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SI ADVANCES IN PHOTOSYNTHESIS

How do vascular plants perform photosynthesis in extreme environments? An integrative ecophysiological and biochemical story

Beatriz Fernández-Marín[1,2,†], Javier Gulías[3,†], Carlos M. Figueroa[4], Concepción Iñiguez[3], María J. Clemente-Moreno[3], Adriano Nunes-Nesi[5], Alisdair R. Fernie[6], Lohengrin A. Cavieres[7], León A. Bravo[8,9], José I. García-Plazaola[2] and Jorge Gago[3,*]

[1] *Department of Botany, Ecology and Plant Physiology, University of La Laguna, Tenerife 38200, Spain,*
[2] *Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), Barrio Sarriena s/n, 48940, Leioa, Spain,*
[3] *Research Group on Plant Biology under Mediterranean Conditions, Universitat de les Illes Balears (UIB), Instituto de Investigaciones Agroambientales y de Economía del Agua (INAGEA), Ctra. Valldemossa km 7.5, 07122 Palma, Spain,*
[4] *UNL, CONICET, FBCB, Instituto de Agrobiotecnología del Litoral, 3000 Santa Fe, Argentina,*
[5] *Departamento de Biologia Vegetal, Universidade Federal de Viçosa, 36570-900, Viçosa, Minas Gerais, Brazil,*
[6] *Central Metabolism Group, Molecular Physiology Department, Max-Planck-Institut für Molekulare Pflanzenphysiologie, Golm, Germany,*
[7] *ECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile,*
[8] *Lab. de Fisiología y Biología Molecular Vegetal, Dpt. de Cs. Agronómicas y Recursos Naturales, Facultad de Cs. Agropecuarias y Forestales, Instituto de Agroindustria, Universidad de La Frontera, Temuco, Chile, and*
[9] *Center of Plant, Soil Interaction and Natural Resources Biotechnology, Scientific and Technological Bioresource Nucleus, Universidad de La Frontera, Temuco, Chile*

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*For correspondence (e-mail xurxogago@gmail.com).

[†] These authors contributed equally to this work.

SUMMARY

In this work, we review the physiological and molecular mechanisms that allow vascular plants to perform photosynthesis in extreme environments, such as deserts, polar and alpine ecosystems. Specifically, we discuss the morpho/anatomical, photochemical and metabolic adaptive processes that enable a positive carbon balance in photosynthetic tissues under extreme temperatures and/or severe water-limiting conditions in C_3 species. Nevertheless, only a few studies have described the *in situ* functioning of photoprotection in plants from extreme environments, given the intrinsic difficulties of fieldwork in remote places. However, they cover a substantial geographical and functional range, which allowed us to describe some general trends. In general, photoprotection relies on the same mechanisms as those operating in the remaining plant species, ranging from enhanced morphological photoprotection to increased scavenging of oxidative products such as reactive oxygen species. Much less information is available about the main physiological and biochemical drivers of photosynthesis: stomatal conductance (g_s), mesophyll conductance (g_m) and carbon fixation, mostly driven by RuBisCO carboxylation. Extreme environments shape adaptations in structures, such as cell wall and membrane composition, the concentration and activation state of Calvin–Benson cycle enzymes, and RuBisCO evolution, optimizing kinetic traits to ensure functionality. Altogether, these species display a combination of rearrangements, from the whole-plant level to the molecular scale, to sustain a positive carbon balance in some of the most hostile environments on Earth.

Keywords: chloroplast ultrastructure, photosynthetic pigments, VAZ, stomatal conductance, mesophyll conductance, RuBisCO.

ECOPHYSIOLOGICAL PERSPECTIVE OF EXTREME ENVIRONMENTS FOR PLANTS: CONCEPTS AND DEFINITIONS

It is difficult to define an 'extreme environment', as hostile microenvironments can be present even in a plant's ideal environment (i.e. a rocky outcrop in a rainforest). Conversely, plants can encounter optimal growth conditions in harsh environments (i.e. annual ephemeral plants after occasional rainfall in the desert). Plants are sessile organisms that have to deal with a series of biotic and abiotic factors that promote or constrain their performance. Such factors define the physiological limits of most processes, either alone or in concert. Furthermore, the relative importance of these factors for determining a physiological process may change depending on the environment. The abiotic factors that are most commonly involved in setting the range of plant physiological processes are temperature, water, nutrients, light and CO_2 (Figure 1) (Crawford, 2008). Plant physiological processes, including photosynthesis, have an optimum range for all these environmental conditions. When plants are outside of this range for a significant amount of time, carbon gain, growth and fitness are compromised; plants are then considered to be under stress (Lambers *et al.*, 2008). In general, the more distant a given factor is from the optimum, the more intense is the stress. Additionally, the timing, duration and frequency of constraining events (e.g. low water availability) are the determinants that together define an extreme environment.

Figure 1. Conceptual 'cage' model symbolizing how the physical environment constraints the growth, reproduction and development of any given species. Background picture shows a cushion of *Silene acaulis* in an alpine tundra 'limited' by the most relevant abiotic factors defining the world's major biomes. Some species (identified as the leaves escaping from the cage) can live in extreme environments, where most of the others cannot. PPFD, photosynthetic photon flux density; UV, ultraviolet.

Under this theoretical framework (see Figure 1), extreme environments are defined as those in which one or more factors are very close to the upper or lower limits for most plant species. These environments are characterized by harsh abiotic conditions that limit the normal functioning of fundamental physiological processes in plants, such as carbon gain, growth, reproduction and fitness (Figure 1). Rather than exceptions, extreme environments extend along a high proportion of our planet's land. For example, Antarctica, which comprises 14 million km^2 of landmass, is the coldest continent in the world. It is, in essence, a cold desert, with less than 1% of its territory being available for land plant colonization (ice-free and snow-free lands) (Peat *et al.*, 2007). It also includes the driest desert on Earth, the McMurdo Dry Valleys, where no liquid water is available (Doran *et al.*, 2002). In maritime Antarctica, where most of the plant diversity on this continent can be found, the growing season lasts 1–4 months per year, with average air temperatures that are slightly over 0°C and a considerable daily range, from −10 to 15°C, on some days (Cavieres *et al.*, 2016). Warm deserts are localized on both sides of the Equator (*c.* 27° latitude) and on the leeward sides of high mountain ranges, where high temperatures and irradiances impose evapotranspiration rates that exceed precipitation rates by several fold (Goudie, 2002). At least 50 deserts can be listed covering *c.* 30% of the total Earth's surface, albeit with different aridity levels. For example, the Atacama, Namib and central/eastern Sahara deserts can experience no rainfall for several years without a predictable pattern (Goudie, 2002). High altitude mountains (such as the Alps, the Rocky Mountains, the Himalayas or the Andes) also cover large landmasses (Körner *et al.*, 2011). All these places are characterized by low water availability and either extreme temperatures or large diurnal/seasonal thermal variations, narrowing the environmental conditions that are suitable for plant life. In mountain ranges, the upper alpine zone is characterized by a growth season that is shorter than 54 days, with average temperatures for the growing season <3.5°C (Körner *et al.*, 2011).

Although harsh abiotic factors strongly constrain the number of species that are able to succeed in extreme environments (Figure 2), these environments are not necessarily devoid of plant life, indicating that species inhabiting these places have adapted to cope with such conditions. As an illustrative example, the terrestrial flora of the entire Antarctic continent comprises 475 lichens, 132 bryophytes and only two angiosperm species (Peat *et al.*, 2007; Ochyra *et al.*, 2008; Øvstedal and Smith, 2011). In

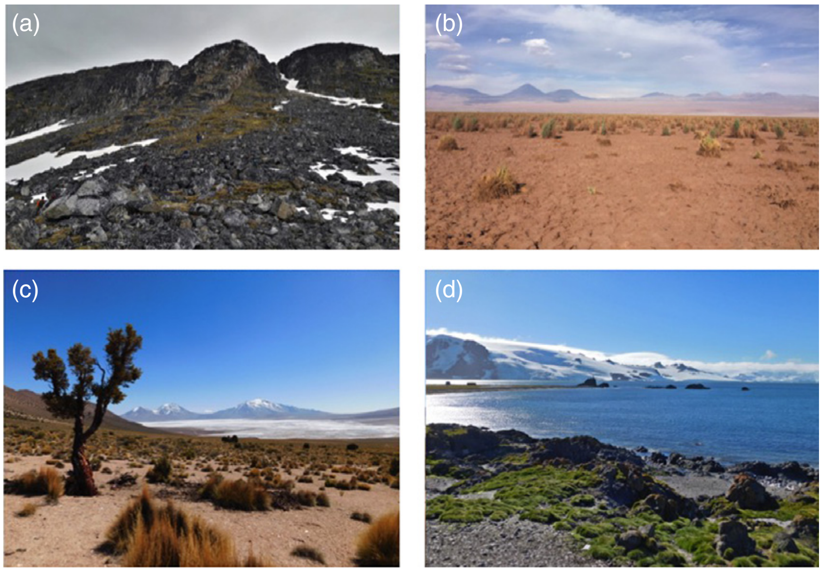

Figure 2. Different extreme environment landscapes with their plant communities. (a) Polar desert in the north of Spitsbergen (Svalbard Islands), showing vegetation patches just under the sea bird cliffs. (b) Atacama desert dominated by the shrub *Atriplex atacamensis* and the herb *Tessaria absinthioides*. (c) Salar de Surire in the Chilean altiplano with the tree *Polylepis tarapacana* that forms the highest altitude forest on the planet [>5000 m above sea level (a.s.l.)]. (d) *Deschampsia antarctica* patches in sheltered sites close to the beach near the Henryck Arctowski Polish Antarctic Station (King George Island, South Shetland, Antarctica). Photographs (b), (c) and (d) are courtesy of Melanie Morales.

general, extreme environments are dominated by non-vascular plants. However, some vascular species can also be found in such places [e.g. Antarctica, the High Arctic or elevations higher than 6150 m above sea level (a.s.l.) in the Himalayas] (Øvstedal and Smith, 2011; Körner, 2011; Angel *et al.*, 2016), evidencing the remarkable ability of plants to adapt to these conditions (Figure 2).

Leaf carbon metabolism is driven by photosynthesis, photorespiration and mitochondrial respiration. These processes control the production/consumption of energy and carbon skeletons that underpin plant physiology and, ultimately, plant life. How vascular plants are able to achieve a positive carbon balance in extreme conditions is key to understanding their ability to colonize and thrive in those environments (Osmond *et al.*, 1987). In this review, we aim to highlight some of the morpho/anatomical, photochemical, and metabolic adaptive mechanisms that enable C_3 evergreen species to maintain a positive carbon balance in extreme environments, such as high mountains, polar tundra and deserts. In the published literature, information on these topics is still scarce. Thus, we complement our review with studies of acclimation to extreme abiotic factors to gain insights into plant responses to changing environments. We also take full advantage of the latest omic technologies to understand the molecular and biochemical mechanisms underlying plant morphophysiological responses in terms of photosynthesis under extreme environments in a highly integrated manner. It is worth noting that, although many species with C_4 and crassulacean acid metabolism (CAM) metabolism are successful in deserts and/or saline environments (Lüttge, 2004; Flexas *et al.*, 2012a,b), we will focus on C_3 species, following studies that have fully characterized the physiological and biochemical limitations of photosynthesis in these species. We developed the ‘four aces’ model, which integrates the major plant responses discussed in this work. The four aces represent the strategies that are required by plants to develop at different levels to succeed in the ‘casino of life’ imposed by extreme environments (Figure 3).

PLANT/LEAF MORPHO/ANATOMICAL ADAPTATIONS IN DESERTS AND POLAR/ALPINE ENVIRONMENTS

Water restriction and extreme temperatures limit the length of the growing season. These two factors, in combination with irradiance (and, to a lesser extent, other factors such as wind and/or abrasion), are the main drivers of growth and leaf morphological traits (Körner, 2003; Larcher, 2003; Crawford, 2008). Thus, whole-plant growth forms, canopy structure, leaf morphology and anatomy are a reflection of the acclimation processes combined with the adaptive responses to the environment (Körner, 2003; Lambers *et al.*, 2008). An excellent example is provided by the circumpolar Arctic/alpine species *Saxifraga oppositifolia*, which inhabits the coldest (4545 m, central Swiss Alps; Körner, 2011) and northernmost (83°40′N, Kaffeklubben Island, Greenland) known places with angiosperm plant life in the world. As a result of autopolyploidy, this species displays considerable morphological and genetic variation throughout its range as a result of autopolyploidy. Diploids can show cushion-like and prostrate/trailing-like forms, while tetraploids only display prostrate/trailing forms and are only present in less extreme environments, despite being more competitive Figure 4a,b) (Eidesen *et al.*, 2013).

In this section, starting from the ‘whole- plant’ level and ending with the ‘internal leaf anatomy’ level, we focus on those above-ground acclimation and/or adaptive features that have direct and/or indirect effects on photosynthesis, with regard to light absorption, water transpiration and

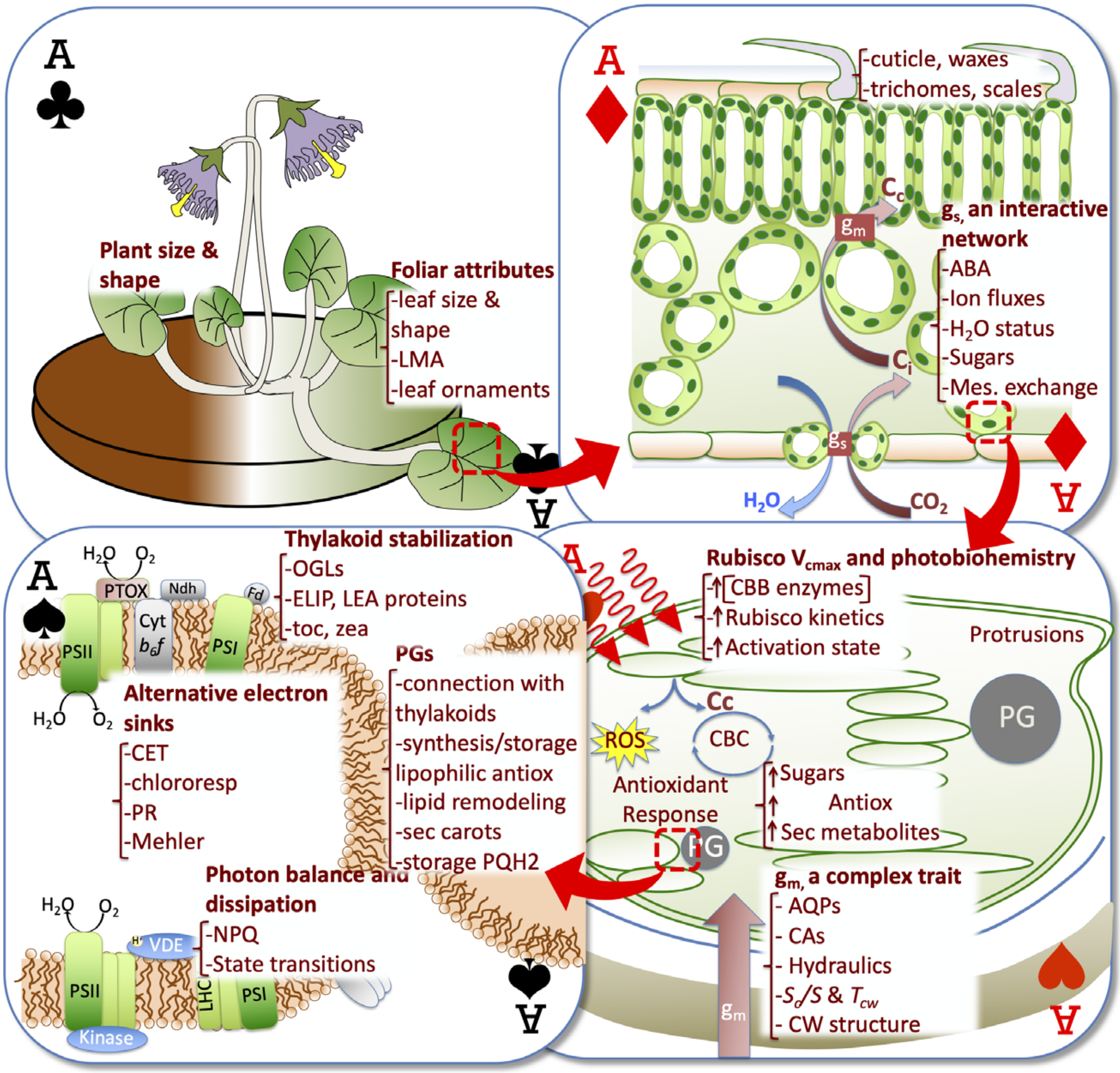

Figure 3. The 'four aces' of plants in the extreme 'casino'. To succeed in extreme environments, plants use a combination of strategies. From the whole-plant level to the thylakoid scale, these strategies shape adaptive responses to hostile environments. None of these are exclusive of plants from those habitats, but their combined actions allows the achievement of a positive carbon balance beyond the reasonable limits of vascular plant life. ABA, abscisic acid; Antiox, antioxidants; AQPs, aquaporins; CAs, carbonic anhydrases; CBC, Calvin–Benson cycle; CET, cyclic electron transport; CW, cell wall; g_m, mesophyll conductance; g_s, stomatal conductance; LMA, leaf mass area; Mes, mesophyll; NPQ, non-photochemical quenching; OGL, oligogalactolipids; PG, plastiglobule; PQH2, reduced plastoquinone; PR, photorespiration; Mehler, Mehler reaction; ROS, reactive oxygen species; S_c/S, chloroplast surface per leaf area; sec carots, secondary carotenoids; sec metabolites, secondary metabolites; T_{cw}, cell wall thickness; toc, tocopherol; VDE, violaxanthin de-epoxidase; zea, zeaxanthin.

carbon fixation. For more detailed information about leaf morpho/anatomical adaptations, see the articles by Wright *et al.* (2004), Reich (2014), and Keenan and Niinemets (2016).

Influence of plant growth properties on the leaf microenvironment

Plant height and size are highly constrained under environments with extreme temperature and water restrictions for three main reasons: (i) to reduce exposure to strong wind (which has both mechanical and desiccation effects) and abrasion; (ii) to facilitate water balance and transport (i.e. by decreasing evapotranspiration and by shortening hydraulic distances from the soil to the leaves); and, the most relevant; and (iii) to buffer extreme (particularly low) temperatures. Early ecophysiological field studies have shown that short-stature plants benefit in cold

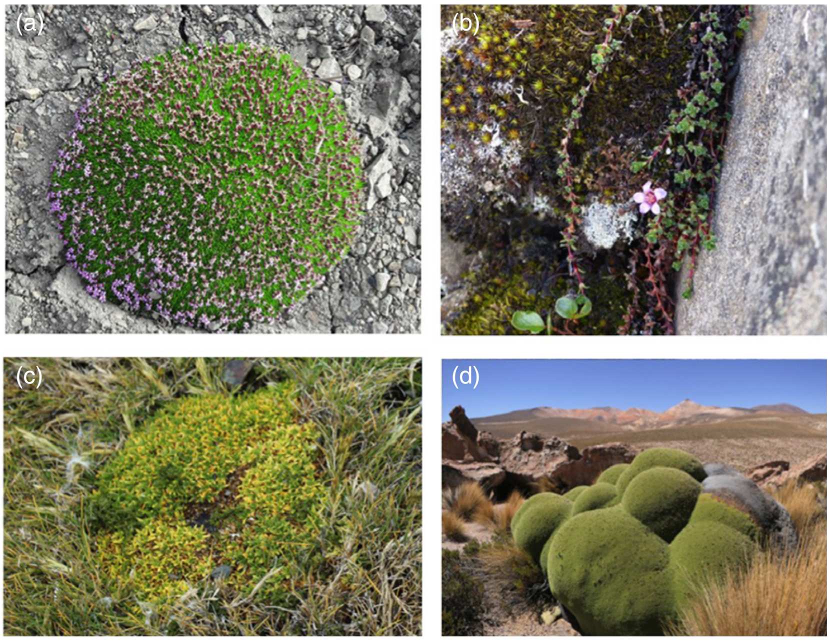

Figure 4. Angiosperm species living in extreme environments: *Saxifraga oppositifolia* in Spitsbergen (Svalbard Islands) showing cushion (a) and trailing (b) forms associated with different (di and tetra) ploidy levels and niche specialization (Eidesen *et al.*, 2013). (c) *Colobanthus quitensis* and *Deschampsia antarctica* growing close to the ground in Livingston Island (Antarctica). (d) *Azorella madresporica* cushion form at Altiplano (Chile).

environments from the higher temperatures produced by radiative heating of the soil surface, strongly decoupling their foliage temperature from the air temperatures (Larcher, 2003; Körner, 2003) (Figures 2a,d, 3, 4c). With the same rationale, a recent study by Bjorkman *et al.* (2018) including 117 tundra sites indicated that plant height tends to increase with warming (over the last 30 years). These authors, however, suggested that size-related traits on the tundra depended on the length of the growing season (e.g. on the potential carbon uptake) more than on extreme events such as low temperatures in winter or water stress in summer. Other related features such as canopy structure and/or leaf arrangement can also greatly affect leaf temperature under high irradiance (Larcher, 1980; Körner, 2003). Thus, decumbent, rosette and cushion are frequent growth forms in many polar and mountain environments. For instance, along the Andes, several *Azorella* species form cushions of tightly knit canopies with small leaves developing compact structures that are sometimes larger than 1 m in diameter; these unique forms promote milder canopy temperatures than the extreme surrounding environment (Cavieres *et al.*, 2007; Anthelme *et al.*, 2014) (Figure 4d). Another example is the Arctic-alpine distributed cushion species *Silene acaulis*, which also decouples its leaf temperature as a consequence of its cushion form from the surrounding habitat (Körner, 2003) and can live longer than 300 years in these extreme environments (Morris and Doak, 1998).

Another structural acclimation strategy to survive the dry season is the partial dormancy that has been described in desert plants such as *Retama raetam*; its stems in the upper canopy, which is exposed to direct sunlight, remain in photosynthetic dormancy but shade the active lower canopy (Mittler *et al.,* 2001). However, this is a double-edged sword, as such plants cannot easily cool down their leaves through transpiration and are continuously exposed to the risk of heat damage (Neuner *et al.*, 2000).

Several species have adapted to the use of fog and dew as major water resources in desert regions, a strategy first described in the species *Nolana mollis* (a succulent-leaved shrub in one of the driest deserts on Earth, Atacama; Mooney *et al.*, 1980) and later observed in other plants from coastal deserts. In the same desert, *Tillandsia landbecki* is able to harvest 25 L m^{-2} per year thanks to its hygroscopic scales (Westbeld *et al.*, 2009). Another example is the Namib grass *Stipagrostis sabulicola*, which is able to collect up to 0.5 L m^{-2} of leaf during a regular nocturnal fog event (Ebner *et al.*, 2011). This species first collects fog droplets and then guides the collected water towards the plant base to promote its absorption in the roots. This process is facilitated by the presence of grooves within the leaf surface, which run parallel to the longitudinal axis of the plant (Roth-Nebelsick *et al.*, 2012). Other species, such as *Combretum leprosum* from semiarid regions in Brazil, directly absorb the dew droplets through leaf trichomes (Pina *et al.*, 2016).

Effect of leaf morphology on photosynthetic capacity

Leaf size and morphology are largely shaped by abiotic factors, in which leaf energy dissipation is highly determined by those traits. In this sense, pinnate, lobulated or dissected leaves would confer an adaptive advantage in dry and hot environments, as has been shown for *Pelargonium* species (Jones *et al.*, 2009). Further, desert plants show an extreme leaf area reduction by decreasing leaf size, or the complete disappearance of leaves and their substitution by other photosynthetic organs such as phyllodes or stems. Large numbers of species from dry environments have the ability to develop leaves only during the first growth stages, to maximize the relative growth rate during those phases, and later to lose them to optimize their water balance (Atkin *et al.*, 1998; Yu and Li, 2007). Alpine tundra species also tend to have small leaves compared with lowland species but with thicker mesophylls (Körner, 2003). These small and thick leaves show greater efficiency in terms of energy balance, are more robust to withstanding strong desiccant winds and are less prone to freezing damage (Körner, 2003). In this sense, the reliance of photosynthesis on thicker or round-section organs largely decreases water consumption and increases water-use efficiency by reducing the surface/volume ratio. Additionally, it decreases light use efficiency due to an uncoupling between CO_2 diffusion and light distribution along the mesophyll tissues in hypostomatic species. Although this may not be a major limiting factor in warm dry deserts with enough sun radiation, it may limit plant growth to a great extent in high-latitude deserts where light availability is much scarcer. Major limitations to photosynthesis in extreme environments may be imposed by the trade-offs between the leaf mass area (LMA), which is determined by leaf thickness and density, and photosynthetic capacity (Wright *et al.*, 2004; Reich, 2014). Moreover, dry and extreme temperature range environments are frequently nutrient-limiting environments, in which thicker and denser leaves are also characterized by long lifespans, a key adaptive trait for these environments in which the growing season length highly limits the formation of new leaves. These thick, dense and long-lived leaves have low N and P contents and display a considerable investment in defensive and support structures, imposing large biophysical constraints that reduce their photosynthetic capacity (Körner, 2003; Wright *et al.*, 2004).

Effect of leaf ornaments on photosynthesis

Plants from arid and high irradiance habitats are frequently hairy, waxy or woolly (Figure 3). The presence of such 'leaf ornaments' is common among alpine plants and helps them increase their energy balance efficiency (Meinzer and Goldstein, 1985; Körner, 2003; Yang *et al.*, 2008), decreasing convective heat loss (Bickford, 2016). These ornaments also reflect ultraviolet (UV)-B, UV-A and excess visible light. However, there is a trade-off between the presence of trichomes and CO_2 diffusion into the leaf, as trichomes increase the boundary layer resistance, potentially limiting photosynthetic gas exchange (Bickford, 2016). Leaf trichomes also play an important role in desert plants (e.g. Ehleringer and Mooney, 1978; Sandquist and Ehleringer, 1998), preventing overheating and excess radiation, providing plants with milder conditions at the leaf level for photosynthesis (Bickford, 2016) and collecting water from dew and the atmosphere (see Section Influence of plant growth properties on the leaf microenvironment). An alternative to these ornaments with no effect on the boundary layer is the accumulation of epidermal anthocyanins. This trait results in a visible purple colour, with positive effects on light shielding, UV-B protection, and camouflage (Niu *et al.*, 2014). There is also a warming effect of anthocyanins that is particularly important in low wind microhabitats and plants with a greater mass per area (Hughes, 2011). In addition to these effects, the metabolic costs in photosynthetic terms of the constitutive presence of anthocyanins in alpine plants is negligible, as described in the Himalayan plant *Corydalis benecincta* (Niu *et al.*, 2014). Other shikimate-derived compounds, such as flavonoids and hydroxycinnamic acids, also contribute to UV screening without affecting light harvesting. The levels of these compounds are usually higher in the epidermis of plants from high altitude and polar habitats (Barnes *et al.*, 2015).

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Limited water availability and very low temperatures produce a strong decrease in enzymatic activity (for most biological reactions, a 10°C reduction causes a two-fold decline in reaction rates) and decreased membrane fluidity. These effects might provoke an uncoupling between temperature-independent photochemical reactions (light absorption and charge separation) and biochemical reactions (electron transport and downstream utilization of electron sinks through metabolism), which could lead to photoinhibition and photooxidation (Falk *et al.*, 1996; Huner *et al.*, 1998; Gollan *et al.*, 2017). Beyond morpho/anatomical leaf features (see Section Plant/leaf morpho-anatomical adaptations in deserts and polar/alpine environments), chloroplast functioning in species growing under extreme environments depends on an effective battery of photoprotective mechanisms. Thus, handling the excess of light energy represents a first and essential step towards acclimation of photosynthetic performance in harsh environments (e.g. extremely contrasting temperatures can occur on a seasonal or daily timescale). The ultrastructural aspects related to the internal organization of chloroplasts and maintenance of thylakoid stability are essential to manage excess energy dissipation/consumption.

Chloroplast ultrastructure

Although the chloroplast ultrastructure has been characterized in several high-elevation and polar plants, few studies on warm and continental desert plants have been reported to date. Among plastidic ultrastructures, the presence of 'chloroplast protrusions' (broad thylakoid-free stromal prolongations of chloroplasts, occurring mostly on the latitudinal ends of chloroplasts; Figure 3; Holzinger *et al.*, 2007) have been reported in a broad range of taxa, including polar and alpine species (Giełwanowska *et al.*, 2005, 2014, 2015; Holzinger *et al.*, 2007; Lütz *et al.*, 2012). Cold stress has been widely related to the induction of chloroplast protrusions (Lütz, 2010; Lütz *et al.*, 2012), although other stressors such as salinity and nutrient deficiency can also trigger the appearance of protrusions in model plants (Vismans *et al.*, 2016). Recent studies have indicated that conditions favouring photorespiration might also promote their appearance (Moser *et al.*, 2015; Buchner *et al.*, 2015a). Thus, the role of chloroplast protrusions in plants living in extreme environments still requires further functional studies.

A second common feature of chloroplasts from plants living in extreme habitats is the presence of osmiophilic lipid droplets, the so-called plastoglobules (PGs; Figure 3). These compartmentalized structures are highly active in metabolism, particularly in the synthesis and storage of prenylquinones, such as tocopherols, tocotrienols, phylloquinone, plastoquinol (PQH2) and plastochromanol (Piller *et al.*, 2012). As all these compounds are antioxidants and PGs are physically connected to thylakoids (Brehelin *et al.*, 2007), transport of prenylquinones to and from PGs is possible, contributing to the alleviation of oxidative damage and over-reduction of the plastoquinone (PQ) pool. Interestingly, although dynamic in size and number, PGs seem to be constitutively present in the leaves of many polar and alpine plants (Giełwanowska *et al.*, 2005). In addition, differences in the size and number of PGs have been reported between different ecotypes of *Colobanthus quitensis*, a high-elevation species that also grows in Antarctica. Andean populations of this species display bigger PGs (occupying a larger proportion of the chloroplast volume) but reduced numbers compared with Antarctic populations (Bascuñán-Godoy *et al.*, 2010). It is known from model plants that the size and number of PGs respond positively to light and oxidative stress (Lichtenthaler, 2007), and they may also serve as storage structures for secondary carotenoids (Solovchenko and Neverov, 2017). Thus, a photoprotective role can be assigned to PGs in extreme environment plants to satisfy the high and variable demand of antioxidants and chloroplast ultrastructure remodelling (Rottet *et al.*, 2015). Additionally, many studies have found that polar populations of several species have a reduced number of thylakoids in the grana compared with their alpine counterparts (Miroslavov *et al.*, 1993; Bascuñán-Godoy *et al.*, 2010). Overall, these data indicate a higher dynamism of chloroplast ultrastructure related to the environment.

In addition to these morphofunctional attributes, maintenance of thylakoid stability under unfavourable conditions is essential to assure its functionality. Basically, biological membranes are in equilibrium with the surrounding water molecules, while temperature determines their biophysical behaviour. Extreme temperatures and water availability also challenge the stability of photosynthetic membranes. Lipid composition is the main factor determining stability under unfavourable thermal or hydric conditions (Moellering *et al.*, 2010; Moellering and Benning, 2011). The presence of a high proportion of oligogalactolipids (lipids with two, three or four galactose residues) is one of the most common responses observed in plants from hostile habitats (Gasulla *et al.*, 2019). It is supposed that lipids with large polar heads maintain a non-micellar structure that improves stability (Gasulla *et al.*, 2019). Conversely, although not always in extreme environments, numerous studies have documented the positive response of lipophilic antioxidants to temperature stress, in particular α-tocopherol, but also the carotenoid zeaxanthin (Z; Figure 3; García-Plazaola *et al.*, 2008; Fernández-Marín *et al.*, 2011; Buchner *et al.*, 2015a). As two illustrative examples: (i) protection by tocopherol, in parallel with a decrease on lipid peroxidation, correlated with an elevation in *Saxifraga longifolia* in the Pyrenees Munné-Bosch *et al.* (2016); and (ii) rises in Z correlated with free radical scavenging activity in response to heat stress in the high mountain species *Rhododendron ferrugineum*, *Senecio incanus* and *Ranunculus glacialis* in the Alps (Buchner *et al.*, 2015a). Freezing of leaves also triggers Z synthesis, even in complete darkness, in the subalpine species *Ramonda myconi* from the Pyrenees (Fernández-Marín *et al.*, 2018b). Finally, it is worth highlighting that tocopherol and Z complement the action of each other and play dual roles as stabilizer and antioxidant molecules (Havaux, 1998). Thus, functional integrity of thylakoid membranes in harsh environments strongly depends on their physical and biochemical stabilities, which are largely guaranteed by a dynamic composition in galactolipids and complemented by efficient lipophilic antioxidants and stabilizers.

Photosynthetic pigment composition

Surprisingly, the photosynthetic pigment composition of vascular plants from the most extreme habitats on Earth has not yet been systematically studied (Fernández-Marín *et al.*, 2018a). The only desert plants for which the detailed carotenoid composition has been studied *in situ* correspond to 'mild' deserts such as the Mojave in the USA (Barker *et al.*, 2002) or the Negev in Israel (Streb *et al.*, 1997). One exception is the tree *Prosopis chilensis,* the photoprotection mechanisms of which were studied in its natural habitat in the Atacama desert (Lehner *et al.*, 2001). However, the deep taproots of this tree are able to access groundwater reserves, and the whole plant is somehow physiologically uncoupled from the surrounding environmental conditions. In the case of Antarctic, Arctic and alpine ecosystems, greater numbers of vascular species and sites are studied due to the research stations strategically located in these environments (Streb *et al.*, 1998; Streb *et al.*, 2003; Lütz and Holzinger, 2004; Bascuñán-Godoy *et al.*, 2010; Laureau *et al.*, 2013; Buchner *et al.*, 2015b; Fernández-Marín *et al.*, 2019).

The revision of the low number of available studies suggests that the photoprotective mechanisms of these plants do not differ in quality or quantity from the rest of the species; this is the case for the xanthophyll cycle carotenoids (VAZ) involved in the modulation of photoprotective thermal energy dissipation (for a review see Müller *et al.*, 2001). The reported values for the VAZ pool range from 60–70 mmol mol^{-1} $\text{Chl}_{\text{a+b}}$ in alpine *R. glacialis* and desert *Atriplex halimus* (Streb *et al.*, 1997, 1998) to 110–160 mmol mol^{-1} $\text{Chl}_{\text{a+b}}$ in species such as *Polylepis tarapacana* from a high elevation in the Andes, the Antarctic *C. quitensis* and the Arctic *Salix pulchra* (Bascuñán-Godoy *et al.*, 2010; García-Plazaola *et al.*, 2015; Magney *et al.*, 2017). These values are within the normal range of VAZ pool sizes described for vascular plants (roughly from 20 to 180 mmol mol^{-1} $\text{Chl}_{\text{a+b}}$ in non-stressed plants; Esteban *et al.*, 2015; Fernández-Marín *et al.*, 2017).

Sustained depression of photochemistry (low predawn optimum quantum yield, F_v/F_m) might be understood as a pre-emptive strategy to prevent the risk of photoinhibition under harsh conditions. This phenomenon has been extensively studied during winter in evergreen conifers (Verhoeven, 2014; Míguez *et al.*, 2015) and is now known to also occur in some alpine species (Míguez *et al.*, 2017; Fernández-Marín *et al.*, 2018b, 2020). Winter depression of predawn F_v/F_m has been observed in shrubs from cold desert ecosystems such as the Alxa Plateau in China (Li *et al.*, 2018) or the Mojave Desert in the USA (Barker *et al.*, 2002). Additionally, during drought stress, perennial herbs that are native to the coastal deserts from southern Africa show low predawn F_v/F_m levels and retain high levels of de-epoxidized xanthophylls (high AZ/VAZ ratio) overnight (Cela *et al.*, 2009). Chilling also induces nocturnal retention of de-epoxidized xanthophylls in the warm desert evergreen shrub *Larrea divaricata* (Medeiros *et al.*, 2015).

Alternative electron transport pathways: chlororespiration, cyclic electron transport and the Mehler reaction

The major electron sinks that consume the redox power originating in the chloroplast electron transport chain (namely, linear electron transport) are the carboxylation and/or the oxygenation activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). Nevertheless, under certain circumstances, three alternative electron sinks (driving three different electron pathways) can operate in the thylakoids, namely cyclic electron transport (CET), chlororespiration and the Mehler reaction, followed by the water–water cycle. These alternative routes alleviate over-reduction of the PQ pool and simultaneously enable the luminal acidification required for energy dissipation in photosystem II (PSII) antennae (Cornic, 2012). While several studies have highlighted the potential photoprotective role of these three different electron pathways for high mountain and polar species, fewer data are available for desert species.

Cyclic electron transport. Cyclic electron transport around photosystem I (PSI-CET) was acknowledged in early studies of electron transport of thylakoids (Whatley *et al.*, 1959) and originally named cyclic photophosphorylation. PSI-CET consists of the donation of electrons from PSI back to *cytochrome* b_6f and involves the transport of protons into the lumen (for further details on the different pathways involved see Yamori and Shikanai, 2016). Functioning of PSI-CET has two consequences related to acidification of the lumen: maintenance of the thermal dissipation of excess energy and maintenance of a driving force for ATP synthesis without NADPH synthesis. Manuel *et al.* (1999) first suggested PSI-CET as a mechanism of energy dissipation to prevent PSII photodestruction when the alpine plant *Geum montanum* was exposed to high light and low temperature (see also Streb *et al.*, 2005). Recently, higher PSI-CET activity was found in populations of the alpine species *Phacelia secunda* from a lower elevation (1600 m a.s.l.) compared with those from higher elevations (2800 and 3600 m a.s.l.) in the Central Chilean Andes (Hernández-Fuentes *et al.*, 2015). Further studies have suggested that the PSI-CET response is associated with an adaptation to recurrent severe summer droughts by the *P. secunda* population from a lower elevation; interestingly the PSI-CET response under drought was almost negligible in upper elevation populations of these species (Hernández-Fuentes *et al.*, 2019). In dry environments, PSI-CET is thought to be crucial for successful rehydration of photosynthetic tissues that are tolerant to desiccation (Gao *et al.*, 2013). In fact, Arabidopsis mutants that are deficient in PSI-CET show an impairment in their capability to repair D1 protein, exacerbating photoinhibition (Takahashi *et al.*, 2009). Additionally, another study has indicated that PSI-CET-dependent ΔpH can protect the oxygen-evolving complex (Huang *et al.*, 2016). Together, these findings suggest that PSI-CET plays an important photoprotective role in tissues when PSII activity has been significantly reduced.

Chlororespiration. The first evidence for a respiratory pathway in the chloroplast was demonstrated by Bennoun (1982). It involves plastid terminal oxidase protein (PTOX), which accepts electrons from reduced PQ (PQH_2) to reduce O_2 in the stroma, thus producing water molecules (Nawrocki *et al.*, 2015). A NAD(P)H dehydrogenase (Ndh) complex also seems to be involved in the chlororespiratory pathway and is associated with the transfer of protons to the lumen (Peltier and Cournac, 2002). The potential role of chlororespiration in photosynthetic organisms has been questioned over the last 2two decades, but there is increasing evidence that it is related to photoprotective responses against abiotic stressors (Cornic, 2012; Streb and Cornic, 2012; Paredes and Quiles, 2017; Nawrocki *et al.*, 2019). Streb *et al.* (2005) first proposed chlororespiration as a photoprotective strategy in alpine plants. They observed extraordinarily high amounts of PTOX in *R. glacialis* and other alpine species, as well as an increase with elevation in *G. montanum* (Streb *et al.*, 2005). By blocking the electron flow to carboxylation, photorespiration and the Mehler reaction, Laureau *et al.* (2013) showed that PTOX maintains a high electron flow and PQ oxidation under saturating light. Thus, they suggested that PTOX acts as a safety valve under rapid light and temperature changes (Laureau *et al.*, 2013). In agreement with these findings, a recent study has shown the crucial role of PTOX in enabling growth under intermittent light conditions (Nawrocki *et al.*, 2019). In model species, PTOX must be transferred to the grana to develop its photoprotective role (Stepien and Johnson, 2018). A recent study of plants originating from the Gurbantünggüt Temperate Desert (north-west China) revealed an increased PQ pool oxidation and enhanced PSI activity when grown under high light, in comparison with *Arabidopsis thaliana* (Tu *et al.*, 2016).

Mehler reaction and the water–water cycle. The photoreduction of oxygen to hydrogen peroxide in thylakoids was first described by Mehler (1951) and then confirmed using $^{18}O_2$ light-dependent uptake (Mehler and Brown, 1952). The Mehler reaction is only the first step in a series of enzymatically catalysed reactions in the chloroplast, a pathway named by Asada (1999) as the water–water cycle. Its name derives from the extraction of electrons from water by PSII to reduce O_2 and then finally re-oxidization to water by ascorbate peroxidase (APX). There is currently no doubt that the Mehler reaction and successive reactions of the water–water cycle are essential for regulating electron transport and detoxifying the unavoidable formation of ROS in the chloroplast. In addition to serving as an electron sink, this cycle can divert electrons from the PQ pool, reducing the intersystem excitation pressure with the electron transport driven by this alternative sink and maintaining the proton gradient and thereby the activity of ATP synthase. For instance, experiments performed in two Antarctic vascular plants have shown that while *Deschampsia antarctica* diverts *c.* 30% of its photosynthetic electron transport through the oxygen-dependent sink, electron transport to oxygen in *C. quitensis* is negligible (Pérez-Torres *et al.*, 2007). The contribution of oxygen as an alternative electron sink relies on efficient detoxification of oxygen anion radicals to hydrogen peroxide and water by chloroplastic antioxidant enzymes, superoxide dismutase (SOD) and APX, respectively, consistent with the observation that *D. antarctica* has much higher SOD activity than *C. quitensis* (Navarrete-Gallegos *et al.*, 2012) and other cultivated Poaceae such as oat, barley or wheat (Pérez-Torres *et al.*, 2004). The importance of this pool of antioxidant enzymes has been confirmed using transgenic strategies. For instance, tobacco overexpressing chloroplast Fe-SOD exhibits enhanced photoprotection of PSII, while overexpression of mitochondrial Mn-SOD does not photoprotect PSII (Van Camp *et al.*, 1996). Enhanced photoprotection against low temperature-induced photoinhibition has also been observed in cotton overexpressing a cluster of genes encoding multiple enzymes from the water–water cycle targeted to the chloroplast (Kornyeyev *et al.*, 2001). Plants from the Tibetan plateau, such as *Stipa purpurea*, *Elymus dahuricus* and *Herpetospermum pedunculosum,* exhibit extreme cold and drought tolerance, concomitantly with exacerbated activity of SOD, APX and glutathione reductase (GR; Yang *et al.*, 2015; Zhao *et al.*, 2019; Cui *et al.*, 2019). Overall, the efficiency of alternative electron sinks and their ecophysiological significance for species inhabiting extreme environments will certainly depend on the interplay of a variety of alternative electron sinks. Unfortunately, there is still limited information on antioxidant metabolism in plants located in extreme environment, an area that merits further research efforts.

PRIMARY METABOLISM AND ANTIOXIDANT BIOCHEMISTRY

Photorespiration, an essential process to sustain primary metabolism under extreme conditions

Photorespiration carries out the detoxification and carbon recovery of 2-phosphoglycolate produced in the RuBisCO oxygenation reaction. The photorespiratory pathway requires energy investment and provokes a loss of fixed C, leading to a reduction in the net photosynthetic rate (Peterhansel *et al.*, 2010). However, in C_3 plants, it has been shown to constitute a major alternative sink for electrons under stress conditions, especially when the CO_2 availability decreases (in drought conditions and/or at elevated temperatures). At 25°C and ambient atmospheric conditions, *c.* 20% of the total electron flux through RuBisCO is diverted to oxygen, increasing when photosynthetic CO_2 assimilation is restricted either by CO_2 diffusion or biochemical limitations (Ort and Baker, 2002). For instance, photorespiration has been reported as a safe alternative pathway for electron transport in many high alpine species (Manuel *et al.*, 1999; Lütz and Engel, 2007; Lütz, 2010). It has also been related to the ultrastructural observation that chloroplasts, mitochondria, and microbodies (peroxisomes) are often observed in close proximity (Lütz, 2010). Additionally, it has been associated with the plastid protrusions observed in alpine plants (Lütz and Engel, 2007; Moser *et al.*, 2015; see Section Photobiochemistry), a phenomenon that is likely related to the lower CO_2 partial pressure and leaf development under low temperatures, which often decrease mesophyll conductance (g_m) and CO_2 assimilation in alpine plants (Saéz *et al.*, 2017). However, in the Andes mountains of central Chile, where severe drought conditions are observed at the end of the growing season (Mediterranean-like climate), photorespiration diminishes with elevation in natural populations of *P. secunda*, but rises after exposure to *in situ* warming under open top chambers (OTCs), mainly at a lower elevation (Hernández-Fuentes *et al.*, 2015). Under controlled laboratory conditions, drought induces a significant increase in photorespiration in plants collected from populations at a lower altitude, suggesting that recurrent drought stress at lower elevations at the end of summer has been a key selective pressure for photorespiration enhancement (Hernández-Fuentes *et al.*, 2019).

The photorespiration response is also associated with hot and dry environments. For instance, the drought-tolerant plant *Caragana korshinskii* and *Reaumuria soongoricaan* (extreme xeric semishrub) from the Loess Plateau in China shows increased photorespiration upon drought exposure (Bai *et al.*, 2008, 2017). An interesting and controversial phenomenon has been observed in *Welwitschia mirabilis*, a plant species from the hyperarid Namib desert. Despite being described as a CAM species, *W. mirabilis* exhibits extremely high photorespiration rates in its natural habitat throughout the day, with a maximum value at the highest air temperature around the leaf (as high as 40°C), when stomata are tightly closed (von Willert *et al.*, 2005). This phenomenon might be related to the observation that CAM processes are weak in this species, with very little contribution of nocturnal CO_2 uptake to the daily CO_2 balance, and that the ecological relevance of the synthesized acids could be to build up a gradient in the leaf along which water can flow at night, rather than to maintain a positive CO_2 balance (von Willert *et al.*, 2005). In contrast, high photorespiration levels have been observed in desiccation-sensitive old leaves, but not in desiccation-tolerant young leaves, of *Sporobolus stapfianus*, a desiccation-tolerant 'resurrection plant' (Martinelli *et al.*, 2007). These results suggested that scavenging excess electrons by photorespiration does not contribute to leaf protection from desiccation. Several lines of evidence indicate a photoprotective role for photorespiration, which has been considered a futile and, moreover, wasteful pathway in terms of energy and carbon loss. New perspectives to improve crop productivity by optimizing photorespiration have been proposed (South *et al.*, 2018).

Alterations in primary and secondary metabolism in response to extreme environments

In the last decade, several studies have used metabolomics to gain insights into the metabolic responses to certain types of stress conditions. These technologies led to the identification of 1000–2000 primary and secondary metabolites, representing a small number considering that the estimation for the whole-plant kingdom is 200 000 metabolites (Obata and Fernie, 2012; Brunetti *et al.*, 2013; Gago *et al.*, 2016). Although the vast majority of these studies was performed with the model plant Arabidopsis, some reports in the literature deal with metabolomics in plants that actually grow in extreme conditions. However, most of the studies cover short-term responses and only one particular stress condition, which is useful for disentangling primary from secondary responses to a certain type of stress. When a plant is faced with any type of abiotic stress condition, several factors account for the observed metabolic changes: inhibition of enzymes, lack of substrates and/or a higher demand for specific compounds (Obata and Fernie, 2012). Upon exposure to a particular type of stress, the whole metabolic network must be reconfigured to sustain metabolism. Acclimation is then achieved by adopting a new steady state (Lambers *et al.*, 2008). This metabolic reprogramming provides particular compounds to the plant, such as compatible solutes, antioxidants and stress-responsive proteins (Obata and Fernie, 2012). The combination of metabolomics, physiological traits and statistical modelling offers new opportunities to understand how metabolic networks regulate physiological traits, and vice versa (Flexas and Gago, 2018).

The metabolic changes associated with different types of abiotic stresses have been reviewed extensively (Shulaev *et al*, 2008; Obata and Fernie, 2012). As a general observation, plants tend to accumulate metabolites upon exposure to any type of abiotic stress. The first rationale indicates that growth is blocked and thus metabolites are not consumed. If plants can acclimate to the new situation, growth resumes based on the accumulated metabolites, which support the synthesis of new cellular components (Obata and Fernie, 2012; Obata *et al.*, 2015). As previously mentioned, there are limited studies describing the metabolic adaptations of plants that grow growing in extreme environments. Ramadan *et al.* (2014) studied the response of *Calotropis procera* growing in the desert to changes in water availability. Analysis of the metabolites demonstrated that plants respond very rapidly to artificial rewatering, increasing the levels of most amino acids and membrane lipids while decreasing sucrose, raffinose and storage lipids. Interestingly, samples harvested 12 h after watering were indistinguishable from the pre-watering stage, suggesting that the ability of *C. procera* to survive in the desert might be related to its rapid adjustments to water status (Ramadan *et al.*, 2014). Angelcheva *et al.* (2014) reported the metabolic changes observed in the conifer Siberian spruce (*Picea obovata*), which occur during cold acclimation caused by natural variations (from 20 to 0°C in a 5-month period). As observed in Arabidopsis, most metabolites (223) accumulated, while a minor proportion (52) showed decreased levels. Among those with higher levels, the authors found sucrose, raffinose (and related metabolites, such as melibiose, *myo*-inositol and galactinol), sugar acids, alcohols, amino acids and polyamines, which might serve as compatible solutes and/or cryoprotectants. Some changes were transient, such as those displayed by γ-aminobutyric acid (GABA) and melibiose, while others (like tryptophan) consistently increased consistently over the whole period (Angelcheva *et al.*, 2014).

Other recent studies on plants growing in extreme environments include an analysis of the altitude acclimation of *Potentilla saundersiana* (Rosaceae family) and *H. pedunculosum* (Cucurbitaceae family) to the Tibetan plateau (Ma *et al.*, 2015; Zhao *et al.*, 2019). The content of sucrose and proline increases with altitude in *P. saundersiana* plants, suggesting a role for these compounds as compatible solutes. The content of anthocyanin increases in parallel, in agreement with the need for the plant to tolerate lower temperatures and higher levels of UV-B radiation at higher altitudes (Ma *et al.*, 2015; see Section Effect of leaf ornaments on photosynthesis). Similarly, most metabolites accumulate in *H. pedunculosum* plants growing at higher altitudes. Among these metabolites, tricetin (a flavonoid), homoserine, levoglucosan, threonine and diglycerol display the highest accumulation. Interestingly, some metabolites that are normally increased in plants subjected to different types of stress are decreased in *H. pedunculosum* plants growing at higher altitudes, including sucrose and raffinose and anthocyanins (Zhao *et al.*, 2019), suggesting that these plants have a particular metabolic machinery to cope with extreme environments.

The accumulation of particular secondary metabolites seems to be a hallmark of vascular plants from extreme environments (see above), with two different but complementary effects. First, the synthesis of flavonols and phenylpropanoids from phenylalanine implies the use of energy and reducing power (Saito *et al.*, 2013; Kutchan *et al.*, 2015). Thus, the synthesis of phenolic compounds facilitates the maintenance of cell homeostasis by utilizing the surplus of NADPH during diminished photosynthesis, which normally occurs under extreme temperatures and reduced water availability (Akhtar *et al.*, 2010; Selmar and Kleinwächter, 2013; Caretto *et al.*, 2015). Second, flavonoids play a key role in reducing the damage produced by UV-B radiation (Kutchan *et al.*, 2015), which is particularly relevant in environments with high and extremely changing irradiance, such as high altitude ranges and Antarctica. Additionally, flavonoids are considered potent antioxidants, as they have the ability to scavenge free radicals (Procházková *et al.*, 2011). Thus, phenolic compounds might play a key role in plants from extreme environments, as almost all abiotic stress conditions ultimately lead to ROS generation.

Enzymatic and non-enzymatic antioxidant responses to stress

The maintenance of cellular homeostasis is an essential priority for all living organisms. The existence of a trade-off between the capacity to achieve high productivity and stress tolerance is generally assumed (Alpert, 2006). Plants from extreme environments are highly constrained in terms of growth rates and biomass (Cavieres *et al.*, 2016). Efficient photoprotective and antioxidant scavenging mechanisms are vital for plant survival in unfavourable environmental conditions, such as extreme temperatures, drought, water availability or nutrient deficiency (Hoermiller *et al.*, 2017). Plants employ enzymatic and non-enzymatic antioxidant defence systems to scavenge and prevent ROS accumulation, thereby avoiding cell damage. Enzymatic antioxidants include SOD, catalase (CAT), APX, GR, monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR), whereas non-enzymatic antioxidants comprise glutathione, ascorbate, carotenoids, tocopherols and phenolic compounds (Shinozaki *et al.*, 2015). Generally, a rapid response of antioxidants (mostly ascorbate and tocopherol) is induced by low-temperature treatments (García-Plazaola *et al.*, 2003) and by high altitudes, as shown in *S. longifolia* from the Pyrenees (Munné-Bosch *et al.*, 2016). For instance, when the role of the antioxidant defence system of 11 species from the Anatolian mountains (1500–2000 m) and 18 species from the Anatolian steppes (850–1000 m) were compared, the mechanisms used to deal with oxidative damage were more effective in species growing at high altitudes (exposed to low temperature and high irradiation) than in plants growing in low-altitude regions. Specifically, SOD activity and carotenoid, proline and soluble proteins concentrations were higher in alpine than in steppe plants (Oncel *et al.*, 2004). Another field study of nine selected high alpine plants to compare antioxidant capacity from different altitudes showed an increase in the total leaf antioxidant content at higher altitudes, with ascorbic acid playing an important role in all of them (Wildi and Lütz, 1996). Biochemical and proteomic assays in the alpine plant *P. saundersiana* showed a positive correlation between antioxidant enzyme activities and altitude, highlighting the importance of active enzymatic ROS scavenging in plants at high elevations. These results agree with an increase in ROS provoked by the extreme environmental conditions at such altitudes (Ma *et al.*, 2015). Another study of five alpine plants species growing at different elevations on the Tibetan plateau revealed a generally positive correlation between antioxidant capacity (total phenols and tannins), protein and fatty acids with altitude, suggesting that these increases are necessary to sustain high metabolic activity as a mechanism to deal with higher oxidative stress (Cui *et al.*, 2016).

Similarly, the desert plant *R. raetam* shows higher antioxidant enzyme activities and amounts of carotenoids than non-desert plants (Streb *et al.*, 1997). The stress tolerance of *Oudneya africana* desert plants is mainly related to the ascorbate–glutathione cycle efficiency and H_2O_2-dependent signals (Talbi *et al.*, 2015), while the antioxidant capacity of the dry-climate population of *Zizyphus jujuba* is also related to flavonoid and proline concentrations, as well as CAT, peroxidase (POX) and GR activities (Wang *et al.*, 2016).

Likewise, several biochemical and physiological mechanisms have been described to occur in response to short-term high light and low temperature treatments in the Antarctic vascular species *D. antarctica* and *C. quitensis* (Perez-Torres *et al.*, 2007). *Deschampsia antartica* shows higher SOD and APX activities than other Poaceae species. These two enzymes are related to ROS scavenging by the water–water cycle. In the same experiment, the authors pointed out that heat dissipation by the xanthophyll cycle allows *C. quitensis* to deal with the energy imbalance (Pérez-Torres *et al.*, 2004, 2007). More recently, it was demonstrated that *C. quitensis* exhibits constitutively high antioxidant capacity that is mainly related to sulphur and secondary metabolism, with normal antioxidant enzyme activities (Clemente-Moreno *et al.*, 2020a). Conversely, *D. antarctica* displays a rather unique pattern of antioxidant enzyme activities after long-term exposure to low temperature. Particularly, POX activity decreases at 4°C, while the opposite pattern has been observed for the model plant wheat (i.e. POX activity increases at low temperature). Moreover, a positive correlation was observed between some physiological traits (A_N, P_R and F_v/F_m) and POX activity, but a negative correlation between the membrane peroxidation level and POX activity in *D. antarctica*. Interestingly, the opposite was observed for wheat, suggesting that *D. antarctica* has a differential mechanism to cope with low temperatures (Clemente-Moreno *et al.*, 2020b).

PHOTOSYNTHESIS IN EXTREME ENVIRONMENTS: TAKING ADVANTAGE OF SCARCE OPPORTUNITIES

Diffusive limitations

It is widely established that photosynthesis is limited by three physiological and biochemical processes: stomatal conductance (g_s), mesophyll conductance (g_m), and photobiochemistry, which drive the final CO_2 fixation rate (Flexas *et al.*, 2012a,b). Thus, when stomata are open (a process mediated by guard cell turgor regulation), CO_2 penetrates the substomatal cavities and water concomitantly evaporates within leaves into the atmosphere. This process becomes crucial in dry environments, where plants should be extremely efficient in balancing CO_2 assimilation and water loss. At the leaf level, this balance can be estimated as the ratio between net photosynthesis (A_N, μmol CO_2 m^{-2} sec^{-1}) and g_s (mmol H_2O m^{-2} sec^{-1}), the intrinsic water-use efficiency (WUE_i) (Leakey *et al.*, 2019). When CO_2 reaches the substomatal cavities, its diffusion pathway is still far from complete, as it has to cross several physical barriers. First, it has to diffuse through the apoplast and across the cell wall, the thickness (T_{cw}) and composition of which affect CO_2 diffusion (Terashima *et al.*, 2011; Tosens *et al.*, 2015; Ellsworth *et al.*, 2018; Clemente-Moreno *et al.*, 2019). Before entering the cytosol, CO_2 must cross the cell membrane and subsequently pass through the chloroplast membranes. This diffusive pathway is facilitated by several specific enzymes, such as carbonic anhydrases and aquaporins (AQP) (Flexas *et al.*, 2016 and references therein). Another important anatomical trait related to g_m is the degree of chloroplast surface that is directly exposed to the mesophyll airspaces (S_c/S) (Gago *et al.*, 2019).

Like other biological processes, both conductances are highly affected by temperature, thus limiting photosynthesis (Berry and Bjorkman, 1980; von Caemmerer and Evans, 2015). It is widely known that stomata respond to different environmental factors, such as light, atmospheric CO_2, vapour pressure deficit (VPD) and temperature. Since the 1970s, temperature has been observed to interact with other major factors driving g_s, such as plant water status and the atmospheric VPD. These interactions can most likely explain several contradictory results observed among species (Berry and Bjorkman, 1980 and references therein) and that A_N and g_s interact with each other (Mott and Peak, 2011, 2013; Gago *et al.*, 2016; de Lima *et al.*, 2019). In general, when leaf water status and VPD remain constant, g_s tends to increase in response to an increasing temperature, in a coordinated manner with photosynthesis, up to a certain temperature threshold (Berry and Bjorkman, 1980; Urban *et al.*, 2017a). Above this threshold, A_N and g_s can be completely uncoupled, and WUE_i becomes highly reduced by decreases in A_N independently of the increase in g_s. In such cases, the higher evaporative cooling driven by a high g_s would help to deal with heat waves, although heat events are frequently associated with drought events (Urban *et al.*, 2017b).

The response of g_m to temperature differs between species with different climatic origins (von Caemmerer and Evans, 2015), but independently of the known 'coupled' behaviour between conductances (Flexas *et al.*, 2013). In this sense, g_m responses to temperature are more likely to be related to the activation energy for membrane permeability and the effective path length for liquid phase diffusion. The first point is related to changes in the membrane lipid composition in response to temperature (Burgos *et al.*, 2011), which in turn affects the direct CO_2 diffusion and activity of transmembrane proteins such as AQP. The second issue is mostly related to the cell wall composition and diffusion through the cytosol and stroma (von Caemmerer and Evans, 2015; Flexas and Díaz-Espejo, 2015). Recently, it has been reported that changes in the cell wall composition in response to stress (mostly pectins and hemicelluloses) are negatively correlated with g_m, suggesting that the cell wall structure and ionic nature of the cell wall nanopores could influence the CO_2 pathway through the cell wall (Clemente-Moreno *et al.*, 2019).

The only two native vascular plants of Antarctica (Figure 4c) have been extensively studied in terms of temperature, water availability and nutrient deficiency (Sáez *et al.*, 2017, 2018a,b; Clemente-Moreno *et al.*, 2019, 2020a). Interestingly, for both species, g_m is the most important limitation under low temperature, drought and nutrient deficiency, as has been previously reported for species from semiarid-arid environments (Galmés *et al.*, 2007). Both Antarctic species present typical anatomical traits related to xerophytic environments; however, these traits do not explain their response to environmental changes, and it is speculated that the responses should be related to the activation energy for membrane permeability and the effective path length for the liquid phase (Clemente-Moreno *et al.*, 2020a,b).

Under water deficit and salinity, g_s and g_m can show the same degree of limitation (observed in plants from non-extreme environments; Flexas *et al.*, 2012a,b), but g_m responses can differ in terms of velocity with respect to the stress, as well as during recovery after rewatering in different herbaceous and woody species (Galle *et al.*, 2009, 2011; Clemente-Moreno *et al.*, 2019). A complex behaviour of g_m would also be associated with additional environmental stimuli and other traits such as water status and hydraulics (Flexas *et al.*, 2013; Carriquí *et al.*, 2019). For example, in *Cistus albidus*, a Mediterranean woody species adapted to a semiarid-arid climate, g_m was observed to acclimate to consecutive drought-rewatering cycles by improving A_N and WUE_i and reducing ROS generation (Galle *et al.*, 2011).

The availability of a complete characterization of photosynthesis in alpine species at a high elevation is scarce. Species living in those habitats are frequently exposed to extreme daily temperature variations, strong winds and high irradiance, and compared with those from polar and warm deserts during the growing seasons. Additionally, they must deal with a low CO_2 partial pressure due to the low atmospheric pressure because of altitude (Körner, 2003; Wang *et al.*, 2017). Wang *et al.* (2017) attempted to disentangle the effect of reduced atmospheric pressure and temperature through an altitudinal gradient in a number of variables affecting A_N, showing that a higher CO_2 drawdown (low ratio of the CO_2 concentration in the substomatal cavities to the atmospheric CO_2 concentration; C_i:C_a) and increased V_{cmax} can be explained by the atmospheric pressure reduction. However, the magnitude of such an effect is increased by low temperatures. For example, Shi *et al.* (2006) showed that *Buddleja davidii* plants from 3400 m a.s.l have a higher A_{max} than the same species growing at 1300 m; this A_{max} is mostly driven by a higher g_m and enhanced photobiochemistry under such environmental conditions.

Biochemical limitations

Biochemical limitations are driven by the processes related to the transformation of inorganic carbon to organic molecules (triose-phosphates) by the Calvin–Benson cycle (CBC). The main enzyme of the CBC is RuBisCO, which catalyses the reaction of CO_2 with ribulose 1,5-bisphosphate (RuBP), producing two molecules of 3-phosphoglycerate. Biochemical limitations of photosynthesis include RuBisCO activity, electron transport-limited rates of RuBP regeneration and triose phosphate utilization (TPU). Modelling of photosynthetic carbon response (A/C_i) curves using the biochemical model of C_3 photosynthesis (Farquhar *et al.*, 1980; von Caemmerer, 2000) allows the calculation of the maximum potential of RuBP carboxylation (V_{cmax}), maximum potential of the electron transport rate (J_{max}) and TPU capacity. These parameters indicate the limiting biochemical process (RuBisCO carboxylation, electron transport rate or TPU) for photosynthesis under a certain environmental condition (Bernacchi *et al.*, 2013), depending on the physiological status of the plant.

The first limiting process is the carboxylation reaction catalized by RuBisCO, which will be determined by [CO_2] and [O_2] at enzyme catalytic sites, the amount of activated enzyme and its catalytic properties (Farquhar *et al.*, 1980). The degree of activation of the RuBisCO pool will depend on the activity of RuBisCO activase, which uses the energy from ATP hydrolysis to convert RuBisCO active sites in an open and catalytically competent conformation (Spreitzer and Salvucci, 2002).

The second process limiting photosynthesis is related to the production of ATP and NADPH by photosynthetic light-dependent reactions, which are used in the CBC for RuBP regeneration. The rate of ATP and NADPH synthesis is directly linked to the rate of linear electron transport (ETR). The third limiting process relates the net CO_2 assimilation to the rate of inorganic phosphate release during the utilization of triose phosphates produced by the CBC (Sharkey, 1985). High rates of sugar-phosphate production can deplete the pool of free inorganic phosphate and limit photophosphorylation (Leegood and Furbank, 1986; Sharkey *et al.*, 1986; von Caemmerer, 2000). A meta-analysis focusing on the relationship among leaf photosynthetic traits has suggested that plants may employ a conservative strategy of J_{max} to V_{cmax} coordination to avoid photoinhibition (see Section Photobiochemistry), based on a strong correlation between both parameters, which is not altered by the nutrient status of the plant (Walker *et al.*, 2014). It is important to note that the authors did not consider g_m to calculate the biochemical parameters based on the CO_2 concentration at the chloroplast carboxylation site (C_c) (instead of on a C_i basis).

Interspecific and intraspecific adaptation, as well as photosynthetic acclimation to a certain environment, have been observed to modulate the response of each biochemical limiting process under changing abiotic conditions (Robakowski *et al.*, 2012; Yamori *et al.*, 2014; Kumarathunge *et al.*, 2019). For instance, low temperatures produce an uncoupling between temperature-independent photochemical reactions and temperature-dependent biochemical reactions, as explained in Section Photobiochemistry. RuBisCO catalytic traits are distinctly affected by temperature, and carboxylation turnover rate (k_{cat}^{c}) is the most responsive trait to temperature changes (Galmés *et al.*, 2019). *In vitro*, k_{cat}^{c} increases with temperature up to a thermal optimum of *c.* 50–55°C (Galmés *et al.*, 2015), beyond which the enzyme undergoes denaturation, while the affinity and specificity of RuBisCO for CO_2 decreases with temperature (Jordan and Ogren, 1984). The strong decrease in k_{cat}^{c} at low temperatures is only partially compensated by an increase in the RuBisCO specificity factor ($S_{c/o}$) and affinity for CO_2, that is, a lower semisaturation constant for CO_2 (K_c) (Bernacchi *et al.*, 2001; Galmés *et al.*, 2016, 2019). Although the higher solubility of CO_2 at low temperatures can also partially attenuate the decrease in RuBisCO activity, CO_2 diffusion is also significantly reduced at low temperatures (see Section Diffusive limitations), so the drop in RuBisCO carboxylation rate may be an important issue in extremely cold environments. Cold acclimation and adaptation of photosynthesis may involve an enhancement of thermal energy dissipation, a reduction in effective photon absorption, metabolic adaptations that increase the antioxidant activity, and/or an increase in electron sink capacity. A higher electron sink capacity might be attained by an increased ratio of unsaturated fatty acids in thylakoid membranes, leading to the stabilization of transmembrane photosynthetic proteins (Falcone *et al.*, 2004; Burgos *et al.*, 2011), and by an increased concentration and activation state of CBC enzymes (Yamori *et al.*, 2006), specially Rubisco (Savitch *et al.*, 1997; Yamori *et al.*, 2005; Jaikumar *et al.*, 2016). Moreover, adaptations in RuBisCO kinetics through increased k_{cat}^{c} and carboxylation catalytic efficiency (k_{cat}^{c}/K_c) have been reported in plants inhabiting cold ecosystems (Sage, 2002; Sáez *et al.*, 2017). Indeed, the highest k_{cat}^{c} ever reported for a C_3 plant was observed in the Arctic–sub-Arctic grass *Arctagrostis latifolia* (Orr *et al.*, 2016).

Apart from the improvement in k_{cat}^{c} of psychrophilic enzymes, other cold adaptations might be related to a reduced enzymatic thermal dependence and a reduced optimum temperature. A reduced temperature sensitivity of RuBisCO kinetic traits of C_3 plants from cold ecosystems – relative to those from warm ecosystems – has been observed (Galmés *et al.*, 2016). Concerning the optimum temperature *in vitro* of RuBisCO for k_{cat}^{c}, the boreal and high-mountain grass *Alopecurus alpinus* has the lowest ever reported optimum temperature of 48.8°C (Tieszen and Sigurdson, 1973) for a vascular plant, while the herbaceous warm desert perennial *Astragalus rafaelensis* has the highest value of 58.7°C (Weber *et al.*, 1977). A very high activation state of RuBisCO has been reported for the two Antarctic vascular plants *C. quitensis* and *D. antarctica* (Salvucci and Crafts-Brandner, 2004; Pérez-Torres *et al.*, 2006). Additionally, an increase in the RuBisCO activation state has been demonstrated as part of a cold-acclimation process in temperate plants (Yamori *et al.*, 2005, 2006).

Conversely, very high temperatures may produce a decrease in enzymatic activity as a result of protein denaturation. Although *in vitro* k_{cat}^{c} has a thermal optimum at *c.* 50–55°C, as explained above, the activation state of RuBisCO significantly decreases at temperatures higher than 30–35°C due to the thermolabile nature of RuBisCO activase (Crafts-Brandner and Salvucci, 2000; Carmo-Silva and Salvucci, 2011), leading to a sharp decrease in *in vivo* carbon fixation. Moreover, the solubility of CO_2 and the ratio of dissolved $[CO_2]/[O_2]$ in chloroplasts decrease at higher temperatures. Biochemical adaptations to extremely warm ecosystems might include expression of heat-stable isozymes (Yamori *et al.*, 2006) and increases in the RuBisCO activase concentration to compensate for the decrease in its activity (Yamori *et al.*, 2005, 2011). Indeed, gene expression analysis in the C_3 warm desert plant *Rhazya stricta* has revealed that two RuBisCO activase isoforms are likely responsible for the maintenance of high photosynthetic rates at leaf temperatures as high as 43°C (Lawson *et al.*, 2014).

Under drought conditions, RuBP oxygenation is favoured over carboxylation, as CO_2 availability within chloroplasts is further reduced due to stomatal closure (Galmés *et al.*, 2011). In this situation, RuBisCO carboxylation may be the main biochemical process limiting photosynthesis (Flexas *et al.*, 2004; Galmés *et al.*, 2011; Niinemets and Keenan, 2014). Decreased RuBisCO activity under water stress may be driven by a reduction in the activation of RuBisCO catalytic sites due to reduced C_c. However, species from semiarid-arid environments, which are adapted to frequent drought events (adapted to low C_c due to strong diffusional limitations), are more capable of maintaining a high activation status of RuBisCO with drought stress intensification (Galmés *et al.*, 2011). In addition, proteomic analysis has confirmed that some photosynthetic proteins, such as RuBisCO and sedoheptulose-1,7-bisphosphatase, are upregulated in plants under water stress (Vincent *et al*., 2007; Zhang *et al*., 2010). However, low nitrogen availability superimposed on water limitation conditions can cause a reduction in the RuBisCO concentration, which may limit the acclimation speed or capacity of some species to extreme environmental temperatures. Therefore, plants that are adapted to extremely xeric and warm ecosystems show higher RuBisCO CO_2 affinity and specificity (Galmés *et al*., 2011; Galmés *et al*., 2014a), which may partially compensate for a lower RuBisCO content due to nitrogen limitation. A similar trend has been reported for Antarctic plants, which also show a higher k_{cat}^{c} (Sáez *et al*., 2017), leading to an even higher carboxylase catalytic efficiency under air conditions than those reported for species from xeric habitats (Galmés *et al*., 2014b). Taken together, these results suggest that the combination of extreme temperatures and low CO_2 concentrations inside the chloroplast has strongly shaped RuBisCO evolution in plants living in extreme environments.

Our knowledge concerning *in vivo* leaf biochemical parameters from plants growing in extreme environments is very limited, and most studies have focused on acclimation processes in non-extreme species. Moreover, information is restricted to biochemical modelling on a C_i basis instead of on a C_c basis, which could affect the shape of the modelled responses (Flexas *et al*., 2008), as explained in Section Diffusive limitations. However, while keeping in mind these limitations, some general trends can be noted based on the currently available pool of data.

The optimum temperatures of V_{cmax} and J_{max} increase with the growth temperature in C_3 plants grown under fertilized, well watered conditions (Smith and Dukes, 2017), but the temperature responses of both parameters might be species and population specific, which will ultimately determine which biochemical process limits photosynthesis in each thermal condition. A predominant limitation of photosynthesis measured at low temperatures in non-acclimated plants seems to be RuBP regeneration, but this limitation is frequently alleviated after plant acclimation to cold temperatures (Sage and Kubien, 2007; Yamori *et al*., 2010, 2014), while acclimation to warmer temperatures tends to have a relatively greater positive effect on the processes limiting carbon assimilation when water and nutrients are not limiting (Smith and Dukes, 2017). Indeed, Kattge and Knorr (2007), based on a meta-analysis of 36 C_3 species, have shown that the J_{max}/V_{cmax} ratio at 25°C decreases with increasing growth temperature and that this moderate temperature acclimation might be sufficient to double photosynthesis at 40°C, if plants are grown at 25°C instead of 17°C. These photosynthetic responses might be modified when water and nutrients become limiting factors, leading to a higher V_{cmax} limitation relative to the J_{max} limitation due to either diffusive constraints or reduced protein synthesis, respectively. A thermal adaptation of the J_{max}/V_{cmax} ratio in mature plants growing in their native environments, including tundra, subalpine and semiarid-arid habitats, has been reported by Kumarathunge *et al*. (2019), again providing a significant negative correlation of J_{max}/V_{cmax}, standardized at 25°C, with the temperature environment, and following the same trend observed for thermal acclimation in other species (Kattge and Knorr, 2007; Kumarathunge *et al*., 2019). Moreover, in low nutrient environments, despite a reduction in V_{cmax}, the J_{max}/V_{cmax} ratio is frequently maintained, reflecting a tight coordination between the photosynthetic gain and costs of energy dissipation (Section Photobiochemistry; Walker *et al*., 2014). After a compilation of previously published V_{cmax} and J_{max} (on a C_i basis due to the scarcity of data on a C_c basis) from temperate, Arctic/alpine and dry warm desert plants standardized or measured at 20–25°C, it is possible to observe that not only are the J_{max}/V_{cmax} ratios from cold-adapted species higher than those from temperate ones, but also some dry warm desert species measured under natural conditions in their respective habitats show equally high ratios (Figure 5). These warm desert species show V_{cmax} values in the range of those from temperate species but higher J_{max} values than those from temperate species, in contrast with the thermal plant acclimation and adaptation trends observed for J_{max}/V_{cmax} in the meta-analysis reported by Kumarathunge *et al.* (2019), which did not include dry warm desert plants. The similarity observed in Figure 5 between the J_{max}/V_{cmax} values compiled for Arctic/alpine and some dry warm desert

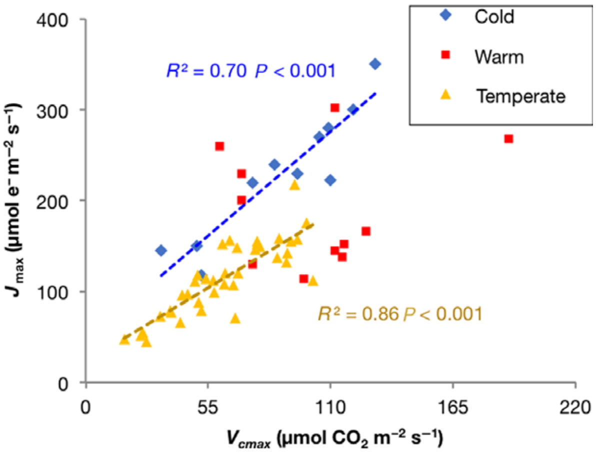

Figure 5. Correlation between V_{cmax} and J_{max} at 20–25°C modelled from A/C_i curves from Arctic/alpine (blue diamond), warm desert (red square) and temperate (orange triangle) species. Data were compiled from Rogers *et al.* (2017), Albert *et al.* (2011), Cai *et al.* (2015), Fan *et al.* (2011), Shi *et al.* (2006), Hamerlynck *et al.* (2002), Huxman and Smith (2001), Shi *et al.* (2008), Utsugi *et al.* (2009), Hinojo-Hinojo *et al.* (2018) and Kattge and Knorr (2007). Only statistically significant linear correlations for each group of species are shown.

plants might be driven by an adaptation pattern to limited water availability, suggesting a preferentially favoured enhancement of electron transport capacity over carboxylation capacity. However, this hypothesis must be confirmed with further *in vivo* leaf biochemical parameters modelled on a C_c basis (i.e. considering g_m) in a larger number of species adapted to different extreme environments.

Regarding TPU capacity, photosynthesis might be limited by P_i regeneration primarily at high CO_2 levels, combined with high irradiance and/or low temperatures (Sharkey, 1985; Labate and Leegood, 1988; Sage, 1994), although TPU limitation is difficult to observe under most of the analysed *in vivo* situations (Kumarathunge *et al.*, 2019). It has been suggested that plants typically maintain a TPU capacity that is slightly greater than the electron transport capacity (Yang *et al.*, 2016). TPU limitation has been observed in warm-grown plants of the high-mountain grass *Calamogrostis canadensis* when the rate of photosynthesis is measured below 15°C, but this limitation was no longer observed after low-temperature acclimation (Kubien and Sage, 2004). TPU limitation has also been observed at high C_i in the cold-tolerant grass *Thinopyrum intermedium* under cold stress (Jaikumar *et al.*, 2016), and the authors suggested that it may be an underrated photosynthetic limitation in future scenarios of increased atmospheric CO_2 in cold environments. Nevertheless, more ecophysiological studies concerning the biochemical limitations of photosynthesis under native growth conditions, including the characterization of RuBisCO kinetics, are needed to corroborate the trends in biochemical adaptation of photosynthesis to extreme environments.

CONCLUDING REMARKS

Ecophysiological studies in plants from extreme environments have been an important focus of scientific attention from the seventies, or even earlier. The most recent technologies offer opportunities to improve our knowledge about plant photosynthesis and ultimately the specific mechanisms that enable plants to sustain a positive carbon balance in hostile environments, where only a small group of vascular plants can live. Adaptation to these hostile environments may involve coordinated enhancements of thermal energy dissipation, reduction of effective photon absorption, metabolic adaptations that increase antioxidant activity and/or an increased electron sink capacity. Despite their exposure to severe photooxidative stress conditions, in general these plants do not possess any particular photoprotection mechanism beyond the known strategies observed widely in plants from more benign environments. However, several gaps of knowledge must be filled regarding the mechanisms that drive chloroplast ultrastructure rearrangements, alternative electron sinks rather than photosynthesis to sustain the cell redox status, the primary and secondary metabolic pathways that sustain the energy balance, and antioxidant metabolism. Additionally, mechanistic approaches are needed to explore the major determinants of the environmental response of g_s and g_m (and the interplay between them) that finally drive the CO_2 supply into the chloroplast. In fact, several works have shown that under low temperature and high elevation, g_m becomes the most important limiting factor driving A_N. Subsequently, a constrained C_c in combination with extreme low temperatures in these environments has shaped photobiochemical adaptations towards an increased CBC enzyme content and activation state, along with improved RuBisCO kinetics, such as higher affinity and specificity for CO_2 and/or elevated k_{cat}^{c}, whereas adaptations to extremely high temperatures may include the expression of heat-stable RuBisCO activase. Nevertheless, our knowledge concerning *in vivo* leaf biochemical limitations of photosynthesis from plants growing in extreme environments remains very limited. Multiple adaptations at different plant levels are required to achieve an annual positive carbon balance due to the very short growing season in extreme environments, in which plants face highly adverse conditions to achieve an annual positive carbon balance, jeopardizing their long-term survival. Therefore, a deeper understanding of the photosynthetic rearrangements of extreme plants will promote more accurate predictions concerning climatic change effects in these environments, as well as biotechnological opportunities regarding productivity and stress tolerance.

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AUTHOR CONTRIBUTIONS

BF-M, JIG-P, JG and JGago designed this work. The different authors participate in the different sections depending of their area of expertise; BF-M, JIG-P, LC and JG developed the section 'Ecophysiological perspective of extreme environments for plants'. The section on 'Plant/leaf morpho/anatomical adaptations in deserts and boreo/alpine environments' was mostly written by BF-M, JIG-P, LC and JG. The section on 'Photobiochemistry' was driven by BF-M, JIG-P, MJCM and LB. The section on 'Primary metabolism and antioxidant biochemistry' was driven by CMF, ARF, ANN, MJCM, CI and JGago. The final section on 'Photosynthesis in extreme environments' was developed by JG, CI, CMF, ARF, ANN and JGago. All authors participate in the Concluding remarks section. BF-M, JIG-P and JGago designed the figures. BF-M, JG, CMF, MJCM and JGago reviewed the entire manuscript and prepared the definitive version.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All relevant data can be found within the manuscript and its supporting materials.

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