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Xanthophyll cycles in the juniper haircap moss (*Polytrichum juniperinum*) and Antarctic hair grass (*Deschampsia antarctica*) on Livingston Island (South Shetland Islands, Maritime Antarctica)

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Abstract

The summer climate in Maritime Antarctica is characterised by high humidity and cloudiness with slightly above zero temperatures. Under such conditions, photosynthetic activity is temperature-limited and plant communities are formed by a few species. These conditions could prevent the operation of the photoprotective xanthophyll (VAZ) cycle as low irradiance reduces the excess of energy and low temperatures limit enzyme activity. The VAZ cycle regulates the dissipation of the excess of absorbed light as heat, which is the main mechanism of photoprotection in plants. To test whether this mechanism operates dynamically in Antarctic plant communities, we characterised pigment dynamics under natural field conditions in two representative species: the moss *Polytrichum juniperinum* and the grass *Deschampsia antarctica*. Pigment analyses revealed that the total VAZ pool was in the upper range of the values reported for most plant species, suggesting that they are exposed to a high degree of environmental stress. Despite cloudiness, there was a strong conversion of violaxanthin (V) to zeaxanthin (Z) during daytime. Conversely, the dark-induced enzymatic epoxidation back to V was not limited by nocturnal temperatures. In contrast with plants from other cold ecosystems, we did not find any evidence of overnight retention of Z or sustained reductions in photochemical efficiency. These results are of interest for modelling, remote sensing and upscaling of the responses of Antarctic vegetation to environmental challenges.

Keywords *Deschampsia antarctica* · *Polytrichum juniperinum* · Photochemical efficiency · Violaxanthin · Zeaxanthin

Introduction

Photosynthesis is the main energy input in the vast majority of Earth's ecosystems, and it is also the key to understanding the long-term changes in atmospheric CO_2 concentrations that ultimately result in climate alterations. Although this process is reasonably well understood at the biochemical level, there are many uncertainties when the scale of observation is moved upwards. For example, it is well known that photosynthesis is dynamically regulated by the amount of energy that reaches the pigment–protein complexes; thus, that when light is in excess, the efficiency of energy conversion is downregulated, decreasing photosynthetic efficiency (Kromdijk et al. 2016). Conversely, under limited light, photochemical efficiency increases. This process is matched, and partially regulated, by the interconversions of three xanthophylls, violaxanthin (V), antheraxanthin (A) and zeaxanthin (Z) within the light-harvesting antenna (Pinnola and Bassi 2018). Thus, under nonstress conditions, when light absorption activates proton pumping in chloroplasts, lumen acidification induces the activity of the enzyme violaxanthin de-epoxidase (VDE), which reduces diepoxide V to Z, via A (Pfündel and Dilley 1993). Under low light or darkness, the reverse reaction takes place and Z is converted into V by the action of the Z-epoxidase (ZE), which is active at neutral pH (Färber and Jahns 1998). These interconversions among the three xanthophylls constitute what is known as the xanthophyll, violaxanthin or VAZ cycle (Demmig-Adams and Adams 1996). Overall, when light is in excess, Z accumulates, downregulating the photochemical efficiency and the higher the energy excess is, the higher the Z content.

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The fact that this cycle correlates with light use efficiency and that it involves three pigments that consequently absorb visible light, has led to the development of methods for its remote detection by spectrometric measurements (Peñuelas et al. 1995). As a result, several optical indices that estimate photosynthetic efficiency have been developed, as is the case of the photochemical reflectance index (PRI) (Gamon et al. 1990). However, when we shift to larger scales of observation, a number of uncertainties appear, and the relationship between optical indices and photosynthetic efficiency is not straightforward (Garbulsky et al. 2011). Among other gaps in knowledge, the relationship between the operation of the VAZ cycle and the photochemical efficiency has not been characterised in all ecosystems and plant functional groups. In addition, it has been shown that particular conditions, such as desiccation, can lead to the accumulation of Z in darkness (Fernández-Marín et al. 2021). Additionally, low temperatures block ZE activity, impeding the reconversion of Z into V during the night (Verhoeven 2014). Additionally, the freezing of tissues activates the de-epoxidation of the xanthophyll cycle in evergreen plants (Fernández-Marín et al. 2018, 2021).

The dynamics of the VAZ cycle under natural conditions have been well characterised for a large series of plants mostly belonging to temperate (Niinemets et al. 2003), alpine (Streb et al. 2003) and tropical biomes (Matsubara et al. 2009), as well as for major crops (Falbel et al. 1994) and cultivated trees (Matsubara et al. 2011). However, the information available for high latitude and polar environments is scarce (Bascuñán-Godoy et al. 2010; Fernández-Marín et al. 2019), in part due to the inherent technical limitations of these "hard to reach" places. These limitations include the collection, storage and transport of samples. In fact a majority of the few studies that have focussed on the VAZ cycle in Antarctic plants have been performed ex situ with specimens collected in the field (Lovelock et al. 1995; Lovelock and Robinson 2002; Pérez-Torres et al. 2004; Bravo et al. 2007; Molina-Montenegro et al. 2016; Sáez et al. 2019), and only a few preliminary studies were carried out directly on field specimens (Post 1990). However, the particular conditions of these ecosystems, such as low average temperatures plus long photoperiods (i.e. > 20 h day or night) throughout the year, together with the global importance of polar areas, demands such field studies. In the Arctic tundra, for example, the effect of constant daylight on the VAZ cycle was studied in a few locations (Magney et al. 2017; Fernández-Marín et al. 2018, 2019). This phenomenon only occurs at very high latitudes and deserves further study to characterise its influence on photosynthetic dynamics. In contrast with the Arctic, higher plant communities in Antarctica are much less developed at latitudes where the sun never sets because of the much harsher environmental conditions. In fact, the only two angiosperm species occurring in Antarctica are almost exclusively found on the shores of the Antarctic Peninsula and the South Shetland Islands (Robinson et al. 2003; Peat et al. 2007), the so-called Maritime Antarctic region. The remaining Antarctic vegetation is basically cryptogamic, comprising approximately 130 bryophyte and 475 lichen species on the whole continent and islands (Øvstedal and Lewis Smith 2001; Robinson et al. 2003; Peat et al. 2007; Ochyra et al. 2008).

During the vegetative period, the climate in this region is typically moist and windy, with mean temperatures slightly higher than zero and frequent cloudiness (Robinson et al. 2003). Under such conditions, and considering the rare occurrence of clear skies and the low temperature-induced enzyme activity limitation, it is uncertain whether the VAZ cycle operates in the same way as it does in warmer ecosystems. To fill this gap, in the present study, we have characterised pigment dynamics under natural field conditions in two representative Antarctic plant species: the moss *Polytrichum juniperinum* (Hedwig) and the grass *Deschampsia antarctica* (É.Desv). Furthermore, given the scarcity of field studies under natural Antarctic conditions, this study provides a substantial contribution to our understanding of the ecophysiology of Antarctic plants.
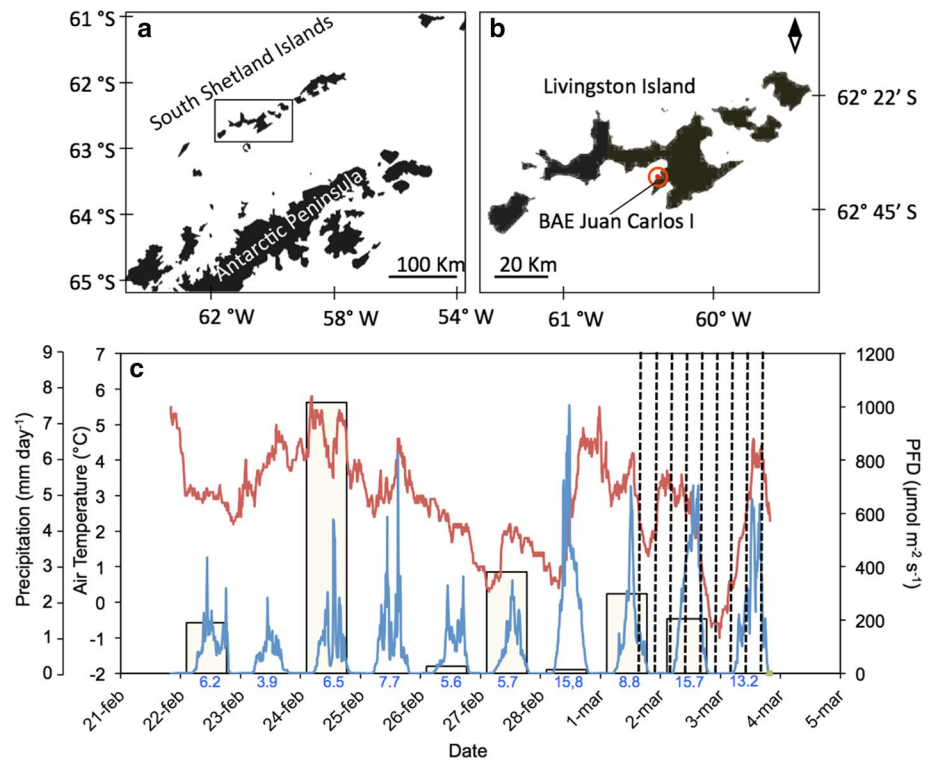
Methods

Field site, plant material and experimental design

Measurements were performed in the surroundings of the Spanish Antarctic Research Station "Base Antártica Española Juan Carlos I" (BAE JCI) in Livingston Island, South Shetland (62°40′ S, 60°23′ W) during the first days of March 2018 (end of the Austral summer) (Fig. 1a, b). During the study period and the preceding week, the air temperature ranged between − 0.7 °C and + 5.6 °C with almost constant cloud coverage and an average daily rainfall of 1.57 mm day^{-1} (Fig. 1c). The cumulative daily irradiance was on average 8.44 mol photons day^{-1}; however, it was 73% higher during the study period than during the previous week.

Two plant species representative of the Antarctic tundra were studied: juniper haircap moss (*Polytrichum juniperinum*) and Antarctic hair grass (*Deschampsia antarctica*). The first is a cosmopolitan, widely distributed moss, while the second is a grass occurring along the Antarctic Islands and Peninsula and the southern tip of South America. Four cushions of each species were monitored every six hours during two consecutive day–night cycles. Thus, two consecutive midnights and three middays were studied. At each time point and cushion, chlorophyll fluorescence was measured in two adjacent leaves, one was dark-adapted with a Leaf-Clip and used for determination of the maximal

Fig. 1 Weather conditions and geographical location of the study site. Upper panels include a map showing the location of the South Shetland Islands (**a**) and the study site adjacent to the Spanish Antarctic Station (BAE Juan Carlos I) in Livingston Island (**b**). Bottom panel show air temperature (red line), daily precipitation (grey bars) and photon flux density (blue line) during the study period and the previous week (**c**). Vertical dashed lines show sampling time points. Numbers in blue at the bottom of the figure represent values of daily cumulative irradiance (mol m^{-2} day^{-1})

efficiency of PSII (F_v/F_m), while the other was used for the determination of the actual efficiency of PSII (Φ_{PSII}) (see description of the fluorescence protocols in the following paragraph). The latter was collected immediately after fluorescence measurements and frozen in liquid nitrogen, for additional photosynthetic pigment analyses. Samples were thereafter stored at -80 °C in the BAE JCI and later transported to Spain at the same temperature in the research ship BIO Hesperides. Once the ship arrived in Spain the cold chain (-80 °C) was always maintained until the samples were finally analysed at the University of the Basque Country.

Chlorophyll fluorescence

Chlorophyll *a* (Chl *a*) fluorescence was measured in the field using a portable modulated Plant Stress Kit fluorometer (Opti-Sciences, Hudson NH, USA). In dark-adapted samples (30 min) the maximum Chl *a* fluorescence (F_m) was induced with a saturating pulse (0.8 s duration, 7000 µmol m^{-2} s^{-1} PFD) while the initial fluorescence (F_o) was recorded with red modulated measuring light (ML < 1 µmol photons m^{-2} s^{-1}). The F_v/F_m was then estimated by the ratio $F_v/F_m = (F_m - F_o)/F_m$. The actual efficiency of PSII (Φ_{PSII}) was measured by using a Y(II) metre from the same manufacturer. In illuminated leaves (i.e. those directly exposed to natural solar radiation) the operating quantum efficiency of PSII was estimated as $\Phi_{PSII} = (F_m' - F_s)/F_m'$, where F_m' is the

maximum Chl *a* fluorescence induced with a saturating pulse and F_s is the actual Chl *a* fluorescence under illumination. The photon flux density reaching the samples during each Φ_{PSII} measurement (PFD$_{\Phi PSII}$) was recorded with the Leaf-Clip built-in irradiance sensor.

Pigment analyses

Approximately 25–60 mg FW per replicate was used for photosynthetic pigment and tocopherol analyses. Plant material was ground under liquid N$_2$. The metabolites were then extracted with an acetone solution buffered with 0.5 g CaCO$_3$ L^{-1} and the extracts were centrifuged at 16,100g and 4 °C. The supernatant was filtered through a 0.2 µm pore size filter (Teknokroma, Barcelona, Spain). Pigment and tocopherol composition were finally analysed by HPLC using a reversed-phase C18 column (Waters, Milford, Massachusetts, USA) as described previously (García-Plazaola and Becerril 1999). We used a photodiode array detector (Waters Model 996) for pigments and a scanning fluorescence detector (Waters Model 474) for tocopherols.

From the analyses, several ratios were derived and used to characterise the structure and function of the photosynthetic apparatus:

- Chlorophyll *a/b* (Chl *a/b*) was calculated as the molar ratio between chlorophyll a and b. Although Chl *b* is located in the light-harvesting complexes (LHCs) Chl *a* can be

present both in the antennae and core complexes (CCs) and is a good indicator of the antenna size (Esteban et al. 2015a). This ratio can also be affected by the stoichiometry of PSI to PSII, as most of the Chl *b* pool is bound to LHCII. However, this relationship is not straightforward, as state transitions can derive energy from LHCII to PSI.

- β-Carotene/neoxanthin (β-Car/Neo) was calculated as the molar ratio between neoxanthin (Neo) and β-carotene (β-Car). Since β-Car is mostly present in CCs in thylakoids (Cazzaniga et al. 2012) while Neo is only bound to antenna proteins (Formaggio et al. 2001), this parameter can be considered a plausible indicator of the CC/LHC ratio. However, this index should be considered with care since β-Car can also be found in the chloroplast envelope, thereby affecting this ratio.

- Xanthophyll cycle pool (VAZ) per chlorophyll (VAZ/Chl): The total VAZ pool was calculated as the sum of violaxanthin (V), antheraxanthin (A) and zeaxanthin (Z) and expressed on a chlorophyll (*a*+*b*) basis. As a consequence, the VAZ pool is usually proportional to the light environment where the plant or tissue develops, and is highly responsive to light fluctuations (Esteban et al. 2015a).

- Total tocopherol pool (Toc) per chlorophyll (Toc/Chl): total Toc was calculated as the sum of α-Toc, γ-Toc and δ-Toc and expressed on a chlorophyll (*a*+*b*) basis. As the main plastidial lipophilic antioxidant, its content usually scales positively with irradiance (García-Plazaola et al. 2004).

- De-epoxidation index (AZ/VAZ): The de-epoxidation index (AZ/VAZ) was calculated as the sum of A and Z divided by the sum of V, A and Z. It represents the state of operation of the VAZ cycle, which is proportional to light excess and/or to the extent of other stress factors (Demmig-Adams and Adams 1996; Fernández-Marín et al. 2021).

Statistical treatments

A *t* test was used to compare pigment ratios to chlorophyll between both species.

Linear regression was applied to analyse the relationships between the main parameters analysed in this study and the relationships between AZ/VAZ and irradiance. Calculated *P* values and regression lines are indicated on the figures whenever significant at $P < 0.05$. Statistical analyses were performed with IBM SPSS v24.0.

Results

The pigment content per unit of dry mass was threefold higher in *D. antarctica* than in *P. juniperinum*, but its composition was qualitatively similar in both species (Fig. 2).

Thus, lutein (Lut) was the dominant carotenoid, followed by the total VAZ pool, β-carotene (β-Car) and neoxanthin (Neo). The carotenoid and tocopherol ratios to chlorophyll differed slightly, but significantly, between both species, with the exception of VAZ/Chl (data not shown, derived from Fig. 2). Thus, Neo/Chl, Lut/Chl and total tocopherol/Chl were 13%, 21% and 43% higher in *P. juniperinum*, respectively. In contrast β-Car/Chl was 4% higher in *D. antarctica*. Chl*a*/*b* also differed between species, being 3.32 ± 0.06 in *D. antarctica* and 3.05 ± 0.05 in *P. juniperinum*.

During the study period, differences between midday and midnight values were not significant (at $P < 0.05$) for any of the pigment to chlorophyll ratios studied, but they were for α-Toc/Chl in *D. antarctica* (Fig. 3). Despite this, significant longer-term trends (48 h) were found between the first midday and the last midday for several of the analysed parameters, in parallel to the overall decrease in temperature and irradiance observed during the sampling period (Fig. 1c). Thus Chl *a*/*b* decreased in both species while Neo/Chl showed the opposite pattern. In addition, α-Toc/Chl and β-Car/Neo decreased in *P. juniperinum*. These parallel responses resulted in the existence of significant correlations between pigment contents. Thus Chl *a*/*b* correlated positively with β-Car/Neo, VAZ/Chl and α-Toc/Chl in *D. antarctica* (Fig. 4). In the case of *P. juniperinum* the correlation was significant only for Chl *a*/*b* vs α-Toc/Chl (Fig. 4c).

In contrast to the stability of VAZ/Chl, the de-epoxidation ratio (AZ/VAZ) varied rhythmically along the daily cycles in both species. This parameter peaked at noon and reached a minimum at midnight that was maintained until dawn, and its values were higher in *P. juniperinum* at all
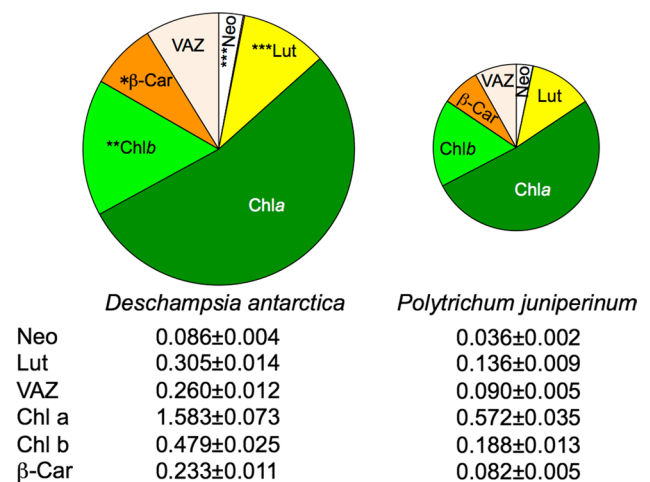

	Deschampsia antarctica	*Polytrichum juniperinum*
Neo	0.086±0.004	0.036±0.002
Lut	0.305±0.014	0.136±0.009
VAZ	0.260±0.012	0.090±0.005
Chl a	1.583±0.073	0.572±0.035
Chl b	0.479±0.025	0.188±0.013
β-Car	0.233±0.011	0.082±0.005

Fig. 2 Pigment composition in the leaves of *Deschampsia antarctica* and *Polytrichum juniperinum* (in µmol g^{-1} DW). Size of the pie charts is proportional to the total pigment content of each species (2.95 and 1.11 µmol g^{-1}DW, respectively). Asterisks denote significant differences between both species in the ratios of each pigment to Chl *a*+*b* at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***)
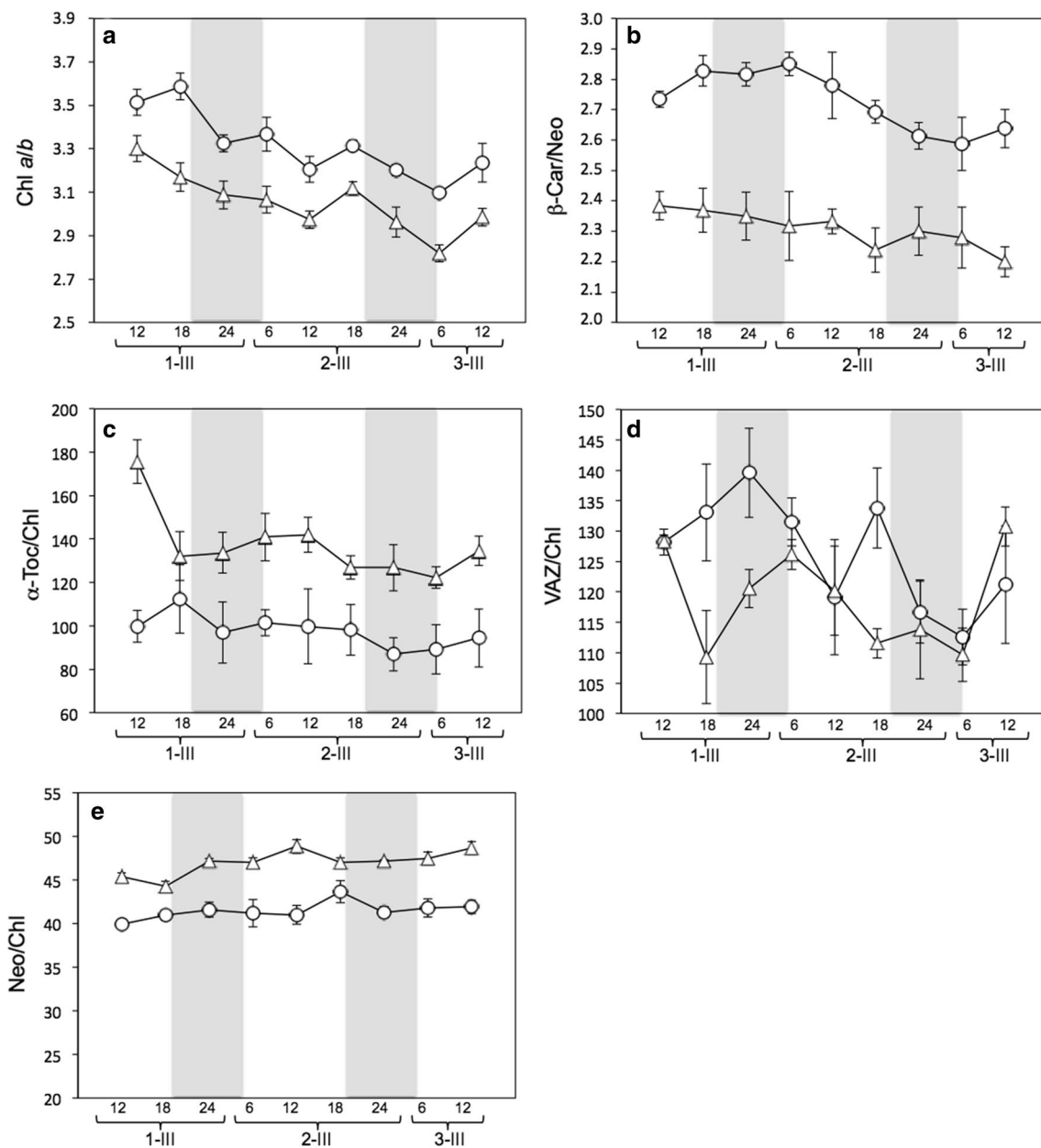
Fig. 3 Daily changes in pigment composition. Time-dependent changes during the study period in pigment ratios indicative of photosynthetic activity and regulation for *Polytrichum juniperinum* (triangles) and *Deschampsia antarctica* (circles): Chl *a*/*b* (**a**), β-Car/Neo (**b**), Toc/Chl (**c**), VAZ/Chl (**d**) and Neo/Chl (**e**). Chl*a*/*b* and β-Car/Neo are expressed in mol mol^{-1} and Toc/Chl, VAZ/Chl and Neo/Chl are expressed in mmol mol^{-1}. Darkened areas denote night periods. Values represent the mean of four replicates $\pm$ SE

timepoints (Fig. 5). Midday values of AZ/VAZ were on average twofold higher in *P. juniperinum* and its daily amplitude of oscillation was on average 70% higher in this species. In contrast with this parameter, F_v/F_m did not show any clear pattern of temporal variation in either of the two species. As a consequence of this distinct behaviour, AZ/VAZ and F_v/F_m were not related in either of the two species studied (Fig. 6). In contrast, AZ/VAZ and

Φ_{PSII} showed a strong negative correlation in both species (Fig. 6), while AZ/VAZ correlated with the actual PFD at the time of sampling only in *P. juniperinum*. The linear correlation coefficient was markedly stronger in both species when AZ/VAZ was plotted against the irradiance accumulated during the two hours prior to sampling instead of to the actual PFD (Fig. 6c, d).
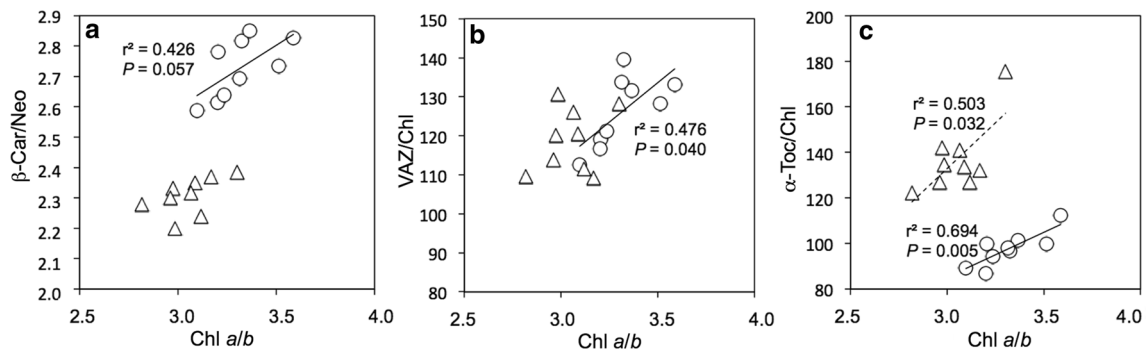
Fig. 4 Correlations between pigment ratios. Regression lines between Chl *a/b vs* β-Car/Neo (**a**), Chl *a/b vs* VAZ/Chl (**b**) and Chl *a/b vs* Toc/Chl (**c**) in *Polytrichum juniperinum* (triangles, dashed lines) and *Deschampsia antarctica* (circles, solid lines). Chl*a/b* and β-Car/Neo are expressed in mol mol^{-1} and Toc/Chl and VAZ/Chl are expressed in mmol mol^{-1}. Linear regression lines, r^2 and P values are shown when statistically significant at $P < 0.05$
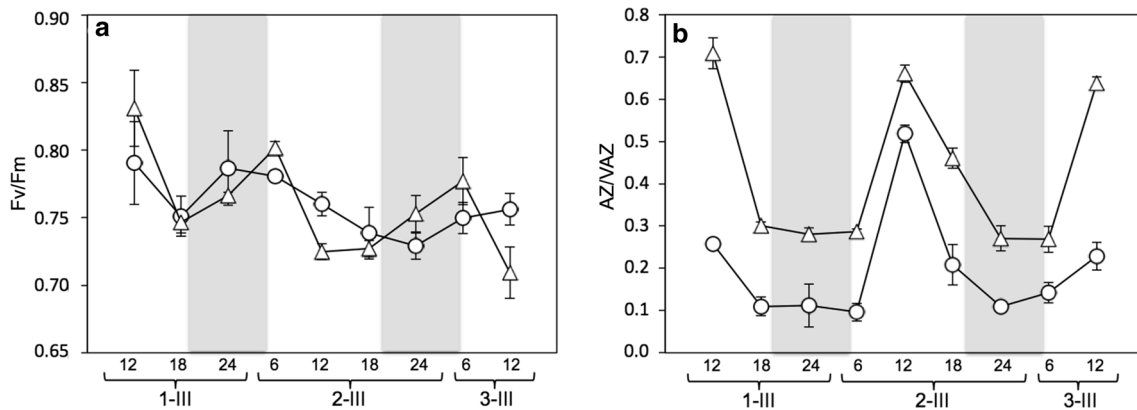

Fig. 5 Daily changes in pigment composition. Time-dependent changes during the study period in F_v/F_m (**a**) and AZ/VAZ (**b**) for *Polytrichum juniperinum* (triangles) and *Deschampsia antarctica* (circles). AZ/VAZ is expressed in mol mol^{-1}. Darkened areas denote night periods. Values represent the mean of four replicates ± SE
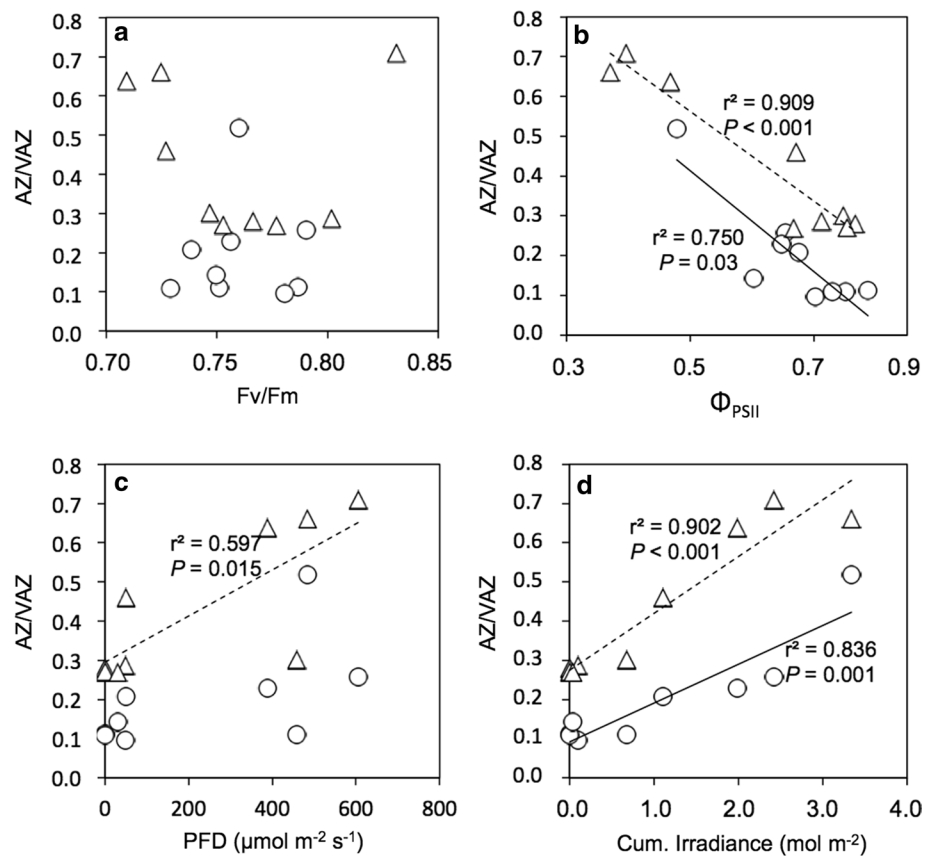
Discussion

Plant life in Antarctica encounters the environmental limits of its survival capacity (Robinson et al. 2003). Maritime Antarctica, which comprises the Antarctic Peninsula and Islands, is comparatively milder than the continent, but even though the growing season is very short, summer temperatures rarely surpass the threshold of ten degrees. Apart from the scarce ice-free area available on the continent and the obvious temperature limitation, the few plant species inhabiting Antarctica have to face an additional stress factor caused by the high cloudiness (80%) (Bañón et al. 2013), which potentially compromises the photosynthetic energy budget. In fact, during the study period, the values of cumulative daily irradiance were similar to those reported in the understorey of temperate forests (Niinemets 2007; Valladares et al. 2008). In addition, sun irradiance not only provides the energy for photosynthesis but also contributes to the temperature difference between air and leaves in Antarctic mosses. Even in Antarctica, moss leaves can easily reach +20 °C during the infrequent sunny periods (Perera-Castro et al. 2020a). Consequently, low irradiance also implies a thermal limitation. During our study, lower irradiance and air temperatures (including sub-zero values) were registered at the end of the sampling time. This could be the reason behind the decreasing trend in the Chl *a/b* and F_v/F_m ratios obtained throughout the study.

The two species studied here can be considered good examples of contrasting strategies of Antarctic plants. Thus, while *P. juniperinum* is a poikilohydric moss that activates or deactivates metabolism in response to water availability, *D. antarctica* is a homeohydric grass. Their photosynthetic responses in Antarctic conditions have been characterised by a number of studies (Sáez et al. 2019; Clemente-Moreno

Fig. 6 Correlations between photochemical parameters and light environment. Regression lines between AZ/VAZ *vs* F_v/F_m (**a**), AZ/VAZ *vs* Φ_{PSII} (**b**), AZ/VAZ *vs* actual photosynthetic photon flux density (PFD) (**c**) and AZ/VAZ *vs* cumulative irradiance (**d**) received during the previous 2 h in *Polytrichum juniperinum* (triangles, dashed lines) and *Deschampsia antarctica* (circles, solid lines). Linear regression lines, r^2 and P values are shown when statistically significant at $P < 0.05$

et al. 2020; Perera-Castro et al. 2020a, b) that show that the optimum temperature for photosynthesis occurs at a range substantially higher than those experienced in their natural environment. This implies that even during frequent cloudy days and due to the low temperatures, leaves suffer an imbalance between the amount of light energy absorbed by chloroplasts and that actually used for photosynthesis. The imbalance could be potentially higher for *P. juniperinum* considering its relatively lower maximal net CO_2 assimilation capacity if compared to *D. antarctica*: roughly 5 *vs.* 20 μmol m^{-2} s^{-1} (Clemente-Moreno et al. 2020; Perera-Castro et al. 2020b). This excess of absorbed light energy exacerbated by close to zero temperatures triggers the activation of photoprotective mechanisms. Among these mechanisms, several authors have highlighted the prominent role of antioxidant defences in Antarctic plants (Pérez-Torres et al. 2004; Clemente-Moreno et al. 2019, 2020). The activation of photoprotective thermal energy dissipation has also been observed in Antarctic species, but direct evidence linking this process to the operation of the xanthophyll cycle is missing (Perera-Castro et al. 2020b).

VAZ cycle activity seems to be higher in Arctic shrubs than in their lower latitude relatives (Magney et al. 2017), but the complete reversion of the cycle seems to be negatively affected by midnight sun (Fernández-Marín et al. 2019). The present study was performed close to the

Equinox, meaning that the photoperiod was close to 12 h. Under these conditions, a strong xanthophyll interconversion was observed, particularly for *P. juniperinum*. Maximum values of AZ/VAZ in both species were observed at noon (0.335 with an amplitude of 0.224 and 0.669 with an amplitude of 0.393 in *D. antarctica* and *P. juniperinum*, respectively), and these values were remarkably similar to those reported in the literature for other Antarctic species: 0.28 (amplitude 0.10) in angiosperms (*C. quitensis*) (Bascuñán-Godoy et al. 2010) and 0.665 (amplitude 0.283) in mosses (Lovelock 1995). Unexpectedly, this ratio only correlated with the actual PFD in *P. juniperinum* (Fig. 6c), suggesting that the operation of the VAZ cycle responds faster to environmental conditions in the moss. However, in both the species, the correlation between AZ/VAZ and the cumulative dose of irradiance received during the previous two hours was much stronger than that with the actual irradiance at the time of sampling. This finding supports that the epoxidation state of the xanthophyll cycle represents a kind of "light memory" (Esteban et al. 2015b) and is not determined by the actual conditions but by the illumination history of the plant. Thus, being proportional to the irradiance received during the last hour, the epoxidation state itself represents a mechanism of information storage that modulates photosynthetic responses, fulfilling the classical definition proposed by Trewavas (2003)

for "plant memory". The time window of such a memory mechanism remains to be elucidated. In fact the reversible accumulation of A and Z did not have any photoinhibitory effect (decrease in F_v/F_m), but it controlled the actual photochemical efficiency (Φ_{PSII}) of energy conversion (Fig. 6b).

The VAZ pool size, which integrates the level of light stress accumulated by the leaf during the previous days (García-Plazaola et al. 2012), was also consistent with the previous data on Antarctic plants. Thus, the mean values of VAZ/Chl were 126 mmol mol^{-1} and 119 mmol mol^{-1} in *D. antarctica* and *P. juniperinum,* respectively*,* while the VAZ/Chl content has been reported to be in the range of 85–144 mmol mol^{-1} in Antarctic bryophytes (Lovelock et al. 1995; Lovelock and Robinson 2002; Robinson et al. 2003; Schroeter et al. 2012) and 117 mmol mol^{-1} in *C. quitensis* (Bascuñán-Godoy et al. 2010). All these values are markedly higher than the average VAZ/Chl for unstressed plants (74 mmol mol^{-1}) (Esteban et al. 2015a), suggesting that Antarctic plants are constitutively under stress.

Apart from daily changes in pigment composition, plants perform long-term adjustments in the structure of the photosynthetic apparatus. The present case study represented the transition from a period of low irradiance (average 5.9 mol photons m^{-2} day^{-1}) to another period of moderate irradiance (average 13.4 mol photons m^{-2} day^{-1}) (Fig. 1). A decrease in some parameters mimicked that change, such as Chl *a/b* in both species (Fig. 2a) and α-Toc/Chl and β-Car/Neo in *P. juniperinum* (Fig. 2b, c), but the direction was the opposite of what was expected, since these parameters usually correlate negatively with antenna size and/or photoprotective demand (Esteban et al. 2015a), but a wider time window is needed to understand the meaning of such changes. A process of desiccation-induced accumulation of tocopherols (Oliver et al. 2011) could contribute to such unexpected results, at least in *P. juniperinum*. The higher responsiveness of *P. juniperinum* supports the result that the physiological responses of moss are comparatively more dynamic than those of grass, probably because bryophytes are generally closer to their optimal range of performance under the environmental conditions of Maritime Antarctica.

Overall, the present study shows that even during the frequent cloudy days that characterise Maritime Antarctica, the VAZ cycle is operative and fully reversible in these two representative examples of the regional flora. Furthermore, we did not find any evidence of sustained Z accumulation or of sustained energy dissipation linked to the accumulation of Z, as is typically observed in the vegetation of other cold ecosystems. Given that the PRI is one of the most promising indices for the remote sensing of the photosynthetic performance (D'Odorico et al. 2021) and that this index captures changes in the state of operation of the VAZ cycle, the present results could be useful for the correct interpretation of remote sensing data in the Antarctic region.

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Data availability Available from corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare they have no competing interests.

Consent for publications All authors agree.

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