UNIVERSITÀ
DI PAVIA

Dipartimento di Scienze della Terra e dell'Ambiente

Corso di Laurea Magistrale in Conservazione della

Biodiversità, Didattica e Comunicazione scientifica

Responses of arctic-alpine vegetation to the combined effects of photoperiod and temperature in a climate change context

Relatore:

Prof. Abeli Thomas

Correlatrice:

Dott.ssa Tarascio Martina

Tesi di Laurea
di Colonna Ginevra

Matr. n. 538751

Anno Accademico 2024-2025

SUMMARY

1 INTRODUCTION

1.1 Climate Change: a focus on Arctic and Alpine regions

The earth's biomes are currently undergoing rapid widespread changes driven by human-induced climate alterations of the main environmental conditions. According to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, Climate Change 2021: The Physical Science Basis), the global mean surface temperature in the 2011-2020 decade was 1.09°C (with a likely range of 0.95°C to 1.20°C) higher than the 1850-1900 baseline, mirroring a significant average acceleration of 0.99°C [0.84 to 1.10]°C during the first two decades of the 21st century, with a larger increase over land (1.59 [1.34 to 1.83]°C) than over the ocean (0.88 [0.68 to 1.01]°C). This warming trend exhibits a marked geographical disparity, often referred to as land–ocean warming contrast. As reported in Chapter 4 of the IPCC AR6 report, this phenomenon describes the disproportionate heating of terrestrial surfaces compared to the oceans, driven by differences in moisture availability and thermal inertia. The global surface is experiencing a thermal increase without precedent, with global temperatures rising more swiftly since 1970 than during any other 50-year span in the last 2000 years. Future climate trajectories, modeled through Shared Socio-economic Pathways (SSPs), hypothesize different warming scenarios by the end of the 21st century (2081–2100), estimating a global temperature increase ranging from 1.4°C (SSP1-1.9, very low greenhouse gas emission) to the catastrophic value of 4.4°C (SSP5-8.5, very high greenhouse gas emission) (see Fig. 1, IPCC, 2021).

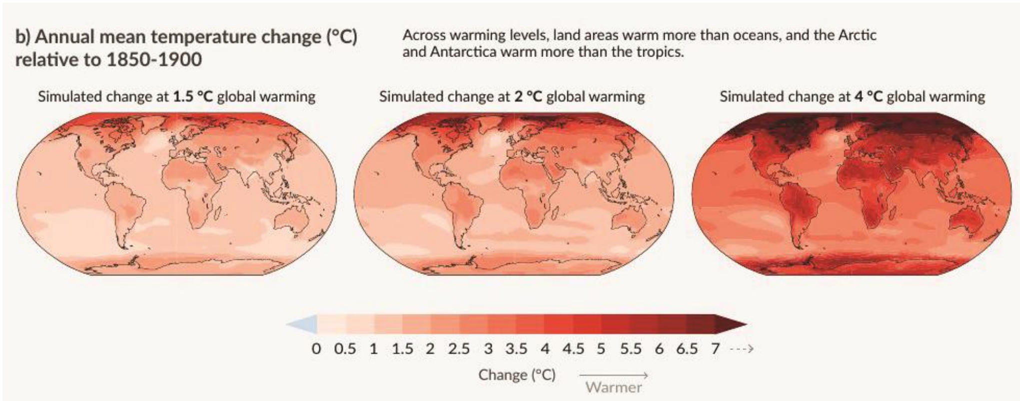

Fig. 1 - Spatial patterns of global warming across three potential future scenarios driven by different anthropogenic emission regimes. ATLAS simulations spanning the period from 1850-1900 to 2100 (IPCC 2021)

Recent observational data reveal that since 1979 the Arctic has warmed nearly four times faster than the global average, a rate far exceeding earlier scientific estimates (Rantanen et al., 2022). This amplification is most extreme in the Eurasian sector of the Arctic Ocean, specifically near the Svalbard archipelago and Novaya Zemlya, where warming rates have reached up to seven times the global mean (Rantanen et al., 2022). This localized high rate, known as Arctic amplification, is primarily driven by the ice-albedo feedback: as rising temperatures melt sea ice, the exposed darker ocean waters absorb more solar radiation instead of reflecting it, creating a self-reinforcing heating cycle. Additionally, the release of stored oceanic heat into the atmosphere during autumn further intensifies this regional warming, a process that current climate models still struggle to fully capture (Serreze & Barry, 2011). The Arctic has experienced a dramatic decline in cryospheric cover, with the summer sea ice extent decreasing by approximately 12.2% per decade while the winter sea-ice maximum recorded in March 2025 reaching its lowest level in the 47-year satellite record (NOAA, 2025). This transformation is characterized by a 95% loss of older, multi-year ice since the 1980s, leaving a fragile environment dominated by thin seasonal ice that accelerates the ice-albedo feedback and regional warming (National

Snow and Ice Data Center, 2024; Maslanik et al., 2011). Glaciers in Arctic Scandinavia and Svalbard experienced the largest annual net loss of ice on record between 2023 and 2024. According to global observational data based on satellite and in situ measurements, the world's glaciers lost approximately 9,179 ± 621 Gt (187 ± 20 Gt per year) of glacier mass between 1976 and 2024, contributing about 25 ± 2 mm to the rise in mean global sea level. About 41 % (~ 10 mm) of this loss occurred in the last decade, with 6 % occurring in 2023 alone, the record-breaking year of glacier mass loss (Dussaillant et al., 2025).

Analogously to Arctic regions, mountain areas - and the European Alps in particular - are among the most sensitive to climate change, displaying visible transformations in both the landscape and cryosphere dynamics (Stucchi et al., 2023). High-elevation areas are experiencing a more pronounced warming trend compared to lowland areas. In the European Alps, this temperature increase is particularly accelerated, occurring at approximately twice the rate of the average warming observed across the Northern Hemisphere (Dumont et al., 2025; Mountain Research Initiative EDW Working Group, 2015). This trend is further corroborated by the rapid degradation of mountain permafrost, which in the last decade has shown warming rates exceeding 1°C per decade (Noetzli et al., 2024)." Research indicates that global warming will influence not only Alpine temperatures but also precipitation patterns, global radiation, and humidity levels. These shifts are projected to impact the frequency of floods and droughts, while simultaneously causing a severe decline in snowpack at elevations below 1500–2000 meters. Furthermore, risks associated with the melting of glaciers and permafrost are likely to intensify (Gobiet et al., 2012). Snow cover is a crucial component of mountain environments, particularly in mid- and high-elevation ranges like the European Alps. It results from the winter accumulation of snowfall, which then gradually melts in the spring or, at higher altitudes, transforms into firn and eventually glacier ice. In the Alps, at elevations above 2000 m, snow blankets the ground for at least 6.5 months per year (Marty et al., 2017; Hüsler et al., 2014). Due to its unique properties, snow serves as a vital water reservoir and a highly effective insulator. Its high air content (50–87%) buffers the soil against extreme temperatures, protecting it from winter cold and delaying spring warming (Bender et al., 2020). Despite its importance, long-term observations reveal a concerning trend: overall, since 1950, the duration of snow cover in the European Alps has shortened by approximately one month at elevations below 2000 m (Matiu et al., 2021).

At low and mid-elevations, winter snow depth has decreased dramatically because rising temperatures shift precipitation from snow to rain (Hock et al., 2019). In contrast, high-elevation sites have maintained stable winter snow volumes, as temperatures there remain well below freezing despite similar warming trends (Marty & Meister, 2012). Nevertheless, the overall duration of the snow season is shrinking across all altitudes due to accelerated spring melting, which now occurs roughly 15 days earlier compared to the average values between the two 30-year periods of 1960–1990 and 1990–2020 considered in the study of Dumont et al., (2025).

Ultimately, climate warming is driving a widespread retreat of alpine snow through a combination of altered precipitation phases at lower altitudes and accelerated spring melting across the board (Dumont et al.,2025).

1.2 Arctic-alpine vegetation and climate change

Covering roughly 2% of the Earth's land surface, arctic and alpine ecosystems span approximately eleven million square kilometers. This total includes five million square kilometers of arctic tundra, three million of alpine tundra, and the rest distributed across intermediate northern highlands (Strimbeck et al., 2019). The current disjunct distribution of arctic-alpine ecosystems, restricted to high latitudes (latitudinal treeline) and mountain summits above the treeline (altitudinal treeline), is a direct legacy of the Pleistocene glaciations. During the post-glacial warming of the Holocene, forest expansion forced these cold-adapted species to migrate northwards and upwards, fragmenting a once-continuous glacial biome into the isolated habitats we observe today (Birsks, 2008). The global presence of arctic-alpine ecosystems is fundamentally driven by temperature, which dictates the climatic treeline worldwide. By preventing tree growth where the seasonal mean temperature drops below 6.4 °C for a minimum of 94 days, this strict thermal threshold creates the life-form boundary that separates forested areas from the treeless polar and alpine tundra ones (see Fig. 2; Paulsen & Körner, 2014; Grace et al., 2002).

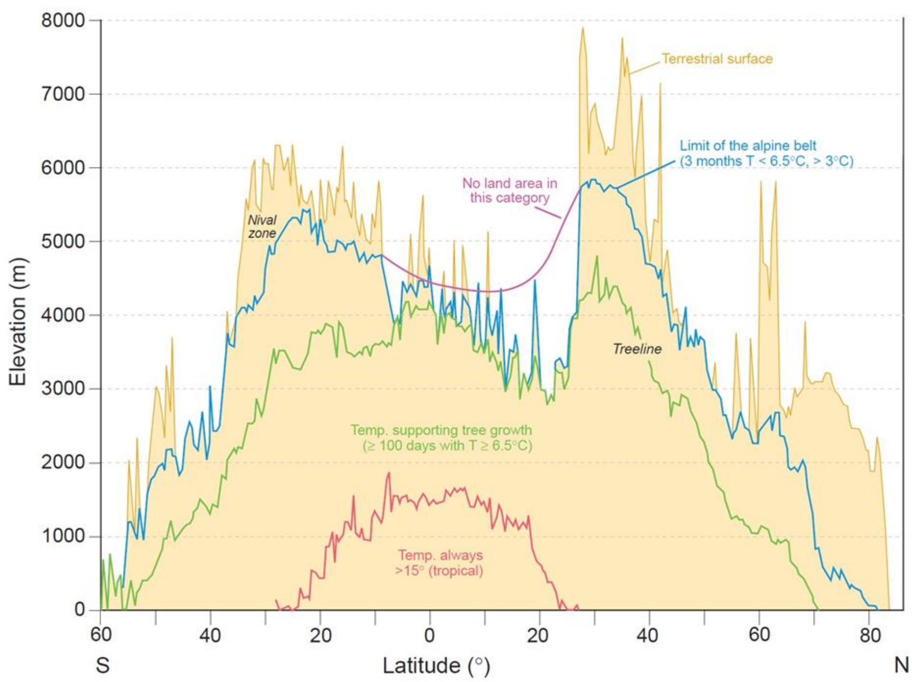

Fig. 2 - Global latitudinal gradient of climatic boundaries: the diagram illustrates the relationship between latitude and the predicted altitudinal position of the climatic treeline with the alpine/nival belt boundaries. The solid line highlights the dramatic descent of the treeline from equatorial regions toward sea level at the poles, driven by thermal limitations (Körner, 2007).

Plants respond to the harsh arctic-alpine environment with a high degree of specializations. These conditions combined with the extremely short growing season - commonly not longer than 6 weeks (of a perhaps 3-month snow-free cover (Körner, 2021) - have driven a strong morphological convergence in their vegetation. The flora is overwhelmingly dominated by dwarf shrubs, bryophytes and lichens, graminoids such as grasses and sedges, mostly forming tussocks, herbaceous perennials plants which frequently adopt cushion or rosette growth forms to exploit the warmer microclimate near the soil surface and protect themselves from freezing temperatures and severe winds (Billings & Mooney, 1968; Körner, 2021). Alpine vegetation, as defined above, represents the only biogeographic unit on land with a global distribution (Körner, 2021). As Ernakovich et al. (2014) emphasizes, cold ecosystems are uniquely vulnerable to climate change because biological and chemical processes in these environments are exceptionally sensitive to temperature fluctuations. The biological repercussions of warming in tundra regions are multifaceted, involving shifts in the seasonal phenology of plant and animal life cycles (Arft et al., 1999; Collins et al., 2021), as well as significant changes in species composition, migration patterns, and extinction rates (Grabherr et al., 1994; Sturm et al., 2005; Bjorkman et al., 2018). In alpine ecosystems, species composition is changing through shifts in the structure of extant species, establishment of subalpine species, and increasing species richness (Pauli et al., 2012.; Grabherr et al., 1994). Alpine species have already demonstrated significant range shifts in response to historical climate change. In the European Alps, comparisons between early 20th-century records and contemporary data reveal upward migrations exceeding 100 meters, with 49 out of 125 observed species now found at higher altitudinal limits than reported a century ago (Winkler et al., 2019). While community-scale changes depend on species-specific responses (Winkler et al., 2019), other severe impacts often arise indirectly through altered species interactions due precisely to this shift in altitude. Direct competition from the "novel competitors" has been explored by Alexander et al. (2015) in the Swiss Alps, demonstrating how new competitors can significantly reduce the survival (by 52–84%) and biomass of pre-established alpine species. This shifts in species distributions can further exacerbate the loss of specialized alpine species not able to sustain competition from lower-land species (Rogora et al., 2018), leading to changes in community dynamics and the potential loss of species unable to migrate (Garamvölgyi & Hufnagel, 2013). This trend triggers a profound reorganization of plant communities, resulting in phenomena such as "thermophilization" and the "homogenization" of alpine vegetation. This occurs because specialized, cold-adapted pioneer species are increasingly being supplanted by more competitive, heat-demanding generalist species due to rapid climate warming (Gottfried et al., 2012). The rate of immigration of lower elevation species into alpine regions is more likely to keep pace with the rate of climate warming, whereas lower latitude species must disperse across much greater distances to reach the Arctic (Loarie et al., 2009).

According to recent satellite data, nearly 77% of the European Alps have experienced a significant increase in vegetation biomass above the treeline since 1984, a phenomenon known as 'greening' (Rumpf et al., 2022). This rapid transformation, driven due to rising temperatures and longer growing seasons, closely mirrors the environmental shifts observed in the Arctic, where high-latitude amplification of global warming is driving similar biomass accumulation (Myers-Smith et al., 2019). While often perceived as a sign of ecosystem vitality, this shift presents several critical challenges, as the self-reinforcing warming loop caused by reducing surface albedo, increase competition, encourage shrubification and destabilizes regional hydrology by significantly increasing water loss through evapotranspiration (Rumpf et al., 2022; Dumont et al., 2025). This "greening" phenomenon is closely connected with the one called shrubification. Shrubification is the climate-driven expansion of woody shrubs in alpine and arctic regions, displacing native species and accelerating warming by lowering surface albedo. Research by Broadbent et al. (2024) demonstrates that this shift can increase shrub biomass by up to 150%, causing a "decoupling" of seasonal plant-soil nutrient cycles, destabilizes regional hydrology and fundamentally altering the biodiversity of tundra and alpine ecosystems (Sturm et al., 2005; Broadbent et al., 2024). The phenological response of Arctic and alpine regions represents one of the most tangible indicators of global climate change. As evidenced by Prevéy et al.

(2017), thermal sensitivity varies significantly between biomes: Arctic plants generally function as direct 'temperature trackers,' advancing their life cycles immediately in response to warming. In contrast, alpine communities often exhibit greater temporal resilience, as their phenology is constrained by photoperiodic cues that prevent premature flowering and protect against sudden high-altitude frost events. However, this generalized advancement, documented since the early meta-analyses of the International Tundra Experiment (ITEX; Arft et al., 1999), carries substantial ecological risks. The primary concern is the phenomenon of 'trophic mismatch' (Post et al., 2009), where the decoupling of plant flowering times from the activity of pollinators or the nutritional needs of large herbivores threatens the biological resilience of these fragile ecosystems. Furthermore, recent historical analyses (Panchen & Gorelick, 2017) indicate that reproductive stages, such as seed dispersal, may be advancing even more rapidly than flowering, suggesting a complex reorganization of Arctic plant life cycles under a warming climate.

1.3 Alpine grasslands and snowbeds: the arctic-alpine sentinels

In the high-altitude and high-latitude landscapes of the arctic-alpine regions, snowbeds constitute one of the most specialized and ecologically constrained habitats. These ecosystems are defined by topographic depressions or leeward slopes where wind-blown snow accumulates to significant depths, persisting long after the surrounding areas have thawed, often for more than eight to nine months of the year (Björk & Molau, 2007). These areas are present in arctic and subarctic lowlands, boreal mountains and temperate high mountains of Central and Southern Europe (2026:https://floraveg.eu/habitat/overview/R41). The ecological character of these sites is dictated by a profound "environmental trade-off": while the deep snowpack provides a stable thermal buffer that insulates the soil and vegetation from lethal sub-zero winter temperatures - maintaining a relatively constant temperature around 0°C - it simultaneously imposes a drastically short growing season (Körner, 2021). Snow accumulation in snowbeds, in fact, can cause in some cases the length of the growing season to vary by 6 weeks across a distance of 10 m, with even larger differences across exposure gradients (e.g., N-S aspect, wind edges) (Körner & Hiltbrunner, 2021). This brief vegetative window, which in some extreme snowbed habitats may last only six to eight weeks, forces plants to adopt an accelerated phenological strategy to complete their reproductive cycles before the onset of autumn frosts (Kudo, 1991; Billings & Bliss, 1959). The soil in these depressions is typically characterized by a high moisture content due to continuous meltwater percolation, which maintains soil saturation long after the beginning of the growing season (Hiller et al., 2005). Furthermore, snowbeds act as sinks for aeolian dust, leading to a significant accumulation of fine silty particles compared to the rocky, well-drained alpine meadows nearby (Litaor et al., 2002), creating a distinct substrate that supports specialized chionophilous (refers to organisms - plants, animals, or fungi - that thrive in cold winter conditions, specifically those that prefer or require significant snow cover for survival) communities. The vegetation structure within these snowbeds is characterized by a high degree of specialization and a dominance of prostrate growth forms like grasses, sedges, herbs and cryptogams. The species composition depends on regional climate, altitude, bedrock and soil type, and sometimes includes endemics, particularly in Southern Europe (2026: https://floraveg.eu/habitat/overview/R41). The prostrate growth form is an evolutionary adaptation to the physical pressure of the snowpack (Björk & Molau, 2007) and the need to remain within the warmer boundary layer of the soil surface (Körner, 2021). One of the critical evolutionary advantages of snowbed specialists is their capacity to start and maintain physiological activity even during the active phase of snowmelt (subnivean growth) (Hamerlynck and Smith, 1994). This "pre-emergence" metabolic vitality allows these plants to reach their maximum photosynthetic capacity rapidly once they emerge through the snow or melt has occurred (Starr and Oberbauer, 2003), penetrating the final 5 cm of the remaining snowpack, often initiating the flowering process within just a few days of their first exposure to full sunlight (Mullen and Schmidt, 1993; Galen and Stanton, 1995). This rapid phenological development is closely synchronized with a sophisticated strategy for resource acquisition. For example, the herb *Ranunculus adoneus* A. Gray and the bryophyte *Kiaeria starkei* (F.Weber & D.Mohr) I.Hagen, possess the unique ability to intercept and exploit the early pulses of nitrogen released into the soil prior to and during the melting process (Mullen et al., 1998; Woolgrove and Woodin, 1996). By capitalizing on this transient "nitrogen flush," these plants secure essential nutrients at a time when most other alpine species remain dormant, thereby maximizing their productivity within a severely restricted growing season. As reported in (Björk & Molau, 2007) snowbed communities, compared to other alpine plant communities, support low species richness in terms of vascular plant species - (up to 18 usually 5 to 10- m2). Generally, the dominant vegetation consists of forbs, but they can be almost completely replaced by bryophytes in very late melting snowbeds. Shrubs usually decrease gradually with shorter snow-free period conditions, except for few dwarf shrubs, e.g. *Salix herbacea* L. and *Harrimanella stelleriana* (Pall.) Coville, that are capable of growing in these environments (Björk & Molau, 2007). In moderate melting snowbeds, graminoids have their largest diversity while they seem to decrease in abundance toward both ends of a snowfree period gradient (Kudo and Ito, 1992). Alpine snowbeds are considered a model plant community for studying the consequences of climate change in alpine vegetation, due to their abundance in ecological specialists (Kliment, Valachovič, 2007), special growth conditions, sensitivity and ability to respond rapidly to changes in annual snowfall patterns, making them particularly vulnerable in a warmer climate (Björk & Molau, 2007). Characterised by a long lasting snow cover (Billings and Bliss 1959), these habitats are increasingly threatened by rising temperatures that contract the snow cover duration and advance spring melt-out dates (Beniston et al., 2003; Körner et al., 2023; Vorkauf et al., 2021). The current characteristic vegetation of snowbeds may change. As demonstrated by transplantation experiments by Shimono and Kudo

(2003), snowbed plants seem to be unable to invade other plant communities (e.g.,fellfields) while fellfield plants can grow in snowbed environments, making this vegetation vulnerable because of the low competitive ability. The predicted advance of spring snowmelt can threaten snowbed communities with invasion of non-specialised species from neighbouring alpine communities, such as *Carex curvula* All. or *Nardus stricta* L., originating from alpine grasslands (Grabherr 2003). The consequences of this invasion of alpine non-snowbed species on snowbed vegetation combined with the lengthening of the growing season, can lead to change in the community composition, with the replacement by strong competitors such as grasses and small shrubs from adjacent communities and lower altitudes (Palaj & Kollar, 2019) and may lead to replacement and local extinction of the least competitive species (Schöb et al., 2008). As a result, contemporary snowbed communities resemble alpine grassland much more than 50 years ago (Matteodo et al., 2016). In conclusion, because their existence is entirely dependent on specific snowfall patterns and temperature thresholds, even minor shifts in climate can lead to a premature melt and the shift to a "thermofilization" process of the habitat, where more competitive, generalist species from lower elevations can consequently invade the snowbeds, outcompeting the highly specialized chionophilous flora (Björk & Molau, 2007). Thus, the study of snowbeds is no longer merely a matter of botanical curiosity but a critical component in understanding the resilience and vulnerability of mountain ecosystems under the pressure of a warming climate.

1.4 Photoperiod and its implications on the vegetation in climate change

Photoperiodism is defined as the biological response of organisms to the relative duration of light and darkness within a 24-hour cycle (Thomas & Vince-Prue, 1997; Jackson, 2009). While it remains constant at the equator - comprising an equal 12 hours split between day and night - the duration diverges as latitude increases. This latitudinal gradient leads to increasingly unequal day and night lengths, culminating in the extreme conditions of the polar regions, where certain times of the year are characterized by continuous 24-hour light or total darkness (Thomas & Vince-Prue, 1997). Unlike other environmental variables such as temperature or precipitation, which exhibit unpredictable daily and seasonal fluctuations, photoperiod follows a highly consistent annual pattern dictated by the Earth's axial tilt. This stability makes it a fundamental latitudinal cue, providing plants with a reliable "astronomical clock" to synchronize their life cycles with the seasons (Jackson, 2009). The importance of photoperiod lies in its role as a primary driver of plant phenology - the study of the relationships between climatic factors and the seasonal manifestation of some phenomena of plant life. By integrating long-term climatic signals, photoperiodic responses allow plants to anticipate environmental shifts rather than merely reacting to them (Chuine, 2010). For instance, in temperate and polar regions, photoperiod can act as a "safety brake," ensuring that critical processes such as flowering or the breaking of bud dormancy do not occur prematurely during unseasonably warm spells, thus protecting the plant from subsequent frost damage (Körner & Basler, 2010). Photoperiodism not only protects plants from risky sprouting before the end of the period of severe frost but also results in a certain degree of synchrony of flowering among individuals within populations, which is essential for cross-pollination and is commonly under strong genotypic control (no ‘‘acclimation’’) (Keller & Körner 2003). The implications of this mechanism are complex and operate at a physiological level. Photoperiodic perception typically occurs in the leaves through specialized photoreceptors, such as phytochromes, and is tightly regulated by the internal circadian clock (Thomas & Vince-Prue, 1997; Singh & Mas, 2018). In the early stages of the growing season, photoperiod acts as a critical "modulating factor," refining the thermal sensitivity of many temperate and boreal species (Tarascio et al., 2025). It frequently functions as a safety brake, preventing premature bud burst during unseasonably warm winters and thus protecting plants from late frost damage (Körner & Basler, 2010). Budburst is regulated by the interplay between thermal cues and photoperiod. When winter chilling is insufficient, the photoperiod can act as a compensatory mechanism, triggering the release of dormancy once a specific daylength threshold is surpassed. This ensures that spring development remains timely even when chilling requirements are not met (Laube et al., 2014). The transition to flowering is shaped by complex interactions where the photoperiod can play an important role. According to Jackson (2009), the photoperiodic control of flowering can be classified into two main categories: obligate - where a specific daylength is a mandatory requirement - or facultative, where the duration of light promotes but does not strictly dictate the floral transition. The "obligate photoperiodic responses, “ensures that reproductive efforts are synchronized with optimal seasonal conditions, regardless of short-term thermal fluctuations. Within this framework, short-day plants (SDPs) are triggered by decreasing daylengths, whereas long-day plants (LDPs) necessitate extended light exposure. It is also important to note that the Critical Daylength (CDL) is a dynamic threshold, varying according to the plant's developmental stage and environmental factors (Jackson, 2009). To avoid reacting prematurely to temporary temperature spikes, many plants and especially long-lived trees and late-successional species, utilize photoperiodic sensitivity as a biological safeguard (Körner & Basler, 2010; Zeng et al., 2024). This mechanism ensures that flowering is synchronized with stable seasonal shifts rather than transient warming events. Furthermore, the intensity of this photoperiodic control is not uniform across all plants: species that bloom later in the season generally exhibit a higher dependence on daylength than those that flower early (Schaber and Badeck, 2003). As the growing season ends, photoperiod emerges as the dominant driver governing the cessation of plant activity, particularly within woody and boreal deciduous species (Tarascio et al., 2025). The progressive reduction in day length during late summer and autumn serves as a reliable environmental cue, signaling the transition toward winter dormancy through growth termination and bud formation (Olsen et al., 1997; Ruttink et al., 2007; Cooke et al., 2012). This photoperiodic shift is fundamental for triggering leaf senescence, a process that enables plants to complete vital nutrient resorption and develop cold hardiness before the onset of dangerous winter temperatures (Körner & Basler, 2012).

Climate change is reshaping plant distributions, exposing species to environmental conditions that may exceed their physiological limits. Photoperiod might significantly limit the responses of plant species to climate change, acting as a constraint that modulates thermal adaptation capacity. While photoperiod-sensitive taxa tend to maintain phenological stability even under rising temperatures, species that are primarily thermally responsive exhibit greater plasticity but face increased risks of frost exposure and seasonal mismatch (Tarascio et al., 2025). This balance between stability and flexibility is crucial as global warming reshapes plant distributions, shifting suitable habitats poleward and upward (Parmesan, 2006; Pauli et al., 2012). In this context, shifting events are constrained not only by temperature but also by photoperiodic regimes, which change predictably with latitude. As species migrate northward, they encounter longer summer days and greater seasonal variation in daylength, factors that can decouple thermal cues from photoperiodic regulation (Huffeldt, 2020). This misalignment can create "photic barriers" that limit northward expansion and alter ecological interactions such as competition and the delicate balance of pollination (Settele et al., 2016; Huffeldt, 2020; Tougeron, 2021), highlighting the photoperiod as one of the key determinant factors of migration capacity (Tomiolo & Ward, 2018). Species differ widely in their photoperiodic sensitivity. Under global warming, those less constrained by daylength control may gain a competitive advantage resulting in increased carbon gain and competitive dominance by responding more directly to rising temperature and extended growing season (Zohner & Renner, 2014; Zohner et al., 2016; Ettinger et al., 2021). Conversely, species with strong photoperiodic regulation, may struggle to adjust to new latitudes where critical daylength thresholds no longer coincide with optimal climatic conditions, potentially reducing their range or requiring assisted colonization to preserve ecosystem stability (Tarascio et al., 2025; IUCN/SSC, 2013). Substantial intraspecific variation in photoperiod sensitivity leads, especially in species with broad latitudinal ranges, to the formation of local ecotypes with specific thresholds, which has critical implications for conservation strategies such as assisted migration and forest management (Aitken et al., 2008; McLachlan et al., 2007; Leech et al., 2011).

Plant phenology, therefore, represents a finely tuned balance where photoperiod, combined with temperature-driven flexibility, acts as a selective filter, making the understanding of these interactions fundamental for forecasting future community changes and species competitiveness under climate change (Tarascio et al., 2025). The importance of the light environment is particularly relevant in the case of arctic-alpine species, whose populations can be scattered across remarkable latitudinal gradients. Climate change in high-latitude and alpine regions is rapidly reshaping the potential growing season and altering key abiotic cues, such as temperature and snowmelt dates, with the potential to alter the phenology of the vegetation and affecting processes ranging from food webs to ecosystem trace gas fluxes (Oberbauer et al., 2013). The capacity of tundra vegetation to adjust to climate-driven shifts is fundamentally regulated by the interaction between temperature and photoperiodic constraints. In alpine regions, where snowmelt typically occurs under shorter day-lengths compared to the continuous light of arctic springs, plants have evolved a more pronounced sensitivity to photoperiod as an evolutionary safeguard against unpredictable spring frosts (Prevéy et al., 2017; Keller & Körner, 2003). Arctic plants, in contrast, seem to be primarily limited by soil temperature and the timing of soil thaw, which delays root growth and nutrient uptake even when air temperatures are high. Because they are less constrained by day length, arctic plants more consistently advance their spring phenological events in response to warming (Ernakovich et al., 2014). Furthermore, the 24-hour photoperiod in the Arctic facilitates a faster rate of greening compared to alpine regions by maintaining warmer nights and accelerating snowmelt (Walker et al., 1999). As suggested in the work of Ernakovich et al. (2014), these divergent strategies might lead to contrasting ecological consequences under continued warming: arctic plants could capitalize on advanced soil thaw and winter-mineralized nitrogen, potentially increasing nutrient uptake, biomass, and ecosystem carbon gain. Conversely, alpine plants may be too constrained by photoperiod to advance their growth in synchrony with earlier snowmelt and microbial activity leading to a competitive disadvantage, nutrient loss and a paradoxically shorter growing season if earlier snowmelt is followed by summer water stress and early senescence (Ernakovich et al., 2014). A likely consequence of all these species-specific responses to a warmer climate and assumed earlier snowmelt is a rearrangement of community composition. Any attempt at predicting or modeling future alpine plant distribution based on warming scenarios needs to consider photoperiodic constraints: warming may be too rapid to track the change in photoperiod by evolutionary adjustment in many of these species. (Keller & Korner, 2003). In arctic and alpine environments, where the growing season is restricted to a narrow window of 8–12 weeks, the precise timing of flowering is fundamental to ensuring reproductive success (Tarascio et al., 2025): the risk of phenological mismatch, in fact, extends to biotic interactions and reproductive success. While temperature-driven species may initiate flowering earlier, facing a heightened risk of frost damage (Wadgymar et al., 2018), those whose flowering remains fixed by photoperiod may lose pace with climate-driven shifts in pollinator activity, such as the advancing flight periods of bumblebees, resulting in reduced pollination success (Pawlikowski et al., 2020; Miller-Struttmann et al., 2022; Rauschkolb et al., 2024). Similar mismatches are predicted between alpine plant growth and the activity of small mammals in the spring (Ernakovich et al., 2014). Summarizing these information, we can expect that differences in photoperiod, cues for plant phenological development, persistence of snow cover, and resource availability will trigger divergent responses between alpine and arctic ecosystems, with alpine ecosystems emerging as potentially more vulnerable to climate change than the arctic ones. Although warmer air temperatures are extending the potential growing season in both arctic and alpine ecosystems, constraints on alpine plants prevent them from realizing a longer growing season. The forecasts support a drastically advance of the life cycle of arctic communities and spring phenological development delays in spring for some alpine plants combined with an earlier senescence in the fall in alpine ecosystems (Ernakovich et al., 2014; Oberbauer et al., 2013; Skyllas et al.,2025).

1.5 Aim of this work

Photoperiod is a fundamental ecological factor regulating the phenological and physiological processes of plants. However, its role remains insufficiently addressed in scientific literature concerning plant responses to climate change. Given that photoperiod is strictly dependent on latitude and remains constant over time, while air temperatures are projected to increase most significantly in Arctic and Alpine systems, a complex interaction between light regimes and global warming is expected. Arctic-alpine plants offer a unique opportunity to investigate phenological responses to climate change: populations across latitudinal gradients, in fact, face markedly different photoperiods, possibly constituting differential phenological cues. However, phenological research in arctic and alpine regions in the past decades has predominantly focused on warming. The fundamental divergence existing between Alpine and Arctic ecosystems regard solar regimes: while alpine growing seasons peak at approximately 16 hours of daylight, arctic populations are subjected to continuous 24-hour photoperiods from April through August. Despite being a stable evolutionary cue for plant regulation, the synergy between this fixed astronomical signal and rising global temperatures remains a critical knowledge gap (Tarascio et al., 2025). This complexity is heightened by contrasting climate projections of rising temperature, changing in the precipitation in both areas and the potential different responses to these factors of the plants. Such divergent scenarios prompt a crucial question: how do photoperiodic constraints and shifting climatic variables interact to determine plant adaptation in these changing environments?

This work is part of the project "PHOTOPLANT: response of arctic and alpine ecosystems to photoperiod-climate interaction in the context of climate change", a pioneering research initiative that investigates, for the first time, the combined effects of photoperiod and global warming (temperature) on Arctic and Alpine vegetation. The project evaluates plant responses in terms of adaptation and plasticity by manipulating both factors and assessing their effects on vegetation samples sourced from the Svalbard Islands (Norway) and the Alpine plateau of Pale di San Martino (Italy). The aim of this work is to contribute to this experimental framework by analyzing the specific mechanisms through which high-altitude and high-latitude species cope with these shifting environmental drivers. Specifically, this research aims to:

1. Test the response of Arctic-Alpine plant species to the synergistic effects of photoperiod and climate warming temperature.
2. Isolate the singular impacts of photoperiod and temperature on plant development and physiology.

By bridging the gap between theoretical ecology and practical conservation, the knowledge gained through PHOTOPLANT will provide essential tools for protecting the planet's most vulnerable ecosystems. The findings will be instrumental in guiding ecological restoration interventions and ensuring the persistence of biodiversity in an increasingly unpredictable climate.

2 EXPERIMENTAL DESIGN

To achieve the purpose of this work, plants and vegetation clods are relocated along a latitudinal gradient between the Arctic and the Alps, allowing for direct observation of how these communities adapt to novel environmental conditions, specifically variations in temperature and light. Samples from both locations were placed in a common garden at the Bruno Peyronel Alpine Botanical Garden, an area located in the Italian Cottian Alps at 2300 m above sea level, as the study area. The target species were specifically selected from snowbed communities, as these habitats are recognized as key indicator sites for monitoring the impacts of climate change. Due to their high sensitivity to shifts in snowmelt timing and temperature fluctuations, snowbeds serve as natural laboratories for ecological research. Within these communities, species with a broad arctic-alpine distribution were prioritized to ensure comparability between different study regions. These include *Salix polaris* Wahlenb., *Salix retusa* L.*, Bistorta vivipara* (L.) Delarbre, *Saxifraga oppositifolia* L. *and* graminoids (Fig. 3). The selection of these taxa allows for a direct comparative analysis of how consistent environmental drivers -specifically the interplay between photoperiod and rising temperatures - influence plant responses across both polar and high-altitude ecosystems.

Fig. 3 - a) *Bistorta vivipara* (L.) Delarbre (Ginevra Colonna); b) Salix retusa L. (Othmar Ortner).

2.1. Experimental study area: Alpine Botanical Garden Bruno Peyronel (Western Alps)

The "Bruno Peyronel" Alpine Botanical Garden represents a site of great ecological and phytogeographical value within the Western Alps, in the Italian Cottian section. Located near Colle Barant in the municipality of Bobbio Pellice (TO), it stands at an elevation of 2290 m a.s.l., making it the highest alpine botanical garden in Europe (Fig.4). Established in 1991 through the joint effort of the University of Turin and local authorities, the Garden is dedicated to the memory of Bruno Peyronel (1919–1982), a distinguished botanist and naturalist, who first recognized the exceptional scientific value of the site (2026: https://www.giardinopeyronel.it/). The Garden is included in the 4.120 ha Site of Community Importance (SCI) IT1110032 'Pra - Barant', subsequently designated as a Special Area of Conservation (SAC) pursuant to the D.M. 27 July 2016. Protected under the European Union's Habitats Directive and included in the Natura 2000 network, the specific conservation measures for the protection of habitats and species were approved by the Piedmont Region with Regional Government Decision No. 19-3112 of 4/4/2016.

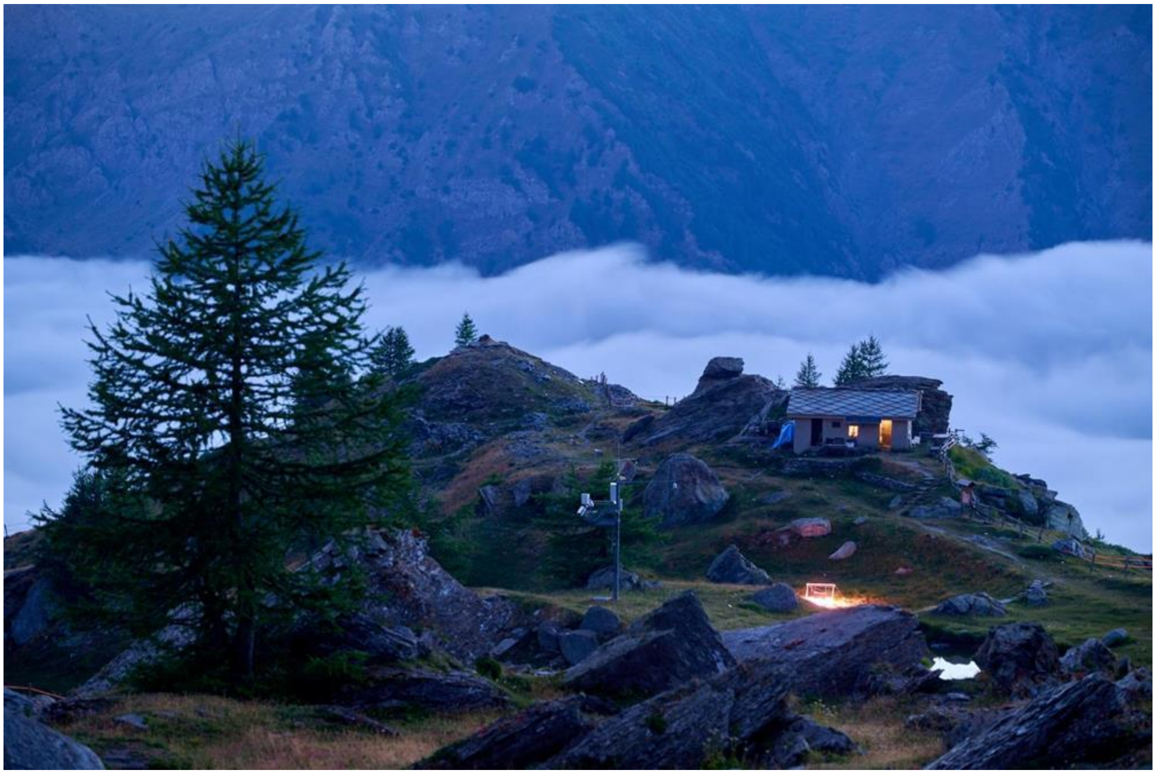

Fig. 4 - Bruno Peyronel Alpine Botanical Garden with the common garden (Othmar Ortner).

Delimited in an area of 17.000 square meters, the Alpine Botanical Garden Bruno Peyronel serves as a high-elevation natural laboratory that represents the most characteristic alpine environments of the Western Alps and the ZSC site itself. The vegetation is entirely spontaneous, in continuity with the surrounding areas, excluding the use of display flowerbeds (2026: https://www.giardinopeyronel.it/). From a phytogeographical perspective, the garden is situated at a unique crossroads where the sub-atlantic character of the Piedmontese valleys meets xeric continental and mediterranean-montane influences (Pascal & Varese, 1997). The climate of the area reflects the typical climatological dynamics of the correspondent altitudinal belt in the

Cottian Alps. Historically, the local climate averages between -3 °C and -5 °C in winter, and 9 °C to 12 °C in summer, with an average annual temperature of 2.8°C (ClimateEU - Marchi et al., 2020). However, rapid warming is severely altering these baselines. Notably, the 2023/2024 winter - the warmest in 67 years - recorded a +2.8 °C regional anomaly. This pushed the freezing level above 3,000 m, resulting in unusual mid-winter positive temperatures at the Barant station (Arpa Piemonte, 2024). Driven by the *Stau* effect (orographic lift), the Peyronel area receives exceptional mean annual precipitation with an average value of 1041 mm (ClimateEU - Marchi et al., 2020). This localized regime is increasingly characterized by extreme peaks, as demonstrated by the 209.2 mm accumulated in a single 24-hour period in May 2023 (Arpa Piemonte, 2023). This climatic complexity is mirrored by the diversity in the lithological substrate belonging to the "Piedmontese Zone," dominated by calc-schists and ophiolites such as serpentinites and prasinites (Pascal & Varese, 1997) with a resulting dominant acid condition in the topsoil layers and active podzolization processes (Nisbet et al., 2000; D'Amico et al.,2009). Such conditions support approximately 300 spontaneous plant species in an area of only 17,000 square meters, including significant endemics of the South-Western Alps like Campanula alpestris All., *Gentiana rostanii* Reut. ex Verl. and *Hedysarum brigantiacum* Bourn., Chas & Kerguélen (2026:https://www.giardinopeyronel.it/). The vegetation structure of the Peyronel Garden is characterized by a mosaic of phytocoenoses, ranging from different facies of *Festuco-Trifolietum thalii* pastures to specialized rupicolous formations like the *Caricetum fimbriatae*, typical of serpentinites. Furthermore, the presence of hygrophilous and snow-bed areas, such as the *Caricion bicolori-atrofuscae* (7240 - priority habitat for the Habitats Directive), highlights the local persistence of the Arctic-Alpine element (Pascal & Varese, 1997). The area was affected by major landslides, which characterize the upper portion of the slope between the Garden and the eastern ridge. Within the Garden, there are several moraine bodies, in which small, semi-permanent drainage channels have formed.

Within some depressions, hydromorphic conditions have developed, with modest peat formation processes still active (Nisbet et al., 2000). Currently, the area exhibits active successional dynamics, with many pastures evolving toward subalpine shrublands and larch-stone pine forests, making the "Bruno Peyronel" garden a critical site for studying the botanical evolution of this still under-researched sector of the Cottian Alps (Pascal & Varese, 1997). The site was selected as the host location for this study due to its suitable climatic and altitudinal conditions, as well as the protection provided during the growing season. This oversight, ensured by the direct supervision of the Garden's volunteers, shielded the implant from both potential anthropogenic disturbances and the destructive impact of livestock grazing (cattle and goats).

2.2 Clod sampling

2.2.1 Ny-Ålesund Station (Svalbard)

The field mission was conducted between the 24th of June and the 2nd of July 2024 at Ny-Ålesund, located on the Brøgger Peninsula (*Brøggerhalvøya*), Spitsbergen. This area represents a classic High Arctic tundra ecosystem, characterized by permafrost-affected soils and proglacial dynamics (Wojcik et al.,2019). A preliminary site inspection was conducted on the western area of the Bayelva River, a glacial meltwater stream primarily fed by the *Austre* and *Vestre Brøggerbreen* glaciers (Blaen et al., 2014). Following the survey, a total of 20 clods were collected. Additionally, representative plant specimens were collected to establish a reference herbarium, ensuring rigorous taxonomic identification of the species present in the sampled clods. In strict accordance with the research authorization granted by the Governor of Svalbard (*Sysselmesteren*), all sampling activities were restricted to the western bank of the Bayelva river. This area is part of the Knudsenheia coastal plain, one of the most extensively studied tundra landscapes in the High Arctic due to its high ecological diversity. The vegetation clods were extracted from four primary sites (see Fig. 5):

1. Bayelva Bridge: 78.93318° N, 11.83590° E
2. Trehyrningen Lakes: 78.93460° N, 11.81908° E & 78.93500° N, 11.80271° E
3. Bayelva Tributary: 78.92614° N, 11.79643° E
4. Knudsenheia Plain: 78.94041° N, 11.83178° E

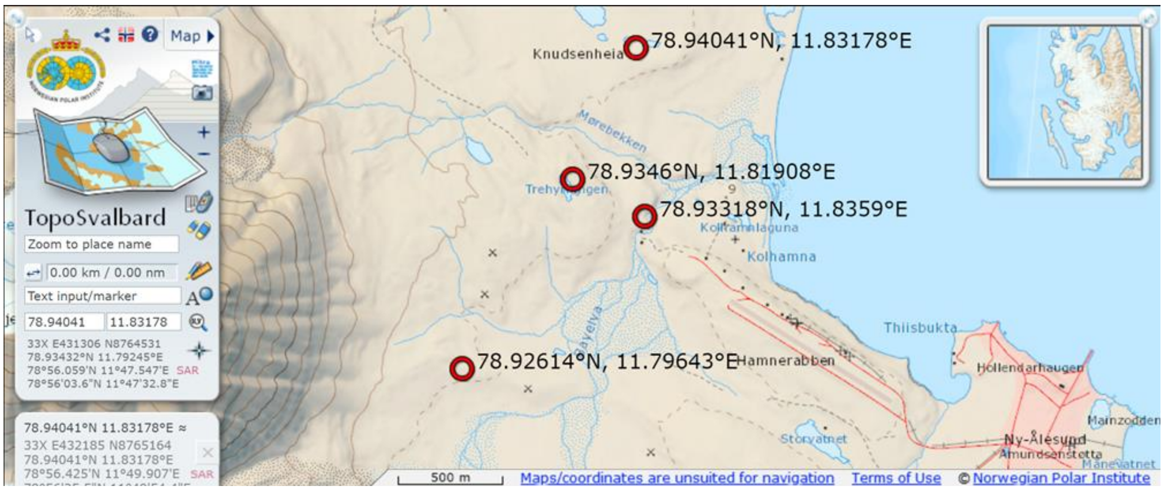

Fig. 5 - Collection site map of the arctic clods from Svalbard archipelago.

The sample selection prioritized vegetation clods containing *Salix polaris* Wahlenb., *Bistorta vivipara* (L.) Delarbre, and *Saxifraga oppositifolia* L. (see Fig 6 for an example). While *S. polaris* is the dominant species in the study area (ecologically replaced by S. herbacea L. and *S. reticulata* L. in alpine calcareous soils), *B. vivipara* and *S. oppositifolia* exhibit a classic arctic-alpine distribution. These species were chosen to facilitate a direct comparison of photoperiod and warming effects across different biomes. Clods were extracted from minimally stony ground using a shovel and a small saw, then placed into 10x8 cm perforated plastic baskets. To ensure environmental restoration, all extraction sites were backfilled with bare soil and local debris. Initial taxonomic identification was performed in the field and subsequently verified at the Italian National Research Council base "Dirigibile Italia". Each clod was individually labelled with an identification code at the time of collection laboratory using a stereomicroscope and photographed to establish a baseline. For transport, samples were placed in hermetically sealed plastic bags to prevent moisture loss.

Fig. 6 - Svalbard clods examples.

2.2.2 Pale di San Martino (Dolomites)

The mission dated 28 August 2024 was conducted to the Pale di San Martino Plateau (Lat. 46.269223° N, Long. 11.838521° E), located at an elevation of approximately 2600 m a.s.l. The site falls within the administrative boundaries of the Primiero San Martino di Castrozza municipality (TN, Italy) and is encompassed by the Paneveggio - Pale di San Martino Natural Park. The sampling involved the acquisition of 24 vegetation clods from snowbed habitats (Fig. 7), following the same methodology used at the Ny-Ålesund site (Svalbard) previously described. The samples were specifically selected based on the presence of arctic-analogous species, focusing on *Salix retusa* L., *Bistorta vivipara* (L.) Delarbre, and *Silene acaulis* (L.) Jacq.

Fig. 7 - the 24 clods freshly collected from Pale di San Martino site.

2.3 Experimental setup

The experimental setup involved initially a total of 48 clods, comprising 24 samples collected from the Ny-Ålesund Station (Svalbard) and 24 from the Pale di San Martino (Dolomites), subsequently adapted for the 20 clods of Svalbard. Clods from each provenance were randomly assigned to four treatments: local photoperiod (approx. 16h) with and without warming and arctic photoperiod (24h) with and without warming (Fig. 8), to simulate climate change-induced thermal stress. This setting results in four experimental treatments, as depicted in figure 9. To ensure structural stability, the OTCs were anchored to the substrate using metal pegs. Environmental conditions within OTC each in the 16h and 24h block were monitored and recorded using data loggers.

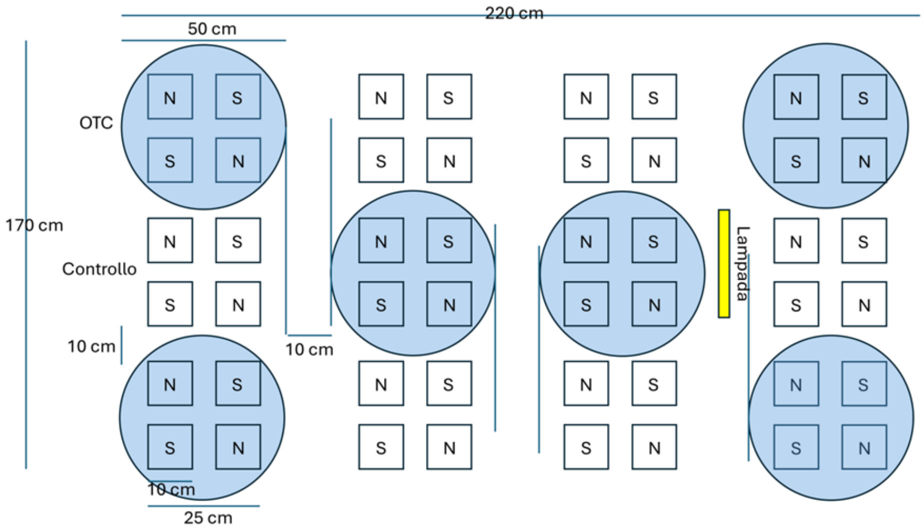

Fig. 8 - Schematic view of the common garden set-up.

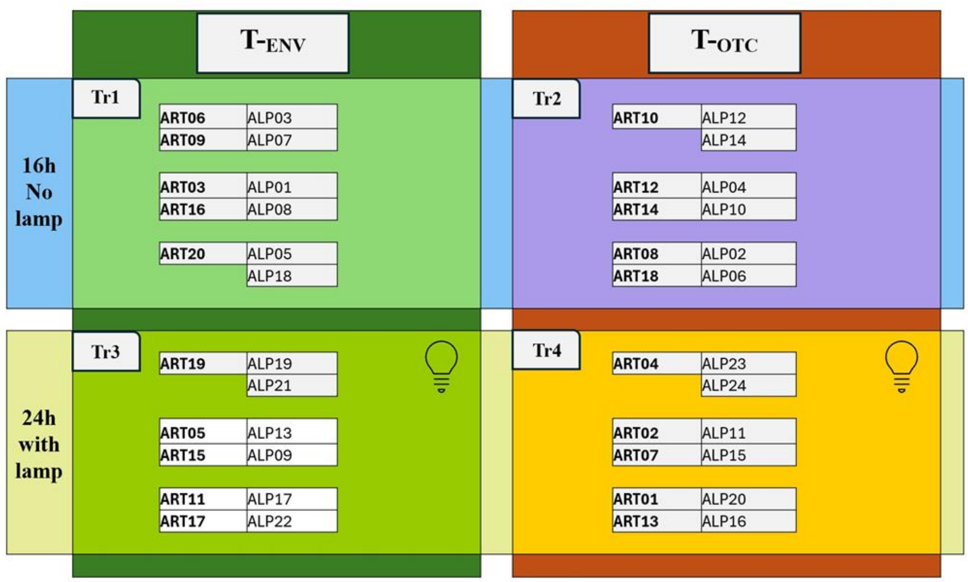

Fig. 9 - schematic view divided for the four treatments: Tr1 (16 h, no OTC); Tr2 (16 h, yes OTC); Tr3 (24 h, no OTC); Tr4 (24 h, yes OTC).

Labeling and Identification

For sample identification, each of the 12 experimental groups was uniquely labelled. Groups in the non-lamp treatment were assigned numbers 1 through 6, while those in the lamp-treatment were assigned letters A through F. The identification tags were secured to the ground adjacent to each experimental block.

Posing of clods and management of local vegetation

A first phase of posing was conducted on July 16, 2024, involving exclusively 20 Svalbard samples (four less compared to the initial design as field collection was limited by permissions). After a preliminary site assessment conducted to identify an optimal location for the permanent transplantation of the experimental clods in the Garden, a snowbed characterized by moist soil and a plant community dominated by *Juncus trifidus* L. and *Carex foetida* All. was selected as the study site. Within this area, a perimeter was excavated to accommodate the samples. The clods were posed while remaining inside their original containers to restrict vegetative spread.

A second posing phase was conducted on August 29, 2024, involving the clods from the Dolomites. These samples were located adjacent to the previously installed arctic samples, following the same experimental protocol. During both installation phases, all reproductive structures - flowers and fruits - were removed from the vegetation to prevent seed dispersal and mitigate the risk of genetic contamination in the surrounding environment. Additionally, a protective metal mesh was placed over the clods, followed by manual irrigation. Finally, a perimeter fence consisting of stakes and wire was installed to protect the experimental units from grazing by local wildlife (Fig 10).

Fig. 10 - Posing of all the vegetation clods with the protection fence.

The final experimental setup was completed between June 19 and 20, 2025, at which time all available clods were posed following the previously described design (Fig. 11).

Fig. 11 - Final set-up: group without the lamp (left); group with the lamp (right).

To minimize environmental disturbance and site impact, the removal of native soil vegetation was performed with high precision using a gardening shovel and small knife. In accordance with the initial protocol, each experimental clod was transplanted while remaining within its original container for the above reasons.

The experimental composition was slightly adjusted due to the low mismatch in the number of samples between clods from Svalbard and the ones from Dolomites. Thus, within each treatment, two groups consisted of three clods - 2 from the Dolomites (N) and 1 from Svalbard (S) - while the remaining groups followed the standard four-samples arrangement.

To accommodate the experimental samples, local clods were temporarily removed from the site. Following irrigation, these clods were transported to the Botanical Garden of Pavia and positioned alongside samples collected during the first phase in the 2024 campaign. At the end of the experiment, the *native clods* were brought back to the site and replaced in their original locations to ensure full site restoration.

Warming simulation using Open Top Chambers (OTC)

Open Top Chambers (OTCs) are portable, translucent structures, often hexagonal or conical in shape, specifically designed to simulate future climate conditions in field experiments. In the early 1990s, these tools were adopted as the recommended warming mechanism by the International Tundra Experiment network (Hollister et al., 2022). According to the study of Marion et al. (1997), recently corroborated by Henry et al. (2022), their unique 'open top' design is crucial because it allows for natural precipitation, gas exchange, and light penetration while simultaneously shielding the internal microenvironment from the cooling effects of wind. The primary function of an OTC is to induce passive warming through a 'mini-greenhouse effect,' which typically increases air and soil temperatures by 1°C to 3°C to study how plants and ecosystems respond to global warming (Healey et al., 2016).

Photoperiod manipulation in the field

For the photoperiod manipulation, the professional Ambralight AE80 LED lamp (100 W) was used, characterised by a photonic flux between 205 and 240 µmol/s and an emission spectrum optimised in the blue (400-500 nm) and red (600-700 nm) regions to maximise the efficiency of the photosynthetic process. The lamp was installed on a clod group and regulated with a timer to activate at sunset and switch off at dawn, thereby providing the plants with a continuous 24-hour photoperiod. The lighting system was powered by a photovoltaic panel coupled with a battery located inside the bivouac within the Alpine Botanical Garden (Fig. 12).

Fig. 12 - the lighting system after the activation of the automatic twilight sensor.

2.4 Data collection

2.4.1 Image Acquisition Protocol

Photographic monitoring of the experimental groups of clods was conducted on a daily basis, supported by the assistance of the Botanical Garden's volunteers. The imaging equipment consisted of a camera mounted on a tripod equipped with an extension arm. To ensure standardization and reproducibility across the entire dataset, the length of the tripod legs and the position of the extension arm were kept strictly constant throughout the study. To achieve consistent framing, three blue reference labels were placed around each block to indicate the exact positioning for the tripod legs. The tripod was oriented so that the extension arm projected outward while the camera body faced inward. Minor adjustments to the tripod's leg spread were permitted solely to align the legs with these specific reference labels. This systematic setup ensured that the camera was perfectly centered over the target block and oriented perpendicularly to the ground, capturing consistent top-down (nadir) images. To ensure the camera was perpendicular to the ground, a bubble level was placed on the camera body prior to each shot. In cases where spatial constraints prevented the use of standard blue labels, one of the reference points was marked directly on the greenhouse anchor. Prior to capturing each image, a reference ruler was placed within the frame of the clods to provide a standardized metric scale for subsequent dimensional analyses. The photographic acquisition period spanned from July 3rd to September 3rd, 2025, and the images were downloaded from the memory cards on a weekly basis. Digital image analysis, focused on assess variation in the total and species-specific percentage cover, was performed using ImageJ software. A 10x10 sampling grid was digitally superimposed onto each photograph, with the grid dimensions calibrated to align precisely with the physical perimeter of the square clod. Both species-specific and total cover data were derived by quantifying the frequency of sub-cell occupancy within the grid. The resulting spatial data were subsequently exported to Excel for statistical processing (Fig. 13).

Fig. 13 - ImageJ data collecting process of the percentage cover.

2.4.2 Fresh and dry biomass

At the conclusion of the field season, the vegetation clods were collected and transported to the labs of the Department of Earth and Environmental Sciences of the University of Pavia. Fresh and dry biomass (measured after samples were placed in an oven at 40°C for 24 hours) were determined for all the vegetation. For *Bistorta vivipara* (L.) Delarbre and graminoid functional groups, the total aboveground biomass was weighed. For *Salix* spp. specimens, woody components were separated and measured independently from the green tissues (including leaves and young stems). The collected data were subsequently organized into a specific Excel spreadsheet for the data analysis stage. Measurements were performed using an analytical balance with a precision of four decimal places (0.1 mg).

2.4.3 Phenological data collection

Phenological monitoring was performed on a weekly basis to track species development and assess treatment effects. Parameters recorded included total leaf count and dates of flowering and fruiting. Additionally, the sex of the inflorescences was identified for dwarf willows (*Salix* sp.).

2.5 Data analysis

2.5.1 Reproductive phenology

The limited number of individuals that successfully reached the flowering, fruiting, or seed production stages (reproductive phenophases) precluded the application of formal statistical analysis. Consequently, these data are presented descriptively in a table, where each observed phase is mapped to its corresponding Day of the Year (DOY).

2.5.2 Modeling temporal vegetation cover dynamics across the treatments

To evaluate the temporal progression of vegetation cover (%) across the different treatments (Tr1–Tr4) and clods types (ALP - alpine vs. ART - arctic), the data were modeled using second-degree polynomial (quadratic) regression. This approach was selected to capture the non-linear nature of plant growth and senescence over the observation period (weeks 27 to 36). The choice of a quadratic model ($y = ax^2 + bx + c$) over a simple linear regression was dictated by the phenological cycle of arctic and alpine vegetation. In these ecosystems, plant greenness typically follows a "bell-shaped" trajectory: an initial increase in leaf area during the peak of the growing season, followed by a gradual decline (senescence) as temperatures drop and photoperiods shorten. A linear model would fail to account for this critical turning point, whereas the quadratic function effectively identifies the seasonal peak and the subsequent rate of decline. Furthermore, the use of binomial/quadratic trends is a well-established standard within the arctic scientific community for describing seasonal vegetation dynamics. This methodology ensures direct comparability with previous longitudinal studies and remote sensing data, as shown for example in the work of Tamstorf et al., (2007), who used similar polynomial functions to describe Normalized Difference Vegetation Index (NDVI) trends in Northeastern Greenland. Adopting this standardized framework, permits us to interpret our results within the broader context of high-latitude ecological monitoring, allowing for a robust comparison between the survival strategies of alpine (ALP) and arctic (ART) clods under transplant and different treatment conditions. The goodness of each model was assessed using the coefficient of determination (R^2), which quantifies the proportion of variance explained by the quadratic trend. Standard errors (SE) were calculated and represented as error bars to indicate the precision of the weekly means. This modeling approach was preferred to more complex non-linear functions (such as sigmoidal or Gaussian models) to avoid overfitting, ensuring that the resulting curves represent the underlying biological signal rather than random sampling noise.

2.5.3 Final Vegetation Cover

The final vegetation cover (%) was analyzed using a Linear Model (LM) to evaluate the influence of environmental treatments and geographical origin. Prior to the analysis, a constant of +1 was added to the raw cover values. This data transformation was implemented to address the presence of zero values, particularly within the arctic samples, thereby stabilizing the variance and ensuring the mathematical robustness of the model without biasing the biological signal. The model defined "Treatment" (four levels: Tr1, Tr2, Tr3, and Tr4) and "Origin" (two levels: alpine vs. arctic) as fixed factors. The interaction term between Treatment and Origin was also included to determine if the response to environmental manipulation varied according to the geographical provenance of the clods. A Two-Way Analysis of Variance (ANOVA) was then performed to assess the significance of these predictors. A simple Linear Model was preferred for this specific parameter as it effectively captures the variance in a factorial experimental design where observations are treated as independent at the final sampling stage. All statistical analyses were conducted in the *Rstudio* software, utilizing the stats package for model fitting (lme4; lmerTest) and ggplot2 for graphical visualization, with results presented as mean values with standard error (SE).

2.5.4 Analysis of Dry Biomass

To evaluate the effects of the four treatments and the origin on plant productivity on dry biomass (DRY) data were analyzed using *Rstudio* software. Due to the non-normal distribution of the raw data, a logarithmic transformation log (x + 1) was applied to ensure normality and homoscedasticity of residuals. A Linear Mixed-Effects Model (LMM) was fitted using the lme4 and lmerTest packages, considering "Treatment" (Tr1, Tr2, Tr3, Tr4) and "Origin" (alpine vs. arctic) as fixed factors, including their interaction. The individual clod ID was included as a random effect to account for the nested experimental design. The significance of the factors was assessed through an analysis of variance (ANOVA) with Satterthwaite's method for the calculation of degrees of freedom (DenDF) and *p-value*. Graphical representations were generated using the ggplot2 library, displaying mean values and standard errors (SE). Woody biomass of *Salix sp.* was excluded from the analysis to avoid potentially misleading results, as woody tissues reflect cumulative growth over multiple years rather than a direct response to a single experimental season. Furthermore, the inclusion of wood would have introduced significant bias, as its weight is heavily dependent on the initial age and size of the individual plants within each clod.

Finally, the final dry biomass of *Salix retusa* (without woody data), graminoids, and *Bistorta vivipara,* the three main studied groups of species present in the clods, was analyzed exclusively for the alpine clods. The arctic clods were excluded from these specific linear models due to the high prevalence of zero values (representing a total lack of biomass in many samples and species). Such a distribution would have violated the fundamental assumptions of normality and homoscedasticity, preventing the generation of valid statistical outputs. For the alpine dataset, a factorial two-way Analysis of Variance (ANOVA) was implemented through linear models in R. To evaluate the potential synergistic effects of environmental stressors, 'Photoperiod' (16h vs. 24h) and 'OTC' (warming treatment: NO vs. SI) were defined as fixed factors, including their interaction term. A logarithmic transformation was applied with the same method as previously described. All models were fitted using the lm() function.

3. RESULTS

3.1. Reproductive Phenology of Experimental Clods

The reproductive phenology of the studied vegetation clods was evaluated across different experimental treatments. The observations revealed that no reproductive stages were recorded in any of the arctic (ART) clods, nor in any clods subject to the Tr4 treatment (24h-OTC). Consequently, reproductive activity was exclusively confined to alpine (ALP) clods. The detailed phenological timings, expressed in Day of Year (DOY), are summarized in figure 14.

	DOY	Bis viv			Sal ret♀			Sal ret♂	
Treatement	Clods	Fl_{on}	Fr_{on}	Sd_{on}	Fl_{on}	Fr_{on}	Sd_{on}	Fl_{on}	Fl_{off}
Tr1	ALP03	202	209	240	188	209	235		
Tr1	ALP08							184	195
Tr1	ALP01				184	195	235		
Tr2	ALP14	195	209	235					
Tr2	ALP10				184	195			
Tr2	ALP02	195	209	235	184	202			
Tr2	ALP06	230	235	246					
Tr3	ALP13	202	216	230	184	195	240		

Fig. 14 - Reproductive phenological timings for the experimental clods across treatments. The numerical values in the cells represent the Day Of the Year (DOY) - the specific day number of the calendar year - on which each phenological stage was recorded.

The detailed data for each reproductive clods are presented below, organized by treatment:

Treatment 1 (Tr1): three out of six clods (50%) advanced to reproductive stages.

- In clod ALP03, *Bistorta vivipara* exhibited flowering onset on DOY 202, fruiting on DOY 209, and seed dispersal on DOY 240. Within the same clod, female *Salix reticulata* recorded flowering on DOY 188, fruiting on DOY 209, and seed dispersal on DOY 235.
- Clod ALP08 contained the only reproductive male individual of *Salix reticulata*, with a flowering onset on DOY 184 and offset on DOY 195.
- Clod ALP01 included a female *Salix reticulata* that flowered on DOY 184, with fruiting on DOY 195 and seed dispersal on DOY 235.

Treatment 2 (Tr2): four out of six clods (approx. 67%) were reproductively active.

- For *Bistorta vivipara*, flowering onset was observed on DOY 195 for clods ALP14 and ALP02. Sward ALP06 displayed an extreme late-season onset on DOY 230, with subsequent phenophases pushed to DOY 235 (fruiting) and DOY 246 (seed dispersal).
- For female *Salix reticulata*, flowering onset began on DOY 184 for clod ALP10 and ALP02, with fruiting onset pushing to DOY 195 and DOY 202, respectively.

Treatment 3 (Tr3): one out of six clods (approx. 17%) exhibited reproductive phenology.

- In clod ALP13, *Bistorta vivipara* had a flowering onset on DOY 202, fruiting on DOY 216, and seed dispersal on DOY 230.
- Within the same clod, female *Salix reticulata* recorded a flowering onset on DOY 184, with fruiting on DOY 195 and seed dispersal on DOY 240.

The single reproductive male *Salix reticulata* (in Tr1) flowered around DOY 184, aligning contextually with the flowering onset of several female individuals (across different treatments) and maintaining its flowers for a duration of 11 days (until DOY 195). Generally, female individuals of *Salix reticulata* exhibited an earlier flowering onset, with all individuals initiating flowering between DOY 184 and 188. In contrast, *Bistorta vivipara* displayed a consistently later flowering onset across all treatments, demonstrating a greater phenological plasticity concerning its flowering onset range (extending from DOY 195 to a late-season date of 230).

3.2 Temporal vegetation cover dynamics

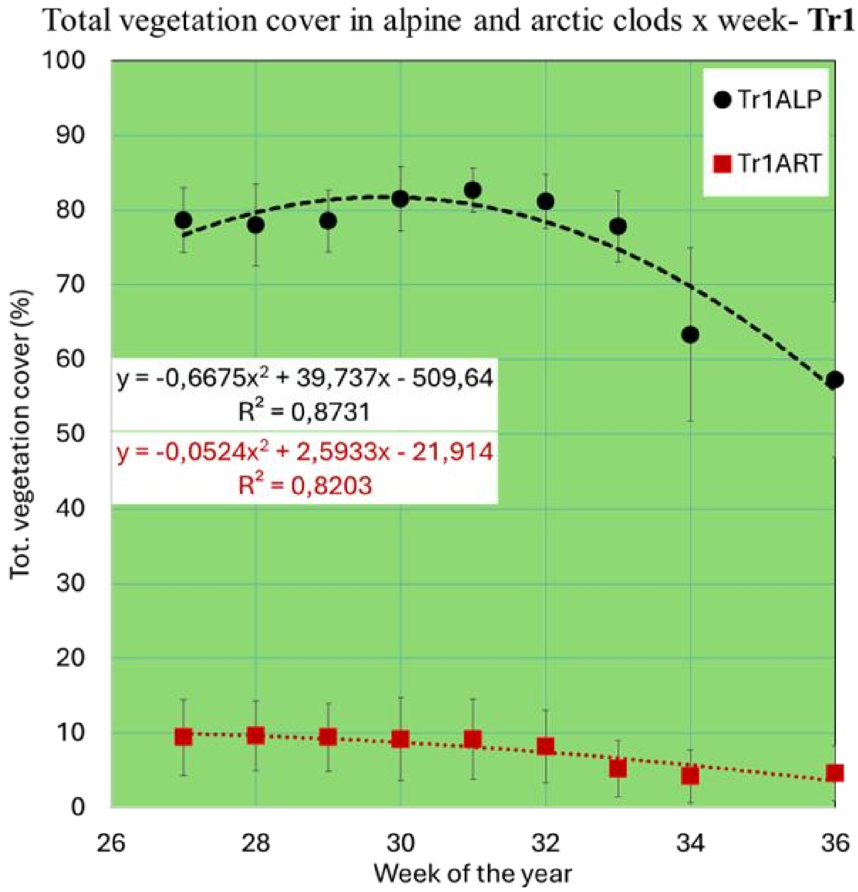

Fig. 15 - Temporal dynamics of total vegetation cover (%) for Treatment 1 (Tr1) from week 27 to 36 for alpine (black) and arctic (red) clods.

In Tr1 (Fig.15), both alpine (ALP) and arctic (ART) clods followed a well-defined convex binomial trend. The ALP clods maintained the highest leaf cover among all groups, starting at approximately 78.7% (week 27), reaching a seasonal peak of 82.7% at week 31, and subsequently declining to 57.3% by week 36. This trend showed a very high goodness of fit ($R^2 = 0.873$). In contrast, ART clods exhibited significantly lower values, maintaining a relatively stable cover between 9.4% and 9.2% for the first five weeks, followed by a decline to 4.6% at the end of the season ($R^2 = 0.820$).

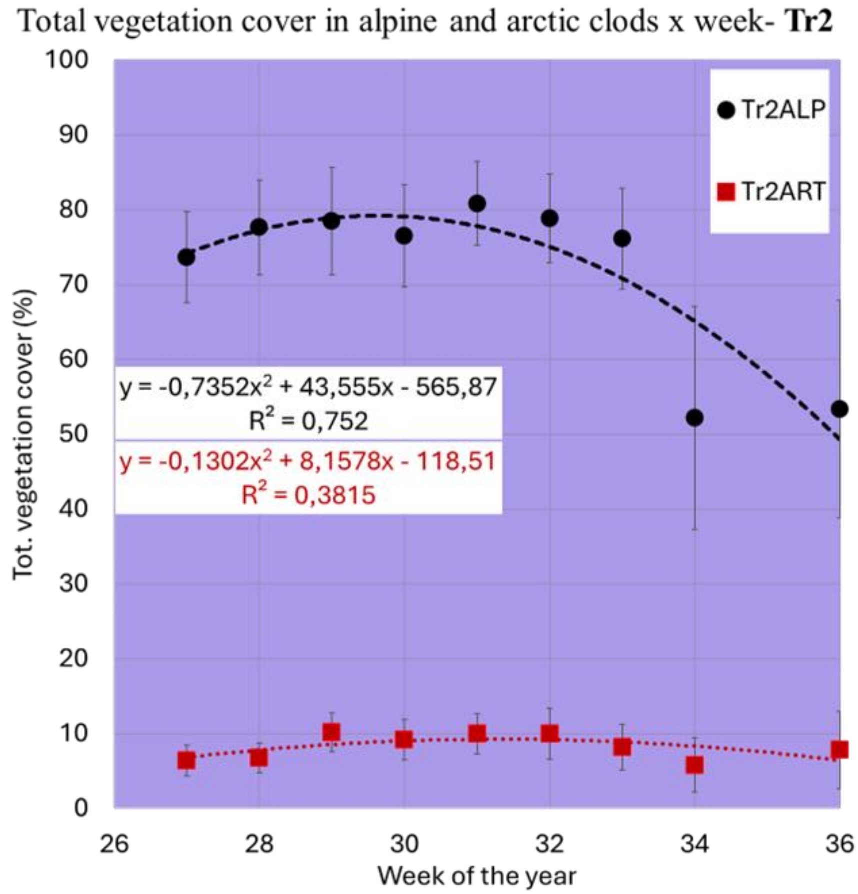

Fig. 16 - Temporal dynamics of total vegetation cover (%) for Treatment 2 (Tr2) from week 27 to 36 for alpine (black) and arctic (red) clods.

Tr2 (Fig.16) showed a similar phenological pattern to Tr1, characterized by a convex trend. ALP clods began with a cover of 73.7%, peaked slightly later at week 31 (80.8%), and ended the season at 53.3%. The quadratic model provided a robust fit ($R^2 = 0.752$). ART clods in this treatment displayed more fluctuation: after an initial cover of 6.4%, they reached a peak of 10.2% (week 29) before dropping to 7.8% by week 36. The R^2 for the ART group (0.381) was the lowest recorded, indicating higher variability in cover maintenance.

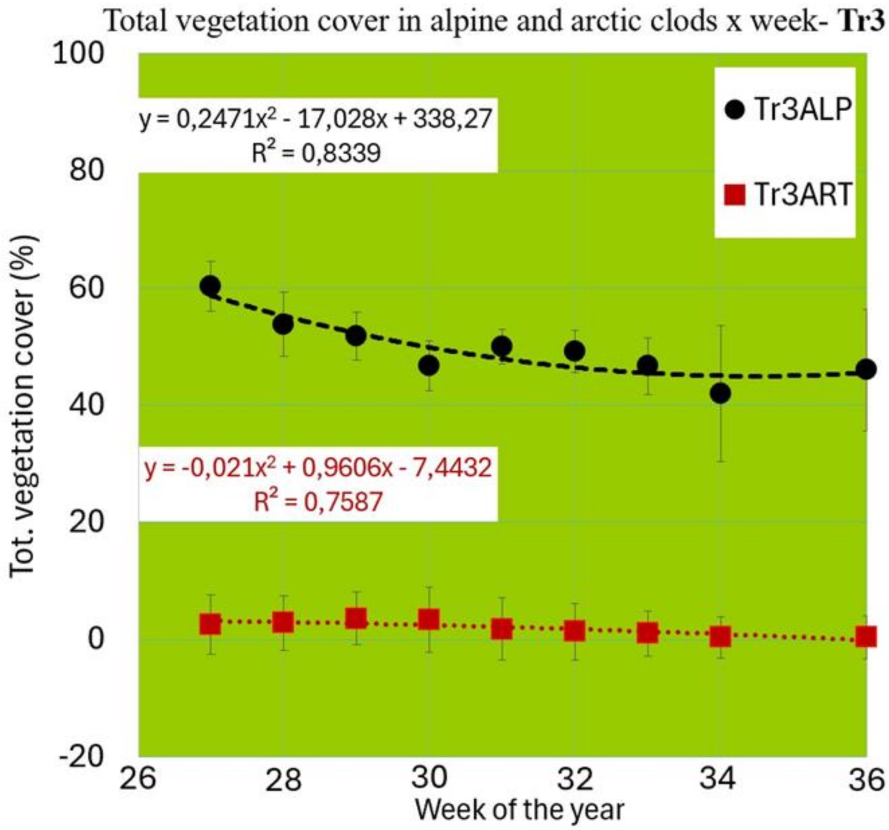

Fig. 17 - Temporal dynamics of total vegetation cover (%) for Treatment 3 (Tr3) from week 27 to 36 for alpine (black) and arctic (red) clods.

Under Tr3 (Fig.17), the overall cover was markedly reduced. ALP swards started at 60.3% and exhibited a steady, near-linear decline throughout the season, ending at 46.0% ($R^2 = 0.833$). Unlike the first two treatments, the peak was observed at the very beginning of the sampling. For the ART swards, the impact was even more severe: starting at a mere 2.6%, the cover dropped consistently until reaching nearly 0% (mean 0.4%) by week 34 and 36 ($R^2 = 0.758$).

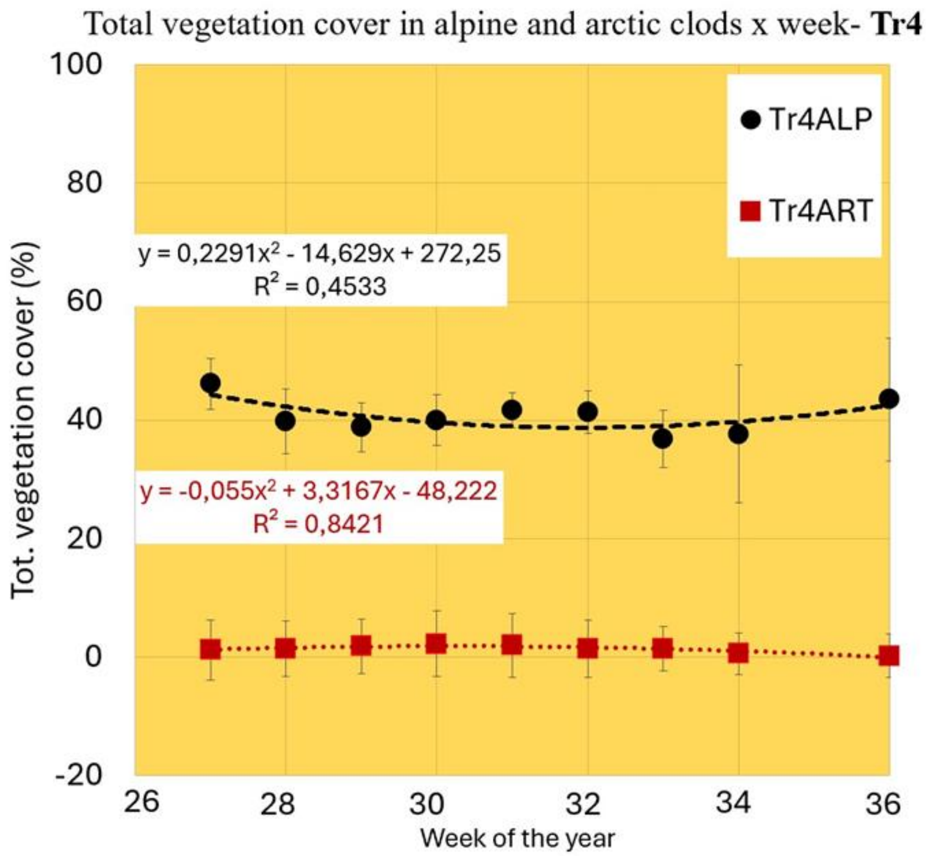

Fig. 18 - Temporal dynamics of total vegetation cover (%) for Treatment 4 (Tr4) from week 27 to 36 for alpine (black) and arctic (red) clods.

Tr4 (Fig. 18) exhibited the lowest performance for the alpine clods. ALP cover fluctuated within a narrow range, starting at 46.2%, dipping to 38.8% (week 29), and recovering slightly to 43.5% by week 36. The quadratic fit was relatively weak (R^2 = 0.453). For the ART clods, the total cover was almost inconsistent from the start: beginning at 1.2%, it reached 0.2% by the end of the season (R^2 = 0.842).

3.3 Final Vegetation Cover

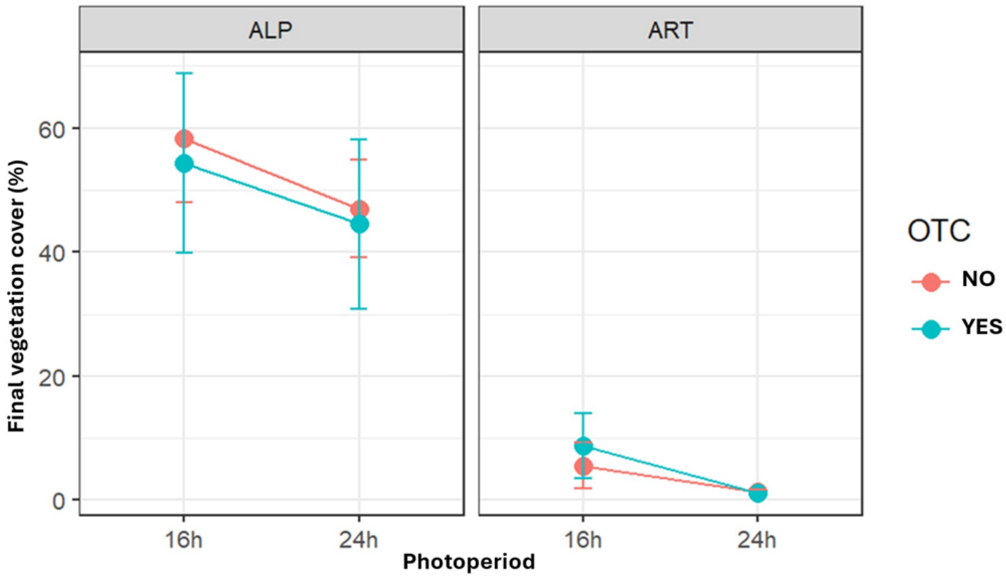

Fig. 19 - Graphic results of the final vegetation cover between treatments and origin.

Factor	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Treatment	3	800.8	266.9	0.5374	0.6597
Origin	1	23885.0	23885.0	48.0848	4.004e-08 ***
Treatment × Origin	3	137.7	45.9	0.0924	0.9637

Fig. 20 - Table results of the Anova analysis of the final vegetation cover.

The analysis of the final vegetation cover revealed the geographical origin of the clods as the main significant driver of vegetative occupancy (Fig.20). Regardless of the experimental conditions, alpine (ALP) clods exhibited a regularly and significantly higher percentage of cover compared to arctic (ART) clods (Fig. 19). Neither the experimental treatment nor the interaction between Treatment and Origin were statistically significant (Fig.20). Visually, the graphical data (Fig.19) confirms this trend, showing a clear and persistent gap in cover percentages between the two origins across all four treatments, with no substantial deviations or crossover effects observed between the groups.

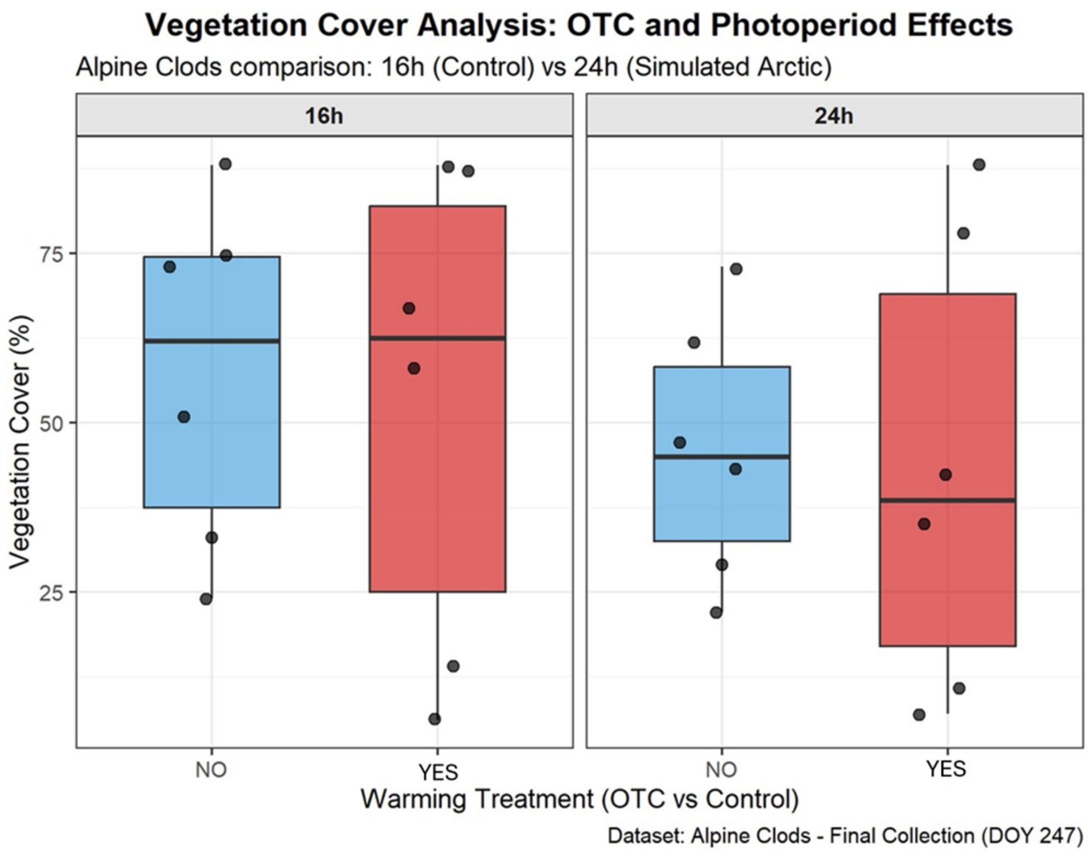

Fig. 21 - Final vegetation cover of alpine clods compared between the different treatments.

The graphic of the final vegetation cover only in alpine clods (Fig.21) shows a slight implication of photoperiod in the decreasing vegetational cover. A reduction in median cover was observed when shifting from the 16h control to the 24h simulated arctic photoperiod. The effect of the Open Top Chambers (OTCs) remained almost inconsistent. Specifically, within the 24h block, the clods with OTC treatment showed a slight decline. Furthermore, the data is characterized by high individual variability, with coverage values ranging from near-total to minimal within the same treatments. The Arctic counterpart was not observed for the reasons explained above.

3.4 Dry Biomass Production

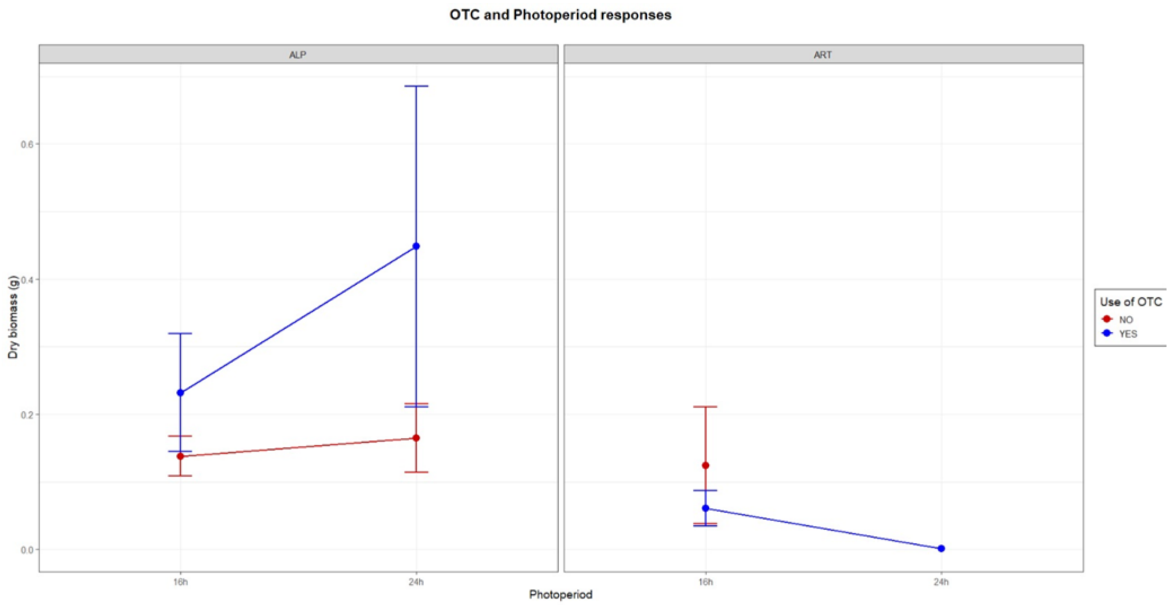

Fig. 22 - Graphic of the dry biomass production between treatments. Measurable leaf dry biomass of arctic clods was not available.

Analysis of Variance Table: Origin and Treatment Effects

Source of Variation	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
ORIGIN	0.06848	0.06848	1	124	2.7316	0.1009
TREATMENT	0.050403	0.008401	6	124	0.3351	0.9173
ORIGIN:TREATMENT	-	-	-	-	-	-

Fig. 23 - Table results of the Anova analysis for dry biomass production data.

The analysis of dry biomass (expressed as log (DRY+1)) revealed that neither geographical origin (ART-ALP) nor experimental treatments exerted a statistically significant influence on final productivity. Although the geographical origin emerged as the most influential factor in the model, it did not reach the conventional threshold of statistical significance (Fig. 23). Similarly, the experimental treatments, encompassing both different photoperiods (16h vs. 24h) and the presence of Open Top Chambers (OTC), did not significantly influence biomass accumulation (Fig.23).

Furthermore, the absence of leaf dry biomass measures of the arctic clods species in the no-OTC-24h condition didn't allow to test differences among all multiple level of Origin and Treatment interaction resulting in missing output for the interaction term.

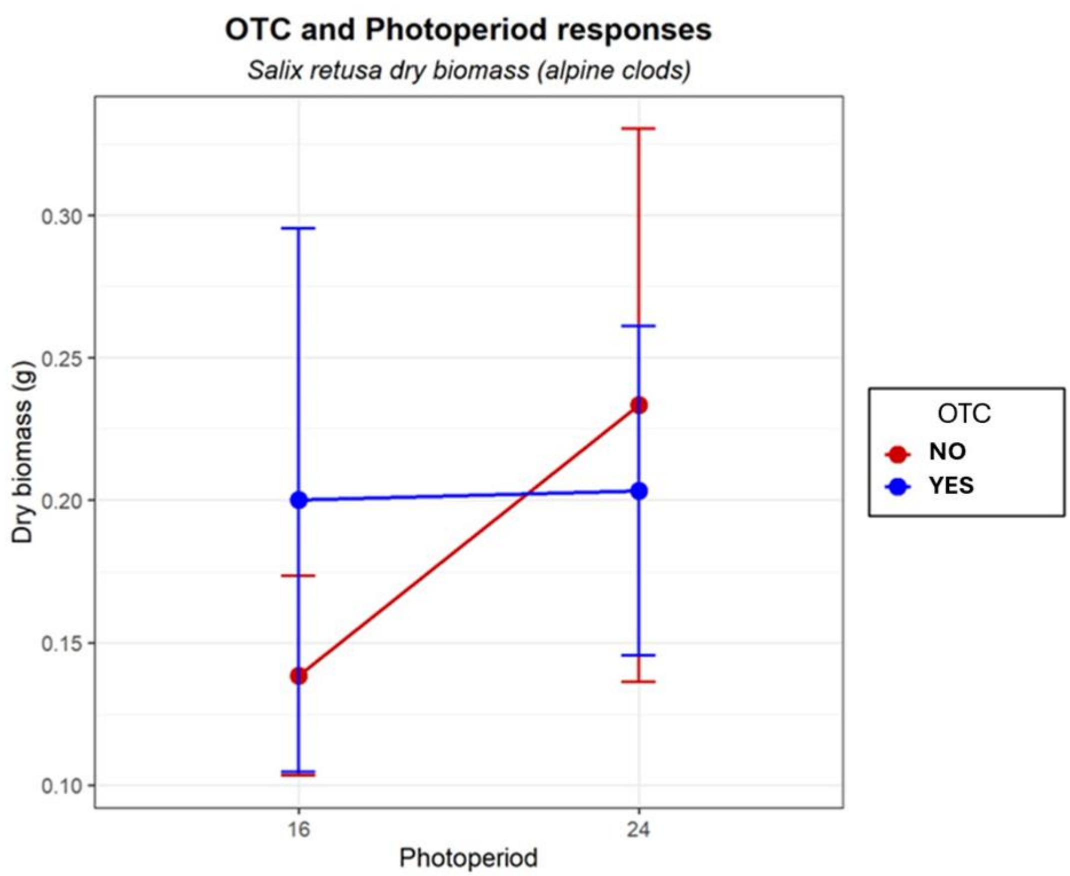

Fig. 24 - Final dry biomass of *Salix retusa* (green) in the alpine clods between the four treatments.

Source of Variation	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PHOTOPERIOD	1	0.01607	0.016065	0.492	0.4931
OTC	1	0.00248	0.002476	0.0758	0.7866
PHOTOPERIOD:OTC	1	0.0097	0.009696	0.2969	0.5933

Fig. 25 - Table results of the Anova analysis of final dry biomass of *Salix retusa* (green) in alpine clods.

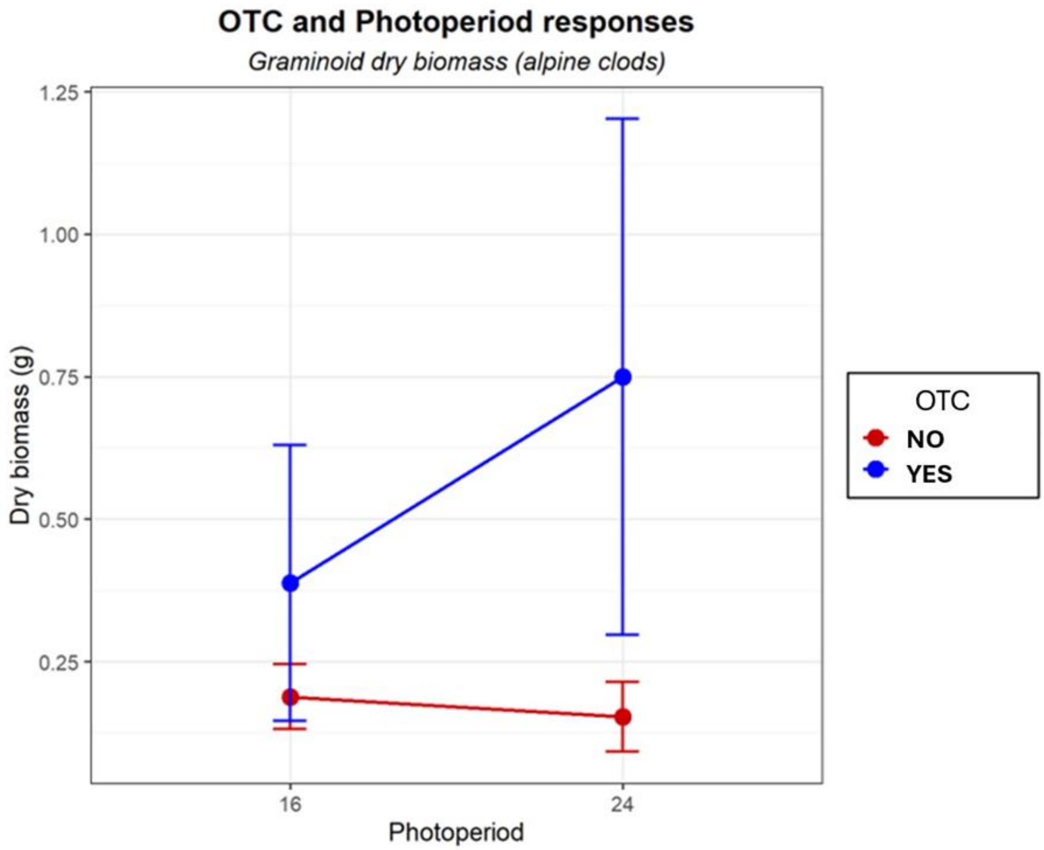

Fig. 26 - Final dry biomass of graminoid group in the alpine clods between the four treatments.

Source of Variation	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PHOTOPERIOD	1	0.03621	0.036206	0.3286	0.5745
OTC	1	0.18598	0.185982	1.6878	0.2123
PHOTOPERIOD:OTC	1	0.04232	0.042319	0.384	0.5442

Fig. 27 - Table results of the Anova analysis of final dry biomass of graminoids group in alpine clods.

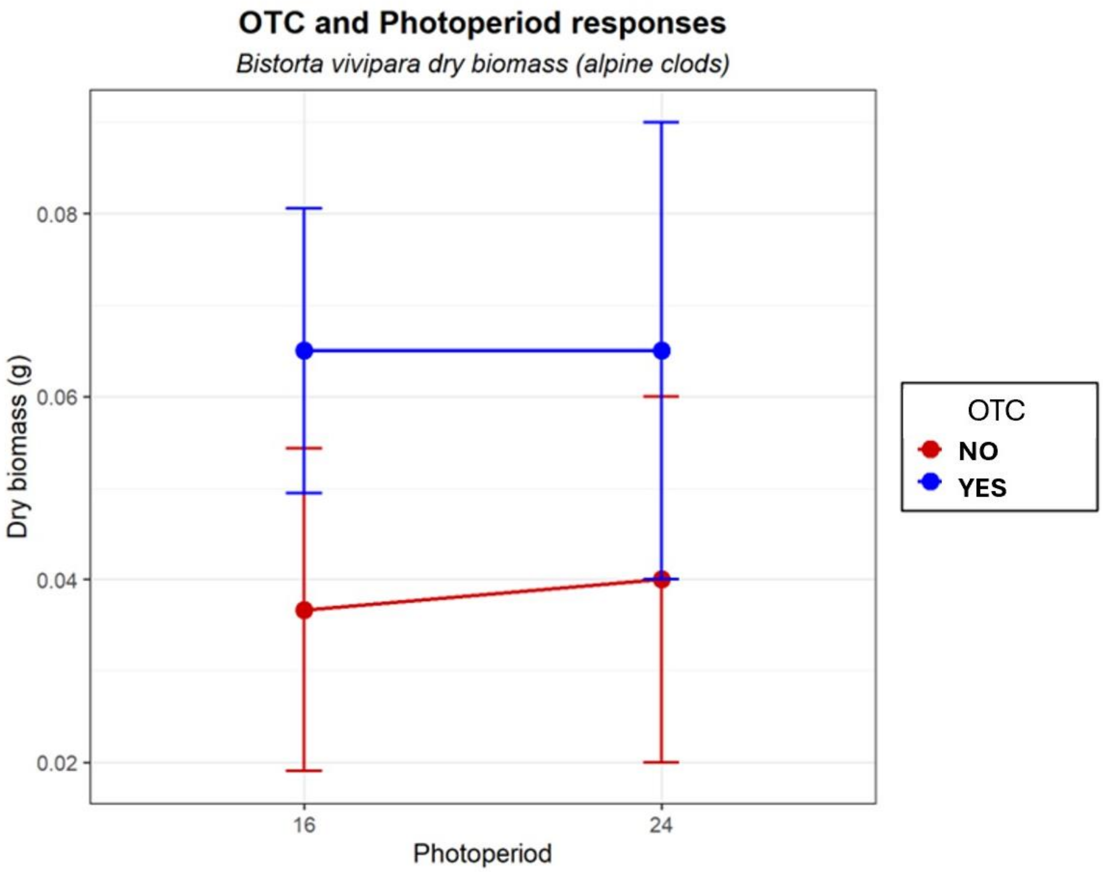

Fig. 28 - Final dry biomass of *Bistorta vivipara* in the alpine clods between the four treatments.

Source of Variation	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PHOTOPERIOD	1	2e-07	1.6e-07	0.0002	0.9897
OTC	1	0.0017971	0.00179711	2.0744	0.193
PHOTOPERIOD:OTC	1	6.8e-06	6.77e-06	0.0078	0.932

Fig. 29 - Table results of the Anova analysis of final dry biomass of *Bistorta vivipara* in alpine clods.

3.5 Data logger control: function of OTCs

The recorded temperature profiles (Fig. 30) indicate that the OTCs didn't induce a consistent warming effect as expected across both experimental blocks. In the 24h photoperiod treatments, the thermal gain appears particularly weak, with visible instances of localized cooling where internal temperatures closely align with or stay slightly below the external values. This suggests that the expected greenhouse effect of the chambers was likely mitigated by site-specific microclimatic factors, such as substrate moisture or evaporative cooling. These substrate-driven conditions appear to have influenced the internal thermal balance, especially within the 24h block, resulting in a less pronounced warming stimulus than expected.

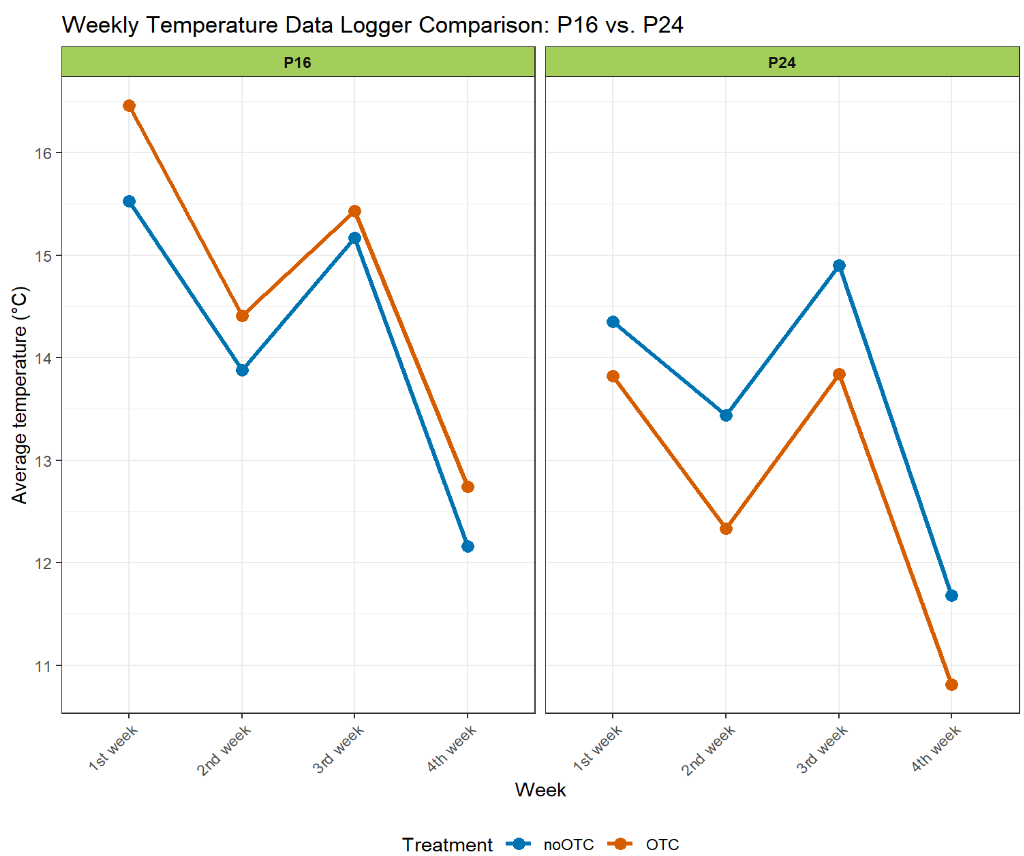

Fig. 30 - Weekly average temperature comparison across four data-loggers, organized by photoperiod blocks (P16 vs. P24) and treatments (OTC vs. no OTC). The data illustrates the temperature trends over a four-week period, showing a consistent warming effect within the OTC in block P16, whereas block P24 displays higher average temperatures in the no OTC control.

4. DISCUSSION AND CONCLUSION

4.1. General Scope and Experimental Constraints

The overarching goal of this study was to establish a comparative framework for evaluating the phenological responses of alpine (ALP) and arctic (ART) vegetation clods. By subjecting these two distinct provenances to controlled experimental treatments in a common garden, the research aimed to uncover how high-altitude and high-latitude grassland communities might respond to shifting environmental stressors (climate change) and a fixed cue (photoperiod). The original experimental design was conceived as a reciprocal transplant experiment, which ideally included a parallel common garden site located in the Svalbard archipelago. This dual-site approach was intended to expose both provenances to "inverted" environmental contexts: observing arctic and alpine clods simultaneously in an alpine setting and a high-arctic setting. Such a symmetrical design is considered the "gold standard" in evolutionary ecology for disentangling the effects of genetic adaptation from phenotypic plasticity (Kawecki & Ebert, 2004). Specifically, a reciprocal design would have enabled the characterization of the population-level plastic responses for both provenances, i.e. the phenotypic reactions of the different groups of plants across different environments (and therefore treatments). By comparing the performance of ALP and ART clods in both sites, we could have tested the 'home-site advantage' hypothesis, which posits that local populations show higher fitness in their native environment compared to not-native ones. However, due to denied authorization from the Svalbard authorities the second common garden could not be performed. Therefore, the interpretation of these results must be contextualized with the fact that we did not have the arctic control data. Moreover, the intended comparative analysis between alpine and arctic samples was profoundly limited by the lack of recovery and subsequent low growth rate of the arctic samples. As evidenced by the vegetation-cover data, the arctic clods almost failed to initiate a standard vegetative cycle, exhibiting nearly null growth activity from the very first weeks of observation. This lack of vitality suggests that the arctic provenance reached a critical physiological threshold even before the experimental variables (such as supplementary temperature and different photoperiod) could be fully assessed. The decline of the Svalbard clods represents a significant biological result in itself: it underscores a severe sensitivity to transport and transplant shock. This phenomenon acted as an immediate environmental filter and is likely a synergistic result of mechanical, thermal, and hydrological stressors. In ecological literature, transplant shock is defined as a period of arrested growth or mortality following the relocation of a plant, often caused by the disruption of the root-soil interface and sudden exposure to a different microclimate (Douglass et al., 2009). The decline of the arctic vegetation can be attributed to a profound environmental mismatch between their native edaphic conditions and the possible drastic changes during the transport and the following experimental site. As documented by Boike et al., (2018) and Migała et al., (2014), high-Arctic soils are characterized by a regime of consistently low temperatures and high, stable moisture availability throughout the growing season - an even more determining factor if we consider the snowbed origin (Björk & Molau, 2007). The logistical phases of transport and transplant likely induced an excessive physiological and mechanical shock. The relocation likely caused a rapid loss of this soil water potential and a thermal spike that exceeded the narrow physiological tolerance of these ecotypes, leading to irreversible collapse, ultimately preventing any viable recovery in the Common Garden. Without the Svalbard trial, it remains unclear whether the observed resilience of the alpine clods is a sign of a superior acclimatation strategy or if they would have suffered a similar physiological collapse when exposed to the constraints of the High Arctic. The dual-site data would have therefore provided the necessary contrast to determine if the mortality of the arctic clods was an absolute response to transplant stress or a relative disadvantage caused by the lack of local adaptation to the mid-latitude common garden conditions.

4.2 Temporal coverage and reproductive phenology

As previously established, the cumulative trauma of transport and transplant shock acted for arctic clods as an insurmountable environmental filter, driving ART vegetative cover to near-zero levels - particularly in the 24h light treatments (Tr3 and Tr4) - well before the official start of the data collection. Consequently, the ART samples failed to initiate any measurable reproductive cycle, reflecting a lack of acclimation capacity to the relocation. Therefore, the following discussion focuses on the significantly higher resilience and plastic responses of the Alpine (ALP) clods. Regarding reproductive phenology and seasonal growth, a clear divergence emerged based on the experimental light regime. In the 16-hour treatments (Tr1 and Tr2), the alpine plants followed a traditional binomial growth curve, reaching a peak in cover between weeks 30 and 31 followed by natural senescence. This pattern is consistent with binomial trends observed in remote sensing studies of similar high-latitude and high-altitude communities (Tamstorf et al., 2007). The observed advancement in reproductive phenology within treatment 2 - 16h plus OTC - reflects a response to the warming effect induced by the Open Top Chambers (OTCs). This acceleration is consistent with the foundational meta-analysis by Arft et al., (1999), which established that experimental warming generally advances the onset of flowering and other reproductive stages across the tundra biome. Furthermore, Oberbauer et al., (2013) and Collins et al., (2021) highlighted that temperature is a primary driver of phenological timing and warming differentially affects vegetative and reproductive phenology, with reproductive phases often exhibiting a more pronounced advancement compared to vegetative ones. In this context, the alpine (ALP) clods in Tr2 leveraged their inherent phenotypic plasticity to take advantage of the increased thermal accumulation. However, as noted in the mentioned studies, the intensity of these responses remained inherently species-specific, reflecting the diverse physiological thresholds and life-history strategies present within the alpine community. The introduction of 24-hour supplementary lighting in Tr3 and Tr4 resulted in a 'suppressed' vegetative trend, significantly diverging from the seasonal growth patterns observed in the 16-hour treatments (Tr1 and Tr2). This fact was most evident in the reproductive output, which demonstrated an almost total inhibition. Specifically, in Treatment 4 (24h light + OTC), no flowering units were recorded, while in Treatment 3 (24h light without OTC), only a single clod showed signs of flowering. This decline is likely attributable to the physiological stress induced by continuous light. While alpine plants are technically long-day species (Keller & Körner, 2003; Körner, 2021) the total absence of a dark phase can trigger a circadian rhythm disruption. Unlike Arctic ecotypes, which have evolved specific mechanisms to thrive under the midnight sun, alpine plants generally require a 'dark repair' or metabolic rest period to manage oxidative stress and the accumulation of reactive oxygen species (ROS). As noted by Barber & Andersson, (1992) and other studies as Baker, 1996 and Velez-Ramirez et al., (2011), constant light exposure can severely impair resource allocation by causing an excessive accumulation of carbohydrates in the leaves. This process, coupled with the overproduction of reactive oxygen species (ROS), shifts energy away from reproductive development toward basic cellular maintenance and stress mitigation. Ultimately, this 'metabolic exhaustion' might have led to premature senescence and the significant reduction in leaf cover and reproductive units observed in our alpine clods under 24h treatments at the end of the season. In Treatment 4, the total absence of flowering phases may also be linked to a counter-intuitive effect of the OTCs, which recorded a cooling effect rather than the intended warming. As highlighted in the ITEX network review by Hollister et al., (2022), and shown in the data-logger graphics, the thermal performance of these chambers is highly context-dependent and can deviate from expected trends under certain experimental setups. Consequently, the combined impact of photoperiodic stress from continuous light and suboptimal temperatures likely created a synergistic environment that suppressed reproductive initiation, ultimately leading to the total failure observed in this specific treatment.

4.3 Phenotypic plasticity and growing trade-offs under experimental conditions

The overall stability observed in the vegetative traits of the studied alpine species reveals a remarkable degree of ecological resilience and phenotypic plasticity. Phenotypic plasticity represents a fundamental evolutionary mechanism that enables plants to maintain functional persistence across fluctuating conditions, allowing for adaptive morphological and physiological adjustments in response to rapid environmental shifts (Schlichting, 1986).

Despite the environmental manipulations, in fact, the plants maintained a high level of vegetative homeostasis. In high-altitude ecosystems, environmental stochasticity, characterized by rapid and unpredictable fluctuations in temperature, snow cover, and light intensity, is the norm rather than the exception. As Körner (2021) observed, alpine plants are not simply "resistant" but are capable of responding with remarkable physiological flexibility. This plasticity allows them to regulate metabolic rates and resource allocation without requiring immediate genetic modification. By maintaining vegetative homeostasis, these plants respond to environmental stresses (such as those induced by continuous photoperiod) by demonstrating acclimation rather than a drastic collapse. This capacity for functional buffering suggests that species like *Salix retusa* L., graminoids, and *Bistorta vivipara* (L.) Delarbre possess a conservative growth strategy, likely evolved to withstand the inherent unpredictability and short growing seasons of high-altitude ecosystems. The absence of statistically significant effects of both OTCs and induced longer photoperiod should not be interpreted as a definitive lack of biological response, especially interpreting the results over long periods. The short temporal window of the experiment may represent a remarkable limiting factor, especially when considering alpine perennials, which are evolutionarily adapted to slow growth and high resource conservation (Körner, 2021). Therefore, structural responses to novel drivers, such as a shifted photoperiod or an altered thermal regime, can exhibit a substantial time-lag. A single growing season may have been insufficient to allow these slow-growing species to translate physiological stress into measurable morphological shifts. In addition, every species in a community tends to react in a different way and with different timing to shifts in environmental parameters and in relation to its ecological requirements (Parolo & Rossi, 2008). Consequently, the observed stability might represent a transitional phase, where the plants are physiologically adapting to the new conditions spanning different rates depending on both intra and inter-specific variability of the phenotypic plasticity (Theurrilat & Guisan, 2001; Orsenigo et al., 2014). Thus, “sharp” structural changes may require either longer or multiple vegetative seasons to manifest at the community level. A particularly interesting result found in this study is the decoupling between biomass accumulation and vegetation cover under the 24h photoperiod visible in the graphics. While total biomass remained statistically stable, an upward trend was observed in the graphics under the 24h photoperiod, contrasting sharply with the noticeable contraction in vegetation cover. This divergence may suggest a physiological trade-off between different growth parameters. The slight gain in biomass may not reflect enhanced 'healthy' productivity: rather, it could be indicative of a stress-induced accumulation of non-structural carbohydrates (NSCs), solutes, and water (Barber & Andersson, 1992). As argued by Körner (2015), the accumulation of biomass is not primarily limited by carbon supply through photosynthesis (source limitation), but rather by the capacity of tissues to undergo cell division and expansion (sink limitation). In this framework, environmental stressors, such as an anomalous photoperiod or unfavorable microclimates, can inhibit structural expansion and lateral growth (explaining the observed reduction in cover) without necessarily halting carbon fixation, leading to an accumulation of these compounds a consequence increase in total dry biomass and tissue density despite the apparent decline in the plant's physical cover. Unlike species strictly native to high-latitude arctic regions, alpine populations may be particularly vulnerable to continuous light because they probably lack specific tolerance mechanisms. In this context, the observed photo-oxidative stress is a non-specific response to a constant light regime that prevents the necessary dark-period recovery, eventually leading to structural damage and less cover development, as a result of circadian asynchrony, situation described in the lighting experiment simulated by Shibaeva et al., (2024) between native and non-native plant species in the subarctic region.

While this study was characterized by certain logistic and technical limitations, the findings offer a compelling glimpse into the physiological and phenotypic resilience of alpine plant communities. The observed trends, though not always crossing the threshold of statistical significance, suggest an ongoing process of functional recalibration in response to novel environmental drivers. It is highly probable that if these populations were subjected to the same stressors over a more extended, multi-year period, the subtle trade-offs and stress responses recorded here would manifest with significantly greater intensity and more pronounced ecological consequences.

5. REFERENCES

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1(1), 95-111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Alexander, J.M., Diez, J.M., & Levine, J.M. (2015). Novel competitors shape species' responses to climate change. Nature, 525(7570), 515-518. https://doi.org/10.1038/nature14952

Arft, Ana & Walker, Marilyn & Gurevitch, Jessica & Alatalo, Juha & Bret-Harte, M. & Dale, M. & Diemer, Matthias & Gugerli, Felix & Henry, Gregory & Jones, Michael & Hollister, Robert & Jónsdóttir, Ingibjörg & Laine, Kari & Lévesque, Esther & Marion, Giles & Molau, Ulf & Nordenhall, Urban & Raszhivin, Valodya & Wookey, Philip. (1999). Response patterns of tundra plant species to experimental warming: a meta-analysis of the International Tundra Experiment. Ecological Monographs. 69. 491-511.

Arpa Piemonte. (2024). *Il Clima in Piemonte - Inverno 2023/2024*. Torino: Dipartimento Rischi Naturali e Ambientali, Arpa Piemonte. https://www.arpa.piemonte.it/sites/default/files/media/2024-04/Inverno_2024.pdf

Arpa Piemonte. (2023). *Il Clima in Piemonte - Maggio 2023*. Torino: Dipartimento Rischi Naturali e Ambientali, Arpa Piemonte. https://www.arpa.piemonte.it/sites/default/files/media/2023- /Maggio_2023_rev.pdf

Baker, N.R. (1996). Photoinhibition of Photosynthesis. In: Jennings, R.C., Zucchelli, G., Ghetti, F., Colombetti, G. (eds) Light as an Energy Source and Information Carrier in Plant Physiology. NATO ASI Series, vol 287. Springer, Boston, MA. https://doi.org/10.1007/978-1-4613-0409-8_7

Barber, J., & Andersson, B. (1992). Too much of a good thing: light can be bad for photosynthesis. Trends in Biochemical Sciences, 17(2), 61-66. https://doi.org/10.1016/0968-0004(92)90503-2

Bender, E., Lehning, M., & Fiddes, J. (2020). Changes in Climatology, Snow Cover, and Ground Temperatures at High Alpine Locations. Frontiers in Earth Science, 8. https://doi.org/10.3389/feart.2020.00100

Billings, W.D., & Mooney, H.A. (1968). THE ECOLOGY OF ARCTIC AND ALPINE PLANTS. Biological reviews/Biological reviews of the Cambridge Philosophical Society, 43(4), 481-529. https://doi.org/10.1111/j.1469-185x.1968.tb00968.x

Birks, H.H. (2008). The Late-Quaternary history of arctic and alpine plants. Plant Ecology & Diversity, 1(2), 135-146. https://doi.org/10.1080/17550870802328652

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S.A., Blach-Overgaard, A., Blok, D., Cornelissen, J.H.C., Forbes, B.C., Georges, D., Goetz, S.J., Guay, K.C., Henry, G.H.R., HilleRisLambers, J., Hollister, R.D., Karger, D.N., Kattge, J., Manning, P., Prevéy, J.S., Rixen, C., Schaepman-Strub, G., Thomas, H.J.D., Vellend, M., Wilmking, M., Wipf, S., Carbognani, M., Hermanutz, L., Lévesque, E., Molau, U., Petraglia, A., Soudzilovskaia, N.A., Spasojevic, M.J., Tomaselli, M., Vowles, T., Alatalo, J.M., Alexander, H.D., Anadon-Rosell, A., Angers-Blondin, S., te Beest, M., Berner, L.T., Björk, R.G., Buchwał, A., Buras, A., Christie, K.S., Cooper, E.J., Dullinger, S., Elberling, B., Eskelinen, A., Frei, E.R., Grau, O., Grogan, P., Hallinger, M., Harper, K.A., Heijmans, M., Hudson, J.M., Hülber, K., Iturrate-Garcia, M., Iversen, C.M., Jaroszynska, F., Johnstone, J.F., Jørgensen, R.H., Kaarlejärvi, E., Klady, R.A., Kuleza, S., Kulonen, A., Lamarque, L.J., Lantz, T.C., Little, C.J., Speed, J.D.M., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S.S., Ninot, J.M., Oberbauer, S.F., Olofsson, J., undefined, ., Rumpf, S.B., Semenchuk, P., Shetti, R., Collier, L.S., Street, L.E., Suding, K.N., Tape, K.D., Trant, A.J., Treier, U.A., Tremblay, J., Tremblay, M., Venn, S., Weijers, S., Zamin, T., Boulanger-Lapointe, N., Gould, W.A., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Jorgenson, J.C., Klein, J.A., & Magnússon, B. (2018). Plant functional trait change across a warming tundra biome. Nature, 562(7725), 57-62. https://doi.org/10.1038/s41586-018-0563-7

Boike, J., Nitzbon, J., Anders, K., Grigoriev, M.N., Bolshiyanov, D.Y., Langer, M., Lange, S., Bornemann, N., Morgenstern, A., Schreiber, P., Wille, C., Chadburn, S., Gouttevin, I., & Kutzbach, L. (2019). Soil data at station Samoylov (2002-2018, level 1, version 201908), link to archive. *Figshare*. https://doi.org/10.1594/pangaea.905233

Blaen, P., Hannah, D.M., Brown, L.E., & Milner, A.M. (2013). Water source dynamics of high Arctic river basins. Hydrological Processes, 28(10), 3521-3538. https://doi.org/10.1002/hyp.9891

Broadbent, A.A.D., Newbold, L.K., Pritchard, W.J., Michas, A., Goodall, T., Cordero, I., Giunta, A.D., Snell, H.S.K., Pepper, V.V.L.H., Grant, H., Soto, D.X., Kaufmann, R., Schloter, M., Griffiths, R.I., Bahn, M., & Bardgett, R.D. (2024). Climate change disrupts the seasonal coupling of plant and soil microbial nutrient cycling in an alpine ecosystem. Global Change Biology, 30(3), e17245-e17245. https://doi.org/10.1111/gcb.17245

Chuine, I. (2010). Why does phenology drive species distribution?. Philosophical Transactions of the Royal Society B Biological Sciences, 365(1555), 3149-3160. https://doi.org/10.1098/rstb.2010.0142

Collins, C.G., Elmendorf, S.C., Hollister, R.D., Henry, G.H.R., Clark, K., Bjorkman, A.D., Myers-Smith, I.H., Prevéy, J.S., Ashton, I.W., Assmann, J.J., Alatalo, J.M., Carbognani, M., Chisholm, C., Cooper, E.J., Forrester, C., Jónsdóttir, I.S., Klanderud, K., Kopp, C.W., Livensperger, C., Mauritz, M., May, J.L., Molau, U., Oberbauer, S.F., Ogburn, E.C., Panchen, Z.A., Petraglia, A., Post, E., Rixen, C., Rodenhizer, H., Schuur, E.A.G., Semenchuk, P., Smith, J.G., Steltzer, H., rjan Totland, ., Walker, M.D., Welker, J.M., & Suding, K.N. (2021). Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. Nature Communications, 12(1), 3442-3442. https://doi.org/10.1038/s41467-021-23841-2

D'Amico, M. E., Calabrese, F., & Previtali, F. (2009). Suoli di alta quota ed ecologia del Parco Naturale del Mont Avic (Valle d'Aosta). *Studi Trentini di Scienze Naturali*, 85, 23-37.

Dumont, M., Monteiro, D., Filhol, S., Gascoin, S., Marty, C., Hagenmuller, P., Morin, S., Choler, P., & Thuiller, W. (2025). The European Alps in a changing climate: physical trends and impacts. Comptes Rendus Géoscience, 357(G1), 25-42. https://doi.org/10.5802/crgeos.288

Dussaillant, I., Hugonnet, R., Huss, M., tienne Berthier, ., Bannwart, J., Paul, F., & Zemp, M. (2025). Annual mass change of the world's glaciers from 1976 to 2024 by temporal downscaling of satellite data with in situ observations. Earth system science data, 17(5), 1977-2006. https://doi.org/10.5194/essd-17-1977-2025

Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis, E., Steltzer, H., & Wallenstein, M.D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology, 20(10), 3256-3269. https://doi.org/10.1111/gcb.12568

Ettinger, A.K., Buonaiuto, D.M., Chamberlain, C.J., Morales-Castilla, I., & Wolkovich, E.M. (2021). Spatial and temporal shifts in photoperiod with climate change. New Phytologist, 230(2), 462-474. https://doi.org/10.1111/nph.17172

Garamvölgyi, Á. and Hufnagel, L., (2013). Impacts of climate change on vegetation distribution No. 1: climate change induced vegetation shifts in the palearctic region.

English, Journal article, Hungary, 1785-0037 1589-1623, 11, (1), Budapest, Applied Ecology and Environmental Research,11 (1). pp. 79-122, Landscape Architecture and Decision Support System.

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2013). 21st century climate change in the European Alps—A review. The Science of The Total Environment, Volume 493, 1138-1151. https://doi.org/10.1016/j.scitotenv.2013.07.050

Gottfried, M.D., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, M.A.F., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puşcaş, M., Rossi, G., Stanisci, A., Theurillat, J., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I., & Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. Nature Climate Change, 2(2), 111-115. https://doi.org/10.1038/nclimate1329

Grabherr, G., Gottfried, M. & Pauli, H.(1994). Climate effects on mountain plants. *Nature* 369, 448. https://doi.org/10.1038/369448a0

Grace, J. (2002). Impacts of Climate Change on the Tree Line. Annals of Botany, 90(4), 537-544. https://doi.org/10.1093/aob/mcf222

Healey, N.C., Oberbauer, S.F., & Hollister, R.D. (2016). Examination of Surface Temperature Modification by Open-Top Chambers along Moisture and Latitudinal Gradients in Arctic Alaska Using Thermal Infrared Photography. Remote Sensing, 8(1), 54-54. https://doi.org/10.3390/rs8010054

Hock, R., G. Rasul, C. Adler, B. Cáceres, S. Gruber, Y. Hirabayashi, M. Jackson, A. Kääb, S. Kang, S. Kutuzov, Al. Milner, U. Molau, S. Morin, B. Orlove, and H. Steltzer (2019): High Mountain Areas. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate - H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)-. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 131–202. https://doi.org/10.1017/9781009157964.004

Hollister, R.D., Elphinstone, C., Henry, G.H.R., Bjorkman, A.D., Klanderud, K., Björk, R.G., Björkman, M.P., Bokhorst, S., Carbognani, M., Cooper, E.J., Dorrepaal, E., Elmendorf, S.C., Fetcher, N., Gallois, E., Guðmundsson, J., Healey, N.C., Jónsdóttir, I.S., Klarenberg, I.J., Oberbauer, S.F., Macek, P., May, J.L., Mereghetti, A., Molau, U., Petraglia, A., Rinnan, R., Rixen, C., & Wookey, P.A. (2022). A review of open top chamber (OTC) performance across the ITEX Network. Arctic Science, 9(2), 331-344. https://doi.org/10.1139/as-2022-0030

Huffeldt, N.P. (2020). Photic Barriers to Poleward Range-shifts. Trends in Ecology & Evolution, 35(8), 652-655. https://doi.org/10.1016/j.tree.2020.04.011

Hüsler, F., Jonas, T., Riffler, M., Musiał, J., & Wunderle, S. (2014). A satellite-based snow cover climatology (1985–2011) for the European Alps derived from AVHRR data. The cryosphere, 8(1), 73-90. https://doi.org/10.5194/tc-8-73-2014

IPCC (2021), Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change - Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.) - Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2391 pp. doi:10.1017/9781009157896.

IUCN/SSC (2013). Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.

Jackson, S. (2008). Plant responses to photoperiod. New Phytologist, 181(3), 517-531. https://doi.org/10.1111/j.1469-8137.2008.02681.x

Jacobs, D.F., Salifu, K.F., & Davis, A.S. (2009). Drought susceptibility and recovery of transplanted Quercus rubra seedlings in relation to root system morphology. *Annals of Forest Science*, 66(5), 504-504. https://doi.org/10.1051/forest/2009029

Kawecki, T.J., & Ebert, D. (2004). Conceptual issues in local adaptation. Ecology Letters, 7(12), 1225-1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Keller, F., & Körner, C. (2003). The Role of Photoperiodism in Alpine Plant Development. Arctic Antarctic and Alpine Research, 35(3), 361-368. https://doi.org/10.1657/1523-0430(2003)035[0361:tropia]2.0.co;2

Körner, C. (2007). Climatic treelines: conventions, global patterns, causes. Erdkunde, 61(4), 316-324. https://doi.org/10.3112/erdkunde.2007.04.02

Körner, C. (2015). Paradigm shift in plant growth control. Current Opinion in Plant Biology, 25, 107-114. https://doi.org/10.1016/j.pbi.2015.05.003

Körner, C. (2021). Alpine Plant Life. https://doi.org/10.1007/978-3-642-98018-3

Körner, C., & Basler, D. (2010). Phenology Under Global Warming. Science, 327(5972), 1461-1462. https://doi.org/10.1126/science.1186473

Kudo, G., & Cooper, E.J. (2019). When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B Biological Sciences, 286(1904), 20190573-20190573. https://doi.org/10.1098/rspb.2019.0573

Leech, S., Almuedo, P.L., & O'Neill, G.A. (2011). Assisted Migration: Adapting Forest Management to a Changing Climate. *Journal of Ecosystems and Management*, 12(3). https://doi.org/10.22230/jem.2011v12n3a91

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., & Ackerly, D.D. (2009). The velocity of climate change. Nature, 462(7276), 1052-1055. https://doi.org/10.1038/nature08649

Lucianetti, G., Cianfarra, P., & Mazza, R. (2017). Lineament domain analysis to infer groundwater flow paths: Clues from the Pale di San Martino fractured aquifer, Eastern Italian Alps. *Geosphere*, 13(5), 1729-1746. https://doi.org/10.1130/ges01500.1

Marchi, M., Castellanos-Acuña, D., Hamann, A., Wang, T., Ray, D., & Menzel, A. (2020). ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. Scientific Data, 7(1), 428-428. https://doi.org/10.1038/s41597-020-00763-0

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J.F., Jones, G.A., Jones, M.H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A.N., Svoboda, J., & Virginia, R.A. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology, 3(S1), 20-32. https://doi.org/10.1111/j.1365-2486.1997.gcb136.x

Marty, C., Schlögl, S., Bavay, M., & Lehning, M. (2017). How much can we save? Impact of different emission scenarios on future snow cover in the Alps. The cryosphere, 11(1), 517-529. https://doi.org/10.5194/tc-11-517-2017

Marty, C., & Meister, R. (2012). Long-term snow and weather observations at Weissfluhjoch and its relation to other high-altitude observatories in the Alps. Theoretical and Applied Climatology, 110(4), 573-583. https://doi.org/10.1007/s00704-012-0584-3

Maslanik, J.A., Strœve, J., Fowler, C.W., & Emery, W.J. (2011). Distribution and trends in Arctic sea ice age through spring 2011. Geophysical Research Letters, 38(13), n/a-n/a. https://doi.org/10.1029/2011gl047735

Matiu, M., Crespi, A., Bertoldi, G., Carmagnola, C.M., Marty, C., Morin, S., Schöner, W., Berro, D.C., Chiogna, G., Gregorio, L.D., Kotlarski, S., Majone, B., Resch, G., Terzago, S., Valt, M., Beozzo, W., Cianfarra, P., Gouttevin, I., Marcolini, G., Notarnicola, C., Petitta, M., Scherrer, S.C., Strasser, U., Winkler, M., Zebisch, M., Cicogna, A., Cremonini, R., Debernardi, A., Faletto, M., Gaddo, M., Giovannini, L., Mercalli, L., Soubeyroux, J., Sušnik, A., Trenti, A., Urbani, S., & Weilguni, V. (2021). Observed snow depth trends in the European Alps: 1971 to 2019. The cryosphere, 15(3), 1343-1382. https://doi.org/10.5194/tc-15-1343-2021

Migała, K., Wojtuń, B., Szymański, W., & Muskała, P. (2014). Soil moisture and temperature variation under different types of tundra vegetation during the growing season: A case study from the Fuglebekken catchment, SW Spitsbergen. CATENA, 116, 10-18. https://doi.org/10.1016/j.catena.2013.12.007

Miller-Struttmann, N.E., Miller, Z., & Galen, C. (2022). Climate driven disruption of transitional alpine bumble bee communities. Global Change Biology, 28(21), 6165-6179. https://doi.org/10.1111/gcb.16348

Mountain Research Initiative EDW Working Group. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*(5), 424-430. https://doi.org/10.1038/nclimate2563

Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K., Bjerke, J.W., Epstein, H.E., Assmann, J.J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P.S.A., Berner, L.T., Bhatt, U.S., Bjorkman, A.D., Blok, D., Bryn, A., Christiansen, C.T., Cornelissen, J.H.C., Cunliffe, A.M., Elmendorf, S.C., Forbes, B.C., Goetz, S.J., Hollister, R.D., de Jong, R., Loranty, M.M., Macias-Fauria, M., Maseyk, K., Normand, S., Olofsson, J., Parker, T.C., Parmentier, F.W., Post, E., Schaepman-Strub, G., Stordal, F., Sullivan, P.F., Thomas, H.J.D., Tømmervik, H., Treharne, R., Tweedie, C.E., Walker, D.A., Wilmking, M., & Wipf, S. (2020). Complexity revealed in the greening of the Arctic. Nature Climate Change, 10(2), 106-117. https://doi.org/10.1038/s41558-019-0688-1

National Snow and Ice Data Center. (2024). *Arctic sea ice continues to be young and thin – loss of multiyear ice.* https://nsidc.org/sea-ice-today/analyses/new-abnormal

Nisbet, Renato & Varese, Paolo & Pascal, Roberto. (2000). Esperienze di didattica ambientale al Giardino Botanico Alpino "Bruno Peyronel", Col Barant (Bobbio Pellice, TO). Associazione Botanica Alpi Cozie, CP 3

NOAA-National Oceanic and Atmospheric Administration. (2025). *Arctic Report Card: 2025*. https://arctic.noaa.gov/report-card/report-card-2025

Noetzli, J., Isaksen, K., Barnett, J., Christiansen, H.H., Delaloye, R., Etzelmüller, B., Farinotti, D., Gallemann, T., Guglielmin, M., Hauck, C., Hilbich, C., Hoelzle, M., Lambiel, C., Magnin, F., Oliva, M., Paro, L., Pogliotti, P., Riedl, C., Schoeneich, P., Valt, M., Vieli, A., & Phillips, M. (2024). Enhanced warming of European mountain permafrost in the early 21st century. Nature Communications, 15(1), 10508-10508. https://doi.org/10.1038/s41467-024-54831-9

Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., Dawes, M.A., Fosaa, A.M., Henry, G.H.R., Høye, T.T., Jarrad, F., Jónsdóttir, I.S., Klanderud, K., Klein, J.A., Molau, U., Rixen, C., Schmidt, N.M., Shaver, G.R., Slider, R.T., Totland, ., Wahren, C.H., & Welker, J.M. (2013). Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Philosophical Transactions of the Royal Society B Biological Sciences, 368(1624), 20120481-20120481. https://doi.org/10.1098/rstb.2012.0481

Olsen, J.E., Junttila, O., & Möritz, T. (1997). Long-Day Induced Bud Break in Salix pentandra Is Associated with Transiently Elevated Levels of GA1 and Gradual

Increase in Indole-3-Acetic Acid. Plant and Cell Physiology, 38(5), 536-540. https://doi.org/10.1093/oxfordjournals.pcp.a029202

Orsenigo, S., Mondoni, A., Rossi, G., & Abeli, T. (2014). Some like it hot and some like it cold, but not too much: plant responses to climate extremes. Plant Ecology, 215(7), 677-688.

Panchen, Z.A., & Gorelick, R. (2017). Prediction of Arctic plant phenological sensitivity to climate change from historical records. Ecology and Evolution, 7(5), 1325-1338. https://doi.org/10.1002/ece3.2702

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology Evolution and Systematics, 37(1), 637-669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pascal R., Varese P. (1997). Le fitocenosi presenti nell'ambito del Giardino Botanico Alpino "Bruno Peyronel" (Alta Val Pellice – Alpi Cozie). Actes Deuxième Colloque Ecologie et Biogéographie Alpines, La Thuile, 6-11 septembre 1997, suppl. Revue Valdôtaine d'Histoire Naturelle, n. 51: 233-238.

Pauli, H., Gottfried, M.D., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., Ghosn, D., Holten, J.I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., Mesa, J.M., Nagy, L., Pelino, G., Puşcaş, M., Rossi, G., Stanisci, A., Syverhuset, A.O., Theurillat, J., Tomaselli, M., Unterluggauer, P., Villar, L., Vittoz, P., & Grabherr, G. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. Science, 336(6079), 353-355. https://doi.org/10.1126/science.1219033

Paulsen, J., & Körner, C. (2014). A climate-based model to predict potential treeline position around the globe. Alpine Botany, 124(1), 1-12. https://doi.org/10.1007/s00035-014-0124-0

Pawlikowski, T., Sparks, T.H., Olszewski, P., Pawlikowski, K., Rutkowski, L., & Jakubowski, R. (2020). Rising temperatures advance the main flight period of Bombus bumblebees in agricultural landscapes of the Central European Plain. Apidologie, 51(4), 652-663. https://doi.org/10.1007/s13592-020-00750-9

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J.M., Wookey, P.A., Schmidt, N.M., & Aastrup, P. (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate Change. Science, 325(5946), 1355-1358. https://doi.org/10.1126/science.1173113

Prevéy, J.S., Vellend, M., Rüger, N., Hollister, R.D., Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Clark, K., Cooper, E.J., Elberling, B., Fosaa, A.M., Henry, G.H.R., Høye, T.T., Jónsdóttir, I.S., Klanderud, K., Lévesque, E., Mauritz, M., Molau, U., Natali, S.M., Oberbauer, S.F., Panchen, Z.A., Post, E., Rumpf, S.B., Schmidt, N.M., Schuur, E.A.G., Semenchuk, P., Troxler, T.G., Welker, J.M., & Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. Global Change Biology, 23(7), 2660-2671. https://doi.org/10.1111/gcb.13619

Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth & Environment, 3(1). https://doi.org/10.1038/s43247-022-00498-3

Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka, D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F., Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R.B., Rosche, C., Shah, M.A., Sporbert, M., Stevens, A., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg, M., Knickmann, B., Nordt, B., Wirth, C., & Römermann, C. (2024). Spatial variability in herbaceous plant phenology is mostly explained by variability in temperature but also by photoperiod and functional traits. International Journal of Biometeorology, 68(4), 761-775. https://doi.org/10.1007/s00484-024-02621-9

Rogora, M., Frate, L., Carranza, M.L., Freppaz, M., Stanisci, A., Bertani, I., Bottarin, R., Brambilla, A., Canullo, R., Carbognani, M., Cerrato, C., Chelli, S., Cremonese, E., Cutini, M., Di Musciano, M., Erschbamer, B., Godone, D., Iocchi, M., Isabellon, M., Magnani, A., Mazzola, L., di Cella, U.M., Pauli, H., Petey, M., Petriccione, B., Porro, F., Psenner, R., Rossetti, G., Scotti, A., Sommaruga, R., Tappeiner, U., Theurillat, J.P., Tomaselli, M., Viglietti, D., Viterbi, R., Vittoz, P., Winkler, M., & Matteucci, G. (2019). Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. arXiv (Cornell University). https://doi.org/10.48550/arxiv.1910.13501

Rumpf, S.B., Gravey, M., Brönnimann, O., Luoto, M., Cianfrani, C., Mariethoz, G., & Guisan, A. (2022). From white to green: Snow cover loss and increased vegetation productivity in the European Alps. Science, 376(6597), 1119-1122. https://doi.org/10.1126/science.abn6697

Ruttink, T., Arend, M., Morreel, K., Storme, V., Rombauts, S., Fromm, J., Bhalerao, R.P., Boerjan, W., & Rohde, A. (2007). A Molecular Timetable for Apical Bud Formation and Dormancy Induction in Poplar. The Plant Cell, 19(8), 2370-2390. https://doi.org/10.1105/tpc.107.052811

Schaber, J., & Badeck, F. (2003). Physiology-based phenology models for forest tree species in Germany. International Journal of Biometeorology, 47(4), 193-201. https://doi.org/10.1007/s00484-003-0171-5

Shibaeva, T.G., Sherudilo, E.G., Rubaeva, A.A., Shmakova, N.Y., Titov, A.F. (2024). Response of Native and Non-Native Subarctic Plant Species to Continuous Illumination by Natural and Artificial Light. *Plants*, 13(19), 2742-2742. https://doi.org/10.3390/plants13192742

Schlichting C D. (1986). THE EVOLUTION OF PHENOTYPIC PLASTICITY IN PLANTS. *Annual Review Ecology, Evolution, and Systematics*. 17:667-693. https://doi.org/10.1146/annurev.es.17.110186.003315

Serreze, M.C., & Barry, R.G. (2011). Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change, 77(1-2), 85-96. https://doi.org/10.1016/j.gloplacha.2011.03.004

Settele, J., Bishop, J., & Potts, S.G. (2016). Climate change impacts on pollination. *Nature Plants*, 2(7), 16092-16092. https://doi.org/10.1038/nplants.2016.92

Singh, M.P., & Más, P. (2018). A Functional Connection between the Circadian Clock and Hormonal Timing in Arabidopsis. Genes, 9(12), 567-567. https://doi.org/10.3390/genes9120567

Strimbeck, G.R., Graae, B.J., Lang, S.I., & Sørensen, M.V. (2019). Functional group contributions to carbon fluxes in arctic-alpine ecosystems. Arctic Antarctic and Alpine Research, 51(1), 58-68. https://doi.org/10.1080/15230430.2019.1578163

Stucchi, L., Dresti, C., & Bocchiola, D. (2023). Centenary (1930–2023) climate, and snow cover changes in the Western Alps of Italy. The Ossola valley. Climatic Change, 176(6). https://doi.org/10.1007/s10584-023-03548-7

Sturm, M., Schimel, J., Michaelson, G.J., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnestock, J.T., & Romanovsky, V.E. (2005). Winter Biological Processes Could Help Convert Arctic Tundra to Shrubland. BioScience, 55(1), 17-17. https://doi.org/10.1641/0006-3568(2005)055[0017:wbpchc]2.0.co;2

Tamstorf, M.P., Illeris, L., Hansen, B.U., & Wisz, M.S. (2007). Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in high arctic Greenland. BMC Ecology, 7(1), 9-9. https://doi.org/10.1186/1472-6785-7-9

Tarascio, M., Brancaleoni, L., Cazzavillan, A., Cutini, M., Gerdol, R., & Abeli, T. (2025). Photoperiod–Temperature Interactions in a Changing Climate: A Review of Plant Phenological Responses. Journal of Biogeography, 53(1). https://doi.org/10.1111/jbi.70113

Theurillat, J. P., & Guisan, A. (2001). Potential impact of climate change on vegetation in the European Alps: a review. Climatic change, 50(1), 77-109. https://doi.org/10.1023/A:1010632015572

Thomas, B., & Vince-Prue, D. (1975). "Photoperiodic Control of Flower Initiation: Some General Principles." In Photoperiodism in plants, 3–28. Elsevier.

Tomiolo, S., & Ward, D. (2018). Species migrations and range shifts: A synthesis of causes and consequences. Perspectives in Plant Ecology, Evolution and Systematics, 33, 62-77. https://doi.org/10.1016/j.ppees.2018.06.001

Tougeron, K. (2021). How Constraining are Photic Barriers to Poleward Range-Shifts?. *Trends in Ecology & Evolution*, 36(6), 478-479. https://doi.org/10.1016/j.tree.2021.02.008

Vélez-Ramírez, A.I., van Ieperen, W., Vreugdenhil, D., & Millenaar, F.F. (2011). Plants under continuous light. Trends in Plant Science, 16(6), 310-318. https://doi.org/10.1016/j.tplants.2011.02.003

Wadgymar, S.M., Ogilvie, J.E., Inouye, D.W., Weis, A.E., & Anderson, J.T. (2018). Phenological responses to multiple environmental drivers under climate change:

insights from a long-term observational study and a manipulative field experiment. New Phytologist, 218(2), 517-529. https://doi.org/10.1111/nph.15029

Walker, M.D., Walker, D.A., Welker, J.M., Arft, A.M., Bardsley, T., Brooks, P.D., Fahnestock, J.T., Jones, M.H., Losleben, M., Parsons, A.N., Seastedt, T.R. and Turner, P.L. (1999), Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Process., 13: 2315-2330. https://doi.org/10.1002/(SICI)1099-1085(199910)13:14/15<2315::AID-HYP888>3.0.CO;2-A

Winkler, D.E., Lubetkin, K.C., Carrell, A.A., Jabis, M.D., Yang, Y., & Kueppers, L.M. (2019). Responses of alpine plant communities to climate warming. Elsevier eBooks, 297-346. https://doi.org/10.1016/b978-0-12-813493-1.00013-2

Wojcik, R., Palmtag, J., Hugelius, G., Weiss, N., & Kuhry, P. (2019). Land cover and landform-based upscaling of soil organic carbon stocks on the Brøgger Peninsula, Svalbard. Arctic Antarctic and Alpine Research, 51(1), 40-57. https://doi.org/10.1080/15230430.2019.1570784

Zeng, K., Sentinella, A.T., Armitage, C., & Moles, A.T. (2024). Species that require long-day conditions to flower are not advancing their flowering phenology as fast as species without photoperiod requirements. Annals of Botany, 135(1-2), 113-124. https://doi.org/10.1093/aob/mcae121

Zohner, C.M., & Renner, S.S. (2014). Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecology Letters, 17(8), 1016-1025. https://doi.org/10.1111/ele.12308

Zohner, C.M., Benito, B.M., Svenning, J., & Renner, S.S. (2016). Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. Nature Climate Change, 6(12), 1120-1123. https://doi.org/10.1038/nclimate3138

WEBSITE

Giardino Botanico Alpino "Bruno Peyronel". *Sito ufficiale*. URL: https://www.giardinopeyronel.it/ (Consultato il: 2026).

REGULATORY REFERENCES

Ministero dell'Ambiente e della Tutela del Territorio e del Mare. *Designazione di 21 zone speciali di conservazione (ZSC) della regione biogeografica alpina insistenti nel territorio della Regione Piemonte*. Decreto Ministeriale 27 luglio 2016. In "Gazzetta Ufficiale della Repubblica Italiana" - Serie Generale n. 193 del 19 agosto 2016.

Regione Piemonte. *L.r. 19/2009 "Testo unico sulla tutela delle aree naturali e della biodiversità". Art. 40 Misure di Conservazione sito-specifiche per la tutela di alcuni siti della Rete Natura 2000 del Piemonte. Approvazione secondo gruppo di misure*. Deliberazione della Giunta Regionale n. 19-3112 del 4 aprile 2016. In "Bollettino Ufficiale della Regione Piemonte".