BioOne COMPLETE

Solar UV Upregulates Photoprotection but Slows Photosynthesis in Subalpine Australian Plants

Authors: Salter, William T., Turnbull, Tarryn L., Rennenberg, Heinz, and Adams, Mark A.

Source: Arctic, Antarctic, and Alpine Research, 49(4) : 673-685

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/AAAR0017-024

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Arctic, Antarctic, and Alpine Research, Vol. 49, No. 4, 2017, pp. 673–685
DOI: http://dx.doi.org/10.1657/AAAR0017-024

Solar UV upregulates photoprotection but slows photosynthesis in subalpine Australian plants

William T. Salter[1,*], Tarryn L. Turnbull[1], Heinz Rennenberg[2,3], and Mark A. Adams[4]

[1]Centre for Carbon, Water and Food, University of Sydney, 380 Werombi Road, Brownlow Hill, NSW 2570, Australia
[2]Institute of Forest Botany and Tree Physiology, Chair of Tree Physiology, University of Freiburg, Georges-Koehler-Allee 53/54, 79110, Freiburg, Germany
[3]College of Sciences, King Saud University, P.O. Box 2455, Riyadh 11451, Saudi Arabia
[4]Department of Chemistry and Biotechnology, Faculty of Science, Engineering and Technology, Swinburne University, PO Box 218, Hawthorn, Victoria 3122, Australia
[*]Corresponding author's email: william.salter@sydney.edu.au

A B S T R A C T

Recent literature suggests a shifting paradigm in relation to photobiology associated with ultraviolet (UV) radiation. UV has been repeatedly shown to be less detrimental to plant performance than previously thought. Nonetheless, relatively few plant species have been studied; too few to make definitive statements about effects of UV on plants at the ecosystem scale. We present findings of a field-based study using natural solar radiation, coupled with UV screening films, to determine physiological costs and benefits of exposure to solar UV for three species representative of subalpine Australian flora: a tree (*Eucalyptus pauciflora*), a forb (*Geranium antrorsum*), and a grass (*Poa hiemata*). Photochemical and photosynthetic responses to UV exclusion varied among species; exposure to UV was of no consequence to the structure, chemistry, or incidence of photoinhibition for *E. pauciflora*. UV was effectively screened at the leaf surface of *P. hiemata*. The response of *G. anstrorsum* to UV exclusion suggests greater susceptibility to photodamage; less successful in screening against UV and exposure reduced rates of photosynthesis, despite increased capacity to scavenge reactive oxygen species (via accumulating ascorbate). This study clarifies that responses to UV are highly species-specific, and that the endemic native flora is seemingly well-adapted to mitigate negative effects.

Introduction

Identifying positive relationships between solar ultraviolet (UV) light and plant performance remains poorly studied, particularly in natural ecosystems. For example, the literature overwhelmingly contains examples of UV causing plant damage, or negatively affecting photobiology and growth, resulting in the general perception that UV radiation is detrimental to plants. Wargent and Jordan's (2013) Tansley Review attributes the balance of findings to methodology, with the dominance of 'negative' studies attributable to unrealistic wavebands or intensity, or targeting exposed mesophyll cells (rather than cells embedded within, and protected by leaf structures, screening compounds, and biochemical processes). Plants reduce their exposure to UV by reflecting around 5% of incident UV radiation at the leaf surface. Of more significance are screening chemicals in the outer leaf structures that together can absorb up to a further 90% of incident UV. Cuticular waxes, particularly of alpine plants, have distinct UV-A and UV-B absorption peaks (Jacobs et al., 2007; Bruhn et al., 2014); the growth of trichomes and accumulation of UV absorbing hydroxycinnamic acids in these cells is promoted by exposure to UV (Karabourniotis et al., 1992; Tattini et al., 2000), and the accumulation of flavonoids and related phenolic compounds in epidermal (and to a lesser extent mesophyll) cells can attenuate UV-B and UV-A wave-

© 2017 Regents of the University of Colorado – 1523-0430/10 $7.00

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

lengths, respectively (Caldwell et al., 1983; Agati and Tattini, 2010). The synthesis of flavonoid compounds is induced by exposure to UV radiation in some plant species; however, many do not act solely to screen UV and have multiple photoprotective roles, including as antioxidants (Agatti et al., 2012; Landi et al., 2015). UV that reaches the mesophyll can affect photosynthetic apparatus in similar fashion to excess radiation of longer wavelengths, in particular via accumulation of reactive oxygen species (ROS) in the thylakoid membrane (Foyer et al., 1994) and/or by inhibiting repair of PSII (Nishiyama et al., 2006). At the cellular level, UV wavelengths can exacerbate oxidative stress (Barta et al., 2004; Snyrychova et al., 2007) via the formation of oxygen radicals from peroxidases and oxidases, chlorophyll molecules and metabolic reactions in peroxisomes, as well as in the electron transport chain (for reviews see Kataria et al., 2014; and Czégény et al., 2016). UV radiation also promotes the production of hydrogen peroxide (H_2O_2), the stable form of oxidized oxygen, and its subsequent photosensitive breakdown to highly oxidizing hydroxyl radical (Czégény et al., 2014). Free radicals can be neutralized by the ascorbate (Asc) and glutathione (GSH) antioxidative system (Foyer and Noctor, 2011; Noctor et al., 2012; Toth et al., 2013), as well as by other enzymatic (including superoxide dismutase, catalases) and non-enzymatic antioxidants (including a-tocopherols, carotenoids, phenolic compounds) (for review see Ahmad et al., 2010).

There is strengthening recognition of positive UV-plant relationships. For example, Day et al. (1992) highlighted that plants do not necessarily have to protect their mesophyll from UV, with herbaceous dicots endemic to mountain ecosystems transmitting 20–40% of UV to the mesophyll (c.f. 4% in adjacent woody dicots and grasses). Similarly, exposure to solar UV is far from universally damaging to plant photosynthetic physiology. UV may directly (via chlorophyll *a* absorption: McCree, 1972; Inada, 1976; Turnbull et al., 2013) and, to a lesser extent, indirectly (via reabsorption of UV-induced blue-green fluorescence: 1% contribution to photosynthesis in Johnson and Day, 2002; 7.8–9.8% in Mantha et al., 2001) drive oxidative photosynthesis in a range of plants. Most recently, Wargent et al. (2015) recorded that the photosynthetic performance of *Lactuca sativa* was enhanced when exposed to UV during early development, and suggested that UV acted as a priming agent for primary productivity.

Australian plants are arguably exposed to some of the brightest (Salby, 2012) and most UV-enriched light environments on Earth (Roy et al., 1995), far in excess of requirements for photosynthesis (Amthor, 2010). In subalpine ecosystems in southeast Australia, plants are exposed to intense visible and UV radiation because of latitude (Gies et al., 2004), altitude (Blumthaler et al., 1997), and albedo and snow cover (Lee et al., 2015). Theory thus suggests that native (well-adapted) plants from these systems should exhibit mechanisms and structures (for example, promotion of antioxidant biosyntheses, alteration of morphology/phenology) that mitigate and limit photobiological stress as, in addition to an inherently energetic light environment, they are also subject to extreme variations in temperature, and availability of water and nutrients, that limit growth and diminish photosynthetic requirements for light (Bornman et al., 2015). We recently provided evidence that *Pimelea ligustrina,* a woody shrub common to Australia's subalpine region, employs a suite of photobiological adaptations in order to utilize UV-A for photosynthesis (Turnbull et al., 2013). *P. ligustrina* has no effective cuticle and limited concentrations of phenols in the epidermal layer. Solar UV-A passes relatively unimpeded to the mesophyll layer, which is in turn enhanced in the UV-A absorbing photo-pigments chlorophyll *a* and lutein (a carotenoid pigment). Consequently, *P. ligustrina* uses UV-A to raise photosynthetic rates ~12% above that driven by the visible component of solar radiation. Furthermore, our data suggest the capacity to use UV-A for photosynthesis features strongly in subalpine flora, with 26 of the 55 most prominent species (mostly herbaceous dicots) also demonstrating that UV-A can directly be absorbed by chlorophyll *a* in intact leaves (Turnbull et al., 2013).

We sought to test if UV-A driven photosynthesis might feature among other major plant genera in the Australian subalpine region. We chose a canopy dominant tree (*Eucalyptus pauciflora*), an herbaceous dicot (*Geranium antrorsum*), and the common snow grass (*Poa hiemata*) as study species. In addition, we sought to test if exposure to UV during leaf development influenced the capacity to utilize UV-A and visible wavelengths together for photosynthesis. We deployed screens above plants growing in situ for the entire growth season, and combined field measurements of gas exchange with laboratory analysis of leaf fluorescence, redox chemistry, and leaf anatomy.

Materials and Methods

Site Description and Treatments

We studied snow gum (*Eucalyptus pauciflora* Sieber x Spreng), rosetted cranesbill (*Geranium antrorsum* Carolin), and soft snow grass (*Poa hiemata* Vickery) growing in a subalpine grassy woodland in the Snowy Mountains region of New South Wales (NSW) (36°05′36″S,

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

148°31′42″E; 1550 m a.s.l.). Photosynthetic measurements were made on clear, sunny days in March 2013 (midday visible photon flux density [PFD] = 1700 μmol photon m^{-2} s^{-1}; midday UVA PFD = 50 μmol photon m^{-2} s^{-1}). Samples for fluorescence, reflectance, microscopy, and chemical analyses were collected upon completion of photosynthetic measurements. The youngest fully expanded leaves (all formed under treatment conditions) were used for all analyses.

To control the spectral quality reaching our chosen plant species, we deployed two filters of contrasting spectral transmissivities (Fig. 1); one that transmits visible light but excludes UV (UV exclusion; #3114; Rosco Australia PTY Ltd., Artarmon, NSW, Australia) and a control filter that transmits visible light and UV (Control; B6191-50; Churchill & Coombes Pty Ltd., Lidcombe, NSW, Australia). We positioned 15 control and 15 UV-exclusion filters along an 800 m transect in locations where the study species grew within a 1 m^2 quadrat. The filters were in place for five months from October 2012 until March 2013.

Leaf Gas Exchange

An infrared gas analyzer (IRGA) (LI-6400; Li-Cor Inc., Lincoln, Nebraska, U.S.A.) was used to measure photosynthetic rates in situ under fully saturating light conditions (PFD > 1500 μmol photon m^{-2} s^{-1}, as determined by a light response curve, data not shown). Chamber temperature and moisture matched ambient, whereas reference CO_2 concentration was 400 ppm and flow rate retained at 350 μmol s^{-1}. The IRGA was fitted with a clear-topped 2 × 3 cm leaf chamber and glass filters to control the spectral quality. To quantify the contribution of UVA to photosynthesis, photosynthetic rates were measured when the leaf was in receipt of wavelengths exceeding 320 nm (PAR + UVA) (N-WG320; Schott Australia Pty. Ltd., French's Forest, NSW, Australia) and at wavelengths greater than 395 nm (PAR – UVA) (GC395; Schott Australia Pty. Ltd., French's Forest, NSW, Australia). Leaves were allowed to stabilize in the chamber for 3 min prior to measurement. Light saturated rates of photosynthesis (A_{sat}) and stomatal conductance (g_s) were logged for 4 min at 30 s intervals.

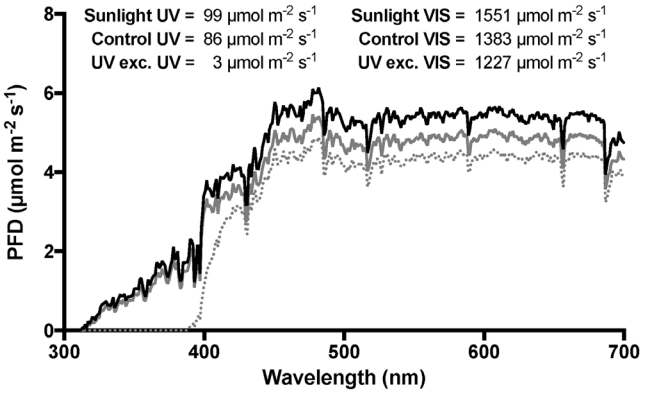


FIGURE 1. Spectral light environment of each treatment in relation to natural insolation; black solid line—sunlight, gray solid line—control, gray dotted line—UV exclusion. The total values shown represent the sum of total PFDs of the UV waveband (λ 280–400 nm) and the VIS waveband (λ 400–700 nm) in μmol m^{-2} s^{-1}.

Fluorescence Spectroscopy

Fluorescence profiles of fresh leaves were captured with a Cary Eclipse fluorescence spectrophotometer (Agilent Technologies, Mulgrave, Victoria, Australia) and a Cary Eclipse fiber optics accessory using a scan rate of 120 nm min^{-1}. Fluorescence emission spectra were collected from samples using excitation λ 380 nm (emission λ scan = 400–700 nm). Epidermal capacity to screen UV was estimated from the ratio of fluorescence emission at λ 440 (epidermal hydroxycinnamic acids) to emission at λ 685 nm (chlorophyll in the mesophyll), and chlorophyll content was estimated from the fluorescence emission at λ 685 to emission at λ 720 nm (Lenk and Buschmann, 2006). To determine chlorophyll *a* fluorescence, excitation spectra were collected for samples at emission λ 685 nm (excitation λ scan = 340–475 nm) and λ 730 nm (excitation λ scan = 370–475 nm). Data points between λ 380 nm and 405 nm were modeled using a sigmoidal curve fitted to the remaining 30 points at an interval of 1 nm between 370 nm and 425 nm (Prism 6; Graphpad Software, La Jolla, California, U.S.A.). All fitted curves had an *R*-squared value greater than 0.99.

Leaf Anatomy

Slides for microscopy analysis were prepared as per Turnbull et al. (2013). Fresh leaf sections (1 cm × 2 mm) were fixed with 2.5% gluteraldehyde solution in 0.1 M phosphate buffer saline (PBS). These were refrigerated at 4 °C for four days to allow full penetration of the fixative. Leaf samples were then dehydrated in a graded series of ethanol, cleared with xylene, and infiltrated with paraffin using an automated processor (TissueTek VIP, Sakura, Tokyo, Japan). The samples were then embedded in blocks of paraffin and cut into 4 μm sections using a microtome (Leica RM2165; Leica Microsystems GmbH, Wetzlar, Germany). The leaf sections were picked up on glass slides and dried at 56 °C. Xylene

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

was used to deparaffinize the slides, which were then rehydrated through a graded series of ethanol. Slides were bathed in 0.1% Toluidine Blue stain, rinsed with distilled water, dehydrated, cleared, and mounted with Ultramount (Fronine, Sydney, NSW, Australia).

Slides were imaged using a light microscope (Olympus BX51; Olympus Imaging Australia, North Ryde, NSW, Australia) connected to a digital camera (Olympus DP70; Olympus Imaging Australia, North Ryde, NSW, Australia). Images were captured at 100× and 400× magnifications and were analyzed using Photoshop software (Adobe Systems Inc., San Jose, California, U.S.A.). Measurements were made of abaxial and adaxial cuticle depth, abaxial and adaxial epidermal depth, and total leaf thickness.

Ascorbate and Its Redox Status

Ascorbate contents were analyzed using the method of Haberer et al. (2007). 20 mg of homogenized frozen leaf material was added to 500 μL of 5% meta-HPO_3, vortexed, and centrifuged for 30 min (12,000 g, 4 °C). Supernatant (100 μL) was transferred to a new tube and neutralized with 20 μL of 1.5 M triethanolamine (TEA) and 100 μL of 150 mM Na-phosphate buffer. Reduced ascorbate was measured directly; total ascorbate was measured after complete reduction by DTT (50 μL, 10 mM, 15 min at room temperature). Excess DTT was removed with NEM (50 μL, 0.5%). Samples for reduced and total ascorbate analysis were then treated in the same way. We added 200 μL of 10% trichloroacetic acid (TCA), 200 μL of 44% ortho-H_3PO_4, and 200 μL of 4% 2,1-dipyridyl to tubes successively. Finally, 100 μL of 3% $FeCl_3$ was added and samples incubated in a water bath at 37 °C for 60 min. Of the final solution, 800 μL was transferred to a cuvette for analysis at l 525 nm in a spectrophotometer (Beckman DU650, Beckman, Krefeld, Germany) as per Okamura (1980). Ascorbate concentrations were quantified using a standard solution (1.5 mg mL^{-1} ascorbate in 0.5% m-H_3PO_4) and normalized per unit fresh weight. Ascorbate extracts were clear, so interference from anthocyanins during analysis was assumed to be negligible. It is possible that a small amount of oxidation of Fe^{3+} could be caused by phenolic compounds also present in the leaves.

Glutathione and Its Redox Status

Thiols were extracted and their redox status of leaves was determined as per Hu et al. (2013). Thiols were extracted from 30 mg homogenized frozen leaf tissue in pre-cooled 750 μL 0.1 M HCl with 50 mg PVPP. Tubes were vortexed and centrifuged for 30 min (14,000 g, 4 °C).

For analyses of reduced plus oxidized thiols, 120 μL aliquots of supernatant were added to 180 μL of 2-(*N*-cyclohexylamino)-ethanesulphonic acid (CHES) buffer (pH 9.3) and 30 μL of 15 mM dithiothreitol (DTT). For oxidized thiols, 20 μL of 20 mM *N*-ethylamide (NEM) was added to tube for 15 min prior to reduction with DTT, to block reduced thiols (Hu et al., 2013). Tubes were incubated for 1 h at room temperature before reduction was terminated with 20 μL of 30 mM monobromobimane (mBBr). Samples were incubated in the dark at room temperature for 15 min to derivatize thiols. The derivatization process was stopped by adding 250 μL of 10% acetic acid, which stabilized the thiol derivatives.

Thiol derivatives were separated by reversed phase high performance liquid chromatography (HPLC) (Beckman Gold System; Beckman, Krefeld, Germany) using a C18-AQ column (Prontosil 120-5-C18, 5 μm particle size, 25 cm × 4.6 mm id; Bischoff Chromatography, Leonberg, Germany) and quantified using a fluorescence analyzer (Shimadzu RF-551-Spectrofluorometric detector; Shimadzu Europe GmbH, Duisberg, Germany) as described by Schupp and Rennenberg (1988). Peaks were identified and quantified using a standard solution (0.2 mM cysteine, 0.1 mM g-glutamyl-cysteine and 1 mM glutathione in 0.01 M HCl) and concentrations normalized per unit fresh mass.

Statistical Analyses

Data were tested for normality and identification of outliers (SPSS Statistics Ver. 21; IBM Australia Ltd., St Leonards, NSW, Australia), and then two-way analyses of variance (ANOVA) were used to determine growth treatment effects and differences between species (Prism 6; Graphpad Software, La Jolla, California, U.S.A.). A paired *t*-test was used to determine the contribution of UV-A to photosynthesis (Prism 6).

Results

Leaf Gas Exchange

Plants grown without exposure to UV exhibited faster rates of light-saturated photosynthesis and stomatal conductance than those exposed to UV ($F_{1,76} = 4.5$, $P < 0.05$, Fig. 2). Photosynthetic rates of *G. antrorsum* plants grown under UV exclusion were 19.7% faster than those grown in full sunlight ($P < 0.05$), corresponding with a 30% faster rate of stomatal conductance ($P < 0.05$, Fig. 2); *E. pauciflora* and *P. hiemata* showed similar trends.

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Net photosynthetic rates of *P. hiemata* were ~60% slower than the other two species ($F_{1,76} = 99.2$, $P < 0.001$). Intrinsic water use efficiency (WUE_i) varied significantly among species ($F_{2,76} = 5.9$, $P < 0.01$) (Fig. 2). Responses of WUE_i to UV exposure were species-specific (interaction between species and UV treatment, $F_{2,76} = 9.5$, $P < 0.001$); WUE_i was reduced in *P. hiemata* exposed to solar UV ($P < 0.001$), whereas *E. pauciflora* and *G. antrorsum* were unaffected ($P > 0.05$). No species was able to utilize UV-A to significantly increase photosynthetic rates (Fig. 3), with the maximum gain in photosynthetic rate from including UV-A in the measurement spectrum being 1.5–2% for *G. antrorsum* ($P > 0.05$).

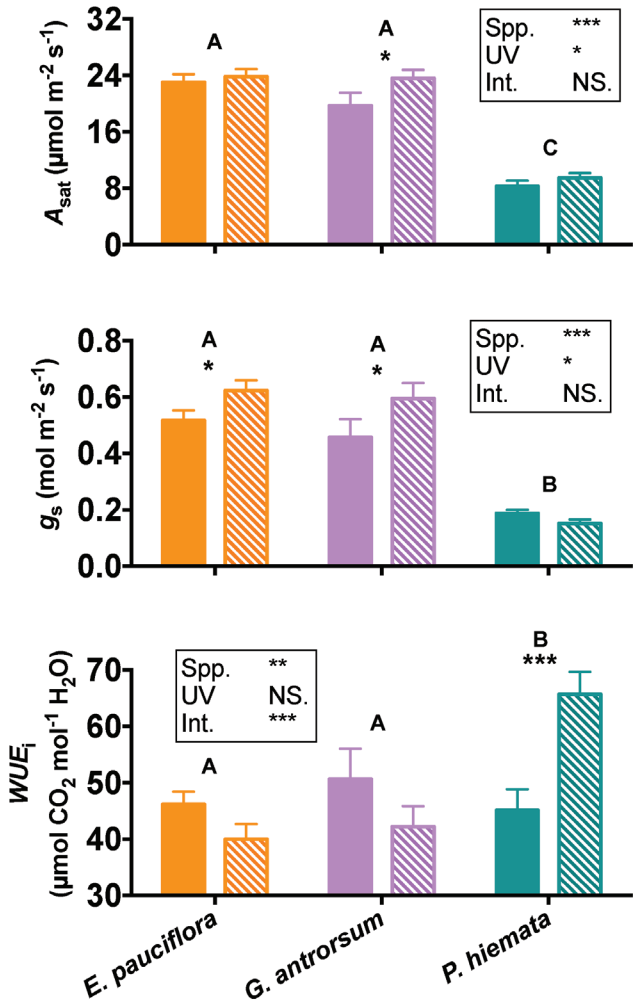


FIGURE 2. (top) Light saturated photosynthetic rates (A_{sat}), (middle) light saturated stomatal conductance (g_s), and (bottom) intrinsic water use efficiency (WUE_i) of *E. pauciflora*, *G. antrorsum*, and *P. hiemata* under UVA+VIS wavelengths (λ > 320 nm). Filled bars represent the full sunlight treatment; dashed bars represent the UV exclusion treatment. Values are means ± SEM ($n = 15$). Asterisks indicate significantly different means (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) between light treatments, within species; upper-case letters denote significantly different means between species identified by Fisher's LSD test ($P < 0.05$).

Fluorescence

Fluorescence emission spectra of fresh leaves varied significantly among species ($F_{2,48} = 28.9$, $P < 0.001$) (Fig. 4), indicating a potential disparity among species in the capacity of leaf surface chemistry to absorb UV-A. The spectra of *E. pauciflora* and *G. antrorsum* had identical peak profiles (λ 423 nm, 445 nm, 460 nm, 486 nm, and 519 nm), indicating comparable chemical profiles, in contrast to *P. hiemata* that maintained a broad peak between λ 410 nm to λ 480 nm and sharp peaks at λ 486 nm and λ 519 nm. Total fluorescence emission, calculated as the area under the emission spectra, and capacity of epidermal cells to screen UV-A were least for *G. antrorsum* (both $P < 0.001$), with *E. pauciflora* leaves emitting the most fluorescence (70% greater than *G. antrorsum*) and *P. hiemata* best able to screen against UV-A (2.8-fold greater ability than *G. antrorsum*). Exposure to UV increased the capacity for epidermal screening against UV ($F_{1,48} = 6.2$, $P < 0.05$, Table 1), with differences most clear in the grass *P. hiemata*, which displayed a 22% greater capacity to screen against UV-A when exposed to UV in the growth environment ($P < 0.01$).

Exposure to UV did not affect the chlorophyll content of leaves ($P > 0.05$; Table 1), although chlorophyll content did vary among species. *E. pauciflora* leaves had,

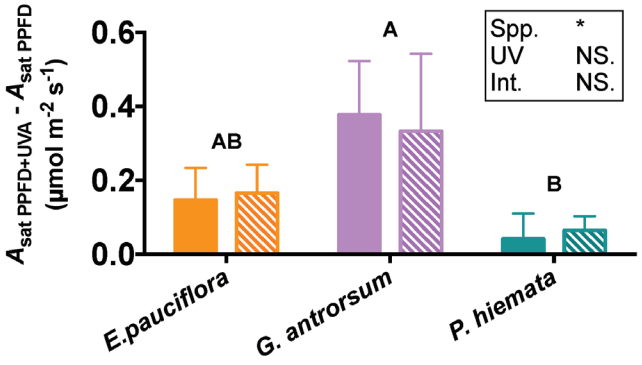


FIGURE 3. Effect of inclusion of UVA wavelengths on the light saturated photosynthetic rate (A_{sat}) for *E. pauciflora*, *G. antrorsum*, and *P. hiemata*. Filled bars represent the full sunlight treatment; dashed bars represent the UV exclusion treatment. Values are means ± SEM ($n = 15$). Asterisks indicate significantly different means (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) between light treatments, within species; upper-case letters denote significantly different means between species identified by Fisher's LSD test ($P < 0.05$).

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

FIGURE 4. Mean fluorescence emission spectra for *E. pauciflora*, *G. antrorsum*, and *P. hiemata*. Excitation wavelength was 380 nm. Black lines represent the full sunlight treatment; gray lines the UV exclusion treatment. Values represent means ± SEM (dashed lines) for $n = 9$.

on average, 22% greater concentrations of chlorophyll than *G. antrorsum* and 58% greater concentrations than *P. hiemata* ($F_{2,48} = 27.0$, $P < 0.001$).

Fluorescence of Chl *a* (emission peak l 685 nm and 730 nm) after excitation with UV-A wavelengths showed UV-A reached the mesophyll in all three species (Fig. 5), albeit the particular wavelengths able to excite Chl *a* varied among species ($F_{2,48} = 494.7$, $P < 0.001$). Chl *a* was excited by wavelengths as low as 378 nm for *P. hiemata* and 386 nm for *G. antrorsum*, whereas the capacity for UV-A to excite Chl *a* in *E. pauciflora* was negligible ($\lambda >$ 395 nm). Exposure to UV during growth had no ef-

TABLE 1

Fluorescence emission peaks and ratios. Fluorescence emission peaks and peak ratios, using an excitation λ of 380 nm. Values represent means ± SEM for $n = 9$. Asterisks indicate significantly different means using a two-way ANOVA (* $P < 0.05$, *** $P < 0.001$). Different lowercase letters represent significantly different means between species by Fisher's LSD multiple comparison test ($\alpha = 0.05$). Dot (•) indicates significantly different means between light treatments within species by Fisher's LSD multiple comparisons test ($\alpha = 0.05$).

	E. pauciflora			*G. antrorsum*			*P. hiemata*			*P*-value		
Characteristic	Full sunlight	UV exclusion		Full sunlight	UV exclusion		Full sunlight	UV exclusion		(species)	(UV)	(Int.)
Emission at λ 423 nm	6.4 ± 0.4	6.1 ± 0.5	**a**	3.4 ± 0.3	2.9 ± 0.3	**b**	3.4 ± 0.4	2.8 ± 0.3	**b**	***		
Emission at λ 445 nm	5.0 ± 0.3	4.6 ± 0.3	**a**	2.6 ± 0.2	2.2 ± 0.2	**b**	3.9 ± 0.5	3.3 ± 0.3	**c**	***		
Emission at λ 460 nm	4.1 ± 0.3	3.9 ± 0.3	**a**	2.2 ± 0.1	1.9 ± 0.1	**b**	3.6 ± 0.5	3.1 ± 0.3	**c**	***		
Emission at λ 486 nm	4.0 ± 0.3	3.8 ± 0.2	**a**	2.1 ± 0.2	1.8 ± 0.1	**b**	3.0 ± 0.3	2.7 ± 0.2	**c**	***		
Emission at λ 519 nm	6.4 ± 0.4	6.3 ± 0.3	**a**	4.8 ± 0.3	4.6 ± 0.3	**b**	4.9 ± 0.4	4.5 ± 0.3	**b**	***		
Total fluorescence (area under spectra)	638 ± 39.5	605 ± 40.1	**a**	376 ± 25.4	336 ± 20.8	**b**	475 ± 47.8	419 ± 33.6	**c**	***		
UV screening capacity (λ 440/685 nm)	5.8 ± 0.2	5.7 ± 0.2	**a**	4.2 ± 0.3	3.5 ± 0.3	**b**	11.7 ± 1.1	9.1 ± 0.7	**c**	•	***	*
Chlorophyll content (λ 685/720 nm)	1.8 ± 0.0	1.9 ± 0.1	**a**	1.6 ± 0.0	1.6 ± 0.0	**b**	1.3 ± 0.1	1.2 ± 0.1	**c**		***	

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

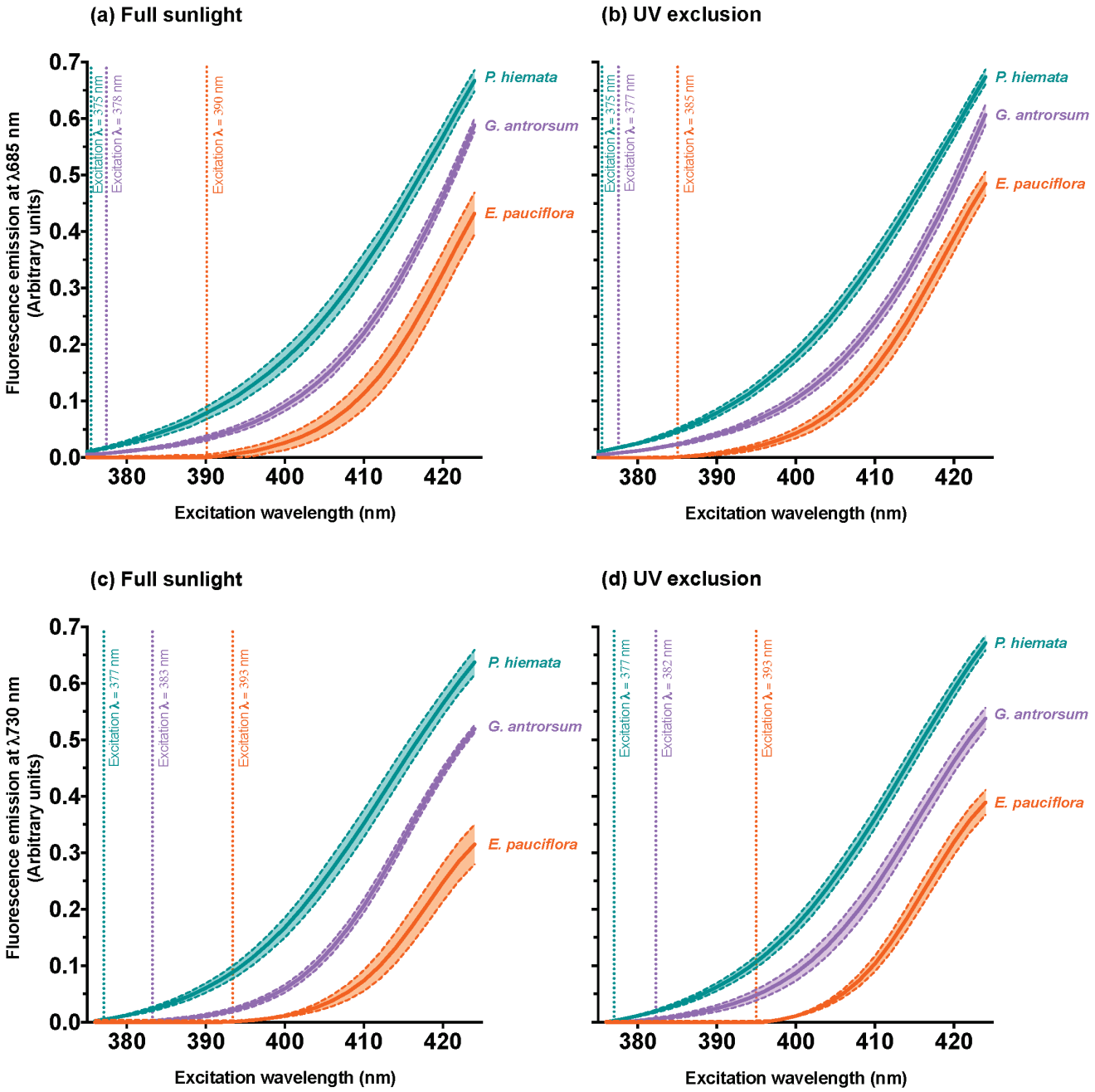


FIGURE 5. Spectral profiles of Chl *a* fluorescence for fresh leaves of *E. pauciflora* (orange), *G. antrorsum* (orchid), and *P. hiemata* (green). Values represent excitation of the Chl *a* emission peak at λ 685 nm for plants grown under (a) full sunlight, and (b) UV exclusion; and of the Chl *a* emission peak at λ 730 nm for plants grown under (c) full sunlight, and (d) UV exclusion. Data shown are means ± SEM for *n* = 9.

fect on profiles of Chl *a* excitation via UV-A ($P > 0.05$; Fig. 5).

Leaf Anatomy

Of the three study species, only the tree, *E. pauciflora*, had a waxy cuticle (Fig. 6; images shown are of leaves grown in full sunlight). Leaves of *E. pauciflora* were also more than twice as thick (463 μm) as those of the other two species (*G. antrorsum* 227 μm, *P. hiemata* 208 μm; $F_{2,73} = 155.3$, $P < 0.001$). The epidermis of *P. hiemata* was significantly thinner than that of the other two species ($F_{2,73} = 88.0$, $P < 0.001$), 13.9 ± 0.5 μm compared to 19.4 ± 0.6 μm in *E. pauciflora* and 21.6 ± 0.7 μm in *G. antrorsum*.

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

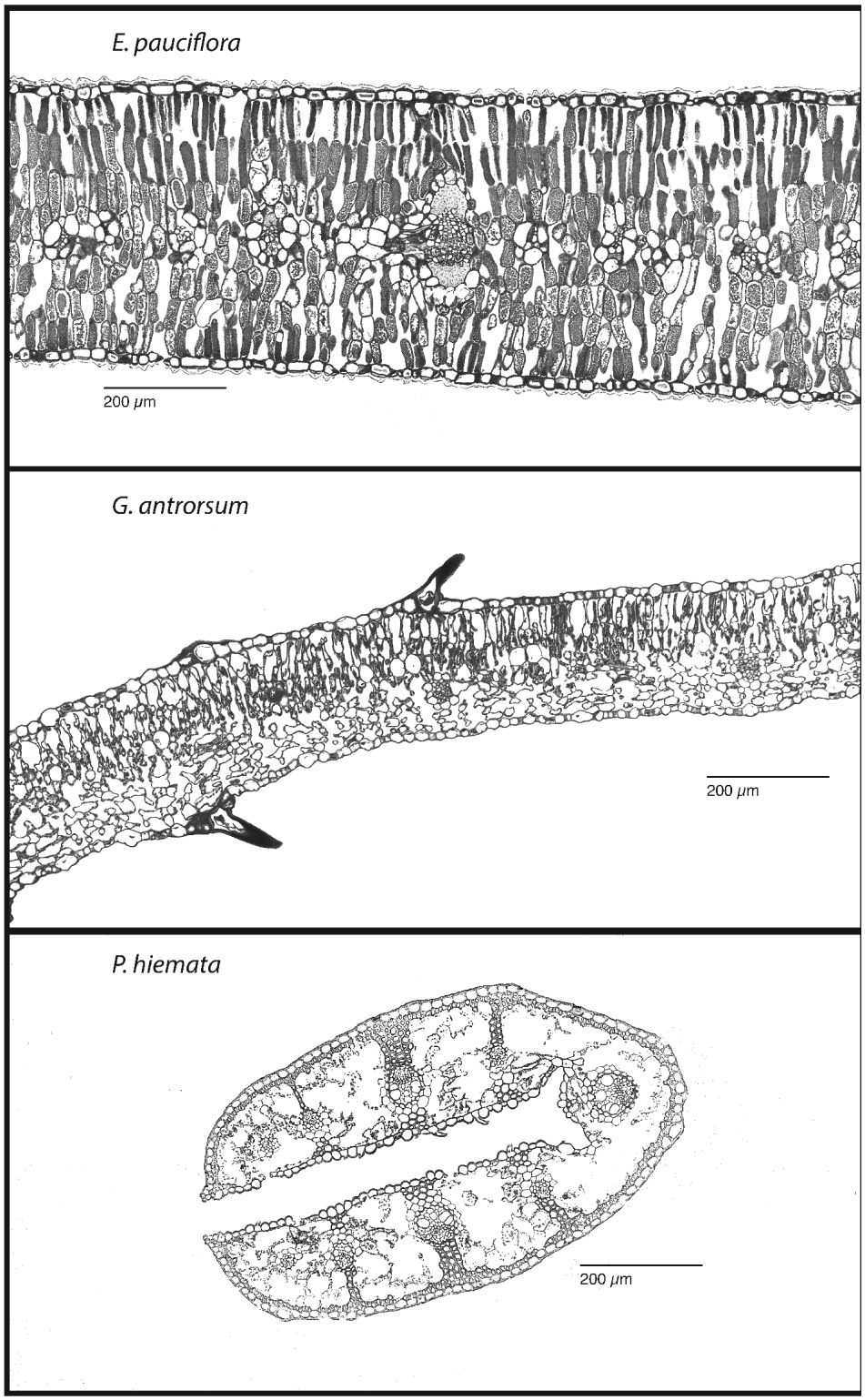


FIGURE 6. Microscopy images of *E. pauciflora* (top), *G. antrorsum* (middle), and *P. hiemata* (bottom) at 100× magnification. Images are from leaves grown in full sunlight.

Adaxial epidermal cells were between 7% (*P. hiemata*) and 15% (*G. antrosum*) thicker than abaxial epidermal cells for all three species ($F_{2,73}$ = 75.4, $P < 0.001$), consistent with a high light environment. Trichomes were present on the adaxial and abaxial surfaces of *G. antrorsum*, but absent in the other two species. There were, however, no discernable anatomical differences between control and UV-exclusion plants in any species ($P > 0.05$).

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Antioxidants and Their Redox Status

Foliar concentrations of ascorbate were, on average, 30% greater in plants exposed to UV ($F_{1,32}$ = 6.3, P < 0.05; Fig. 7), albeit of unaltered redox state (P > 0.05). UV-induced ascorbate accumulation was greatest in *G. antrorsum*, with 50% greater concentrations in leaves grown in full sunlight than those grown without UV (P < 0.05). Concentrations of ascorbate differed among all three species ($F_{2,32}$ = 69.9, P < 0.001), being greatest in *E. pauciflora* (40.8 ± 3.8 μmol g^{-1} FW) and the least in *P. hiemata* (6.5 ± 1.7 μmol g^{-1} FW). The ascorbate redox state of *P. hiemata* leaves was significantly greater than the other two species ($F_{2,32}$ = 31.5, P < 0.05).

Leaf concentrations of glutathione (GSH), glutathione disulphide (GSSG) (Fig. 7), and the glutathione precursors cysteine (Cys) and γ-glutamylcysteine (γ-EC) (Table 2) were unaffected by exposure to solar UV during growth (P > 0.05) but varied considerably among species (GSH, $F_{2,42}$ = 30.2, P < 0.001; GSSG, $F_{2,42}$ = 126.0, P < 0.001; Cys, $F_{2,42}$ = 55.2, P < 0.001; γ-EC, $F_{2,42}$ = 19.0, P < 0.001; Fig. 7 and Table 2), with greatest levels of these compounds found in *G. antrorsum*. Glutathione redox state was also unaffected by solar UV (P < 0.05), but was much lower in *E. pauciflora* than the other two species ($F_{2,42}$ = 118.4, P < 0.001).

Discussion

Our results show clearly that whereas the reported capacity of *P. ligustrina* to utilize UV-A for photosynthesis (Turnbull et al., 2013) is not necessarily shared by other subalpine Australian species, neither can UV wavelengths be regarded as universally detrimental to the functioning of these plants. These results add to the emerging body of literature showing natural levels of UV radiation are not necessarily damaging to plants.

Despite their contrasting anatomy and chemistry, all three of the study species demonstrated capacity to use

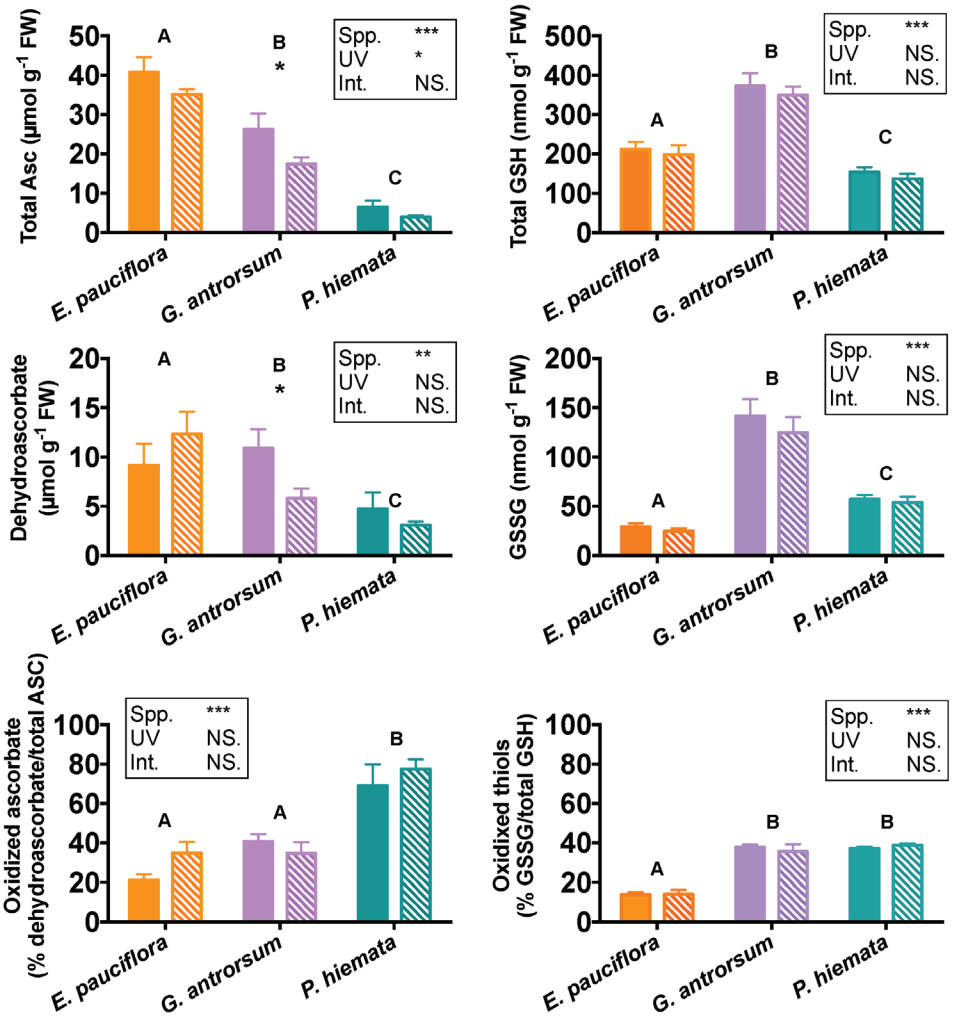


FIGURE 7. Total ascorbate concentration, dehydroascorbate concentration, ascorbate redox state (dehydroascorbate/total ascorbate), total glutathione concentration, GSSG concentration, and glutathione redox state (GSSG/total glutathione) in leaves of *E. pauciflora*, *G. antrorsum*, and *P. hiemata*. Filled bars represent the full sunlight treatment; dashed bars the UV exclusion treatment. Values are means ± SEM (n = 15). Asterisks indicate significantly different means (* P < 0.05, ** P < 0.01, *** P < 0.001) between light treatments, within species; upper-case letters denote significantly different means between species identified by Fisher's LSD test (P < 0.05).

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 2

Glutathione precursors. Concentrations of the glutathione precursors cysteine and γ-glutamylcysteine (γ-EC). Values represent means ± SEM for $n = 15$. Asterisks indicate significantly different means using a two-way ANOVA (* $P < 0.001$). Different lowercase letters represent significantly different means between species by Fisher's LSD multiple comparison test ($\alpha = 0.05$).**

	E. pauciflora			*G. antrorsum*			*P. hiemata*			*P*-value		
Redox component	Full sunlight	UV exclusion		Full sunlight	UV exclusion		Full sunlight	UV exclusion		(species)	(UV)	(Int.)
Cysteine (nmol g^{-1} FW)	8.4 ± 1.10	5.7 ± 0.66	a	22.2 ± 2.54	22.4 ± 5.03	b	9.1 ± 0.68	9.8 ± 0.88	a	***		
γ-EC (nmol g^{-1} FW)	3.7 ± 0.48	3.3 ± 0.31	a	6.0 ± 0.39	5.0 ± 0.83	b	2.7 ± 0.23	2.7 ± 0.31	c	***		

UV-A for photosynthesis as indicated by Chl *a* fluorescing at wavelengths less than 400 nm (Fig. 3). As for *P. ligustrina* (Turnbull et al., 2013), *G. anstrorsum* displayed negligible blue-green fluorescence when leaf surfaces were exposed to UV-A (Fig. 2) and had no cuticle (Fig. 4). Both *E. pauciflora* and *P. hiemata* strongly fluoresced under UV-A, a feature associated with the ability to use UV-A for photosynthesis (Turnbull et al., 2013). Whereas the excitation fluorescence profiles (Fig. 3) suggest the grass *P. hiemata* should have the greatest capacity to utilize UV-A wavelengths for photosynthesis, both the emission profile (Fig. 2) and capacity for UV-A absorption (Table 1) suggest that Chl *a* was stimulated to fluoresce upon receipt of blue-green fluorescence rather than directly by UV-A photons (Johnson and Day, 2002; Mantha et al., 2001). Regardless of whether UV-A was directly or indirectly (via blue green fluorescence) used for photosynthesis, including UV-A in the photosynthetic spectrum increased photosynthetic gain but by less than 2%. Work with lower plants (red algae) has highlighted that contributions of UV-A to photosynthesis are more important close to dawn and dusk, when visible light is limited (Gao and Xu, 2008). In higher plants, contributions of UV-A under light-limiting conditions are less clear. Of some relevance are diurnal fluctuations in UV screening compounds (Barnes et al., 2008) that offer increased protection during the middle of the day but allow additional UV to penetrate to the mesophyll closer to nighttime.

Plants mostly adapt to UV exposure via modified structures and chemistry such that evaluating impacts of UV wavelengths on photosynthesis and carbon gain is complex for terrestrial ecosystems (Jansen et al., 1998; Jordan, 2002). Removing exposure to UV did not instigate any structural change in our three study species over the course of our study period. Although this contrasts with some reports (Grammatikopoulos et al., 1998), it is consistent with strong co-regulation of leaf anatomy by light intensity (Krauss et al., 1997; Liakopoulos et al., 2006), which is also intense in subalpine areas. Leaves of *E. pauciflora* have thick cuticles and thick epidermal layers and exhibit strong structural screening against UV (Day et al., 1992). These are traits typical of woody perennials (Jordan et al., 2005) that have evolved in receipt of more direct radiation than understory grasses and herbs (Brodersen and Vogelmann, 2007). The literature contains many records of exposure to UV altering the array of leaf photoprotective compounds by increasing "sunscreens" such as flavonols and hydroxycinnamic acids (Wargent et al., 2015), which dissipate high-energy UV either as heat (Demmig-Adams and Adams, 2006) or by re-fluorescing it as lower energy photons (i.e., visible photons, Johnson et al., 2000). Even so there is wide variation among life forms (Day et al., 1992) and diurnally (Barnes et al., 2008).

One of our study species, the grass *P. hiemata*, emitted more blue-red fluorescence (an analogue for UV screening capacity, Lenk and Buschmann, 2006) when exposed to solar UV. Similar responses to non-UV wavelengths have been recorded in dicot species (Wargent et al., 2015). Our data diverges from those of Day et al. (1992), who found grasses of subalpine areas in North America less able than the dominant woody plants to screen against UV. *P. hiemata* is widely distributed in subalpine areas of SE Australia and is often the dominant species on lower, treeless plains within inverted treeline landscapes. Our data show that *P. hiemata* has more than twice the capacity to screen against UV than the tree *E. pauciflora* and more than three-fold the capacity of the herb *G. antrorsum*.

Whereas *E. pauciflora* and *P. hiemata* rely heavily on structural and chemical screens against UV, *G. antrorsum* does not. Herbaceous species generally show weaker screening capacity than other life forms (Day et al., 1992). A likely consequence is that significant amounts of UV reach the underlying mesophyll, stimulating generation of reactive oxygen species (ROS) (Czégény et al., 2016) and potentially damaging cellular organelles involved with photosynthesis (Ivanova et al., 2008). Fittingly, *G. antrorsum* maintained the greatest concentrations of glutathione

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(Noctor et al., 2012) and synthesized ascorbate upon exposure to UV (Foyer et al., 1994; Gao and Zhang, 2008; Kataria et al., 2012). Ascorbate and glutathione scavenge and detoxify ROS to prevent cellular damage (Foyer et al., 1994), ascorbate being the most responsive to light intensity (Grace and Logan, 1996; Peltzer and Polle, 2001). Whereas the constant oxidative state upon exposure to solar UV suggests the varying photoprotective strategies employed by each species prevent oxidative stress, we still observed reduced rates of photosynthesis for *G. anstrorsum* plants exposed to UV. We speculate that this could be because of direct damage to photosynthetic reaction centers (PSII being particularly sensitive to UV, Ivanova et al., 2008), as has been found in other alpine ecosystems (Albert et al., 2010; Shi et al., 2011), or to diffusional limitations arising from reduced stomatal conductance that accompanies exposure to UV (Nogues et al., 1999), as illustrated by both *G. anstrorsum* and *E. pauciflora*. Increased expression of the UV resistance locus8 (UVR8), a UV-B specific photoreceptor, has been used to explain decreased stomatal conductance following UV-B exposure (Brown et al., 2009). As UVR8 evolved with unicellular algae (Parihar et al., 2016) it is likely also present in monocots as well as dicots. We observed no regulation of g_s by UV for the grass *P. hiemata*. Regardless, it appears diffusional limitations are unlikely to explain our decreased photosynthetic rate in *G. anstrorsum* exposed to UV as WUE_i remained constant among treatments.

Conclusions

Recent studies show that exposure to solar UV can upregulate photosynthetic capacity for agricultural crops in temperate regions (Wargent et al., 2011, 2015; Davey et al., 2012). Here we demonstrate highly species-specific photobiological responses of native plants adapted to high UV exposure. Across three study species there were varying strategies to dissipate incoming UV radiation. Mild photoinhibition was recorded for one species, *G. anstrorsum*, the species least structurally or chemically able to screen against UV wavelengths. We also found that increased photosynthetic rates do not necessarily follow the inclusion of UV-A wavelengths in the photosynthetic spectrum for plants that transmit UV wavelengths to the mesophyll, and finally, that UV exposure during growth appears an important regulator of plant water loss in dicots.

Acknowledgments

We thank Barry Aitchison for site access; David Coleman, Helen Liang, Svetlana Ryazanova, and Robin Shrestha for assistance with fieldwork; and Laura Leone for microscopy preparation. We also thank the staff and students at the lab of Prof. Rennenberg at the University of Freiburg for their assistance with redox analyses, with particular thanks to Dr. Jürgen Kreuzwieser, Monika Eiblmeier, and Ursula Scheerer.

References Cited

Agati, G., and Tattini, M., 2010: Multiple functional roles of flavonoids in photoprotection. *New Phytologist,* 186(4): 786-793.

Agati, G., Azzarello, E., Pollastri, S., and Tattini, M., 2012: Flavonoids as antioxidants in plants: location and functional significance. *Plant Science,* 196: 67-76.

Ahmad, P., Jaleel, C. A., Salem, M. A., Nabi, G., and Sharma, S., 2010: Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. *Critical Reviews in Biotechnology,* 30(3): 161-175.

Albert, K. R., Mikkelsen, T. N., Ro-Poulsen, H., Michelsen, A., Arndal, M. F., Bredahl, L., Hakansson, K. B., Boesgaard, K., and Schmidt, N. M., 2010: Improved UV-B screening capacity does not prevent negative effects of ambient UV irradiance on PSII performance in High Arctic plants. Results from a six year UV exclusion study. *Journal of Plant Physiology,* 167(18): 1542-1549.

Amthor, J. S., 2010: From sunlight to phytomass: on the potential efficiency of converting solar radiation to phytoenergy. *New Phytologist*, 188(4): 939–959.

Barnes, P. W., Flint, S. D., Slusser, J. R., Gao, W., and Ryel, R. J., 2008: Diurnal changes in epidermal UV transmittance of plants in naturally high UV environments. *Physiologia Plantarum,* 133(2): 363-372.

Barta, C., Kalai, T., Hideg, K., Vass, I., and Hideg, E., 2004: Differences in the ROS-generating efficacy of various ultraviolet wavelengths in detached spinach leaves. *Functional Plant Biology,* 31(1): 23-28.

Blumthaler, M., Ambach, W., and Ellinger, R., 1997: Increase in solar UV radiation with altitude. *Journal of Photochemistry and Photobiology B: Biology,* 39(2): 130-134.

Bornman, J. F., Barnes, P. W., Robinson, S. A., Ballare, C. L., Flint, S. D., and Caldwell, M. M., 2015: Solar ultraviolet radiation and ozone depletion-driven climate change: effects on terrestrial ecosystems. *Photochemical & Photobiological Sciences,* 14(1): 88-107.

Brodersen, C. R., and Vogelmann, T. C., 2007: Do epidermal lens cells facilitate the absorptance of diffuse light? *American Journal of Botany,* 94(7): 1061-1066.

Brown, B. A., Headland, L. R., and Jenkins, G. I., 2009: UV-B action spectrum for UVR8-mediated HY5 transcript accumulation in *Arabidopsis*. *Photochemistry and Photobiology,* 85(5): 1147-1155.

Bruhn, D., Mikkelsen, T. N., Rolsted, M. M. M., Egsgaard, H., and Ambus, P., 2014: Leaf surface wax is a source of plant methane formation under UV radiation and in the presence of oxygen. *Plant Biology,* 16(2): 512-516.

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Caldwell, M. M., Robberecht, R., and Flint, S. D., 1983: Internal filters: prospects for UV-acclimation in higher-plants. *Physiologia Plantarum,* 58(3): 445-450.

Czégény, G., Wu, M., Dér, A., Eriksson, L. A., Strid, Å., and Hideg, E., 2014: Hydrogen peroxide contributes to the ultraviolet-B (280–315 nm) induced oxidative stress of plant leaves through multiple pathways. *FEBS Letters,* 588(14): 2255-2261.

Czégény, G., Mátai, A., and Hideg, É., 2016: UV-B effects on leaves - Oxidative stress and acclimation in controlled environments. *Plant Science,* 24857-63.

Davey, M. P., Susanti, N. I., Wargent, J. J., Findlay, J. E., Quick, W. P., Paul, N. D., and Jenkins, G. I., 2012: The UV-B photoreceptor UVR8 promotes photosynthetic efficiency in *Arabidopsis thaliana* exposed to elevated levels of UV-B. *Photosynthesis Research,* 114(2): 121-131.

Day, T. A., Vogelmann, T. C., and Delucia, E. H., 1992: Are some plant life forms more effective than others in screening out ultraviolet-B radiation. *Oecologia,* 92(4): 513-519.

Demmig-Adams, B., and Adams, W. W., 2006: Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytologist,* 172(1): 11-21.

Foyer, C. H., and Noctor, G., 2011: Ascorbate and glutathione: the heart of the redox hub. *Plant Physiology,* 155(1): 2-18.

Foyer, C. H., Lelandais, M., and Kunert, K. J., 1994: Photooxidative stress in plants. *Physiologia Plantarum,* 92(4): 696-717.

Gao, K., and Xu, J., 2008: Effects of solar UV radiation on diurnal photosynthetic performance and growth of *Gracilaria lemaneiformis* (Rhodophyta). *European Journal of Phycology,* 43(3): 297-307.

Gao, Q., and Zhang, L. X., 2008: Ultraviolet-B-induced oxidative stress and antioxidant defense system responses in ascorbate-deficient vtc1 mutants of *Arabidopsis thaliana*. *Journal of Plant Physiology,* 165(2): 138-148.

Gies, P., Roy, C., Javorniczky, J., Henderson, S., Lemus-Deschamps, L., and Driscoll, C., 2004: Global solar UV index: Australian measurements, forecasts and comparison with the UK. *Photochemistry and Photobiology,* 79(1): 32-39.

Grace, S. C., and Logan, B. A., 1996: Acclimation of foliar antioxidant systems to growth irradiance in three broad-leaved evergreen species. *Plant Physiology,* 112(4): 1631-1640.

Grammatikopoulos, G., Kyparissis, A., Drilias, P., Petropoulou, Y., and Manetas, Y., 1998: Effects of UV-B radiation on cuticle thickness and nutritional value of leaves in two mediterranean evergreen sclerophylls. *Journal of Plant Physiology,* 153(3-4): 506-512.

Haberer, K., Herbinger, K., Alexou, M., Tausz, M., and Rennenberg, H., 2007: Antioxidative defence of old growth beech (*Fagus sylvatica*) under double ambient O_3 concentrations in a free-air exposure system. *Plant Biology,* 9(2): 215-226.

Hu, B., Simon, J., and Rennenberg, H., 2013: Drought and air warming affect the species-specific levels of stress-related foliar metabolites of three oak species on acidic and calcareous soil. *Tree Physiology,* 33(5): 489-504.

Inada, K., 1976: Action spectra for photosynthesis in higher plants. *Plant and Cell Physiology,* 17(2): 355-365.

Ivanova, P. I., Dobrikova, A. G., Taneva, S. G., and Apostolova, E. L., 2008: Sensitivity of the photosynthetic apparatus to UV-A radiation: role of light-harvesting complex II-photosystem II supercomplex organization. *Radiation and Environmental Biophysics,* 47(1): 169-177.

Jacobs, J. F., Koper, G. J. M., and Ursem, W. N. J., 2007: UV protective coatings: a botanical approach. *Progress in Organic Coatings,* 58(2-3): 166-171.

Jansen, M. A. K., Gaba, V., and Greenberg, B. M., 1998: Higher plants and UV-B radiation: balancing damage, repair and acclimation. *Trends in Plant Science,* 3(4): 131-135.

Johnson, G. A., and Day, T. A., 2002: Enhancement of photosynthesis in *Sorghum bicolor* by ultraviolet radiation. *Physiologia Plantarum,* 116(4): 554-562.

Johnson, G. A., Mantha, S. V., and Day, T. A., 2000: A spectrofluorometric survey of UV-induced blue-green fluorescence in foliage of 35 species. *Journal of Plant Physiology,* 156(2): 242-252.

Jordan, B. R., 2002: Molecular response of plant cells to UV-B stress. *Functional Plant Biology,* 29(8): 909-916.

Jordan, G. J., Dillon, R. A., and Weston, P. H., 2005: Solar radiation as a factor in the evolution of scleromorphic leaf anatomy in Proteaceae. *American Journal of Botany,* 92(5): 789-796.

Karabourniotis, G., Papadopoulos, K., Papamarkou, M., and Manetas, Y., 1992: Ultraviolet-B radiation absorbing capacity of leaf hairs. *Physiologia Plantarum,* 86(3): 414-418.

Kataria, S., Dehariya, P., Guruprasad, K. N., and Pandey, G. P., 2012: Effect of exclusion of ambient solar UV-A/B components on growth and antioxidant response of cotton (*Gossypium hirsutum* L.). *Acta Biologica Cracoviensia Series Botanica,* 54(2): 47-53.

Kataria, S., Jajoo, A., and Guruprasad, K. N., 2014: Impact of increasing ultraviolet-B (UV-B) radiation on photosynthetic processes. *Journal of Photochemistry and Photobiology B: Biology,* 137: 55-66.

Krauss, P., Markstadter, C., and Riederer, M., 1997: Attenuation of UV radiation by plant cuticles from woody species. *Plant Cell and Environment,* 20(8): 1079-1085.

Landi, M., Tattini, M., and Gould, K. S., 2015: Multiple functional roles of anthocyanins in plant-environment interactions. *Environmental and Experimental Botany,* 119: 4-17.

Lee, Y. G., Koo, J. H., and Kim, J., 2015: Influence of cloud fraction and snow cover to the variation of surface UV radiation at King Sejong station, Antarctica. *Atmospheric Research,* 164: 99-109.

Lenk, S., and Buschmann, C., 2006: Distribution of UV-shielding of the epidermis of sun and shade leaves of the beech (*Fagus sylvatica* L.) as monitored by multi-colour fluorescence imaging. *Journal of Plant Physiology,* 163(12): 1273-1283.

Liakopoulos, G., Nikolopoulos, D., Klouvatou, A., Vekkos, K. A., Manetas, Y., and Karabourniotis, G., 2006: The photoprotective role of epidermal anthocyanins and surface

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

pubescence in young leaves of grapevine (*Vitis vinifera*). *Annals of Botany,* 98(1): 257-265.

Mantha, S. V., Johnson, G. A., and Day, T. A., 2001: Evidence from action and fluorescence spectra that UV-induced violet-blue-green fluorescence enhances leaf photosynthesis. *Photochemistry and Photobiology,* 73(3): 249-256.

McCree, K. J., 1972: The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agricultural Meteorology,* 9(3/4): 191-216.

Nishiyama, Y., Allakhverdiev, S. I., and Murata, N., 2006: A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. *Biochimica et Biophysica Acta-Bioenergetics,* 1757(7): 742-749.

Noctor, G., Mhamdi, A., Chaouch, S., Han, Y., Neukermans, J., Marquez-Garcia, B., Queval, G., and Foyer, C. H., 2012: Glutathione in plants: an integrated overview. *Plant Cell and Environment,* 35(2): 454-484.

Nogues, S., Allen, D. J., Morison, J. I. L., and Baker, N. R., 1999: Characterization of stomatal closure caused by ultraviolet-B radiation. *Plant Physiology,* 121(2): 489-496.

Okamura, M., 1980: An improved method for determination of L-ascorbic-acid and L-dehydroascorbic acid in blood-plasma. *Clinica Chimica Acta,* 103(3): 259-268.

Parihar, P., Singh, R., Singh, S., Tripathi, D. K., Chauhan, D. K., Singh, V. P., and Prasad, S. M., 2016: Photoreceptors mapping from past history till date. *Journal of Photochemistry and Photobiology B: Biology,* 162: 223-231.

Peltzer, D., and Polle, A., 2001: Diurnal fluctuations of antioxidative systems in leaves of field-grown beech trees (*Fagus sylvatica*): responses to light and temperature. *Physiologia Plantarum,* 111(2): 158-164.

Roy, C. R., Gies, H. P., and Toomey, S., 1995: The solar UV radiation environment: measurement techniques and results. *Journal of Photochemistry and Photobiology B: Biology,* 31(1-2): 21-27.

Salby, M. L., 2012: Physics of the atmosphere and climate. Cambridge, New York: Cambridge University Press.

Schupp, R., and Rennenberg, H., 1988: Diurnal changes in the glutathione content of spruce needles (*Picea abies* L). *Plant Science,* 57(2): 113-117.

Shi, S.-B., Shang, Y.-X., Zhu, P.-J., and Zhang, D.-G., 2011: Effects of UV-B exclusion on photosynthetic physiology in alpine plant *Saussurea superba*. *Chinese Journal of Plant Ecology,* 35(2): 176-186.

Snyrychova, I., Kos, P. B., and Hideg, E., 2007: Hydroxyl radicals are not the protagonists of UV-B-induced damage in isolated thylakoid membranes. *Functional Plant Biology,* 34(12): 1112-1121.

Tattini, M., Gravano, E., Pinelli, P., Mulinacci, N., and Romani, A., 2000: Flavonoids accumulate in leaves and glandular trichomes of *Phillyrea latifolia* exposed to excess solar radiation. *New Phytologist,* 148(1): 69-77.

Toth, S. Z., Schansker, G., and Garab, G., 2013: The physiological roles and metabolism of ascorbate in chloroplasts. *Physiologia Plantarum,* 148(2): 161-175.

Turnbull, T. L., Barlow, A. M., and Adams, M. A., 2013: Photosynthetic benefits of ultraviolet-A to *Pimelea ligustrina*, a woody shrub of sub-alpine Australia. *Oecologia,* 173(2): 375-385.

Wargent, J. J., and Jordan, B. R., 2013: From ozone depletion to agriculture: understanding the role of UV radiation in sustainable crop production. *New Phytologist*, 197(4): 1058–1076.

Wargent, J. J., Elfadly, E. M., Moore, J. P., and Paul, N. D., 2011: Increased exposure to UV-B radiation during early development leads to enhanced photoprotection and improved long-term performance in *Lactuca sativa*. *Plant Cell and Environment,* 34(8): 1401-1413.

Wargent, J. J., Nelson, B. C. W., McGhie, T. K., and Barnes, P. W., 2015: Acclimation to UV-B radiation and visible light in *Lactuca sativa* involves up-regulation of photosynthetic performance and orchestration of metabolome-wide responses. *Plant Cell and Environment,* 38(5): 929-940.

MS submitted 26 February 2017
MS accepted 25 August 2017

Downloaded From: https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use