

Beneficial effects of solar UV-B radiation on soybean yield mediated by reduced insect herbivory under field conditions

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Ultraviolet-B radiation (UV-B: 280–315 nm) has damaging effects on cellular components and macromolecules. In plants, natural levels of UV-B can reduce leaf area expansion and growth, which can lead to reduced productivity and yield. UV-B can also have important effects on herbivorous insects. Owing to the successful implementation of the Montreal Protocol, current models predict that clear-sky levels of UV-B radiation will decline during this century in response to ozone recovery. However, because of climate change and changes in land use practices, future trends in UV doses are difficult to predict. In the experiments reported here, we used an exclusion approach to study the effects of solar UV-B radiation on soybean crops, which are extensively grown in many areas of the world that may be affected by future variations in UV-B radiation. In a first experiment, performed under normal management practices (which included chemical pest control), we found that natural levels of UV-B radiation reduced soybean yield. In a second experiment, where no pesticides were applied, we found that solar UV-B significantly reduced insect herbivory and, surprisingly, caused a concomitant increase in crop yield. Our data support the idea that UV-B effects on agroecosystems are the result of complex interactions involving multiple trophic levels. A better understanding of the mechanisms that mediate the anti-herbivore effect of UV-B radiation may be used to design crop varieties with improved adaptation to the cropping systems that are likely to prevail in the coming decades in response to agricultural intensification.

Introduction

Solar ultraviolet-B (UV-B: 290–315 nm) radiation is a narrow but important band of the solar spectrum reaching the biosphere. Since the discovery of the Antarctic ‘ozone hole’ and general depletion of the stratospheric ozone layer in the mid 1980s there has

been significant interest in documenting global trends in levels of UV-B radiation and the effects of UV-B on organisms and ecosystems (for reviews, see Ballaré et al. 2011, Hader et al. 2011, Zepp et al. 2011). Current projections predict a general recovery of stratospheric ozone in the next decades as a consequence of the successful implementation of the Montreal Protocol (McKenzie et al. 2011). However, several models predict reductions in cloud cover and increased aridity for

Abbreviations – UV-B, ultraviolet-B radiation; DAS, days after sowing; APx, ascorbate peroxidase; CAT, catalase; Amb_{UV}, ambient UV-B; MG, maturity group; Red_{UVB}, reduced UV-B.

low- to mid-latitudes, and increased cloudiness and precipitation at high latitudes in both hemispheres (IPCC 2007, Trenberth and Fasullo 2009, Ballaré et al. 2011). These alterations in cloud patterns associated with climate change could have strong effects on the levels of UV radiation, which could increase in tropical and subtropical regions and decrease at higher latitudes (Ballaré et al. 2011, McKenzie et al. 2011). In addition, the global trend for agricultural intensification, which commonly involves increased crop density and fertilization, can have strong impacts on the levels of UV-B radiation received by individual plants within the crop canopy, with consequences for plant function and plant–consumer interactions.

Solar UV-B radiation can affect organisms and modulate ecosystem processes. At the level of organisms, UV-B radiation has negative impacts on several biological processes, because UV-B quanta can disrupt important molecules such as proteins, lipids or nucleic acids, and lead to oxidative stress through the generation of reactive oxygen species (Strid et al. 1994, Jordan 2002, Caldwell et al. 2003). Direct effects of natural or enhanced levels of UV-B radiation on plant morphology, growth or yield have been detected under field conditions; however, in quantitative terms, these effects tend to be modest, with growth reductions rarely exceeding 20% (Searles et al. 2001, Newsham and Robinson 2009, Wargent et al. 2009, Ballaré et al. 2011). This limited impact reflects the activity of protective mechanisms, which include accumulation of UV-absorbing sunscreens (Robberecht and Caldwell 1978, Tevini et al. 1991, Li et al. 1993, Landry et al. 1995, Sheahan 1996, Mazza et al. 2000, Xu et al. 2008), activation of DNA-repairing enzymes (Landry et al. 1997, Giordano et al. 2004, Yoshihara et al. 2005) or production of enzymatic and non-enzymatic antioxidants (Malanga and Puntarulo 1995, Mazza et al. 1999a, Giordano et al. 2004). At the ecosystem level, direct effects of UV-B radiation on organisms could have consequences for ecological interactions (reviewed in Caldwell et al. 2003, Paul and Gwynn-Jones 2003, Stratmann 2003, Caldwell et al. 2007, Andrady et al. 2009, Ballaré et al. 2011, Kuhlmann and Müller 2011, Paul et al. 2012). It has been shown in many field studies that plants or plant parts often suffer less herbivory when they receive solar UV-B than when they grow under attenuated levels of UV-B radiation (for reviews, see Caldwell et al. 2007, Ballaré et al. 2011, Kuhlmann and Müller 2011). UV-B can directly affect herbivorous insects, reducing their growth, fecundity and survival (Bothwell et al. 1994, McCloud and Berenbaum, 1999), and eliciting behavioral (avoidance) responses (Mazza et al. 1999b, Mazza et al. 2002). In addition, UV-B can

change the chemistry of plant tissues, thus indirectly acting upon consumer organisms. It is well documented that insect herbivores often avoid leaves that have been previously exposed to UV-B radiation (Ballaré et al. 1999, Zavala et al. 2001, Rousseaux et al. 2004, Caputo et al. 2006, Foggo et al. 2007) and that UV-B radiation can reduce the nutritional quality of plant tissues (McCloud and Berenbaum 1994, Caasi-Lit 2005). Some of the effects of UV-B radiation on plant tissue chemistry parallel those elicited by insect herbivory (Izaguirre et al. 2003, Izaguirre et al. 2007), and several secondary compounds (particularly phenolics) appear to have a dual function as UV screens and anti-herbivore defenses (Harborne and Williams 2000). Surprisingly, there have been few studies that attempted to quantify the net result of detrimental direct effects and potentially beneficial indirect effects of solar UV-B radiation on plant biomass accumulation or yield; a notable exception being the study of Bothwell et al. (1994) in aquatic ecosystems.

Soybean is one of the major crops produced worldwide. Argentina is a world leading producer of this legume, ranking third (after United States and Brazil) in harvested area (19 Mha), production (52 MTn) and grain exports (10 MTn) and is the world's first soybean oil exporter (data from USDA: <http://www.usda.gov>; friendly accession to same data in Index Mundi: <http://www.indexmundi.com>). Similar to many other plant species, soybean can be affected by solar UV-B radiation. Several classic studies have shown that enhanced UV-B radiation can reduce grain yield and alter many plant morphological, physiological and biochemical characteristics (Teramura and Sullivan 1987, Teramura et al. 1990, Yuan et al. 2002).

Soybean yields per hectare have increased steadily in the last four decades (around 60% worldwide) (data from FAO: <http://www.fao.org/> – accessed November 2011). These increased yields reflect the success of breeding programs and improved management. A trend in modern soybean production in Argentina and other regions is the reduction of row spacing (from 70 cm to as low as 35 cm) with the purpose of increasing canopy light interception early in the season and crop yield per unit area (Harder et al. 2007, De Bruin and Pedersen 2008). Given the increasing pressure for raising crop yields to match the world demand for food, it is likely that this trend will continue in future. Reduced row spacing and increased leaf area index are expected to dramatically reduce whole-plant exposure to UV-B radiation early in the growing season, as could be inferred from studies that measured penetration of visible wavelengths through the crop canopy (Flénet et al. 1996, Maddonni et al. 2001). Reduced UV-B (Red_{UVB}) exposure is likely to have consequences for plant growth and resistance to

biotic stress. Interestingly, a frequently reported caveat of reducing inter-plant spacing in other crops is the increase in the incidence of crop diseases (Burdon and Chilvers 1982, Alexander and Holt 1998, Jurke and Fernando 2006). This negative effect of crop density could result, at least in part, from a weakening of the plant defense system, as a consequence of reduced exposure to UV-B radiation (Demkura et al. 2010).

The experiments reported in this paper were designed to evaluate the responses of soybean canopies to the attenuation of the UV-B component of solar radiation. We were interested in both the direct growth responses of the soybean crop to UV-B attenuation, and in the indirect effects, mediated by changes in the intensity of insect herbivory. To this end, we conducted UV-B attenuation experiments under field conditions. In one experiment the crops were protected with standard pesticide applications, thus minimizing the incidence of insect herbivores, whereas in a second experiment no chemical control was applied.

Materials and methods

Plant material and experimental setup

The experiments were conducted in the experimental field of the School of Agronomy – IFEVA, Buenos Aires (34°35'S, 58°28'W). Five soybean (*Glycine max*) cultivars were used in this study, which were selected on the basis of previous work showing that these genotypes have contrasting levels of soluble leaf phenolics and UV protection (Mazza et al. 2000): Williams [Will; maturity group (MG): III], Dekalb CX458 (DK; MG: IV), A5308 (A53; MG: V), A5634RG (A56; MG: V) and Charata (Cha; MG: VII). Seeds were sown directly in the field in late spring (first week of December). Each genotype was sown in a different row in each of the 16 2 × 1 m plots, and there were two border rows (Cha), one on each side of the plots. Inter-row spacing was 35 cm, and spacing between plants within each row was 8 cm, which produced a final crop density of 360 000 plants per ha. This is a recommended commercial density currently used in Buenos Aires (<http://www.niderasemillas.com.ar/NideraSemillas>). One day after sowing the experimental site was treated with Roundup® (glyphosate; Monsanto Co., St Louis, MO) and Scepter® (imazaquin; BASF SE, Limburgerhof, Germany) in order to eliminate weeds.

Immediately after sowing, plastic filters were placed to cover the plots. Half of the plots were covered with 0.022-mm Stretch film (Bemis Co., Minneapolis, MN), which has a very high transmittance in the UV and visible regions of the solar spectrum (ambient UV-B

treatment, Amb_{uvb}); the other plots were covered with Mylar-D® (0.1 mm; DuPont, Wilmington, DE) clear polyester, which excludes almost all radiation below 320 nm (Red_{uvb} treatment). For transmittance details of the filters, see Izaguirre et al. 2007. Filters were raised daily, following plant growth, in order to keep a constant distance of 15 cm between the films and the upper canopy leaves. There were four true replicates of each genotype × UV-B treatment combination.

In experiment I, the plots were regularly treated with a crop protection package that included acaricide, fungicide and insecticide. Adult and egg acaricide [Fenpropathrin (Danitol®) and Hexythiazox (Nissorum®), respectively] were applied 90 days after sowing (DAS). The fungicide methyl-thiophanate (Topsin®) was applied 28, 60, 77, 91 and 101 DAS. The insecticide Lorsban Plus® (chlorpyrifos + cypermethrin) was applied 41, 54, 105 and 119 DAS, whereas dimethoate (Glacoxan D-Sist®) was applied 130 DAS. Each chemical was applied at the labeled rates and in accordance with the manufacturer's indications. In addition, anti-frost non-woven gauze curtains were erected around the plots to prevent insect movement. These curtains slightly reduced PAR, which may have reduced potential yield in the plots.

In experiment II, there were no chemical treatments applied to the plots (with the exception of the herbicide combination described above applied 1 DAS). To avoid differences in temperature or radiation with experiment I, these plots were also encircled with the anti-frost fabric. These curtains were kept down during the day, but were lifted up during nighttime to allow free movement of canopy arthropods. Because the influence of the curtains was not exactly the same between the first and the second experiment, the absolute biomass data cannot be compared between experiments.

Herbivory levels and yield determinations

Regular inspection of the plots indicated the presence of typical soybean pests, including thrips, sting bugs and grasshoppers. Herbivory damage was assessed by counting the number of visible herbivory marks in the leaves of all the plants in each plot.

At the end of the season, plants were harvested and manually threshed. Plant parts (stems, pods and seeds) were manually separated and weighted. Crop yield was estimated by multiplying the average genotype yield in each plot by the final crop density.

Chlorophyll fluorescence and enzyme activity determinations

Chlorophyll fluorescence induced by UV excitation (RF_{UV}) was used for rapid estimation of transmittance

of the leaf epidermis to UV radiation, essentially as explained in Mazza et al. 2000. Briefly, leaf discs (8 mm diameter) were taken at noon from the central leaflet of upper canopy, and placed with the abaxial surface facing upward on moist paper. Immediately after collection, samples were placed in a Bio-Rad Fluor-S Multimager (Bio-Rad, Hercules, CA) and epi-illuminated with UV light. Red fluorescence was acquired with a cooled CCD camera fitted with appropriate Schott long pass filters ($\lambda > 720$ nm).

For determinations of total catalase (CAT) and ascorbate peroxidase (APx) activities, we followed the protocols described in Mazza et al. (1999a). Very briefly, leaf samples from exposed positions at the top of the canopy were collected at noon, wrapped in aluminum paper, kept on ice and processed immediately. Samples (100 mg) of fully expanded middle leaflets were homogenized in buffer, centrifuged, and enzyme activities were spectrophotometrically analyzed in the supernatant by following the consumption of H_2O_2 at 240 nm in a reaction mixture. APx activity was measured spectrophotometrically by the decrease in absorbance of ascorbate at 290 nm in a reaction mixture. For additional details, see Mazza et al. (1999a).

Statistical analysis

Statistical analyses were performed using PROC GLM in the SAS V 8.0 package (SAS Institute, Cary, NC); appropriate transformations of the primary data were used when needed to meet the assumptions of the analysis of variance. For all the variables measured in this study, there were four true replicates per genotype and UV-B treatment in each of the experiments (I and II). Because of the limitations associated with the design of the experiments (i.e. handling of anti-herbivore curtains, discussed in the foregoing), the absolute biomass data cannot be compared between experiment I and II.

Results

In experiment I, five soybean cultivars were grown in the field to examine their responses to the attenuation of solar UV-B radiation under conditions in which the crops were routinely sprayed with chemicals to control phytophagous arthropods and microbial diseases. Crop responses were measured in terms of basic acclimation parameters, such as accumulation of UV-absorbing sunscreens and antioxidant capacity, biomass accumulation and herbivory levels, and grain yield at the end of the growing season. All five cultivars responded to solar UV-B attenuation (Red_{UVB}) with a reduction in the accumulation of epidermal UV-absorbing sunscreens, as

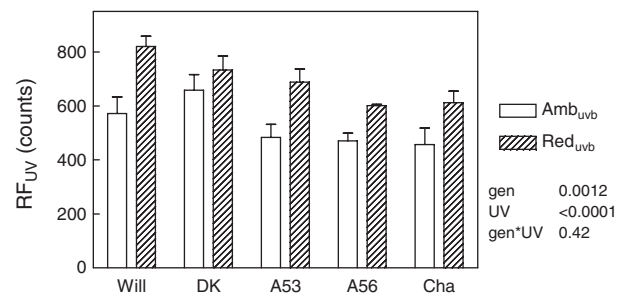


Fig. 1. Epidermal transmittance (RF_{UV}) of five soybean cultivars grown under ambient (open bars) or reduced (hatched bars) solar UV-B radiation. Cultivars are ordered according to their maturity group.

indicated by measurements of UV-induced chlorophyll fluorescence (RF_{UV}) (Fig. 1). Interestingly, the basal levels of epidermal transmittance (i.e. in the absence of UV-B, hatched bars in Fig. 1) correlated with maturity group (MG; $r^2 = 0.85$; $P = 0.026$). Since MG is associated with photoperiod sensitivity, high MG cultivars are planted at low latitudes (where UV levels are naturally high). Therefore, the correlation we found between RF_{UV} and MG strongly suggests that low epidermal transmittance is a UV-resistance trait that was inadvertently selected throughout the breeding process.

UV-B transmittance of the epidermis (estimated though RF_{UV}) appeared to have an important effect on the levels of oxidative stress of the inner leaf tissues. We measured the activity of two H_2O_2 -scavenging enzymes (CAT and APx). These two enzymes showed a tight correlation with RF_{UV} in the Amb_{UVB} treatment, whereas no significant correlation was found in the Red_{UVB} treatment (Fig. 2A, B). These results highlight the importance of epidermal sunscreen accumulation as a resistance trait for solar UV-B radiation: a lower screening capacity demands a stronger antioxidant response.

At the end of the growing season, plant material was harvested for determination of crop yield. Excluding solar UV-B from the radiation received by the crops caused a significant yield increase in all the genotypes tested (Fig. 3; average yield response = $36.0 \pm 7.7\%$; $P = 0.095$). RF_{UV} explained a large fraction of the yield variation among cultivars (Fig. 4). Varieties with higher UV-B epidermal transmittance yielded significantly less than those with higher levels of UV-absorbing sunscreens.

Although the crops were regularly treated with pesticides (see section Materials and methods), residual populations of herbivorous arthropods were observed throughout the growing season. Interestingly, we found that a fraction of the variability in crop yield that was not explained by RF_{UV} (i.e. the residuals in Fig. 4) tended

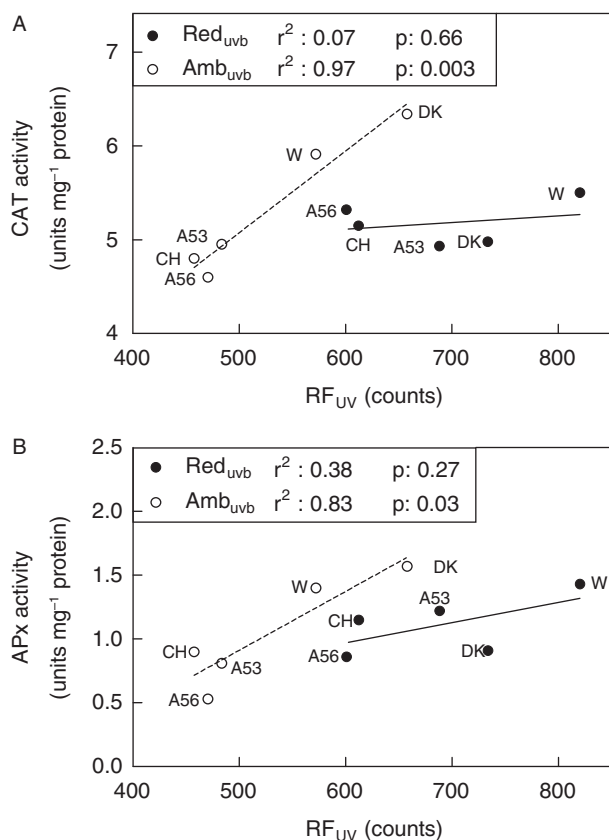


Fig. 2. Antioxidant responses of five soybean cultivars to solar UV-B radiation. CAT (A) and APx (B) activities and their relation to epidermal transmittance (RF_{UV}) under ambient (open symbols) and reduced (closed symbols) solar UV-B radiation. A unit of CAT and APx activity is defined as the consumption of 1 μmol of $\text{H}_2\text{O}_2 \text{ min}^{-1}$.

to correlate with the incidence of herbivores in the crop ($r^2 = 0.36$, $P = 0.069$; data not shown).

In experiment II, without applications of insecticides and fungicides, leaf damage by chewing insects was much more common than in the first experiment, as expected [mean bite marks per leaf ($\pm\text{SE}$): 1.45 ± 0.26 in experiment I vs 18.9 ± 1.8 in experiment II]. In this second experiment, insect damage was significantly higher in the plots that received attenuated solar UV-B than in those receiving the full solar spectrum (Red_{UVB} vs Amb_{UVB}, Fig. 5). This anti-herbivore effect of solar UV-B radiation was present in all the cultivars tested in this study, as indicated by the non-significant UV $\times$ genotype interaction. Under these conditions (i.e. in the presence of insect herbivory) plants grown in the Red_{UVB} environment tended to yield less than those exposed to solar UV-B radiation (Fig. 6). This result suggests that the reduction in arthropod herbivory caused by solar UV-B radiation could compensate the direct deleterious effect of UV-B on soybean yield documented in Fig. 3.

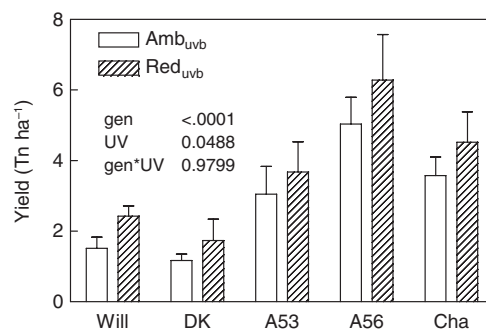


Fig. 3. Yield of five soybean cultivars grown under ambient (open bars) or reduced (hatched bars) solar UV-B radiation in the experiment I (with pest control).

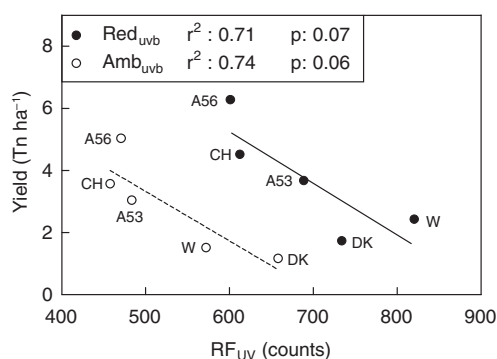


Fig. 4. Relationship between soybean yield and epidermal transmittance for crops grown under ambient (open symbols) or reduced (closed symbols) solar UV-B radiation.

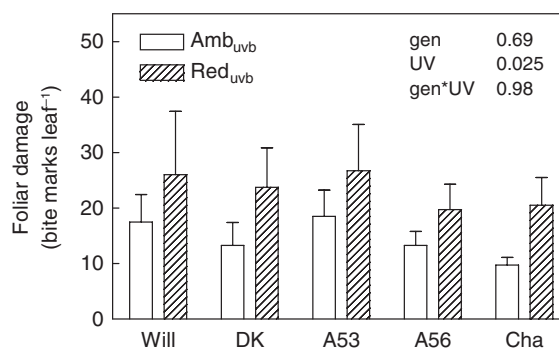


Fig. 5. Leaf damage caused by chewing insects in experiment II (no chemical control) measured in the five soybean cultivars grown under ambient (open bars) or reduced (hatched bars) solar UV-B radiation.

Discussion

Current levels of solar UV-B radiation can have important effects on plants and ecosystems. Moreover, although recent reports predict a recovery of the stratospheric ozone layer by the middle of this century

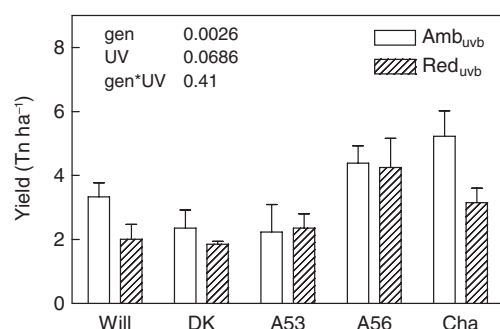


Fig. 6. Yield of five soybean cultivars grown under ambient (open bars) or reduced (hatched bars) solar UV-B radiation in experiment II (without chemical control).

(Harris et al. 2008, McKenzie et al. 2011), projected changes in cloud patterns may have important impacts increasing or decreasing (depending on latitude) the levels of UV radiation reaching the ground (Ballaré et al. 2011, McKenzie et al. 2011). Moreover, the reduced precipitation associated with predictions of reduced cloud cover at low to mid-latitudes (IPCC 2007) could also alter plant growth and canopy structure, thereby affecting the UV-B environment perceived by individual plants. In agroecosystems, in addition to those climate-related factors, management practices directed to increase canopy leaf area index early in the season can substantially reduce the levels of UV-B radiation reaching the plants. The net effect of projected changes in UV-B radiation on plants and agroecosystems is likely to depend on a complex web of interactions involving negative effects of UV-B radiation on plant growth as well as effects on plant–consumer interactions. In our experiments, we sought to separate these effects in a soybean agroecosystem.

Our results showed that solar UV-B directly reduced yield in all the cultivars tested when the crops were grown under the usual pesticide practices (Fig. 3). This result is in agreement with previous UV-B attenuation studies in barley crops carried out in the same field site (Mazza et al. 1999a). In the present experiments, a yield reduction occurred in spite of photoprotection responses activated by the plants through reduced epidermal UV-transmittance (Fig. 1) and increased antioxidant activity (Fig. 2A, B). Accumulation of phenolic compounds in the epidermal tissue is one of the most consistent plant responses to UV-B radiation (Searles et al. 2001), and its functional significance for DNA damage protection has been documented in field-grown soybean plants (Mazza et al. 2000). The activities of the two antioxidant enzymes measured in our experiments were directly related to the epidermal transmittance, which further

emphasizes the functional role of screening by epidermal accumulation of UV-absorbing compounds. The weight of the evidence obtained in these field studies is consistent with the idea that present levels of solar UV-B radiation represent a mild environmental stress for plants, which causes modest, but detectable reductions in growth and yield (Newsham and Robinson 2009, Ballaré et al. 2011). This reduced growth could result from direct damage or as a consequence of the diversion of plant resources to damage repair and protection.

In our second experiment without pest control, an anti-herbivory effect of UV-B radiation was readily detected (Fig. 5). Several explanations for the effects of UV-B radiation on plant–herbivore interactions have been postulated, which include direct deleterious effects on the animals, direct avoidance responses and indirect (i.e. plant-mediated) effects on insect growth and behavior (for recent reviews, see Ballaré et al. 2011, Kuhlmann and Müller 2011).

Plant-mediated effects are generally assumed to be the result of changes in the levels of secondary compounds. Several plant metabolites (mainly phenolic compounds) elicited by solar UV-B radiation are known to possess a dual function, serving as photoprotectants and anti-herbivory defenses, and there is evidence that solar UV-B radiation can trigger plant responses that resemble those elicited by insect herbivory. A partial convergence between the effects of solar UV-B and insect herbivory has been observed at the levels of gene expression (Izaguirre et al. 2003), accumulation of phenolic compounds (Izaguirre et al. 2007), and tissue quality determinations in herbivory bioassays (review in Ballaré et al. 2011). Molecules capable of simultaneously protecting the plant from biotic and abiotic stressors could be regarded a priori as cost-saving compounds, which may have been selected during evolution. In some environments it is also possible that the levels of UV-B radiation received by individual plants are positively correlated with the risk of herbivory (e.g. isolated, visible plants vs plants ‘hidden’ within a dense canopy). Furthermore, it has been postulated that UV-B radiation is among the light signals that plants use to gauge the risk of competition, and the allocation to anti-herbivore defense compounds frequently increases under conditions of reduced competition pressure (Ballaré 2009, Moreno et al. 2009, Demkura et al. 2010). The recent description of a UV-B photoreceptor in *Arabidopsis* (Rizzini et al. 2011) opens exciting perspectives for the study of the roles of solar UV-B as an environmental signal affecting plant photomorphogenesis and the interactions with competitors and consumer organisms (Demkura and Ballaré 2012).

Agricultural production must increase during the next decades in order to keep up with the global food

demand (Rosegrant and Cline 2003), and an increased agricultural output per unit area would be required, in order to avoid continued encroachment into natural ecosystems. The need for improved crop production will be even more pronounced in the face of anticipated negative effects of climate change on global agriculture (IPCC 2007). In order to achieve this goal, new varieties with improved performance will have to be developed, and the use of fertilization, irrigation, herbicides and pesticides is likely to increase (Oerke and Dehne 2004, Jaggard et al. 2010). Although extrapolation of our results to real field conditions should be done with caution, the results described in this paper highlight the importance of ambient solar UV-B radiation as an abiotic factor that reduces the incidence of insect pests, which could hint to plausible strategies for the production of healthy crops. Further studies are needed to properly characterize the UV-B environment inside crop canopies, and its relationship with crop density, ontogeny or plant structure, as well as to improve our understanding of the effects of UV-B radiation on plant defenses. In soybean crops, the use of short-season varieties could enhance UV-B availability in a proportionally longer period of crop development, whereas open architectures could increase UV-B : PAR ratio inside the canopy (Flint and Caldwell 1998, Grifoni et al. 2008). These changes in the canopy light environment could increase the contribution of natural resistance traits to plant defense, thereby reducing the need for pesticide applications. The results reported here for soybean could also be valuable for improved horticultural management, where small cultivation areas and mixed crop production schemes are particularly apt to canopy structure and density manipulations. Under conditions where the light environment is difficult to manipulate through technologically viable cropping strategies, a better understanding of the mechanisms whereby solar UV-B radiation boosts the expression natural plant defenses could provide important elements for biotechnological and traditional crop breeding programs.

In conclusion, the results of our experiments suggest that the anti-herbivore effect of solar UV-B radiation can counterbalance the negative, direct effects of this radiation on plant growth and soybean yield. This beneficial effect of UV-B on crop yield could be an important element of agronomic practices aimed at reducing the use of pesticides, and should be taken into account when selecting planting densities and patterns, which affect light penetration into the canopy. Under a broader perspective, the results reported in this paper stress the need for holistic approaches when considering the biological effects of current and projected levels of UV-B radiation on agroecosystems.

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