

Global Change Biology (2009) 15, 2493–2502, doi: 10.1111/j.1365-2486.2009.01970.x

Solar UVB and warming affect decomposition and earthworms in a fen ecosystem in Tierra del Fuego, Argentina

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Abstract

Combined effects of co-occurring global climate changes on ecosystem responses are generally poorly understood. Here, we present results from a 2-year field experiment in a Carex fen ecosystem on the southernmost tip of South America, where we examined the effects of solar ultraviolet B (UVB, 280-315 nm) and warming on above- and belowground plant production, C:N ratios, decomposition rates and earthworm population sizes. Solar UVB radiation was manipulated using transparent plastic filter films to create a near-ambient (90% of ambient UVB) or a reduced solar UVB treatment (15% of ambient UVB). The warming treatment was imposed passively by wrapping the same filter material around the plots resulting in a mean air and soil temperature increase of about 1.2 °C. Aboveground plant production was not affected by warming, and marginally reduced at near-ambient UVB only in the second season. Aboveground plant biomass also tended to have a lower C:N ratio under near-ambient UVB and was differently affected at the two temperatures (marginal UVB × temperature interaction). Leaf decomposition of one dominant sedge species (Carex curta) tended to be faster at near-ambient UVB than at reduced UVB. Leaf decomposition of a codominant species (Carex decidua) was significantly faster at near-ambient UVB; root decomposition of this species tended to be lower at increased temperature and interacted with UVB. We found, for the first time in a field experiment that epigeic earthworm density and biomass was 36% decreased by warming but remained unaffected by UVB radiation. Our results show that present-day solar UVB radiation and modest warming can adversely affect ecosystem functioning and engineers of this fen. However, results on plant biomass production also showed that treatment manipulations of co-occurring global change factors can be overridden by the local climatic situation in a given study year.

Keywords: biomass production, Carex curta, Carex decidua, decomposition, Dendrobaena octaedra, earthworms, ecosystem functioning, global change, global warming, ozone depletion, soil heterotrophs

Received 10 October 2008; revised version received 16 April 2009 and accepted 21 April 2009

Introduction

Elevated solar ultraviolet-B radiation (UVB, 280–315 nm) and global warming are two important con-

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sequences of human-induced climatic change and may affect ecosystem function in coming years (IPCC, 2001, 2007). Increased solar UVB radiation due to stratospheric ozone depletion is most pronounced at higher latitudes and UVB radiation is assumed to have reached a maximum at the beginning of this century, but the increased UVB levels are predicted to last for another 50 years (Madronich *et al.*, 1998; McKenzie *et al.*, 2007). The Earth's climate has warmed by approximately 0.6 °C

over the past 100 years and average surface temperature is projected to increase up to 4.0 °C by 2100 (IPCC, 2007). Global warming is also more pronounced at higher latitudes (e.g., Mitchell *et al.*, 1990) and can accelerate the depletion of the stratospheric ozone layer (Hartmann *et al.*, 2000).

Ambient solar and moderately enhanced UVB radiation has been shown to alter different aspects of ecosystem function under field conditions (e.g., Björn et al., 1997; Rozema, 1999; Ballaré et al., 2001; Caldwell et al., 2007) including the growth of primary producers (Rousseaux et al., 2001; Robson et al., 2003; Zaller et al., 2004), microbial activity (Newsham et al., 1997; Searles et al., 2001b), root symbionts (Zaller et al., 2002), herbivores (e.g., Salt et al., 1998; Rousseaux et al., 2001; Zaller et al., 2003), soil heterotrophs (Verhoef et al., 2000), decomposition (Gehrke et al., 1995; Pancotto et al., 2003; Austin & Vivanco, 2006), and biogeochemical cycling (Zepp et al., 2007). Warming is believed to primarily affect ecosystems in colder climates (Rustad et al., 2001) and has been shown to increase primary production (Nadelhoffer et al., 1997; Day et al., 2008), soil nutrient mineralization (Hobbie & Chapin, 1998; Grogan & Chapin, 2000), ecosystem and belowground respiration (Grogan & Chapin, 2000), decomposition (Aerts, 2006), and alterations in soil faunal communities (Coulson et al., 1996; Convey et al., 2002; Briones et al., 2004; Bokhorst et al., 2008). Of course, UVB radiation and warming affect ecosystems together (Caldwell et al., 2003; Zepp et al., 2007), yet, these two global change factors have seldom been studied simultaneously in the field (Day et al., 1999; Lud et al., 2001; Convey et al., 2002; Sonesson et al., 2002; Bjerke et al., 2003; Day et al., 2008).

Here, we present findings of an experiment conducted during two growing seasons in a sedge fen in Tierra del Fuego (Argentina). Ecosystems in this region are constrained by temperature (sub-Antarctic climate) and experience more stratospheric ozone reduction ('ozone hole') than any other terrestrial ecosystem outside of Antarctica (Booth *et al.*, 1994; Madronich *et al.*, 1998). The aim of this study was to examine whether solar UVB radiation and warming affect autotrophic and heterotrophic/detritivorous elements of this fen ecosystem.

Materials and methods

Study site

The study site is located near the city of Ushuaia, Tierra del Fuego, Argentina (200 m a.s.l.; 54°47′S, 68°16′W). The climate there is sub-Antarctic with an annual precipitation of about 500 mm uniformly distributed over the year at a mean annual air temperature of about 5.5 °C (FAO, 1985). Experimental plots were situated in

a fen ecosystem interspersed among scattered trees of *Nothofagus antarctica* (Forster f.) Oersted (up to 1 m tall) and were dominated by the sedges *Carex curta* Gooden and *Carex decidua* Boott. Less frequent species were *Carex magellanica* Lam., *Acaena magellanica* (Lam.) Vahl, *Gunnera magellanica* Lam., *Caltha sagittata* Cav., *Blechnum penna-marina* (Poiret) Kuhn and *N. antarctica* (nomenclature follows Moore, 1983). The soil in the plots is mainly peat (pH = 6.0, N = 1.7%, C:N ratio = 19.7) with a water table about 5-10 cm below the surface.

Manipulation of UVB radiation and temperature

Starting in October 1999, 10 experimental plots $(1.4 \,\mathrm{m} \times 1.5 \,\mathrm{m})$ were installed under two types of plastic film filters to selectively manipulate the solar UVB transmission. Five plots were under a filter material (polyester film, 100-μm thick, DuPont Co., Wilmington, DE, USA) that absorbed UVB but was transparent to longer wavelength radiation (reduced UVB treatment). The other five plots were under a filter material (Aclar type 22A, 38 µm thick; Honeywell Inc. formerly Allied Signal, Pottsville, PA, USA) that was similarly transparent to all wavelengths in the UV and visible spectrum (near-ambient UVB treatment). The filters were suspended 35 cm above the ground and 10 cm above the tallest vegetation. All filter material was perforated with louvers to allow precipitation to penetrate to the plots below and to purposely not exclude all UVB radiation. Plots in the reduced-UVB treatment received about 15% of the ambient solar UVB and those in the near-ambient treatment about 90% (weighted with the generalized plant action spectrum at 300 nm after Caldwell, 1971; Searles et al., 1999). Both filter materials transmitted nearly 90% of the photosynthetic active radiation (400-700 nm, Searles et al., 1999). Occasionally filters would be destroyed by wind, but these were always promptly replaced. The UVB- manipulation treatments were maintained each year during the growing season from about early October following snowmelt until mid-March when plants in the plots started senescing and solar UVB radiation was quite low (Searles et al., 1999; Searles *et al.*, 2001b).

In the same plots, temperature was manipulated passively by wrapping 30-cm-broad strips of transparent UVB filter film along two sides and the diagonal of the plots enclosing a triangle (further called windscreens). Thus, each experimental plot consisted of a UVB treatment divided in an ambient (i.e., no filters wrapped around) and an elevated temperature treatment. For each plot, windscreens were made of the same filter material as used to manipulate UVB. In order to allow some wind circulation under the filters in the plots and to keep temperature increases moderate, the

Table 1 Climatic conditions at field site (UVB radiation, precipitation) and on experimental plots maintained at either reduced or near-ambient UVB radiation and ambient or elevated temperatures located in Ushuaia, Tierra del Fuego, Argentina

	Season 1999/2000						Season 2000/2001					
	UVB $(kJ m^{-2} day^{-1})$	Precipitation (mm)	Air temperature		Soil temperature		UVB	Precipi- tation	Air temperature		Soil temperature	
Month			Ambient (°C)	Elevated (°C)	Ambient (°C)	Elevated (°C)	$(kJ m^{-2} day^{-1})$	(mm)	Ambient (°C)	Elevated (°C)	Ambient (°C)	Elevated (°C)
October	4.19	72	5.7	6.1	4.5	4.0	3.47	36	4.4	5.8	3.5	5.1
November	5.98	24	9.5	10.2	9.1	10.7	2.44	71	6.7	8.8	7.6	9.3
December	6.98	49	10.2	11.5	10.5	11.2	4.00	69	8.0	10.4	9.1	9.2
anuary	6.25	59	9.8	10.8	10.6	10.6	3.53	70	9.5	11.7	10.4	12.4
February	4.40	29	9.5	10.5	10.3	11.9	2.00	40	7.3	9.2	8.9	10.5
March	nd	nd	9.8	10.7	9.6	11.0	nd	nd	9.4	10.8	8.9	9.8

Near-ambient UVB plots received about 90% of given UVB radiation, reduced UVB plots received about 15% of given values. Amb, ambient daily mean temperature; Elev, elevated temperature treatment; nd, no data available.

windscreens started 5-cm above the surface and were also perforated like the main filter material. Air (at 10 cm above the soil surface) and soil temperature (5 cm soil depth) in the plots was monitored throughout the field season in three representative treatment plots by using fine-wire copper-constantan thermocouples connected to a datalogger (Campbell Scientific, Logan, UT, USA). Our temperature treatments significantly increased mean daily air temperature across seasons by $1.4\,^{\circ}\text{C}$ (P<0.001) and soil temperature by $1.1\,^{\circ}\text{C}$ (P < 0.001; Table 1). The waterlogged soil conditions in this fen precluded a monitoring of the soil moisture since neither time-domain reflectrometry nor gravimetrical soil moisture measurements would render reliable results (Sala et al., 2000). Ambient solar UV was monitored every 15 min using a erythemically weighted broadband UV meter (Solar Light Co., Model PMA2102, Philadelphia, PA, USA) connected to the same datalogger (Table 1). There was a close relationship between readings of the broadband UV meter and those of a scanning double monochromator installed in Ushuaia as part of the US National Science Foundation UV Radiation Monitoring Network (SUV 100, Biospherical Instruments, San Diego, CA, USA; Diaz et al., 2001). Ambient precipitation amounted to 233 mm in the first season and was on average 25% greater each month in the second season (Table 1).

Plant biomass production

In late February/early March of 2000 and 2001, aboveground plant biomass was cut on a 0.63 m²-center-area of each plot 3 cm above the soil surface, dried at 70 °C and weighed. Carbon (Ctot) and nitrogen (Ntot) concentrations of dried and powdered plant material were determined using a CHN analyzer (LECO Instruments, St Joseph, MI, USA).

Ecosystem root production was assessed using two root ingrowth cores per plot. Ingrowth cores were custom-made of plastic mesh (1 mm × 1 mm mesh size, 10 cm long, 5.5 cm diameter) and filled with local, rootfree peat soil. Ingrowth cores were inserted in early October 1999, removed in March of the following year and replaced with a new set of ingrowth cores for the following 2000/2001 season. After removal of the cores, all live roots were washed free of soil by using a uniform amount of water and time for each core. Roots were dried at 70 °C for at least 2 days and root mass determined.

Earthworm sampling

Earthworm biomass was determined in October 2000 after extracting earthworms with an aqueous mustard solution (Gunn, 1992). Therefore, a plastic collar (diameter 22 cm) was pressed 5-cm-deep into the ground in the center of each experimental plot and the extraction solution of 4 g of mustard powder (Coleman's Mustard) per 4L of tap water was poured into the collar. All earthworms appearing at the soil surface within 30 min were collected, identified, counted and weighed. Mustard extraction has been shown to provide comparable estimates of earthworm population size to other more conventional sampling methods like the destructive hand sorting or extraction using toxic chemicals such as formalin (Lawrence & Bowers, 2002).

Decomposition of leaves and roots

To determine whether UVB or warming had an influence on decomposition of leaf and root material of

C. curta and C. decidua tissues samples that had been grown under simulated ambient UVB in growth chambers was used (Zaller et al., 2004). In September 2000, we placed 0.20 g of dry leaf and root material of each species into plastic mesh bags (5 cm × 5 cm, mesh openings 3 mm × 2 mm), that would allow smaller decomposer organisms and earthworms access to the material (Coleman & Crossley, 1996). In the field, leaf litter bags were placed on the soil surface using U-shaped wire pinned into the ground and covered with dead leaf material in order to avoid direct exposure to sunlight. Root litter bags were vertically inserted into the ground near the leaf litter bags. After 5 months in the field we collected the litter bags and dried them at 70 °C for 48 h. Residual leaf and root material was carefully cleaned of attached soil material before weighing.

Statistical analyses

All data were analyzed using a nested ANOVA model with the 'proc mixed'model in SAS (vers. 9.1 for Windows; SAS Institute Inc., Cary, NC, USA) with UVB treatment and temperature as fixed and block as random factors. Data were arcsine-transformed when needed to meet assumptions of ANOVA. In our model we used the general Satterthwaite approximation for the denominator degrees of freedom. Experimental units here were five blocks, UVB treatment nested within blocks and temperature treatments nested with-

in UVB treatments nested within blocks. All anova analyses were performed using Type III sums of squares. Values given throughout the text are means \pm SE.

Results

Across treatments, aboveground plant biomass production was twice as high in the second (wetter) season than in the first season (average 237 vs. $117 \,\mathrm{g\,m^{-2}}$). Aboveground plant biomass was marginally reduced by solar UVB in the second season ($F_{1,7.3.6} = 5.23$, P = 0.0655) but unaffected by the warming treatments (Fig. 1).

Belowground plant biomass production was only 6% higher in the second than in the first season (average 212 vs. 200 g m⁻²), and remained unaffected by the experimental treatments (Fig. 1).

Plant C and N concentrations were unaffected by the experimental treatments (data not shown). In the first season, aboveground land area-based biomass C was not affected by the treatments (averaged across treatments: $53.25 \pm 9.33\,\mathrm{g\,C\,m^{-2}}$); however in the second season aboveground biomass C tended to be higher under reduced UVB than under near-ambient UVB (112.58 \pm 15.11 vs. $103.90 \pm 10.01\,\mathrm{g\,C\,m^{-2}}$, respectively; UVB: $F_{1,8.05} = 3.99$, P = 0.0839, Temp.: ns, UVB × Temp.: $F_{1,7.75} = 5.22$, P = 0.0666); warming had no influence on C m⁻². Aboveground biomass N m⁻² was unaffected by the treatments (data not shown). Plant shoot and root biomass C: N ratio was not affected by treatments in the

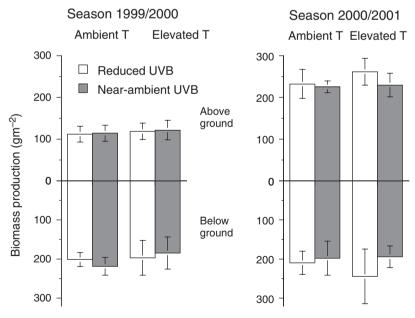


Fig. 1 Plant biomass production in a fen ecosystem in Tierra del Fuego, Argentina maintained at reduced or near-ambient UVB radiation and ambient or elevated temperature. We observed a marginal reduction in shoot biomass under near-ambient UVB in the second year. Means \pm SE, n = 5. UVB, ultraviolet B.

first year, however in the second year C:N tended to be lower under near-ambient than under reduced UVB (UVB: $F_{1,8.08} = 5.36$, P = 0.0555, Temp.: ns, UVB × Temp.: $F_{1,7.99} = 4.82$, P = 0.0619; Fig. 2).

C. curta leaf decomposition tended to be higher at nearambient UVB than under reduced UVB ($F_{1,7.95} = 4.12$, P = 0.0795) but was unaffected by temperature treatments; root decomposition of this species was unaffected

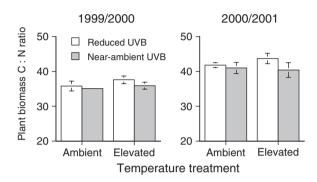


Fig. 2 Plant biomass C:N ratio in a fen ecosystem in Tierra del Fuego, Argentina maintained at reduced or near-ambient UVB radiation and ambient or elevated temperature. We observed a marginal reduction in C:N ratio under near-ambient UVB in the second year. Means \pm SE, n=5. UVB, ultraviolet B.

by the treatments (Fig. 3). *C. decidua* leaves decomposed significantly faster under near-ambient UVB than under reduced UVB ($F_{1,7.93} = 11.93$, P = 0.0141); decomposition was not affected by the temperature treatments (Fig. 3). Roots of *C. decidua* tended to decompose faster under warming but decomposition was unaffected by UVB (UVB: ns, Temp.: $F_{1,7.96} = 4.79$, P = 0.0620, $F_{1,7.89} = 5.22$, UVB × Temp.: P = 0.0543).

We only found the cosmopolitan, epigeic earthworm species, *Dendrobaena octaedra* Sav. (Lumbricidae: Oligochaeta) in our experimental plots. Earthworm numbers m^{-2} and earthworm biomass m^{-2} in warming plots were significantly lower than in plots exposed to ambient temperature ($F_{1,8.05} = 16.41$, P = 0.0106 and $F_{1,7.99} = 11.89$, P = 0.0132, respectively), however, they were unaffected by UVB treatments (Fig. 4).

Discussion

Although we tested the effects of UVB and warming in an ecosystem of rather low productivity, several alterations of ecosystem processes were apparent. The observation of a marginal UVB treatment effect on plant biomass suggests that the species dominating this fen might have been to some extent detrimentally affected

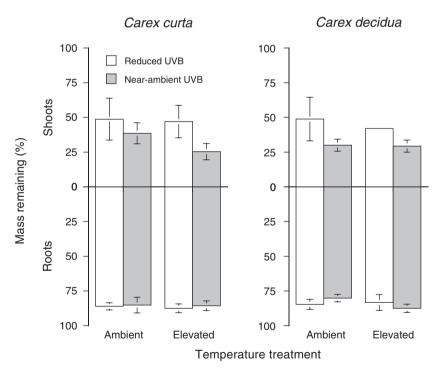


Fig. 3 Shoot and root decomposition in the season 2000/2001 of two most dominant sedge species in a fen ecosystem in Tierra del Fuego, Argentina maintained at reduced or near-ambient UVB and ambient or elevated temperature. Treatment effects: *Carex curta* shoots decomposed marginally faster under near-ambient UVB; *Carex decidua* shoots decomposed significantly faster under near-ambient UVB, *C. decidua* roots decomposed marginally slower under warming. Means \pm SE, n = 5. Small error bars are not depicted. UVB, ultraviolet B.

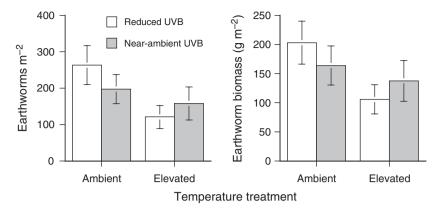


Fig. 4 Epigeic earthworm numbers m⁻² and biomass m⁻² in October 2000 in experimental plots of a fen ecosystem in Tierra del Fuego, Argentina which have been maintained at reduced or near-ambient UVB radiation and ambient or elevated temperature. Only the temperature treatment significantly affected earthworm abundance and biomass. Means \pm SE, n = 5. UVB, ultraviolet B.

by increased doses of UVB radiation under conditions of ozone depletion. In contrast to a previous study in this ecosystem (Zaller et al., 2002), UVB did not affect root growth in the current study. This can perhaps be explained by the averaged 30% higher productivity of the experimental plots in the former study since more productive ecosystems tend to be more responsive to UVB than less productive ecosystems (Searles et al., 2001a). The lack of interactions between UVB and warming on plant production confirms results of the few other studies that simultaneously studied UVB and warming (Day et al., 1999; Lud et al., 2001; Sonesson et al., 2002; Bjerke et al., 2003), and suggests that warming does not counteract the negative effects of UVB or that synergistic or additive effects between the two global change factors occur.

In the current study, C: N ratios of aboveground plant biomass under near-ambient UVB tended to be lower than under reduced UVB. Since, the observed plant biomass C:N ratio of around 40 is considered to be rather high, litter with lower C:N ratios is expected to decompose more readily (Swift et al., 1979). This corresponded with our results that the leaves of both dominating Carex species decomposed faster under near-ambient UVB than under reduced UVB. Direct photodegradation or effects on decomposer organisms by UVB radiation were likely not responsible for this UVB effect, because we covered the mesh bags containing the decomposing material with plant litter. Thus, if we consider decomposition as an integrative measure of the activity of various decomposer organisms, this finding suggests that decomposers are indirectly affected by UVB radiation, perhaps through an altered chemical composition of the plant litter. This increased decomposition under enhanced UVB is well in line with other field studies conducted both in the Northern

(Gehrke et al., 1995; Rozema et al., 1997; Day et al., 2007) and Southern Hemisphere (Pancotto et al., 2005; Austin & Vivanco, 2006). However, our current results seem to be in contrast to findings of another experiment conducted in the study region where litter of a native perennial creeping herb (G. magellanica) had significantly less mass loss under near-ambient UVB than litter that decomposed under reduced UVB (Pancotto et al., 2003). In the former study this was related to UVB induced changes in the fungal community while changes in photochemical breakdown appeared to be less important. An explanation for this discrepancy may be related to a species-specific effect of UVB on the chemical composition of litter: Pancotto et al. (2003) did not find any significant effects of UVB on nutrient content of the herbaceous litter, whereas, in this study, for our sedges we found a decrease in C:N ratios in higher UVB treatments. Since high latitude ecosystems are generally characterized by slow decomposition (Hobbie et al., 2000), it was interesting to see that of the dominant sedge species only about 50% of the initial plant biomass was left after 6 months at reduced UVB and only about 30% left at near-ambient UVB. We expected that, in this temperature-limited fen ecosystem, a higher temperature would accelerate decomposition and were surprised that only a marginal increase in leaf and root decomposition was measured in the warming plots. Explanations for this could be (i) that the potential influence of warming was slightly attenuated because we covered the decomposition bags with plant litter in order to avoid direct effects of UVB radiation through photodegradation and/or (ii) that our moderate warming slightly decreased moisture on the soil surface and thereby limited decomposition rates (Aerts, 2006).

warming caused suboptimal conditions for earthworm populations. Although there was no significant interaction between UVB and warming on earthworm populations, UVB tended to reduce earthworm populations at ambient but increase them at elevated temperatures.

Our results that shoot decomposition tended to be faster in warming plots where earthworm populations were reduced seem counterintuitive and might suggest that earthworms play only a minor role for decomposing plant litter in these systems. However, it is also very plausible, as observed at elevated atmospheric CO₂ (Zaller & Arnone, 1997, 1999), that fewer earthworms are more active and consume more plant litter leading to a higher loss of plant material in these plots.

An important observation of the current study was the difference in ecosystem plant production responses between years, with a tendency toward stronger responses in the second (wetter) season. This can be the case because (i) treatments become effective in these low fertility ecosystems only after a prolonged period of time, (ii) regional climatic situations within a given year (e.g., precipitation, waterlogging, solar radiation, ambient temperature) interact differently with the treatment factors (Zaller et al., 2004). In any case, this observation strongly emphasizes the importance that especially in such slow growing systems, investigations should run over a longer period of time in order to enable effects to be expressed when many other confounding environmental variables might adversely affect ecosystem parameters (Press et al., 1998; Day et al., 1999; Aphalo, 2003).

Taken collectively, we found that UVB radiation and warming can adversely affect some important parameters in this ecosystem and potentially alter the functioning of this Sub-Antarctic fen ecosystem in a period of just 2 years. A UVB-induced increase of the aboveground decomposition rate of a dominant sedge species might result in a decreased C-storage, while a warming-induced decrease in earthworm population size might positively affect C-storage.

Acknowledgements

We thank Oscar Bianciotto for providing his property to establish our experimental sites. We are grateful to Eduardo Olivero and Susana Diaz and their teams at the Centro Austral de Investigaciones Científicas, Ushuaia for providing logistic and technical support. Cecilia Rousseaux and Peter Searles established and maintained sites through the first years of this study. Thanks to Nancy Lozano, Ricardo Saenz-Sarmiento and Nicolas Garibaldi for assistance during laboratory and field work. Prof. A. Zisci, Budapest, Hungary, helped with identification of earthworm species. This work was supported by by the NSF/DOE/NASA/USDA/EPA/NOAA Interagency Program on Terrestrial Ecology and Global Change (TECO) by the United States National Science Foundation (IBN 9524144 and IBN 9814357), CONICET and Inter-American Institute for Global Change Research. SDF was also supported by USDA/CREES 2008-34263-19485.

Previous field studies already demonstrated altered plant-animal interactions in terrestrial ecosystems by UVB radiation (Rousseaux et al., 1998; Salt et al., 1998; Gwynn-Jones, 1999; Convey et al., 2002; Veteli et al., 2003; Zaller et al., 2003; Rousseaux et al., 2004; Caputo et al., 2006). Although, earthworms are generally considered to be sensitive to direct exposure to UV radiation (Edwards & Bohlen, 1996; Chuang et al., 2006), in the present study epigeic earthworm population size remained unaffected by UVB radiation. This suggests that this earthworm species that is active on the soil surface also during the day is well protected from UVB radiation by their pigmentation (Sicken et al., 1999). We also expected that besides direct effects of UVB also indirect effects via UVB-induced changes in the chemical composition of plant material might influence earthworms. When the vertical burrowing earthworms Lumbricus terrestris and the epigeic Lumbricus rubellus were offered leaf litter produced under zero and ambient UVB (at 52°N) in a laboratory experiment, L. terrestris tended to be detrimentally affected by 'UV-B treated' litter while the latter benefited from the UVBtreated litter (Gwynn-Jones et al., 2003). The effect of warming on soil microarthropods are very variable ranging from limited responses of abundances of Acari, Collembola and soil oribatid mites (Webb et al., 1998; Bokhorst et al., 2008) to increases in arthropod or nematode communities (Kennedy, 1994; Coulson et al., 1996) to a decline of Collembola (Convey et al., 2002). It is generally believed that litter shredders like earthworms and large arthropods are absent in cold biomes and that this functional role is taken over by microarthropods (mites and springtails), Enchytraeidae and nematodes (Ruess et al., 1999). In our study, earthworm population sizes of on average 185 individuals m⁻² and a biomass of $150\,\mathrm{g\,m^{-2}}$ were surprisingly high for this type of ecosystem and this climatic conditions (Edwards & Bohlen, 1996) suggesting that they are among the most important decomposer organisms in this ecosystem. To the best of our knowledge, the current study is the first field study to demonstrate effects of warming on ecosystem engineers (Jones et al., 1994) such as earthworms. The finding that warming detrimentally affected the number and biomass of litter-dwelling earthworms can have far-reaching consequences for the breakdown of organic matter, nutrient cycling and seedling establishment (Zaller & Saxler, 2007). Because the earthworm species found in this fen is distributed in various climatic regions around the world, it is even more interesting that warming led to a dramatic 36% reduction in earthworm numbers and biomass. This suggests that the local population of this species seems to be well adapted to ambient temperatures and that perhaps a reduced water availability at the soil surface under

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