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REVIEW PAPER

What can we learn from the ecophysiology of plants inhabiting extreme environments? From 'sherplants' to 'shercrops'

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Abstract

In the 19th century it was proposed that ecophysiology was best studied in regions with extreme climatic conditions. In the present perspective, we argue that perhaps this is more timely than ever. The main reason is the need to improve crops to be simultaneously more productive—due to the increased population—and more stress tolerant—due to climate change. Climate change induces plants to face not just harsh but also 'unexpected' (unpredictable) climatic conditions. In this sense, we hypothesize that 'sherplants', namely plants living in the extremes of plant life (e.g. hot deserts, Arctic and Antarctica, or high elevations) can provide cues on how to break the trade-off between productivity and stress tolerance, as they need to be produced quickly due to the very short growing period while being stress tolerant due to the harsh and unpredictable climate endured during most of the year. We present glimpses of results from three consecutive projects developed over the last 10 years, in which hundreds of species from different regions of the world have been studied. In particular, we propose a pathway for developing 'shercrops' learning from 'sherplants', debate whether some of the already studied species may have really broken the aforementioned trade-off, and present a number of interesting unforeseen discoveries made when studying plants from extreme climates.

Keywords: Climate change, ecophysiology, extreme environments, photosynthesis, sherplants, stress tolerance, trade-off.

Introduction

The idea is not new, nor is it ours. As early as the late 19th century, Simon Schwendener proposed that the relationship between the environment and the morphological habit of plants (i.e. ecophysiology) could be best studied in regions with extreme climatic conditions (reviewed in Lüttge and Scarano, 2004). Prominent plant ecophysiologists such as Hal Mooney, Otto Lange, Detlef Schulze, Chris Field, Olle Björkman, Phil Rundel, Arthur Gibson, Barry Osmond, Joe Berry, and Jim Ehleringer, among others, made the idea their own in the 1970s and 1980s by, for example, devoting efforts to building 'portable' instruments to measure gas exchange in the Death Valley, Negev desert, and other remote sites (quoted in Field *et al.*, 1989), leading to an explosion in knowledge on how photosynthetic processes adapted to environmental stress (Berry, 1975). In the last three decades, however, such adventurous field ecophysiological campaigns have become scarcer, even though nowadays systems are indeed portable. However, perhaps applying Swendener's idea is more timely than it has ever been. The increasing global human population and climate change are currently challenging our capacity to cope with food security (Schmidhuber and Tubiello, 2007; Morison *et al.*, 2008; Andrade, 2016; ONU, 2019; Ortiz-Bobea *et al.*, 2021). On the one hand, increasing crop yield per hectare is urgent to feed the growing population (Kay *et al.*, 2013; Fischer *et al.*, 2014; Lal, 2016); on the other, this has to be achieved with varieties or species not only more tolerant to a global higher average temperature and drought (Rivero *et al.*, 2022; IPCC 2023) but also enduring an increased frequency of extreme events, including more

frequent heatwaves (i.e. periods of substantially above-average ambient temperature) whose effects remain largely understudied (Breshears *et al.*, 2021; Ostria-Gallardo *et al.*, 2023). Additionally, and counterintuitively, plants are faced with extreme freezing periods in regions distant from the Arctic, which are related to Arctic warming provoking changes in atmospheric circulation (Francis and Vavrus, 2012), such as those which occurred in Texas in 2021 or in several parts of the USA in 2024 (CNN, 2024; The Conversation, 2024; The Guardian, 2024). When combined, multi-stress effects can be devastating for plants (Gu *et al.*, 2008; Zandalinas and Mittler, 2022). Hence, crops must now face not only increased average temperatures, but also extreme episodes of freezing and heat waves often combined with pre-existing drought.

Consequently, we are urged to improve crop productivity and tolerance to multiple stresses simultaneously. This is challenging because of the well-known trade-off between productivity and stress tolerance (Moles, 1994; Crawley, 1997; Alpert, 2006; Reich, 2014; Niinemets, 2020). This trade-off is also apparent in crops, showing negative correlations between yield and stress tolerance indicators (Conway, 1993; Cunha da Silva *et al.*, 2020). Another trade-off exists between yield and yield stability under stress (i.e. less productive varieties under non-stress conditions show larger yield stability under stress) (Marten, 1988; Conway, 1993; Blum, 2005). Plant physiology and plant ecophysiology in particular are key to deciphering whether this trade-off can be broken since they address the underlying mechanisms for both productivity and stress tolerance. Indeed, such a trade-off has a reflection at the leaf level in the worldwide leaf economics spectrum, consisting of negative correlations between some leaf traits enhancing productivity—such as photosynthesis, nitrogen, and phosphorus contents—and those enhancing either tolerance or resource use efficiencies—such as leaf mass per area, leaf life span, and mesophyll cell wall thickness—(Wright *et al.*, 2004; Onoda *et al.*, 2017; Xue *et al.*, 2023)—or turgor loss and hydraulic safety (Nadal *et al.*, 2018, 2023; Xiong and Flexas, 2022). It also has a reflection in the well-known antagonistic crosstalk among hormones, although it has been proposed that there are opportunities to break this (Karasov *et al.*, 2017). The bad news is that photosynthesis—the ultimate driver, alongside respiration, of plant productivity—is already very high in crops (Flexas *et al.*, 2014a; Nadal and Flexas, 2019), derived from already highly photosynthetic wild ancestors (Gómez-Fernández *et al.*, 2024)—hence presumably low stress-tolerant species—but reportedly having endured further reductions in their tolerance to, for example, drought during domestication (Koziol *et al.*, 2012). In general, most crops have low tolerance to stresses (e.g. Schmitt and Edwards, 1981; Ergo *et al.*, 2021; Vico *et al.*, 2023), while the model species *Arabidopsis thaliana* also has low tolerance to stress (Chaves *et al.*, 2009) in addition to a very modest photosynthetic capacity (Flexas *et al.*, 2007; but see Demmig-Adams *et al.*, 2017; Adams *et al.*, 2018). At the leaf level, ~10 years ago, we proposed a central hypothesis

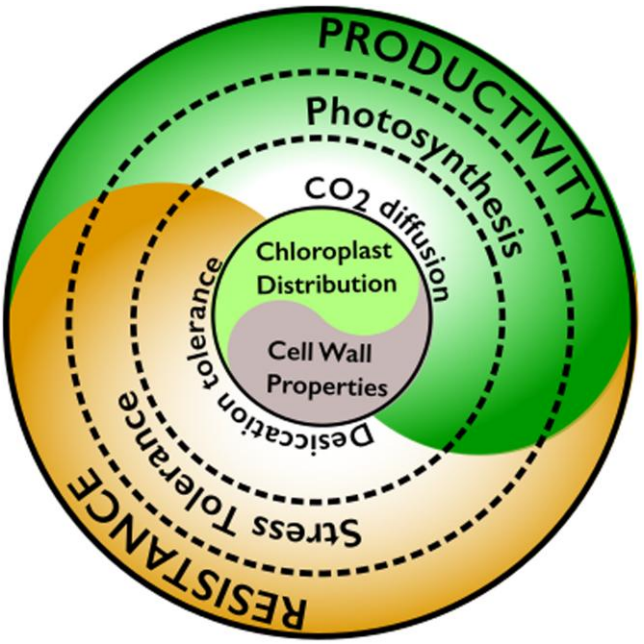

Fig. 1. Downscaling of the trade-off between productivity and resistance (ecosystem level) through photosynthesis-stress tolerance (organism level) and CO_2 diffusion-desiccation tolerance (organ-to-cell level) to the proposed anatomy-based conditioner of the trade-off (subcellular level).

for projects TOPSTEP, EREMITA, and POPEYE (all of them funded by the Spanish Ministry of Science since 2015; see the Acknowledgements for details). It stated that the general trade-off may have a specific conditioner in subcellular anatomy, where a large chloroplast surface area facing intercellular air spaces (S_c) and a low cell wall thickness (T_{cw}) contribute to large photosynthetic capacity—by enhancing mesophyll conductance to CO_2 (g_m)—while the opposite situation promotes cell desiccation tolerance but reduces photosynthesis due to reduced g_m (Fig. 1).

While we were able to prove this anatomy-based trade-off across the phylogeny of land plants (Gago *et al.*, 2019; Flexas *et al.*, 2021), the intra-group dispersion is large enough to believe that it might be possible to find outliers to this trade-off. Interestingly, resurrection ferns and angiosperms (able to completely desiccate and recover physiological activity upon rewatering) were shown to have a significantly different ratio of photosynthesis to both S_c and T_{cw} (Nadal *et al.*, 2021), yet it remains to be discerned whether they are real outliers to the general rule. Different functional types of tracheophytes also present less marked but still significantly distinct g_m/anatomy ratios (Knauer *et al.*, 2022), although these were not apparent when pooling tracheophytes with non-tracheophytes (Flexas *et al.*, 2021). So, the key question is: can the trade-off between productivity and stress tolerance be broken? To answer this question, we should look at both what ecophysiology has proven thus far and what might be expected from it in the future.

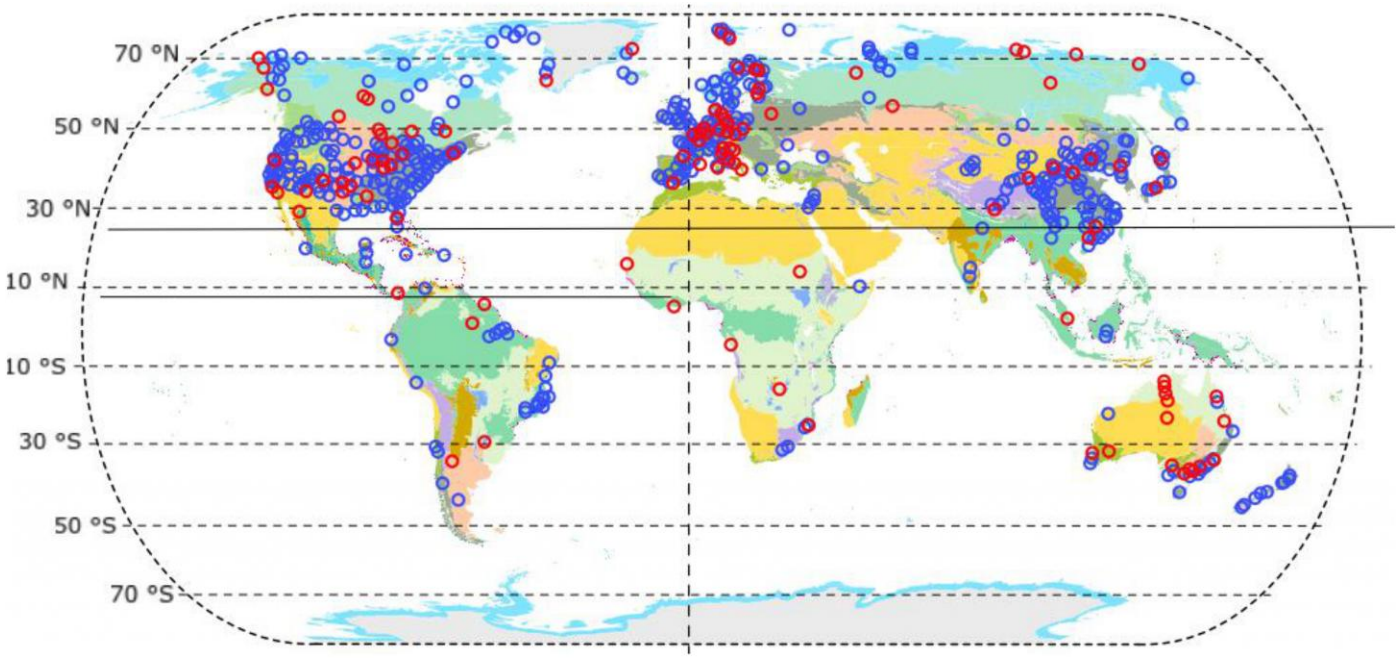

Fig. 2. Global distribution of studies on climate change effects on plant physiology (blue circles) and FLUXNET eddy covariance towers (red circles). Redrawn after Song *et al*. (2019) and Gao *et al*. (2021), respectively.

Current reality for past and present plant ecophysiology studies

A large number of studies on plant ecophysiology have been performed in Northern Hemisphere countries plus Australia. Moreover, most of these studies have focused on a very restricted number of species, namely crop plants or model species such as *A. thaliana* (Marks *et al*., 2023).

To provide just two examples of this, Fig. 2 shows world distributions of studies on climate change effects on plant physiology and the operating FLUXNET eddy flux towers (Song *et al*., 2019; Gao *et al*., 2021). It appears that more than three-quarters of studies on climate change and more than half the operating eddy flux towers concentrate between 30° and 50° North, suggesting that even studies in non-crop plants deal mostly with plants from temperate and Mediterranean biomes. Hence, many important biomes of the world have been missed in such studies.

In other words, ecophysiological studies of plants facing extreme conditions are very scarce. There is a remarkable scarcity of datapoints in the vast yellow areas (hot deserts and xeric shrublands) and in the largest mountain systems of the world (Himalayas and Andes). Moreover, they are completely absent in Antarctica according to Gao *et al*. (2021), although we have made significant advances there (Sáez *et al*., 2018; Sierra-Almeida *et al*., 2018; Ramírez *et al*., 2024). Furthermore, studies of, for example, the physiological determinants of photosynthesis, stress tolerance, or responses to simulated climate change have mostly focused on a narrow range of plant functional types and phylogenetic groups, namely land plants including angiosperms and a limited number of gymnosperm species (Veromann-Jürgenson *et al*., 2020). It has already been discussed that very different responses can be expected from plants belonging to different phylogenetic groups and functional types (Niinemets *et al*., 2011; Flexas *et al*., 2014b; Gago *et al*., 2019). For this reason, it is a priority to begin experimental studies in groups of basal land plants, such as mosses, hornworts, and liverworts (Bryophyta), because many of their species are colonizers of cold, windy, and nutrient-poor microenvironments, ideal for exploring the trade-offs between productivity and environmental tolerance. Of course, this requires field protocols and analyses adjusted to the poikilohydric biology of their gametophytes and the small size of their phyllidia, but this has been proven to be feasible although tricky (e.g. Troncoso *et al*., 2013; Flexas and Carriquí, 2020; Perera-Castro *et al*., 2022a, b; Morales-Sánchez *et al*., 2022, 2023; Wuyun *et al*., 2024). Comparative work with the poikilohydric algal relatives of land plants can pinpoint conserved molecular programs (Dadras *et al*., 2023; Feng *et al*., 2024) and gene regulatory networks (Dong *et al*., 2024; Goldbecker and de Vries, 2025; Rieseberg *et al*., 2025). It would also be interesting to study fern gametophytes, which are considered highly dependent on water and fragile but, nevertheless, have been demonstrated to be far more tolerant than the sporophytes, at least for non-resurrection ferns (Pittermann *et al*., 2013; López-Pozo *et al*., 2018). Perhaps gametophytes of non-studied species could be outliers from which we could learn novel strategies to cope

with stress and a good model for understanding the gene regulation leading to stress tolerance since gametophytes and sporophytes have the same genes (but in one or two copies) but different ways to cope with stress.

In addition, it has been already recognized that 'any single plant species cannot fully embody the characteristics of all others' in reference to the limits of Arabidopsis as a model species (Woodward and Bartel, 2018), which became so precisely due to its small genome size and short life cycle (Stitt *et al.*, 2010). For the same reason, attempting to improve crop yields and stress tolerance based on Arabidopsis-driven knowledge is an even more distant goal than gaining insights into human physiology based on studies in laboratory mice (*Mus musculus*). Lab mice are mammals as are humans, and their genome size is only 26% smaller than ours (2.5 Gbp versus 3.4 Gbp). However, the genome size of Arabidopsis is as much as 100 times smaller than that of, for example, wheat (0.136 Gbp versus 17 Gbp), with other plants having even larger genome sizes (Michael, 2014; Pellicer *et al.*, 2018), the current record peaking at >160 Gbp for the fern *Tmesipteris oblanceolata* (Fernández *et al.*, 2024). Therefore, while it is undisputed that model species such as Arabidopsis are essential to understanding basic physiological and biochemical mechanisms, particularly those well conserved across plants, the plant kingdom offers much greater diversity beyond them at the gene, molecular, and physiological levels (García-Plazaola *et al.*, 2012; Flexas and Gago, 2018).

Current perspective for future plant ecophysiology studies

Since we need to increase yield per hectare while agronomic practices are already optimized, increasing photosynthesis is envisaged as a major means to achieve this goal. Certainly, there have been theoretical (Flexas, 2016; Flexas *et al.*, 2016; Bayley-Serres *et al.*, 2019; Galmés *et al.*, 2019; Wu *et al.*, 2019; Smith *et al.*, 2023) and applied approaches (Ort *et al.*, 2015; Simkin *et al.*, 2019; South *et al.*, 2019; López-Calcagno *et al.*, 2020; Salesse-Smith *et al.*, 2024) to improve crop yields by enhancing different photosynthetic traits. However, these efforts have focused mostly on non-stress conditions, yet acknowledging the importance of dynamic environmental changes, such as fast changes in the incoming irradiance on leaves (Kromdijk *et al.*, 2016; De Souza *et al.*, 2023). This said, climate change will impose (in fact, it is imposing) on crops and wild vegetation an ongoing progressive change towards more adverse 'average' environmental conditions and a higher frequency of extreme events. This will potentially lead to plant tissue desiccation and/or temperatures surpassing metabolic limits. Also do not forget that extreme events may last days to weeks! So, we absolutely do need to improve yields using more stress-tolerant plants.

We hypothesize that, if we are to find any plant species that have evolutionarily overcome the trade-off between productivity and stress tolerance, it will certainly be found in those places which at the extremes of plant life. The reason is that to achieve a positive seasonal carbon balance, plants inhabiting extreme environments may require a large photosynthetic capacity to produce sufficient new organic matter during the very short period in which environmental conditions are optimal (Fernández-Marín *et al.*, 2020a). However, at the same time, because of the very unfavorable weather conditions during the rest of the year and its great unpredictability during the growing season, plants may also possess intrinsic defense mechanisms or adaptive functional traits to tolerate harsh conditions and fluctuations during the optimal periods (Liancourt *et al.*, 2020; Chlumská *et al.*, 2022). On the other hand, life in extreme environments is expected to be almost devoid of biological competition. Thus, traits increasing competitive ability might have been largely lost during evolution for improving survival under extreme abiotic pressures. Expression of traits improving competition is typically expensive, and thus modern crops have been bred such that they hardly tolerate biological competition at all (Niinemets, 2020). Therefore, in theory, extreme environment plants with superior physiology under abiotic stress might constitute a promising platform for breeding high-yielding crops. However, it is evident that many plants inhabiting extreme environments are not at their optimum there, for instance being below their photosynthetic optimal temperature, as observed for Antarctic mosses (Perera-Castro *et al.*, 2020) and angiosperms (Clemente-Moreno *et al.*, 2020a, b; Ramírez *et al.*, 2024). While the only two higher plants that have been able to colonize maritime Antarctica—*Deschampsia antarctica* and *Colobanthus quitensis*—are not fully adapted to Antarctic conditions based on their physiological responses (Clemente-Moreno *et al.*, 2020a, b), nevertheless they are experiencing significant expansion there by colonizing new habitats, which has been related to progressive warming of the zone (Grobe *et al.*, 1997; Vera, 2011). In the case of *C. quitensis*, this may reflect the large plasticity of the species as, looking at its distribution (e.g. https://www.gbif.org/), it ranges all along the Andes, even to Ecuador (in fact, its name *quitensis* was given for Quito), although towards the North it just grows at high elevations. The case of *D. antarctica* is more intriguing, as its distribution is periantarctic, reaching north only to Tierra del Fuego and Patagonia (although it has been rarely mentioned in the Andes; Moore, 1970), so one would expect it to be really adapted to the prevailing cold conditions of these regions. On the other hand, in other extreme regions of the world—such as the Atacama Desert and surrounding ecotones—plants are not undergoing expansion and, indeed, their recruitment is very rare and might occur in only one out of many years (e.g. ENSO years, Holmgren *et al.*, 2006; Carvajal *et al.*, 2014).

It is likely that the cause of non-adaptation is related more to the speed of climate change rather than to its magnitude. Besides recruiting only in some years, plants from harsh environments tend to show longer leaf life spans but also delayed sexual maturity (Rosbakh and Poschlod, 2018; Chondol

et al., 2023). For instance, sexual maturity is delayed by as much as 15–20 years in high-elevation populations as compared with lower elevation conspecifics in *Potentilla pamirica* (Dolezal *et al.*, 2021). Now imagine a species recruiting only once per decade or two and then requiring several additional decades to flower. This is well known, for example for baobabs and sequoias, but it can be extreme in species such as the Andes bromeliad *Puya raimondii*, which can take 40–100 years to flower (Liu *et al.*, 2024). Owing to the rules of natural selection, only the best adapted seedlings will survive and reach sexual maturity. However, since it takes decades for this, adult individuals nowadays are those adapted to the prevailing conditions of decades ago. Between 1960 and 2020, the CO_2 concentration rose in the atmosphere by ~109 ppm (NOAA, 2024), which is a somewhat larger change than that having occurred during the last two deglaciations, except that at that time it took ~14 000 years! Therefore, the fast speed of global change coupled with the slow development of many species from harsh environments results in most currently observed individuals being adapted to the past rather than the prevailing conditions. Of course, it is conceivable that some plant species really adapted to harsh environments can still be found. An example could perhaps be *Schrenkiella parvula*, a *Brassicaceae* herb which grows faster under stress than under non-stress conditions, because of rewiring in the regulatory network between hormones [specifically abscisic acid (ABA)] and growth (Sun *et al.*, 2022). Of course, it is also essential—but outside the scope of this review—to examine how these plants utilize the elevated atmospheric CO_2 that is now widespread globally. CO_2 itself could be a key factor that explains the increase in distribution range for some extremophiles (see Box 1 for some open questions on this).

In summary, adaptation in species inhabiting extreme environments is not general, which may have at least two potential causes: (i) the fact that they might not be at their physiological optimum but surviving due to reduced competition; and/or (ii) the instability of these habitats owing to ongoing climate change. Whatever the cause, the result is that we expect that just a small fraction of all plants inhabiting extreme environments may prove to be really adapted to those conditions and, importantly, might have overcome the trade-off between productivity and stress tolerance. Understanding such plant responses will deepen our knowledge of carbon use patterns within these species, ultimately shedding light on the trade-off between productivity and stress tolerance.

Box 1. Open questions regarding the effects of increasing CO_2 in extremophile plants

Do plants in harsh environments fully capitalize on this extra CO_2 surrounding their leaves?

Do they acclimate to increased CO_2 by closing their stomata?

Will they use the additional carbohydrates produced to enhance growth, accelerate their life cycle, maintain high respiration rates, or reinforce their defense mechanisms?

These are just a few of the questions that remain unanswered. Although considerable research studies have explored the effects of elevated CO_2 on plants (Jauhiainen and Silvola, 1999; Leakey *et al.*, 2009; Dusenge *et al.*, 2019), studies specifically focusing on plants in extreme environments are scarce. Given that plants in extreme environments typically have robust leaves and high CO_2 diffusion resistance from substomatal cavities to chloroplasts, elevated CO_2 is expected to enhance their photosynthesis more than in species with mesophytic leaves (Niinemets *et al.*, 2011). Thus, CO_2 itself can be a key factor that explains the range increase for some extremophiles or explains why they can hold their ground when life becomes more extreme due to increases in temperature and reductions in water availability.

What should we expect from studies on plants from extreme environments?

As said, we expect to find some but few outliers of the trade-off between photosynthesis and stress tolerance. At the same time, understanding the stress tolerance mechanisms of non-outlier plants inhabiting extreme environments might be of great help for designing an outlier crop using biotechnology tools. If the deciphered mechanisms do not have systematic negative effects on photosynthesis, they could eventually even be used to introduce stress tolerance to crops without losing productivity. In this sense, we introduced the concept of 'sherplants' (Flexas and Gago, 2018) in analogy to the conquest of Himalayan summits by European alpinists starting in the middle of the last century. European alpinists were well trained and technically prepared for climbing, having reached the major summits in the Alps. However, as soon as they attempted much higher elevations in the Himalayas, they realized that their physiology was not acclimated. Native sherpas—who were essential to conquer the >8000 m summits—instead were physiologically adapted! Current crops—like European alpinists—are 'technically' prepared for high productivity but they are not physiologically ready for multi-stress tolerance and, hence, facing current climate change challenges. In contrast, 'sherplants' are generally not good in terms of fast growth and production, but they can survive in the harshest conditions. This is why we propose that it is urgently necessary to study the physiology of 'sherplants'. If a given sherplant is an outlier of the trade-off (i.e. with the 'technical capacity for climbing like Tenzing Norgay or nowadays sherpas'), then even better (in terms of plants not only being highly tolerant to multi-stress but also having large photosynthetic capacity).

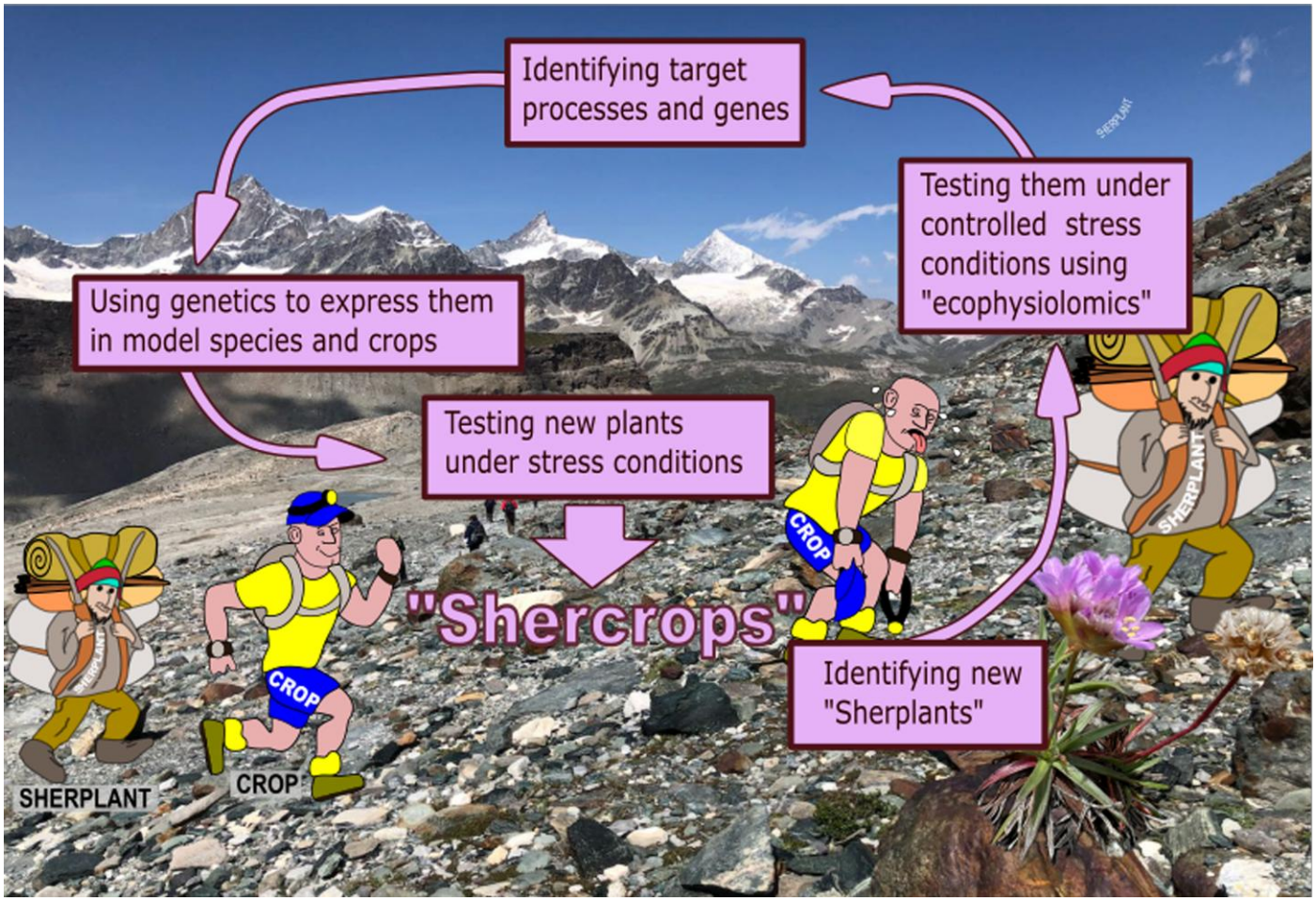

Fig. 3. A cartoon parallel between non-native climbers or trail runners versus sherpas and current crops versus 'sherplants'. The diagram shows the proposed step sequence to achieve 'shercorps'–highly productive crops with high tolerance to environmental stresses (Design: J.I. Garcia-Plazaola).

The final goal should be developing productive crops with simultaneously high tolerance to multiple stresses, in other words 'shercrops' (Fig. 3). Please note that the diagram presented in Fig. 3 and, more generally, the whole purpose of the present review, can be applied to any aspect of plant ecophysiology—and ideally should be (e.g. root-to-shoot ratios, carbon balance, use efficiencies of water, nitrogen, and other minerals, the relationships between carbon balance, growth, and development, senescence mechanisms, etc.). In the next section we will just briefly summarize some of the works that we have developed at or slightly beyond the phase 'identifying new sherplants' shown in Fig. 3.

Preliminary results: for a research effort lasting for about 10 years!

The title of this section is not intended to be provocative but rather to reflect a reality, meanwhile warning future plant 'ecofizzers' aiming to deal with extreme/remote environments about several aspects to be considered, which can be summarized by stating that the logistics in remote places are often very complicated. They include, among others, the lack of a true lab, restricted access to power supplies or expendables—even to daily food in some cases—difficult access to plants, complex interactions with dangerous and/or protected fauna, the necessary acquisition of visiting and/or sampling permissions, and many more such challenges. More site-specific issues may, in our experience, include, for example, the need to pass a detailed and time-consuming military health exam to reach Antarctica under Spanish regulations, or to gain adequate capacities and permissions to carry high ammunition weapons, compulsory in many places in the High Arctic. In addition, of course, one might be ready for unexpected issues, such as what happened to us: for example a car motor burning in the Namibian desert or being questioned by the police and later required to leave a town on the Qinghai–Tibet Plateau for having unintentionally spent the night in a prohibited area. For those who are used to ecophysiological field work—involving power-driven instruments and time-

consuming measurements—it is easy to imagine how all the aforementioned circumstances limit the capacities to conduct research at remote sites. For this reason, in order to identify potential outliers based on the simple leaf-level principles outlined in Fig. 1, we decided to keep sampling to a minimum three steps: (i) leaf sampling in small Eppendorf tubes for later analysis of subcellular anatomy; (ii) measuring *in situ* gas exchange and chlorophyll fluorescence using portable commercial instruments (aiming to travel to each site during its most favorable season for plants, based on meteorological recordings, so that the measured net CO_2 assimilation is close to the light-saturated and ambient CO_2 photosynthetic capacity); and (iii) determining the tolerance of the photosynthetic tissue to several abiotic stresses. Concerning the latter, in our first project starting on 2015, we focused on desiccation tolerance, for which we developed the so-called 'Falcon test' (López-Pozo *et al.*, 2019). This consists of a relatively portable kit, including a high-precision balance (again the need for a power supply, in remote sites meaning car batteries with suitable adaptors, fuel-based electric generators, or direct supply through transformers from a motorhome battery), plus Falcon tubes previously filled with different desiccants of known equilibrium water potential at a range of usual temperatures. Adding a pocket fluorometer to the kit it is possible to determine the sample relative water content (RWC) and the maximum quantum efficiency of PSII (F_v/F_m) at each point, from which several quantitative indexes can be estimated (e.g. initial minus final F_v/F_m over the initial value, ranging from 0% to 100%) as a proxy for dehydration tolerance (DT) of PSII to severe desiccation (López-Pozo *et al.*, 2019). More recently, additional leaf-level stress tolerance indices have been added—resulting in increased logistic complexity even though all the analytical tests are based on pocket fluorometer measurements of F_v/F_m—including UV-B test, high irradiance test, and freezing and heating tolerance tests, the latter three based on a device protected under Spanish invention patent (ES2960435) and a pending application under the Patent Cooperation Treaty (WO2024/028532 A1).

As mentioned, our main goal was measuring the photosynthetic capacity (A_N) and the abiotic stress tolerance (DT) of the leaf, hypothesizing a trade-off betewwn these two parameters. These two parameters are plotted in Fig. 4 for the data collected in a >2000 km field transect from Manas's steppes in Western China to the Qinghai–Tibet Plateau at Delingha, passing through the Turpan depression and the Taklamakan desert (data published in Flexas *et al.*, 2022). While no significant correlation is observed between photosynthesis and DT, the graph can be tangentially divided into two corners by tracing a line from the maximum photosynthesis measured among all species to the maximum possible DT (Fig. 4). All the species analyzed fall into the bottom left corner of that line, except *Peganum harmala* (Supplementary Fig. S1), located in the upper right corner but still close to the division line. Whether *P. harmala* is or is not a real outlier to the general trade-off is yet to be confirmed

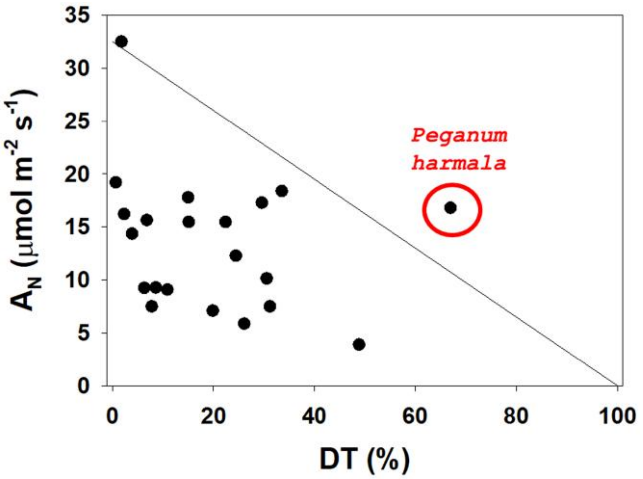

Fig. 4. The relationship between photosynthesis (A_N, measured with an IRGA during the supposedly optimal season for each plant at their site) and leaf tissue dehydration tolerance (DT, *sensu* López-Pozo *et al.*, 2019) in an ~2000 km transect from the Manas steppes through the Turpan depression (–100 m a.s.l.) and the Taklamakan desert to the Qinghai–Tibet Plateau (QTP) at Delingha (+3000 m.a.s.l.). Each dot represents one species at one site. The line was drawn from the maximum photosynthesis measured among all species (corresponding to 32.5 μmol CO_2 m^{-2} s^{-1} found in *Hedysarum multijugum* at the QTP) to the maximum possible DT (100%). Only one species (*Peganum harmala*, sampled at Manas steppe) lay on the upper right corner, being a potential outlier of the trade-off (replot from Flexas *et al.*, 2022).

based on more detailed analysis. In general, the picture confirms that it might be hard to find a true outlier and that most of the plants found at the environmental limits of plant growth inhabit these sites because they can survive better than potential competitors at those sites, but not because they are at their physiological optimum there. A trade-off leading to similar conclusions was shown by Karabourniotis *et al.* (2014) as a negative exponential relationship between photosynthesis and total leaf soluble phenolics and/or condensed tannin contents. While the study compiled data from more species than those in Fig. 4, from two distant locations and belonging to very diverse growth forms, no outlier was found. However, due to the proposed dual role of cell walls in photosynthesis and stress tolerance (Fig. 1), phenolic compounds and other antioxidant systems might be especially relevant to understanding these trade-offs, as a large fraction of the antioxidant activity of leaves occurs in the apoplast, and negative correlations between CO_2 diffusion in photosynthesis and apoplastic antioxidant activity have been shown (Clemente-Moreno *et al.*, 2019; Roig-Oliver *et al.*, 2020).

Recently, a comparison of phylogenetically related tree species inhabiting the Atacama Desert (*Strombocarpa tamarugo*, *Neltuma alba*, and *Neltuma chilensis*) using the Falcon-based test and a freezing test, revealed that *S. tamarugo* (Supplementary Fig. S1) seems to qualify as an outlier of the trade-off, exhibiting the expression of genes and the synthesis of metabolites capable

of conferring dehydration tolerance and freezing avoidance without jeopardizing its photosynthetic performance (Gajardo *et al.*, 2024). The photosynthetic machinery of *S. tamarugo* was efficiently protected from oxidative stress by the synthesis of tryptophan derivatives and complex antioxidant metabolites. Additionally, the high allocation of nitrogen for the synthesis of chlorophylls could be favored by the synthesis of non-nitrogen osmoprotectants (ciceritol and mannitol). Additional metabolomic and transcriptomic studies on phylogenetically diverse species from the Atacama Desert provided new insights into an evolutionarily convergent strategy with a unique set of traits associated with multi-stress tolerance (Eshel *et al.*, 2021; Dussarrat *et al.*, 2022, 2024).

Interesting unforeseen discoveries on sherplants made so far

The pioneer ecophysiological work in extreme climates during the 1970s and 1980s was probably powered by a genuine aim of understanding nature and, perhaps, to be amazed about how this has overcome environmental problems. In this sense, those early observations based on a huge effort and home-made instrumentation were extremely useful and are nowadays found in textbooks: for example, Schulze *et al.* (1972) discovered for the first time that stomata responded to surrounding air humidity in the Negev Desert; Mooney (1976) discovered an unexpected and surprisingly large photosynthetic rate (~60 μmol m^{-2} s^{-1}!) in the desert C_3 species *Camissonia claviformis*; while Keeley *et al.* (1984) discovered that the stomata-lacking Andean plant *Stylites andicola* performed photosynthesis by absorbing CO_2 through its roots! It was also shown that desert plants present a variety of photosynthetic organs other than leaves, which increase their water use efficiency (reviewed in Gibson, 1998). Therefore, nature has plenty of surprises if one seeks to look at its whole diversity, so even if no real outlier of the trade-off was finally found, prospecting physiological traits in plants from the environmental limits to plant life is still of interest.

Several examples of interesting findings based on our recent research include the following.

(i) We found that the only two vascular species native to Antarctica (*C. quitensis* and *D. antarctica*) present a high score in DT and in other tolerance tests while having a photosynthetic capacity that is quite average for angiosperms. Additionally, their leaves possess characteristics of plants adapted to dry environments, such as a high water use efficiency and substantially thicker cell walls than the angiosperm average (Sáez *et al.*, 2018; Gago *et al.*, 2019) coupled with a remarkably high Rubisco affinity for the limiting intracellular CO_2 (Sáez *et al.*, 2017). Interestingly, this finding agrees with the cross-tolerance to desiccation and to freezing we have also found in resurrection angiosperms and ferns at higher latitudes (Verhoeven *et al.*, 2018; Fernández-Marín *et al.*, 2018, 2021a; Georgieva *et al.*, 2022). Returning to Antarctica, it is remarkable that *C. quitensis* additionally presented a very large total antioxidant capacity in its leaves without penalty in photosynthetic capacity (Clemente-Moreno *et al.*, 2020a). Controlled low temperature experiments in both species confirmed that, although neither of the two was at its photosynthetic optimum at the temperatures most frequently experienced in Antarctica, both tolerate low temperatures better than temperate crops belonging to their respective families (i.e. carnation for *Colobanthus* and wheat for *Deschampsia*). While the metabolomic responses of Arabidopsis and crop species to a wide range of stresses have been extensively investigated (Obata and Fernie, 2012; Bulut *et al.*, 2025), the responses of extremophile plants have received less attention. Interestingly, metabolomic analyses revealed that the two species achieved similar tolerance using substantially different mechanisms. *Colobanthus*, in agreement with its reported very high respiration rate as compared with worldwide respiration datasets (Atkin *et al.*, 2015; Sáez *et al.*, 2018; Tcherkez and Atkin, 2021), links its tolerance to the production of energetically expensive but low N-content metabolites (Clemente-Moreno *et al.*, 2020a), such as (a) those requiring *S*-adenosylmethionine (SAM), which in turn is necessary for methylation reactions involved in the synthesis of polyamines and flavonoids (Long *et al.*, 2015); and (b) the phenylalanine pathway that leads both to secondary metabolism through the synthesis of flavonoids/phenylpropanoids and to the formation of salicylic acid (SA) and tocopherols, both reportedly related to increased stress tolerance (Morales and Munné-Bosch, 2016; Saleem *et al.*, 2021). In contrast, *Deschampsia* faced chilling stress by means of partial defoliation and nutrient remobilization. Nitrogen in particular was remobilized but, still, the routes of polyamine synthesis and the phenylalanine pathway found in *Colobanthus* were also enhanced in *Deschampsia* (Clemente-Moreno *et al.*, 2020b), as they were in the resurrection angiosperm *Ramonda myconi* during the winter season (Fernández-Marín *et al.*, 2020b).

(ii) Another example of how relevant prospecting physiological traits in plants towards their environmental limits can be was exemplified in the finding of complete operation of the so-called xanthophyll cycle in darkness, and solely activated by freezing (Fernández-Marín *et al.*, 2021a, b).

(iii) A remarkable finding was that mangrove species, such as *Avicennia marina*, can re-hydrate through absorption of liquid water that accumulates through deliquescence of salt secreted onto their leaf surfaces (Coopman *et al.*, 2021). Deliquescence is the dissolution of a hydrophilic particle in water vapor and occurs when atmospheric vapor pressure equals the equilibrium vapor pressure above a saturated solution of the dissolved substance (Zhao *et al.*, 2008). Deliquescence depends on relative humidity

(RH), occurring, for example, at 75% RH for NaCl (Langlet *et al.*, 2011) and at 80–85% RH for sea salt (Zeng *et al.*, 2013), thus enabling extraction of liquid water from unsaturated atmospheres. The amounts extracted increase (and the solutions become more diluted) with an increase in RH above the deliquescence point (Zhao *et al.*, 2008). However, access to this salty water must be selective to prevent both uncontrolled entry of excess ions into the leaf and uncontrolled water loss from the leaf. Fuenzalida *et al.* (2019) suggested that hydraulic conductance from the leaf surface to the leaf interior of *A. marina* was regulated by epidermal features such as salt secretion glands (Tan *et al.*, 2013), trichomes (Nguyen *et al.*, 2017a), or stomata (Eichert *et al.*, 2008), instead of cuticular permeability. Salt secretion glands may provide a pathway for the extraction of freshwater from the saline solutions that were initiated through deliquescence. Selective water uptake by salt secretion glands depends on PIP2;1 aquaporins (Tan *et al.*, 2013), which have dual water and ion channels (Kourghi *et al.*, 2018) whose separate functions are achieved by individual regulation of the different channel types (Byrt *et al.*, 2017; Qiu *et al.*, 2020). Indeed, rates of foliar water uptake estimated from the density and activity of salt secretion glands per unit leaf area in *Avicennia officinalis* (Tan *et al.*, 2013) compare well with bulk measurements of foliar water uptake in *A. marina* (Fuenzalida *et al.*, 2019; Coopman *et al.*, 2021). Finally, studies on sap flow showed a strong correspondence between the occurrence of reverse (downwards) sap flow and the initiation of deliquescence of salts secreted onto leaves in *A. marina* (Coopman *et al.*, 2021). The rates of reverse sap flow increased with increasing RH from the point of deliquescence (75% RH), showing that water extracted from unsaturated atmospheres could supply sufficient water to rehydrate leaves and even drive greater top-down rehydration depending on the intensity and duration of the wetting events. The potential importance of this water source is reflected in leaf water relations that indicate increased necessity for absorption of atmospheric water to maintain or enhance turgor with increasing salinity or aridity of the environments where *A. marina* grows (Nguyen *et al.*, 2017b). Similarly, a desert salt-secreting species, *Tamarix aphylla*, also shows enhanced hydration in response to wetting driven by deliquescence, but at a much lower RH (55%) due to the composition of secreted salts (Al-Handawi *et al.*, 2023). The capacity to extract water from unsaturated atmospheres may provide inspiration for greater understanding of the diversity of salt-tolerant species, and traits that might enhance salt and drought tolerance in crop plants.

(iv) Samples for leaf anatomy belonging to these ∼10 years of field campaigns are under current analysis, but even at this stage we can at least say that we have found some 'surprises' in them (Fig. 5). The figure illustrates three concepts at a time: (a) that, despite the existence of some dedicated apps, when an expert taxonomist is not present at the expedition to remote places, sometimes one ends up with samples and measured traits for a fully (bottom right image) or partially (upper right image) unidentified species; (b) that one may eventually find unexpected leaf structures with unknown function—such as those separating two palisade (upper left) or two spongy (upper right) mesophyll tissues (two different types of sclerenchyma?)—or those air (or water?) 'chambers' perfectly defined by clearly differentiated cells separating two sides of spongy mesophyll (bottom right and left images); (c) that even these unexpected and 'rare' leaf structures show convergence, as illustrated by these two examples from South Africa and Chile (observations backing the early ones of von Humboldt, but this time aided by a microscope!).

(v) Also, from Flexas *et al.* (2022), two additional useful issues were raised besides the discussed trade-off and its potential outlier *P. harmala*: the first opening up a new routine testing method when performing gas exchange measurements—in general, but particularly useful when analyzing unknown species in remote sites (a); and the second challenging our current understanding of C_4 physiology (b). (a) It was shown [after more than three decades of having been proposed as a useful parameter to diagnose stress in plants (Krall and Edwards, 1992; Flexas *et al.*, 2002)] that the ratio between the electron transport rate (ETR)—measured by a chlorophyll fluorometer, which are nowadays optionally incorporated into almost any commercial gas exchange system—to A_N—measured with the infra-red gas analyzer (i.e. the ETR/A_N ratio) can be used to estimate the actual-to-potential photosynthesis ratio of a given plant without need of *a priori* knowledge on the maximum expected photosynthesis of the species (provided that the stomatal conductance is not extremely low, i.e. it is larger than ∼0.05–0.1 mol H_2O m^{-2} s^{-1}). This means that a 'standard' measure of combined gas exchange and chlorophyll fluorescence using commercial equipment can provide a diagnosis of plant stress in the field without any previous knowledge about the plant (you might even not be able to identify it, as in one example in Fig. 5). Besides this interesting application, the ETR/A_N ratio provides a fast way to test both the accurate functioning of the two instruments (infra-red gas analyzer and fluorometer) and the absence of stress in experimental control plants, for which we have proposed it as a routine test to be reported in every work presenting photosynthesis rates at the leaf level (Perera-Castro and Flexas, 2023). In brief, in control C_3 species, the ratio should range from 7.5 to 12, while lower ratios indicate instrument malfunctioning and larger ratios indicate that control plants are enduring some

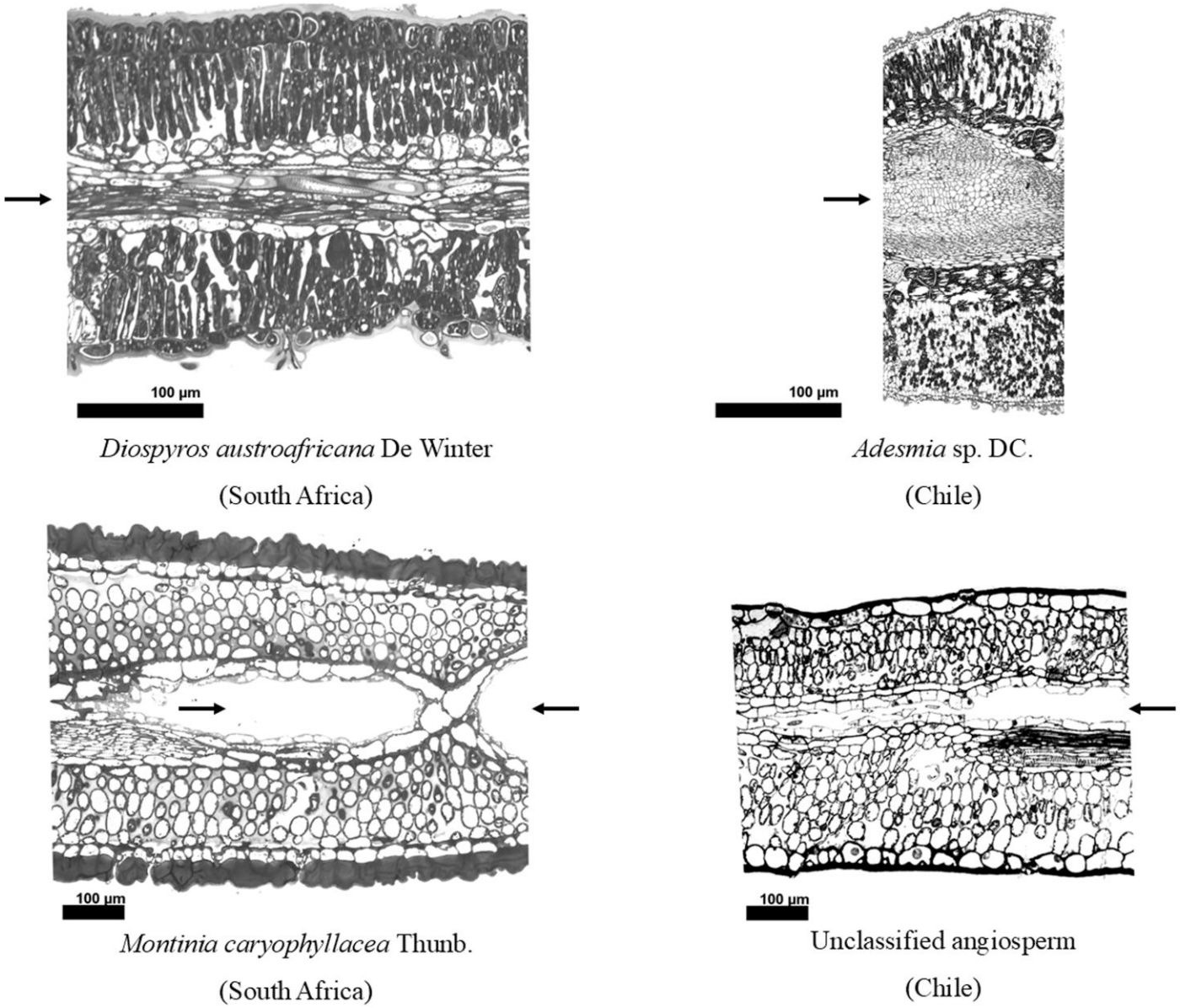

Fig. 5. Examples of unexpected structures found at sampled species from remote sites in South Africa (savanna, at Aquila Private Game Reserve, –33°36′ N, 19°93′W) and Chile (coastal desert ecotone, at Parque Natural Llanos de Challe, –2°89′N, 71°16′W). The upper pictures show a 'structure' (sclerenchyma?) physically separating upper and lower mesophylls. In *Dyospiros* they are clearly two palisade tissues, while in *Adesmia* it is less clear what kind of mesophyll is on both sides. The lower pictures show clearly defined structures (as they are surrounded by a clearly distinctive cell layer) but, are these air or water cavities?

undesired stress. (b) It was also shown that co-existing C_3 and C_4 species sharing identical average potential photosynthesis and midday leaf water potential strongly differed in their actual photosynthesis, with C_3 species displaying much higher current-to-maximum photosynthetic rates than their C_4 co-habiting species. In other words, under identical water stress at the leaf level, C_4 species presented more reduced carbon assimilation. This is counter-intuitive since C_4 species are reputed to be more water use efficient and to better tolerate dry environments than C_3 species, but is nevertheless in agreement with previous findings (Ripley *et al.*, 2007; Taylor *et al.*, 2014; Quirk *et al.*, 2019). The current perspective is that C_4 species are very tolerant/efficient under mild-to-moderate water stress (such as those endured by C_4 crops in their traditional seeding areas, e.g. the US corn belt) but they collapse rapidly after reaching a given water potential threshold denoting the start of severe stress. This severe stress threshold might be surpassed year-round at the climatically extreme environments of

Western China. Nevertheless, the mechanism(s) for the proposed collapse are unknown and may be a battle horse of C_4 research in the next years. Very recently, we have proposed bundle sheath collapse at low relative water content as a major non-stomatal limitation in C_4 species under drought (Bellasio *et al.*, 2023, 2024).

(vi) When considering the Himalayas, we often picture snow-capped high mountains and freezing cold. However, the westernmost part of the Himalayan Range is very arid because the region is on the leeward side of the Great Himalayan Range, and the monsoon wind from the Indian subcontinent loses almost all its moisture after colliding with the amazing heights of the mountains there on the southern slopes. Hence, this landscape is a cold desert. In the northwestern part of the Indian Himalayas lies the extremely cold and dry region of Ladakh (often known as Little Tibet). Ladakh provides a unique natural setting for ecophysiological studies due to its contrasting habitats (Dvorský *et al.*, 2011), such as arid steppe at the lower elevations (susceptible to seasonal drought), but relatively moist alpine and subnival habitats near the glaciers (prone to soil freezing). Some plants growing there are angiosperms occurring at the highest elevations (~ 6150 m a.s.l.) (Klimeš and Doležal, 2010; Dolezal *et al.*, 2016). Our first ecophysiological expedition to this region was in August 2022, although we were unable to reach the uppermost plants since special permission was required due to the region's sensitive location on the border of India–China and Pakistan, nevertheless we learnt from people who been there that those plants are no longer present due to permafrost solifluction. Certainly, in the present climate change scenario, the region is exposed to more frequent unpredictable extreme events such as summer snowfall, or warming, both causing disturbances due to frequent free–thaw cycles resulting in solifluction that hampers plant regeneration, because of plant population removal or habitat shift (Dvorský *et al.*, 2016). Coming back to the idea of 'cold' in high elevation areas in the Himalayas, we used thermographic measurements to assess stones, soil, and plant canopy temperatures at midday on sunny days at two sites there (Fig. 6). The results of this prospective exercise were surprising. As seen in Fig. 6A, above 4000 m a.s.l. at Sakti (steppe), where the air temperature was slightly above 25 °C, the five most abundant species analyzed showed large differences in their canopy temperature. Two erect species (*Ajania fruticulosa* and *Eriophyton tibeticum*) were well below ambient temperature, probably because of combined dissipation by transpiration and convection. In contrast, prostrate species with their leaves in contact with the soil have canopy temperatures close to or above air temperature. Among the three, the only pubescent species—*Oxytropis microphylla*—was closer to air temperature, probably because of its partial avoidance of incoming irradiance, while the other two (*Schistophyllidium bifurcum* and *Heteropappus semiprostratus*) were above the air temperature. Of course, the temperatures of inert bodies (white stones, soil, and dark stones) were much higher (Fig. 6). At a higher elevation above 5000 m a.s.l. (Tanglang La, subnival), where the ambient air temperature was <25 °C and all the species were prostrate (Fig. 6B), the results were even more amazing, with differences of >20 °C in canopy temperatures in plants inhabiting a few meters apart from each other on a flat area over a hill. In this case, highly pubescent, whitish species, showed canopy temperatures ~10 °C below the ambient air temperature, while the green darkest-leaved species *Sibbaldia tetrandra* showed canopy temperatures >10 °C above the surrounding atmosphere and even above the soil temperature. Cushion plants such as *Thylacospermum*

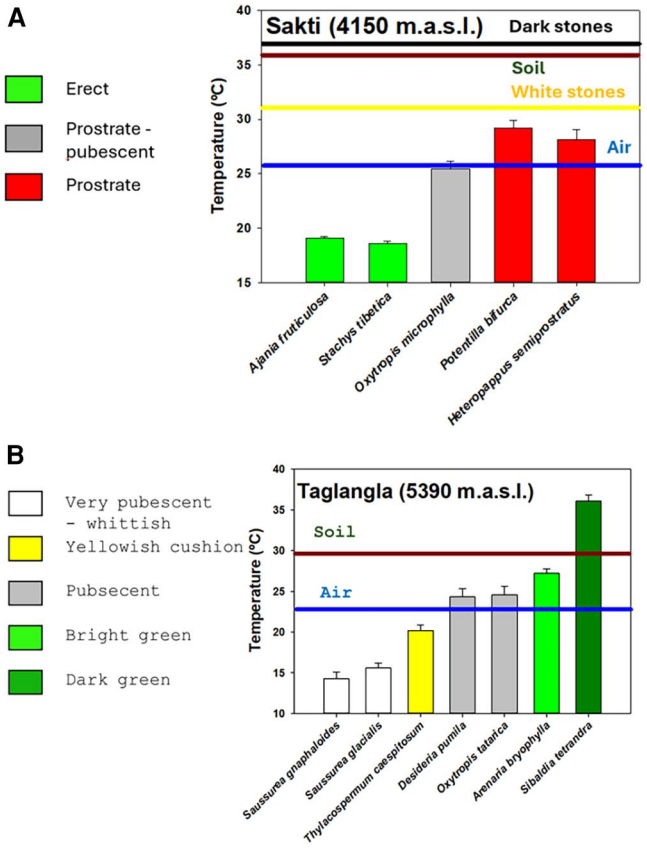

Fig. 6. Unexpected and variable canopy temperatures at two sites in Ladakh (Western Himalayas): Sakti (A) and Taglang La (B). Data were acquired with a thermographic camera and averaged for a minimum of 10 replicates per case. Small meteorological devices (Onset HOBO MX1101, Onset brand, Bourne, MA, USA) were used, placed under an aluminum foil tunnel with ventilation, to assess the ambient air temperature. The observed differences in canopy temperature are consistent with data collected by Liancourt *et al.* (2020), among others, and illustrate an established pattern observed under comparable conditions.

caespitosum and *Arenaria bryophylla* showed canopy temperature close to the ambient air temperature. These results amazingly illustrate the concept of microclimate and the strategy of decoupling from the ambient temperature in a way in which the growth form and morphology (i.e. the phenotype) of the plant have a strong influence (Liancourt *et al*, 2020).

In summary, besides identifying potential outliers and observing intriguing results, seeking and sampling plants from the extremes of plant life may allow us to be amazed by nature—which we guess is not a trivial issue nowadays, in the light of the social aspect of science—and to deepen into understanding the multi-stress tolerance traits, eventually deciphering the metabolites, transcripts, and genes involved. Since in many of these remote and climatically extreme environments, tracheophytes have a reduced presence while, in contrast, lichens and bryophytes are dominant, our studies also indirectly led us to a substantial understanding of how physiological traits vary along the land plant phylogeny (Tosens *et al.*, 2016; Nadal *et al.*, 2018, 2023; Carriquí *et al.*, 2019; Gago *et al.*, 2019; Flexas *et al.*, 2021; Roig-Oliver *et al.*, 2020) and even along the phylogeny of terrestrial and intertidal algae (Fernández-Marín *et al.*, 2019; Arzac *et al.*, 2023, 2024; García-Plazaola *et al.*, 2023; Ruiz-Medina *et al.*, 2023).

Conclusion

While already pinpointed by Simon Schwendener in the 19th century, studying the physiology of plants from extreme environments is more timely than ever due to the need to concomitantly enhance crop productivity and stress multi-tolerance. However, as illustrated by examples throughout this review, even if we are not to find any true outlier of the trade-off between productivity and tolerance, studying plants inhabiting the limits of vegetation distribution is still interesting as it might increase our understanding of particular phylogenetic, anatomical, and physiological trends and/or help in finding new mechanisms for stress tolerance. Taken together, such findings will help improve our knowledge of plant functions and the boundaries or limits for their potential distribution.

Supplementary data

The following supplementary data are available at *JXB* online.

Fig. S1. Aspect of *Peganum harmala* growing in the Manas steppe (Western China) and *Strombocarpa tamarugo* in the Atacama Desert (Chile).

Conflict of interest

The authors have no conflict of interest to declare.

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