B and ambient UV-B plus the UV-B supplement, it is not uncommon for individual plants within a plot to be used as the replicates in the statistical analysis. Individual plants within a plot are not independent experimental units and the plot should be used as the treatment replicate. Approximately 50% of the reports of leaf area response to elevated UV-B were pseudoreplicated and tended to report larger reductions in leaf area than studies using the plot as the replicate. This more pronounced response to UV-B likely cannot be explained by pseudoreplication per se because the average response should not be greatly affected by using the individual plant as the replicate when considering a large number of studies in a combined analysis.

If the plot is used appropriately as the replicate, the small sample size of these studies provides little statistical power to detect UV-B effects if they are present and confidence intervals are often large. For example, in a recent field study with five ambient UV-B plots and five plots where UV-B was supplemented, interplot variability was such that the smallest differences in reproductive yield between UV-B levels that could be detected as significant at $P = 0.05$ were 8.5% in pea and 21.6% in barley (Stephen et al. 1999). Stephen et al. (1999) suggest that greater replication would be a prerequisite for better quantifying the response of barley to UV-B given the limited ability to see statistical differences in their experiment. For leaf area response to UV-B in our meta-analysis, no study where the experimental unit could be adequately determined used more than six control and six treatment plots. Clearly, a greater numbers of plots is needed in most UV-B studies.

Apart from pseudoreplication and adequate replicate number, the accurate measurement of UV-B represents a serious difficulty in conducting these studies. The UV-B supplement represents a very small amount of absolute energy and requires accurate measurements at individual wavelengths by a spectroradiometer. Thus, even seemingly minimal errors can lead to serious inaccuracies in the UV-B supplement. This may explain some of the variance in UV-B effects between studies in this meta-analysis. Additionally, the irradiance at each wavelength is traditionally weighted by the generalized plant action spectrum (Caldwell 1971) when calculating the UV-B supplement. This generalized action spectrum does not consider UV radiation to affect plant response beyond 313 nm. Some recent studies in agricultural species indicate that plant aboveground biomass and leaf area can be decreased by UV-A as well as UV-B wavelengths (Holmes et al. 1997; Krizek et al. 1997, 1998), but UV-A can also mitigate UV-B damage (Flint and Calwell 1996). The implication of the wavelength sensitivity of plant response to UV radiation is an important issue that still needs to be addressed for evaluating supplemental lamp studies.

Ultraviolet-B radiation has often been proposed to affect a suite of morphological plant traits under glasshouse conditions including plant height, internode lengths, leaf insertion heights, leaf mass per area, and branching or tillering (e.g., Barnes et al. 1990, 1993) Several lines of evidence suggest these responses may be controlled by photoreceptors including a specific UV-B photoreceptor and are not necessarily damage responses to UV-B (e.g., Wellman 1983; Ballaré et al. 1995). Field studies of wheat (*Triticum aestivum*) and wild oat (*Avena fatua*) in monocultures have also shown small reductions in leaf insertion height for both species under supplemental UV-B even though production of the monocultures was not affected (Barnes et al. 1988, 1995). In mixtures of these two species, leaf insertion height of wild oat was reduced to a greater extent than wheat under enhanced UV-B, which resulted in greater light interception and canopy photosynthesis for wheat. Our meta-analysis shows only a minor influence of UV-B on plant height and no effect on leaf mass per area. However, subtle differences in species sensitivity to UV-B may still lead to shifts in competitive relationships as suggested for the wheat and wild oat system. Leaf insertion heights, internode lengths, and branching or tillering were not reported with sufficient frequency to be used in our analysis.

No UV-B effects on variables related to photosynthesis including leaf chlorophyll content, chlorophyll fluorescence (a measure of photosystem II activity), and leaf gas exchange were found in the meta-analysis. These results are consistent with recent critical reviews that have concluded that increased UV-B due to ozone depletion at current predicted levels will not be a threat to photosynthetic competence in the vast majority of species (Fiscus and Booker 1995; Allen et al. 1998). Laboratory experiments indicated that photosystem II was the main target of UV-B damage to photosynthesis (reviewed by Teramura and Sullivan 1994). However, field studies show no indication of photosystem II inhibition by UV-B. Allen et al. (1998) suggested Calvin cycle enzymes such as Rubisco and stomatal closure may be more sensitive to UV-B than photosystem II, but only under very high levels of UV-B that are not relevant to ozone depletion predictions.

Overall, only a few subtle plant responses to enhanced UV-B simulating stratospheric ozone depletion were seen in this meta-analysis of 62 field-based research papers published over 20 years. It is uncertain whether the modest decrease in aboveground vegetative biomass in plant exposed to elevated UV-B will be important since the increase in UV-B at currently predicted levels of ozone depletion will be much lower than the UV-B supplements in most experimental studies. The increase in UV-B-absorbing compounds (i.e., flavonoids and other phenolics) was not dependent in our analysis on the ozone depletion simulated, and their role in altering insect herbivory on plants and leaf decomposition is likely to be a critical area for assessing UV-B effects on ecosystem function. Such indirect effects of UV-B may be more important in nonagricultural ecosystems than agricultural systems since management is less intensive in natural ecosystems. Feedbacks to vegetation mediated through direct UV-B effects on other organisms like pathogens and fungal decomposers of leaves also should be further examined.

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Table 10 Summary of the 62 research papers included in the analysis. The categorical variables of growth form, degree of simulated ozone depletion, duration of experiment, and latitude of the study are reported for agricultural and nonagricultural plants. Three classes (or subcategories) are used for each categorical variable. The number of papers may be less than or greater than 62 if a paper could not be classified or was included in more than one class

	Class		
Growth Form	monocots	dicots	gymnosperms
agricultural	14	22	--
nonagricultural	1	21	6
Duration (days)	≤60	61-365	>365
agricultural	17	19	0
nonagricultural	4	12	11
Ozone Depletion (%)	10-20 %	>20 %	10-20 % and >20%*
agricultural	18	9	9
nonagricultural	19	4	4
Latitude (°)	≤35°	35-45°	>45°
agricultural	10	23	2
nonagricultural	1	15	10

* Indicates research papers that included both levels of ozone depletion

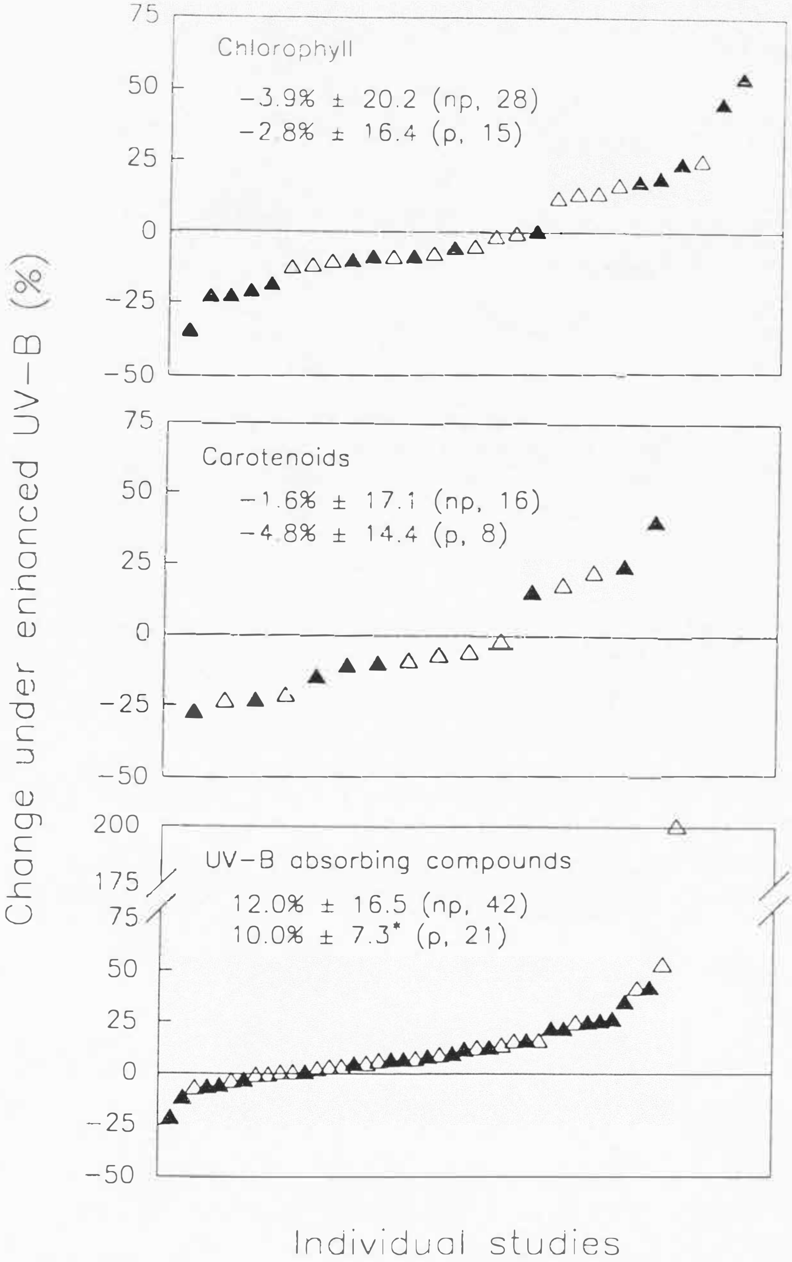

Fig. 16 The response of total chlorophyll, carotenoids, and UV-B-absorbing compounds to enhanced UV-B radiation. Filled triangles represent reports (i.e., studies) from published, field-based papers where statistical information was sufficient for inclusion in the parametric (p) analyses. The hollow triangles represent studies that could not be included in the parametric analyses. All of the data points were used in the nonparametric (np) analyses. The mean ± the 95% confidence interval is shown along with the method of analysis and the sample size in parentheses. * $P < 0.05$

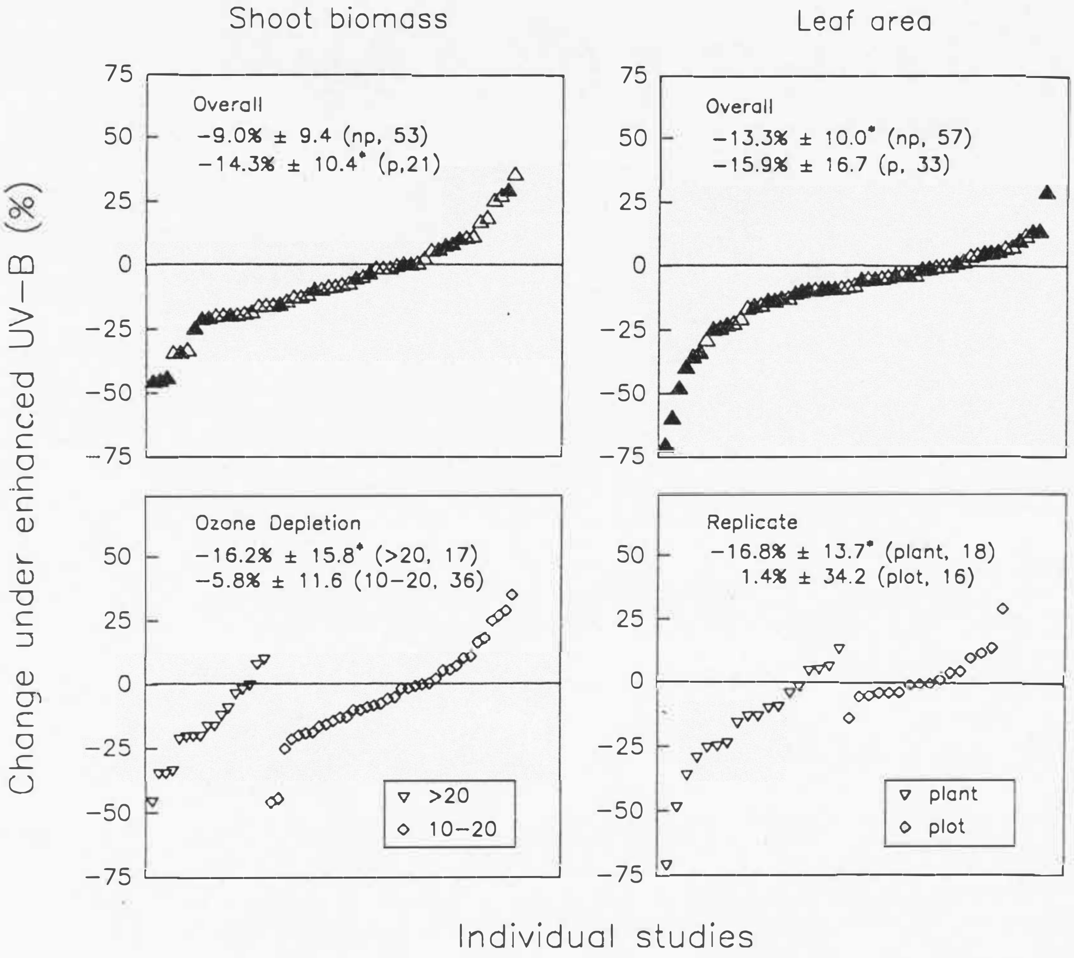

Fig. 17 The response of shoot biomass and leaf area to enhanced UV-B radiation. Symbols for the overall response are the same as Fig. 16. The shoot biomass is further classified by the percentage of ozone depletion (10-20% or >20 %) simulated and leaf area is classified by the experimental replicate (individual plant or plot) chosen by the authors. The mean ± the 95% confidence interval is shown along with the method of analysis and the sample size in parentheses. * $P < 0.05$

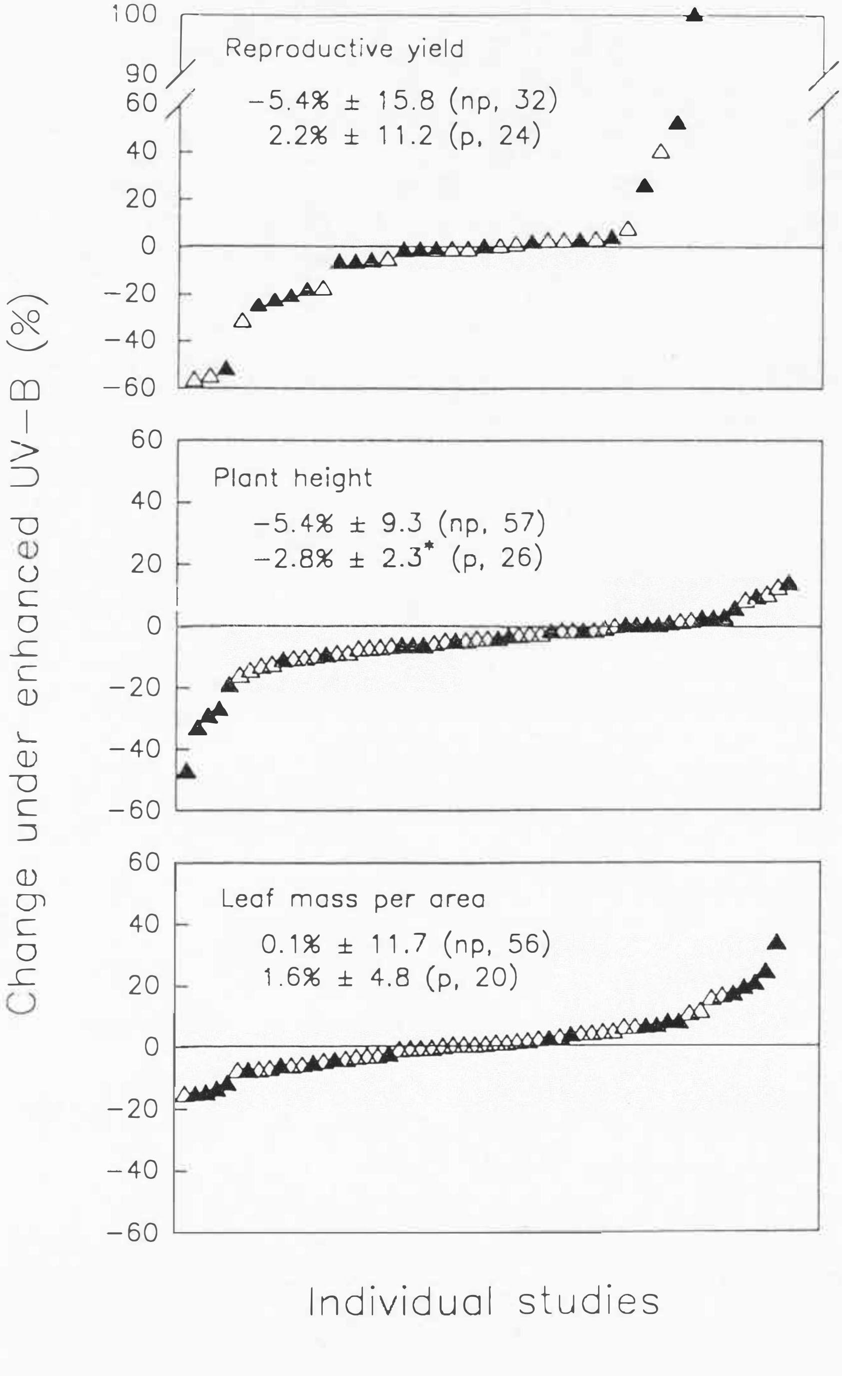

Fig. 18 The response of reproductive yield, plant height, and leaf mass per area to enhanced UV-B radiation. Symbols are the same as Fig. 16. The mean ± the 95% confidence interval is shown along with the method of analysis and the sample size in parentheses. * $P < 0.05$

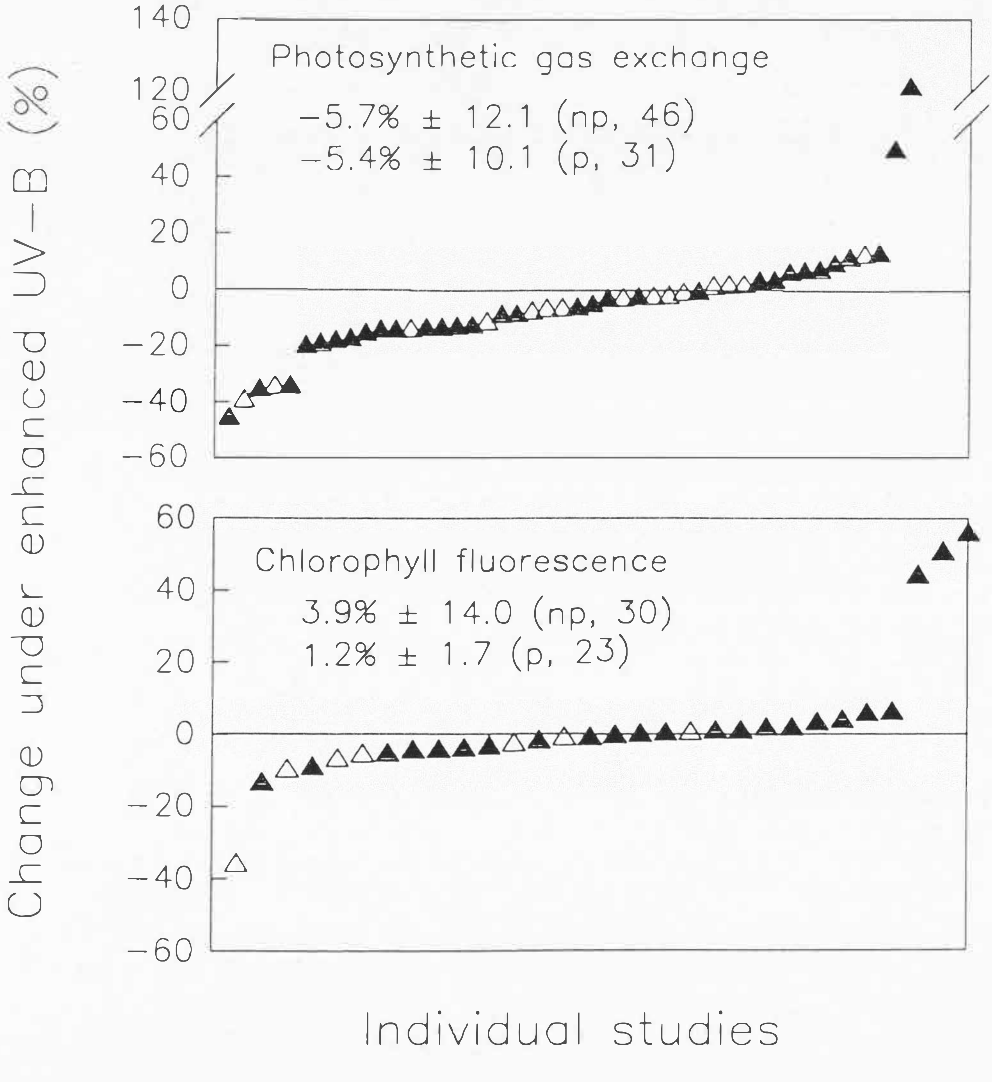

Fig. 19 The response of leaf photosynthetic gas exchange and chlorophyll fluorescence (a measure of photosystem II activity) to enhanced UV-B radiation. Symbols are the same as Fig. 16. The mean ± the 95% confidence interval is shown along with the method of analysis and the sample size in parentheses.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Summary

The number of ozone-depleted days over Tierra del Fuego, Argentina, in the austral spring has increased greatly over the last two decades due to the Antarctic "ozone hole" (Rousseaux *et al.* 1999). This has led to increased levels of solar ultraviolet-B radiation (UV-B, 280-320 nm) in Tierra del Fuego (e.g., Bojkov *et al.* 1995; Kirchhoff *et al.* 1997; Orce & Helbling 1997). These increases in UV-B can occur not only in the springtime due to the "ozone hole," but during the summer months as well (Frederick *et al.* 1994). The general deterioration of the stratospheric ozone layer throughout much of the Southern Hemisphere is likely responsible for these summertime increases. The presence of relatively high levels of solar UV-B throughout the growing season has prompted concerns about the sensitivity of terrestrial vegetation and ecosystems to UV-B radiation in Tierra del Fuego.

In Chapter 2, the effects of solar UV-B on growth-related parameters of plants were examined in a *Sphagnum* peatland and a *Carex* fen in Tierra del Fuego, Argentina. These first season findings did not indicate any influence of UV-B radiation on a number of plant species including the moss *Sphagnum magellanicum*. During the second and third growing seasons (Chapter 3), the height growth of *S. magellanicum* was less under near-ambient solar UV-B than reduced UV-B, while volumetric density was greater. These morphological effects of UV-B on *S. magellanicum* are similar to the effects reported for *S. fuscum* in Abisko, Sweden (Gehrke 1998). In both studies, no changes in *Sphagnum* biomass production were apparent. Solar UV-B had little influence on the morphology of the three vascular plant species in the *Sphagnum* peatland even during the second and third years. However, two of the three species showed somewhat greater UV-B-absorbing compounds under near-ambient UV-B than reduced UV-B. These species were *Empetrum rubrum* and *Tetroncium magellanicum*. UV-B-absorbing compounds are often considered to protect plants from UV-B damage. In the *Carex* fen, no UV-B effects were apparent on the aboveground growth or UV-B-absorbing compounds of *Carex decidua* and *Carex curta* after 3 years of study (unpublished data).

In Chapter 4, the effects of solar UV-B on microbial communities inhabiting the *S. magellanicum* moss and the leaf surfaces of vascular plants were assessed for the second and third growing seasons. Initial results from the first field season (Chapter 2) suggested that testate amoebae (i.e., shelled amoebae) and rotifers in the *S. magellancium* might be affected by UV-B. Similar to the earlier findings, the number of testate amoebae was counterintuitively greater under near-ambient solar UV-B than under reduced UV-B during the second and third growing seasons. The UV-B response of the testate amoebae occurred both for the 0-5 mm depth in the *S. magellanicum* moss where UV-B penetrates to some extent and the 5-10 mm depth where UV-B penetration is negligible. This suggests that the effect of solar UV-B on the amoebae is not direct. It appears that the response of the testate amoebae to UV-B is possibly mediated by UV-B-induced changes in the height growth of the *S. magellanicum*. No response to UV-B was apparent for rotifers, nematodes, bacteria, fungi, and a common microalga (*Euglena* *mutabilis*) in the *S. magellanicum*. Fungi on the leaves of the tree *Nothofagus antarctica* were significantly lower under near-ambient solar UV-B than under reduced UV-B, and appeared to be directly inhibited by UV-B.

A quantitative literature review of UV-B effects on vascular plants in Chapter 5 addressed the potential effects of increased UV-B radiation simulating stratospheric ozone depletion. Of 10 plant response variables, meta-analysis revealed some significant inhibition of leaf area, aboveground biomass, and plant height due to increased UV-B. These inhibitions were 10-15% for leaf area and aboveground biomass and about 5% for plant height. A significant 10% increase in UV-B-absorbing compounds was also apparent. The decrease in aboveground biomass only occurred under levels of supplemental UV-B radiation that are much higher than the current predicted UV-B increases due to stratospheric ozone depletion. Additionally, the response of leaf area to UV-B was only detected in studies using inappropriate statistical analyses. The increase in UV-B-absorbing compounds appears to be the most robust general response to increased UV-B radiation.

Conclusions

Removal of 80% of the solar UV-B led to few changes in growth-related parameters in the *Sphagnum* and *Carex* peatlands after 3 years. The most significant responses were the UV-B effects on height growth and volumetric density in *S. magellanicum*. *S. magellanicum* is central to the ecosystem functioning of these systems in Tierra del Fuego because of its accumulation as peat.

The impact of solar UV-B on *Sphagnum* peatlands will depend on the severity of ozone depletion over the next several decades. The increase in solar UV-B (approx. 10% under clear sky conditions) associated with ozone depletion since 1980 in Tierra del Fuego is much less than the 80% reduction of UV-B used in our study. If the ozone layer substantially recovers by the middle of the 21st century as predicted (World Meteorological Organization 1999), only some minor effects of increased UV-B on ecosystem function mediated through production-related changes in *S. magellanicum* may be expected. The UV-B effects on microbial communities such as testate amoebae may ultimately influence the decomposition of *S. magellanicum*, but this assertion is difficult to test. A concurrent study in a shrub-steppe ecosystem by the University of Buenos Aires also indicates only some small responses of plant growth to solar UV-B, although UV-B does increase the number of DNA lesions in the plant *Gunnera magellanica* (Rousseaux *et al.* 1999; Rousseaux, unpublished data).

The results of the meta-analysis provide some perspective to interpret the findings from Tierra del Fuego. The average responses to increased UV-B in the literature using meta-analysis are fairly modest. This is the case even though many researchers have used high UV-B doses that are not entirely relevant to the current predictions of stratospheric ozone depletion. The magnitude of my findings in Tierra del Fuego using solar UV-B reduction is similar to the overall responses for plants under supplemental UV-B radiation.

Ultimately, these studies have provided much needed information about the integrity of peatlands in southern South America. While the effects of solar UV-B reported in this dissertation are not particularly striking, recovery of the stratospheric ozone layer is still crucial to avoid the potential accumulation of UV-B effects over decades. The presence of the Antarctic "ozone hole" over South America should continue to be a concern for the functioning of biological systems.

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APPENDICES

APPENDIX A. LETTERS

b
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www.blackwell-science.com

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8 June 2000

Fax: 001 435 797 3796

Peter Searles
Dept. of Rangeland Resources
and The Ecology Center
Utah State University
Logan, UT 84322-5230
USA

Dear Mr Searles

Thank you for your recent e-mail requesting permission.

I can confirm that we would be happy to grant you permission to reproduce in your dissertation, pages 225-234 from Vol 5 of ***Global Change Biology***, subject to the full acknowledgements of source.

Regards.

Yours sincerely

Tracey Davies (Mrs)
Senior Reprints and Permissions Assistant
email tracey.davies@blacksci.co.uk

IFEVA
CONICET y UNIVERSIDAD DE BUENOS AIRES
Av San Martin 4453
1417 Buenos Aires, ARGENTINA
Tel 11 4524 8071
Fax 11 4514 8730

Mr. Peter S. Searles
Dept. of Rangeland Resources
Ecology Center
Utah State University
Logan, UT 84322

FAX.: 435 797 3796

Dear Peter:

This is simply to confirm that, as a co-author, I give my consent for you to include the following published paper as a chapter in your dissertation:

Searles PS, Flint SD, Diaz SB, Rousseaux MC, Ballaré CL, Caldwell MM. 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. **Global Change Biology** 5:225-234

Best wishes,

Carlos L. Ballaré
Senior Research Scientist
Associate Professor

Ministerio de Cultura y Educación
Secretaría de Ciencia y Tecnología
Consejo Nacional de Investigaciones Científicas y Técnicas
CENTRO AUSTRAL DE INVESTIGACIONES CIENTÍFICAS

Ushuaia, June 20th, 2000

Dear Mr Searles:

As a co-author, you have my permission to include the following papers in your dissertation:

Solar ultraviolet-B radiation influence on Sphagnum bog and Carex fen ecosystems: first field season findings in Tierra del Fuego, Argentina (chapter 2; published previously in Global Change Biology, volume 5, 225-234)

Plant response to solar ultraviolet-B radiation in a southern South America Sphagnum peatland (chapter 3)

UNIVERSITY OF CALIFORNIA, DAVIS

BERKELEY • DAVIS • IRVINE • LOS ANGELES • RIVERSIDE • SAN DIEGO • SAN FRANCISCO SANTA BARBARA • SANTA CRUZ

COLLEGE OF AGRICULTURAL AND
ENVIRONMENTAL SCIENCES
AGRICULTURAL EXPERIMENT STATION
COOPERATIVE EXTENSION
DEPARTMENT OF VEGETABLE CROPS
MANN LABORATORY
FAX (530) 752-4554

ONE SHIELDS AVENUE
DAVIS, CALIFORNIA 95616-8631

Davis, June 2 2000

As a co-author, I give my consent for you to include the following published paper as a chapter in your dissertation:

Serales PS, Flint SD, Diaz SB, Rousseaux MC, Ballare CL, Caldwell MM. 1999. Solar ultraviolet-B radiation influence on Sphagnum bog and Carex fen ecosystems: first field season findings in Tierra del Fuego, Argentina. Global Change Biology 5: 225-234

Maria Cecilia Rousseaux

UtahState
UNIVERSITY

DEPARTMENT OF RANGELAND RESOURCES
Logan UT 84322-5230
Telephone (435) 797-2471
FAX (435) 797-3796
E-mail rangesci@cc.usu.edu

June 14, 2000

Dear Peter,

As a coauthor, I am pleased to give my consent to the use of the following papers as chapters in your dissertation:

Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. (chapter 2; previously published in Global Change Biology, volume 5, 225-234 (1999).)

Plant response to solar ultraviolet-B radiation in a southern South America *Sphagnum* peatland (chapter 3)

The influence of solar ultraviolet-B radiation on some microbial communities in peatlands in Tierra del Fuego, Argentina (chapter 4)

A meta-analysis of plant field studies simulating stratospheric ozone depletion (chapter 5)

Sincerely,

Stephan Flint
Research Associate

COLLEGE OF NATURAL RESOURCES

UtahState
UNIVERSITY

DEPARTMENT OF BIOLOGY
5305 Old Main Hill
Logan UT 84322-5305

20-June-00

Peter:

As a co-author, you have my permission to include the following paper in your dissertation: The influence of solar UV-B radiation on some microbial communities in peatlands of Tierra del Fuego, Argentina.

Sincerely,

Bradley R. Kropp

Phone (435) 797-2485
Fax (435) 797-1575

biomail@biology.usu.edu
www.biology.usu.edu

APPENDIX B. ANALYSIS OF VARIANCE STATISTICAL TABLES

Table B.1. ANOVA of *Assulina muscorum* population number

Source	df	SS	MS	F-value	*P*-value
UV-B	1	1634488	1634488	10.57	0.0830
Block	2	29387154	14693577	95.07	0.0104
Error	2	309127	154563		

Table B.2. ANOVA of total testacean population number

Source	df	SS	MS	F-value	*P*-value
UV-B	1	2315779	2315779	13.39	0.0672
Block	2	34290775	17145387	99.17	0.0100
Error	2	345772	172886		

Table B.3. ANOVA of rotifer population number

Source	df	SS	MS	F-value	*P*-value
UV-B	1	456629	456629	8.36	0.1016
Block	2	695379	347689	6.37	0.1357
Error	2	109182	54591		

Table B.4. ANOVA of *Sphagnum magellanicum* height growth

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	4.24	0.0542
Year	2	Residual	41.02	0.0001
UV-B*Year	2	Residual	2.07	0.1404

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.01277609
Residual	36	0.03438274

Table B.5. ANOVA of *Sphagnum magellanicum* volumetric density

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Residual	5.13	0.0361

Covariance Parameter Estimates

Parameter	df	Estimate
Residual	18	0.00088098

Table B.6. ANOVA of *Tetroncium magellanicum* leaf length

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	2.56	0.1270
Year	1	Residual	4.22	0.0458
UV-B*Year	1	Residual	0.27	0.6076
Month	1	Residual	8.85	0.0047
UV-B*Month	1	Residual	2.81	0.1007
Year*Month	1	Residual	0.02	0.8983
UV-B*Yr*Mo	1	Residual	0.41	0.5250

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	6.71877835
Residual	46	3.92802883

Table B.7. ANOVA of *Nothofagus antarctica* leaf length

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	0.04	0.8366
Year	1	Residual	3.39	0.0713
UV-B*Year	1	Residual	0.01	0.9344
Season	1	Residual	21.46	0.0001
UV-B*Season	1	Residual	4.62	0.0362
Year*Season	1	Residual	0.46	0.4997
UV-B*Yr*Seas	1	Residual	0.16	0.6906

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	6.71877835
Residual	54	3.92802883

Table B.8. ANOVA of *Empetrum rubrum* leaf number per stem length

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	4.16	0.0563
Year	1	Residual	0.83	0.3731
UV-B*Year	1	Residual	0.00	0.9841

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.01522463
Residual	18	0.00721392

Table B.9. ANOVA of *Sphagnum magellanicum* absorbance at 305 nm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	2	Plot(UV-B)	0.03	0.8587
Year	1	Residual	0.77	0.4704
UV-B*Year	2	Residual	3.51	0.0406

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.00008995
Residual	36	0.00009868

Table B.10. ANOVA of *Empetrum rubrum* absorbance at 305 nm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	2	Plot(UV-B)	3.54	0.0761
Year	1	Residual	53.70	0.0001
UV-B*Year	2	Residual	0.12	0.8875

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.00022221
Residual	36	0.00017726

Table B.11. ANOVA of *Tetroncium magellanicum* absorbance at 305 nm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	4.43	0.0504
Year	1	Residual	43.28	0.0001
UV-B*Year	1	Residual	0.21	0.6518

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	17	0.00061909
Residual	17	0.00508663

Table B.12. ANOVA of *Tetroncium magellanicum* absorbance at 360 nm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	11.27	0.0037
Year	1	Residual	6.66	0.0195
UV-B*Year	1	Residual	0.07	0.7945

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	17	0.00135241
Residual	17	0.01199220

Table B.13. ANOVA of *Tetroncium magellanicum* absorbance at 400 nm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	8.61	0.0093
Year	1	Residual	75.03	0.0001
UV-B*Year	1	Residual	0.11	0.7420

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	17	0.00027778
Residual	17	0.00286993

Table B.14. ANOVA of *Assulina* testate amoebae at 0-5 mm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	5.09	0.0368
Year	1	Residual	2.69	0.1182
UV-B*Year	1	Residual	1.60	0.2226

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.3433
Residual	18	1.3518

Table B.15. ANOVA of total testate amoebae at 0-5 mm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	4.25	0.0540
Year	1	Residual	2.40	0.1385
UV-B*Year	1	Residual	1.24	0.2793
			4.25	0.0540

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.4419
Residual	18	1.2526

Table B.16. ANOVA of *Assulina* testate amoebae at 5-10 mm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	3.71	0.0701
Year	1	Residual	4.65	0.0448
UV-B*Year	1	Residual	0.09	0.7667

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.3658
Residual	18	0.4830

Table B.17. ANOVA of total testate amoebae at 5-10 mm

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Plot(UV-B)	4.15	0.0567
Year	1	Residual	3.32	0.0851
UV-B*Year	1	Residual	0.62	0.4410

Covariance Parameter Estimates

Parameter	df	Estimate
Plot(UV-B)	18	0.3760
Residual	18	0.4452

Table B.18. ANOVA of the ratio of *Aureobasidium* on adaxial-to-abaxial leaf surfaces

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Residual	4.41	0.0501

Covariance Parameter Estimates

Parameter	df	Estimate
Residual	18	0.8127

Table B.19. ANOVA of the ratio of total fungi on adaxial-to-abaxial leaf surfaces

Test of Fixed Effects

Source	df	Error term	F-value	*P*-value
UV-B	1	Residual	3.34	0.0840

Covariance Parameter Estimates

Parameter	df	Estimate
Residual	18	0.08745422

APPENDIX C. META-ANALYSIS

Table C.1. The species used and variables measured for each of the 62 references in the meta-analysis database. The variables are abbreviated as follows: leaf pigments on a mass basis -- carotenoids (Cm), chlorophyll (CHm), UV-B-absorbing compounds (UVm); leaf pigments on an area basis -- UV-B-absorbing compounds (UVa); growth and morphological variables -- height (H), shoot mass (M), reproductive yield (Y), leaf area (LA), leaf mass per area (LMA); and leaf photosynthetic parameters -- gas exchange including CO_2 uptake and O_2 evolution (GX), chlorophyll fluorescence as variable-to-maximal fluorescence (Fl). The number of reports for a given variable are shown for each species for each reference. More than one report for a variable may occur if a paper includes multiple cultivars or ecotypes, seasons of study for annual species, or ozone depletion levels (see Methods for further details). The total number of reports for each variable is given at the bottom of the table.

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Allen et al. 1999	*Pisum sativum*				1	1			1		1	1
Ambasht and Agrawal 1995	*Zea mays*	1	1	1			1				1	
Ambasht and Agrawal 1997	*Oryza sativa*	1	1	1			1				1	
Ambasht and Agrawal 1998	*Sorghum vulgare*	1	1	1							1	
Antonelli et al. 1997	*Phaseolus vulgaris*	1	1		1	1	1		1	1	1	
Antonelli et al. 1998	*Quercus robur*					1						
Balakumar et al. 1997	*Lycopersicon esculentum*			1		1			1			
Barnes et al. 1987	*Lupinus spp.*			1	1					2	2	
	Plantago lanceolata			1	1					2	2	

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	FI
Barnes et al. 1987 (cont.)	*Rumex acetosella*			1	1					2	2	
	Taraxacum spp.			1	1					2	2	
Barnes et al. 1995	*Avena fatua*								2			
	Triticum aestivum								2			
Beyschlag et al. 1988	*Avena sativa*										1	
	Triticum aestivum										1	
Björn et al. 1997	*Calluna vulgaris*						1					
	Vaccinium myrtillus						1					
Booker et al. 1992	*Glycine max*		2		1		2					
Conner and Zangori 1997	*Brassica spp.*					2	2	2				
Correia et al. 1998	*Zea mays*					1	1		1	1		
D'Surney et al. 1993	*Glycine max*			2			2	2		2		

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	FI
Dai et al. 1995	*Oryza sativa*			6					6	6	3	
Dai et al. 1997	*Oryza sativa*					2		3				
Day et al. 1996	*Pisum sativum*				2							
Dillenburg et al. 1995	*Liquidambar styraciflua*		2		2					2		
Drilias et al. 1997	*Nerium oleander*						2		2	2		
Fiscus et al. 1996	*Glycine max*								2	2		
Flint et al. 1985	*Vicia faba*			2	2						2	
Grammatikopoulos et al. 1998	*Mentha spicata*				6		2	2	2	2		
Gwynn-Jones et al. 1997	*Empetrum hermaphroditum*					1						
Gwynn-Jones et al. 1997	*Vaccinium myrtillus*					1		1				
Harley et al. 1996	*Acer platanoides*									1		
	Mucana pruriens									1	1	

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Harley et al. 1996 (cont.)	*Quercus gambelii*									1	1	
Huang et al. 1997	*Oryza sativa*					4			4			
Johanson et al. 1995	*Empetrum hermaphroditum*					1						
Johanson et al. 1995	*Vaccinium spp.*					3			3	3		
Kim et al. 1996	*Oryza sativa*					1	1		1	1		
Manetas et al. 1997	*Pinus pinea*			1			1					2
Mepsted et al. 1996	*Pisum sativum*				4	4		4			1	4
Miles 1993	*Glycine max*											4
Miller et al. 1994	*Glycine max*							6				
Moody et al. 1998	*Calluna vulgaris*			2								
	Vaccinium myrtillus			1							1	
Murali and Teramura 1986a	*Glycine max*		4		4				4	4	4	

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Murali and Teramura 1986b	*Glycine max*		1	1		1	1		1	1	1	
Musil 1996	*Dimorphotheca sinuata*	1	1	1			1	1	1	1		1
Naidu et al. 1993	*Pinus taeda*					1	1		1		1	2
Nedunchezhian and Kulandaivelu 1997	*Vigna unguiculata*		1		1	1	1		1			
Newsham et al. 1996	*Quercus robur*					1						
Nikolopoulos et al. 1995	*Phlomis fruticosa*				4		1		1	1	1	1
Nouchi and Kobayashi 1995	*Oryza sativa*				3	3						
Petropoulou et al. 1995	*Pinus halepensis*	6	6	6			3				4	4
Salt et al. 1998	*Calluna vulgaris*			1								
Sinclair et al. 1990	*Glycine max*							2				
Singh 1996	*Glycine max*	1	1	1		1			1			

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Singh 1996 (cont.)	*Phaseolus mungo*	1	1	1		1			1			
	Vigna radiata	1	1	1		1			1			
Sisson et al. 1976	*Rumex patientia*										1	
Sprtova et al. 1999	*Picea abies*										1	
Stephanou and Manetas 1997	*Cistus creticus*				2							
Stephanou and Manetas 1998	*Cistus creticus*					1	1	1		1	1	1
Sullivan and Teramura 1990	*Glycine max*					1	1	1	1	1	1	
Sullivan and Teramura 1992	*Pinus taeda*					8	8					
Sullivan et al. 1994	*Glycine max*	2	2	2		2	2	2	2	2	2	2
Sullivan et al. 1994	*Liquidambar styraciflua*		2		2		2		2	2	4	4
Sullivan et al. 1996	*Pinus taeda*				2				2			
Teramura et al. 1990	*Glycine max*							4				

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Tosserams et al. 1997	*Bromus spp.*			2		2	2		2	2		
	Oenethera biennis			1		1	1		1	1		
	Plantago lanceolata			1		1	1		1	1		
	Rumex obtusifolius			1		1	1		1	1		
	Verbascum thapsus			1		1	1		1	1		
Weih et al. 1998	*Betula pubescens*						1			1		
Yuan et al. 1998	*Triticum aestivum*					4	4	4	3	3		
Yuan et al. 1999	*Avena fatua*				2			1				
	Triticum aestivum				1			1				
Yue et al. 1998	*Triticum aestivum*						3	3				
Zeuthen et al. 1997	*Fagus sylvatica*											1

Table C.1. Continued

Reference	Species	Cm	CHm	UVm	UVa	H	M	Y	LA	LMA	GX	Fl
Ziska et al. 1993	*Manihot esculentum*					1	1		1		1	3
												30
Total # of reports *		16	28	42	44	57	55	40	57	56	46	

* A few reports of shoot mass and reproductive yield included greater than 100 replications. These reports were not included in the nonparametrically-weighted analyses to avoid biasing of the dataset by individual studies.

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Examples of Meta-analysis Statistics

Below are examples of output from the meta-analysis software, MetaWin 1.0, designed by Rosenberg et al. (1997); see chapter 5 for the full reference. The parametric and nonparametric output is shown for aboveground biomass.

Parametric output

```
Meta-Analysis Results, MetaW16 1.00

Analysis begun on 6/3/99  1:45:21 PM

Data from C:\METAW16\MASS99\MASS992.DTA

Data sorted by plotcode
  Excluded the following studies:  27nai, 51mus, 67ant, 82Wei, 28dsu
        28dsu, 74tos, 74tos, 74tos, 74tos, 74tos, 74tos, 36pet
        36pet, 36pet, 23sul, 23sul, 23sul, 23sul, 23sul, 23sul
        23sul, 23sul, 26zis, 32sul, 32sul, 46nou, 87gra, 87gra
        77yua, 77yua, 77yua, 77yua, 97ste

----------Parametric Methods----------

 Sample Statistics: Effect values for each study

Study     Class    ln RR      95% CI        V          W        W*

25boo       X      0.095   -0.099  0.290  0.010    101.297   13.510
25boo       X      0.077   -0.119  0.273  0.010     99.750   13.482
88amb       X      0.070    0.050  0.090  0.000   9327.390   15.563
73ned       X      0.055   -0.048  0.159  0.003    357.992   14.938
70amb       X     -0.583   -0.795 -0.372  0.012     85.951   13.195
66bjo       X      0.000   -0.111  0.111  0.003    312.681   14.848
66bjo       X     -0.104   -0.192 -0.016  0.002    496.473   15.114
10mur       X     -0.223   -0.291 -0.155  0.001    828.928   15.301
64man       X      0.256    0.129  0.383  0.004    236.857   14.626
59dri       X     -0.289   -0.426 -0.152  0.005    204.447   14.484
59dri       X     -0.058   -0.228  0.112  0.008    132.889   13.952
38nik       X     -0.611   -0.870 -0.352  0.017     57.333   12.256
18sul       X     -0.423   -0.756 -0.090  0.029     34.619   10.749
```

Sample Statistics: Effect values for each study (cont.)

Study	Class	ln RR	95% CI		V	W	W*
68con	X	-0.329	-0.475	-0.183	0.006	179.993	14.346
68con	X	-0.234	-0.385	-0.082	0.006	166.528	14.254
33sul	X	0.000	-0.244	0.244	0.015	64.752	12.564
33sul	X	-0.036	-0.310	0.239	0.020	51.037	11.941
94cor	X	-0.237	-0.348	-0.126	0.003	310.215	14.843
95yue	X	-0.170	-0.225	-0.115	0.001	1267.510	15.399
95yue	X	-0.241	-0.295	-0.186	0.001	1294.592	15.403
95yue	X	-0.604	-0.658	-0.551	0.001	1344.379	15.410

Meta-analysis results for groups

--- Fixed Model ---

Class	#Studies	ln RR+	95% CI		Qwi
X	21	-0.0687	-0.0838	-0.0537	753.7142

Class	#Studies	RR+	95% CI	
X	21	0.9336	0.9196	0.9477

--- Mixed Model ---

Class	#Studies	ln RR+*	95% CI		Pooled Variance
X	21	-0.1667	-0.2806	-0.0528	0.0641

Class	#Studies	RR+*	95% CI	
X	21	0.8465	0.7554	0.9486

Final Statistics

Group	Qwi	DF	P-value (Chi-Square Test)
X	753.7142	20	0.00000

	95% CI	
ln RR++	-0.083788	-0.053683
RR++	0.919627	0.947732
ln RR++*	-0.280568	-0.052792
RR++*	0.755355	0.948577

Nonparametric output

```
Meta-Analysis Results, MetaW16 1.00

Analysis begun on 6/21/99  2:22:57 PM

Data from C:\METAW16\MASS99\MASS992.DTA

Data sorted by plotcode
  Excluded the following studies:  68con, 68con

Resampling tests generated from 4999 iterations.

 Nonparametric Weights

          ---Fixed Model---

study          W

25boo        2.000
25boo        2.000
27nai        6.000
88amb        4.500
73ned        6.000
70amb        4.500
51mus       12.000
67ant       15.000
82Wei       15.000
28dsu        3.733
28dsu        4.000
66bjo        5.000
66bjo        5.000
74tos        9.000
74tos        9.000
74tos        9.000
74tos        9.000
74tos        9.000
74tos        9.000
36pet        5.000
36pet        5.000
36pet        5.000
10mur        4.000
23sul       11.000
23sul       11.000
```

```
Nonparametric Weights (cont.)

study          W

23sul        11.000
23sul        11.000
23sul        11.000
23sul        11.000
23sul        11.000
23sul        11.000
64man         5.000
59dri        10.000
59dri        10.000
38nik         5.000
18sul        10.000
33sul        10.000
33sul        10.000
26zis        12.000
32sul         1.500
32sul         1.500
46nou         7.000
87gra         5.000
87gra         5.000
77yua         3.000
77yua         3.000
77yua         3.000
77yua         3.000
94cor         4.000
95yue         3.000
95yue         3.000
95yue         3.000
97ste         1.500


----------Results of Resampling Tests----------

 Meta-analysis results for groups

    --- Fixed Model ---

Class  #Studies   ln RR+         95% CI            Qwi
X         53      -0.0947    -0.1974     0.0080    11.0290
```

```
Class    Bootstrapped CI       Bias-Corrected CI
X      -0.1387    -0.0516    -0.1400    -0.0523

Class  #Studies      RR+             95% CI
X          53      0.9097     0.8209      1.0081

         Bootstrapped CI       Bias-Corrected CI
X        0.8705     0.9497     0.8693     0.9491


      --- Mixed Model ---

Calculation of SSpool for the mixed effects model was less
than or equal to zero.  The mixed effects model was
therefore invalid or identical to the fixed effects model,
so no mixed effect model calculations were performed.
```

CURRICULUM VITAE

Peter S. Searles
(July 2000)

Education: B.S. (in biology) University of Maryland at College Park, 1991; M.S. (in ecology) Utah State University, 1994; PhD (in ecology) Utah State University, expected Fall 2000

Professional Employment: Intern, Crop Genetics International, Microbial Ecology Unit, 1990; Graduate Research Assistant, Department of Rangeland Resources and the Ecology Center, Utah State University, 1991-2000; Post-doctoral Associate, Department of Vegetable Crops, University of California at Davis, starting July 2000

Professional Interests: plant physiological ecology, photobiology, global climate change. As a graduate student, my research focused on ultraviolet-B radiation and stratospheric ozone depletion in natural ecosystems including tropical rainforests (Barro Colorado Island, Panama) and subantarctic *Sphagnum* and *Carex* bogs (Tierra del Fuego, Argentina).

Publications:

Searles PS, Flint SD, Díaz SB, Rousseaux MC, Ballaré CL, Caldwell MM (1999) Solar ultraviolet-B radiation insfluence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. *Global Change Biology*, **5,** 225-234

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Barnes PW, Searles PS, Ballaré CL, Ryel RJ, Caldwell MM (2000) Non-invasive measurements of leaf epidermal transmittance of UV radiation using chlorphyll fluorescence: field and laboratory tests. *Physiologia Plantarum*, **109,** 274-283

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Rousseaux MC, Ballaré CL, Scopel AL, Searles PS, Caldwell MM (1998) Solar ultraviolet-B radiation affects plant-insect interactions in a natural ecosystem of Tierra del Fuego (southern Argentina). *Oecologia*, **116,** 528-535

Rousseaux MC, Ballare CL, Giordano CV, Scopel AL, Zima AM, Szwarcberg-Bracchitta M, Searles PS, Caldwell MM, Diaz SB (1999) Ozone depletion and UVB radiation: Impact on plant DNA damage in southern South America. *Proceedings of the National Academy of Science (USA)*, **96,** 15310-15315

Fellowships and Awards:

Smithsonian Graduate Student Fellowship, 1995 (declined)
Don Dwyer Award for Excellence in Range Science, Utah State University, 1994
Mellon Foundation Pre-Doctoral Fellowship, 1992-1994
Graduate Student Fellowship, Utah State University, 1991-1992
Appleman-Norton Award (Outstanding Undergraduate Botany Student), University of Maryland at College Park, 1991