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Solar ultraviolet-B radiation can affect slug feeding preference for some plant species native to a fen ecosystem in Tierra del Fuego, Argentina

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Abstract

The objectives of this study were to test potential effects of solar ultraviolet-B (UV-B) radiation on (i) foliage nutritional quality and foliage decomposition rates of six plant species of this fen ecosystem (*Nothofagus antarctica*, *Carex curta, C. decidua* and *C. magellanica*; *Acaena magellanica* and *Gunnera magellanica*) and (ii) feeding preferences for these plant species of the slug *Deroceras reticulatum* prevalent in this ecosystem. In a mixed-diet selection slugs were offered leaves of the six species that had been grown for three years in experimental field plots under either near-ambient or reduced solar ultraviolet-B (UV-B) radiation. The chosen characteristics of leaf quality (nitrogen concentration, carbon:nitrogen ratio, specific leaf area) and leaf decomposition rates of the six species varied significantly among species but were not affected by the UV-B treatments. However, there were UV-B treatment effects on slug feeding preference for two plant species. For the tree species, *Nothofagus*, slugs had consumed only one-third as much foliage grown under near-ambient UV-B radiation as of foliage grown under reduced UV-B by the end of the feeding experiment. In contrast, leaves of the sedge *C. decidua* that had been grown under near-ambient UV-B were consumed twice as much as leaves grown under reduced UV-B radiation. Consumption of foliage for the other four species was similar for the two UV-B treatments. Additionally, diet selection of the slugs was also significantly affected by prior UV-B conditions under which foliage had been grown. *Nothofagus* leaves were consumed proportionately less and *C. decidua* proportionately more if the foliage had been grown under near-ambient UV-B radiation.

Introduction

Since the mid-1980s stratospheric ozone concentrations over the Antarctic and most southerly latitudes of South America have declined markedly during the austral spring (Farman et al. 1985; Crutzen and Arnold 1986). Since ozone is the principal absorber of ultraviolet-B radiation (UV-B, 280–315 nm), the ground-level solar UV-B flux has correspondingly increased during this time period (Bojkov and Fioletov 1995; Madronich et al. 1998). While much of the ozone reduction has been associated with the presence of the Antarctic Vortex containing the "ozone hole", there has also been a general erosion of the ozone layer during the summer months after the Antarctic Vortex has disappeared (McKenzie et al. 1999). Both damaging and regulatory effects of solar UV-B radiation can occur in biological systems (e.g., Caldwell and Flint (1994) and Rozema et al. (1997)). For example, the passage of the "ozone hole" over Tierra del Fuego and the concomitant increases in solar UV-B radiation has been shown to result in significant increases in DNA damage in a native herbaceous species (Rousseaux et al. 1999). An example of regulatory effects of solar UV-B radiation are changes in foliage chemistry and morphology that, while not interpreted as damage *per se*, can have important secondary effects on ecosystem processes. Such secondary effects include changes in plant susceptibility to disease and herbivory (e.g., Berenbaum (1988) and Rousseaux et al. (1998), Mazza et al. (1999a, 1999b), Gwynn-Jones (1999)) and changes in decomposition rates of dead foliage (Gehrke et al. 1995).

Reports on effects of UV-B radiation on herbivory of native plant species are mixed. Sometimes herbivory is increased (e.g., Lavola et al. (1998) and Gwynn-Jones et al. (1997), Buck and Callaghan (1999)) and sometimes reduced (e.g., Gwynn-Jones et al. (1997) and Rousseaux et al. (1998)). For most of these studies, changes in foliage quality such as leaf chemistry, appears to be largely responsible for the altered herbivory. Both changes in foliage primary and secondary chemistry appear to mediate these plant-insect interactions (Caldwell et al. 1999; Gwynn-Jones 1999). However, identification of particular compounds that are increased or decreased by UV-B radiation and that are directly responsible for the changes in herbivory remains elusive.

All the studies of UV-B effects on herbivory of which we are aware have involved insect herbivory. Nothing is known about potential effects of UV-B radiation on herbivory by slugs and snails. Slugs have received attention primarily because of the economic damage they inflict in agricultural systems (e.g., Godan (1979) and South (1992)). However, in non-agricultural ecosystems slugs also play an important role in nutrient cycling by reducing the size of detritus particles and therefore accelerating decomposition and mineralization of plant litter (Petersen and Luxton 1982). In the moist fen ecosystem where we conducted the current study, we estimated a slug density of 20–50 individuals per square meter during favorable periods of the year (JG Zaller, unpublished data). The dominant slug species in this ecosystem is *Deroceras reticulatum* Müller (Gastropoda, Agrolimacidae), a species with worldwide distribution, largely due to human activities. It has even been introduced onto sub-Antarctic islands (Dell 1964). *Deroceras reticulatum* is also known as one of the most abundant and harmful agricultural slug species on arable land worldwide (e.g., Godan (1979) and South (1992)). It is unlikely that UV-B radiation would directly affect the feeding behavior of slugs because they are primarily active at night or under very cloudy and rainy conditions when UV-B radiation is typically quite low. However, similar to the findings of several studies with insect herbivory, we hypothesized that UV-B radiation might affect feeding behavior of slugs due to changes in foliage quality.

We conducted a diet-selection experiment in which slugs were offered leaves of the six most abundant plant species of this *Carex* fen system that had previously been subjected to different solar UV-B conditions. These species represented different functional groups including two herbs, three graminoids and one tree species. The foliage was collected from plants grown in an ongoing field experiment, in which experimental plots had been maintained under either near-ambient or reduced solar ultraviolet-B radiation for three growing seasons (corresponding to 20% and 90% of ambient solar UV-B radiation, respectively, Searles et al. (1999)). The objectives of this study were to test potential effects of solar ultraviolet-B radiation on (i) foliage nutritional quality and foliage decomposition rates of the six plant species of this fen ecosystem and (ii) feeding preferences to these plant species of the slug *Deroceras reticulatum* prevalent in this ecosystem.

Materials and methods

Study site

The study site is located at an elevation of about 200 m a.s.l. near the city of Ushuaia, the southernmost city on Earth, in Tierra del Fuego, Argentina (54°47′ S, 68°16′ W). This location experiences more stratospheric ozone reduction than any other location in the world where terrestrial ecosystems with appreciable plant cover occur. The climate at the site is sub-Antarctic with annual precipitation of 500 mm which is uniformly distributed over the year. Mean annual air temperature is 5.5 °C (FAO 1985). The fen ecosystem occurs in peat soil (pH = 6.0, N = 1.7 mg g^{-1}, C/N ratio = 19.7) with a water table about 5–10 cm below the soil surface. Experimental plots were 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 *C. 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*. Plant nomenclature follows Moore (1983).

Manipulation of UV-B radiation

The experimental area was established in October 1996 with ten 1.4 × 1.5 m plots under two different types of plastic film filters to selectively manipulate the solar UV-B transmission. The filters were suspended 35 cm above the ground and 10 cm above the tallest vegetation. The sides were open to allow for ventilation provided by the nearly constant wind. Five plots in the "Reduced-UV-B" treatment were under a filter material that absorbed UV-B but was quite transparent to longer wavelength radiation (polyester film, 100-μm thick, DuPont Co, Wilmington, DE, USA). The other five plots in the "Near-ambient UV-B" treatment were under a filter material that was equally transparent to all wavelengths in the UV and visible spectrum (Aclar type 22A, 38 μm thick; Honeywell Inc. formerly Allied Signal, Pottsville, PA, USA). All filter material was perforated with louvers using a custom melting device to allow precipitation to penetrate to the plots below. Furthermore, since in the Reduced-UV-B treatment, a reduction of UV-B levels rather than complete exclusion of UV-B was intended, the louvers also allowed some UV-B radiation to reach the canopy level. Thus, plots in the Reduced-UV-B treatment received about 20% of the ambient solar UV-B and those in the Near-ambient treatment about 90% (weighted with the generalized plant action spectrum at 300 nm after Caldwell (1971) and Searles et al. (1999)). Plants growing under the near-ambient UV-B filter experienced the enhanced UV-B levels presently occurring in Tierra del Fuego which are due both to the passage of the ozone hole (polar vortex) over the experimental site and also due to the general erosion of the ozone layer at high latitudes (Madronich et al. 1998). These UV-B levels are believed to currently be at the highest levels that will be observed if the ozone depletion phenomenon decreases as projected (Madronich et al. 1998). The reduced UV-B treatment, except on days with particularly high UV-B irradiation levels, has UV-B levels that are somewhat below levels characteristic of pre ozone-hole times. Thus the UV increment responsible for the observed effects is somewhat greater than the increment due to ozone depletion, but is an inevitable consequence of the available filter materials. 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 UV-B- 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 UV-B radiation was quite low. For further details concerning the experimental design see Searles et al. (1999).

Leaf quality characteristics and decomposition

In an attempt to explain any differences in slug herbivory, we measured certain leaf quality parameters that are known to affect herbivory and that could be affected by UV-B exposure. Since slugs also feed on detrital leaf material, we allowed the slugs to feed to decaying leaf material as well as fresh foliage. Another aspect of detrital leaf composition, is that UV-B radiation has been shown to affect decomposition rates of foliage (Gehrke et al. 1995). Thus, we were interested in how potential UV-B induced changes on leaf decomposition rate combined with changes in food quality of the fresh foliage might change the feeding preferences of slugs. We placed leaves of the two herbaceous species *Acaena magellanica* and *Gunnera magellanica*, the three graminoid species *Carex curta*, *C. decidua* and *C. magellanica* and the tree species *Nothofagus antarctica* that had been grown under either near-ambient or reduced UV-B conditions in the fen field plots into ten plastic boxes (15 × 10 × 5 cm high) on a 1-cm thick layer of moist soil. Each box was covered with fine mesh to prevent animals from entering the boxes; boxes were placed in the understory of *Nothofagus* trees for one month. Because the experiment was conducted in a cool, high-latitude environment, decomposition rates are low and the foliage material did not fully decompose during the course of the experiment.

For the selected leaf quality characteristics, leaf subsamples for each plant species and prior UV-B treatment were taken at the beginning and at the end of the decomposition experiment. Carbon and nitrogen concentrations of dried and powdered leaves from each individual plant (about 10 leaves per plant species) were determined using a CHN analyzer (LECO Instruments, St. Joseph, Michigan, USA). Specific leaf area (SLA, $cm^2\ g^{-1}$) was determined as an indicator of leaf toughness, and as a possible indicator of decomposition rates (i.e., lower SLA values meaning greater leaf toughness and slower decomposition rates (Lambers et al. 1998)). Decomposition of leaves was expressed as the proportion of leaf dry mass remaining at the end of the experiment relative to the initial dry mass.

Slug herbivory

The overall goal of our experiment was to mimic realistic field conditions where a variety of plant species are usually available for herbivores. Therefore, we offered the slugs leaf material of the different species and pretreatments (prior radiation conditions) at the same time and in the same containers. Since there is considerable evidence that herbivores, including slugs, are selective feeders and seldom consume plants simply in proportion to their abundance we considered the leaves to be independent and available for free choice by the slugs. We used ten plastic boxes with a 1-cm thick layer of moist soil, similar to those used for the decomposition experiment, to conduct the feeding preference experiment with slugs. In each box, leaves of the six plant species grown under the two UV-B treatments in the fen field plots were offered to slugs. In each box we placed three individuals of the slug species *Deroceras reticulatum* (each 20–30 mm long) collected from outside of the experimental plots in the fen ecosystem (i.e., ambient solar UV-B conditions). In these boxes, slugs had the opportunity to freely feed on any leaves from the six species and two UV-B radiation histories. In each box the same leaf area was offered from each of the six species and the two treatments. The leaf material remained in the feeding boxes throughout the duration of the experiment (31 days). We covered the boxes with a fine mesh to prevent escape of the slugs and invasion of other animals that could feed on the plant material. All ten boxes were placed next to the decomposition boxes in the understory of *Nothofagus* trees at our field site in order to avoid exposure to direct sunlight, which might influence the activity of the slugs.

Feeding activity of the slugs was usually monitored every second day from January 12 until February 12, 1999 by measuring the leaf area consumed by the slugs using graph paper with millimeter gradation. In order to take species-specific differences in leaf thickness into account, leaf consumption is expressed as leaf dry mass for the different species and UV-B treatments. This was calculated by dividing the leaf area consumed by the mean SLA for a given species and UV-B treatment. Initial SLA values were used for calculating the masses consumed in the first half of the experiment and post-experiment SLA values for calculating the masses in the second half of the experiment. Diet selection of the slugs was expressed as the proportion of total leaf mass consumed for each of the species in the two UV-B treatments.

The experiment was terminated after one month since by then slugs had completely consumed leaves of one plant species (*Acaena magellanica*) and most of the slugs were in their reproductive stage and starting to age. We did not want the free choice of the slugs to be limited by not having foliage material from all species available. At the end of the experiment, slugs usually weighed less than at the beginning (0.73 ± 0.03 g start vs. 0.55 ± 0.03 g fresh mass end) mainly due to egg laying (on average seven eggs per box). Three slug individuals died early in the course of the experiment and were replaced by newly collected individuals.

Statistical analyses

To test UV-B effects on leaf quality and decomposition among species, we used two-way ANOVA with previous UV-B history and species as independent variables. Additionally, we used one-way ANOVA to identify UV-B effects on leaf quality parameters and decomposition for each individual species. The UV-B treatment effect on the cumulative leaf mass consumed by slugs at each measurement date was analyzed using repeated measures ANOVA (Sokal and Rohlf 1981). Diet selection of slugs relative to total biomass consumed was analyzed by using one-way ANOVA for each plant species. To assess the relationship between slug herbivory and leaf quality parameters and decomposition rates, we performed a stepwise multiple linear regression analysis (Sokal and Rohlf 1981) regressing the total leaf mass consumed against the initial leaf N concentration, C/N ratio, SLA and percentage of dry mass remaining after decomposition. When necessary, data were log or arcsin transformed (e.g., percentage values) prior to statistical analyses to conform with assumptions of normality (Zar 1996). All statistical analyses were performed using SYSTAT (version 5.2.1. for Macintosh, Wilkinson et al. (1992)).

Results

Although leaf N, C/N and SLA values varied significantly among the six species (species difference for

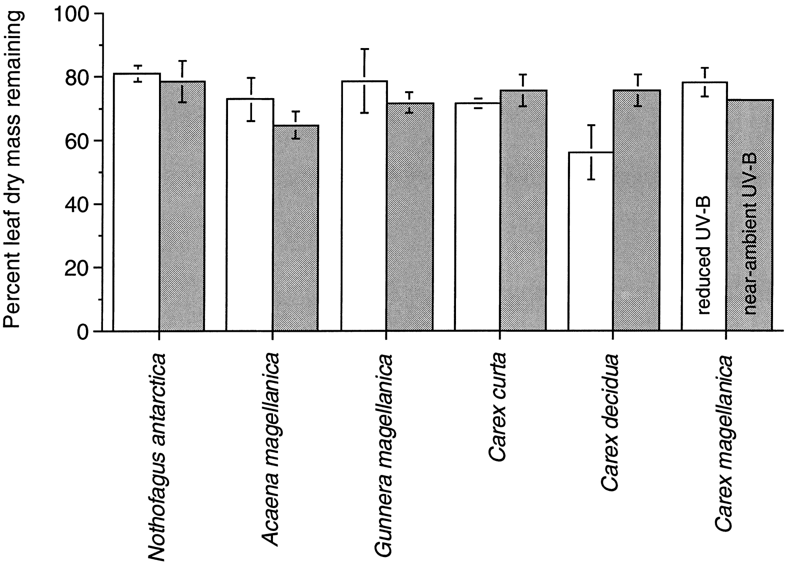

Figure 1. Decomposition of leaves expressed in percent dry mass remaining at the end of the experiment relative to the dry mass present at the start of the experiment from plants which had been grown under either reduced or near-ambient UV-B radiation in a *Carex* fen ecosystem in Tierra del Fuego, Argentina. Mean ± SE (n = 10).

Table 1. Leaf nitrogen concentration, leaf carbon: nitrogen ratio and, specific leaf area of plants grown under either reduced or near-ambient (near amb.) UV-B radiation in a *Carex* fen ecosystem in Tierra del Fuego, Argentina. Mean ± SE (n = 10).

	Nitrogen conc. (mg/g)		Carbon: nitrogen ratio		Specific leaf area (cm^2/g)	
	reduced UV-B	near amb. UV-B	reduced UV-B	near amb. UV-B	reduced UV-B	near amb. UV-B
Nothofagus antarctica	1.32 ± 0.23	1.55 ± 0.22	44.53 ± 4.07	35.23 ± 5.91	118.49 ± 6.21	99.84 ± 8.55
Acaena magellanica	1.44 ± 0.10	1.50 ± 0.12	31.22 ± 2.36	29.98 ± 2.71	99.17 ± 6.20	85.74 ± 8.10
Gunnera magellanica	2.38 ± 0.11	2.28 ± 0.12	18.92 ± 0.84	19.78 ± 0.97	104.49 ± 11.01	94.33 ± 4.01
Carex curta	1.05 ± 0.06	1.09 ± 0.10	44.61 ± 4.40	43.71 ± 2.48	134.85 ± 9.75	135.78 ± 7.47
Carex decidua	1.40 ± 0.08	1.24 ± 0.07	34.89 ± 2.38	38.69 ± 2.07	73.59 ± 9.47	60.39 ± 8.76
Carex magellanica	1.64 ± 0.29	1.65 ± 0.19	34.22 ± 5.65	31.00 ± 4.23	90.53 ± 5.02	90.37 ± 7.37

Note: ANOVAs showed no significant UV-B or UV-B × species effects. Across UV-B levels N, C/N and SLA were significantly different among species.

all three parameters: $P < 0.001$, Table 1), these leaf quality characteristics did not differ between the UV-B treatments (Table 1). Similarly, decomposition rates for leaves of individual species were not affected by UV-B treatment, but varied significantly among species across UV-B treatments (mean levels ranged from 80% mass remaining for *Nothofagus* to 70% mass remaining for *Acaena*, species difference: $P = 0.071$, Figure 1).

Slugs began to consume measurable amounts of leaf material three to eight days after initiation of the experiment (Figure 2). For two of the species there were large differences in consumption as a result of the prior UV-B exposure. Over the course of the experiment, slugs consumed only one-third the leaf mass of *Nothofagus* that had been grown under near-ambient UV-B radiation than of leaves grown at reduced UV-B ($P = 0.069$, Figure 2). In contrast, leaves of *Carex decidua* that had been grown at near-ambient UV-B were consumed twice as much as leaves grown under reduced UV-B radiation ($P = 0.088$, Figure 2). Consumption of foliage for the other species was not influenced by prior UV-B radiation exposure (Figure 2). Also, consumption during the first week of the feeding experiment when leaf material was still rather fresh was not affected by prior UV-B radiation (data not shown). Daily rates of leaf area consumption fluctuated over the measurement period but ex-

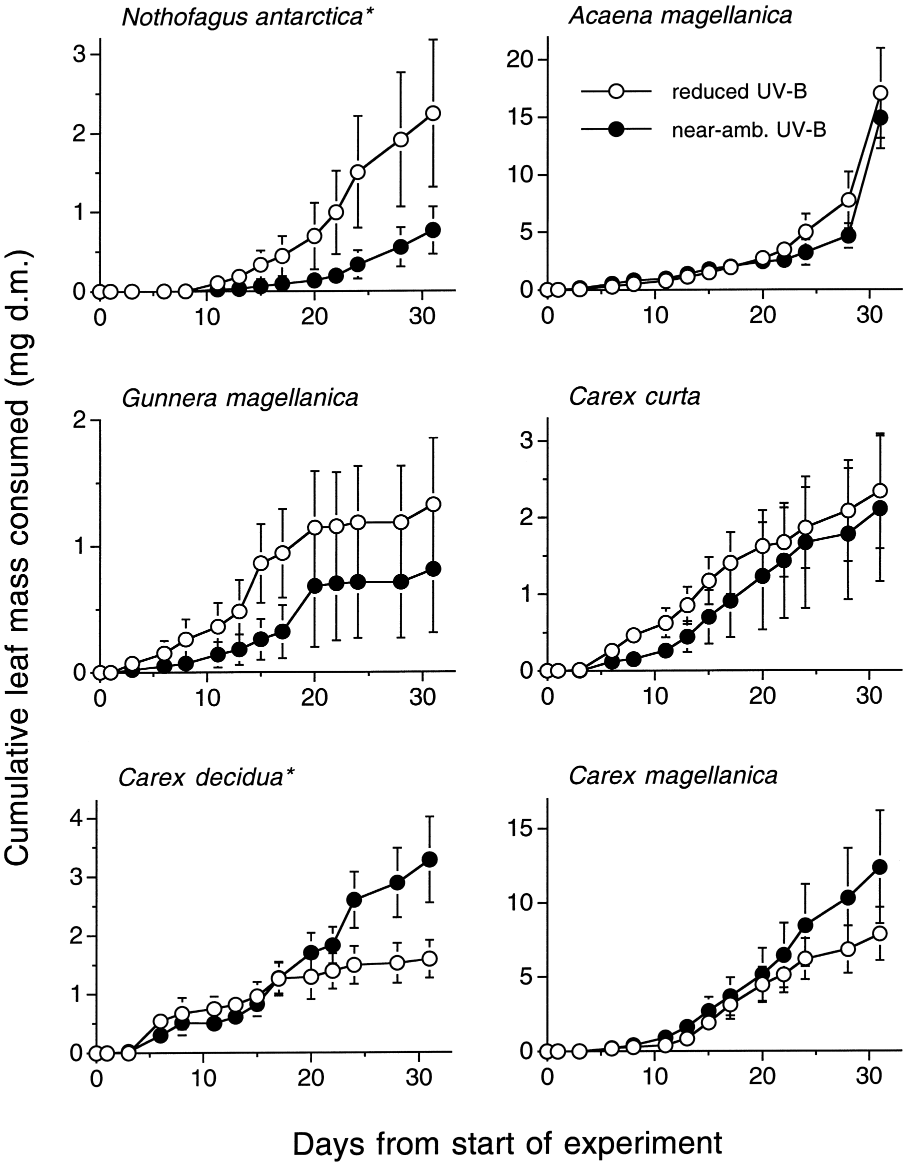

Figure 2. Cumulative leaf mass consumption by slugs feeding on plants which had been grown under either reduced or near-ambient UV-B radiation in a *Carex* fen ecosystem in Tierra del Fuego, Argentina. An asterisk behind the species name denotes differences in cumulative consumption derived from repeated measurement ANOVAs ($P < 0.09$). Mean ± SE (n = 10).

hibited similar patterns for plants previously grown under the two different UV-B radiation conditions; daily consumption rates tended to increase during the experiment (data not shown).

Additionally, diet selection by slugs was significantly altered by the previous UV-B radiation conditions under which the plants had been grown. Relative to the total leaf mass consumed for all six species, *Nothofagus* leaves were consumed to a lesser extent ($P = 0.067$) and *Carex decidua* to a greater degree ($P = 0.057$) when plants had been grown under near-ambient UV-B than when they had been grown under reduced UV-B radiation (Figure 3).

Consumption of foliage material by slugs was not significantly related to any single characteristic of the leaf quality parameters chosen for this study. In trying to explain the pattern of total leaf mass consumed by slugs, no single leaf quality parameter served as a significant predictor. However, when species leaf N, C, C/N, SLA and percentage of mass remaining were

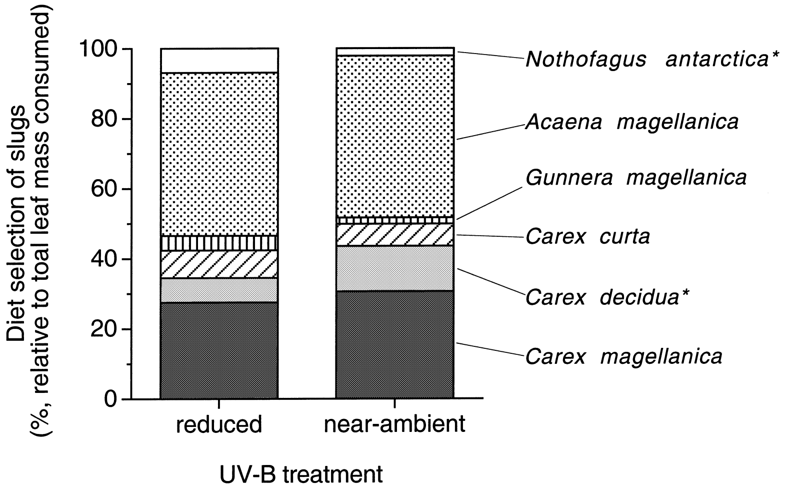

Figure 3. Diet selection of slugs for plant species grown under reduced or near-ambient UV-B conditions in a *Carex* fen ecosystem in Tierra del Fuego, Argentina. An asterisk behind the species name denotes differences in percentage consumption between UV-B treatments ($P < 0.07$). Mean (n = 10).

combined as predictors for the total leaf mass consumed in a multiple regression analysis we could explain more than 70% of the variation ($r^2 = 0.731$, $P = 0.091$). UV-B did not influence these relationships (data not shown).

Discussion

Our results showed that slugs that inhabit these fen ecosystems consumed significantly greater amounts of Southern beech (*Nothofagus antarctica*) foliage which had been grown under reduced UV-B radiation than of foliage grown under near-ambient UV-B (Figure 2). In contrast, leaves of *Carex decidua* grown under reduced UV-B were significantly less consumed than leaves grown under near-ambient UV-B (Figure 2). For both species, this UV-B-induced difference in leaf consumption by slugs became more pronounced towards the end of the experiment. One explanation of this increased food consumption later in the experiment might be due to the greater body size of the slugs and requirements for egg production. Also, later in the experiment as the season progressed, mean air temperatures were lower and these conditions are generally more favorable for the slugs. Furthermore, during the course of the experiment, the progressive decay of the foliage may have facilitated consumption by the slugs.

For the leaf quality parameters chosen, we were not able to detect UV-B-treatment effects for *Nothofagus* and *Carex decidua* apart from the hint ($P = 0.111$) of thicker leaves of *Nothofagus* and thinner leaves of *C. decidua* ($P = 0.085$) grown under near-ambient UV-B. However, other unmeasured indices of leaf quality may have shown distinct differences as it is clear that the UV-B treatment influence was mediated through changes in the foliage, rather than direct UV-B effects on the slugs. Certain slug species have been shown to be affected in their feeding by chemical deterrents in plant tissues such as terpenoids, lignin, tannins and phenolics (Harborne 1988). Gehrke et al. (1995) were not able to detect changes in lignins or tannins when they exposed vegetation to supplemental UV-B in a subarctic environment. However, in various studies, UV-B has been shown to affect several other characteristics of foliage that might play roles in the feeding preference of slugs, including increased epicuticular wax production (Steinmüller and Tevini 1985; Gordon et al. 1998), increased leaf hair density (McCloud and Berenbaum 2000) and singlet oxygen production (Berenbaum and Larson 1988). There is also the possibility that the total amount of secondary chemicals might remain unaffected by UV-B radiation but that UV-B could cause changes in the distribution of these substances within plant tissues such accumulation of phenolics in the upper epidermal cell layers (Robberecht and Caldwell 1978; Schmelzer et al. 1988; Grammatikopoulos et al. 1998) which could conceivably alter herbivory patterns. An earlier herbivory experiment in Tierra del Fuego with Lepidoptera larvae and a native herb species, *Gunnera magellanica*, also showed that manipulating ambient solar UV-B radiation in a manner similar to our experiments resulted in sizeable differences in feeding. Leaves grown at reduced UV-B exhibited considerably more lesions from feeding than those grown under near-ambient UV-B (Rousseaux et al. 1998).

Since slugs feed on dead as well as living plant materials, the decomposition rate of leaves may be an important influence on the feeding behavior of slugs. While decomposition rates in our study varied greatly among species, they were apparently unaffected by the prior UV-B exposure. Had the decomposition trials been allowed to continue for a longer period of time, UV-B treatment effects may have become apparent similar to what has been found in some other UV-B radiation experiments (Rozema et al. (1997) and Gehrke et al. (1995); but see Findlay et al. (1996)). However, in those experiments, direct effects of UV-B radiation on fungal decomposer organisms also contributed to the UV-B effects on decomposition rates (Newsham et al. 1997). In our study, the decomposition trials were conducted in the understory of trees where solar UV-B radiation would be very low (e.g., Brown et al. (1994) and Flint and Caldwell (1998)). Thus, any possible effects of UV-B treatment on decomposition in our study would be indirect, mediated by changes in the foliage.

We also observed significant differences in the relative diet selection resulting from the prior UV-B treatments. When a mixture of foliage from the six species was offered to the slugs, they consumed less leaf material of *Nothofagus* and more of *Carex decidua* if the foliage had been previously exposed to near-ambient UV-B radiation compared with foliage exposed to reduced UV-B. The sedge constitutes as much as half of the aboveground biomass of our experimental area (J.G. Zaller, unpublished data), thus, changes in consumption of this species may have important implications for the plant community, the slug populations and detritus turnover in the system. For very small seedlings of *Nothofagus*, reduced consumption of living foliage by slugs might enhance tree seedling growth and establishment.

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