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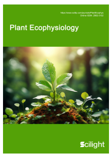

Review

Cold Air Pools (CAPs) as Natural Freezers for the Study of Plant Responses to Low Temperatures

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Abstract: The stratification of cold air is a phenomenon that typically occurs under certain topographic (closed ground depressions) and atmospheric conditions (stability and nocturnal radiative cooling). Under such conditions the drainage of the heavier cold air from the higher elevations causes its accumulation for days or weeks in the bottom of these depressions, leading temperatures to dramatically decrease and to decouple from regional climatic conditions. These particular locations which are frequent in karstic, volcanic and glacial landscapes, have been proposed to act as microrefugia of biodiversity in the context of climate warming. The existence of these cold air pools (CAPs) has been reported worldwide, and their biotic communities differ from equivalent sites out of these locations. However, there is an almost complete absence of ecophysiological studies concerning plant communities inhabiting CAPs. Thus, one of the objectives of this review is to hypothesize the effects of these specific conditions on the biology of the soil and the manner in which these plants should respond to such particular environmental conditions. Furthermore, given that temperature can decrease dramatically over short distances inside CAPs, in the present review we also propose their use as natural freezers for the study of plant responses to low temperatures.

Keywords: Cold Air Pool (CAP); microrefugia; low temperature; plant ecophysiology; freezing-tolerance

1. Introduction

Primary production in terrestrial ecosystems is essentially constrained by the availability of water (liquid or vapor) (Grossiord et al., 2020) and by air temperatures (Whittaker, 1975). In fact, the active metabolism of plants is only possible in a comparatively low range of leaf temperatures from around 70 °C in sun exposed CAM desert plants to a few degrees below the freezing point in cold acclimated species. In contrast, the range of temperatures that allow plant survival is considerably wider than for metabolic activity, ranging from the boiling point in orthodox seeds to the liquid nitrogen (−196 °C) in desiccated vegetative tissues (Larcher, 2003). However, despite this wide range of survival temperatures, plants need to encounter periodically thermal conditions favorable to metabolic activity to achieve a positive carbon balance, otherwise plant life is not possible. This is for example the case of the highest world elevations in the Himalayas or the Antarctic Plateau, that are completely devoid of plant life. Consequently, latitude and elevation are considered to be the main factors determining the thermal boundaries of plant life. Although this general picture is correct at a coarse scale, it ignores the influence of local topographic factors on the fine scale of temperature distribution. This is notably the case of the well characterized orientation effect (Körner, 2021), where microclimatic conditions of sun-exposed slopes are uncoupled from those of the regional climate. Another example of a microtopographic effect is the occurrence of cold air pools (CAPs) (Pastore et al., 2022), the subject of present review, where the denser cold air accumulates at the bottom of topographic depressions.

2. Where, When and Why Do CAPs Occur

Air density decreases with temperature, and as a consequence, cold air tends to descend. Thus, during clear nights, ground radiative cooling causes cold air to accumulate wherever air drainage is topographically restricted and atmospheric conditions are stable enough to prevent air mixing (McCaffrey et al., 2019). When these two conditions are met, air temperature decreases to values much lower than those of the surroundings, leading to the formation of cold air pools through a process that is particularly noticeable when air stability and clear skies last for several consecutive days. This causes a thermal inversion, with colder temperatures at lower elevations. As a consequence, CAPs typically occur at the bottom of fluvial valleys or basins (Vosper et al., 2014). Cold air pooling typically occurs during clear and stable nights, disappearing when sunlight favors air mixing, but it can also be maintained during longer periods, particularly in winter or high latitudes (McCaffrey et al., 2019).

This phenomenon has been theoretically modeled using predictive algorithms (Chung et al., 2006; Lundquist, Pepin, & Rochford, 2008; Daly et al., 2007) and confirmed by numerous theoretical and observational studies (John et al., 2024; Iijima & Shinoda, 2002). CAPs have been reported in a diversity of environments and geographical locations such as the sub-escarpment lowlands of South Africa (Duker et al., 2020), Sierra Nevada in California (Curtis et al., 2014), the mountains of central Japan (Iijima & Shinoda, 2002), Southwest Australia (Matusick et al., 2014) or the mountains of central Europe (Frei et al., 2023). In addition to the above-mentioned factors, cold air pooling and thermal decoupling from the regional climate is enhanced in those sites with a large collecting basin and in those forming close topographic depressions, ranging in depth from a few to hundreds of meters (Pastore et al., 2022). Examples of such topographic sites prone to the formation of CAPs are karstic depressions (dolinas) (Frei et al., 2023), glacio-karstic closed depressions (Giovagnoli & Tasinazzo, 2014), glacial cirques closed by frontal moraines, salt diapirs or volcanic craters and calderas. Figure 1 illustrates four distinct examples of topographic locations in Spain that are susceptible to the formation of CAPs. Thus, CAPs can be considered as a global widespread phenomenon that is observed wherever topography favors it (Pastore et al., 2022). Furthermore, in these particular locations, typically sheltered from the wind, the phenomenon of cold air stratification is further amplified by the reduction of air mixing, finally resulting in surprisingly large thermal gradients in very short distances. Apart from their intrinsic scientific and environmental interest, the specific features of these small topographic locations, particularly their steep thermal gradients, make them natural freezers for the study of plant responses to low temperatures, as will be discussed in Section 7.

Figure 1. Examples of CAPs: (**A**) a glacial cirque with a frontal moraine, notice the long-lasting snow accumulation (Corral de Veleta, Sierra Nevada, 37°03′, −3°22′); (**B**) a volcanic crater (Pico Viejo, Canary Islands, 28°15′, −16°40′); (**C**) a glacio-karstic depression (Hoyo Sin Tierra, Picos de Europa, 43°10′, −4°50′) and (**D**) a karstic dolina (Lubierri, Sierra de Urbasa, 42°51′, −2°05′).

3. Environmental Conditions inside CAPs

The direct effect of radiative cooling and subsequent atmospheric stratification is a significant decrease of air temperature, particularly during nighttime and close to ground. This generates relevant differences between the conditions inside and outside CAPs which are especially relevant for living organisms, which depend on these microclimatic conditions and not on temperatures prevailing in the free atmosphere (Lembrechts et al., 2020). Figure 2 illustrates the atmospheric characteristics occurring on CAPs, and their main impacts on vegetation. Many observational studies have described temperature gradients between the bottom and upper part of CAPs ranging between 2 and 20 °C (Pastore et al., 2022). For example, microclimatic studies in karstic areas of Hungary show that mean temperatures are between 1.5 °C and 2.4 °C lower at the bottom of CAPs compared to the surrounding plateaus (Frei et al., 2023), while in the mountains of Central Japan the maximum temperature difference measured in the bottom of a hollow was 12.5 °C with respect to the summit (Iijima & Shinoda, 2002). Another biologically significant factor is the occurrence of extreme minimum temperatures that may fall below the survival limits for many organisms, constraining the presence of freezing-sensitive species. In fact, the regional absolute minimum temperatures are sometimes measured in CAPs, as is the case of Vega Liordes in the Cantabrian Mountains where the coldest temperature ever in Spain (−35.8 °C) was recorded in 2021 (Iglesisas, 2021). These conditions of thermal stress can be exacerbated by much larger diurnal and seasonal temperature fluctuations (John et al., 2024). Another physical consequence of the lower temperatures inside CAPs is the higher air relative humidity (on average 15%) (Frei et al., 2023). The primary factor influencing the disparity in air temperature and relative humidity within dolines is the sun's trajectory throughout the day, combined with the bowl- or funnel-like structure of these depressions. For instance, eastward slopes capture more sunlight in the morning, whereas westward slopes absorb greater sunlight during the afternoon and evening (Bátori et al., 2023).

In this review, the focus has been on natural areas where the phenomenon of CAPs occurs. However, it is important to note a particular phenomenon studied in urban areas that can also affect natural areas, even if to a lesser extent. The accumulation of pollutants generated in urban areas has been observed to coincide with the occurrence of CAPs phenomena, due to the strong atmospheric stability. This phenomenon has been studied in different valleys or cities, such as Salt Lake (Utah) using air quality simulations (Sun et al., 2021), Coimbra, using field data loggers (Cordeiro, Orenlas, & Silva, 2023) or Wasatch Mountains (Utah) were they study the ion concentrations in different snowpacks (Hall et al., 2014).

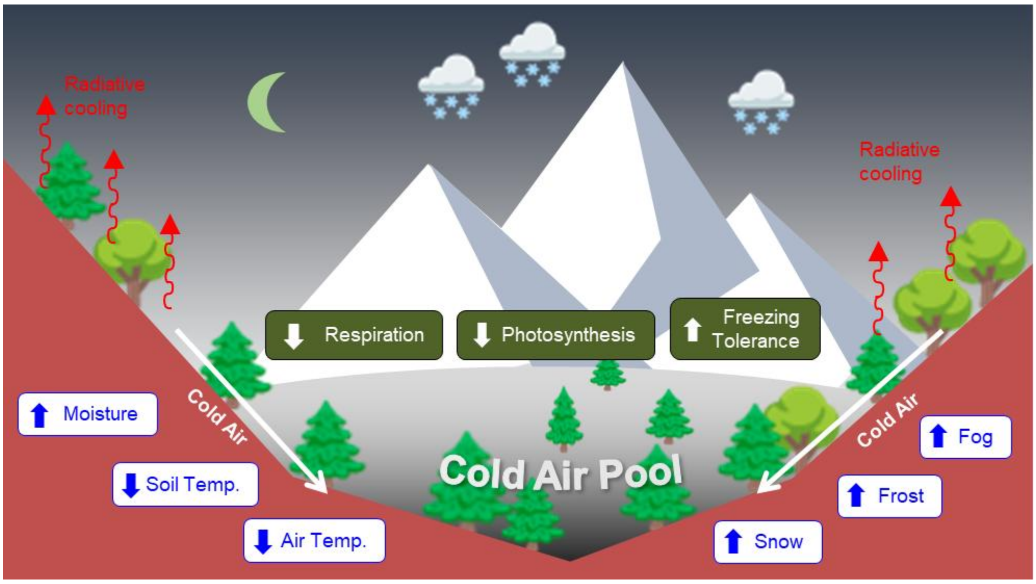

Figure 2. Schematical representation of main environmental conditions in CAPs (blue boxes) and their effects over main physiological responses of plant (green boxes).

4. Effects on the Biology of Soils

4.1. General effects of CAPs on soil properties

As a result of the air temperature decrease in CAPs, soil temperatures reach lower temperatures than those prevailing in the surrounding areas, which has a determinant effect on the biology of the soil (Novick, Oishi, & Miniat, 2016; Soler et al., 2002). One of the principal characteristics of CAPs is the potential for an extended duration of the snowpack (see Figure 1A). This phenomenon can be attributed to two key factors: the lower soil temperatures and the influence of microgeomorphic features of the ground surface and wind action on snowpack distribution, which removes snow from small, exposed ridges to accumulate in shallow depressions (Giovagnoli & Tasinazzo, 2014). Several studies have demonstrated this empirically, for example Curtis et al. (2014), at Sierra Nevada (California), using a water-balance approach for modeling snowpack duration. As a porous medium with high air content snow has high insulation properties. Its thermal insulation capacity mitigates ground temperature fluctuations and, in winter, keeps soil temperatures relatively high as compared to the surroundings above the snow (Vuosku et al., 2022). Therefore, a snow cover protects underlying vegetation and soil against very low temperatures, creating conditions that are favorable to plant survival and plant metabolism (Körner, 2021). However, under snow, plants experience other stresses such as light deprivation (Robson et al., 2019) and prolonged snow cover, which could weaken plants by impeding metabolic processes and reducing the length of the growing season (Larcher, 2003; Sakai & Larcher, 1987).

Apart from temperature and light, gas diffusion represents another significant factor, which is also conditioned by the snow cover. The presence of snow (especially when ice layers are formed), impedes the flow of gases, such us; soil-atmosphere gas exchange, plant tissues and soil microorganisms gas exchange (Martz et al., 2016). In conditions of low light intensity, the rate of respiration in plants will exceed the rate of net CO_2 assimilation. While oxygen will be consumed by heterotrophic respiration, CO_2 will be released, which can lead to periodic anoxia beneath the snow cover (Körner, 2021; Martz et al., 2016; Edwards, Scalenghe, & Freppaz, 2007). These conditions can be detrimental for plant life by reducing the efficiency of cellular ATP production and lead to the accumulation of toxic metabolites as a result of anaerobic metabolism (Vuosku et al., 2022). Nevertheless, it is important to highlight that snow presence depends on CAPs location and latitude and may not always play a significant role in the biology of the soil. In fact, soils in snow-free CAPs can experience lower temperatures and be subjected to more extreme freeze-thaw cycles compared to those outside CAPs during the winter season.

Water and moisture accumulate in CAP soils because of two main reasons. First, cold air pooling itself can affect dew formation and vapor pressure deficit and thus, indirectly affect soil moisture through effects on plant ecophysiological processes (Pastore et al., 2024). Additionally, cold air pooling events may contribute to the retention of soil moisture due to the lower vapor pressure deficit and reduced wind speed that accompany these events (Frei et al., 2023). Second, due to the concave topography and location (low-lying regions), CAPs can retain more water upon precipitation events, potentially enhancing water availability in soil. Besides, these low- laying areas are frequently covered by deep soils with high water retention capacity (Frei et al., 2023; Bátori et al., 2017). Apart from moisture, higher nutrient and organic matter concentration can be found in these locations. For example, it is known, that soils in CAPs of karst landscapes have high nitrogen and phosphate concentration (Frei et al., 2023).

Cold, wet (or waterlogged) and snow covered (if it is the case) soils protect organic matter from decomposition, preserving soil carbon. Low temperatures reduce gaseous soil carbon losses and wetter soils may favor lower rates of soil respiration when oxygen becomes limiting and as a consequence, soil carbon storage is higher (Pastore et al., 2022). A more persistent snowpack can reduce soil freeze-thaw cycles (Pastore et al., 2022; Wipf et al., 2015). The frequency and duration of freeze-thaw events are critical to nutrient and carbon cycling, so reducing freeze-thaw cycles limits soil carbon loses through respiration and leaching (Edwards, Scalenghe, & Freppaz, 2007). For example, this reduction of soil respiration in CAPs was observed in a southeastern US Appalachian Mountain site (Novick, Oishi, & Miniat, 2016). It should be noted, however, that, in addition to temperature and moisture, the influence of local soil properties on plant community development may outweigh the influence of cold air pooling microclimates.

4.2. Potential CAPs-effects on soil microbiology

To the best of our knowledge the specific microbial communities present in soils where cold air pooling events occur have never been studied. Nevertheless, we hypothesize that their composition and dynamics could be driven by three interacting factors: lower temperatures, longer and thicker snow coverage and higher soil water content. Additionally, it is crucial to acknowledge that these characteristics can exhibit considerable variability depending on the location, topography and soil type.

In regard to low soil temperatures, Schnecker et al. (2023) observed a notable increase in microbial activity during the winter season and postulated a number of potential explanations for this phenomenon. One possibility is that microbial carbon use efficiency (CUE) rises at cooler temperatures (Frei et al., 2023), which can derive from respiration being more temperature-sensitive than growth (Pietikäinen, Pettersson, & Bååth, 2005; Cruz-Paredes, Tájmel, & Rousk, 2021). Alternatively, at lower temperatures, predators may become inactive while their prey microorganisms can continue to increase in biomass. A third potential explanation is that soil microorganisms augment their cellular contents during winter, either as reserves (Manzoni et al., 2021; Mason-Jones et al., 2022) in anticipation of substrate scarcity, or as osmotic agents or cryoprotective substances.

As previously stated, the coverage of snow on a CAP may be longer-lasting than on the surrounding area, contingent on the location and altitude of the CAP. In such instances, microbial activity will manifest in a different way. Under the snowpack, as microorganisms decompose organic matter and release minerals, they accumulate nitrogen, and microbial biomass reaches an annual peak at snowmelt. This safeguards nutrients from being depleted from the soil during this moist period, and as the season advances, these nutrients are released for plant uptake, while microbial biomass diminishes (Körner, 2021; Brooks, Williams, & Schmidt, 1998; Lipson et al., 1999). Microbial activity under snow recycles a large fraction of growing season primary production and thus determines the following season's nutrient availability.

Soil may be subjected to a multitude of physicochemical transformations in response to flooding, a phenomenon that can occur frequently in CAPs. The saturation of soil pores, which typically facilitate gas exchange between the atmosphere, soil, and soil microorganisms, results in a significant reduction in gaseous diffusion. Oxygen levels can rapidly decline due to the activity of aerobic microorganisms, reaching anoxic conditions even in the soil surface layers within the first hours of flooding. This alteration in oxygen availability can then result in a gradual transition in the microbial community from aerobic species to facultative anaerobic organisms, and ultimately to strict anaerobic organisms (Hartman & Tringe, 2019).

5. Plant Communities inside CAPs

5.1. Species present

The exceptional microclimatic conditions typically associated to CAPs can strongly determine the vegetation stablished within them. Thus, the extent and recurrence of low temperature events can play a detrimental effect on non-tolerant species but also a favoring effect on tolerant species, as it has been reported in different geographical locations (Pastore et al., 2022). For example, deleterious effects of low temperatures associated to topographic depressions caused strong seedling mortality on a plantation of spruce and pine in central Sweden (Blennow & Lindkvist, 2000). By contrast, the current distribution of the rare endemic alpine plant *Saxifraga florulenta* in the Maritime Alps matches CAPs microtopography, more than regional macroclimate (Patsiou et al., 2017). This species is favored by cold-air pooling sites where current macroclimate warming effects are buffered and its persistence over the last millennia in that area is explained by topo-climatic cold-microrefugia (Patsiou et al., 2017). Similarly, a recent study in a Hungarian Karst landscape demonstrates higher species cover and richness at the bottom of dolines than on their corresponding plateaus and this correlates with events of lower temperatures (Frei et al., 2023). Additionally, cold-adapted species are more frequent in coldest dolines (Bátori et al., 2017). Similarly, it has been described in the mountains of Japan the existence of a vegetation inversion, with tundra communities occupying the bottom of CAPs and the surrounding higher elevation slopes covered by subalpine conifer forests (Iijima & Shinoda, 2002). Thus, specific microclimate of CAPs can either limit or favor the presence of particular species, likely being low temperature the main selective factor.

5.2. Changes on the biology of present species

The species and/or individuals present in CAPs can also show biological differences when compared to nearby areas out of the CAPs. Although these evidences directly obtained from CAPs are very scarce, information can be inferred from basins recurrently subjected to temperature inversions. Alterations in phenology have already been reported. For example, in a year with frequent anti-cyclonic weather that promoted cold-air pooling at Cascade Range (USA), spring bud break of many species was delayed at low elevation sites (Ward, Schulze, & Roy, 2018). Timing of leaf expansion and of leaf fall is also related with the occurrence of nocturnal temperature inversions at small basin in Central Japan (Kusunoki & Ueno, 2022). Most of the scarce studies available so far, are mainly focused on community assembly and species composition (Pastore et al., 2022; Frei et al., 2023), being physiological studies virtually unavailable. Two further aspects that are misrepresented in bibliography are: climatically warm environments (since most of the literature is centered at mid latitudes) and cryptogamic vegetation (i.e. very little is known on ferns, and nothing on lichens or bryophytes potentially inhabiting CAPs). While temperature is the primary factor influencing species presence in CAPs, other elements such as soil moisture, nutrient availability, and snow cover (see Section 5) frequently interact with it (Frei et al., 2023).

6. Physiological Adaptations. General Effects of Low Temperatures

As previously mentioned, low temperatures can significantly influence vegetation establishment. Despite the absence of direct evidence, the ecophysiological responses of CAP plant communities can be inferred from the better characterized responses to low temperatures. In general, these plants will be subjected to a significantly greater degree of temperature stress than adjacent populations situated outside of CAPs. Therefore, plants in CAPs require activation of signaling pathways that enable processes and structures to minimize climatic impact by either avoiding or tolerating it. Since plant survival under low temperature stress has been reviewed extensively (Körner, 2021), Figure 3 will focus briefly and directly on the most relevant plant strategies in response to low temperatures. Within the lower end of the thermal range, two distinct yet overlapping types of plant stress can be identified: chilling and freezing. Chilling stress occurs at temperatures ranging from 0 to 15 °C, while freezing stress occurs at temperatures below 0 °C. Chilling stress typically interferes with plant metabolism and growth while freezing temperatures lead to ice formation causing structural damage and cell dehydration. Plants respond to such stresses with a series of strategies ranging from stress avoidance to tolerance of ice formation in the apoplast.

Considering these strategies, supercooling is generally effective for brief frost periods, lasting only a few hours. However, if the frost period extends inside CAPs, ice formation may occur, which is often fatal. In such cases, it is more advantageous for the plant to rely on tolerance mechanisms.

As it has been previously mentioned, most of the limited studies available so far primarily focus on community structure and species composition (Pastore et al., 2022; Frei et al., 2023), with physiological research being almost nonexistent. A more specific focus should be placed on the subject of how CAP plants cope with freezing temperatures, with particular attention to the role of antifreeze proteins and solutes, as well as ice nucleation. Additionally, further exploration is warranted into the function of cryoprotectants or ROS-scavenging mechanisms, supercooling, and extracellular freezing tolerance. Further avenue of investigation lies in the comparison of photosynthetic performance between CAP and non-CAP plants. In Section 8, we present preliminary results from our research on this topic, which includes the analysis of osmotic potential, freezing tolerance, and photosynthetic performance of plants both inside and outside of CAPs. Undoubtedly, a more in-depth study in this area would be highly beneficial.

Whether ecophysiological strategies of photosynthetic organisms inhabiting CAPs differ much from those already studied in polar or alpine plants is a key point. Unfortunately, currently available knowledge on plant physiology inside CAPs is so scarce that we are unable to give answer to these and other more specific questions. On the light of main environmental differences between CAPs and other potentially cold emplacements (such as Alpine and Polar ecosystems), could be reasonable to expect that plants adapted to CAPs may have unique morphophysiological characters. Very likely, these could be strongly related with the possibility of importantly low temperature at vegetatively relevant periods along the year. Complementarily, some of the morphosysiological features could be related to attenuated irradiance and wind. In consequence, it could be reasonable to expect that plants adapted to CAPs may have unique morphophysiological characters, i.e. big leaves (as inferred from plants adapted to shade), but constitutive physiological adaptations to low temperatures, i.e., low osmotic potential.

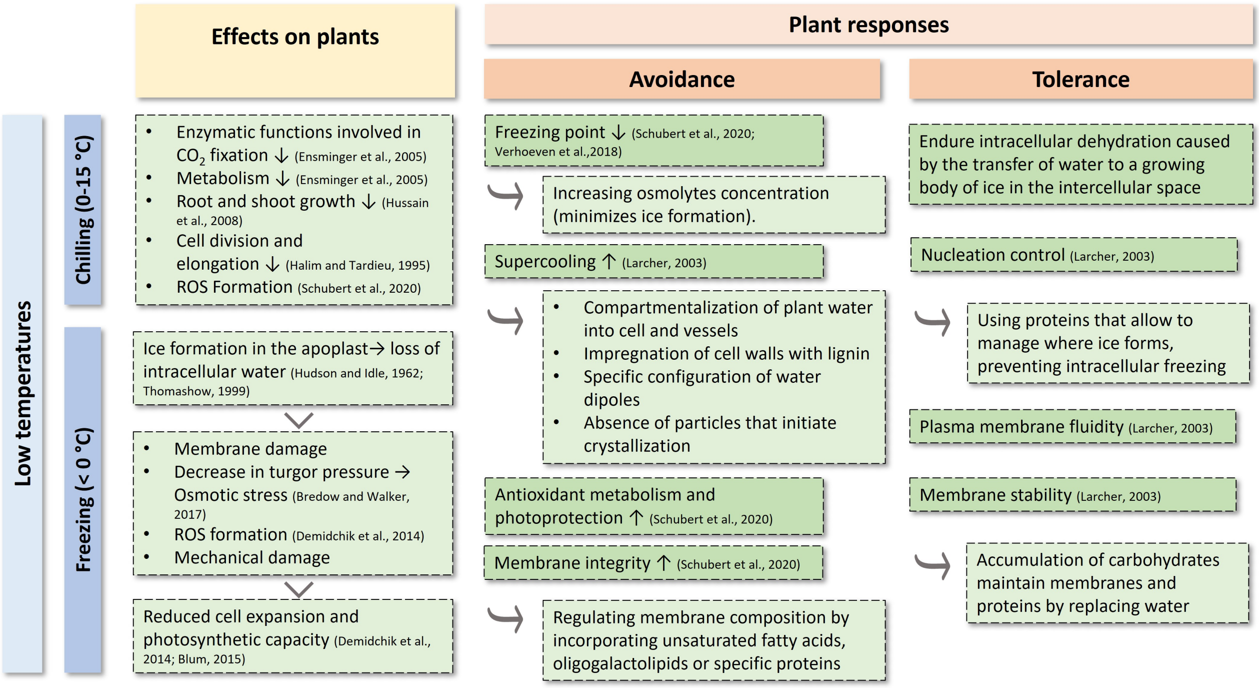

Figure 3. Effects of chilling and freezing temperatures and plant mechanisms in response to low temperatures, avoidance and tolerating strategies (Larcher, 2003; Ensminger, Busch, & Huner, 2005; Hussain et al., 2018; Ben-Haj-Salah & Tardieu, 1995; Schubert et al., 2020; Hudson & Idle, 1962; Thomashow, 1999; Bredow & Walker, 2017; Demidchik et al., 2014; Blum, 2015; Verhoeven, García-Plazaola, & Fernández-Marín, 2018).

7. CAPs as Natural Freezers for the Study of Plant Responses to Low Temperatures

Geodiversity sometimes offers unique opportunities for the study of relevant ecophysiological issues. This is for example the case of the geothermal CO_2 springs in central Italy where a natural plant community grows in a naturally enriched CO_2 environment, providing the opportunity to study long-term responses of vegetation to future atmospheric conditions (Körner & Miglietta, 1994; Miglietta, 2006). In an analogous way, we propose here the use of CAPs as natural freezers to deepen into the study of plant responses in situ to low and freezing temperatures.

Manipulative treatments of temperature stress have been applied in situ to study the responses to both heating stress (Buchner et al., 2015) and freezing tolerance (Buchner, Neuner, & Ball, 2011) thanks to temperature control devices adapted for their use in the field. An alternative approach to study thermal stress is to take advantage of the periodic occurrence of heat (Esteban et al., 2008; Schär et al., 2004) or cold waves (García-Plazaola et al., 2003). However, these extreme meteorological events are essentially unpredictable, which constrains their systematic use in ecophysiological studies. Given that temperature decreases with elevation, another option is to study plant traits across steep altitudinal gradients (Cabrera, Rada, & Cavierers, 1998). However, at high elevations, low temperatures are accompanied by reduced atmospheric pressure, leading to a decrease in oxygen partial pressure. This reduction has been found to decrease frost resistance in some plant species (Larcher, 2003), while enhancing it in others (Halloy & González, 1993). Thus, CAPs offer the opportunity to study variations in low temperatures by comparing nearby positions situated inside and outside the CAPs, avoiding the influence of different oxygen partial pressure for the same species. However, in any study that using CAPs as an experimental model, it must always be taken into consideration that CAPs are natural systems and not experimental chambers, implying that temperature always co-varies with other key environmental factors such as atmospheric humidity, snow cover, or hidden precipitation in the form of dew or fog.

In the context of a climate change scenario, the role of CAPs as microrefugia for cold-adapted species is well-established in this review. However, the future stability of CAPs remains uncertain, and the existing literature on the subject is limited. CAP persistence is contingent on stable nocturnal radiative cooling, a process that may be influenced by factors such as increasing cloud cover and changes in air circulation patterns. It is also plausible that climate change could lead to a reduction in snowfall, which could in turn affect the thermal insulation properties of CAPs.

8. CAPs at Teide National Park, a Case Study at Subtropical Latitude

8.1. Characteristics of studied CAPs in Teide volcanic caldera

Teide National Park (28°16′N, 16°38′W) features the Teide stratovolcano which has its highest elevation at 3715 m. The peak itself is surrounded by a much wider volcanic caldera, which is delimited by a huge escarpment and consists of a series of natural sedimentary basins locally called “cañadas”, where all the eroded material from escarpments accumulates (see Figure 4A). The characteristic configuration of Cañadas del Teide is formed by a huge caldera with a diameter of 17 km in its largest radius (NE-SW) and 7 km in the smallest radius (NW-SE). On days with lower wind speed, the cold air accumulates at lower altitudes resulting in the typical CAP inversion. Figure 5A illustrates the temperature inversion on the nights of 27–28 and 28′29 of December 2018. Temperature at the bottom, where sensor P5 is located (2049 m), was lower than at Montaña Blanca, situated at 2727 m (see Figure 4B), contrary to what would be expected under usual wind speed conditions that prevent air stratification. It should be noted that these sensors are installed at a height of 1.5 m from the ground, measuring air temperature in the free atmosphere and temperatures at ground level might be lower. In Figure 4A, the location of every sensor is displayed.

There are also occasional CAPs of smaller extension, within the large pool of circumstantial cold air of the Caldera, such as Seven Cañadas. This is a local geographic depression that extends for more than 10 km into the base of the great caldera at its southern end and is up to 75 m deep. Here, the stratification events that lead to the formation of CAPs occur at night, when wind speed is at a minimum, and last until dawn, when the sun illuminates this area and generates turbulence that breaks up the air stratification. Figure 5B shows how the process of thermal inversion occurs as the night progresses and the wind speed slows down, so that, if at noon the temperature inside the caldera is higher than at the top of the surrounding area, at midnight and until daylight, the opposite occurs.

This phenomenon is relatively common in the Seven Cañadas and, to a lesser extent, in the whole of the large caldera that makes up the Teide National Park. It affects one third of the days of the year and occurs in every season, even in summer, depending on the characteristics of the local wind regime (López-Díez et al., 2022). It is also known in other summit areas, such as the Ucanca plain (Lazar, 1996). Probably any endorheic basin inside the Cañadas del Teide caldera and surrounding high altitude area could behave as a CAP. This is the case of the basin at 3000 m in the Pico Viejo crater. López-Díez et al. (2021) pointed out several locations of these CAPs in the Teide National Park (López-Díez et al., 2022).

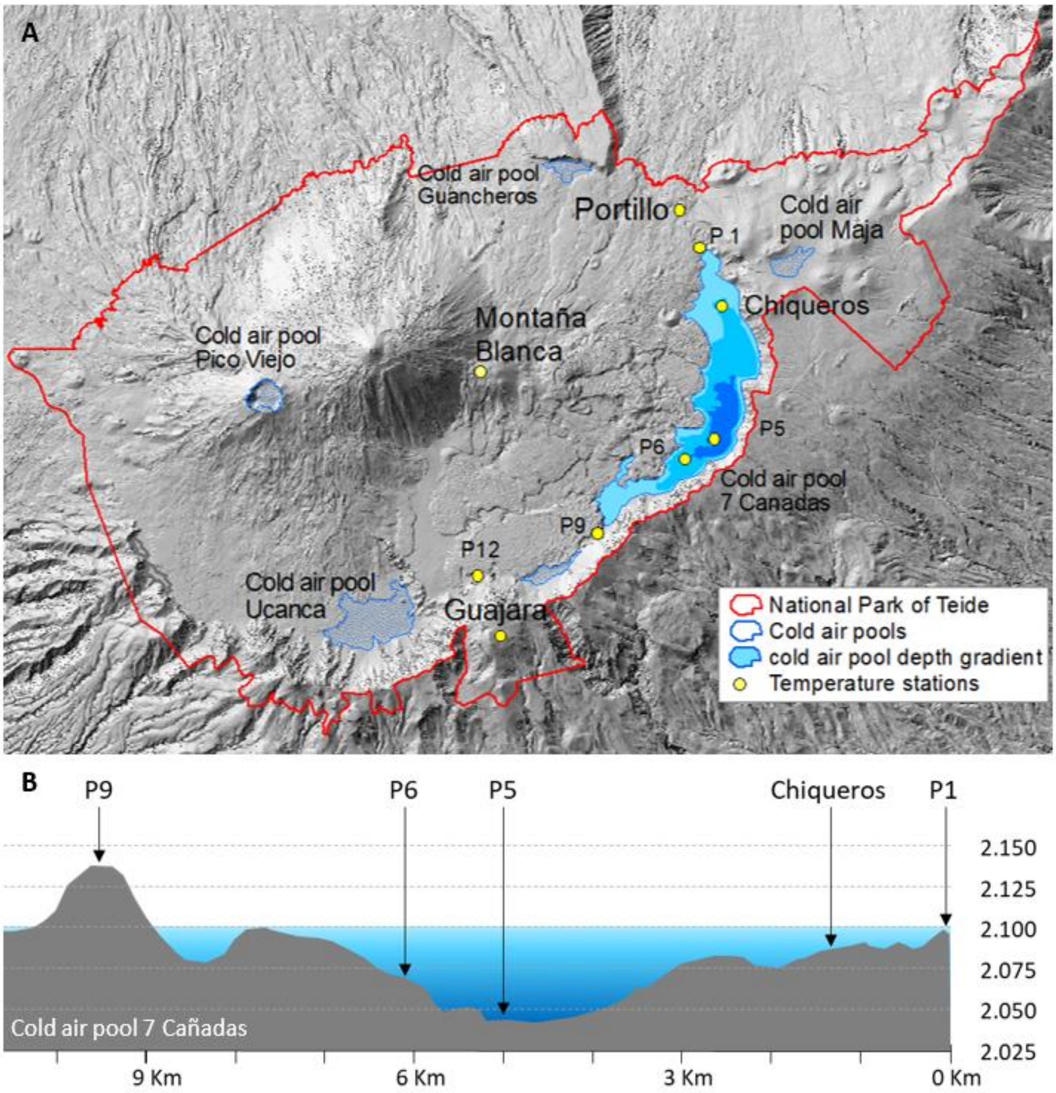

Figure 4. (**A**) Cañadas del Teide map. Yellow points indicate the position of temperature sensors at 1.5 m height from the ground. Red line indicates the limits of the National Park of Teide. In blue CAPs of different depth. (**B**) Elevation profile of the CAP 7 cañadas and the corresponding location of each temperature sensor. Data kindly provided by the National Park "El Teide".

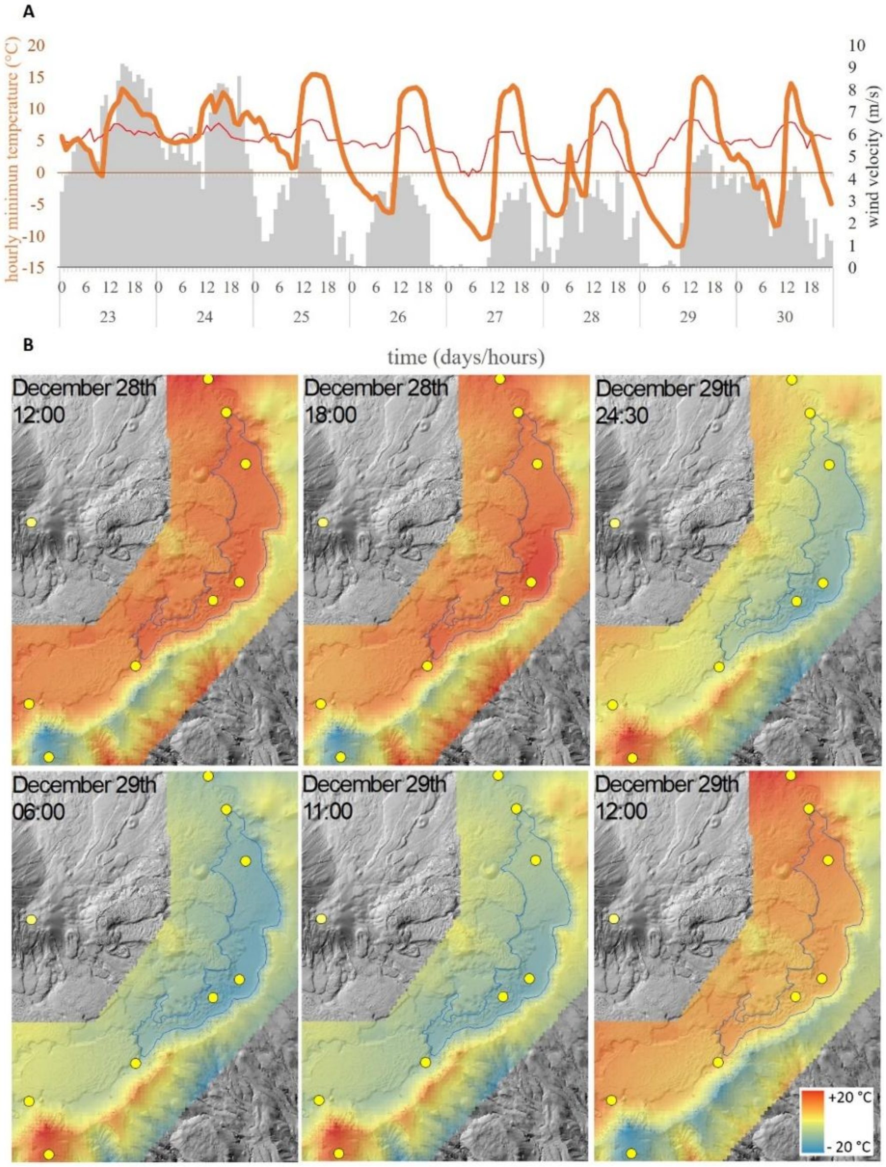

Figure 5. (**A**) Representation of time evolution between 23 and 30 December 2018 of the Caldera de Las Cañadas. The thick orange line belongs to the station P5, in the deepest part of the cold lake of Seven Cañadas (2049 m) and the thin red line belongs to the station Montaña Blanca (2727 m). Note how in the event of the night of 27–28 the phenomenon is repeated twice, as the wind, once activated, slows down again. (**B**) Digital terrain model of a CAP event on the night of 29 December 2018, from weather data from ground stations. Interpolation was performed using multiple linear regression with hourly minimum temperature as the dependent variable and longitude, latitude and elevation from a digital terrain model with 100 m resolution as independent variables. The result was adjusted by adding an inverse distance weighted interpolation of the residuals, according to the methodology proposed by Ninyerola et al. (2000). Data kindly provided by the National Park "El Teide".

8.2. Plant performance on Cañada del Portillo (Teide National Park)

Temperature profiles were followed in a particular location, Cañada del Portillo (see Figure 4A) within the large CAP of Seven Cañadas throughout the growing season (from May to September) of 2024. Figure 6A depicts a photograph of the CAP at Cañada del Portillo, while Figures 6B, 6C and 6D present a schematic representation of the position of the various sensors. Four of them were placed at the bottom of the basin (two on the ground and the other two on rocks), two of them were placed outside and the other four at the southeast-facing slope.

The resulting analysis showed that there was a thermal gradient greater than 2 °C on 96.5% of the days, during the recorded period, while the average gradient was 5.14 °C. As can be seen in Figure 6B, freezing nights (temperatures below zero) occurred 44 % of days at the bottom, while at the plateau never occurred. The absolute minimum recorded by a sensor placed at ground level was −9.36 °C during a cold air pooling event on 6 September 2024 (Figure 6C).

The surroundings of the hollow were occupied by a plant community dominated by two shrubs: *Descurainia bourgeana* (E.Fourn.) and *Pterocephalus lasiospermus* (Link ex Buch*)*, with the first being dominant in the bottom of the hollow and the latter in the upper plateau (Figure 6A). The physiological responses of both populations (upper and lower) of *Descurainia bourgeana* were characterized in late spring when thermal inversions are large (Figure 6C) and freezing events are still frequent (Figure 6B) at the bottom of the hollow. While no differences were observed between individuals from the bottom and plateau areas in basic photosynthetic or hydraulic parameters (Figure 7A–C,E,F) when examining the species' tolerance to freezing temperatures (Figure 7D), a notable divergence emerges, with individuals from the bottom area exhibiting a considerably higher tolerance to freezing. The physiological basis of this enhanced freezing tolerance remains to be elucidated, but current analysis clearly provides preliminary evidence in support of the hypothesis that CAPs can be understood as natural freezers, thereby facilitating the study of plant responses to low temperatures. In addition, a statistically significant difference was observed in the osmotic potential (Figure 7B), suggesting that a response to freezing temperatures in this species could be the accumulation of osmolytes as it is described in Section 5.

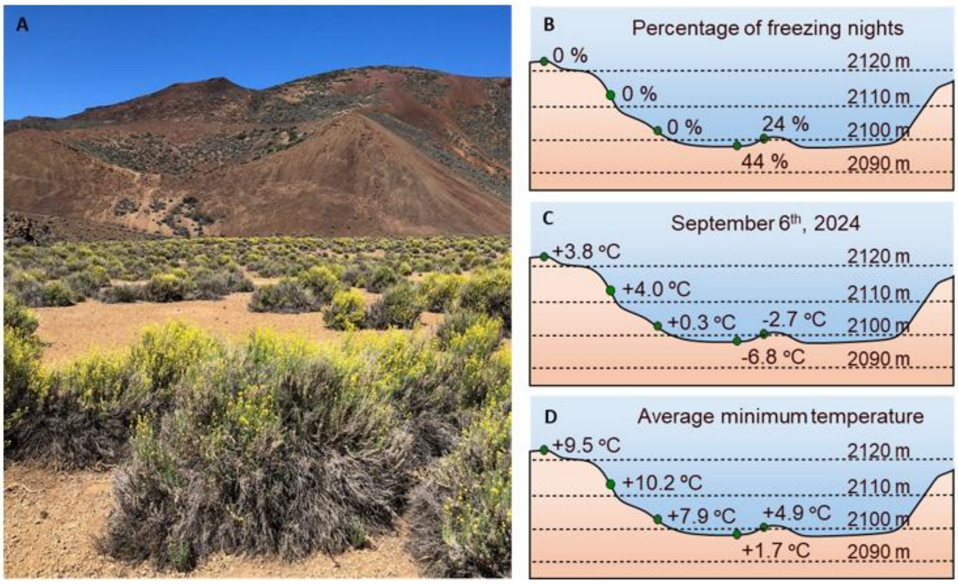

Figure 6. (**A**) Late Spring at the bottom of the "Cañada del Portillo". Vegetation is dominated by flowering bushes of Descurainia bourgeana. (**B**) Percentage of freezing nights at different points at "Cañada del Portillo" during the growing season of 2024. (**C**) Minimum temperatures profile at "Cañada del Portillo" during a cold air pooling event on 6 September 2024. (**D**) Average minimum temperatures at different points at "Cañada del Portillo" during the growing season of 2024.

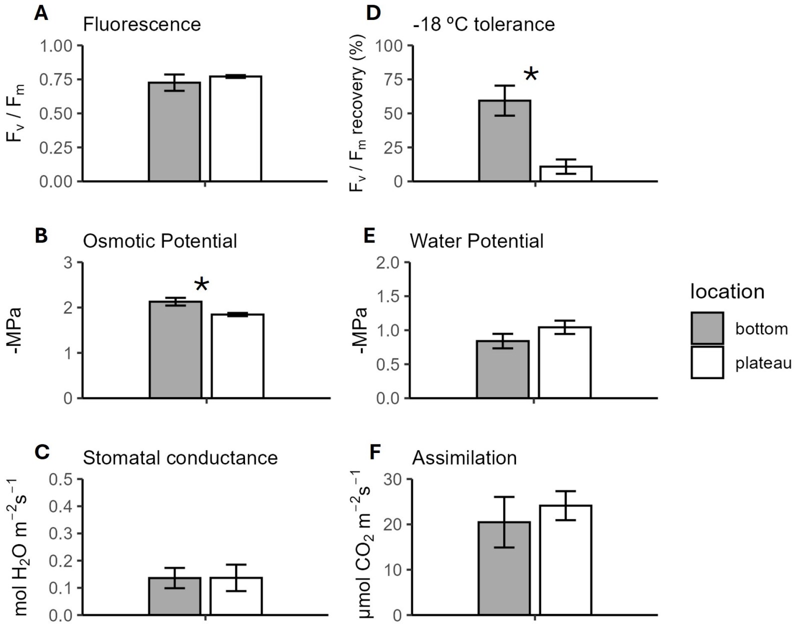

Figure 7. Physiological parameters measured in Descurainia bourgeana, dominant species at "Cañada del Portillo" comparing the response of the individuals growing outside the CAP (plateau, white) and inside the CAP (bottom, grey). Represented as mean ± SE (n = 4) the statistical difference at $p < 0.05$ between bottom and plateau was determined by t-test, indicated by * in the graphs. (**A**) Fluorescence measured *in situ*. (**B**) Osmotic potential measured in sampled leaves. (**C**) Stomatal conductance measured *in situ*. (**D**) Freezing tolerance to -18 °C measured in sampled leaves. (**E**) Water potential measured in sampled leaves. (**F**) CO_2 assimilation measured *in situ*. See Supplementary Materials for Materials and Methods.

9. Concluding Remarks

In light of the aforementioned considerations, it becomes evident that numerous aspects of CAPs remain subject to investigation. A shortage of literature exists about the biological differences between the species in and out of CAPs or about the specific microbial communities present in CAP soils. It is also important to highlight that the formation of these events occur in a diversity of environments and geographical locations with markedly disparate characteristics, which can make challenging to identify the common attributes. Taking this into account, here we focused on the potential of CAPs as natural freezers and their utility in elucidating the plant response to cold and freezing temperatures. Cañadas del Teide has been identified as an appropriate location for further research concerning this aspect of the CAPs and the results of the preliminary tests suggest that the proposed hypothesis is valid. The current analysis offers preliminary evidence that CAPs can be conceptualized as natural freezers, thereby facilitating the study of plant responses to low temperatures. These initial findings serve as a foundation for future investigations in diverse CAPs and in various species.

Supplementary Materials

The additional data and information can be downloaded at: https://www.sciltp.com/journals/PlantEcophys/2025/1/558/s1.

Author Contributions

The conceptual framework of the manuscript was devised by the author J.I.G.P. E.A. had a major contribution in the original draft preparation. All authors contributed to the writing and figure preparation and agreed to the final version of the manuscript.

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Data Availability Statement

Original data are available upon request to the corresponding author.

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Conflicts of Interest

The authors declare no conflict of interest.

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