



**UNIVERSITY  
OF TURKU**

# **The impact of population origin on the survival and performance of Antarctic hairgrass *Deschampsia antarctica*: a comparison between two latitudes**

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Ecology and Evolutionary Biology

Master's thesis

Credits: 30 ECTS

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5.12.2023

Turku

The originality of this thesis has been checked in accordance with the University of Turku quality assurance system using the Turnitin Originality Check service.

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**Number of pages:** 46 pages, 3 appendices

**Date:** 5.12.2023

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The Antarctic climate is warming at an accelerating rate, driving the retreat of continental ice sheets in Antarctica. This decline in glacial formations relaxes dispersal barriers and allows the distribution ranges of terrestrial plant species to spread further inland and toward higher latitudes. At higher latitudes, species must adapt to the more extreme seasonal variation in day length. Thus, an extreme light environment may function as a bottleneck for the successful establishment of species in these areas.

In this thesis, I studied the adaptability of Antarctic hairgrass, *Deschampsia antarctica*, in response to two latitudes characterized by differences in the seasonal variability of day length and temperature. I conducted a common garden experiment at two sites in Finland: Ruissalo, Turku (60°26'N) and Kevo, Utsjoki (69°45'N). These sites represent the current and future day-length conditions experienced by *D. antarctica* as the species disperses to higher latitudes. The study design consisted of plants collected from populations of two origins: southern Patagonia and coastal Antarctica. Despite fewer Antarctic replicates, it was possible to compare differences in the performance of plants from two genetic backgrounds in response to two latitudinal environments. To analyze these differences, I recorded plant growth and fitness-correlated traits over two consecutive growing seasons in 2022 and 2023.

The results of this study demonstrate that *D. antarctica* is not restricted by the light environment in establishing and regulating its reproductive timing at higher latitudes. I found evidence of divergent adaptation between the two plant origins and latitudes in the initial growth following transplantation. This supports my hypothesis that genetic background affects the plants' acclimatization to different light environments. Furthermore, the two sites and plant origins diverged significantly in survival and flowering rates. These results support previous studies of genetic distinctiveness between *D. antarctica* populations. In general, plants performed better in Kevo compared to Ruissalo, likely due to a lower amplitude of temperature variation and a more consistent snow cover during the winter season. Regardless of the site, plants of Antarctic origin had a lower survival rate but flowered more readily than Patagonian plants. This suggests a divergent allocation of resources to sexual reproduction and vegetative growth between the two origins.

Although the low number of Antarctic replicates limits these comparisons, my results highlight the importance of genetic background in predicting the future dynamics of *D. antarctica*. Photoperiodism together with other selection pressures is likely to affect the genetic structure of *D. antarctica* populations, as the species disperses toward higher latitudes. Further research is needed to identify specific responses to different light environments, especially regarding the species' flowering phenology and resource allocations between vegetative and generative growth.

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**Key words:** Antarctic hairgrass, Antarctica, Patagonia, climate change, distribution range, photoperiodism.

## Pro gradu -tutkielma

**Pääaine:** Ekologia ja evoluutiobiologia

**Tekijä:** Emilia Mäkinen

**Otsikko:** Populaation alkuperän vaikutus antarktiksenuhan (*Deschampsia antarctica*) elossasäilyvyyteen ja menestykseen: vertailu kahden latitudin välillä

**Ohjaajat:** Kari Saikkonen, Benjamin Fuchs

**Sivumäärä:** 46 sivua, 3 liitettä

**Päivämäärä:** 5.12.2023

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Antarktinen ilmasto lämpenee kiihtyvällä tahdilla, voimistaen mannerjäätiköiden perääntymistä Etelämantereella. Näiden massiivisten jäätiköiden vetäytyminen vähentää jään muodostamia leviämiseiteitä, mahdollistaen terrestristen kasvilajien levittäytymisen syvemmälle sisämaahan ja kohti korkeampia latituteja. Korkeammilla latituteilla lajin tulee kuitenkin sopeutua huomattavasti rajumpaan päivän pituuden kausittaisvaihteluun. Tällöin valoilmasto voi toimia pullonkaulana lajeille, jotka onnistuvat asettumaan perääntyvän jään paljastamille maa-alueille.

Tässä tutkielmassa tarkastelin antarktiksenuhan (*Deschampsia antarctica*) adaptiivisuutta kahteen eri latitudiin, jotka eroavat toisistaan päivän pituuden ja lämpötilan vuodenaikaisvaihtelun suhteen. Suoritin common garden -tyyppisen kokeen kahdella koealalla, joista toinen sijaitsi Ruissalossa (Turku, 60°26'N) ja toinen Kevolla (Utsjoki, 69°45'N). Nämä koealat edustavat antarktiksenuhan nykyistä ja tulevaa valo-olosuhteiden kausittaisvaihtelua lajin levittäytyessä korkeammille latituteille. Koeasetelma koostui kasveista, jotka oli kerätty kahdesta eri alkuperästä: Chilen Patagoniasta ja Etelämantereen rannikolta. Etelämantereelta tuotujen kasvien alhaisemmasta replikaattimäärästä huolimatta tämä koeasetelma mahdollisti kasvumenestyksen vertailun eri alkuperien välillä kahdella eri latitudilla. Eroja tutkiakseni mittasin kasvien kelpoisuus- sekä kasvuominaisuuksia kahtena peräkkäisenä kasvukautena vuosina 2022 ja 2023.

Tämän tutkimuksen tulokset osoittavat, että valoilmasto ei rajoita antarktiksenuhaa sen levittäytyessä ja ajoittaessa lisääntymistään korkeammilla latituteilla. Erot ensimmäisen kasvukauden vegetatiivisessa kasvussa viittasivat eriyvään adaptaatioon eri alkuperien ja koealojen välillä. Tämä tulos tukee hypoteesiani geneettisen taustan vaikutuksesta antarktiksenuhan sopeutumiseen eri valoilmastoihin. Koealat ja alkuperät erosivat toisistaan merkitsevästi sekä elossasäilyvyyden että kukinnan suhteen. Nämä tulokset ovat linjassa aikaisempien tutkimusten kanssa, joissa on havaittu antarktiksenuhan populaatioiden olevan geneettisesti eriytyneitä. Kasvit menestyivät paremmin Kevolla kuin Ruissalossa, todennäköisesti johtuen Kevon pienemmästä lämpötilavaihtelusta ja pysyvämmästä lumipeitteestä. Koealasta riippumatta Etelämantereelta tuotujen kasvien elossasäilyvyys oli alhaisempi ja kukkivuus korkeampi kuin Patagoniasta tuotujen kasvien. Erot alkuperien kukinnassa viittaavat mahdollisesti resurssien erilaiseen allokoimiseen seksuaalisen lisääntymisen ja vegetatiivisen kasvun välillä.

Vaikka Etelämantereelta tuotujen kasvien pienempi replikaattimäärä rajoittaa vertailuja, nämä tulokset korostavat geneettisen taustan tärkeyttä antarktiksenuhan tulevaisuutta mallinnettaessa. Fotoperiodismi yhdessä muiden valintapaineiden kanssa tulee todennäköisesti vaikuttamaan antarktiksenuhan populaatioiden geneettiseen rakenteeseen lajin levittäytyessä korkeammille latituteille. Lisää tutkimusta kuitenkin tarvitaan koskien antarktiksenuhan adaptiivisia responsseja erilaisiin valoilmastoihin, erityisesti suhteessa kukinnan fenologiaan sekä resurssien allokaatioon vegetatiivisen ja generatiivisen lisääntymisen välillä.

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**Avainsanat:** antarktiksenuha, Etelämanter, Patagonia, ilmastomuutos, levinneisyysalue, fotoperiodismi.

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# 1 Introduction

## 1.1 Changing climate in the Antarctic

Human-mediated climate change is the most prominent threat to ecosystems around the world. Globally, the dynamics of ecological communities are forced to change, as the distribution ranges of many species shift toward higher latitudes (Pecl *et al.*, 2017). This effect is especially strong in the polar regions, with Arctic climates warming nearly four times more rapidly than the global average (Rantanen *et al.*, 2022). An accelerating trend has also been recorded in the Antarctic, specifically in the fall and winter months of the western Antarctic Peninsula region (Vaughan *et al.*, 2003; Bozkurt *et al.*, 2021). In the Antarctic, this warming drives the accelerating retreat of massive continental ice sheets. The West Antarctic ice sheet may have already reached a critical tipping point, leading to further amplification of the retreat and irreversible damage to the functionality of the ecosystem (Armstrong McKay *et al.*, 2022). While the retreat of these major glacial formations poses a considerable threat to many ice-dependent species, it also provides opportunities for adaptive radiation and primary succession in the newly exposed terrestrial areas (Favero-Longo *et al.*, 2012; Lee *et al.*, 2017).

The climate of Antarctica is generally characterized by extremely low temperatures that even in the northern maritime regions rise only slightly above freezing (Weather, 2015). Ground-level winds blow in harsh gusts, regularly reaching levels of moderate to high speeds. The annual precipitation over the continent is minimal, but highest on the coastline where the amount of annual precipitation is around 350-500 mm (Green, Schroeter and Sancho, 1999). While precipitation is usually received in the form of snow in the interior parts of Antarctica, some is received as rain during the summers of the maritime climate region. These coastal areas are also characterized by milder temperatures relative to the inland, with mean summer temperatures reaching slightly above freezing and mean winter temperatures rarely dropping below -10°C (Green, Schroeter and Sancho, 1999). Although long-term temperature monitoring has shown southern Antarctica to experience varying changes in mean temperature, rapid warming has been recorded in the Antarctic Peninsula region for the last 60 years (Turner *et al.*, 2005; Bromwich *et al.*, 2013). Still, Antarctica can currently be classified as a cold semidesert (Green, Schroeter and Sancho, 1999).

As continental ice sheets diminish, the positive feedback loop caused by lower albedo will amplify both climate warming and further retreat of the glacial formations (Frezzotti and Orombelli, 2014). While only 1% of Antarctica's surface area is currently ice-free, models predict an increase of nearly 25% in the land area of the Antarctic Peninsula region by the end

of the century (Lee *et al.*, 2017). As shown in a study conducted by Lee *et al.* (2017), the dynamics of glacial retreat have been somewhat irregular, with the foreground moving in small patches of ice-free land area. However, as climate warming progresses these patches are expected to coalesce, forming a more unified front of retreat (Lee *et al.*, 2017).

In the Antarctic, vegetation is forced to adapt to an extremely harsh environment and a chronically cold climate. As a result of this, the vegetation of Antarctica consists mainly of stress-tolerant bryophyte and lichen species. Only two vascular plant species are found native to the continent: *Deschampsia antarctica* and *Colobanthus quitensis* (Chown *et al.*, 2015). The Antarctic hairgrass, *D. antarctica*, is a hardy grass species distributed roughly between 50°S and 69°S in southern Patagonia and the maritime regions of Antarctica. The abiotic conditions of the Antarctic are limiting for any plant species, but *D. antarctica* shows remarkable extremophilic adaptations to such an environment (Alberdi *et al.*, 2002; Robinson *et al.*, 2018). As only 1% of Antarctica's surface area is currently ice-free, the distribution of vegetation is strongly limited by habitat availability and accessibility to water (Chown *et al.*, 2015; Lee *et al.*, 2017). In general, the habitats available for plants range from cold deserts to mountain ranges, with terrestrial flora often growing within relatively isolated islands surrounded by ice (Convey and Peck, 2019). Thus, the growth and survival of plants in the Antarctic are limited by factors that determine soil quality and microclimate, such as soil microbiology, ground-level wind speed, and moisture availability (Beyer, Bölter and Seppelt, 2000).

## 1.2 Variation in light environment over a latitudinal gradient

As climate warming induces the retreat of Antarctica's continental ice sheets, dispersal barriers formed by the ice are relaxed (Lee *et al.*, 2017). While plant dispersal is strongly inhibited by ice, the melting of major glacial formations allows the expansion of distribution ranges further inland (Favero-Longo *et al.*, 2012; Lee *et al.*, 2017). However, as species disperse toward greater latitudes at the forefront of retreating ice sheets, they will experience a gradient of continuously more extreme seasonal light conditions. The light environment of polar regions is characterized by polar day, a period of continuous daylight, and polar night, a period of no sunrise and very limited solar radiation. In the Northern regions of the Antarctic Peninsula, day length varies from 21 h in the summer to 3 h in the winter (Alberdi *et al.*, 2002). For photosynthesizing organisms, it's essential to follow photoperiodic signals to appropriately time phenological functions (Körner and Basler, 2010). Thus, the vegetation of polar regions must adapt to a strong seasonal variation in day length, an extremely short growing season, as well as the unique phenomena of polar night and day. Previous approaches have largely ignored

the effect of day length and light intensity on species' biogeographical adaptations in the context of climate change (Saikkonen *et al.*, 2012).

Compared to factors such as temperature or precipitation, the seasonal variation in day length, light intensity, and spectral composition remains relatively stable (Nelson, Denlinger and Somers, 2009). Changes in the characteristics of solar radiation are governed by cycles in the tilt of the Earth's axis, the direction of the axis tilt, and the ellipticity of the Earth's solar orbit (Nelson, Denlinger and Somers, 2009). Therefore, it has been hypothesized that the extreme light environment of high latitudes could function as an ecological bottleneck for the dispersal success of plants (Saikkonen *et al.*, 2012). Although the simultaneous effect of temperature and other environmental cues on plant dispersal is significant, the constraints of the light environment are yet little studied and often excluded from models projecting range shifts.

In the case of *D. antarctica*, studies have shown the overall genetic diversity of the species to be relatively low (Androsiuk *et al.*, 2021). However, individual populations are both genetically and morphologically distinctive, even when separated by small distances (Fasanella *et al.*, 2017; Parnikoza *et al.*, 2018; Androsiuk *et al.*, 2021). Such distinctness is theorized to result from the species' colonization history, which has likely been aided by seabirds (Fasanella *et al.*, 2017). As birds spread plants scarcely across the geographically extensive Antarctica, the plants established small, locally propagating, and self-fertilizing populations. These populations were likely reproductively isolated and strongly affected by founder effects (Fasanella *et al.*, 2017). Currently, populations of *D. antarctica* are observed to be well-adapted to the specific microclimatic factors of their surroundings. As a result of the unique genetic backgrounds of populations, *D. antarctica* communities may exhibit significant differences in their photoperiodic adaptability (Holderegger *et al.*, 2003; Androsiuk *et al.*, 2021).

### 1.3 Competition with an introduced species

Climate change induces changes in the dynamics of ecological communities, driving the distribution ranges of *D. antarctica* and many other species to shift toward higher latitudes (Favero-Longo *et al.*, 2012; Lee *et al.*, 2017; Pecl *et al.*, 2017). Thus, species that have been previously isolated may come into contact, potentially leading to increased levels of interspecific competition (Norberg *et al.*, 2012). Currently, the only non-native plant species reported in Antarctica is *Poa annua*, a cosmopolitan grass species introduced to the continent through human mediation (Olech and Chwedorzewska, 2011). Since its original introduction, *P. annua* has escaped anthropogenic sites to natural conditions (Galera *et al.*, 2017). Despite



excessive eradication efforts, the species persists in the seed bank of the Antarctic Peninsula region (Chwedorzewska *et al.*, 2015).

Studies have shown *P. annua* to possess greater competitiveness and the ability to dominate over *D. antarctica* in common garden conditions (Molina-Montenegro *et al.*, 2012, 2016, 2019). Thus, the alien species poses a considerable threat to native plant communities in the Antarctic. Moreover, *P. annua* is characterized by high adaptability to unstable and varying environmental conditions (Chwedorzewska *et al.*, 2015). However, beyond observations on increased epigenetic changes in its genome, little is known about the species' adaptive responses to the more extreme light environment of latitudes greater than its current distribution (Chwedorzewska *et al.*, 2015). As *D. antarctica* has already had to acclimatize to the harsh climate of the Antarctic throughout its evolutionary history, the competing species may reach a latitudinal threshold where their adaptive advantages are reversed (Barnes *et al.*, 2006; Mosyakin, Bezusko and Mosyakin, 2007; Fasanella *et al.*, 2017).

#### 1.4 Potential hybridization as a result of range shifts

The shorter growing season of higher latitudes can force the timing of reproductive cycles to overlap (Nelson, Denlinger and Somers, 2009). In polar regions, where the growing season is extremely short, the flowering times of plants are restricted to a particularly narrow window of time. This reduction in temporal reproductive isolation could potentially lead to an increase in interspecific hybridization between related species. Genomic studies suggest that such hybridization events may have played a major role in the evolution of *D. antarctica* during interglacial periods (González *et al.*, 2016). However, present-day Antarctica is isolated and relatively inaccessible from other continents by long distances of strong ocean currents (Barnes *et al.*, 2006). Thus, the natural colonization of alien plants to the continent is rare. The prevailing geographic isolation is also demonstrated by the generally low genomic variability of Antarctica's plant biota (Androsiuk *et al.*, 2021). Anthropogenic activity has increased the risk of alien plant introduction to Antarctica, particularly by grasses of the Poaceae family (Olech and Chwedorzewska, 2011; Colesie *et al.*, 2023). Although warming may increase the chance of successful plant introduction, interspecific hybridization is unlikely to occur under the current climate conditions of Antarctica.

On the other hand, the rate of intraspecific hybridization would be expected to increase with the warming of the Antarctic climate (Lee *et al.*, 2017). Generally, populations of *D. antarctica* have been found to be genetically distinct and reproductively isolated (Chown *et al.*, 2015;

Convey and Peck, 2019; Androsiuk *et al.*, 2021). *D. antarctica* spreads mostly via asexual propagation, which may have aided the persistence of the species in a patchy environment (Gielwanowska and Kellmann–Sopyła, 2015). However, the relaxation of dispersal barriers via climate warming increases the connectivity between previously isolated populations, potentially strengthening the role of sexual reproduction (Best *et al.*, 2007; Lee *et al.*, 2017). Thus, cross-breeding and hybridization events between populations are expected to occur more frequently, especially at high latitudes where the time window for flowering is particularly narrow (Best *et al.*, 2007; Nelson, Denlinger and Somers, 2009; Lee *et al.*, 2017; Chan, Hoffmann and van Oppen, 2019). The increase in connectivity and change in population dynamics would affect the gene composition of locally adapted and inbreeding populations (Fasanella *et al.*, 2017; Androsiuk *et al.*, 2021). An increase in genetic material would likely be advantageous for communities in their dispersal toward higher latitudes, as thriving in these conditions requires adaptive adjustments via photoperiodism and phenology (Alberdi *et al.*, 2002; Robinson *et al.*, 2018). The shift in gene exchange across populations of *D. antarctica* could also increase its competitiveness against alien species, such as *P. annua* (Leger and Espeland, 2010; Rius and Darling, 2014).

The ecological dynamics of *D. antarctica* are expected to change substantially, as population connectivity and gene flow between distinct communities increases (Chown *et al.*, 2015; Lee *et al.*, 2017). Through changes in the Antarctic climate, a shift in the species' ecophysiology may also affect population dynamics. Under current climate conditions, the photosynthetic rate of *D. antarctica* is often limited by below-optimal temperatures (Xiong, Ruhland and Day, 1999). However, as the Antarctic climate is predicted to warm rapidly, temperatures could occasionally reach supraoptimal levels ( $>20^{\circ}\text{C}$ ) (Xiong, Ruhland and Day, 1999). At these temperatures, the rate of photosynthesis is reduced, most likely due to increased cell respiration or structural breakdown on a molecular level (Xiong, Ruhland and Day, 1999). However, reaching such supraoptimal temperatures is still very rare in the Antarctic Peninsula region. In comparison, temperatures in the optimal range lead to notable increases in the photosynthetic rates of *D. antarctica*. Such increases in metabolism may partly explain the growth in the species' abundance recorded over the past decades (Smith, 1994; Day *et al.*, 1999; Xiong, Ruhland and Day, 1999). A continuous increase in abundance together with relaxed dispersal barriers is likely to further facilitate the population connectivity of *D. antarctica*.

## 1.5 Aims of the thesis

In this thesis, I study how latitude characterized by differences in light environment and temperature affects the performance and survival of the Antarctic hairgrass, *Deschampsia antarctica*. To investigate this, I conducted an experiment over two consecutive growing seasons in two corresponding common garden settings, one in Ruissalo, Turku (60°26'N) and the second in Kevo, Utsjoki (69°45'N). The chosen locations represent the current and predicted day-length conditions experienced by *D. antarctica*, as the species disperses toward higher latitudes in the Antarctic. To capture the intraspecific variation of *D. antarctica*, I used genotypes collected from several populations of two geographic origins: Chilean Patagonia and coastal Antarctica. By comparing survival, flowering, and growth at the two sites, I can assess differences in establishment and performance between plants of different origins. The results of this study can be used to predict the adaptive abilities of *D. antarctica* in future settings.

I predict plants of both origins to diverge in their performance between the two experimental sites. Furthermore, I expect plants originating from Antarctica to be better adapted to more extreme polar day and night cycles. Plants collected from coastal Antarctica have already acclimatized to higher seasonal variation in day length compared to plants from Chilean Patagonia. Thus, I predict the phenological rhythm of plants from Antarctica to be better adapted to the subarctic climate of Kevo. In contrast, I expect plants of Patagonian origin to establish and perform better in Turku, where the latitudinal day-length conditions resemble southern Patagonia more closely.

## 2 Materials and methods

### 2.1 *Deschampsia antarctica*

*Deschampsia antarctica* E. Desv., the Antarctic hairgrass, is a monocot species in the Poaceae family. *D. antarctica* is currently found between latitudes of 50°S and 69°S in the ice-free maritime regions of Antarctica, the South Shetland Islands, and southern parts of Chile and Argentina. So far, the southernmost recording of *D. antarctica* has been made on Alexander Island at a latitude of 69°22'S (Green, Schroeter and Sancho, 1999; Wali, Evrendilek and Fennessy, 2009, p. 21; Androsiuk *et al.*, 2021). The species is especially significant to its local communities as it's one of only two vascular plant species found native in the Antarctic. With its relatively fast growth rate and ability to withstand unfavorable conditions, *D. antarctica* makes an excellent candidate for transplant experiments.

*D. antarctica* is a low-growing grass that can form dense cushion-like stands (*Deschampsia antarctica* É.Desv. | *Plants of the World Online* | Kew Science, 2022). Its leaf-blades are 10–30 cm long, filiform, and usually smooth-surfaced. Like most grasses, *D. antarctica* photosynthesizes via the C3 pathway. The sexual reproduction of these plants usually occurs by wind pollination with unassuming bisexual panicles, the inflorescences reaching heights of 5–20 cm. In addition to this, the species can spread vegetatively by tiller growth, as large enough tiller nodes are capable of surviving independently from the mother plant (Moore and Moser, 1995; Gurevitch, Scheiner and Fox, 2021, pp. 95–96). *D. antarctica* is also known to express cleistogamy, i.e. self-fertilization within closed flowers, which may have aided in its adaptation to specific microclimates (Yudakova *et al.*, 2016). The reproductive timing of *D. antarctica* is restricted to the austral summer season, which in optimal weather conditions lasts from November to March (Gielwanowska and Kellmann–Sopyła, 2015). While the plants flower nearly every year, the production of fruit is more variable and erratic (Convey, 1996). Additionally, the flowering process may sometimes be postponed by retaining late flowers to the next growing season (Gielwanowska and Kellmann–Sopyła, 2015).

*D. antarctica* is well-adapted to polar environments and has been previously studied as an ecological marker species (Alberdi *et al.*, 2002). Its morphological adaptations to the chronically cold and dry climate include high water-use efficiency and resistance to transpiration, which helps prevent both heat and water loss. However, studies suggest these temperature-related physiological characteristics are plastic reactions to environmental differences, rather than evolutionary adaptations as a result of natural selection (Alberdi *et al.*, 2002). Nevertheless, *D. antarctica* can tolerate very low temperatures by cold acclimation

through cryoprotective mechanisms (Bravo *et al.*, 2001; Alberdi *et al.*, 2002). As the seasonal variation in day length in the species' native range is severe, the plants must be able to effectively utilize a very short growing season. *D. antarctica* expresses metabolic reactions to changes in day length, accumulating carbohydrates such as sucrose and fructans in the summer season (Bravo *et al.*, 2001; Alberdi *et al.*, 2002). The plants are better capable of cold acclimating in periods of long day length, which may be due to the increased concentrations of these solubles and a positive carbon balance. Efficient carbon metabolism is likely a part of the mechanism by which growth is stimulated in response to day-length cues (Bravo *et al.*, 2001; Alberdi *et al.*, 2002). The optimal temperature range for the photosynthesis of *D. antarctica* is 10-20°C, with net photosynthesis being highest at 10-13°C (Edwards and Smith, 1988; Xiong, Ruhland and Day, 1999). With the warming climate, the photosynthetic rate of *D. antarctica* is likely to improve via increased biomass allocation to leaf tissues (Xiong, Ruhland and Day, 1999; Alberdi *et al.*, 2002).

*D. antarctica* is characterized by relatively low genetic diversity both overall and within populations (Holderegger *et al.*, 2003; Androsiuk *et al.*, 2021). Furthermore, the species' genetic diversity gradually decreases toward the southern parts of its distribution range (Androsiuk *et al.*, 2021). Despite this, the phenotypic variation between individuals can be strikingly high (Figure 1). Populations are often genetically distinct, expressing great levels of morphological and genetic differentiation from each other. This may be a heritage of the species' colonization history, which was likely affected by seabirds (Fasanella *et al.*, 2017; Parnikoza *et al.*, 2018). Carried by birds, the plants would have been distributed across geographically wide regions, establishing small populations affected by founder effects. The morphological plasticity of *D. antarctica* and the formation of distinguishable ecotypes are likely a result of the species' extensive geographical range (Androsiuk *et al.*, 2021). Epigenetic mechanisms and polymorphisms behind this plasticity may be essential for the plants, allowing them to respond to various microclimatic stressors in their local environments.



Figure 1: Intraspecific morphological variation of *D. antarctica*. On the left, a plant collected from coastal Antarctica has wide leaf blades. In comparison, a Patagonian plant on the right has needle-like leaves.

## 2.2 Field sampling

The plants used in this study were collected from Chilean Patagonia and coastal Antarctica in the spring of 2022 over expeditions led by the multidisciplinary MICROBIPOLAR project. The collection of samples in Antarctica was carried out by a Chilean team from the University of Talca in collaboration with MICROBIPOLAR. The sampling process at all sites was conducted between January and early February 2022. During these expeditions, samples of 20 *D. antarctica* individuals were collected from 7 distinct populations across Chilean Patagonia, in addition to 3 individuals from 2 island populations off the coast of Antarctica (Figure 2; Table 1). In this thesis, these plant individuals will be referred to as genotypes. Only two populations were sampled from coastal Antarctica, as the global COVID-19 situation prevented travel to sites further inland. Despite this, the sampled populations cover a wide latitudinal range: the northernmost collected population, La Leona, is found at a latitude of 52°33'S, whereas the southernmost population, Lagotellerie, is found at 67°52'S (Figure 2; Table 1).

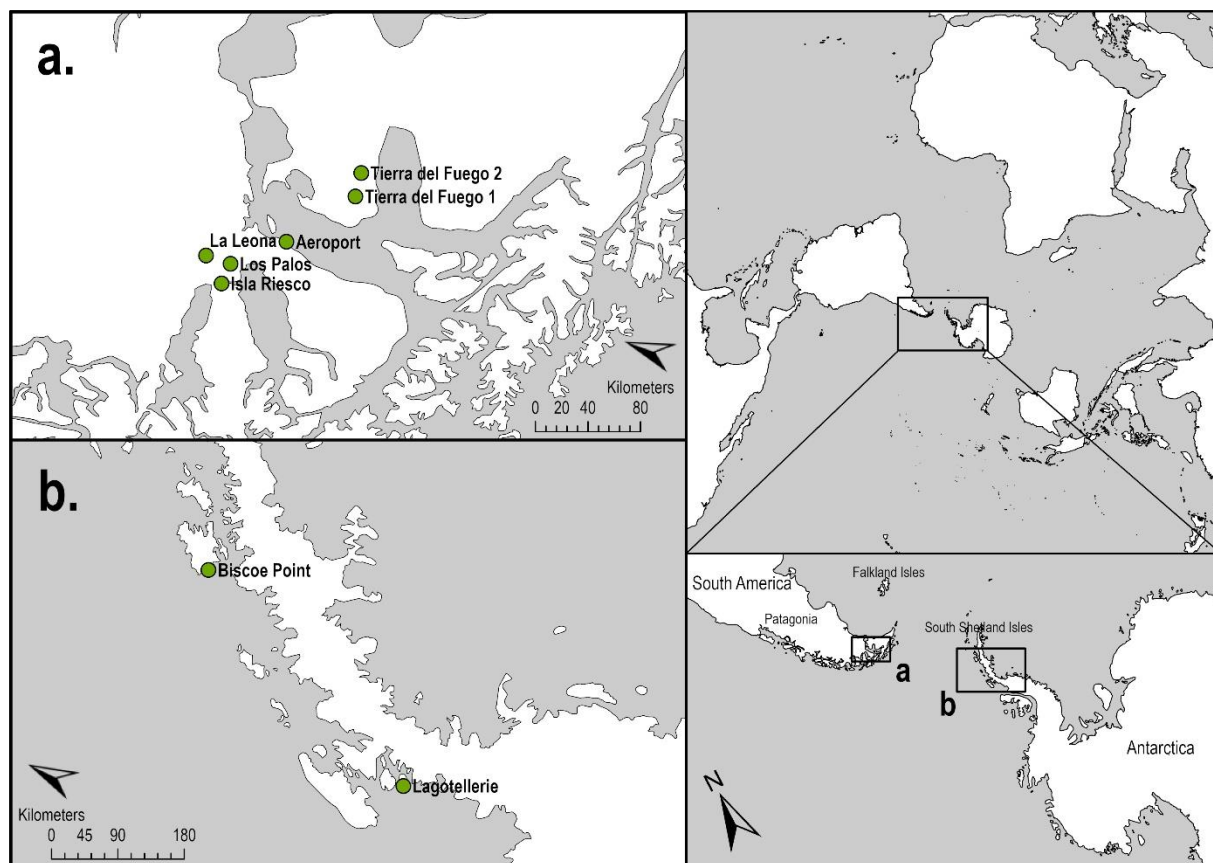


Figure 2: The locations of the *D. antarctica* populations where plants were collected. Plants were sampled from two regions, Chilean Patagonia (a) and coastal Antarctica (b).

Table 1: Region of origin, latitude, longitude, altitude, and habitat type of all sampled populations.

Origin	Population	Latitude	Longitude	Elevation (m a.s.l.)	Habitat
Patagonia	Aeropuerto	52°59'58,1"S	70°49'09,8"W	20	<i>Nothofagus</i> forest
Patagonia	Isla Riesco	52°42'18,1"S	71°26'01,1"W	35	Mixed grassland
Patagonia	La Leona	52°33'34,1"S	71°12'54,4"W	144	Mixed grassland
Patagonia	Los Palos	52°43'04,4"S	71°03'40,6"W	26	Mixed grassland
Patagonia	Tierra del Fuego 1	53°18'23,1"S	70°08'42,1"W	200	Heath-shrubland
Patagonia	Tierra del Fuego 2	53°17'25,9"S	69°53'55,7"W	273	Heath-shrubland
Antarctica	Biscoe Point	64°46'38,3"S	64°3'7,11"W	NA	Near penguin colony
Antarctica	Lagotellerie	64°52'49,9"S	64°26'10,2"W	NA	Far from penguin colonies

In their natural habitat, the Patagonian *D. antarctica* plants were found in rocky grasslands and low shrublands dominated by heath-type vegetation (Table 1). Almost all areas surrounding the sampled populations were noted to experience heavy grazing by various large herbivores, such as guanacos and sheep. In Antarctica, the plants were commonly found on moss-covered slopes between glacial formations. In comparison to Patagonia, herbivory is very limited in

Antarctica (Convey and Stevens, 2007; Parnikoza *et al.*, 2018; Maggio *et al.*, 2022). Thus, the Antarctic plants were most often found in areas of high bird activity, as bird feces can act as a strong fertilizer (Bokhorst *et al.*, 2022).

The collected *D. antarctica* samples were exported from Chile with the permission of the Chilean Antarctic Institute INACH and transported to the Botanic Garden of the University of Turku, Finland (60°26'N, 22°10'E). In Turku, the plants were grown and maintained in a greenhouse for future use. Upon arrival, the roots of the plants were thoroughly washed and all soil from the collection sites was autoclaved and discarded. This was done to reduce the chance of introducing invasive alien species or pathogens to Finland, under import permissions granted by the Finnish Food Authority (Appendices 1-3).

Once the plants had recovered from the transportation, samples of individual genotypes were further split into clonal replicates and repotted. Grasses can be replicated by splitting tussocks into smaller pieces, as rooted tillers can survive independently from the mother plant (Gurevitch, Scheiner and Fox, 2021, pp. 95–96). The repotting was done in 5 cm square pots with two soil types, black potting soil (Kekkilä Viherkasvimulta) and a sand-peat-soil mixture. The plants were then maintained at the Botanic Garden of Turku in quarantine conditions for 3 months. After this quarantine period, the plant samples were inspected by a representative from the Finnish Food Authority who determined that they were safe for release. While in the greenhouse, plants were watered both manually when needed and by an automated misting system programmed to keep a constant moisture level. The plants were also fertilized using a water-soluble fertilizer (Kekkilä Kastelulannoite), first weekly and later on a biweekly basis. Watering and fertilization of the plants were controlled to help the small replicates establish themselves in new pots.

## 2.3 Common garden experiment

Using the plants sampled from Chilean Patagonia and Antarctica, I established a common garden style transplantation experiment in the early summer of 2022. The experiment was run for two consecutive growing seasons and consisted of two field sites: one at the Botanic Garden of Ruissalo in Turku, and the other at the Kevo subarctic research station in Utsjoki. Both facilities are managed by the University of Turku, enabling a smooth collaboration with this project. The chosen locations represent the current latitudinal range of *D. antarctica* and the species' projected future distribution as it expands its range to higher latitudes. The latitudinal location of Ruissalo (60°26'N) is invertedly equivalent to central parts of the



distribution range of *D. antarctica* in the southern hemisphere. In contrast, the site in Kevo (69°45'N) mirrors the current southernmost edge of the species' distribution range. Plants of Patagonian origin were collected from populations found at less extreme latitudes than either of the study sites (Table 1). In comparison, Antarctic plants were collected from populations found invertedly at latitudes roughly between Turku and Kevo (Table 1). As day-length conditions change rapidly at high latitudes, the plants were accustomed to considerably milder seasonality in their light environment before transplantation. For example, plants collected from the Antarctic population Lagotellerie (64°52'S) had previously experienced an approximately 5-day period of polar day. In comparison, the polar day lasts nearly two months in Kevo (69°45'N). The plants collected from Patagonian populations had previously experienced seasonal day-length conditions comparable to Central Europe in the northern hemisphere. Thus, these sites present an exceptional opportunity to study the plants' performance in a more extremely seasonal light environment.

In Turku, the study site was established on a square 9 m x 9 m field. In Kevo, the site was comprised of two parts: a larger 14,5 m x 5,5 m area and a smaller 4,0 m x 5,5 m area adjacent to it. Both fields were fenced off to keep out any larger herbivores such as hares, deer, or reindeer. Despite the fencing, however, it was noted that some plants at the Kevo site had been grazed on by voles during the 2023 growing season. To control for any gradient or edge effects in the study sites, I arranged plant replicates in a fully randomized block design at both locations. Each site had 5 blocks, with all populations and genotypes represented within each block. To fit all blocks evenly inside the fields, some empty positions needed to be added among the plants. In Turku, I randomized these positions between all replicates. In Kevo, I arranged the empty spots in the middle of the field to form a walkway across. To eliminate the effect of intraspecific competition on plant performance, I planted each plant inside a 50 cm grid (Figure 3).



*Figure 3: The experimental site in Turku is pictured on the left and the site in Kevo on the right.*

Due to the global COVID-19 situation in the spring of 2022, only 2 populations (Biscoe Point and Lagotellerie) were collected from coastal Antarctica, compared to 6 populations from Chilean Patagonia. The Patagonian populations had 10 genotypes each, whereas the Antarctic populations together had only 3 genotypes (1 genotype from Biscoe Point and 2 genotypes from Lagotellerie). Because of these discrepancies in the sampling process, the experimental design was biased toward the Patagonian replicates. However, I controlled for this bias by fully randomizing the block design and including as many clonal replicates of the available genotypes as possible. Genotypes of all populations were clonally replicated 5 times for each experimental site (6 Patagonian populations x 10 genotypes x 5 replications + 3 Antarctic genotypes x 5 replications). Thus, each block consisted of 63 plants, each site of 315 plants, and both sites together had a total of 630 plants.

The study site in Turku was located within an oak-dominated temperate forest zone, common for the oak groves found in southernmost Finland. Contrarily, the site in Kevo was located within a pine-dominated xeric heath forest, characteristic of the subarctic climate. Finland and Antarctica are characterized by divergent climate and environmental conditions, including soil quality, temperature, and precipitation. However, these variabilities were considered in the experimental design. As the soil base diverges between the two locations from clayey in Turku to sandy in Kevo, a shovel-full of potting soil was always added around the plants as a barrier

against the natural soil medium. The addition of a soil barrier helped control for the environmental differences between the two sites, in addition to aiding the plants in their initial establishment outside greenhouse conditions. As climate variables such as temperature and precipitation differ between Turku and Kevo, both fields were also monitored during the growing seasons and watered with sprinklers as needed. This was done to prevent any lengthy periods of drought and to control for the climate differences between Turku and Kevo. Furthermore, the watering helped the plants overcome the initial transfer from constant moisture levels in the greenhouse to natural weather conditions outside. Both sites were also weeded to control for the effect of interspecific competition. Maintenance of the fields, including watering and weeding, was done with the help of summer trainees from HelanderSaikkonenLab and seasonal trainees from the Kevo research station. To record temperature variation at each site, I installed two Tomst TMS-4 dataloggers on both experimental plots. This way temperature variation could be considered when analyzing differences between the experimental sites.

Throughout the first field season in 2022, it was noted that some genotypes initially thought to be *D. antarctica* had been misidentified. These non-target replicates (included in populations Tierra del Fuego 1 and 2) were removed from the fields at the end of the growing season and kept in paper bags before being safely disposed of. The positions of removal in the plots were from then on treated as empty, both in the field and in the data analysis. Due to the removals, the number of replicates for Tierra del Fuego 1 was reduced from 50 to 46 in Kevo. For Tierra del Fuego 2, the number of replicates was reduced from 50 to 38 in Ruissalo and from 50 to 33 in Kevo.

## 2.4 Measured traits

I measured the plants twice during each of the two growing seasons. I took the first set of measurements as the experimental sites were established between 17.6. and 24.6.2022. The same measurements were repeated at the end of the first growing season between 24.8. and 31.8.2022. I timed the initial measurements of the second year to a similar stage of the early growing season as the first year, between 21.6.2023 and 29.6.2023. At the end of the experiment, I took final measurements between 15.8. and 22.8.2023. All measurements were taken with the help of summer trainees from HelanderSaikkonenLab.

During the first field season, I collected data on survivorship and phenotypic growth traits. The recorded growth traits included stem height, circumference, and tiller counts. I measured stem height with a standard ruler from each plant replicate's tallest living leaf blade, and

circumference with measuring tape from the base of the plant tussocks. All circumference measures under 1,0 cm were rounded to 0,5 cm, as it was not feasible to measure them more precisely. Tiller counting is a common method of measuring the size and growth of grasses (Moore and Moser, 1995). I did this by approximating the number of tillers from aboveground as precisely as possible. However, counting the tillers became increasingly time-consuming as the plants grew in circumference. As such, I did not continue the tiller counts in the second field season. During the second field season in 2023, the plants had accumulated a considerable amount of dead biomass, affecting the assessment of circumference. Although I included the dead biomass in the circumference mark, the measurements still give adequate insight into the size differences between plant groups, as this dead tissue tends to accumulate with overall growth.

To assess the general establishment success of *D. antarctica*, I measured the survival and reproductive activity of the plants. I first recorded survival at the end of the first growing season and continued the monitoring at each following data collection. To give the plants time to establish themselves after being transplanted, I only recorded flowering rates over the second growing season. As the plants varied in their initial size, flowering in the first year was more likely related to the plants' developmental stage rather than their adaptive responses to the latitudes. During the second growing season, I collected data on flowering rates by recording all replicates with inflorescences both in June and August. Due to unexpectedly high mortality over the winter season of 2022-2023, temporal phenology was not possible to quantify in more detail that would be statistically informative. Furthermore, all inflorescences of *D. antarctica* had to be cut and carefully collected before seeds were fully developed to prevent the species from spreading to surrounding areas. This was done under the official importation and experimental use agreements of *D. antarctica* with the Finnish Food Authority (Appendices 1-3).

At the end of the experiment in August of 2023, I collected the above-ground biomass of all living plants. I did this by cutting the plants near ground level to include all above-ground parts in the sample. After individually bagging all plants, I recorded their fresh biomass within a day of initial collection. At this time, I also cleaned the plants of any weeds and soil residues to get the most accurate measure of *D. antarctica* biomass. After initial weighing, I kept the plants in drying cabinets set at 60°C for a minimum of two days. When the plants were completely dry, I weighed the samples for dry biomass. I measured both fresh and dry biomass but used only dry biomass in further analysis. Dry biomass is a clearer indication of accumulated tissue as the effect of water retention is excluded.

In addition to plant traits, I recorded temperature variation at the sites using Tomst TMS-4 temperature loggers. The loggers were activated on 17.6.2022 and the data was collected at the end of the experiment on 16.8.2023. Each logger recorded temperature at three different depth levels: below-ground soil temperature at a depth of 6 cm, ground-level temperature at 2 cm above-ground, and aerial temperature at 15 cm above ground. The loggers recorded the temperature every 15 minutes for the duration of the experiment. Both fields had two separate loggers, and the final temperature data for each site was derived by averaging from the two.

## 2.5 Statistical analysis

I conducted all data exploration and statistical analysis using version 4.2.1 of RStudio (RStudio Team, 2023). I examined the data by creating descriptive plots using the packages ‘tidyverse’, ‘ggplot2’, ‘reshape2’, and ‘scales’ (Wickham, 2007, 2016; Wickham *et al.*, 2019; Wickham and Seidel, 2022). To estimate fitness-correlated responses in the plants, I first compared differences in survival, the clearest indicator of plant performance. To analyze survival, I conducted a generalized linear mixed model using the glmmTMB procedure from package ‘glmmTMB’ (Brooks *et al.*, 2017). In this model, survival rates (recorded as living/dead for each replicate) were predicted by experimental site, plant origin, and interaction as fixed effects. Additionally, I used genotype nested within population as a random factor to control for autocorrelation between clonal replicates. As the plant genotypes were collected separately and planted in a fully randomized way, genotypes can be treated as statistically independent. The model was based on the logit link function, which is suitable for binomial data. I assessed the fit of the model by running a dispersion test and simulated residual plots with the ‘DHARMA’ package (Hartig, 2022). According to a visual interpretation of the simulated residual plots and a dispersion factor of 1,007, the model’s assumptions were fulfilled. The predictors of the model were tested using the type II Wald Chi-square test from the package ‘car’ (Fox and Weisberg, 2019). Although environmental variation at the experimental sites likely led to a block effect in the data, I did not include block in this or the following models due to insufficient degrees of freedom. Thus, the models treat replicates as fully randomized within the experimental sites. Though this may bias the results, the models were built based on the biological relevance of the determinants to the research questions of this thesis.

As a second fitness-correlated trait, I compared differences in the reproductive activity of the plants. To analyze these differences, I conducted a generalized linear mixed model using the glmmTMB procedure from package ‘glmmTMB’ (Brooks *et al.*, 2017). In this model, flowering rates over the second growing season (recorded as flowering/not flowering for each replicate)

were predicted by experimental site, plant origin, and interaction as fixed effects. The model was based on the logit link function, which is suitable for binomially distributed data. To control for the autocorrelation between clonal replicates, genotype nested within population was added as a random factor. The fit of the model was assessed by running a dispersion test and simulated residual plots using the 'DHARMA' package (Hartig, 2022). With no residual patterns and a dispersion factor of 1,010, the model assumptions were met. The model predictors were tested using the type II Wald Chi-square test from the package 'car' (Fox and Weisberg, 2019). Due to low numbers of late-flowering replicates, I did not analyze flowering rates separately between June and August.

To assess plant establishment over the first growing season, I analyzed tiller growth. For this analysis, I conducted a linear mixed model with the lme procedure from package 'nlme' (Pinheiro and Bates, 2000). In this model, tiller growth calculated by subtracting the initial tiller number (June 2022) from the final tiller number (August 2022) was used as the dependent, and experimental site with origin and interactions as fixed effects. Additionally, I included the initial tiller number as a covariate and genotype nested within population as a random factor. The initial tiller number was added as a covariate, as this improved model fit based on AIC. The fit of the model was further assessed by visually interpreting diagnostic plots. Although a few outliers in the data caused some deviations in the residual tail, the distribution of the model's residuals was otherwise normal. As such, I determined the model's assumptions as fulfilled. The outliers were retained in the data, as they represent natural biological variation in the plants' growth rate.

To explore differences in growth over the whole experimental period, I calculated an estimation of plant volume by using height and circumference. Volume is known to be a good estimator of plants' above-ground biomass (Faeth, Helander and Saikkonen, 2004). I estimated volume by using the formula of a cylinder ( $V=\pi^2h$ ), which approximately represents the growth form of a bunchgrass. The total growth of plants over the two growing seasons was calculated by subtracting the initial volume measured in June 2022 from the final volume in August 2023. To analyze both final biomass and volume growth, I conducted linear mixed models with the lme procedure from package 'nlme' (Pinheiro and Bates, 2000). Both mixed models had the experimental site and plant origin as fixed effects, in addition to genotype nested within population as a random factor. The interaction between site and origin was left out of the models, as the low number of living Antarctic replicates at the end of the experiment (specifically at the Ruissalo site) did not allow for meaningful analysis. I added initial plant volume in the volume growth model as a covariate, as this improved model fit based on AIC. I further assessed the fit of both models by visually interpreting diagnostic residual plots. As with

the tiller model, outliers caused some deviations in the residual tails. However, as the distribution of the residuals was otherwise normal, the assumptions of the models were determined as fulfilled. The outliers were again retained in the data, as they represent natural biological variation in plant growth.

### 3 Results

#### 3.1 Survival

I found both the experimental site and plant origin to significantly predict differences in survival rates, with the effect of the site being stronger than the origin's (Table 2). Overall, survival was significantly lower at the Ruissalo site (29%) compared to Kevo (73%). While survival rates differed considerably between the two sites, they also diverged between plant origins. The survival rate of Patagonian plants was significantly higher (48%) than the survival rate of Antarctic plants (23%). At the Ruissalo site, the survival rate of Antarctic plants was 7%, compared to 33% for Patagonian plants (Figure 4). In Kevo, the survival rate of Antarctic plants was 47%, compared to 73% for Patagonian plants. Although survival rates diverged between the two sites and origins, the interaction between site and origin remained non-significant (Table 2). Temporally, most of all mortality occurred over the winter period between growing seasons, while mortality during growing seasons remained relatively minor (Figure 4). At almost all recorded time points, the survival of Antarctic genotypes was lower relative to Patagonian genotypes. The only exception was at the end of the first growing season in Ruissalo (Figure 4).



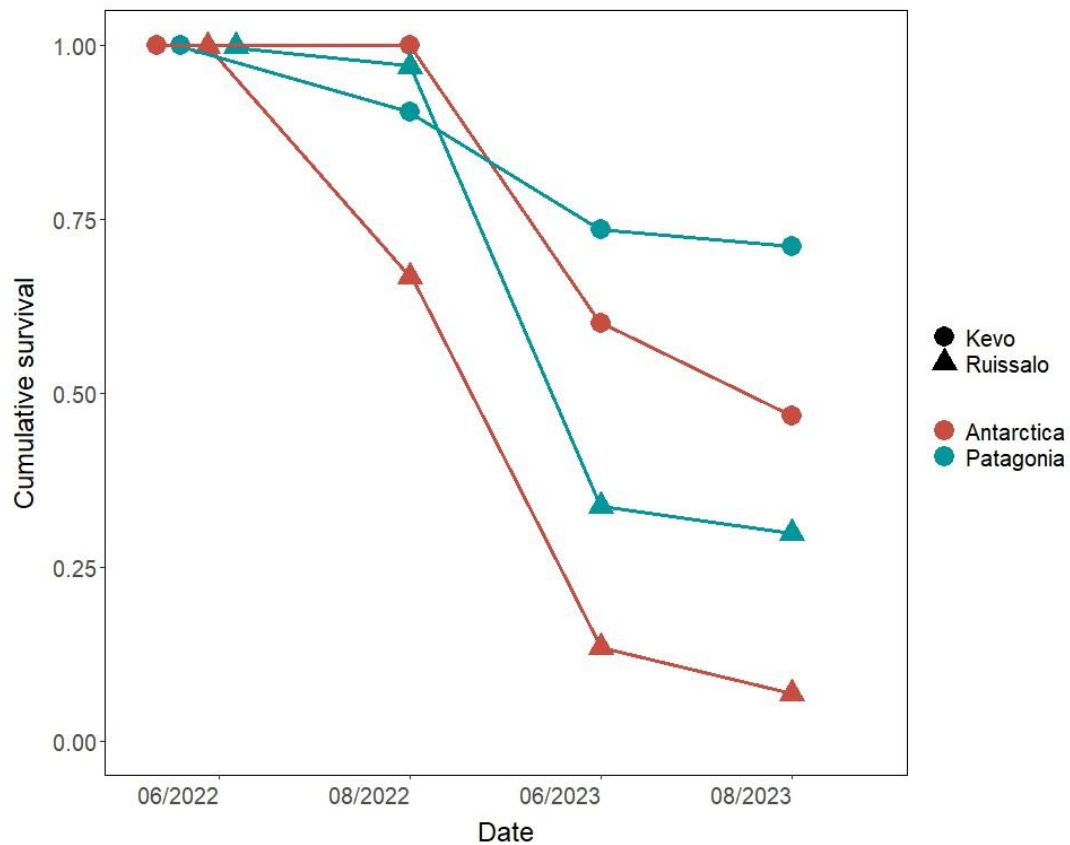


Figure 4: The cumulative survival of different origins of *D. antarctica*. Survival was recorded over two consecutive growing seasons in Ruissalo and Kevo.

Table 2: Results of the statistical comparison of survival between the experimental sites, origins, and their interactions. The analysis is based on a generalized mixed model with a binomial distribution and a logit link. Significant differences are marked with asterisks: \*\*\* =  $P < 0,0001$ , \*\* =  $P < 0,001$ , \* =  $P < 0,05$ , ° =  $P < 0,1$ . Df = degrees of freedom.

	Df	X <sup>2</sup>	P	
Site	1	104,112	< 0,0001	***
Origin	1	5,726	0,017	*
Site x Origin	1	0,045	0,831	

### 3.2 Flowering

Populations exhibited varying responses in reproductive activity over the 2023 growing season. I found the experimental site to significantly predict differences in flowering rates, as well as a marginal effect by plant origin (Table 3). In Ruissalo, the flowering rate remained minor, with only 6% of all initially planted replicates flowering. In Kevo, the flowering rate was higher at 14% of all initially planted replicates. Overall, plants of Antarctic origin were more

reproductively active than Patagonian plants. In Ruissalo, 7% of initially planted Antarctic plants flowered, whereas 40% flowered in Kevo. In comparison, 6% of initially planted Patagonian plants flowered in Ruissalo, and 13% in Kevo. Although flowering rates diverged between the two sites and plant origins, the interaction between site and origin remained non-significant (Table 3). As seen in Figure 5, the flowering rates of distinct populations are generally higher in Kevo relative to Ruissalo. Only the population Tierra del Fuego 2 shows a divergent response, with a higher flowering rate in Ruissalo. The difference between experimental sites is especially notable in the Antarctic plants, which were very active at the Kevo site.

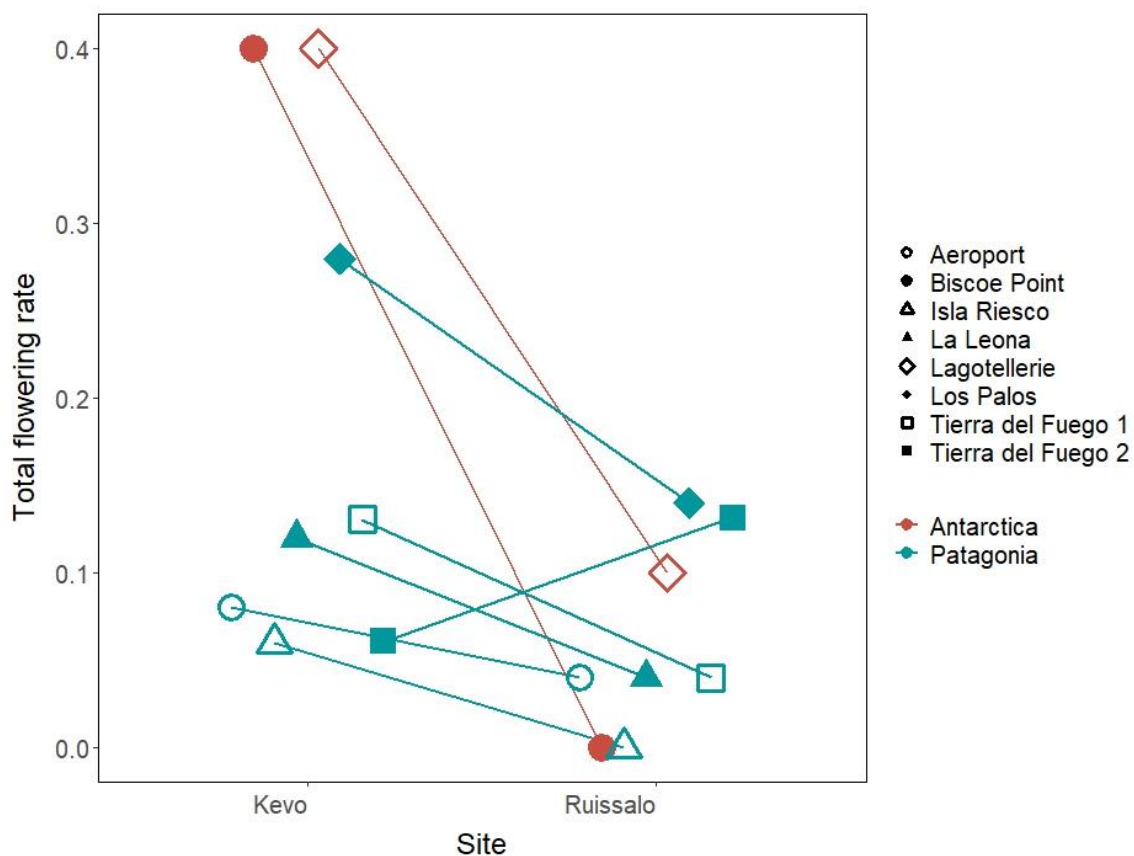


Figure 5: The flowering rates of *D. antarctica* populations based on the number of flowering replicates relative to initial sample sizes.

*Table 3: Results of the statistical comparison of flowering between the experimental sites, origins, and their interactions. The analysis is based on a generalized mixed model with a binomial distribution and a logit link. Significant differences are marked with asterisks: \*\*\* =  $P < 0,0001$ , \*\* =  $P < 0,001$ , \* =  $P < 0,05$ , ° =  $P < 0,1$ . Df = degrees of freedom.*

	<i>Df</i>	<i>X<sup>2</sup></i>	<i>P</i>	
Site	1	10,268	0,001	*
Origin	1	2,991	0,084	°
Site x Origin	1	1,445	0,229	

The rate at which plants flowered in June and August also diverged between experimental sites. The flowering rate at each site was highest in June, with 21% of all surviving plants flowering in Ruissalo and 16% in Kevo. Only a few plants produced inflorescences after the initial monitoring in June, and all the late inflorescences were produced at the Kevo site. Thus, the flowering rates were very minor in August: none of the plants in Ruissalo and 3% of all living plants in Kevo. As seen in Figure 6, the flowering rates of surviving Antarctic plants are considerably higher than Patagonian plants both in the early growing season and at the end of the experiment. However, the number of surviving Antarctic replicates at these time points is only a fraction of the number of surviving Patagonian replicates (Figure 6). Despite this, a difference between the plant origins can be seen at both sites in the early summer: 56% of Antarctic plants and 15% of Patagonian plants flowered at the Kevo site, compared to 50% and 20% in Ruissalo (Figure 6).

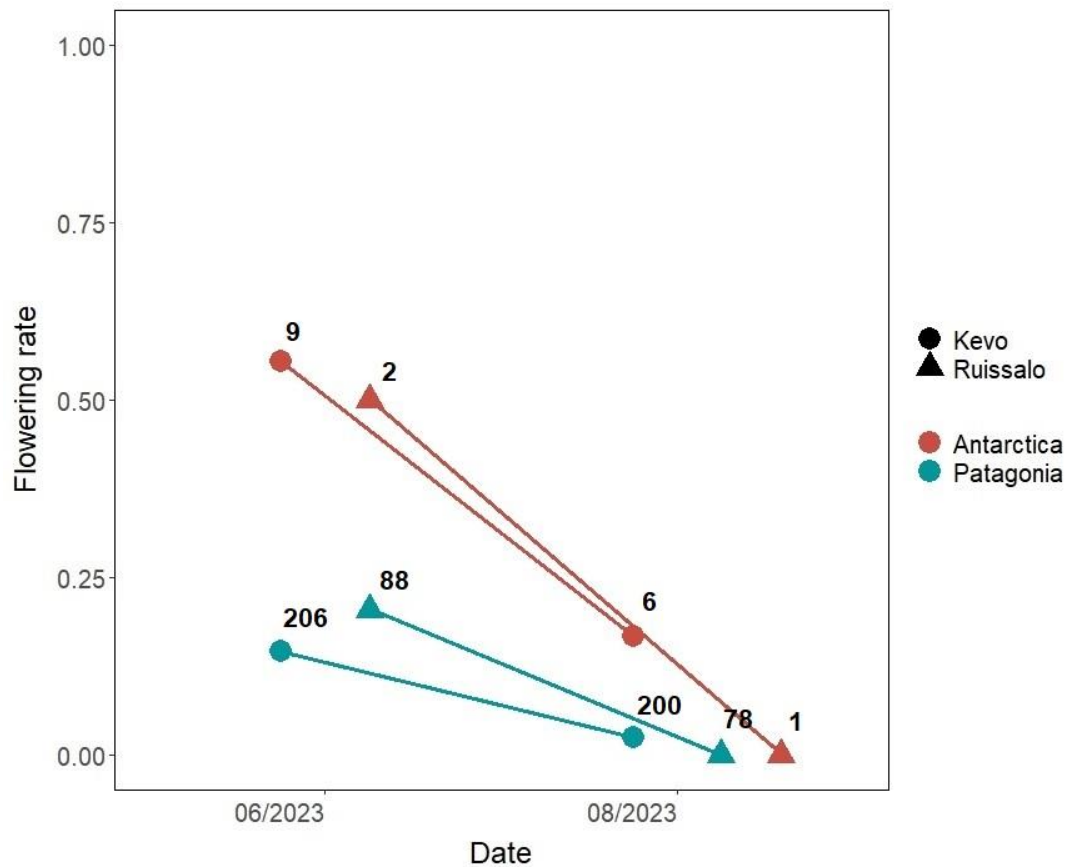


Figure 6: The flowering rates of *D. antarctica* in June and August of 2023, relative to the number of plants alive at each time point. The number of living replicates is visualized above each point.

### 3.3 Growth

The plants exhibited a relationship between site and origin in the tiller growth of the first growing season. As seen in Figure 7, the mean tiller growth of Patagonian plants was generally higher in Ruissalo ( $78,15 \pm 87,11$  tillers) compared to Kevo ( $49,19 \pm 53,55$  tillers). Plants of Antarctic origin showed an opposite pattern, as plants grew more in Kevo ( $100,67 \pm 48,69$  tillers) compared to Ruissalo ( $48,07 \pm 87,11$  tillers). While the variation in tiller growth within populations and origins was higher in Ruissalo relative to Kevo, a distinct pattern between site and origin can be seen (Figure 7). This is also supported by statistical analysis, which showed site and the interaction between site and origin to significantly predict differences in tiller growth (Table 4). Though the effect of origin remained non-significant, tiller growth was strongly predicted by the initial tiller number (Table 4). This effect implies that initially large plants tended also to grow larger.

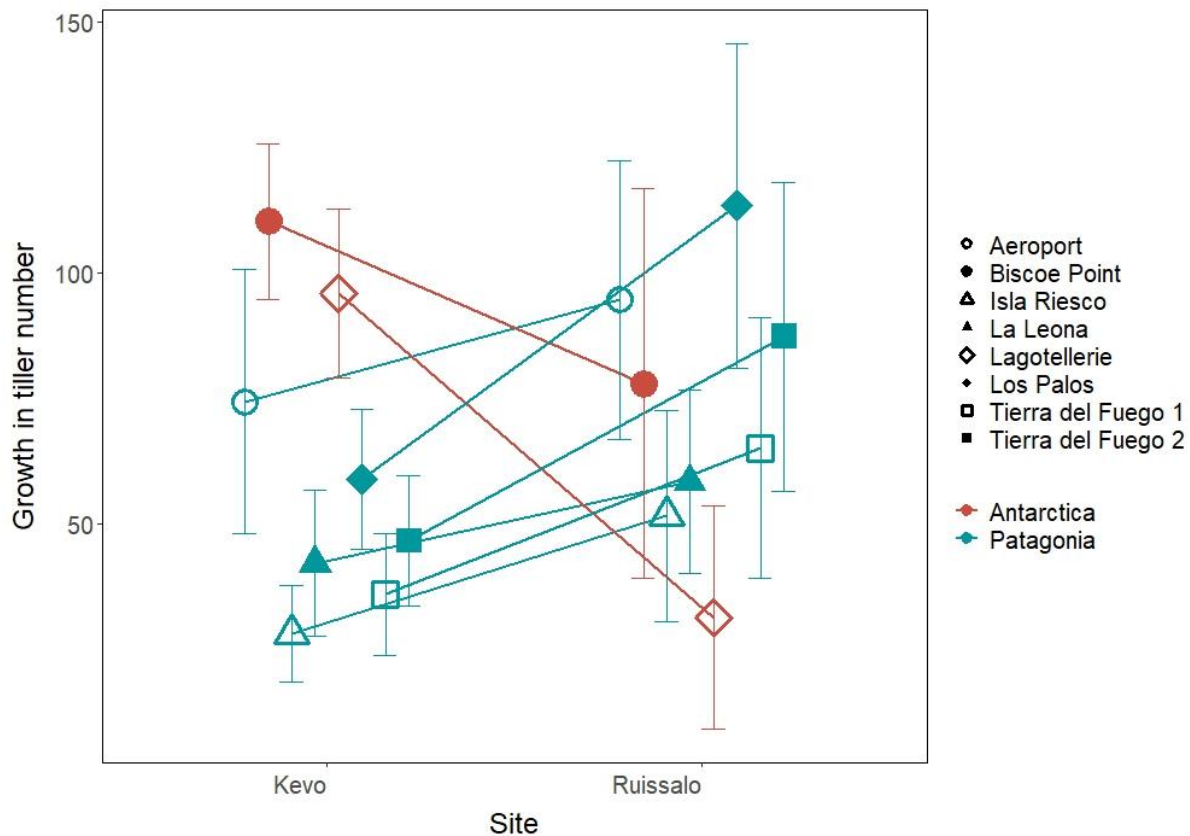


Figure 7: The mean tiller growth of *D. antarctica* populations over the 2022 growing season in Kevo and Ruissalo. The whiskers indicate standard errors.

Table 4: Results of the statistical comparison of tiller growth between the experimental sites, origins, and their interactions. The initial tiller number was used as a covariate. The analysis is based on a linear mixed model. Significant differences are marked with asterisks: \*\*\* =  $P < 0,0001$ , \*\* =  $P < 0,001$ , \* =  $P < 0,05$ , ° =  $P < 0,1$ . Df = degrees of freedom.

	numDf	denDf	F	P	
(intercept)	1	497	182,271	< 0,0001	***
Site	1	497	20,521	< 0,0001	***
Origin	1	6	0,746	0,421	
Site x Origin	1	497	10,326	0,001	*
Initial Tiller number	1	497	62,668	< 0,0001	***

Most of the total plant growth showed in circumference, whereas the height of the plants generally decreased (Figure 8). The single Antarctic replicate which survived to the end of the experiment in Ruissalo lost  $-11,10$  cm in height, whereas Antarctic plants in Kevo lost  $-13,43 \pm 3,63$  cm on average. In comparison, Patagonian plants only lost  $5,31 \pm 4,11$  cm in Ruissalo and  $2,18 \pm 4,74$  cm in Kevo. On the other hand, circumference growth was mostly positive. Patagonian plants in Ruissalo gained  $66,31 \pm 7,78$  cm in circumference, compared to  $6,41 \pm 4,74$  cm in Kevo. The surviving Antarctic replicate in Ruissalo gained circumference (9,00 cm),

but in Kevo the Antarctic plants lost  $6,41 \pm 4,74$  cm. Within populations, considerable variation can be seen both in height and circumference growth (Figure 8).

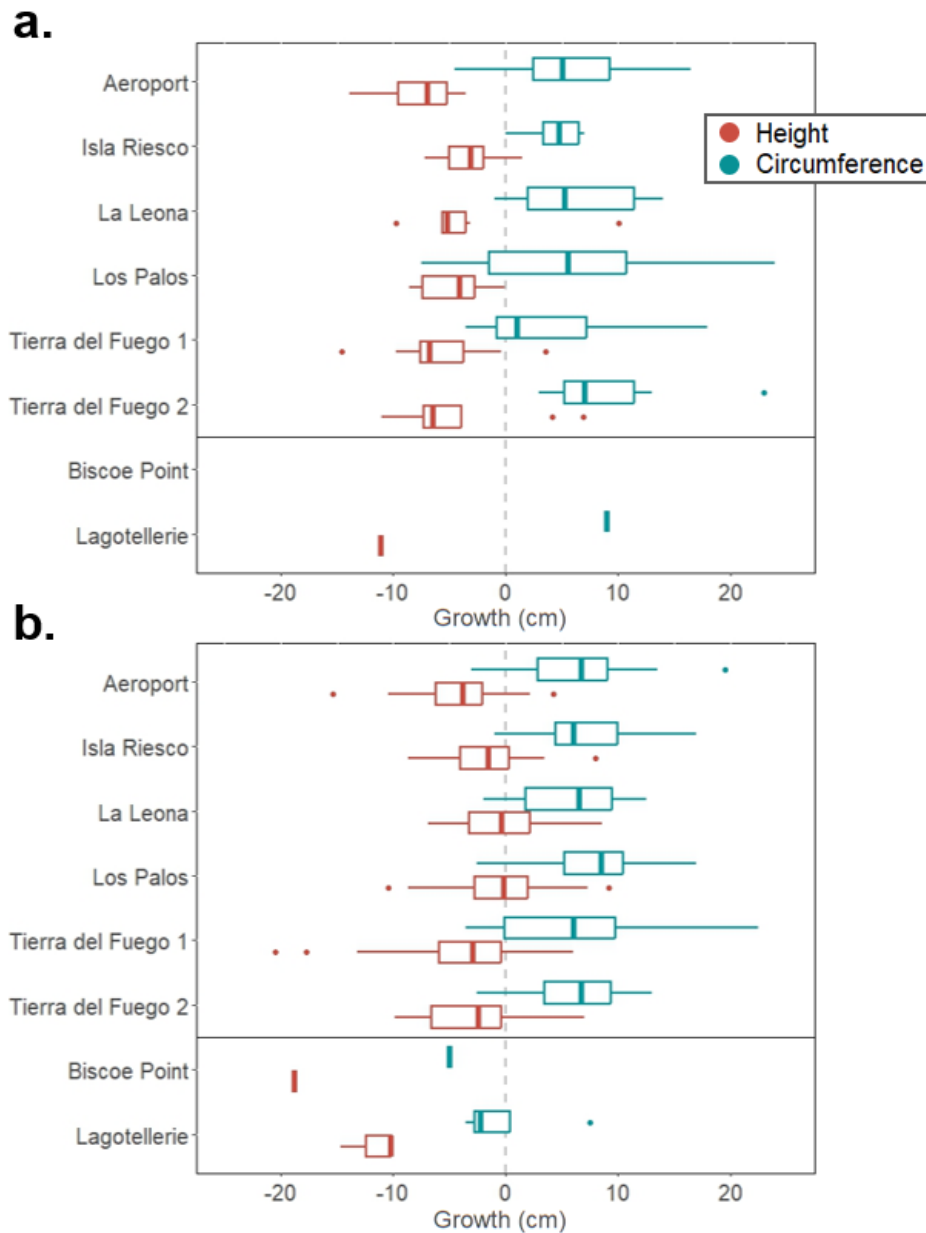


Figure 8: The distribution of *D. antarctica* populations' height and circumference growth in Ruissalo (a) and Kevo (b). The boxes visualize the first and third quantiles with the median. The vertical lines represent minimum and maximum values excluding outliers, which are shown in points. Populations Biscoe Point and Lagotellerie originate from Antarctica and the rest from Patagonia.

The mean volume of nearly all populations grew over the two growing seasons (Figure 9). However, neither site nor plant origin predicted differences in total growth rates (Table 5). The Patagonian population Tierra del Fuego 2 was notably successful at the Ruissalo site, reaching a volume growth of  $430,04 \pm 561,31$  cm<sup>3</sup>. Despite the success of this population, I found no

significant differences in growth rates between the two sites (Figure 9). Although the difference between origins also remained non-significant, Patagonian plants accumulated a positive volume growth ( $114,27 \pm 191,61 \text{ cm}^3$ ) compared to Antarctic plants with a negative growth rate ( $-5,56 \pm 39,49 \text{ cm}^3$ ). In Ruissalo, the single surviving Antarctic replicate reached a small growth ( $54,05 \text{ cm}^3$ ), but in Kevo the growth rate of Antarctic plants was negative ( $-17,48 \pm 31,91 \text{ cm}^3$ ). In comparison, the volume growth rates of Patagonian plants were higher both in Ruissalo ( $121,57 \pm 273,64 \text{ cm}^3$ ) and in Kevo ( $111,43 \pm 147,80 \text{ cm}^3$ ). Though the mean level of volume growth was higher for Patagonian populations, the variation in the growth rates of these populations was also high (Figure 9). However, it should be considered that the comparison of growth rates was limited by the small number of Antarctic replicates that survived to the end of the experiment (1 in Ruissalo and 6 in Kevo). As such, the interaction between site and latitude was not analyzed.

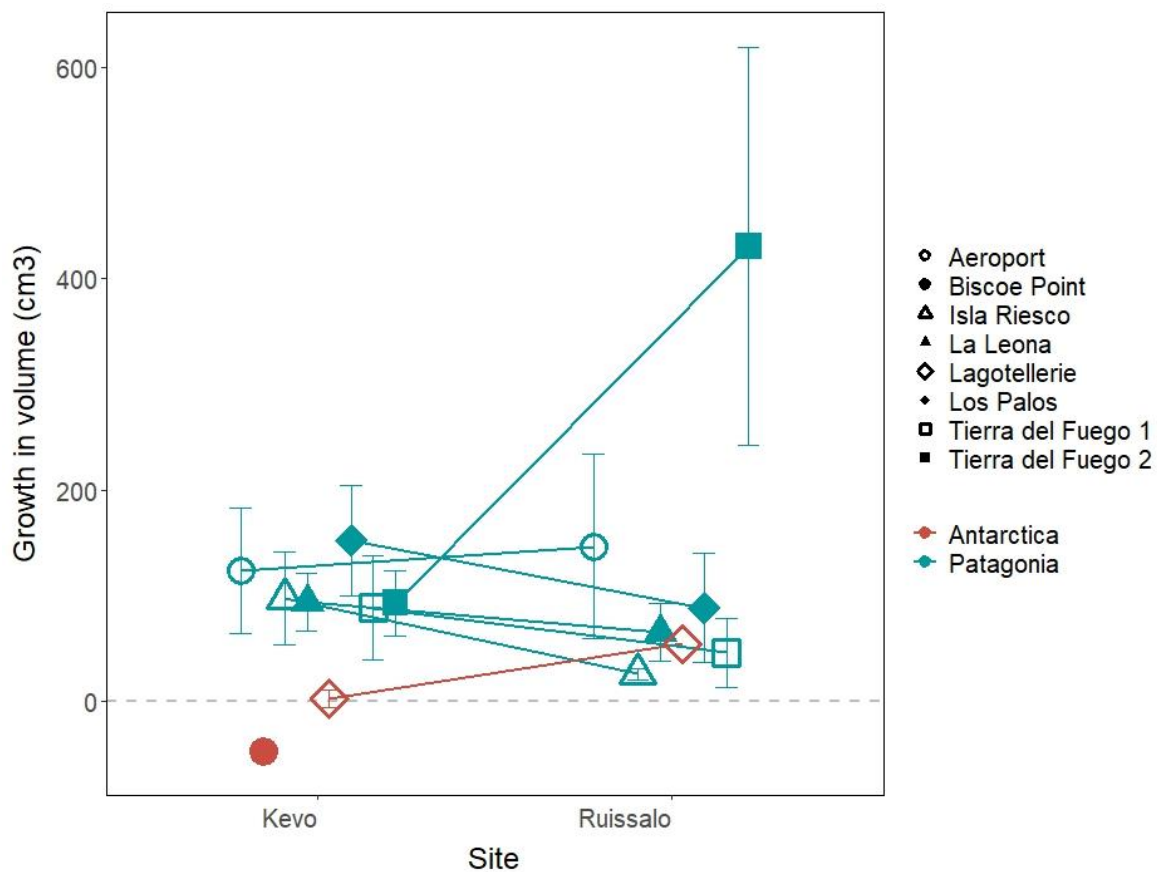


Figure 9: The mean volume growth of *D. antarctica* populations over two consecutive growing seasons in Ruissalo and Kevo. The whiskers indicate standard errors.

*Table 5: Results of the statistical comparison of volume growth between the experimental sites and origins, with the initial volume used as a covariate. The interaction between site and origin was not analyzed due to low replicate numbers of Antarctic plants. The analysis is based on a linear mixed model. Significant differences are marked with asterisks: \*\*\* =  $P < 0,0001$ , \*\* =  $P < 0,001$ , \* =  $P < 0,05$ , ° =  $P < 0,1$ . Df = degrees of freedom.*

	<i>numDf</i>	<i>denDf</i>	<i>F</i>	<i>P</i>	
(intercept)	1	217	57,168	< 0,0001	***
Site	1	217	0,253	0,616	
Origin	1	6	2,176	0,191	
Site x Origin			Not analyzed		
Initial volume	1	217	1,9439	0,165	

The responses in the final biomass of the plants were similar to responses in volume growth. I found neither the experimental site nor plant origin to predict differences in final biomass (Table 6). Although the difference remained non-significant, Patagonian plants reached a higher final biomass ( $2,01 \pm 3,36$  g) compared to plants of Antarctic origin ( $0,31 \pm 0,50$  g) (Figure 10). The Patagonian population Tierra del Fuego 2 was notably successful in Ruissalo, reaching a final biomass of  $6,00 \pm 11,16$  g. Despite the success of this population, differences between the sites remained non-significant. In Ruissalo, the final biomass of the single surviving Antarctic replicate was 0,45 g. In comparison, the Antarctic plants in Kevo reached a final biomass of  $0,28 \pm 0,54$  g. On the other hand, the Patagonian plants reached a higher final biomass both in Ruissalo ( $1,62 \pm 4,18$  g), and in Kevo ( $2,16 \pm 2,96$  g). Although the mean final biomass of Patagonian populations was higher, the variation in the final biomass of these populations was also considerably high (Figure 10). In a further examination of the statistical model's variance components, I found the variance explained by random factors to be infinitesimally small. Therefore, genotype did not predict any of the variance in final biomass. However, it should be considered that these comparisons were limited by the minimal number of surviving Antarctic replicates. Consequently, the interaction between site and latitude was not analyzed.



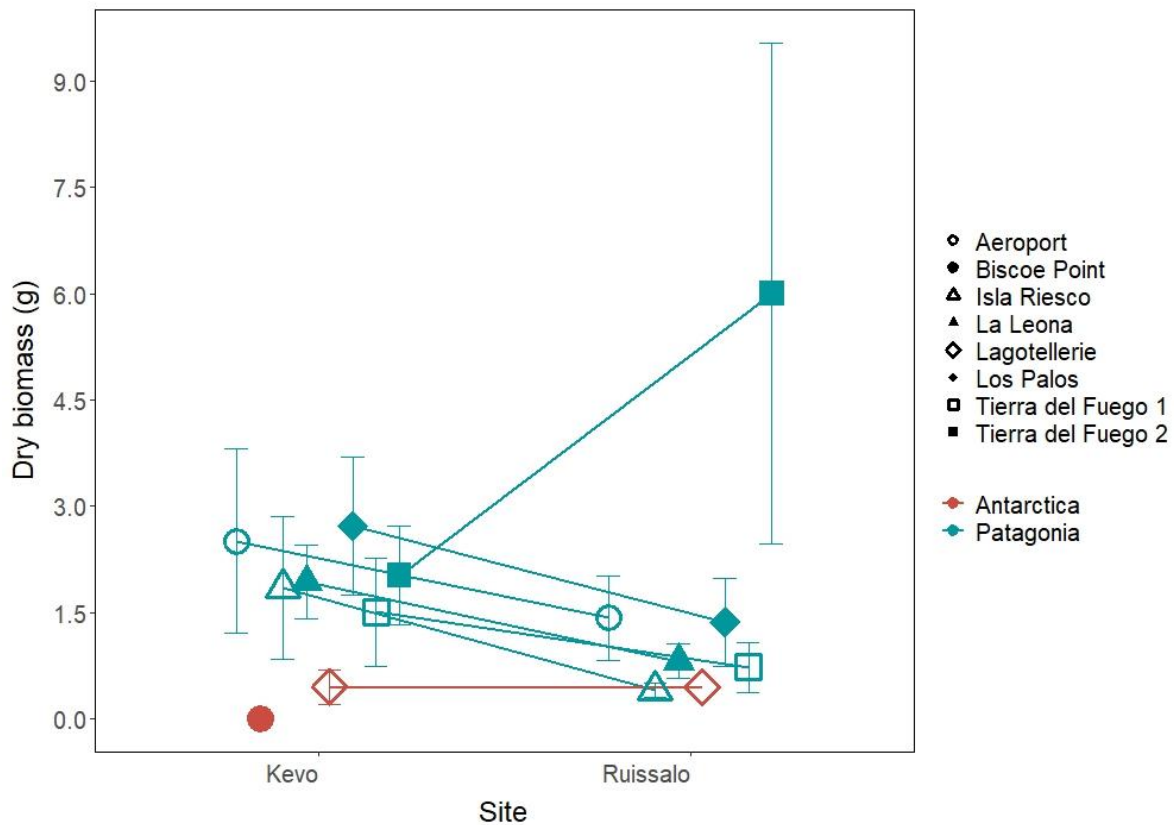


Figure 10: The mean final dry biomass of *D. antarctica* populations in Ruissalo and Kevo. The whiskers indicate standard errors.

Table 6: Results of the statistical comparison of final biomass between experimental sites and origins. The interaction between site and origin was not analyzed due to low replicate numbers of Antarctic plants. The analysis is based on a linear mixed model. Significant differences are marked with asterisks: \*\*\* =  $P < 0.0001$ , \*\* =  $P < 0.001$ , \* =  $P < 0.05$ , ° =  $P < 0.1$ . Df = degrees of freedom.

	numDf	denDf	F	P	
(intercept)	1	219	64,640	< 0,0001	***
Site	1	219	1,243	0,266	
Origin	1	6	1,575	0,256	
Site x Origin			Not analyzed		

### 3.4 Temperature variation

The temperature climate experienced by plants varied considerably between the two experimental sites. In Kevo, the temperature remained more uniform at different depth levels (below-ground, ground-level, and above-ground) compared to Ruissalo (Figure 11). At both sites, temperature varied most during the summer season, but the amplitude and frequency of temperature variation were higher in Ruissalo. During the thermal winter period (mid-November – early April in southern Finland), the above-ground temperature was more unstable

in Ruissalo compared to Kevo. Thermal winter lasted longer in Kevo, where daily mean aerial temperature didn't permanently rise above 0 °C until late April. However, the beginning of winter and the drop in mean temperature was more abrupt in Ruissalo. At the Kevo site, thermal winter began earlier (around mid-October) but the temperature dropped more gradually (Figure 11).

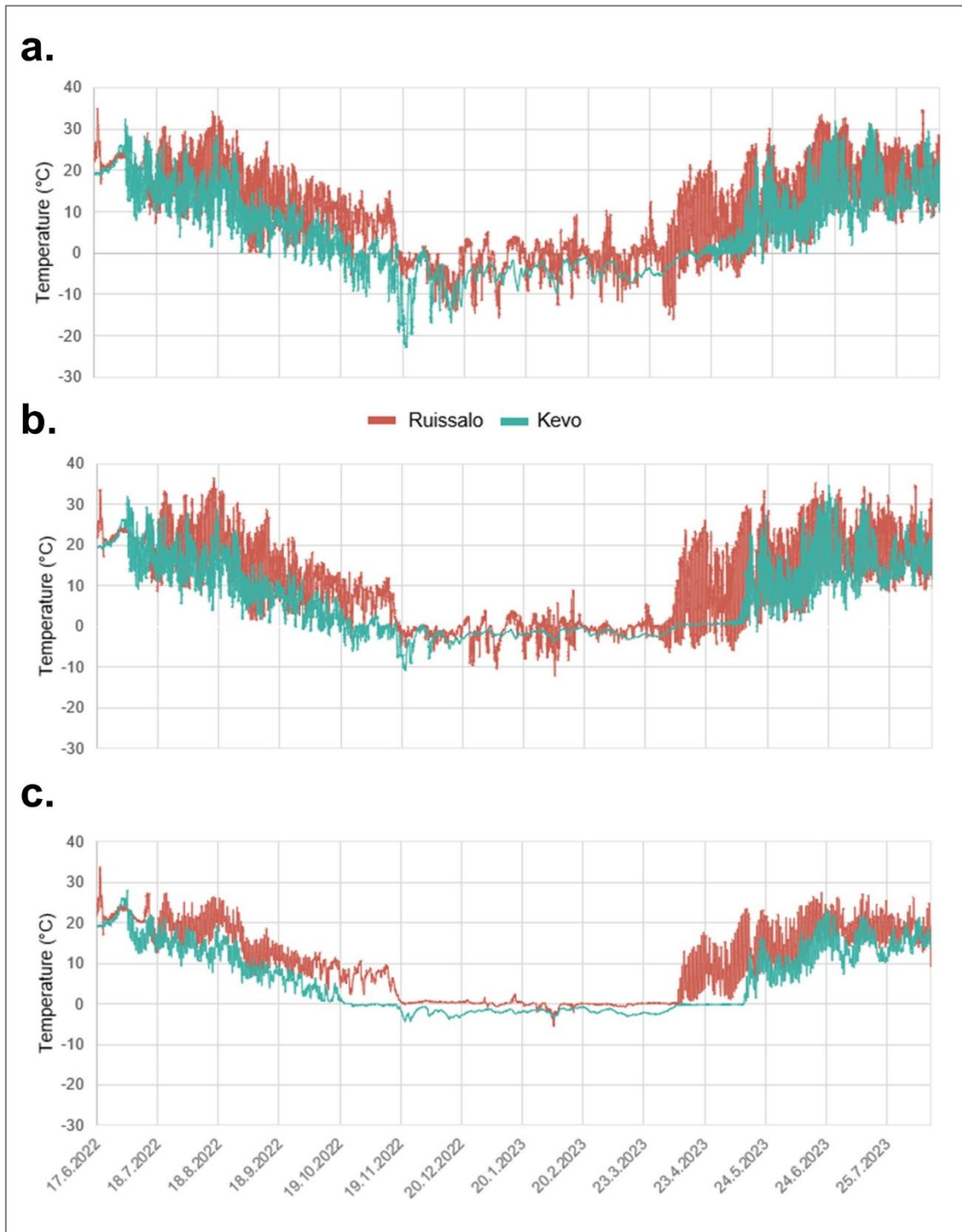


Figure 11: Temperature variation in Ruissalo and Kevo over the experimental period. Temperature was recorded at three depth levels: above-ground (a), at ground level (b), and below-ground (c).

In the summer season, the mean above-ground temperature was three degrees higher in Ruissalo (18,3 °C) compared to Kevo (15,3 °C) (Table 7). Though below-ground temperature varied less than above-ground temperature, the mean below-ground temperature in Ruissalo (19,2 °C) was higher than above-ground (18,3 °C). In the summer, the differences between minimum and maximum temperatures at different depth levels were higher in Kevo compared to Ruissalo. However, the effect was reversed in the winter season (Table 7). Although mean winter temperatures were lower in Kevo at all depth levels, the variation between minimum and maximum temperatures was larger in Ruissalo. The below-ground temperatures, which directly affect plant roots, remained relatively stable in Kevo during winter (between -3,7 °C and -0,8 °C). In Ruissalo on the other hand, the below-ground temperatures varied more (between -5,6 °C and 2,3 °C). The ground-level and above-ground temperatures, which affect plants' above-ground tissues, showed even greater variation over the winter season (Table 7). In Ruissalo, the above-ground winter temperatures varied between -15,8 °C and 12,5 °C. In comparison, the above-ground temperatures in Kevo remained more stable, varying between -17,0 °C and -0,8 °C.

*Table 7: Characteristics of temperature climates in Ruissalo and Kevo. Temperature values for the winter season are calculated from the beginning of December 2022 to the end of March 2023. Values for summer are calculated from the beginning of June to the end of August, combined between 2022 and 2023.*

<b>Above-ground</b>						
	<b>Winter</b>			<b>Summer</b>		
	Mean °C	Min °C	Max °C	Mean °C	Min °C	Max °C
Ruissalo	-2,1	-15,8	12,5	18,3	0,5	35,0
Kevo	-5,1	-17,0	-0,8	15,3	-0,2	32,5
<b>Ground-level</b>						
	<b>Winter</b>			<b>Summer</b>		
	Mean °C	Min °C	Max °C	Mean °C	Min °C	Max °C
Ruissalo	-1,0	-12,1	9,1	18,9	1,1	36,6
Kevo	-1,9	-7,8	-0,2	15,9	1,4	34,8
<b>Below-ground</b>						
	<b>Winter</b>			<b>Summer</b>		
	Mean °C	Min °C	Max °C	Mean °C	Min °C	Max °C
Ruissalo	0,0	-5,6	2,3	19,2	7,1	33,8
Kevo	-2,0	-3,7	-0,8	15,3	4,4	28,0

## 4 Discussion

These results demonstrate that *Deschampsia antarctica* is not restricted by the light environment in expanding its distribution to higher latitudes. In this thesis, I studied the effect of latitude on the performance and survival of the Antarctic hairgrass, *D. antarctica*, in a common garden experiment. Genotypes of *D. antarctica* were sampled from populations of two origins: southern Patagonia and coastal Antarctica. The experiment was conducted at two sites characterized by differences in light environment and temperature: Ruissalo, Turku (60°26'N), and Kevo, Utsjoki (69°45'N). I found *D. antarctica* to be significantly more successful in Kevo compared to Ruissalo, with a 1,43 x higher survival rate and a 1,21 x higher flowering rate. Regardless of latitude, plants of Antarctic origin had a 47% lower survival rate but flowered 1,51 x more actively than Patagonian plants. Furthermore, I found a potentially adaptive relationship between plant origin and latitude regarding the plants' initial vegetative growth. This result supports the hypothesis that genetic background affects the acclimatization of *D. antarctica* to different light environments. Contrary to predictions, I found no evidence of adaptation between plant origin and latitude regarding survival or flowering rate. Moreover, differences in final biomass and total volume growth remained non-significant. Nonetheless, my results demonstrate that *D. antarctica* can establish and successfully regulate its reproductive timing in novel environments at high latitudes. This study provides new insight into the adaptive capabilities of *D. antarctica* beyond its current range in the Antarctic.

### 4.1 Survival and flowering

I found significant differences in the performance of *D. antarctica* across the two study sites and between plants originating from Antarctica and Patagonia. This was evidenced especially clearly by survival, the most distinct fitness-correlated trait and an indicator of establishment success. Overall, the survival rate of the plants was much lower at the Ruissalo site (29%) compared to Kevo (73%). This could be explained by the species' long history of adaptation to the climates of southern Patagonia and maritime Antarctic, which the general climate of Kevo resembles more closely (Fasanella *et al.*, 2017). Regardless of site, however, the survival rate of Antarctic plants was significantly lower (23%) compared to Patagonian plants (48%). While both site and plant origin predicted differences in survival, the interaction between these components remained non-significant. This indicates that, in terms of survival, there was no clear adaptation to the two latitudes by genetic background.

The overwintering success of the plants was generally low, likely explained by temperatures exceeding critical physiological thresholds. Most of all mortality occurred over the winter season, with the rate of overwinter mortality being higher in Ruissalo (88% of all mortality at the site) compared to Kevo (60% of all mortality at the site). This suggests that mortality was affected by differences in climate or, more specifically, temperature variation between the two latitudes. Temperature variation over the experimental period was generally higher in Ruissalo compared to Kevo, especially during the winter season. As a result of this, a protective snow cover was likely maintained more consistently at the Kevo site, with the Ruissalo site experiencing more frequent freezing and thawing cycles. The lack of thermal buffering by a stable and deep-enough snow cover allows ground-level and below-ground soil temperatures to reach much colder degrees (Slatyer, Umbers and Arnold, 2022). For example, the lowest ground-level temperature of January recorded at the Ruissalo site was 7,4 degrees lower than in Kevo. It must also be taken into account that the plants were brought from an austral summer season to a second summer in Finland. This transition may have disrupted the plants' normal physiological preparations for wintering, reducing their overall wintering success.

In addition to mortality, there was significant variation in the reproductive activity of *D. antarctica* between the two sites and origins. Overall, the flowering rate was significantly higher in Kevo compared to Ruissalo, corresponding with the site's significantly higher survival rate. Although the effect of plant origin on flowering remained marginal, the flowering rate of Antarctic plants was 1,56 x higher than the flowering rate of Patagonian plants. As with the pattern seen in survival, site and origin predicted differences in flowering rates, but no adaptive relationship between genetic background and latitude was found. However, populations still varied in their reproductive activity. For example, while other Patagonian populations flowered more readily in Kevo compared to Ruissalo, the Patagonian population Tierra del Fuego 2 was more reproductively active in Ruissalo. Although the replicate number of this population was reduced due to a misidentification of species, this contrasting pattern demonstrates variation in the responses of populations sampled from similar geographic origins. Such variation supports previous studies on the genetic distinctiveness of *D. antarctica* populations (Holderegger *et al.*, 2003; Androsiuk *et al.*, 2021).

The flowering of *D. antarctica* was timed accurately in the early summer, with only a few inflorescences developing later in the season. This ratio contradicts the other results on plant performance, as *D. antarctica* would be expected to prolong the flowering process with late inflorescences in unfavorable climate conditions (Gielwanowska and Kellmann-Sopyła, 2015). Although I did not monitor the flowering phenology in detail, I found that 10% of all initially planted replicates flowered, and nearly all of these plants flowered in the spring. Late

inflorescences developed only at the Kevo site, suggesting a response to the shorter growing season or a connection to the generally high performance of the plants. Both Antarctic and Patagonian plants were able to successfully regulate their reproductive timing at the two latitudes. However, as only a cross-section of the flowering process was measured, it's unknown whether there were significant differences in the flowering span between Ruissalo and Kevo. Despite the limitations, these results imply a high plasticity in the ability of *D. antarctica* to regulate its reproductive timing at latitudes beyond its current range.

## 4.2 Vegetative reproduction and growth

During the first growing season, plants of different origins diverged significantly in their tiller growth between the two experimental sites. Plants of Antarctic origin accumulated more tillers in Kevo, whereas Patagonian plants in Ruissalo. This potentially adaptive relationship between site and origin supports the hypothesis, that plants have an advantage in their establishment based on their genetic adaptation history. In general, vegetative growth is thought to be advantageous in resource-limiting or highly disturbed environments, as it facilitates establishment in a patchy habitat (Smith, 1971; Jaenike, 1978). Tiller production is a form of vegetative propagation, with individual tillers being capable of surviving independently from the mother plant (Moore and Moser, 1995; Gurevitch, Scheiner and Fox, 2021, pp. 95–96). Thus, tiller growth can be interpreted as direct evidence of establishment success after transplantation. On the other hand, tiller growth was also predicted by the initial tiller number, implying that initially large plants tend to grow faster than smaller plants. Such a correlation is to be expected, as larger plants are more likely to have better-developed root structures and a higher capacity to utilize resources after stress or disturbance (Moreira, Tormo and Pausas, 2012). Furthermore, the number of tillers can be greatly affected by seasonal climate conditions. Unfavorable conditions can result in a loss of tillers, including tillers that would later become reproductively active (Moore and Moser, 1995). The loss of reproductive tillers due to temperature or drought stress may be connected to the relatively low flowering rate of plants at the Ruissalo site.

The adaptive responses seen in initial tiller growth are contradicted by the results on final biomass and total volume growth. Over the two consecutive growing seasons, plants generally grew in circumference but declined in height. The loss of height is likely a result of tiller mortality, followed by a subsequent change in tiller demography (Moore and Moser, 1995). On the other hand, circumference growth is linked to tiller production following establishment.

Although individual plant replicates reached very large final volumes, most plants only experienced minimal or moderate total growth. Above-ground growth likely remained relatively minor, as more resources were allocated to root structures following transplantation (Poorter *et al.*, 2012). In terms of final biomass and total volume growth, there was no significant effect by site or plant origin. Moreover, genotype failed to predict any of the variance in final biomass. These results contrast with the plants' potentially adaptive responses in initial tiller growth. Thus, although the plants' initial establishment at different latitudes is affected by genetic background, the long-term growth rate may be more strongly determined by environmental factors. However, it's unknown whether an adaptive response in final biomass or total volume growth would have been revealed, as the effect of the interaction between site and latitude was not analyzed. Despite the limitations of these comparisons, my results demonstrate that plants of different origins exhibit adaptations to latitude in their initial establishment. These adaptations may be advantageous for *D. antarctica*, as the species disperses toward higher latitudes in a patchy environment.

### 4.3 Implications for *D. antarctica* in a warming climate

The high winter mortality observed in Ruissalo is most likely explained by the continuous thawing and re-freezing of soil at the site. In comparison, plants at the Kevo site experienced relatively low temperature fluctuations under a protective snow cover. The results of my study suggest that alternating freeze-thaw events and consecutive fluctuations in soil and ground-level temperatures may decrease the wintering success of *D. antarctica*. In the last 50 years, studies have shown a general decline in snow duration and cover, especially in the maritime regions of the world (Slatyer, Umbers and Arnold, 2022). In the Antarctic, climate models predict a considerable increase in annual precipitation with an additional increase in extreme snowfall events by the end of the century (Colesie *et al.*, 2023). Although there is yet no consistent data on the snow cover variation in Antarctica, the crucial insulating effect of snow cover has been demonstrated on multiple sites in the Antarctic Peninsula region (Cannone *et al.*, 2006; Hrbáček, Láška and Engel, 2016). With the increase in aerial and permafrost temperatures, the dynamics of snow are likely to change in the maritime Antarctic as they have in other polar regions (Slatyer, Umbers and Arnold, 2022). Following climate warming in the coastal regions of Antarctica, *D. antarctica* may become exposed to similar fluctuations in snow cover and more frequent freeze-thaw events as seen in Ruissalo.

Regardless of site, plants of Antarctic origin had a lower survival rate compared to Patagonian plants. This may be explained by the Antarctic plants' acclimatization to a lower variability in

climate. Since the establishment of *D. antarctica* in Antarctica in the mid-late Pleistocene, the species has persisted in a harsh but climatically stable environment (Fasanella *et al.*, 2017). Though survival in the Antarctic requires the ability to withstand major physiological stress, the climate conditions at the two experimental sites may have reached suboptimal levels for some genotypes (Androsiuk *et al.*, 2021). A study by Xiong *et al.* (2000) shows that *D. antarctica* collected from coastal Antarctica does not photosynthetically acclimate to rising day-time temperatures, and the upper limit for photosynthetic optima is 20°C. The lack of acclimation is likely connected to the relatively stable temperature regime of the maritime Antarctic's growing seasons. As such, Patagonian plants may be adapted to a higher amplitude of temperature variation compared to plants of Antarctic origin. The optimal temperature range for photosynthesis was often exceeded during my experiment, likely inhibiting the growth and establishment of plants not able to acclimate to the amplitude of temperature variation. Furthermore, successful wintering requires acclimation to cold during fall (Androsiuk *et al.*, 2021). Cold acclimation may have been disturbed by irregular temperature variation or by the transplantation process itself, as plants were brought from one summer season to another. Although previous studies suggest that regional warming would lead to increased growth of *D. antarctica*, an increase in the amplitude of seasonal temperature variation may disrupt the acclimation processes of plants adapted to stable temperature regimes (Xiong, Mueller and Day, 2000).

Sporadic drought stress combined with temperature variation may have exceeded critical physiological thresholds for the plants. Due to genetic divergence and local microclimatic adaptations, different geographic backgrounds of *D. antarctica* can have divergent responses to climate-related stressors (Holderegger *et al.*, 2003; Androsiuk *et al.*, 2021). The habitats from which the plants were sampled varied in environmental characteristics, such as soil type, water availability, and nutrient flow (Table 1). Previous studies on pasture grasses demonstrate that plants of different environmental origins can have very divergent physiological reactions to climate extremes, especially drought (Beierkuhnlein *et al.*, 2011). Although the experimental fields were manually watered during summer, the plants may have been exposed to drought in the time between snow melt and the beginning of the summer season, especially in Ruissalo where temperature varied more strongly. Furthermore, small-scale spatial differences in soil quality and water drainage at the sites likely affected the microclimatic conditions experienced by plants. In following studies, a controlled watering system would minimize differences in moisture levels between and within sites. Nonetheless, plants of Antarctic origin would be expected to be better adapted to low water availability, as they have persisted in an environment where water is extremely limiting, (Green, Schroeter and Sancho, 1999; Beyer, Bölter and Seppelt, 2000). However, the combined variation in temperature and water



availability at the experimental sites may be connected to the low survival of the Antarctic plants. In Antarctica, plants are predicted to become more frequently exposed to drought combined with high temperatures, as aerial temperatures rise and receding permafrost leads to increased drainage (Colesie *et al.*, 2023).

In addition to climate variation, Antarctic plants may be less adapted to physical disturbance, such as trampling, root damage, or herbivory (Colesie *et al.*, 2023). Although the experimental sites were fenced to prevent damage by large grazers, the plants were exposed to herbivory by smaller herbivores such as insects or rodents. For example, it was noted during the second growing season that some replicates had been grazed on by voles. Herbivores are largely absent in Antarctica, aside from small decomposers and seabirds that rip plants for nest material (Convey and Stevens, 2007; Parnikoza *et al.*, 2018; Maggio *et al.*, 2022). In comparison, Patagonian plants are exposed to a wide range of enemies, including large herbivores such as guanacos and geese. With the Antarctic climate warming, the relatively defenseless Antarctic genotypes of *D. antarctica* are especially vulnerable to invasions by novel herbivores (Pearse *et al.*, 2013).

Simultaneous with external effects of disturbance or climate-related stressors, the population dynamics of *D. antarctica* are affected by the species' intrinsic dispersal mechanisms. Although total growth was not affected by the origin of *D. antarctica*, my results suggest that initial establishment success was dependent on the plants' adaptive responses to latitude. Such adaptability could be an advantage for the Antarctic populations of *D. antarctica*, as they disperse to higher latitudes in a patchy habitat (Lee *et al.*, 2017). Through resource competition between meristems, resources are allocated between patch persistence via vegetative growth, and the colonization of new patches via sexual reproduction (Smith, 1971; Jaenike, 1978; Ronce *et al.*, 2005). In my study, plants of Antarctic origin expressed low vegetative growth and high reproductive activity compared to Patagonian plants, especially at the Kevo site. Although these results are only tentative due to the low replicate number of Antarctic plants, this suggests plants of Antarctic origin exhibit increased allocation to sexual reproduction over vegetative growth. In comparison, Patagonian plants exhibit a relatively low reproductive allocation. A difference in the allocation of resources to reproduction between the two origins is in line with the results of a previous study by Convey (1996). In the study, it was demonstrated that *D. antarctica* collected from Antarctic sites had higher reproductive biomass compared to plants from a subantarctic site.

Traditional models on life history strategies predict that species exposed to chronically stressful environments will exhibit reduced investment in reproductive structures due to increased costs

of survival (Greenslade, 1983). Contrarily, studies conducted on perennial grassland species conclude that increased disturbance, such as grazing or competition, generally leads to increased allocation to reproductive output and seed production (Pakeman, 2004; Jongejans, De Kroon and Berendse, 2006). As mentioned above, Antarctic plants may be less adapted to climate variation or physical disturbance. Thus, Antarctic plants are likely more prone to a response in terms of reproductive allocation. Such responses may explain the differences in reproductive activity between Antarctic and Patagonian plants. On the other hand, the flowering rates of both plant origins were higher in Kevo compared to Ruissalo. As flower formation in *D. antarctica* is promoted by a long day, the light environment of the Kevo site may have provided optimal day-length conditions for flower development (Gielwanowska and Kellmann-Sopyła, 2015). Additionally, the higher reproductive activity in Kevo is likely connected to the plants' overall performance and size (Weiner, 2004). Based on this study, it's unknown how much of the plants' reproductive success can be attributed to size-dependent investment in flowering intensity or trade-offs between vegetative growth and sexual reproduction. Increased allocation to sexual reproduction at a higher latitude may be an adaptive response to escape unfavorable environmental conditions, whereas vegetative growth facilitates establishment in a patchy habitat (Smith, 1971; Jaenike, 1978; Ronce *et al.*, 2005; Androsiuk *et al.*, 2021).

As proposed by other studies, the temporal overlap in flowering cycles creates a possibility for intraspecific hybridization between populations, especially at high latitudes where the growing season is extremely short (Best *et al.*, 2007; Nelson, Denlinger and Somers, 2009; Chan, Hoffmann and van Oppen, 2019). Despite the limitations of this flowering assessment, my results tend to suggest that genetically distinct populations experience overlap in their reproductive timing. As the connectivity between distinct populations is predicted to increase due to relaxed dispersal barriers, intraspecific hybridization is likely to occur more frequently (Best *et al.*, 2007). The general reproductive isolation of *D. antarctica* populations has been maintained by physical dispersal barriers and the significant role of vegetative growth over sexual reproduction in the species' dispersal (Chown *et al.*, 2015; Fasanella *et al.*, 2017; Convey and Peck, 2019; Androsiuk *et al.*, 2021). However, the role of sexual reproduction is likely to become more significant, as climate conditions develop more favorable for flower induction (Gielwanowska and Kellmann-Sopyła, 2015).

Increased geneflow between Antarctic populations may also increase the competitive ability of *D. antarctica* against invasive species. The risk of plant invasions to Antarctica has been recorded to increase in the last decades due to anthropogenic activity (Colesie *et al.*, 2023). Highly invasive species, such as *Poa annua*, threaten the native flora of Antarctica with their

competitive ability to suppress other plants (Molina-Montenegro *et al.*, 2012, 2016, 2019; Chwedorzewska *et al.*, 2015). However, the epigenetic mechanisms and polymorphisms that enable the morphological plasticity of *D. antarctica* may also be an adaptive advantage against invasive species in extreme climate conditions (Androsiuk *et al.*, 2021). As the genetic diversity of invaders is limited by their colonization history in the Antarctic, the increase in gene flow between populations of *D. antarctica* is likely to be advantageous (Leger and Espeland, 2010; Rius and Darling, 2014). However, highly invasive species may be more resilient than *D. antarctica* in withstanding disturbance, such as high amplitudes of temperature variation combined with drought stress. Such an effect may be one factor behind the low success of plants at the Ruissalo site. Although both sites were weeded, the plants may have been exposed to competition by aggressive weeds able to withstand strong abiotic stress. However, the results of my study demonstrate that *D. antarctica* is not restricted by the light environment in its dispersal toward higher latitudes. Thus, a critical latitudinal threshold may be reached where the adaptive advantages between *D. antarctica* and potential invaders are reversed.

In conclusion, the results of this study highlight the importance of considering population origin when predicting the future dynamics of *D. antarctica*. Despite limitations, this study provides valuable insight into the species' general adaptive capabilities at high latitudes. My results suggest that plants of different origins exhibit divergent adaptations to latitude via their initial vegetative growth. Such adaptive responses could prove advantageous, as the species disperses toward higher latitudes in a patchy habitat (Lee *et al.*, 2017). However, the lower survival of Antarctic plants compared to plants from Patagonia implies a higher susceptibility to disturbance and unfavorable environmental conditions. This could pose a threat to genotypes unable to acclimate to variations in temperature, drought caused by receding permafrost, or changes in snow cover dynamics (Xiong, Mueller and Day, 2000; Vaughan *et al.*, 2003; Bozkurt *et al.*, 2021; Slatyer, Umlers and Arnold, 2022; Colesie *et al.*, 2023). On the other hand, the higher reproductive activity of Antarctic plants tends to suggest divergence in resource allocations to vegetative and generative growth between plant origins. Thus, the effect of photoperiodism together with other selection pressures may lead to changes in the genetic structure of *D. antarctica* populations and the species' population dynamics via increased reproductive connectivity. Changes in gene flow could affect the adaptive advantage of *D. antarctica* against invasive species, such as *P. annua* (Molina-Montenegro *et al.*, 2012, 2016, 2019; Chwedorzewska *et al.*, 2015). This study demonstrates that different genetic backgrounds of *D. antarctica* are capable of establishment, growth, and regulation of their reproductive timing at latitudes beyond their current range.

#### 4.4 Future directions

Although these results demonstrate that *Deschampsia antarctica* is not restricted by latitude in expanding its distribution range, it will be crucial to study how the light environment together with temperature affects species interactions and community composition. More long-term research is required both in the field and in a more controlled setting to further separate the effect of the light environment from other climatic influences on plant performance. With a more balanced collection of plant samples, especially from Antarctic populations further inland, new insights may be uncovered by future studies.

This study provides a cross-section of the flowering phenology of *D. antarctica*, but more detailed monitoring of flower development is needed to identify differences in flowering span across latitudes. The reproductive characteristics of *D. antarctica* have been previously studied in field and greenhouse conditions, but little is known about the differences in reproductive allocation between genetic backgrounds (Convey, 1996; Gielwanowska and Kellmann-Sopyła, 2015). Further understanding of the role of sexual reproduction and the reproductive timing in different light environments would provide valuable insight into the population dynamics of *D. antarctica*, as connectivity between populations is predicted to increase (Best *et al.*, 2007).

Studying the adaptability of *D. antarctica* in a more extreme light environment and a more variable climate is essential, as Antarctic biota is threatened by an increasing risk of species invasions (Colesie *et al.*, 2023). At its current range, *D. antarctica* exhibits lower plasticity and competitiveness against highly invasive plant species, such as *P. annua* (Molina-Montenegro *et al.*, 2012, 2016, 2019; Chwedorzewska *et al.*, 2015; Colesie *et al.*, 2023). However, the competitive interaction between *D. antarctica* and potential plant invaders may change as the species disperse toward higher latitudes in a warming climate. Furthermore, Antarctica has remained generally enemy-free for terrestrial plants, leaving present species potentially unadapted to novel herbivory (Convey and Stevens, 2007; Pearse *et al.*, 2013; Parnikoza *et al.*, 2018; Maggio *et al.*, 2022). With the Antarctic climate warming, the risk of successful invasions by novel herbivores is increasingly heightened (Pearse *et al.*, 2013). The intraspecific dynamics of plants and their interactions with potential invaders are also influenced by their microbiomes, which may diverge in response to climate warming or changes in day-length conditions (Saikkonen *et al.*, 2012). Thus, studying the combined effect of light environment and temperature on species interactions, for example between *D. antarctica* and microbial communities, will be crucial to predict the population dynamics of the species in future settings.

## **5 Acknowledgements**

I would like to thank members of the MICROBIPOLAR project and collaborators from Talca University for providing the plants and materials used in this study, as well as their support with fieldwork. I wish to also thank Turun Yliopistosäätiö for funding my thesis work and travels to Kevo during the summer of 2023.

I thank my supervisors Kari Saikkonen and Benjamin Fuchs for their guidance and feedback throughout this thesis. I also extend my gratitude to Jeannie Mounger for her help in designing the study setup. Lastly, I would like to acknowledge Irma Saloniemi, Satu Ramula, and Tero Klemola for their expertise and support with the statistical analyses.

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## Appendices

### Appendix 1: Export permit by the Chilean Antarctic Institute INACH



#### CERTIFICADO N° 174 /2022

El Director Nacional del Instituto Antártico Chileno, INACH, que suscribe, en virtud de la Resolución Exenta N° 647 del INACH, de fecha 24 de octubre de 2017, mediante este documento autoriza, conforme a lo establecido en el Anexo II del Protocolo al Tratado Antártico sobre Protección del Medio Ambiente, y por los principios del Comité Científico de Investigaciones Antárticas, SCAR, la recolección de las muestras científicas que se indican, para el siguiente proyecto científico:

**1. INVESTIGADORES:** Dra. Marjo L. Helander y Dr. Kari Saikkonen.

**3. INSTITUCIÓN y PAÍS:** Universidad de Turku. Finlandia.

**4. MUESTRAS COLECTADAS:**

a) Plantas antárticas (*Deschampsia antarctica*): 140 plantas individuales con raíces y algo de suelo asociado contenidas en 14 bolsas plásticas cada una con 10 plantas (cada planta de aproximadamente 50-100 g, peso bolsa 0.5-1 kg)

Peso total 10 kg

b) Semillas: 100 sobres con 10-20 semillas en una bolsa plástica. Peso total 0,1 kg

c) Plantas antárticas (*Deschampsia antarctica*): 2 plantas in dos bolsas plásticas. Peso total 250 g.

Se extiende este certificado a solicitud del investigador, para facilitar su tránsito hacia Finlandia.

  
**DR. MARCELO LEIPE CARTES**  
Director Nacional  
Instituto Antártico Chileno

JGA/

## Appendix 2: The Finnish Food Authority's importation permit for *Deschampsia antarctica*



**RUOKAVIRASTO**  
Livsmedelsverket • Finnish Food Authority

### Päätös

1 (2)

Kasvintuotannon osasto  
Kasvinterveys- ja lannoiteyksikkö

Pvm/Datum/Date  
24.11.2021

Dnro/Dnr/DNo  
7015/04.00.05.01.01/2021

Kari Saikkonen / Turun yliopisto  
Biodiversiteettiyksikkö, Natura  
20014 Turun Yliopisto

Hakemuksenne kasvinterveydellistä maahantuonnin poikkeuslupaa varten, saapunut 12.11.2021

### Päätös maahantuonnin poikkeusluvasta

#### Hakemus

Kari Saikkonen / Turun yliopisto hakee maahantuonnin poikkeuslupaa Antarktikselta ja Arktiselta alueelta (Pohjois-Eurooppa) tutkimustarkoitukseen kerätyille mikrobi- ja kasvinäytteille (Kasvit: *Deschampsia arctica*. Siemenet: *Poa annua*. Sammalpaakut: *Pohlia nutans*, *Ceratodon purpureus* ja *Polytrichum juniperinum*). Maahantuonti tapahtuisi kolmessa erässä vuosien 2022, 2023 ja 2024 aikana. Tutkimustoimintaa varten on haettu tilapäisen eristystilan hyväksyntää.

Poikkeuslupan tarve on se, että kyseisten tuotteiden maahantuonti on kielletty tai vaadittavaa kasvinterveystodistusta luonnosta kerätyille kasveille tai muille tuotteille ei ole mahdollista saada.

#### Päätös

Ruokavirasto hyväksyy hakemuksessa mainittujen maanäytteiden maahantuonnin tutkimustarkoitukseen poikkeusluvalla seuraavasti:

1. Alkuperämaa: **Antarktis ja Arktinen alue (Pohjois-Eurooppa)**
2. Tuote ja määrä: **Näytteitä kolme lähetystä, yhdessä lähetyksessä *Deschampsia antarctica* kasveja 250 kpl, *Poa annua*, siemeniä 250 kasvista ja sammalpaakkuja *Pohlia nutans*, *Ceratodon purpureus* ja *Polytrichum juniperinum* halkaisijaltaan n. 5 cm paakkuja, 100 kpl kutakin**
3. **Näytteet tuodaan ja niitä säilytetään hyväksytyssä tilapäisessä eristystilassa; Ruissalon kasvitieteellinen puutarha, Turun yliopisto Tutkimuskasvihuone 6 (karanteenikasvihuone) Ruissalon puistotie 215, 20100 Turku**
4. **Lähetäjä/tuoja: Kari Saikkonen / Turun yliopisto, Biodiversiteettiyksikkö, Natura, 20014 Turun Yliopisto, 040-6683468, karisaik@utu.fi**
5. **Tutkimuksesta vastaa: Kari Saikkonen, 040-6683468, karisaik@utu.fi ja Marjo Helander 050-3369566, helander@utu.fi**
6. **Näytteiden tuontiajankohta: kolme lähetystä vuosien 2022, 2023 ja 2024 aikana**
7. **Tutkimustoiminnan kesto: 1.1.2022-31.8.2025**

**Ruokavirasto**  
PL 200, 00027 RUOKAVIRASTO  
Puh. 029 530 0400 (vaihe)  
ruokavirasto.fi  
Y-tunnus: 2911686-7

**Livsmedelsverket**  
PB 200, 00027 LIVSMEDELSVERKET  
Tfn 029 530 0400 (växel)  
livsmedelsverket.fi  
FO-nummer: 2911686-7

**Finnish Food Authority**  
P.O. Box 200, FI-00027 FINNISH FOOD AUTHORITY, FINLAND  
Tel. +358 29 530 0400 (switchboard)  
foodauthority.fi  
Business ID: 2911686-7





2 (2)  
**RUOKAVIRASTO**  
Livsmedelsverket • Finnish Food Authority

## Päätös

Kasvintuotannon osasto  
Kasvinterveys- ja lannoiteyksikkö

Pvm/Datum/Date Dnro/Dnr/DNo  
24.11.2021 7015/04.00.05.01.01/2021

8. Hakemuksessa mainitut varotoimenpiteet ja Ruokaviraston ohjeen (1171/04.00.00.01/2020) vaatimukset tulee huomioida ja noudattaa mahdollisten tuhoojien leviämisen estämiseksi.

### Tuotteiden vapauttaminen karanteenista

Jos kyseiset tuotteet on tarve siirtää pois tilapäisestä eristystilasta, edellyttää se Ruokaviraston erillistä hyväksyntää, joka perustuu vähintään Ruokaviraston tekemään tuotteiden fyysiseen tarkastukseen.

### Maksut

88,00 euroa, laskutetaan

### Hyväksymistodistus

Tähän päätökseen on annettu kyseistä tuontia koskeva hyväksymistodistus (Letter of Authority), johon tulee hankkia lähettäjämäärä kasvinsuojeluviranomaisen hyväksyntäallekirjoitus ja todistus tulee esittää Suomeen tuotaessa tulli-/rajaviranomaiselle ohjeen 1171/04.00.00.01/2020 mukaisesti. Hyväksymistodistus on voimassa enintään yhden vuoden ja sen jälkeen toimijan tulee pyytää Ruokavirastolta uusi todistus. Hyväksymistodistus tulee säilyttää, kuten muutkin kyseiseen toimintaan liittyvät asiakirjat.

### Päätöksen perusteena olevat säädökset:

Kasvinterveyslaki (1110/2019)  
Kasvinterveysasetus (EU) 2016/2031  
Poikkeuslupa-asetus (EU) 2019/829  
Tuontivalvonta-asetus (EU) 2019/2122

### Muutoksenhaku

Tähän päätökseen saa hakea oikaisua Ruokavirastolta.

Yksikönjohtaja Tuula Mäki-Valkama

Ylitarkastaja Miia Pasanen

**Ruokavirasto**  
PL 200, 00027 RUOKAVIRASTO  
Puh. 029 530 0400 (vaihe)  
ruokavirasto.fi  
Y-tunnus: 2911686-7

**Livsmedelsverket**  
PB 200, 00027 LIVSMEDELSVERKET  
Tfn 029 530 0400 (växel)  
livsmedelsverket.fi  
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**Finnish Food Authority**  
P.O. Box 200, FI-00027 FINNISH FOOD AUTHORITY, FINLAND  
Tel. +358 29 530 0400 (switchboard)  
foodauthority.fi  
Business ID: 2911686-7



**RUOKAVIRASTO**  
Livsmedelsverket • Finnish Food Authority

Tämä asiakirja on laadittu ja allekirjoitettu sähköisesti.  
Dokumentet har uppsatts och undertecknats elektroniskt.  
This document has been digitally prepared and signed.

Tuula Mäki-vaikama  
Hyväksytty 25.11.2021

Miia Pasanen  
Esitehty 24.11.2021

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**Ruokavirasto**  
PL 100, 00027 RUOKAVIRASTO  
Puh. 029 530 0400 (vaihte)  
ruokavirasto.fi  
Y-tunnus: 2911686-7

**Livsmedelsverket**  
PB 100, 00027 LIVSMEDELSVERKET  
Tfn 029 530 0400 (växel)  
livsmedelsverket.fi  
FO-nummer: 2911686-7

**Finnish Food Authority**  
P.O. Box 100, FI-00027 FINNISH FOOD AUTHORITY, FINLAND  
Tel. +358 29 530 0400 (switchboard)  
foodauthority.fi  
Business ID: 2911686-7

## Appendix 3: The Finnish Food Authority's permit to release *Deschampsia antarctica* samples from quarantine in 2022



**RUOKAVIRASTO**

Livsmedelsverket • Finnish Food Authority

**PÄÄTÖS**

1554357

1 (2)

Kasvintuotannon osasto

Kasvinterveys- ja lannoiteyksikkö

Pvm/Datum/Date

18.5.2022

Dnro/Dnr/DNo

7015/04.00.05.01.01/2021

Kari Saikkonen/ Turun yliopisto  
Biodiversiteettisyksikkö, Natura  
20014 Turun yliopisto

Poikkeusluvalla tuotujen kasvien vapauttaminen karanteenista

### Päätös karanteenista vapauttamisesta

#### Hakemus

Ruokavirasto on hyväksynyt Kari Saikkosen / Turun yliopisto kasvien (*Deschampsia antarctica*) maahantuonnin tutkimustarkoitukseen poikkeusluvalla. Kasvit on tuotu Suomeen poikkeusluvalla Antarktikselta ja Patagoniasta helmikuussa 2022. Kasveille haetaan karanteenista vapauttamista.

#### Päätös

#### Ruokavirasto hyväksyy mainittujen kasvien (*Deschampsia antarctica*) vapauttamisen karanteenista.

Kasvit (*Deschampsia antarctica*) on tuotu tilapäiseen hyväksytyyn karanteenitilaan. Kasveista on poistettu maa-aines, ja maa-aines on hävitetty asianomaisella tavalla (kuumennus 120 asteessa, 1 bar, 30 min ja kompostointi). Tämän jälkeen kasveja on säilytetty kolmen kuukauden ajan hyväksytyssä tilapäisessä karanteenitilassa. Kasvit (*Deschampsia antarctica*) on käyty tarkastamassa mahdollisten karanteenituhoojien varalta 16.5.2022. Kasveissa (kasvusto/juuristo) ei havaittu tarkastuksella karanteenituhoojia eikä karanteenituhoojien oireita.

Tämän päätöksen perusteella kasvit (*Deschampsia antarctica*) voidaan vapauttaa karanteenista ja ottaa tutkimuskäyttöön.

**Maksut** 70,00 euroa, laskutetaan

#### Päätöksen perusteena olevat säädökset:

Kasvinterveyslaki (1110/2019)  
Kasvinterveysasetus (EU) 2016/2031  
Poikkeuslupa-asetus (EU) 2019/829  
Tuontivalvonta-asetus (EU) 2019/2122  
Asetus Karanteenituotteiden luovuttamisesta karanteenitilasta (EU) 2019/2148

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1554357

Kasvintuotannon osasto  
Kasvinterveys- ja lannoiteyksikkö

Pvm/Datum/Date      Dnro/Dnr/DNo  
18.5.2022              7015/04.00.05.01.01/2021

**Muutoksenhaku**

Tähän päätökseen saa hakea oikaisua Ruokavirastolta.

Päätös allekirjoitetaan sähköisesti.

Ylitarkastaja              Sari Haikola

Ylitarkastaja              Miia Pasanen

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This document has been digitally prepared and signed.

Sari Haikola  
Hyväksytty 18.5.2022

Miia Pasanen  
Esitelty 18.5.2022

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