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Direct and indirect effects of solar ultraviolet-B radiation on long-term decomposition

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Abstract

As a result of stratospheric ozone depletion, more solar ultraviolet-B radiation (UV-B, 280–315 nm) is reaching the Earth's surface. Enhanced levels of UV-B may, in turn, alter ecosystem processes such as decomposition. Solar UV-B radiation could affect decomposition both indirectly, by changes in the chemical composition of leaves during growth, or directly by photochemical breakdown of litter and through changes in decomposer communities exposed to sunlight. In this experiment, we studied indirect and direct effects of solar UV-B radiation on decomposition of barley (*Hordeum vulgare*). We used barley straw and leaf litter grown under reduced UV-B (20% of ambient UV-B) or under near-ambient UV-B (90% of ambient UV-B) in Buenos Aires, Argentina, and decomposed the litter under reduced or near-ambient solar UV-B for 29 months in Tierra del Fuego, Argentina.

We found that the UV-B treatment applied during growth decreased the decay rate. On the other hand, there was a marginally significant direct effect of elevated UV-B during the early stages of decomposition, suggesting increased mass loss. The effect of UV-B during growth on decomposition was likely the result of changes in plant litter chemical composition. Near-ambient UV-B received during plant growth decreased the concentrations of nitrogen, soluble carbohydrates, and N/P ratio, and increased the concentrations of phosphorus, cellulose, UV-B-absorbing compounds, and lignin/N ratio. Thus, solar UV-B radiation affects the decomposition of barley litter directly and indirectly, and indirect effects are persistent for the whole decomposition period.

Key words: barley decomposition, global change, long-term study, ozone depletion, plant litter quality, solar ultraviolet-B radiation, terrestrial ecosystem, Tierra del Fuego, UV-B

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Introduction

The amount of solar ultraviolet-B radiation (UV-B, 280–315 nm) reaching the Earth's surface has increased significantly as a consequence of stratospheric ozone depletion. The most pronounced depletion occurs every year over Antarctica during the austral spring (September–November) because of the annual formation of the 'ozone hole' (Farman *et al*., 1985; Kirchhoff & Echer, 2001). A general erosion of the ozone layer throughout much of the Southern Hemisphere also contributes to increased solar UV-B at other latitudes, and throughout the entire year (Randel *et al*., 1999). Tierra del Fuego (55°S) possesses the most austral fully developed terrestrial ecosystems of the Southern Hemisphere. The flora includes large and diverse vascular plant communities, which are frequently influenced by the Antarctic ozone hole. This location thus offers an ideal setting to evaluate the effects of the increased solar UV-B that have already occurred (Ballaré *et al*., 2001).

Several studies have examined the influence of increased solar UV-B radiation on plants, and specifically the effects on DNA damage, growth, and morphology (Ballaré *et al*., 1996; Britt, 1996; Searles *et al*., 2001). In contrast, fewer studies have evaluated the UV-B effects on plant litter decomposition, the process

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by which essential mineral elements are made available to plants and microbes in inorganic form. Plant litter decomposition may be affected directly or indirectly by UV-B radiation. Direct effects of UV-B, caused by UV-B exposure during decomposition, may alter decomposition rates, as a consequence of the photodegradation of plant material or through changes in the abundance and community composition of decomposers. Indirect effects of UV-B result from UV-B exposure during plant growth causing differences in the chemical composition and physical properties of plant parts, which subsequently affect their decomposition rate in soil.

Evidence of direct effects showed that elevated UV-B increased mass loss as a consequence of accelerated photodegradation of lignin (Rozema *et al*., 1997) or decreased decomposition by directly affecting decomposer organisms (Gehrke *et al*., 1995; Newsham *et al*., 1997; Moody *et al*., 2001; Pancotto *et al*., 2003). Indirect effects of UV-B exposure on leaf chemistry during growth include increased α-cellulose (Rozema *et al*., 1997), decreased soluble carbohydrates, increased N content (Yue *et al*., 1998), decreased lignin : N ratio (Cybulski *et al*., 2000), and increased UV-B-absorbing compounds, including flavonoids and polyphenols such as tannins (Gehrke *et al*., 1995). Although there is considerable evidence of indirect UV-B effects on decomposition, some studies report no evidence of UV-B exposure during plant growth on litter chemistry and decomposition (Newsham *et al*., 2001b; Hoorens *et al*., 2004).

UV-B effects on decomposition vary considerably among different experiments and plant species and this limits our ability to make generalizations. The differences among experiments may, in part, be because of environmental conditions and the UV-B fluxes involved, but also may be attributed to differences among the plant species used. The use of the same species of plant litter in several different experimental settings can help to isolate the effects of different environmental conditions in decomposition experiments (Berg *et al*., 1993; Bottner *et al*., 2000; Coüteaux *et al*., 2002). We selected barley as a material for our experiments because it has often been used in decomposition experiments. In several field studies, the effects of initial nutrient content (Christensen, 1985a, 1986), soil type, and biological activity (Christensen, 1985b; Henriksen & Breland, 2002) on decomposition of barley or similar plant material, such as wheat, have been investigated.

Decomposition of *Gunnera magellanica*, a native species from Tierra del Fuego, Argentina, was affected by manipulation of solar UV-B during decomposition, but was unaffected by similar solar UV-B manipulations during growth of the species in the same environment (Pancotto *et al*., 2003). While UV-B conditions received by plants during growth did not affect mass loss and nutrient composition of litter, colonization of fresh litter by bacterial and fungal communities was different. The ambiguous responses to UV-B, with changes in decomposer community composition that were not expressed in mass loss changes, suggested that the UV-B levels received by vegetation in Tierra del Fuego during growth may not have been sufficient to elicit detectable changes in mass loss, masking the potential importance of indirect UV-B effects. The aim of this study was to evaluate independently direct and indirect effects of solar UV-B radiation on the mechanisms that regulate decomposition. In order to maximize the effects of UV-B during the growing season, we grew barley plants under near-ambient or reduced fluxes of solar UV-B radiation at mid latitude (34°S), where UV-B fluxes are much greater than those at high latitude (54°S) (Orce & Helbling, 1997); and then decomposed the resulting litter under near-ambient or reduced fluxes of solar UV-B radiation at high latitude (Tierra del Fuego, 54°S) under similar UV-B conditions as in the *Gunnera* experiment. We assessed indirect effects of UV-B by monitoring changes in nutrient content of the litter and how these changes affected subsequent decomposition. We also quantified direct UV-B effects as changes in nutrient content and mass loss during decomposition.

Materials and methods

Experimental design and UV-B manipulation

The experimental design was a 2×2 factorial using litter from plants grown under two UV-B treatments and then decomposed in a factorial design under the two UV-B treatments, reduced ($UV\text{-}B^R$) or near-ambient ($UV\text{-}B^A$) solar UV-B radiation, control treatment. We manipulated the UV-B radiation received during plant growth and during decomposition using plastic filters. Solar UV-B radiation was attenuated using 100 μm clear polyester (optically equivalent to 'Mylar-D', DuPont Co., Wilmington, DE, USA), which absorbs radiation below 310 nm but is transparent to longer wavelengths. We used a 38 μm Aclar plastic film (Aclar Fluoropolymer Film type 22A, Honeywell, Pottsville, PA, USA), transparent to nearly all solar radiation, including UV, to provide the near-ambient UV-B treatment. We replaced filters when damaged or brittle, and they were never used for more than 2.5 months to avoid changes in their optical properties because of photodegradation. We perforated the filters to let natural rainfall penetrate to the experimental plots. Polyester filters transmitted 10–20% of the biologically effective

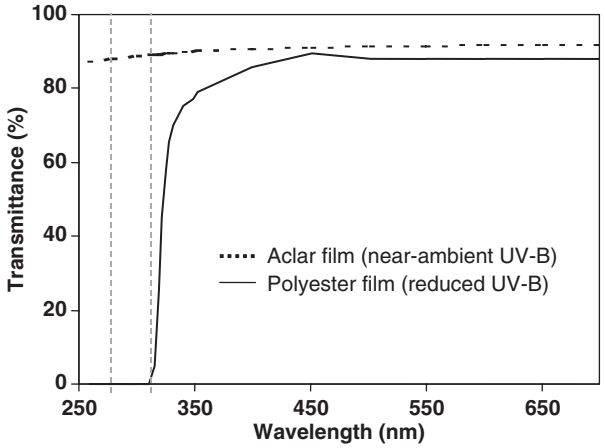


Fig. 1 Transmission spectra of polyester (solid line) and Aclar films (dashed line) used to achieve reduced and near-ambient UV-B conditions, respectively, during growth and decomposition periods.

solar UV-B (UV-B_{BE} Caldwell (1971), normalized at 300 nm) while Aclar plastic transmitted 90% UV-B_{BE} (for more details, see Searles *et al*. (1999)) (Fig. 1). Mean UV-B levels registered during plant growth were 26.5 kJ m^{-2} in winter and 78 kJ m^{-2} in spring. During decomposition, UV-B mean levels were 66.5 55.8, and 57.8 kJ m^{-2}, from October to February for 1999–2000, 2000–2001, and 2001–2002 seasons, respectively (based on data from the GUV-511 radiometer, from Argentina Solar Ultraviolet Radiation Monitoring Network).

Plant growth and decomposition experiment

We used straw and leaves of barley (*Hordeum vulgare* L., Maris Mink wild-type line), which was grown from seed to maturity for 6 months (June 15–December 15) under field conditions at the IFEVA experimental field, Buenos Aires, Argentina (34°35′ S; 58°29′ W). From emergence to harvest, plants were exposed to near-ambient or reduced UV-B conditions as explained above. The UV-B exposure during growth reduced both biomass accumulation and grain yield and increased UV-absorbing pigments (Mazza *et al*., 1999). At senescence, we collected plant material (stems and leaves), and air-dried it in paper bags at room temperature (20 °C). We then filled fiberglass litterbags ($15 \times 5\,cm^2$), of 2 mm^2 mesh size, with 4 g of this senescent plant material. Mesh bags partially block incoming UV-B (45%), which may lead to underestimation of the direct UV-B effects. We placed litterbags in a fully randomized design under both types of filters in an experimental field site in Tierra del Fuego, Argentina (54°51′ S 68°36′ W).

Decomposition was evaluated for 29 months from October 1999 to March 2002. Barley litter produced under UV-B^A was decomposed in paired plots under UV-B^A and under UV-B^R. Similarly, barley litter produced under UV-B^R was decomposed under UV-B^R and UV-B^A. For clarity of presentation, we use a notation where $(UV\text{-}B)^{grown,\ decomp}$ represents the UV-B treatment under which leaves were grown and subsequently decomposed. For example, $(UV\text{-}B)^{A,R}$ denotes plant litter produced under near-ambient UV-B and decomposed under reduced UV-B conditions.

We used 10 independent replicates per treatment. We placed four litterbags from each of the two UV-B growth treatments in 10 plots with near ambient UV-B and in 10 plots with reduced UV-B radiation (total number of litterbags = 160). We harvested litterbags from each plot time, after 2, 12, 17, and 29 months.

Mass loss and chemical analyses

We calculated the relative organic mass loss of barley litter at each sampling date, estimating ash-free dry mass (AFDM) by the muffle-furnace method (0.250 g of sample was oven-dried and heated at 500 °C for 4 h) (Harmon *et al*., 1999).

We estimated the annual decay rate constants (k, $g\,g^{-1}\,yr^{-1}$) using all the collection dates for each replicated combination of litter type and decomposition UV-B treatments, by regressing the logarithm of the fraction of mass remaining against time, using the equation:

$$\ln(X_t/X_i) = \alpha - kt,$$

where X_t (g) is the mass of barley litter remaining at the sampling time t, X_i is the initial mass (g), k is the decay constant, and α the intercept (Olson, 1963). In order to detect UV-B effects during early stages of decomposition, we also calculated k values for the periods 0–12 and 0–17 months.

We performed chemical analyses to evaluate the effects of growth and decomposition conditions on litter quality and nutrient release. We oven-dried litter at 65 °C for 48 h, and estimated carbon, nitrogen, and phosphorus concentration at each sampling date, and also estimated soluble carbohydrates, cellulose, and lignin concentration before and at the end of the decomposition period. We determined total organic carbon (C) as 50% of AFDM (Gallardo & Merino, 1993), total nitrogen and phosphorus by a standard Kjeldhal acid-digestion procedure, and lignin content using the Van Soest acid-detergent method (Harmon & Lajtha, 1999). We also determined the concentration of UV-B-absorbing compounds in acidified methanol extracts. Approximately 2.5 mg of senescent leaves were

extracted in 3 mL methanol : HCl (99 : 1) for at least 48 h at −20 °C and then we measured the absorbance in a spectrophotometer at 305 nm. The UV-B absorbing compounds were expressed as absorbance units (AU) per mg of dry mass. Changes in the concentrations of soluble carbohydrates, cellulose, lignin, and lignin/nitrogen ratio during decomposition were calculated as the difference per gram of AFDM and expressed as percentage of the concentration at the start of decomposition. Nutrient release (nitrogen and phosphorus) during decomposition was calculated as the percentage of the original nutrient content remaining (Harmon *et al*., 1999):

$$\text{Nutrient release} = \frac{\%N_t \times \text{Mass}_t}{\%N_0 \times \text{Mass}_0},$$

where $\%N_t$ is the nutrient concentration at time t, Mass_t is the dry mass at time t, $\%N_0$ is the initial nutrient concentration, and Mass_0 is the initial dry mass.

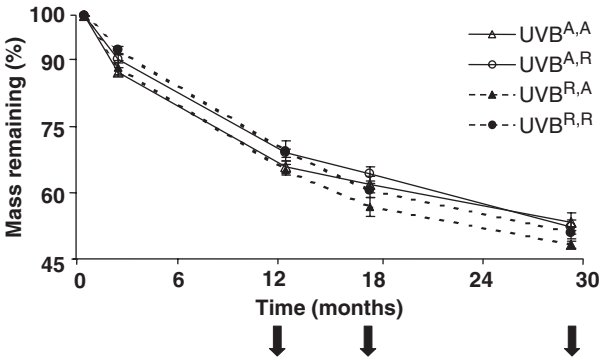
Statistical analyses

To test effects of reduced and near-ambient solar UV-B radiation on the decay rate (k) and on the relative dry mass of organic matter loss, we used a two-way analysis of variance (ANOVA) (Sokal & Rohlf, 1981), with growth and decomposition conditions as main factors. We assessed differences in initial chemical composition of plant material with a one-way ANOVA (Sokal & Rohlf, 1981). We estimated the slopes of nutrient release (N and P) regressing the logarithm of nutrient content of each plot against time, and then we compared the slopes with two-way ANOVA, with growth and decomposition conditions as main factors (Sokal & Rohlf, 1981). The values were transformed if necessary to achieve normality.

Results

Mass loss

Combined analysis of the results from the four collection dates encompassing 29 months indicated that the UV-B treatment applied during growth significantly affected decomposition rate (k) but UV-B treatment received during decomposition did not (Fig. 2). Barley litter produced under near-ambient UV-B decomposed more slowly than litter produced under the reduced UV-B treatment (Fig. 2). We found a similar pattern when we considered just the first 17 months of decomposition (Fig. 2, Table inset), in that the UV-B treatments during growth had a significant effect on decomposition. For the UV-B treatments applied during decomposition, we detected a marginally significant



	k (years^{-1}, first 12 months)			k (years^{-1}, first 17 months)			k (years^{-1}, total 29 months)		
	UVB^A	UVB^R	P	UVB^A	UVB^R	P	UVB^A	UVB^R	P
G	0.38 (0.01)	0.39 (0.02)	0.51	0.33 (0.01)	0.38 (0.01)	**0.01**	0.26 (0.01)	0.30 (0.01)	**0.01**
D	0.40 (0.01)	0.36 (0.02)	**0.08**	0.37 (0.01)	0.34 (0.01)	**0.09**	0.28 (0.01)	0.28 (0.01)	0.49

Fig. 2 Effect of UV-B conditions during growth and decomposition on the fraction of initial mass remaining for barley litter at each collection date over 29-month decomposition trial in the field (mean ± SE, $n = 10$). $(UVB)^{A,A}$, grown and decomposed under near-ambient UV-B conditions; $(UVB)^{A,R}$, grown under near-ambient UV-B and decomposed under reduced UV-B conditions; $(UVB)^{R,A}$, grown under reduced UV-B and decomposed under near-ambient UV-B conditions; $(UVB)^{R,R}$, grown and decomposed under reduced UV-B conditions. The table below the x-axis shows mean decay rate (k, years^{-1}) and standard error for different time periods during the process of decomposition for plants grown or decomposed under near-ambient ($UV\text{-}B^A$) or reduced ($UV\text{-}B^R$) UV-B radiation. The rates were compared with two-way ANOVA. Factorial analysis: G, main effect of UV-B during growth; D, main effect of UV-B during decomposition; G × D, growth by decomposition interaction. The growth by decomposition interaction was not significant for the three k-constant analyses. Bold letter indicates significant ($P < 0.05$) or marginally significant ($P < 0.1$) effect.

($P < 0.1$) UV-B effect when we calculated k for the first 12- and 17-month intervals, with higher decomposition rate when litter decomposed under near-ambient UV-B than under reduced UV-B conditions (Fig. 2, Table inset). We did not find a significant interaction between growth and decomposition UV-B treatments ($P = 0.36$).

UV-B effects on initial litter quality

The UV-B treatment during plant growth resulted in significant changes in litter quality. The concentrations of phosphorus, cellulose, UV-B absorbing compounds and lignin : N ratio were respectively 35%, 11%, 30%, and 26%, higher under near-ambient UV-B than under reduced UV-B, while the concentrations of nitrogen and soluble carbohydrates were 14% and 7% lower under the same conditions (Table 1). N : P ratio was significantly lower (30%) under near-ambient UV-B than

Table 1 Mean, standard error, and ANOVA *F* and *P* values of initial chemical composition (before the decomposition period) for litter of barley grown under near-ambient UV-B radiation (UVB^A) and reduced UV-B radiation (UVB^R)

	UVB^A	UVB^R	*F*	*P*
Phosphorus (%)	0.43 (0.01)	0.28 (0.02)	44.6	<0.01
Nitrogen (%)	0.72 (0.02)	0.84 (0.04)	4.8	0.04
Soluble carbohydrates (%)	48.60 (0.46)	52.20 (0.45)	15.6	<0.01
Cellulose (%)	33.90 (0.56)	30.20 (0.68)	8.7	0.01
Lignin (%)	4.36 (0.10)	3.94 (0.13)	3.1	0.10
C/N ratio	60.70 (1.93)	53.50 (2.95)	2.9	0.11
Lignin/N ratio	6.21 (0.31)	4.57 (0.30)	5.1	0.05
N/P	1.67 (0.05)	3.02 (0.12)	95.5	<0.01
UV-B-absorbing compounds (AU)	0.47 (0.04)	0.33 (0.04)	11.7	<0.01

Statistical significance of UV-B effect on litter quality was tested with a one-way ANOVA.

under reduced UV-B. Lignin content and C:N ratio were unaffected by UV-B exposure, their tendencies were higher under $UV\text{-}B^A$, however they were not statistically significant (Table 1).

Changes in chemistry during decomposition

The UV-B conditions received during growth influenced nitrogen dynamics during the decomposition period. Nitrogen release during decomposition was slower from litter of plants that had grown under near-ambient UV-B than from litter of those grown under reduced UV-B conditions ($P<0.01$). The UV-B treatment received during decomposition did not modify nitrogen release ($P>0.05$, Fig. 3). The UV-B conditions during growth also modified phosphorus dynamics during decomposition, there was greater release of phosphorus from material grown under near-ambient UV-B ($P<0.01$). However, the phosphorus dynamics were not influenced by the UV-B treatments during decomposition ($P>0.05$, Fig. 4). In both cases, we found no interactions between the effects of UV-B during decomposition and growth. The UV-B treatment received during growth affected changes in soluble carbohydrates, cellulose, and lignin content during decomposition (Table 2). These different changes in litter constituent concentrations resulted in similar concentrations among treatments by the end of the decomposition experiment (data not shown), and tended to obscure the UV-B treatment differences observed prior to the decomposition experiment (Table 1). Soluble carbohydrates loss was higher from litter of plants grown under reduced UV-B conditions than from litter of plants grown under near-ambient conditions. The relative content of cellulose, lignin, and lignin/nitrogen ratio increased less in litter from plants grown under near-ambient UV-B than under reduced

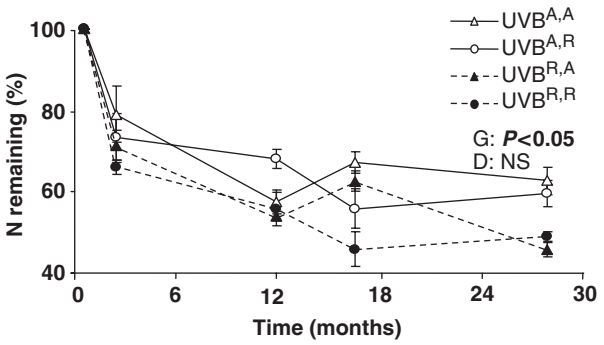


Fig. 3 Effects of UV-B treatments during growth and during decomposition on relative nitrogen concentration remaining (expressed as percentage of original amount) over 29 months of decomposition in the field (mean ± SE, $n = 5$–6). Slope values of N remaining were compared with ANOVA. For abbreviations, see Fig. 2. The treatment interactions were not significant.

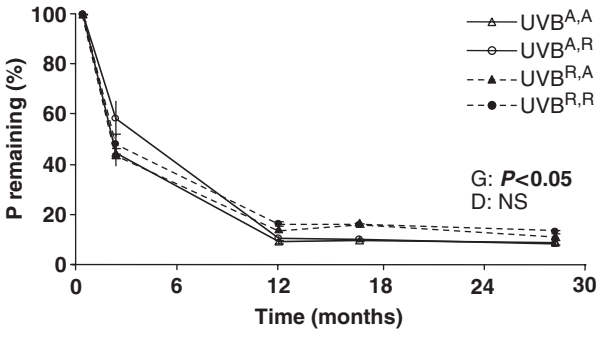


Fig. 4 Effects of UV-B conditions during growth and during decomposition on the relative concentration of phosphorus remaining (expressed as percentage of original amount) over 29 months of decomposition in the field (mean ± SE, $n = 5$–6). Slope values of P remaining were compared with ANOVA. For abbreviations, see Fig. 2. The interactions were not significant.

Table 2 Changes in the concentration of soluble carbohydrates, cellulose, lignin, and the lignin/N ratio of barley litter during the decomposition period

	$UVB^{A,A}$	$UVB^{A,R}$	$UVB^{R,A}$	$UVB^{R,R}$	G	D	G × D
CH sol	−12.30 (1.35)	−11.80 (0.65)	−16.90 (1.37)	−17.36 (1.32)	<0.01	0.97	0.67
Cellulose	11.97 (3.13)	9.28 (3.51)	24.70 (3.47)	29.03 (5.17)	<0.01	0.83	0.37
Lignin	87.87 (9.46)	98.31 (8.46)	116.50 (6.81)	118.65 (9.21)	<0.05	0.48	0.64
Lignin/N	68.28 (8.33)	56.94 (10.87)	145.68 (13.42)	151.46 (4.79)	<0.01	0.78	0.40

Data were calculated as (final %−initial %)/initial %. Negative values indicate that the relative concentration decreased during decomposition, positive values indicate that the relative concentration increased during decomposition. For abbreviations, see Fig. 2.

UV-B, because of the lower overall mass loss recorded under this treatment.

Discussion

Exposure of barley to near-ambient UV-B radiation during growth indirectly decreased the decomposition rate compared with litter produced under the reduced-UV-B treatment. There was also a marginally significant effect of near-ambient UV-B during early stages of decomposition, suggesting accelerated rates of mass loss caused by direct exposure to UV-B. The indirect effect of UV-B during growth was more apparent in the latter stages of the decomposition process.

The indirect effects of UV-B on the decomposition of barley litter were largely attributable to chemical changes in plant tissues caused by solar UV-B exposure during growth. Exposure to near-ambient UV-B during growth of the barley increased concentrations of cellulose, UV-B absorbing compounds, and lignin/N ratio. Such changes increased recalcitrant fractions, which soil microbes, are less able to break down, decreasing decomposition rates, as reported by Melillo *et al*. (1982). During decomposition, soluble carbohydrates breakdown more readily than cellulose and lignin (Swift *et al*., 1979). Thus, greater lignin concentrations in litter following 29 months of decomposition are not surprising. Nitrogen release also differed in response to UV-B exposure during growth, in that litter from plants grown under near-ambient UV-B (with less initial nitrogen, higher lignin/N ratio, and UV-B absorbing compounds) released less N than litter from plants grown under reduced UV-B. Similarly, Cybulski *et al*. (2000) reported that *Pinus taeda* litter produced under enhanced UV-B simulating a 16% and 25% ozone reduction had a higher lignin : nitrogen ratio, however it decomposed faster than litter produced under control conditions. Unexpected, phosphorus release was higher under near ambient UV-B than under reduced UV-B, maybe because of the higher availability of P in the litter in this treatment, doing more readily accessible to organisms (Table 1).

Our results are also consistent with reports that elevated UV-B applied during growth indirectly reduces the decomposition rate of *Vaccinium* sp. (Gehrke *et al*., 1995) and *Calamagrostis* sp. (Rozema *et al*., 1997) litter. However, our results contrast with previous studies reporting increased decomposition rates of litter exposed to enhanced UV-B during growth, observed both for *Quercus* sp. (Newsham *et al*., 2001a) and for wheat (*Triticum* sp.) litter (Yue *et al*., 1998). Comparisons among studies are complicated because of different methodologies used to simulate increased UV-B, specific plant species responses, or differences in growing conditions. Moreover, experiments in different locations suggest that this UV-B effect may be dose-dependent (Warren *et al*., 2002; Lavola *et al*., 2003) and might be undetectable when plants were grown under relatively low UV-B conditions. In a study of the native *Gunnera magellanica*, also carried out at our Tierra del Fuego study site, litter decomposition was unaffected by the UV-B treatment applied during growth (Pancotto *et al*., 2003). The apparently contradictory results with our current study on barley litter may be because of the much greater UV-B fluxes during growth of the barley. The UV-B dose received by barley during November/December in the Buenos Aires growth site (96 kJ m^{-2} day^{-1}, based on data from the GUV-511 radiometer, from 'Argentina Solar Ultraviolet Radiation Monitoring Network'), was greater than the UV-B received by *G. magellanica* in Tierra del Fuego at this time of year (52 kJ m^{-2} day^{-1}).

Our results contribute to an understanding of the multiple effects of UV-B radiation on decomposition. The decomposition process can be affected both by UV-B radiation received by plants during growth and by litter during decomposition. High fluxes of UV-B during growth may result in increased concentrations of UV-B absorbing compounds and lignin, and decreased soluble carbohydrates (Rozema *et al*., 1997; Yue *et al*., 1998) as we observed in this study with barley. During decomposition of the litter, greater UV-B fluxes may exert influence on the decomposition process by two mechanisms: (1) a biotic effect,

manifested through changes in the community of decomposer organisms or their activity (Newsham *et al*., 1997; Moody *et al*., 1999; Duguay & Klironomos, 2000; Pancotto *et al*., 2003; Robson *et al*., 2004) and (2) an abiotic effect, caused by differences in the direct photodegradation of the litter (Gehrke *et al*., 1995; Rozema *et al*., 1997). These two UV-B effects during decomposition might be expected to work in opposite directions, with greater fluxes of UV-B increasing photodegradation, but decreasing the activity of decomposer organisms. In our earlier study on litter decomposition of *Gunnera*, greater UV-B flux during decomposition altered the decomposer community composition and these changes corresponded with decreased decomposition rates (Pancotto *et al*., 2003). Litter quality may influence the relative importance of mechanisms by which UV-B affects decomposition. For example, the magnitude of the biotic effect of UV-B during decomposition may depend on the litter quality. Litter quality of the barley, was likely much lower than the quality of the *Gunnera* litter, considering nitrogen, lignin and UV-B absorbing compounds content. Thus, the effects of UV-B during decomposition may have played out more in photodegradation (abiotic effect) than in altered decomposer activity (biotic effect). To sum up, the relative importance between abiotic vs. biotic effects would be modulated by litter quality; when litter quality is low, it limits the activity of microorganisms (Swift *et al*., 1979), and decomposition processes are driven mostly by abiotic factors.

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