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# Solar UV-B radiation affects leaf quality and insect herbivory in the southern beech tree *Nothofagus antarctica*

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**Abstract** We examined the effects of solar ultraviolet-B (UV-B) radiation on plant-insect interactions in Tierra del Fuego (55°S), Argentina, an area strongly affected by ozone depletion because of its proximity to Antarctica. Solar UV-B under *Nothofagus antarctica* branches was manipulated using a polyester plastic film to attenuate UV-B (uvb−) and an Aclar film to provide near-ambient UV-B (uvb+). The plastic films were placed on both north-facing (i.e., high solar radiation in the Southern Hemisphere) and south-facing branches. Insects consumed 40% less leaf area from north- than from south-facing branches, and at least 30% less area from uvb+ branches than from uvb− branches. The reduced herbivory on leaves from uvb+ branches occurred for both branch orientations. Leaf mass per area increased and relative water content decreased on north- versus south-facing branches, while no differences were apparent between the UV-B treatments. Solar UV-B did lead to lower gallic acid concentration and higher flavonoid aglycone concentration in uvb+ leaves relative to uvb− leaves. Both the flavonoid aglycone and quercetin-3-arabinopyranoside were higher on north-facing branches. In laboratory preference experiments, larvae of the dominant insect in the natural community, Geometridae "Brown" (Lepidoptera), consumed less area from field-grown uvb+ leaves than from uvb− leaves in 1996–97, but not in 1997–98. Correlation analyses suggested that the reduction in insect herbivory in the field under solar UV-B may be mediated in part by the UV-B effects on gallic acid and flavonoid aglycone.

**Keywords** Flavonoids · Gallic acid · Herbivory · *Nothofagus* · Ozone depletion

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## Introduction

Ultraviolet-B radiation (UV-B; 280–315 nm) is increasing throughout the spring and summer over southernmost Argentina due to stratospheric ozone depletion (Frederick et al. 1994; Rousseaux et al. 1999, 2001). This region experiences both the passage of the Antarctic 'ozone hole' several times each spring and the general depletion of the ozone layer in the Southern Hemisphere. Studies in the terrestrial ecosystems of Tierra del Fuego, Argentina, have indicated mostly modest effects of solar UV-B on plant growth (see review by Ballaré et al. 2001). However, changes in solar UV-B may lead to larger effects on plant-insect interactions (Caldwell et al. 1999, 2003; Ballaré et al. 2001). For example, leaf area of the perennial herb *Gunnera magellanica* only decreased by 12% due to solar UV-B in manipulative experiments, whereas the leaf area removed by insects (primarily Lepidopteran larvae) decreased by 75% (Rousseaux et al. 2001).

Solar UV-B can affect insect herbivores in various ways. Thrips in field soybean canopies appeared to detect solar UV-B even in full sunlight and to subsequently avoid UV-B exposure (Mazza et al. 1999, 2002). What is more, the thrips consumed less leaf tissue and Lepidopteran larvae had lower survivorship in laboratory assays when presented with leaves that had been grown in the field under near-ambient solar UV-B compared to leaves from UV-B exclusion plots (Mazza et al. 1999; Zavala et al. 2001). The lower caterpillar survivorship was likely related to the higher levels of soluble phenolics and lower lignin content in the foliage receiving solar UV-B. In Tierra del Fuego, greater nitrogen concentration in *G. magellanica* leaves receiving solar UV-B appeared to at least partially explain the decrease in herbivory by Lepidopteran larvae under solar UV-B radiation (Rousseaux et al. 1998). No changes in other measured parameters including soluble phenolics, hemicellulose, leaf mass per area, and relative water content were found.

Foliar UV-B-absorbing compounds include phenolics such as flavonoids, which may play important roles as either deterrents or attractants of insect herbivores (Harborne 1988). These compounds commonly respond to changes in UV-B radiation such as the increase in solar UV-B that occurs with ozone depletion (Searles et al. 2001). For example, the foliar content of several phenolics increased in silver birch seedlings (*Betula pendula*) over a wide range of UV-B doses in growth chamber and glasshouse experiments in Finland (Lavola et al. 1998; De la Rosa et al. 2001). An increase in Lepidoteran larval feeding occurred on the silver birch leaves that had been grown under UV-B, although direct involvement of specific phenolics could not be determined (Lavola et al. 1998). In contrast, increases in soluble phenolics in soybean due to solar UV-B were correlated with a decrease in herbivory as mentioned earlier (Zavala et al. 2001). These differing results indicate the potential complexity of insect herbivory responses to UV-B radiation. Effects of UV-B radiation on other secondary compounds, such as cyanogens (Lindroth et al. 2000), may also influence herbivory.

The primary aims of this study with the southern beech tree *Nothofagus antarctica* were to: (1) assess solar UV-B effects on insect herbivory by manipulating solar UV-B at the branch level using plastic filters; and (2) investigate whether the influence of UV-B on insect herbivory could be attributed to indirect effects mediated through changes in leaf quality, particularly phenolic compounds.

## Materials and methods

### Experimental site

Experiments were carried out at the experimental fields of the Centro Austral de Investigaciones Científicas (CADIC) near Ushuaia, Argentina (54°S, 68°W), and in the Parque Nacional Tierra del Fuego 20 km to the west of CADIC. Mean annual temperature is 5.5°C, and mean annual precipitation is 524 mm with precipitation distributed fairly evenly throughout the year (FAO 1985). The natural vegetation in the area is predominately deciduous forest composed of two southern beech tree species, *Nothofagus pumilio* and *N. antarctica* (Moore 1983). Bud break starts in October (early spring) and leaf expansion, to about 1.5 cm in length, is completed by mid-December (early summer). Leaf senescence starts as early as mid-February (late summer).

Most of the herbivory at our sites is caused by moth larvae (Lepidoptera: Geometridae). Identification to the species level has not been possible due to limited knowledge about the phytophagous insects of this region (McQuillan 1993; Spagarino et al. 2001). However, several aspects of the ecology of the caterpillars have been documented in our field observations. The larvae of one lepidopteran species (Geometridae "Brown") camouflage as a small twig, whereas the larvae of another species camouflage as a leaf (Geometridae "Green"). These larvae display solitary behavior, are mostly nocturnal in their feeding, move between branches, and rest primarily on *Nothofagus* branches not exposed to direct sunlight during the day. Other herbivores include coleopteran larvae (Coleoptera: Chrysomelidae) and adult specimens of a leaf beetle (Coleoptera: Curculionidae).

Field studies were performed at the CADIC experimental station. Leaves for feeding preference experiments in the laboratory were collected from *N. antarctica* trees at the Parque Nacional Tierra del Fuego. Ten trees were used at each site. The trees were 3–4 m tall, spaced at least 5 m apart, and were naturally growing in grass- or shrub-dominated communities. Measurements of solar UV-B and photosynthetic photon flux density (PPFD) were made above north- and south-facing branches and in the open under clear-sky and cloudy conditions using a broadband UV-B sensor (YMT, Interscience Technologies, Silver Spring, Md., USA) and a quantum sensor (LiCor, Lincoln, Neb., USA), respectively. The midday leaf temperature was also measured on a sunny day during the summer on north- and south-facing branches of each tree using an infrared thermometer (Instatherm 14–220D, Barnes Engineering, Stanford, Calif.).

### Branch orientation field experiment

In the 1996–97 field season, insect herbivory was assessed on north- and south-facing branches of ten trees. The measurements were conducted in late summer using the distal portion (0.40 m long) of three branches (at breast height) for each branch orientation. The number of lesions per leaf from leaf mining and chewing insects was used as our measure of herbivory intensity. Each of the ten trees was considered to be an experimental block.

### Solar UV-B attenuation field experiment

A manipulative experiment was carried out during the 1998–1999 growing season to test whether differences in herbivory between north- and south-facing branches could be explained by differences in UV-B irradiances. To create different UV-B levels, plastic filters that are either mostly transparent or opaque to UV-B were placed over branches before bud-break at the beginning of the growing season (mid-October). Clear 38 μm Aclar plastic film (Honeywell, formerly Allied Signal, Pottsville, Pa., USA) was used to obtain the near-ambient UV-B (uvb+) environment. Clear 50 μm Mylar-D film (Dupont, Wilmington, Del., USA) was used to attenuate solar UV-B (uvb−). The transmittance of both filters is similar at longer UV and visible wavelengths (Searles et al. 2002). The filters (25×35 cm in size) were maintained 10 cm above the upper side of each branch using a chicken wire mesh frame. No filter was used on the lower side of the branch to allow adequate ventilation. We are using the term attenuation rather than exclusion for the uvb− treatment because the lower side of the branches received some solar UV-B that reflected from vegetation and the ground surface (i.e., <10% of ambient solar UV-B).

The wire frames and accompanying filters were placed on north- and south-facing branches following a split-plot design. One Aclar and one Mylar branch filter was employed for each of the two azimuth directions (i.e., a total of four filters per tree). The branches were harvested at the end of January after 3 months of UV-B manipulation. The leaves of each branch were removed and mounted between two layers of transparent tape. Leaf area per branch was then measured by passing the leaves on the tape through an area-meter (LI-3100, Li-Cor, Lincoln, Neb.). The leaf area removed by the insects was darkened on the transparent tape using a permanent black marker, and the total leaf area was measured again to calculate the leaf area removed by the insects.

### Feeding preference experiments

To test whether differences in herbivory were related to leaf characteristics, we carried out a series of feeding preference (choice) experiments in the laboratory. During the 1996–1997 growing season, leaves of *N. antarctica* were grown under uvb+ or uvb− filters on north-facing branches in the Parque Nacional Tierra del Fuego. In 1997–98, the UV-B filters were placed on both north- and south-facing branches using a split-plot design similar to the solar UV-B attenuation experiment. The UV-B treatments in both growing seasons were started before bud-break. After 3 months of treatment, twigs were collected from the branches and offered to larvae in a UV-B free environment in the laboratory. The insect larvae were collected at breast height from *N. antarctica* and *N. pumilio* at our two field sites or from the nearby forest. The larvae of each species used in the experimental trials were not all of the same instar because it was not possible to collect enough larvae in the field. The trials started 48 h after collecting the larvae.

The experimental trials were conducted for 48 h in plastic feeding boxes (15×10×5 cm) on a laboratory bench at CADIC. Five boxes per larvae species were used in each trial with 14 trials in 1996–97 and 17 in 1997–98. The leaf area consumed in the five boxes for each insect species was pooled together, and 'feeding trial' was considered as the experimental unit in subsequent analyses.

Each feeding box contained 16 small twigs (4 cm long) for a total of approximately 150 fully expanded leaves per box. Freshly collected twigs from the various field treatments were intermixed and the larvae of a given species were placed randomly on the twigs. An average of 12 larvae was used per trial. The air temperature was 20°C and dim room light was provided 12 h per day. High humidity levels were maintained by covering the bottom of the boxes with blotting paper saturated by water. Leaf consumption was measured using a leaf area meter and expressed as the total leaf area removed during each feeding trial.

### Leaf characteristics

Leaves were collected simultaneously with the field measurements of herbivory to perform leaf analyses of relative water content (RWC), leaf mass per area (LMA), and phenolic compounds. Leaves were also sampled from the twigs used in the laboratory feeding preference experiments. The RWC and LMA were calculated as: RWC = (fresh mass−dry mass) / (water saturated mass−dry mass) and LMA = (dry mass / leaf area), using five leaf disks per branch. Crude UV-B-absorbing phenolic compounds were measured after extracting five fresh leaf disks in methanol (99%): 1 *N* HCl (1%) for at least 48 h at −20°C (Beggs and Wellmann 1985). Absorbance was measured at 305 nm with a spectrophotometer.

In addition to the crude phenolic leaf extracts, individual leaf phenolic compounds were characterized by high performance liquid chromatography (HPLC) for the various treatments of the solar UV-B attenuation experiment. The samples were collected in December 1998 (i.e., late spring) to coincide with the high daily UV-B levels of the approaching summer solstice (21 December). This sampling was also done before most of the insect herbivory for the growing season occurred to better assess UV-B effects on phenolic compounds rather than the induction of phenolics by herbivory. The plant material was air dried at room temperature, extracted with methanol, and analyzed by HPLC (Julkunen-Tiitto et al. 1996). The identification of secondary compounds was based on their retention time and spectral data (monitored at 220 nm, 270 nm and 360 nm), and quantification used commercial standards. Compounds identified by HPLC included: quercetin-3-arabinopyranoside, quercetin-3-arabinofuranoside and myricetin-3-arabinoside; a flavonoid glycoside; flavonoid aglycones 1 and 2; catechin; gallocatechin and hydrolysable tannin precursors or tannins (gallic acid, digalloylglucose, trigalloylglucose, tetragalloylglucose, pentagalloylglucose).

### Statistical analyses

Standard analyses of variance were performed in SAS (SAS, Cary, N.C., USA) for both the field and laboratory experiments. Non-parametric Freidman tests were employed for two phenolic compounds, quercetin-3-arabinofuranoside and flavonoid aglycone 1, in the solar UV-B attenuation experiment (1998–99) since the data were not normal even when transformed. Additionally, correlation coefficients ($r$) were calculated in the attenuation experiment to assess the relationship between leaf characteristics (i.e., phenolic compounds, leaf mass per area) and the % leaf area consumed. The correlations either included all data values ($n$ =40; 2 UV-B treatments ×2 orientations ×10 trees), or north- and south-facing branches were pooled by UV-B level ($n$ =20; uvb+ or uvb− ×2 orientations ×10 trees) to assess the role of the UV-B treatments.

## Results

### Solar microenvironment

North-facing *N. antarctica* branches received more UV-B and PPFD than south-facing branches (as expected in the Southern Hemisphere) based on ratios of irradiance above the branch to irradiance in the open (Fig. 1). The north versus south differences in PPFD were much greater on clear, sunny days than on cloudy days, whereas the differences in UV-B exposure were less affected by cloudiness. The midday leaf temperature on a sunny day also varied with branch orientation during the summer (13.5±0.6°C north vs 10.7±0.5°C south; $P$ <0.05).

### Branch orientation and UV-B attenuation

During the initial branch orientation experiment (1996–97), the number of leaf lesions caused by phytophagous insects in the *N. antarctica* trees was 43% less on north-facing branches than on south-facing branches when exposed to ambient solar UV-B (Fig. 2). Similarly, the leaf area removed was 39% lower on north-facing branches receiving near-ambient UV-B (Nuvb+) than in south-facing branches receiving near-ambient UV-B (Suvb+) during the solar attenuation experiment (1998–99) (Fig. 3). In both the branch orientation and solar UV-B attenuation experiment, leaf mass per area was consistently higher in leaves from north-facing branches (Table 1). Relative water content (%) was lower in leaves of north-facing (51.9±0.05) than of south-facing branches

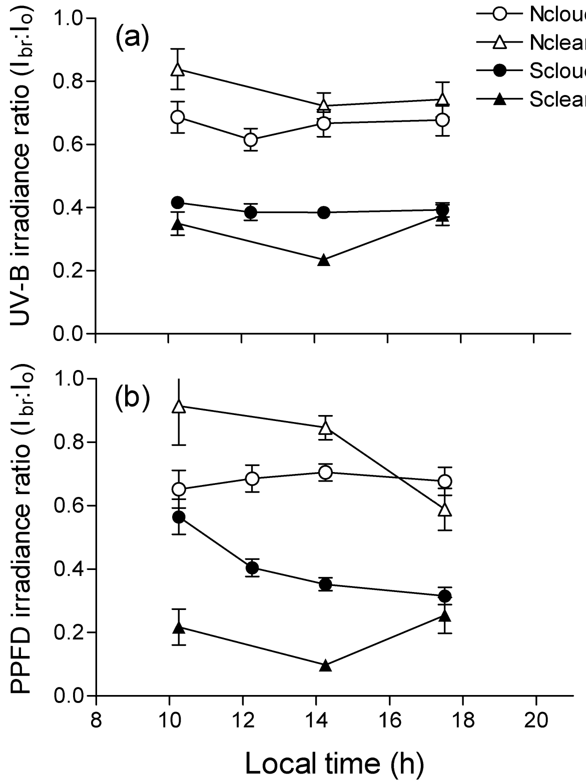


**Fig. 1** The ratio of irradiance above the branch ($I_{br}$ ) to irradiance in the open ($I_o$ ) for north- and south-facing branches of *Nothofagus antarctica* trees. Irradiance ratios are given for **a** ultraviolet-B (UV-B) radiation and **b** photosynthetic photon flux density (PPFD) under clear-sky and cloudy conditions. Values represent the mean ($n$ =10) ± SE

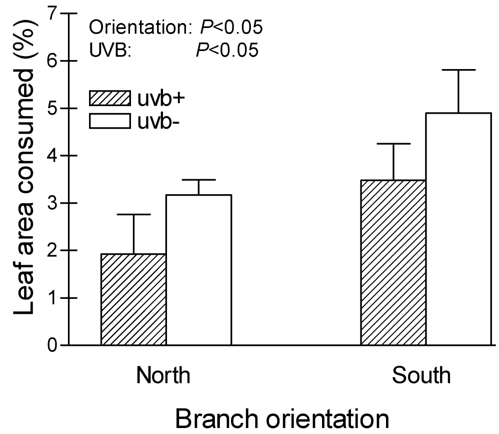


**Fig. 3** Percentage of leaf area consumed by insects on north- and south-facing *N. antarctica* branches under near-ambient (uvb+) or attenuated UV-B (uvb−) radiation. Data are from the solar UV-B attenuation experiment (1998–99). Plastic filters were used to obtain the near-ambient and attenuated UV-B levels. Values represent the mean ($n$ =10) ± SE

(54.5±1.0) in the branch orientation experiment. No measurements of RWC were conducted in the solar UV-B attenuation experiment. Crude UV-B-absorbing phenolics were not affected by branch orientation in either experiment (Table 1).

In the solar UV-B attenuation experiment, the leaf area removed by herbivores from both north- and south-facing branches was at least 30% less under the near-ambient UV-B filters than under the attenuation filters (Fig. 3). No significant effects of solar UV-B on crude UV-B-absorbing phenolics or LMA were apparent (Table 1). Thus, UV-B significantly affected not only the leaf area consumed by insects, but leaf mass consumed as well (i.e., 32.2±8.2 mg per branch for uvb+ and 56.9±9.1 mg per branch for uvb− when data are pooled by UV-B treatment). Leaf mass consumption was not statistically different in north- versus south-facing branches.

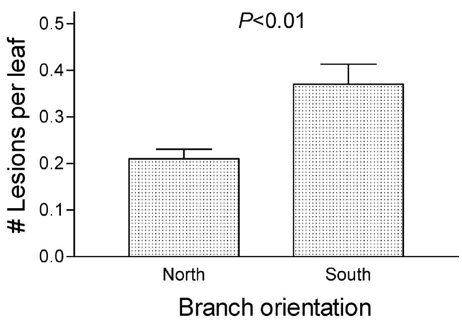


**Fig. 2** Number of insect lesions per leaf on north- and south-facing branches of *N. antarctica* trees under ambient UV-B radiation. Data are from the branch orientation experiment (1996–97). Counts were made on all leaves of each sampled branch at the end of the growing season. There were no less than 170 leaves per branch. Values represent the mean ($n$ =10) ± SE

## Individual phenolic compounds and herbivory

In the solar UV-B attenuation experiment, leaves that developed under near-ambient UV-B had a lower concentration of gallic acid ($P$ <0.01; Fig. 4a) and of some other related compounds including digalloylglucose, trigalloylglucose, and tetragalloylglucose ($P$ <0.05; data not shown). Pentagalloylglucose did not appear to be affected by the UV-B treatment (Fig. 4b). Only the concentration of flavonoid aglycone 1 was significantly higher under near-ambient UV-B ($P$ <0.05; Fig. 4c). Flavonoid aglycone 1 was also higher for leaves of north- versus south-facing branches ($P$ <0.01) as was quercetin-3-arabinopyranoside ($P$ <0.05; Fig. 4d).

Gallic acid was positively correlated with leaf area consumed ($P$ <0.01) when all data values were considered independent of UV-B treatment and branch orientation. Additionally, this correlation was somewhat greater under attenuated UV-B than under near-ambient UV-B conditions. In contrast, both flavonoid aglycone 1 and LMA were negatively correlated with leaf area consumed ($P$ <0.05; Table 2). Within the same leaves, a strong negative correlation between gallic acid and flavonoid aglycone 1 was not apparent (data not shown).

**Table 1** Leaf mass per area (LMA) and crude leaf phenolic compounds of north- and south-facing *Nothofagus antarctica* branches under ambient, near-ambient, or attenuated UV-B radiation. Plastic filters were used to obtain the near-ambient and attenuated UV-B levels in the solar UV-B attenuation experiment (1998–99). No filters were used in the earlier branch orientation experiment (1996–97). Units are on a dry mass basis, and absorbance (*Abs.*) is for a 1-ml extract. Values represent the mean ($n$=10) ± SE. Different letters indicate statistically significant differences ($P$<0.05) between treatments for a given experiment

| Experiment | Orientation | UV-B | LMA (g $m^{-2}$) | Crude UV-B phenolics (Abs. at 305 nm $mg^{-1}$) |
|---|---|---|---|---|
| Branch orientation | North | Ambient | 58.7±1.4 a | 7.03±0.54 a |
| | South | Ambient | 47.9±0.2 b | 5.76±0.99 a |
| Solar UV-B attenuation | North | Near-ambient | 49.8±1.8 a | 5.47±0.40 a |
| | North | Attenuated | 50.0±1.4 a | 5.13±0.40 a |
| | South | Near-ambient | 44.3±2.6 b | 5.45±0.38 a |
| | South | Attenuated | 45.8±1.2 b | 5.92±0.56 a |

Feeding preference experiments

Choice bioassays were performed in the laboratory to more directly assess the role of leaf quality on herbivory. During 1996–97, leaf area consumption by Geometridae (Brown) larvae was 21% lower for leaves grown in the field under near-ambient UV-B filters than for leaves grown under solar UV-B attenuation filters ($P$<0.05; Fig. 5a). In contrast, leaf area consumed by Chrysomelidae larvae and Geometridae (Green) larvae in the choice bioassays was not affected by the UV-B conditions during leaf growth (Fig. 5a). Geometridae (Brown) represented about 60% of the larval community in the trees at our field site and the surrounding forest during 1996–97. No significant UV-B effect on LMA or crude UV-B-absorbing phenolics was apparent for foliage collected for the choice bioassays (data not shown).

During 1997–98, leaves were collected from under the UV-B filters in the field on both north- and south-facing branches. In laboratory choice bioassays with this leaf material, leaf area consumed by Geometridae (Brown) and Chrysomelidae from south-facing branches was slightly greater than from north-facing branches ($P$ =0.07; Fig. 5b). No differences in herbivory were apparent when expressed on a leaf mass basis. Leaves from north-facing branches had a higher LMA (54.4±1.4, north; 50.5±2, south) and lower % RWC (53.7±2, north; 57.8±1.5, south) than leaves from south-facing branches. In contrast to the 1996–97 feeding experiment, UV-B conditions during leaf growth did not affect the leaf area consumed by any of the insect larvae during 1997–98 (Fig. 5b). Geometridae (Brown) represented only 24% of total larvae in 1997–98.

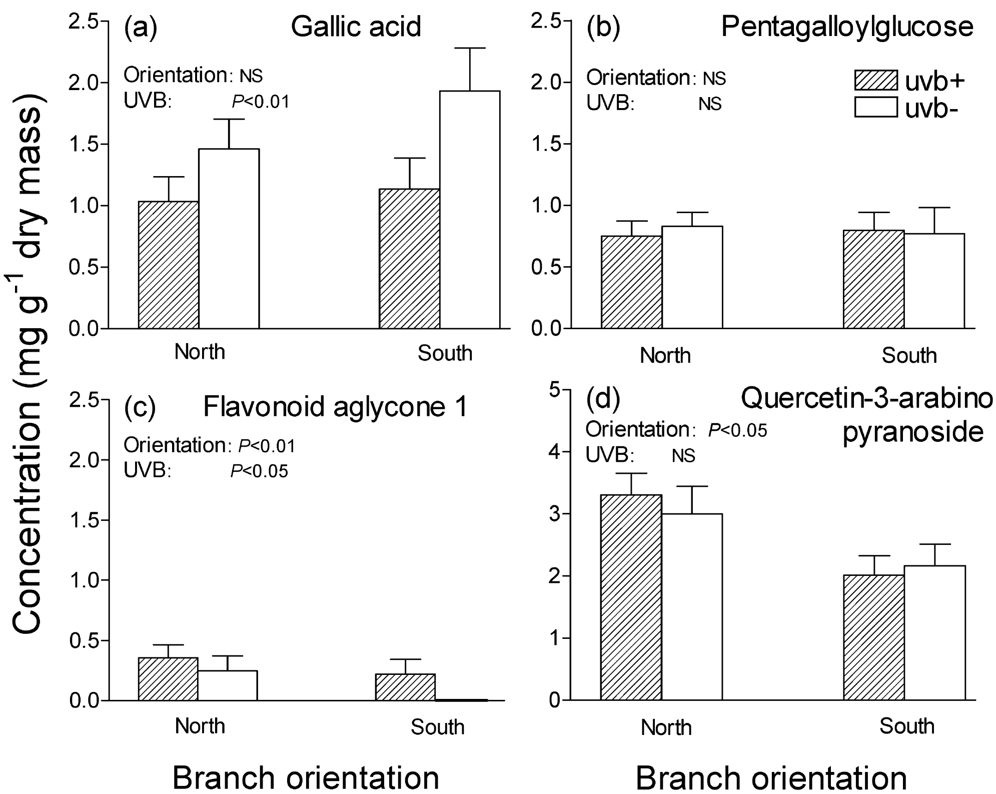


**Fig. 4** Leaf concentration of **a** gallic acid, **b** pentagalloylglucose, **c** flavonoid aglycone 1, and **d** quercetin-3-arabinopyranoside from north- and south-facing *N. antarctica* branches under near-ambient solar UV-B (uvb+) or attenuated UV-B (uvb −) radiation. Data are from the solar UV-B attenuation experiment (1998–99). Plastic filters were used to obtain the near-ambient and attenuated UV-B levels. Values represent the mean ($n$ =10) ± SE. Flavonoid aglycone 1 was not detected in south facing, uvb− leaves

**Table 2** Correlation coefficients between some leaf characteristics and leaf area consumption of *Nothofagus antartica* by insects. *All data* represents all sample values regardless of treatment. Near-ambient UV-B values were pooled from north- and south-facing branches. Attenuated UV-B values were similarly pooled except for flavonoid aglycone 1, which was not detected in leaves of south-facing branches. ** $P$<0.01, *$P$<0.05

| Variable | Data used in correlation | | |
|---|---|---|---|
| | All data ($n$=40) | Near-ambient UV-B ($n$=20) | Attenuated UV-B ($n$=20) |
| Gallic acid | 0.47** | 0.35 | 0.50* |
| Flavonoid aglycone 1 | −0.33* | −0.28 | −0.25 |
| Leaf mass per area | −0.31* | −0.30 | −0.29 |

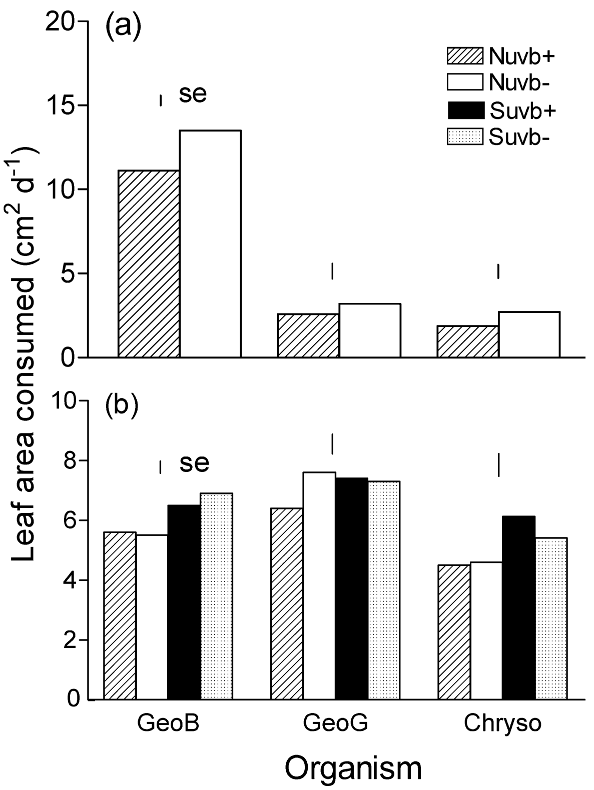


**Fig. 5** Leaf area of *N. antarctica* consumed by insects in laboratory feeding preference experiments. Leaves were collected from **a** under near-ambient solar UV-B (uvb+) and UV-B attenuation (uvb−) filters on north-facing branches (January 1997), or **b** under the filters on both north- and south-facing branches (January 1998). The results are given for the larvae of Geometridae "Brown" (*GeoB*), Geometridae "Green" (*GeoG*), and Chrysomelidae (*Chryso*). Five boxes were used per insect group in each experimental trial. The experimental trials were repeated 14 times ($n$=14) during January 1997 and 17 times ($n$=17) during January 1998

## Discussion

Our field experiments demonstrated that leaf area consumption of *N. antarctica* by phytophagous insects was much less on branches receiving more total solar radiation (i.e., north- vs south-facing branches) or more UV-B radiation (i.e., near-ambient vs attenuated UV-B). Less consumption is often found in sunny relative to shaded habitats (e.g., Louda et al. 1987; Mole and Waterman 1988; Dudt and Shure 1994). Similar to our findings, solar UV-B has led to decreased herbivory in several plant species in cultivated and natural communities in Argentina (Ballaré et al. 1996; Rousseaux et al. 1998, 2001; Mazza et al. 1999; Zavala et al. 2001; Izaguirre et al. 2003). In contrast, enhanced UV-B from supplemental lamps has led to increased insect herbivory in some cases including mountain birch (*Betula pubescens* ssp. *tortuosa*) in Sweden and cottonwood (*Populus trichocarpa*) in Washington State (USA) (Buck and Callaghan 1999; Warren et al. 2002). Opposing responses to enhanced UV-B were reported in the dwarf shrub *Vaccinium* with one species showing an increase in herbivory and another species a decrease (Gwynn-Jones et al. 1997).

Measurements of several physical and chemical leaf properties allowed us to assess some potential mechanisms of herbivore response. For the branch orientation experiment, north-facing branches had higher LMA and lower RWC than south-facing branches. These are common leaf responses to sunny environments (Björkman 1981). Leaf mass per area and leaf area consumption were negatively correlated in our study, and this may partially explain the reduced area consumption on north-facing branches. Leaves with higher LMA may be tougher (Choong 1996; Hanley and Lamont 2002), or insects may merely consume less leaf area due to the greater leaf mass per area. A statistically significant difference in leaf consumption was not observed on a mass basis although variation was high (37.1±6.9 mg per north-facing branch; 51.9 ±10.6 mg per south-facing branch). Our solar UV-B filtering experiments did not indicate any specific UV-B effects on LMA or RWC.

Effects of solar UV-B on herbivory were correlated with changes in individual secondary compounds, as seen in several other UV-B studies (e.g.; McCloud and Berenbaum 1994; Lavola et al. 1998; Lindroth et al. 2000). The concentration of flavonoid aglycone 1 was greater in leaves of north-facing branches and in leaves receiving a significant amount of solar UV-B (i.e., the near-ambient UV-B treatment). Flavonoid aglycones have been suggested to have antifeeding activity (Hedin and Waage 1986), and were indeed negatively correlated with leaf area consumed in our study. In contrast, gallic acid was lower under near-ambient solar UV-B and surprisingly had a strong positive correlation with leaf area consumed. A similar relationship between herbivory by *Epirrita autumnata* caterpillars on mountain birch (*Betula pubescens* ssp. *czerpanovii*) and gallotannins has been found in Finland (Kause et al. 1999; Lempa et al. 2000). These studies propose that because gallotannins have a high protein precipitation capacity, they lead to increased leaf consumption as a compensatory feeding behavior. It is not presently known if the decrease observed in gallic acid levels is a general response to solar UV-B. A range of responses to UV-B by individual phenolic compounds were recently reported in willow *(Salix myrsinifolia*) including decreases in some compounds (Tegelberg and Julkunen-Tiitto 2001).

Our laboratory, feeding preference experiments further examined the sensitivity of the insect community to indirect effects of UV-B. As expected, larvae of the most prevalent insect group during 1996–97, Geometridae (Brown), consumed less leaf material from leaves grown under near-ambient solar UV-B. Interestingly, no UV-B response was observed the second year. Geometridae (Brown) represented a much greater component of the insect community in 1996–97 (60%) than in 1997–98 (24%), and only an earlier, less active larval instar was available for collection from our field sites and neighboring forest in 1997–98 possibly due to cooler temperatures. Larvae of a Chrysomelidae species were the most common (58%) in 1997–98.

Direct effects of UV-B on insects can include reduced survivorship (Bothwell et al. 1994; McCloud and Berenbaum 1999), or behavioral changes such as UV-B avoidance (Mazza et al. 2002). The larvae of the Geometridae on *N. antarctica* are nocturnal and predominately found on the abaxial side of leaves during the day. Thus, direct effects of UV-B are likely less important than indirect effects similar to herbivory by nocturnal moth larvae on another Tierra del Fuego plant, *Gunnera magellanica* (Rousseaux et al. 1998, 2001). A preliminary laboratory experiment using UV-B lamps did not show any avoidance or attraction to UV-B over several hours (M. Cecilia Rousseaux, unpublished results).

A growing body of evidence suggests that UV-B affects plant-insect interactions in complex ways. In our study, the significant reduction in herbivory (i.e., ≥30%) on *N. antarctica* under solar UV-B was consistent with the results of our previous experiments with herbaceous species. The concomitant effects of solar UV-B on foliar gallic acid and flavonoid aglycone levels suggest that these phenolic compounds may play a functional role mediating UV-B effects on caterpillar feeding. Reductions in insect herbivory (Rousseaux et al. 1998, 2001, this study) under current UV-B conditions in Tierra del Fuego along with studies of plant growth and DNA damage, microbial population densities, and mycorrhizal infection rates (see review by Ballaré et al. 2001) all suggest that increased UV-B accompanying stratospheric ozone depletion has been of ecological importance at this site.

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