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Impacts of solar ultraviolet-B radiation on terrestrial ecosystems of Tierra del Fuego (southern Argentina) An overview of recent progress

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Abstract

The southern part of Tierra del Fuego, in the southernmost tip of South America, is covered by dense *Nothofagus* spp. forests and *Sphagnum*-dominated peat bogs, which are subjected to the influence of ozone depletion and to increased levels of solar ultraviolet-B radiation (UV-B). Over the last 5 years we have studied some of the biological impacts of solar UV-B on natural ecosystems of this region. We have addressed two general problems: (i) do the fluctuations in UV-B levels under the influence of the Antarctic ozone 'hole' have any measurable biological impact, and (ii) what are the long-term effects of solar (ambient) UV-B on the Tierra del Fuego ecosystems? In this paper, we provide an overview of the progress made during the first 4 years of the project. We highlight and discuss the following results: (1) ambient UV-B has subtle but significant inhibitory effects on the growth of herbaceous and graminoid species of this region (growth reduction ≤12%), whereas no consistent inhibitory effects could be detected in woody perennials; (2) in the species investigated in greatest detail, *Gunnera magellanica*, the inhibitory effect of solar UV-B is accompanied by increased levels of DNA damage in leaf tissue, and the DNA damage density in the early spring is clearly correlated with the dose of weighted UV-B measured at ground level; (3) the herbaceous species investigated thus far show little or no acclimation responses to ambient UV-B such as increased sunscreen levels and DNA repair capacity; and (4) ambient UV-B has significant effects on heterotrophic organisms, included marked inhibitory effects on insect herbivory. The results from the experiments summarized in this review clearly indicate that UV-B influences several potentially important processes and ecological interactions in the terrestrial ecosystems of Tierra del Fuego.

Keywords: *Gunnera magellanica*; *Nothofagus*; *Sphagnum*; DNA damage; Herbivory; Ozone hole; Tierra del Fuego; UV-B

1. Introduction

The study of the biological effects of ultraviolet-B radiation (UV-B; 280–315 nm) has attracted considerable attention during the last two decades because the thinning of the stratospheric ozone layer leads to elevated solar UV-B at ground level [1–3]. In 1996 we set up a long term experiment to study the impacts of solar UV-B radiation on natural ecosystems of Tierra del Fuego (southern Argentina). The choice of this experimental location is based on two major factors: the unique physical environment of Tierra del Fuego, characterized by the influence of the Antarctic ozone hole, and the structural and biological diversity of the region.

Satellite data from the total ozone mapping spectrometer (TOMS), which are available since 1978, indicate that the area of the ozone hole has increased from ca. 2×10^6 km^2 in the early 1980s to $>25\times10^6$ km^2 in the late 1990s [4]. Consequently, the area of influence of the ozone hole now includes the southern regions of mainland Argentina and Chile. Under the direct influence of the ozone hole, in early spring, the thickness of the ozone layer above southern Argentina and Chile drops from its normal level of around 330 Dobson units (DU) to almost half of this value within a time interval of less than 2 days [5–7]. But

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ozone depletion is not limited to this transient episodes: parcels of ozone-poor air also linger over the region during the summer, and TOMS ozone records indicate a significant decline in ozone levels for every month of the growing season (October to March) relative to 20 years ago. This decline represents, on average, an 11% reduction in ozone levels [8].

Regarding the biological component, Tierra del Fuego is unique in that it is the only area of the world regularly affected by severe ozone depletion that is covered by well developed terrestrial ecosystems. These ecosystems are productive and diverse, particularly in comparison with the ecosystems of Antarctica, where most of the UV-B research has been carried out. Tierra del Fuego harbors the southernmost forest ecosystems of the world, which cover most of the southern part of the island [9].

This combination of rich biology and heavily perturbed atmospheric conditions prompted us to study the biological impacts of solar UV-B radiation under natural field conditions. We have addressed two basic questions:

1. Do the fluctuations in UV-B levels during the spring have any measurable biological impact?
2. What roles does present-day, ambient UV-B play in the control of plant growth and trophic level interactions in the native ecosystems of Tierra del Fuego?

In this paper, we briefly review the most recent results of this study.

2. Ecosystems studied

The experiments were established near the city of Ushuaia, Province of Tierra del Fuego, Argentina (54° 4′ 23″ S, 68° 35′ 77″ W, sea level). The area receives an average annual precipitation of 520 mm; mean annual temperature is 5.5°C. The experimental plots were located in three contrasting sites (Fig. 1): (a) a shrubland, dominated by the evergreen shrub *Chiliotrichum diffusum* (Forster f.) O. Kuntze ('mata negra') and surrounded by a deciduous *Nothofagus* forest; (b) a *Sphagnum* bog; and (c) a *Carex*-dominated fen. The shrubland and bog sites are located in the Tierra del Fuego National Park about 20 km west of Ushuaia; the fen is located in Andorra Valley about 5 km north-east of Ushuaia. For a detailed description of the experimental setup see Rousseaux et al. [8] and Searles et al. [10].

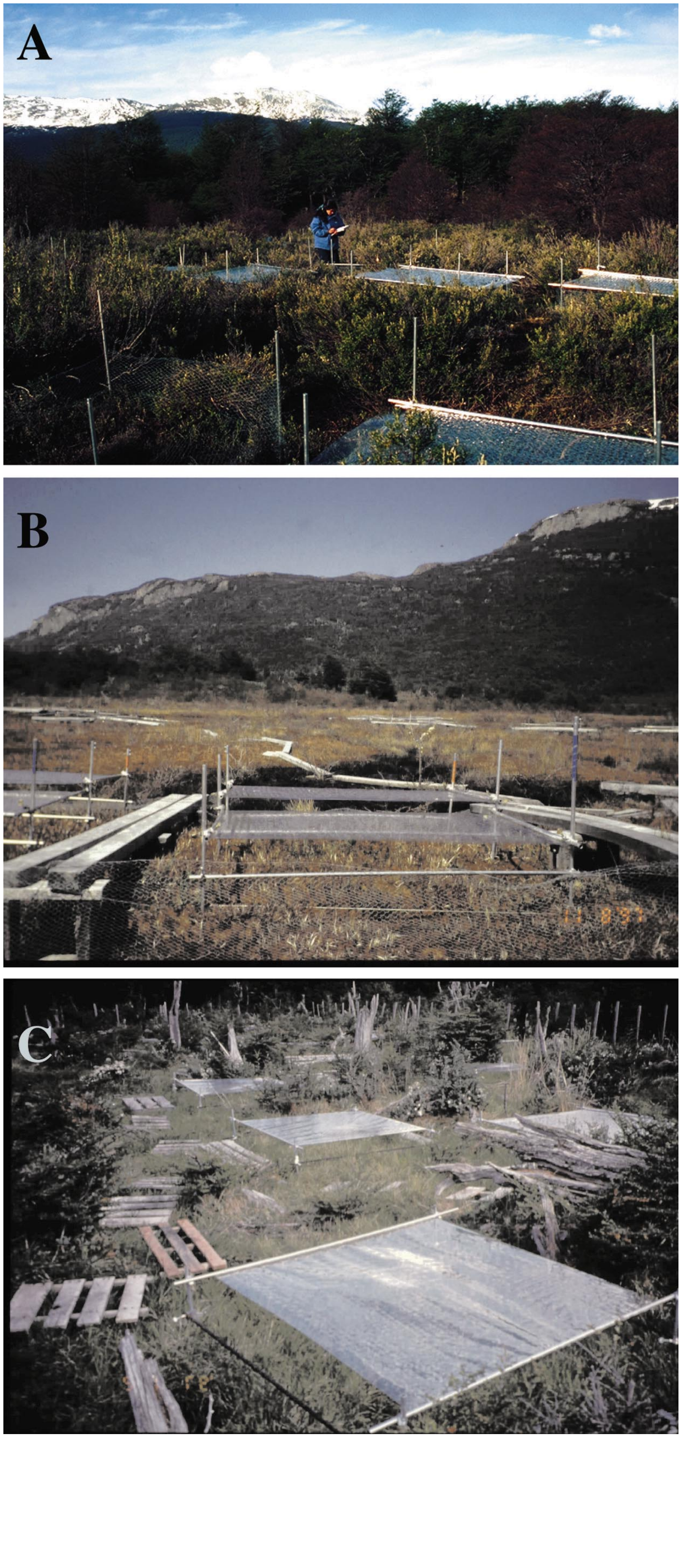
Because we were interested in two interrelated, yet different problems, the short-term responses to abnormally high UV-B levels during the spring, and the long-term effects of ambient UV-B on ecosystem biology, we used two separate experimental approaches. To study short-term impacts of UV-B fluctuations during the period in which the region is subjected to the influence of the Antarctic ozone hole, we correlated the doses of UV-B received at ground level with the intensity of a particular biological effect: the induction of DNA damage in native plants. To study the impacts of present-day, ambient UV-B over longer periods of time, we designed a manipulative experiment that had two treatments: attenuated UV-B and near-ambient UV-B. These treatments were imposed using especially-designed plastic films that were suspended over the vegetation using adjustable aluminum frames. The attenuated UV-B treatment reduced the current flux of biologically effective UV-B by ca. 80%, whereas the near-ambient UV-B treatment attenuated the UV-B flux by less than 10%. Both types of filters were perforated to allow precipitation to pass through (for details see Refs. [8,10]). We set up ten permanent plots of each treatment at the shrub and bog sites, and fourteen permanent plots in the fen. This manipulative experiment started in the spring of 1996.

Because it was technically not feasible to place filters on top of whole trees, we did some branch-level experiments to test the impact of attenuating UV-B on growth, acclimation, and trophic level interactions in *Nothofagus* trees (*N. antarctica*, *N. pumilio*, and *N. betuloides*). In this case, the filters were supported by chicken-wire frames (30×40 cm) to cover a small branch area; they were set on the trees before bud break, and remained on the branches until the end of the growing season.

3. Short-term impacts of ozone and UV-B fluctuations

We documented a significant inverse correlation between column ozone in early spring and the ground-level, biologically-effective UV doses derived from spectral data collected by the United States National Science Foundation spectroradiometer in Ushuaia (Fig. 2). Similar results have been reported for other years in Ushuaia and nearby Punta Arenas (Chile) [5,7]. As expected, the correlation between ozone column thickness and effective UV was stronger when we used functions to weight the radiation in which the quantum effectiveness declines sharply with the increase in wavelength. This is because only the shorter

Fig. 1. The three ecosystems chosen for study in the Tierra del Fuego area. (a) Shrubland dominated by *Chiliotrichum diffusum*; (b) minerotrophic bog dominated by *Sphagnum magellanicum*; and (c) fen dominated by the sedges *Carex decidua* and *Carex curta*. The first two sites (a and b) are within the boundaries of the Tierra del Fuego National Park, in the Laguna Negra area, approximately 20 km to the west of the city of Ushuaia. The fen ecosystem is located on private property, in the Andorra Valley area, near Ushuaia. For detailed descriptions see Rousseaux et al. [8] (site a) and Searles et al. [10] (sites b and c).


A
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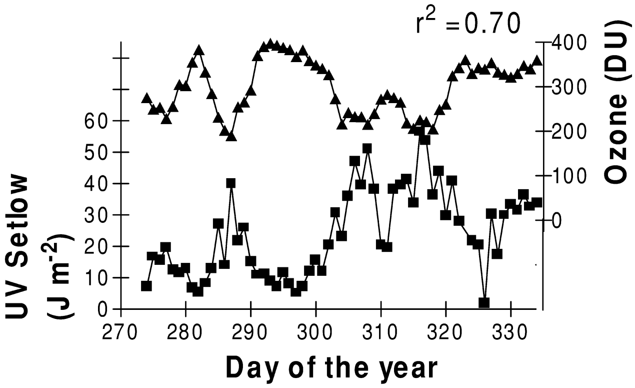

Fig. 2. Inverse relationship between ozone column and UV-B dose measured at ground level in the early spring. Ozone data were obtained from the TOMS database (see http://jwocky.gsfc.nasa.gov, overpass data file for the city of Ushuaia, October and November of 1997). UV-B was measured at ground level with a scanning spectroradiometer of the US NSF monitoring network based at CADIC (city of Ushuaia). The irradiance data were weighted for biological effectiveness using Setlow's action spectrum for DNA damage, and integrated between dawn and 13:30 h to obtain a pre-noon biologically-effective UV dose (For details, see Ref. [6]).

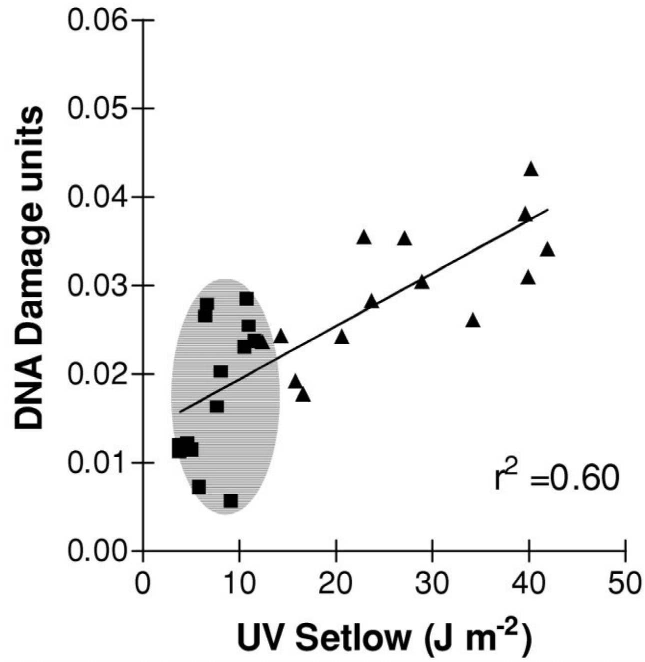

Fig. 3. Effects of variations in pre-midday UV dose at ground level during October and November 1997 (see Fig. 2) on the steady state levels of CPDs measured in leaves of *G. magellanica*. The leaf tissue was obtained from plants that occurred naturally in our field plots. The squares in the shaded ellipse represent samples collected from plants covered with filters that attenuated the UV-B component of solar radiation (For details see Ref. [6]).

wavelengths of the UV spectrum (i.e. the UV-B) are significantly affected by ozone depletion. These results indicate that, in spite of the large day-to-day variations in cloud cover, the passage of the ozone hole over the southern tip of South America causes large increases in biologically effective UV radiation at the ground level in the early spring [3,6].

Do these ozone-related UV peaks in the early spring have any measurable biological impact? In order to address this question it is necessary to choose a response variable with a fast response kinetics, and which can be unequivocally attributed to the variations in UV-B levels. We chose to measure the density of cyclobutane pyrimidine dimers (CPDs) in DNA extracted from leaves of plants that occurred naturally in our field site. CPDs constitute the major fraction (ca. 75%) of the aberrant DNA photoproducts induced by UV [11]. Eco-physiological studies have provided indirect, correlative evidence suggesting that the plant growth inhibition caused by high [12] and ambient [13,14] UV-B doses may be related to DNA damage.

Using the herbaceous *Gunnera magellanica* as a model species, we found that the steady-state levels of CPDs measured at midday in leaf tissue were linearly correlated with the pre-midday UV dose measured at ground level (Fig. 3).

The relationship between UV dose and CPD load was particularly strong when we weighted the radiation for biological effectiveness using spectra that assume a sharp decline in quantum efficiency with increasing wavelength from the UV-B into the UV-A regions of the spectrum [6]. That weighting functions which strongly discount the UV-A component gave the best prediction of CPD accumulation under real ozone variation probably reflects the influence of UV-A-driven photoreactivation under natural conditions. Photoreactivation would reduce the apparent contribution of the UV-A waveband to the generation of DNA damage. Of course, other factors, such as accumulation of phenolic sunscreens, may also affect the shape of the weighting function that best predicts the impacts of ozone-related UV fluctuations on a particular biological process

Are the variations in CPD density that we measured in response to ozone-related UV fluctuations physiologically significant? Genetic tools (i.e. DNA repair mutants) are not available in *G. magellanica*, and detailed kinetic analyses of growth inhibition are not feasible in field studies with species that show slow rates of growth. Therefore, the evidence for a functional link between DNA damage and alterations in plant growth remains circumstantial, and it is based on three pieces of information: (1) present levels of solar UV-B in the early spring do inhibit leaf area expansion in *G. magellanica* (as well as in other herbaceous species, see below); (2) studies with DNA repair mutants of *Arabidopsis thaliana* have clearly demonstrated that CPDs have growth inhibitory effects in terrestrial plants [15,16]; and (3) in all cases studied thus far the inhibitory effects of solar UV-B on growth were found to be accompanied by increased levels of DNA damage in the form of CPDs ([14,17,18] and C.A. Mazza unpublished results).

4. Long-term effects of solar UV-B attenuation on plant growth and physiological acclimation

4.1. Growth and morphology

In terms of effects of ambient UV-B on growth, the data that we have collected in Tierra del Fuego indicate that: (1) ambient UV-B inhibits the growth of some species under natural field conditions; and (2) the effects are different for different species (Table 1).

In the 'mata negra' shrubland site, we found significant inhibitory effects of ambient UV-B on frond elongation in the fern *Blechnum penna-marina* and leaf expansion in *G. magellanica* (growth reductions between 10 and 12%). In contrast in the dominant shrub, *C. diffusum*, we were not able to detect any significant growth response to solar UV-B [8]. In the *Carex*-dominated fen ecosystem, shoot growth of the dominant *Carex* species was unaffected by solar UV-B [10,19]; however, recent results show that root length growth can be significantly inhibited by ambient UV-B in this fen [20]. In the *Sphagnum* bog we detected a small, but significant inhibitory effect of ambient UV-B on *Sphagnum* height growth, particularly after the second growing season of the experiment [19,21]. Similarly, ambient UV-B reduced leaf production and total leaf area in *Tetroncium magellanicum* (a perennial monocot) [19,21]. No effects of UV-B attenuation were apparent on the growth of the two woody species that emerge from the *Sphagnum* carpet (dwarf *N. antarctica* trees and *Empetrum rubrum*) [19,21]. The experiments with full size *Nothofagus* spp. trees have been limited to branch-level manipulations of the UV climate, and the data collected thus far do not show significant effects of ambient UV-B on leaf area expansion [22].

4.2. Phenolic sunscreens and internal UV filtration

We measured accumulation of methanol-soluble UV-absorbing compounds and changes in leaf thickness (or specific leaf mass) in most of the species, as indicators of long-term screening acclimation to solar UV-B. In some species of the shrubland site these measurements were complemented with determinations of epidermal UV transmittance. In the majority of the species investigated we did not detect a significant effect of ambient UV-B levels on concentration of UV-absorbing compounds (*G. magellanica*, *B. penna-marina*, *C. diffusum*, *S. magellanicum*) or specific leaf mass (*G. magellanica*, *B. penna-marina*, *C. diffusum*) [8,17]. In contrast, in the *Nothofagus* trees, both UV-B absorbing compounds and leaf thickness increased in response to ambient UV-B radiation [22]. Searles [19] also reported small effects of ambient UV-B on UV-absorbing compounds in *Empetrum rubrum* and *Tetroncium magellanicum*. Using UV-induced chlorophyll fluorescence to estimate epidermal transmittance [18,23], Barnes et al. [23] confirmed the lack of effect of ambient UV-B on sunscreen accumulation in all three species of the shrubland site (*G. magellanica*, *B. penna-marina*, *C. diffusum*). These measurements also demonstrated that most of these species have very high constitutive levels of phenolic sunscreens, and correspondingly very low epidermal transmittance to UV-B (Fig. 4).

Table 1
Summary of effects of solar UV-B on the growth of various plant species of the Tierra del Fuego ecosystems

Site	Species	Life form	Effect of solar UV-B	Ref.
Shrubland	*G. magellanica*	Perennial herb	Inhibited leaf growth	[8,17]
(+adjacent	*B. penna marina*	Perennial herb	Inhibited frond growth	[8]
forest)	*C. diffusum*	Shrub	No effects detected	[8]
	N. antarctica	Deciduous tree	No effect on leaf area	[22]
	N. pumilio	Deciduous tree	No effect on leaf area	[22]
	N. betuloides	Evergreen tree	No effect on leaf area	[22]
Bog	*S. magellanicum*	Moss	Inhibited height growth	[19,21]
	E. rubrum	Shrub	No effects detected	[19,21]
	T. magellanicum	Perennial graminoid	Inhibited leaf growth	[19,21]
Fen	*C. curta* and *C. decidua*	Perennial graminoid	No effects on shoot growth; reduced root length	[20]

Effects were determined by comparing the near-ambient with the attenuated UV-B treatments. Inhibitory effects are reported only if the difference between treatments was statistically significant in the original study.

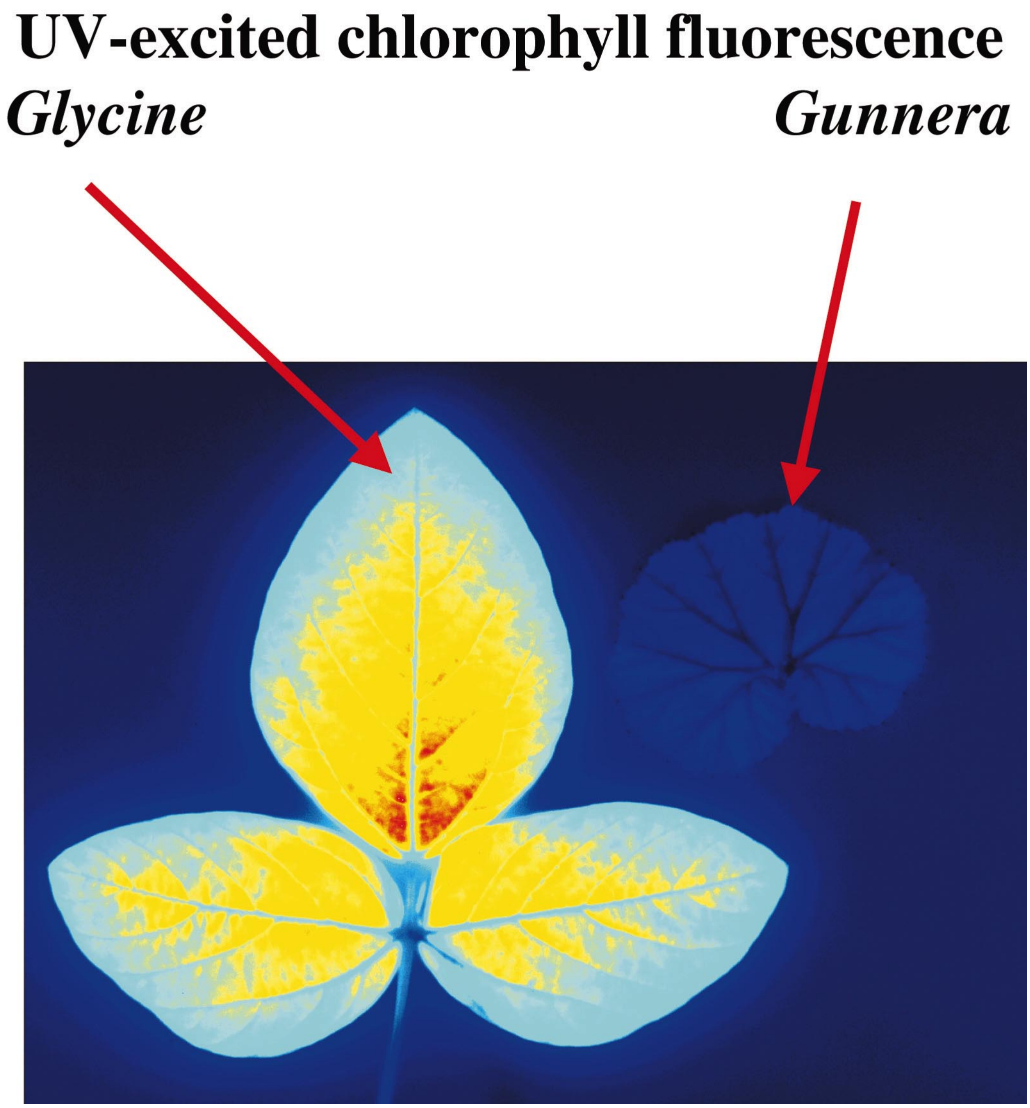

Fig. 4. False color image indicating the intensity of chlorophyll fluorescence excited by UV in leaves of *G. magellanica* and soybean (*Glycine max*), which is used here as a reference. In this system (for details see Ref. [18]), a low intensity of chlorophyll fluorescence indicates a low penetration of UV through the epidermis and to the photosynthetic mesophyll. Notice the very dark appearance of the *G. magellanica* leaf in comparison with the soybean leaf.

4.3. DNA repair

Another attempt to characterize the long-term physiological acclimation to solar UV-B is based on measuring the effects of exposure to different UV regimes on DNA photorepair capacity in *G. magellanica*. Preliminary results indicate that leaves from plants that occur naturally under the filters that attenuate solar UV-B display CPD photorepair rates that are not very different from those of plants exposed to ambient UV-B levels. In general, the CPD photorepair capacity of *G. magellanica* appeared to be low, compared to other species of temperate origin [24]. This reduced CPD repair capacity might explain why *G. magellanica* is affected by the ambient levels of UV-B in Tierra del Fuego, in spite of the fact that this species has efficient UV-absorbing sunscreens.

5. Long-term effects of solar UV-B attenuation on trophic-level interactions

We found significant effects of solar UV-B attenuation on heterotrophic organisms in all three ecosystems (Table 2). The effects of solar UV-B on plant–herbivore interactions have received the most study, and will be summarized first.

In the shrubland site we have documented consistent

Table 2
Summary of effects of near-ambient UV-B on heterotrophic organisms in the Tierra del Fuego ecosystems

Site	Organism/s	Effect of solar UV-B	Ref.
Shrubland (+adjacent forest)	Insects feeding on *G. magellanica* leaves	Reduced leaf herbivory	[8,17]
	Insects feeding on *N. antarctica* leaves	Reduced leaf herbivory	[26]
Bog	Microfauna in *Sphagnum* capitulae	Increased density of testate amoebae	[10,19,27]
Fen	Symbiotic mycorrhizae	Increased symbiotic mycorrhizal infection of *Carex* roots in fen	[28]
	Slugs feeding on leaves of most abundant species in fen	Reduced and increased herbivory; changed diet selection of slugs	[25]

Effects were determined by comparing the near-ambient with the attenuated UV-B treatments. Positive or negative effects are reported only if the difference between treatments was statistically significant in the original study.

effects of solar UV-B on insect herbivory, which was particularly intense early in the season on the perennial herb *G. magellanica*, one of the first species to resume growth at the end of the winter. Plants covered by filters that attenuate solar UV-B radiation were significantly more consumed by chewing insects than plants exposed to near-ambient UV-B levels [8,17]. Moth larvae (Lepidoptera: Noctuidae) were the most important consumers.

Are the impacts of solar UV-B on herbivory mediated by changes in the host plants or through direct effects of UV-B on the insects? The moth larvae that feed on *G. magellanica* leaves are active during the night, and hide under the litter layer during the day. Therefore, it is most unlikely that the effects of UV-B on herbivory are mediated by direct effects of the radiation on the caterpillars. Rousseaux et al. [17] tested the effects of UV-B on host plant quality using 'choice' experiments. They found that the plants that grew under attenuated UV-B were chosen significantly more often by the natural fauna of insect consumers than plants collected from under the near-ambient UV-B treatment. These results indicate that solar UV-B can alter parameters of tissue quality that insects use in their host-selection decisions, and are consistent with the idea that at least part of the effects of solar UV-B on insect herbivory are mediated by UV-B-induced changes in the plants.

Herbivory appeared to be much less intense in the *Carex* fen and *Sphagnum* bog than in the drier shrubland. Nonetheless, in the *Carex* ecosystem, Zaller et al. [25] found that slugs in this fen consumed less decaying leaf material of *N. antarctica* but more of *C. decidua* when plants had been grown at ambient UV-B than when plants grew at reduced UV-B. Also, the diet selection of slugs among the six most abundant plant species in this fen was affected by UV-B treatments [25].

The leaves of *N. antarctica* trees are also consumed by a variety of herbivores, particularly lepidopteran larvae. Using branch filters Rousseaux et al. [26] found that, in the field, folivore insects consumed significantly more leaf area in *N. antarctica* branches covered with UV-B-attenuating film than in control branches that received near-ambient UV-B. These effects of ambient UV-B on herbivory are likely to be mediated by changes in tissue quality because lepidopteran larvae showed preference for leaves that had expanded under reduced UV-B when they were tested in choice bioassays [26]. Chemical analysis of *N. antarctica* leaf samples collected at the beginning of the summer (before the start of insect damage) showed that part of the variation in herbivory intensity could be explained by a multiple regression model that included levels of three specific phenolic compounds. The levels of two of these phenolics (gallic acid and a non-identified flavonoid-aglycone) were significantly affected by artificial UV-B attenuation in the field [26].

In the *Carex* fen and *Sphagnum* bog sites, solar UV-B also appeared to be an important factor regulating the populations of other components of the ecosystems besides plants and herbivorous insects. Searles et al. [10] reported significantly larger densities of testate amoebae under near-ambient UV-B levels than under attenuated UV-B. This difference was confirmed by Searles [19] and Robson et al. [27] in subsequent years. In the fen site, Zaller et al. [28] found large increases in symbiotic mycorrhizal infection of the *Carex* roots in the near-ambient UV-B plots, compared with the attenuated UV-B treatment. The effects were consistent over the seasons. The mechanisms that mediate these effects of solar UV-B on microfauna and symbiotic organisms are presently unknown.

6. Response patterns and comparisons with other ecosystems

The series of experiments described in this paper represents one of the first attempts to study the impacts of ambient UV-B on the biology of intact terrestrial ecosystems in an area of the world that is already exposed to ozone depletion. Therefore, direct comparisons with other studies are difficult to establish. In the following we will: (1) draw some generalizations from the data collected in the three ecosystems of Tierra del Fuego and compare our results with those of other UV-B attenuation studies; and (2) discuss them in connection with UV-B supplementation studies carried out at high latitudes in the Northern hemisphere.

6.1. Generalizations from the Tierra del Fuego data set and comparison with other UV-B attenuation studies

We will highlight three general features of our data set: (i) the subtle inhibitory effect of solar UV-B on the growth of herbaceous plants; (ii) the reduced physiological plasticity to UV-B attenuation in all the plant species investigated; and (iii) the effects of solar UV-B on insect herbivory.

6.1.1. Growth responses to solar UV-B

As summarized in Table 1, in nearly all the herbaceous species investigated in our experiments in Tierra del Fuego solar UV-B (near-ambient level) had subtle, but significant inhibitory effects on growth or morphological development. In contrast, in our survey of woody perennials, which included the shrubs *C. diffusum* and *E. rubrum* and three species of *Nothofagus* trees, we could not detect growth inhibitory effects of solar UV-B. Many previous studies carried out at lower latitudes in both hemispheres (i.e. $<40°$ latitude) reported inhibition of growth by ambient UV-B in herbaceous species. These studies include those carried out with *Datura ferox* [13] and cultivated species such as cucumber [29], lettuce [30], and barley [14]. In UV-B attenuation experiments carried out at mid and high latitudes in the Northern hemisphere ($>40°$), inhibitory effects of UV-B on the growth of herbaceous species were found in some studies [31], but not in others [32,33]. The series of experiments that is most similar to ours, in terms of method and geographical location, is that of Day and co-workers in the Antarctic Peninsula [34–36]. They examined the influence of solar UV-B on the performance of *Colobantus quitensis* and *Deschampsia antarctica*, two vascular species, in a multi-year field study. In both species, ambient UV-B had significant inhibitory effects on leaf elongation and leaf area. The difference in relative UV-B levels between the near-ambient and attenuated UV-B treatments in our experiments was similar to that imposed by Day and associates (ca. 85% ambient for the near ambient UV-B treatment vs. 20% ambient for the attenuated UV-B treatment). However, the magnitudes of the UV-B effects detected by Day and co-workers (up to 43% reduction in leaf elongation in *D. antarctica*, and up to 25% reduction in number of green leaves in *C. quitensis*) [36] were much larger than the responses that we have measured in our experiments (12% growth inhibition or less). There may be several reasons for the difference in the magnitude of biological response between Day's studies and ours; we believe that the simplest explanation is that ozone depletion has been more pronounced over the Antarctic Peninsula than over Tierra del Fuego. Day et al. [36] estimate that ozone depletion over their field site has resulted in a 62% enhancement of (early-season) biologically effective UV-B (plant action spectrum; Ref. [37]), whereas from the ozone data reported by Rousseaux et al. [8] (11% reduction in ozone column), we estimate that the increase in biologically effective UV-B over Tierra del Fuego during the last two decades should not exceed 25% (assuming constant sky transmission and a radiation amplification factor of 2.2). Therefore, while the relative attenuation level imposed by Day and co-workers is similar to that used in our studies, the current (ambient) UV-B dose should be much more out of the range of the presumed evolutionary niche for Antarctic plants than for the plants of Tierra del Fuego.

Regarding growth responses of woody species to ambient UV-B, Hunt and McNeil [38] studied the effects of solar UV-B on mountain beech (*N. solandri* var. *cliffortioides*) and broadleaf (*Griselinia litoralis*) in New Zealand. In *N. solandri*, they found that UV-B attenuation caused increased height growth and average leaf size (by as much 45%); however, leaf number was reduced under attenuated UV-B and the average total leaf area per seedling was not affected by UV-B attenuation. Growth of *G. litoralis* was not affected by UV-B attenuation. We are not aware of other UV-B attenuation studies with woody perennials except those conducted by Searles et al. [39] in Panama and Schumaker et al. [40] in Pullman (WA, USA). No significant effects of UV-B attenuation on leaf area expansion were found in these studies.

6.1.2. Physiological acclimation to solar UV-B

All the species investigated in Tierra del Fuego had high constitutive levels of phenolic compounds in their leaves and these levels increased only slightly in response to solar UV-B (*Nothofagus* spp.) or were not affected at all (all species in the shrubland site). These large constitutive levels of phenolic sunscreens did not prevent, however, the transient accumulation of deleterious photoproducts in DNA during days in which UV-B increased in response to ozone depletion [6]. It is apparent from our preliminary results that *G. magellanica*, the only species investigated in detail with respect to DNA damage, has constitutively low repair rates [24]. Whether or not this is a general feature of all the plants native to this high latitude region is presently unknown.

6.1.3. Effects of solar UV-B plant–herbivore interactions

The third general feature that we identified in our data set from Tierra del Fuego is the negative effect of solar UV-B on levels of leaf herbivory in various species. Again, this is consistent with the results of previous UV-B attenuation studies in other systems. In terrestrial systems, Ballaré et al. [13] found that exposure of *D. ferox* seedlings to the UV-B component of solar radiation resulted in reduced levels of herbivory by a diverse guild of chewing insects. Similar results were reported by Mazza et al. [41], who worked with thrips and soybean plants, and by Zavala et al. [42], who studied the effects of solar UV-B attenuation on soybean herbivory by the velvetleaf worm *Anticarsia gemmatalis*. In all the experiments reported to date involving terrestrial plants, it could be demonstrated that exposure to solar UV-B induces persistent changes in the quality of plant tissues that the insects can recognize in choice experiments carried out under controlled environmental conditions. The nature of these changes is unknown, but they may involve alterations in the levels of specific phenolic compounds [43], as it may be the case for *N. antarctica* trees (see discussion above), or changes in specific defense proteins such as proteinase inhibitors [44].

6.2. Comparisons with UV-B supplementation studies carried out at high latitudes in the Northern hemisphere

UV-B supplementation studies involving natural vegetation have been conducted at a few locations in the Northern hemisphere. One of the most complete series of experiments has been conducted at a field site near Abisko (68° Northern latitude, Sweden) [45–47], in a system that has ecological convergence with our Tierra del Fuego field site (for further discussion see Ref. [48]).

In terms of UV-B impacts on plant growth, the Abisko supplementation studies that simulated ozone depletion levels of ca. 15% on clear days yielded UV-B treatment effects that were either similar or more intense than those of our UV-B attenuation experiments. For example, the studies at the Abisko site showed a 15% decrease in leaf growth of *Vaccinium myrtillus*, 27% and 33% reduction in stem growth of *V. vitis-idaea* and *Empetrum* sp., respectively [45], and 25% decrease in *Sphagnum fuscum* height [46].

In terms of trophic-level interactions, Gwynn-Jones and co-workers [49] reported that enhanced UV-B decreased the intensity of herbivory in *V. uliginosum*, which is consistent with the results of our experiments. However, UV-B supplementation was found to increase herbivory by 70% in another species (*V. myrtillus*) included in the Abisko study. Given the complex effects of UV-B on plant secondary chemistry, and the complex sensory interactions between plant and insects, it is hardly surprising to find system-dependent effects of UV-B on insect herbivory.

7. Outlook

Is ozone depletion affecting the functioning of terrestrial ecosystems in Tierra del Fuego? If we focus our analysis on short-term impacts, it is clear from the data collected by our group [6] that the increases in solar UV-B during the early spring cause proportional increases in the density of aberrant photoproducts in the leaves of naturally occurring plants. To the extent that these photoproducts have toxic or mutagenic effects [15,16], it is reasonable to expect that the increased UV-B levels in the spring have transient negative impacts on the native flora of the Tierra del Fuego ecosystems. If, on the other hand, we focus on long-term effects of enhanced UV-B on plant growth, our ability to draw robust conclusion is much more limited. Any inference in this regard would involve several assumptions about (i) the UV-B climate that prevailed over the region before the beginning of ozone depletion; and (ii) the responses of the biological system to alterations in UV-B over long time scales. We did find small but consistent inhibitory effects of ambient UV-B levels on the growth of herbaceous species in all three ecosystems (Table 1), and it is reasonable to assume that solar UV-B plays now a greater role as an environmental stressor than 20 years ago, due to ozone depletion. This idea is strongly supported by the comparison between our data and the data collected by Day and co-workers [34–36] in the Antarctic Peninsula. This comparison shows that a similar fractional level of UV-B attenuation has impacts on plant growth that increase with the level of ozone depletion (i.e. from Tierra del Fuego to Antarctica). If there were a linear correspondence between UV-B dose and plant growth inhibition, the inhibitory effect of enhanced springtime UV-B in Tierra del Fuego should be around 3–4% for herbaceous species (i.e. one-quarter to one-third of the inhibitory effect that we detected when comparing the near-ambient UV-B with the 80% attenuation treatments) [8]. The magnitude of this predicted effect compares well with the results of a recent meta-analysis of UV-B supplementation studies [50]. This analysis indicated that UV-B supplementation treatments that simulated a 10–20% ozone depletion resulted, on the average, in a 6% reduction in plant biomass.

Current UV-B levels also had effects on plant consumers and other heterotrophic organisms in the three ecosystems that we studied. Due to limitations associated with extrapolating over large spatial and temporal scales it remains unclear if these organisms have different dynamics or densities now than under the previous UV-B climate. Our demonstration of strong effects of solar UV-B on biotic interactions in natural systems suggests that further research on the underlying mechanisms and ecological implications is warranted.

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