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Growth responses to ultraviolet-B radiation of two *Carex* species dominating an Argentinian fen ecosystem

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Abstract

Solar ultraviolet-B radiation (UV-B, 280–315 nm) in the Southern Hemisphere has been increasing over the last few decades due to seasonal stratospheric ozone depletion associated with the 'ozone hole' and a more general erosion of the stratospheric ozone layer. We studied the effect of UV-B radiation on growth responses of *Carex curta* and *C. decidua,* the two most dominant sedges in a fen ecosystem in Tierra del Fuego (Argentina) in field plots and growth chambers where UV-B radiation was manipulated using different transparent plastic films that either transmitted or attenuated UV-B radiation. In the field, leaf and spike elongation of both species was unaffected by UV-B treatments in all four seasons studied (1997/98 through 2000/2001). Specific leaf areas (SLA) were only measured in the last two seasons and remained unaffected by UV-B for both species in the third field season. However, SLA decreased for *C. curta* in the fourth season but increased for *C. decidua* under near-ambient UV-B. Ecosystem specific root length was unaffected by UV-B. Although UV-B did not have a statistically significant effect on biomass production, there was a trend for a 15% higher production under near-ambient UV-B in the fourth year ($P = 0.064$). In the growth chambers, simulated ambient UV-B approximately equivalent to ambient UV-B in Tierra del Fuego stimulated seedling emergence of *C. curta* but reduced emergence of *C. decidua*; leaf elongation remained unaffected in both species. While plant morphology of *C. curta* remained unaffected by UV-B radiation, *C. decidua* had fewer tillers per plant, however tillers had more leaves and biomass under simulated ambient UV-B than under reduced UV-B radiation. The SLA of *C. curta* was unaffected by UV-B treatments; however, it was significantly lower for *C. decidua* under simulated ambient UV-B. Root morphology remained unaffected by UV-B for *C. curta* but roots of *C. decidua* were significantly thicker under simulated ambient UV-B. Taken collectively, our findings demonstrate that even moderate changes in UV-B radiation (e.g., corresponding to those expected with current stratospheric ozone depletion) may influence growth, morphology and biomass allocation in a species-specific manner for these native sedges in growth chambers and might also affect competitive relationships of these species in the field.

Die ultraviolett-B-Strahlung (UV-B, 280–315 nm) über der Südhemisphäre ist in den letzten Dekaden bedingt durch eine saisonale Abnahme an stratosphärischem Ozon ("Ozonloch") und einer zusätzlichen, eher generellen Erosion der stratosphärischen Ozonschicht angestiegen. Wir untersuchten den Effekt von UV-B-Strahlung auf verschiedene Wachstumsparameter von *Carex curta* und *C. decidua*, den zwei dominierenden Seggenarten in Seggenried-Ökosystemen in Tierra del Fuego (Feuerland, Argentinien) in einem Feldversuch (Versuchsdauer: vier Saisonen von 1997/1998

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bis 2000/2001) und in Wachstumskammern (Versuchsdauer: 3 Monate). Die Manipulation der UV-B-Strahlung erfolgte dabei durch transparente Kunststofffilm-Filter, welche die solare UV-B-Strahlung entweder transmittieren (Behandlung: "normale UV-B-Strahlung") oder abschwächen (Behandlung: "reduzierte UV-B-Strahlung"). Im Feldversuch war das Längenwachstum von Blättern und Ähren beider Seggen-Arten in keiner der vier Vegetationsperioden von den UV-B Behandlungen beeinflusst. Die spezifische Blattfläche der beiden Seggen wurde nur in den letzten beiden Vegetationsperioden gemessen und war in der dritten Vegetationsperiode für beide Seggen-Arten unbeeinflusst von der UV-B-Strahlung. Im vierten Jahr jedoch war die spezifische Blattfläche unter normalem UV-B bei *C. curta* reduziert und bei *C. decidua* erhöht. Die spezifische Wurzellänge im Ökosystem war unbeeinflusst von der UV-B-Strahlung. Die Biomasse-Produktion des Ökosystems war im dritten Versuchsjahr unbeeinflusst von der UV-B-Strahlung, im vierten Jahr war jedoch ein Trend zu einer um 15% höheren Produktion bei normalem UV-B im Vergleich zu reduziertem UV-B erkennbar ($P = 0.064$). In den Wachstumskammern hat eine die Feldbedingungen in Tierra del Fuego simulierende UV-B-Strahlung das Aufkommen von *C. curta*-Keimlingen erhöht aber jenes von *C. decidua* reduziert; das Längenwachstum der Blätter war bei beiden Arten unbeeinflusst von der UV-B-Strahlung. Während die Morphologie von *C. curta* von der UV-B-Strahlung unbeeinflusst war, zeigte *C. decidua* weniger Sprosse pro Pflanze, diese Sprosse hatten jedoch mehr Blätter und Biomasse unter simulierten normalen UV-B Bedingungen als unter reduziertem UV-B. Die spezifische Blattfläche von *C. curta* war unbeeinflusst von der UV-B-Strahlung, hingegen war sie bei *C. decidua* unter simuliertem normalen UV-B-signifikant kleiner. Die Wurzelmorphologie von *C. curta* blieb unbeeinflusst von der UV-B-Strahlung, die Wurzeln von *C. decidua* waren jedoch signifikant dicker unter simuliertem normalen UV-B. Zusammenfassend zeigen unsere Ergebnisse, dass selbst moderate Änderungen in der UV-B Strahlung, wie sie beispielsweise im Zuge der gegenwärtigen stratosphärischen Ozonabnahme vorkommen können, artenspezifische Modifikationen im Wachstum, der Morphologie und der Biomasse-Allokation dieser Seggen in Wachstumskammern bewirken und somit potentiell auch die Konkurrenzbeziehungen dieser Arten in den Seggenriedern beeinflussen können.

Key words: biomass allocation – biomass production – global climate change – morphological responses – ozone depletion – sedges – specific leaf area – specific root length – ultraviolet radiation

Introduction

The intensification of UV-B radiation due to a general erosion of the stratospheric ozone layer (McKenzie et al. 1999) and especially the pronounced seasonal ozone depletion (i.e., "ozone hole") over southern South America has the potential to alter ecosystem function (e.g., Caldwell et al. 1999, Rozema 1999). Most plants that are normally exposed to sunlight have means of protection from solar UV-B. This includes the shielding of sensitive radiation targets by structural characteristics and pigments that screen out the most damaging radiation (Caldwell et al. 1983). Nevertheless, solar UV-B radiation has been shown to cause direct damage in plants in the form of nucleic acid damage, photooxidative effects and injury to specific targets in processes such as the photosystem II reaction center of photosynthesis (e.g., Ziska et al. 1993, Teramura & Sullivan 1994, Rousseaux et al. 1999). Beside these physiological responses, morphological alterations in plants due to UV-B radiation such as greater leaf thickness, shorter internode length, increased branching or tillering have been identified as sensitive response parameters to UV-B radiation (e.g., Barnes et al. 1995, Day et al. 1999). Most of these morphological alterations represent mainly shifts in allocation without changes in biomass production (e.g., Flint & Caldwell 1996) and have been shown to affect competitive interactions for several species (Gold & Caldwell 1983, Ryel et al. 1990, Barnes et al. 1995). However, there is a great variation in the response to UV-B radiation among different plant functional types and even different genotypes of the same species (e.g., Caldwell & Flint 1994, Tegelberg et al. 2003). While considerable attention in UV-B research has been focused on the growth and ecological interactions of economically important annual crops (e.g., Tevini & Teramura 1989, Barnes et al. 1990, Barnes et al. 1993, Mazza et al. 1999), there is still little knowledge of how UV-B radiation might affect native plant species in unmanaged ecosystems (but see Gehrke et al. 1995, Björn et al. 1997, Day et al. 1999, Searles et al. 1999, Rousseaux et al. 2001). Also, mainly due to differences in radiation applied, there is a general trend that plants grown in open sunlight are generally much more resistant to UV-B radiation than those grown under growth-chamber or greenhouse conditions (Tevini et al. 1990, Caldwell & Flint 1994, Fiscus &

Booker 1995, Dai et al. 1997, Antonelli et al. 1998, Stephanou & Manetas 1998).

In the current study, we focus on UV-B responses of the two sedges *Carex curta* and *Carex decidua*, which make up more than 90% of the herbaceous biomass in a fen ecosystem in Tierra del Fuego, southernmost South America. This location has already experienced up to 13% decrease in springtime and summertime ozone within the last two decades (Rousseaux et al. 2001) and the consequences of the concomitantly altered UV-B radiation to ecosystem processes may already be occurring (Ballaré et al. 2001). Manipulative UV-B experiments indicate UV-B effects on microbial populations in a peat bog (Searles et al. 1999, 2001, 2002), changes in herbivory in a shrub (Rousseaux et al. 1998, 2001) and a fen ecosystem (Zaller et al. 2003), changes in root growth and mycorrhizal infection in a fen (Zaller et al. 2002) and changes in leaf morphology of Southern beech trees (M. Robson, personal communication). Here we present results summarizing four years of a long-term field experiment located in Tierra del Fuego where we manipulated the solar UV-B radiation with two types of selective plastic filters providing either near-ambient or reduced UV-B radiation. In addition, we also set up a growth chamber experiment complementary to the field experiment in which these two species have been grown under radiation conditions simulating the level of UV-B radiation in the field.

The central aims of this study were to determine how UV-B radiation affects (1) growth, biomass responses, and seed production of mature specimens of two *Carex* species in the field, and (2) the emergence, growth, morphology and biomass production of seedlings of these species using growth chamber facilities. Since solar UV-B is already greater than historical levels due to ozone depletion, our goal was to determine if present-day solar UV-B is exerting effects on this system, rather than testing the effects of levels of UV-B elevated above current levels.

Materials and methods

Field experiment

The field site is located in a fen ecosystem at an elevation of about 200 m (a.s.l.) near the city of Ushuaia, Tierra del Fuego, Argentina (54°47′S, 68°16′W) where the climate is sub-Antarctic (annual precipitation: 500 mm, mean annual air temperature of 5.5 °C). The fen ecosystem grows in peat soil (pH = 6.0, N = 1.7%, C/N ratio = 19.7) with the water table about 5–10 cm below the soil surface. Experimental plots were located between scattered saplings of *Nothofagus antarctica* (Forster f.) Oersted (up to 1 m tall) and are dominated by the sedges *Carex curta* and *C. decidua*. Other less dominant species are *Carex magellanica* Lam., the herbaceous species *Acaena magellanica* (Lam.) Vahl, *Gunnera magellanica* Lam., *Caltha sagittata* Cav., and the fern *Blechnum penna-marina* (Poiret) Kuhn. (nomenclature after Moore 1983).

Manipulation of UV-B radiation started in October 1996 with nine 1.4 m × 1.5 m experimental plots maintained under near ambient UV-B conditions by covering the plots with UV-transparent plastic film (Aclar type 22A, 38-µm thick; Honeywell Inc. formerly Allied Signal, Pottsville, PA, USA) and nine plots maintained at reduced UV-B conditions using clear polyester film (100-µm thick, optically equivalent to ‘Mylar-D’, DuPont Co, Wilmington, DE, USA). Filters were perforated to allow precipitation and a small amount of unfiltered solar radiation to penetrate to the plots. Plots maintained at reduced UV-B radiation received about 20% of the ambient solar UV-B and those maintained at near-ambient UV-B received about 90% of ambient UV-B radiation (when weighted with the generalized plant action spectrum normalized to 300 nm after Caldwell 1971, Searles et al. 1999). Both filters transmitted nearly 90% of the photosynthetic active radiation (Searles et al. 1999). Filters were installed horizontally about 35 cm above the soil surface and about 10 cm above the tallest vegetation. We replaced filters with new ones when they were destroyed by wind. Experimental plots of the two treatments were randomly interspersed between saplings of Southern Beech. Every year, UV-B manipulation treatments were maintained during the growing season from about early October until mid-March. By then plants in the plots were starting to senesce. Micro-meteorological parameters (e.g., precipitation, air and soil temperature) have been shown to be similar between filtered plots and adjacent unfiltered areas (see Searles et al. 1999 for further details).

Field experiment measurements

In the field, we monitored above-ground growth of *Carex curta* and *C. decidua* at least once per growing season between December 1997 and March 2001 (on a total of 7 dates). Due to the different growth form of the two sedge species we measured different growth parameters for each species. For *C. curta* we measured length of the youngest leaf starting from the tip of the ligula to the tip of the leaf, stem length was measured between the ligula of that leaf and the beginning of the spike. Spike length was measured from the lowest spikelet until the tip of the spike. For *C. decidua* we measured the length of the three longest spike leaves, stem length from the beginning of the spike until the ligula of the first leaf inserted at the stem. Spike length and density was determined similarly as for *C. curta*. Seed number and seed dry mass (oven-dried at 60 °C for 48 h) were determined on a per plant basis. Below-ground growth was determined by four ingrowth cores (5.5 cm diameter, 10 cm depth) made of 1-mm plastic screen inserted in each plot. Ingrowth cores were filled with root-free peat soil derived near the field site. In late February of 2000 and 2001, ingrowth cores were collected and roots grown into the cores carefully washed free of soil and stored in ethanol until root length could be measured using a root length scanner (Commonwealth Aircraft Corporation ltd., Melbourne, Australia). Above-ground biomass production was measured by harvesting above-ground plant biomass in a center area of 70 cm × 70 cm in each plot to a height of 2 cm above the soil surface in early March, 2000 and late February, 2001. Vegetation of a 10-cm border strip of the plot border was cut and discarded. Below-ground biomass production was determined by drying roots that accumulated until the end of the season in the ingrowth cores. Above- and below-ground biomass was dried at 70 °C for at least two days before weighing.

Growth chamber experiment

The experiment was conducted between June and September, 1999 in two growth chambers (Mallory Inc., Salt Lake City, USA). Seeds of *Carex curta* Gooden and *Carex decidua* Boott. were collected in January 1997, in a fen ecosystem in Ushuaia, Tierra del Fuego, Argentina (55°S, 68°W) and stored at room temperature until they were used for this experiment. We planted one seed per species in a separate conical plastic container (40-mm diameter, 210 mm length, 85 containers per species) filled with moist peat soil (pH = 6.0, N = 1.34%, C/N = 29) and stored the containers for stratification at 5 °C under opaque plastic. After five weeks (seeds still had not emerged from the soil surface), we transferred the racks holding the containers to the growth chambers where we maintained the different UV-B treatments (see below). Because of the uncertain germination rates of these native sedge species, we planted many more containers than would be used in the actual measurements (42 in one chamber and 43 in the other). For the measurements, a random sample of 15 individuals per species and treatment were used (see below). Plant containers with the two different species were randomly mixed on the racks and watered frequently with tap water to keep soil moist throughout the experiment. No additional nutrients were added over the course of the experiment.

Because the growth chamber experiment was designed to complement field experiments conducted in Ushuaia, Tierra del Fuego, Argentina (see below), we attempted to simulate solar UV-B conditions of late spring and early summer under present-day conditions (i.e. October–December; see Searles et al. 1999). We set the duration of the photoperiod accordingly to this time at the location (14, 16, and 17 hours for the first, second, and third month of the growth chamber experiment, respectively). However, in order to accelerate plant growth in the chambers we increased the daily temperatures resulting in an average 15% higher monthly mean temperatures than in the field as measured at 10 cm height near our field plots using copper-constantan thermocouples connected to a datalogger (Campbell Scientific, Logan, Utah, USA). In order to also simulate the highly variable weather conditions at the field site, we occasionally allowed the temperature in the chambers to drop below 0 °C over night. We used one 6000-W-xenon lamp per growth chamber as a source for photosynthetic active radiation (PAR, 400–700 nm, 800 µmol m^{-2} s^{-1} at the soil surface) as well as for UV-B radiation (150 mW m^{-2}, weighted with the generalized plant spectrum normalized to 300 nm). Midday PAR at the field site during this time is around 2000 µmol m^{-2} s^{-1} for clear skies and around 700 µmol m^{-2} s^{-1} for overcast skies, which are frequent in this region (J. G. Zaller, unpublished data).

To create the two UV-B treatments within each growth chamber we used two different transparent plastic films to filter out different amounts of UV-B radiation emitted from the xenon lamps. Filters were suspended about 10 cm above the soil surface or vegetation allowing us to have both UV-B treatments in each chamber. Spectral irradiance under filters was measured frequently with a double-monochromator spectroradiometer (Optronic Laboratories, Model 742, Orlando, Florida, USA), which was calibrated for wavelength accuracy and intensity before each use. Spectral irradiance was weighted according to a generalized plant action spectrum (Caldwell 1971, normalized to 300 nm) to obtain biologically effective UV-B radiation (UV-B_{BE}). Cellulose di-acetate filters (different combinations of 125-µm and 75-µm thick filters dependent on lamp characteristics) were used to simulate ambient UV-B conditions ("simulated ambient UV-B", mean daily UV-B_{BE} radiation: 4.9, 5.2, and 5.5 kJ m^{-2} d^{-1} for a 14, 16, and 17-hour photoperiod, respectively). Clear-sky UV-B_{BE} radiation in Ushuaia is about 5.5 kJ m^{-2} d^{-1} in December for a 17-hour photoperiod (abstracted from Searles et al. 1999). Clear polyester film (100-µm-thick) was used to create low UV-B treatments which allowed about 5% of the UV-B radiation of the simulated ambient UV-B treatment reach the soil surface. Both filter types transmitted on average 85% of PAR as measured with a quantum sensor (LiCor, Lincoln, Nebraska, USA). To compensate for differences in radiation between the centers and borders of racks, we rotated the racks within chambers every second day. Racks were also rotated between growth chambers at biweekly intervals to minimize chamber effects. Filters were changed on average every second week to avoid photodegradation of the filter material.

Growth chamber measurements

During the first three weeks after starting the growth chamber experiment we monitored seedling emergence every day. We recorded the day of emergence, seedling height and the number of leaves produced. With further development of seedling growth, we also measured the number of tillers and the number of leaves per tillers. At the end of the experiment, we divided the plants into above-ground and below-ground parts, measured the parameters mentioned above and additionally determined the leaf area and root length on a random subsample of 15 plants per species and treatment. Above-ground plant material was weighed after drying the samples for 24 hours at 65 °C, roots were dried for 48 hours at 65 °C before weighing. We also calculated the specific leaf area (SLA, $cm^2 g^{-1}$) and specific root length (SRL, $m g^{-1}$).

Statistical analyses

Field SLA and SRL data were analysed using a two-way ANOVA with the GLM procedure in SAS (release 8.2 for Windows; SAS Institute, Cary, NC, USA) with UV-B treatment and Species as factors. Data were arcsine-transformed when needed to meet assumptions of ANOVA. Above- and below-ground plant biomass production in the system was analysed separately for each season using a two-way ANOVA (factors: UV-B treatment and Biomass component (above vs. below-ground) within the GLM procedure. Data analysis for the growth chamber experiment were conducted using a nested ANOVA model with the “proc mixed” procedure in SAS with UV-B treatment and Species as factors. In our model we used the general Satterthwaite approximation for the denominator degrees of freedom. Experimental units here were Growth chambers, UV-B treatment nested within Growth chambers and Plant racks nested within UV-B treatments nested within Growth chambers. The basic replication unit for the growth chamber experiment was the two racks per UV-B treatment. For each individual plant, the number of days under UV-treatment (counted since the first emergence on the soil surface) was used as a co-variable in the statistical analysis. For the analysis of the time course of seedling establishment in the growth chambers a repeated measurement nested ANOVA including 23 dates was conducted using the GLM procedure in SAS. All ANOVA analyses were performed using Type III sums of squares and were followed by Tukey’s least squares means test for multiple comparisons. Values given throughout the text are means ± SE.

Results

Field experiment

In the field, leaf and stem elongation of both species remained unaffected by UV-B radiation for the four seasons we present here (Table 1). Seed number, seed dry mass, and number of plants with reproductive spikes were not affected by the implemented UV-B radiation (Table 2). The SLA for both species remained unchanged by UV-B in the third season (Fig. 1), however in the fourth season *C. curta* had a 15% lower SLA (Tukey; $P = 0.015$) and *C. decidua* a 10% higher (Tukey; $P = 0.0384$) under near-ambient UV-B and also had a significant UV-B × Species interaction term (Fig. 1). The SRL was not assessed separately due to difficulties in distinguishing roots of the two species, however ecosystem SRL remained unchanged by UV-B treatment (season 1999/2000: 242.98 ± 7.96 mg^{-1} vs. 227.70 ± 22.24 mg^{-1} at reduced vs. near-ambient UV-B; season 2000/2001: 143.64 ± 9.24 mg^{-1} vs. 129.68 ± 11.94 at reduced vs. near-ambient UV-B, respectively).

Table 1. Leaf length, stem and spike length of *Carex curta* and *C. decidua* in plots of a fen ecosystem receiving reduced or near-ambient UV-B radiation. For data of the 1996–1997 season see Searles et al. 1999. T-tests showed no significant differences between treatments. Means in cm ± SE (n = 9).

Species	Plant part	1997–1998		1998–1999		1999–2000		2000–2001	
		reduced UV-B	near-amb. UV-B	reduced UV-B	near-amb. UV-B	reduced UV-B	near-amb. UV-B	reduced UV-B	near-amb. UV-B
C. curta	leaf	18.4 ± 0.8	20.1 ± 0.8	19.9 ± 0.9	21.2 ± 0.9	18.3 ± 7.7	18.7 ± 4.6	15.8 ± 4.5	16.0 ± 5.3
	stem+spike	28.9 ± 2.0	30.5 ± 2.9	27.2 ± 1.2	28.3 ± 1.1	27.7 ± 10.3	28.7 ± 5.7	24.3 ± 9.3	26.2 ± 11.1
C. decidua	3rd spike leaf	7.9 ± 0.4	8.0 ± 0.4	8.7 ± 0.4	8.7 ± 0.3	6.8 ± 3.2	7.0 ± 2.9	5.5 ± 1.8	5.4 ± 1.8
	stem+spike	16.3 ± 0.7	16.0 ± 0.5	12.3 ± 0.5	13.0 ± 0.5	15.2 ± 6.9	15.7 ± 6.5	14.3 ± 5.2	14.5 ± 4.4

Table 2. Number of seeds and seed mass of *Carex curta* and *C. decidua* in plots of a fen ecosystem receiving reduced or near-ambient UV-B radiation. T-tests showed no significant differences between treatments. Means ± SE (n = 9).

Variable	Species	1996–1997		1997–1998		1998–1999	
		reduced UV-B	near-amb. UV-B	reduced UV-B	near-amb. UV-B	reduced UV-B	near-amb. UV-B
Seed number	*C. decidua*	228 ± 12	240 ± 12	238 ± 12	235 ± 9	266 ± 11	254 ± 14
	C. curta	110 ± 10	110 ± 5	124 ± 8	114 ± 9	107 ± 7	124 ± 9
Seed mass	*C. decidua*	104 ± 5	99 ± 6	105 ± 6	104 ± 8	102 ± 6	91 ± 7
(mg/seed)	C. curta	51 ± 5	46 ± 2	44 ± 3	42 ± 4	27 ± 4	35 ± 4
Plants with seeds	*C. decidua*	152 ± 18	197 ± 32	178 ± 38	153 ± 25	176 ± 29	218 ± 26
(Individuals m^{-2})	*C. curta*	95 ± 14	109 ± 18	143 ± 35	124 ± 12	71 ± 14	89 ± 10

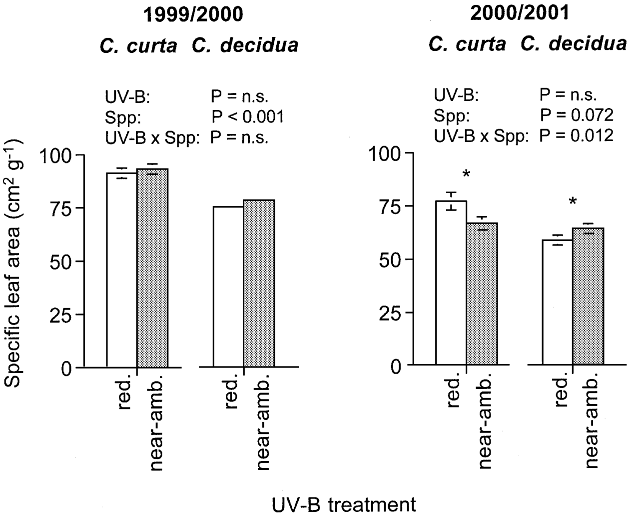

Fig. 1. Specific leaf area of mature plants of *Carex curta* and *C. decidua* in field plots of a fen ecosystem in Tierra del Fuego, Argentina, maintained at reduced (red.) and near-ambient (near-amb.) UV-B radiation. Two-way ANOVA results presented for each season. Asterisks indicate significant treatment effects (Tukey; P < 0.05). Means ± SE (n = 9). Small error bars are not depicted.

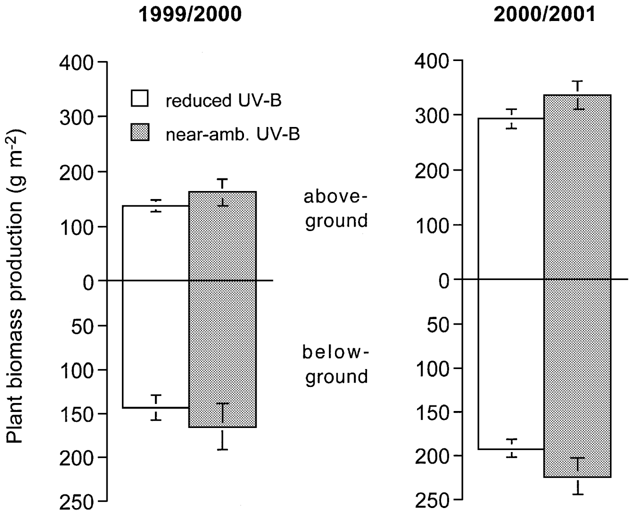

Fig. 2. Above- and below-ground biomass production in field plots with dominating mature *Carex curta* and *C. decidua* in a fen ecosystem in Tierra del Fuego, Argentina, maintained at reduced and near-ambient UV-B radiation. Two-way ANOVA results: season 1999/2000, all effects non-significant; season 2000/2001, UV-B: $F_{1,32}$ = 3.70, P = 0.064; Biomass component (above- vs. below-ground): $F_{1,32}$ = 30.05, P < 0.001; UV-B × Biomass component: n.s.. Means ± SE (n = 9).

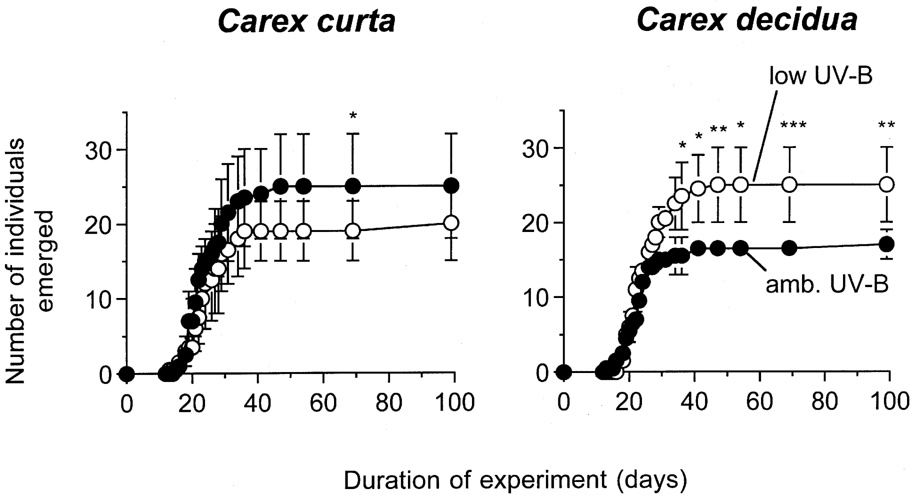

Fig. 3. Seedling emergence of *Carex curta* and *C. decidua* in growth chambers maintained at low and simulated ambient (amb.) UV-B radiation. Repeated measures ANOVA results: UV-B: $F_{1,11}$ = 39.36, P < 0.001; Spp: n.s., Spp × UV-B: $F_{1,11}$ = 5.56, P = 0.038; Time × UV-B: $F_{22,242}$ = 17.06, P < 0.001; Time × Spp: n.s.; Time × UV-B × Spp: $F_{22,242}$ = 2.69, P < 0.001. Asterisks indicate significant treatment effects for individual dates (Tukey; * P < 0.05, ** P < 0.001, *** P < 0.001). Means ± SE (n = 2). Small error bars are not depicted.

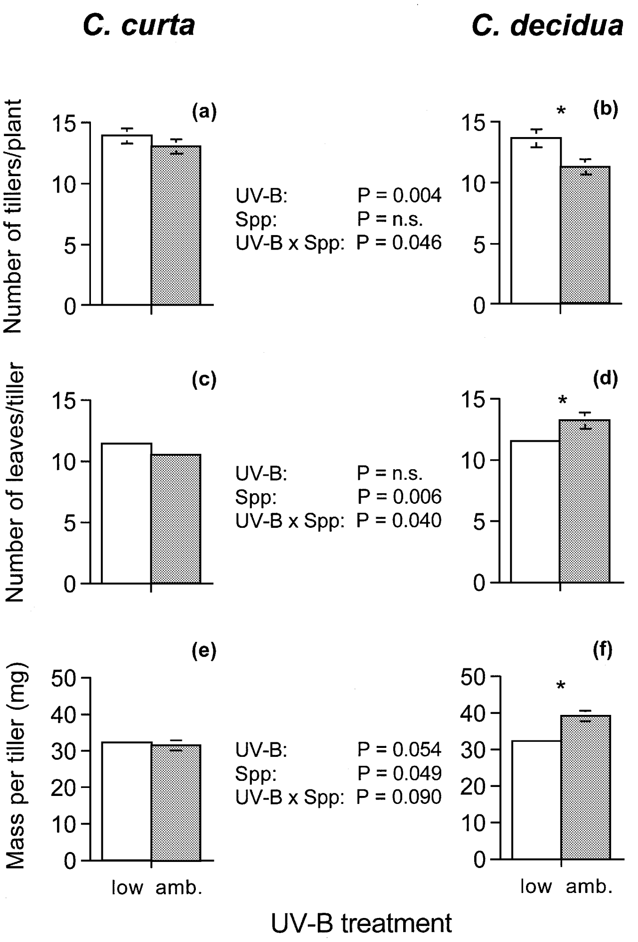

Fig. 4. Number of tillers per plant (a, b), number of leaves per tiller (c, d), and biomass per tiller (e, f) of juvenile plants of *Carex curta* and *C. decidua* in growth chambers maintained at low and simulated ambient (amb.) UV-B radiation. Two-way ANOVA results presented for each parameter. Asterisks indicate significant treatment effects (Tukey; $P < 0.05$). Means ± SE ($n = 2$). Small error bars are not depicted.

In the field, both above- and below-ground biomass production also remained unaffected by UV-B treatment for both seasons studied, however total biomass tended to be 15% higher under near-ambient UV-B in the fourth season (Fig. 2).

Growth chamber experiment

UV-B treatment significantly influenced the seedling establishment of both *Carex* species differently, also demonstrated by a significant UV-B × Species interaction term (Fig. 3). Simulated ambient UV-B increased the seedling emergence of *Carex curta* seedlings by 25%, but, in contrast decreased seedling emergence of *Carex decidua* by 36% (Fig. 3). Cumulative leaf elongation remained for both species unaffected by UV-B radiation treatment and amounted across UV-B treatments at the end of the experiment to 131.35 ± 19.91 mm for *C. curta* and to 121.14 ± 16.36 mm for *C. decidua*.

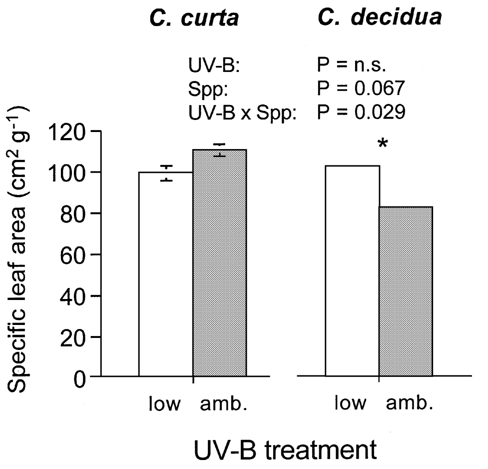

Fig. 5. Specific leaf area of juvenile plants of *Carex curta* and *C. decidua* in growth chambers maintained at low and simulated ambient (amb.) UV-B radiation. Results presented are from a two-way ANOVA. The asterisk indicates a significant treatment effect (Tukey; $P < 0.05$). Means ± SE ($n = 2$). Small error bars are not depicted.

Number of tillers per plant, number of leaves per tiller and dry mass per tiller of *Carex curta* seedlings remained unaffected by imposed UV-B radiation (Fig. 4a,c,e). However, *Carex decidua* seedlings had 17% less tillers (Tukey; $t = 4.08$, $P = 0.010$; significant UV-B × Species interaction; Fig. 4b), tillers tended to be 33% heavier (Tukey; $t = 3.06$, $P = 0.060$; significant UV-B × Species interaction; Fig. 4d) and had 15% more leaves (Tukey; $t = 3.15$, $P = 0.043$; marginally significant UV-B × Species interaction; Fig 4f) under simulated ambient UV-B than under low UV-B radiation. Also, leaf and root morphology was significantly affected by UV-B radiation. Specific leaf area of *Carex curta* remained unaffected by UV-B (Fig. 5), however was 20% lower for *Carex decidua* at simulated UV-B compared to low UV-B (Tukey; $t = 3.16$, $P = 0.043$; significant UV-B × Species interaction; Fig. 5). Specific root length of *Carex curta* remained unaffected by UV-B treatments (averaged across UV-B treatments: 11.10 m/g), but was 20% lower for *Carex decidua* under simulated ambient UV-B than under low UV-B radiation (12.69 ± 1.11 m/g vs. 9.98 ± 1.09 m/g for low vs. ambient UV-B, respectively; Tukey; $t = 3.52$, $P = 0.024$).

Despite these alterations in growth and morphology, the above-ground biomass production of neither species was affected by the treatments (Fig. 6). However, under simulated ambient UV-B, the below-ground biomass production of *Carex curta* was 15% lower than under low UV-B radiation and this resulted in a marginally significant 11% reduction in total biomass production of *Carex curta* grown at simulated ambi-

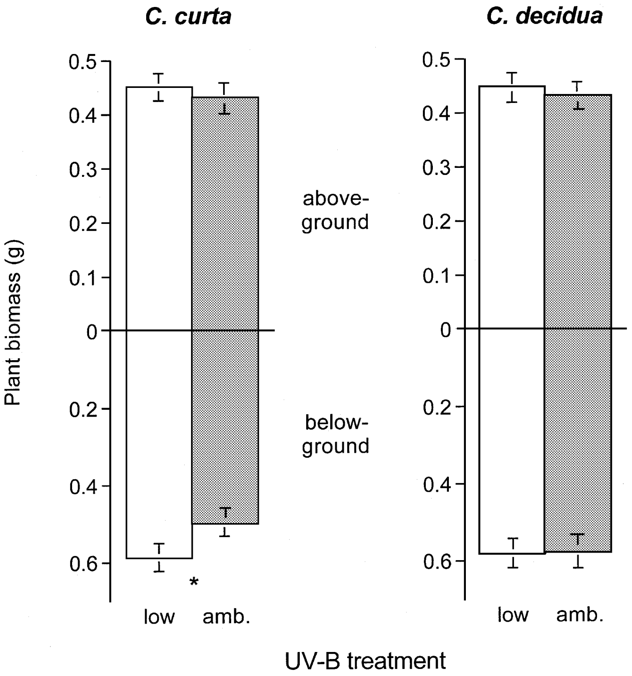

Fig. 6. Above- and below-ground biomass production of juvenile plants of *Carex curta* and *C. decidua* grown in growth chambers maintained at low and simulated ambient (amb.) UV-B radiation. Two-way ANOVA results for total biomass: UV-B: $F_{1,4} = 4.98$, $P = 0.089$; Spp: n.s.; UV-B × Spp: n.s. The asterisk indicates a significant treatment effect (Tukey; $P < 0.05$). Means ± SE ($n = 2$).

ent UV-B (Tukey; $t = 4.98$, $P = 0.089$; Fig. 6). Root biomass and total biomass production of *Carex decidua* remained unaffected by UV-B treatment (Fig. 6).

Discussion

In the field, where mature plants of the two *Carex* species have been growing in plots maintained at reduced or near-ambient UV-B for more than five seasons, we were unable to detect UV-B effects on leaf elongation, stem elongation, and seed production (also, results in the first year did not show any UV-B effects on above parameters, see Searles et al. 1999). In contrast, in our growth chamber experiment, UV-B greatly affected the emergence, tillering, and morphology of seedlings of the two *Carex* species from Tierra del Fuego (Argentina). The UV-B response of the sedges was highly species-specific, and for some parameters indicated responses in opposite directions (e.g., seedling emergence or specific leaf area). Although, we detected substantial changes in the morphology of both species, leaf elongation and biomass production was unaffected by UV-B radiation (see also Barnes et al. 1988, Barnes et al. 1990). Similar morphological responses to UV-B, such as reduced total leaf area and numbers of leaves and branches were also reported for seedlings of two Antarctic vascular plant species (Ruhland & Day 2000). Also, the grass *Deschampsia antarctica* showed a reduced leaf elongation under near-ambient UV-B (Ruhland & Day 2000).

Sedge SLA, ecosystem SRL and biomass production data are only available for two seasons: the two sedges showed no response in the third season but significant, UV-B responses for SLA in the fourth season in opposite directions for the two species. These responses may be due to climatic differences between the two seasons where SLA was unaffected in the season with average precipitation but was affected in the year with above average precipitation. Due to difficulties in separating roots of the two *Carex* species we only were able to determine ecosystem SRL and ecosystem root mass which remained unaffected by UV-B treatment. Thus, it remains unclear whether UV-B radiation may also have evoked species-specific root responses as we showed in the growth chamber experiment. Above- and below-ground biomass production was 70% greater in the wet season than in the “normal” season, however apart from a trend towards an average 15% higher biomass production under near-ambient UV-B for both years, UV-B did not affect biomass production in a statistically significant manner in this fen ecosystem.

One of the central aims of this study was to compare the response of seedlings grown under controlled conditions to the response of plants in the field. We showed both in the growth chamber and the field experiment that the parameters of leaf elongation and above-ground biomass production were insensitive to UV-B for both *Carex* species. On the other hand, various UV-B-induced alterations were species-specific either in the growth chambers (e.g., leaf, root and tiller morphology) or in the field experiment (e.g., leaf morphology). Although UV-B radiation conditions in the growth chamber and the field were fairly similar, it must be recognized that (1) in the chambers we studied the response of seedlings, but primarily mature plants in the field, (2) plants in the growth chamber grew in a non-competitive environment, and (3) other differences between plants growing in the growth chambers and the field might have affected plant response to UV-B. Taking these considerations into account, the observed morphological responses of the two *Carex* species to UV-B radiation are still likely to have consequences for the development and performance of these species. For instance it has been demonstrated that the number of leaves per tiller is positively correlated to plant survival (Carlsson & Callaghan 1990b) and flowering probability (Carlsson

& Callaghan 1990a) for another *Carex* species. For *Carex decidua* this could mean that once it is established it is more successful under high UV-B than *Carex curta*.

To what extent the UV-B induced differences on the seedling emergence could also have consequences on the species composition of these ecosystems is difficult to predict. However, it is evident that seedlings that emerge earlier tend to gain a disproportionate advantage in size, space pre-emption and resource capture relative to their neighbours (e.g., Ross & Harper 1972, Abul-Faith & Bazzaz 1979) and small initial differences among plants in size and growth may have become greatly magnified over time (Weiner & Thomas 1986, Thomas & Bazzaz 1993). The number of seeds, seed dry mass, and viability were not affected by the differences in UV-B radiation in either species (Searles et al. 1999).

Taken collectively, our findings showed that (1) UV-B radiation affected the growth and morphology of seedlings of the two most dominant *Carex* species native in a fen ecosystem in Tierra del Fuego (Argentina) when grown under controlled conditions, (2) that responses to UV-B in many cases varied between species, and (3) that results from studies carried out under controlled conditions cannot be used to predict ecosystem responses in the field. Finally, our results also showed that the effect of UV-B radiation in the field is obviously influenced by the vicissitudes of weather variations (e.g., precipitation), thus highlighting the importance of long-term field experiments in the study of climatic change effects on ecosystems, including solar UV-B radiation.

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