

Freezing resistance in high arctic plant species of Svalbard in mid-summer

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It is well known that freezing temperatures put arctic and alpine plants at risk during the growing period only. Here we explore responses of high arctic plant species to a simulated early summer freezing event of $-7\text{ }^{\circ}\text{C}$. After gradual cooling, several hours at target conditions and slow thawing over 21 hours, the 12 species tested exhibited a broad damage spectrum from zero to 100%. We conclude that $-7\text{ }^{\circ}\text{C}$ is a critical temperature for many arctic taxa, and repeated freezing episodes like this would exert major changes in species abundance.

Es ist bekannt, dass arktische und alpine Pflanzen nur während der Wachstumsperiode wirklich frostgefährdet sind. Hier untersuchten wir die Reaktionen hocharktischer Pflanzenarten auf ein simuliertes fröhsommerliches Frostereignis von $-7\text{ }^{\circ}\text{C}$. Nach langsamem Abkühlen, einigen Stunden Exposition bei der Zieltemperatur und langsamem Auftauen über insgesamt 21 Stunden zeigten die untersuchten 12 Arten ein breites Schadenspektrum von null bis 100%. Wir schliessen daraus, dass $-7\text{ }^{\circ}\text{C}$ eine kritische Temperatur für viele arktische Pflanzen darstellt und wiederholte derartige Frostepisoden die Häufigkeit der Arten beträchtlich verändern würde.

Freezing resistance is the first and most fundamental environmental filter plant species have to pass to establish sustainably in periodically cold environments. The taxa found in areas with periodic freezing temperatures have to be resistant, otherwise they would not be there. However, freezing tolerance of plants has two aspects. One is the loss of certain (above-ground) organs such as leaves and flowers, another one is the complete extinction of an individual. The repeated occurrence of the first may, however, pave the way to the second. Another facet of freezing tolerance is time, which again has two dimensions, a short term and a long term. In the short term, freezing tolerance goes through seasonal cycles of acclimation, with hardening and dehardening associated with both photoperiod and experienced temperature (SAKAI & LARCHER 1987, HEIDE 2005). Plants are commonly much more susceptible when they are active, i.e. during the growing season, than during the dormant season (winter). Tissues of arctic and alpine plants may tolerate almost any temperature (some even liquid nitrogen) when they are dormant, but might be killed at temperatures between -2 and $-9\text{ }^{\circ}\text{C}$, when actively growing and flowering. Hence it is well established that extreme summer events are the critical issue to look at (for a review see KÖRNER 2003).

The climate of Svalbard is quite untypical for the given latitudinal position between 76.5° and 80.5° of northern latitude, because the Archipelago is hit by the gulf stream, causing its temperatures to lack extremes known for other high arctic and

Keywords: cold climate, frost, low temperature, Spitsbergen

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Angenommen: 20. November 2007

antarctic latitudes, both in terms of winter minima and summer maxima (ENGELSKIØN et al. 2003, PRZYBYŁAK 2007). Although the annual mean temperature is ca. $-5\text{ }^{\circ}\text{C}$ at sea level at the Longyearbyen airport station (a comparatively warm area for Svalbard; for a climate description see RØNNING 1996), the 30 year absolute minima there are $-10\text{ }^{\circ}\text{C}$ for June and $0\text{ }^{\circ}\text{C}$ for July (the lowest temperature ever measured, $-46\text{ }^{\circ}\text{C}$ in March; annual absolute maximum $+23\text{ }^{\circ}\text{C}$ in July). At sea level and in favorable regions, such as the inner Fjords, the growing season normally does not last longer than 80–100 days in the warmest places. It may be as short as 6 weeks in less sheltered coastal sites and there is hardly any higher plant growth in the polar desert north of 80° . Even the most favorable locations do not permit upright shrubs to grow. The about 165 higher plant species known for Svalbard (BROCHMANN & STEEN 1999, RØNNING 1996, ELVEN & ELVEBAKK 1996), all have their growing points (apical meristems) within a few centimeters above ground or below the soil surface (the majority), only exposing leaves and flowers to atmospheric conditions. These tissues may thus be experiencing short term low temperature extremes, while sub-surface structures would profit from the moderating influence of immersion in soil.

Although the sun is shining 24 hours in summer, and even midnight sun is quite intense, slope inclination and slope direction can cause a periodic screening of vegetation from direct insolation. While direct solar radiation is commonly causing plant temperature to rise above air temperature in the arctic (by 4–17K according to BIEBL 1968), the lack of direct insolation can cause ground surface temperatures to drop below air temperature by radiative cooling under clear sky conditions (KÖRNER 2003). Temperatures may be 2–4K below the air temperature a meteorological station might record under standard measurement conditions. In addition, altitude causes a mean reduction of 0.7K per 100 m in this area and flowering plants grow above 500 m a.s.l. in some places. Hence, plants may experience temperatures as low as $-15\text{ }^{\circ}\text{C}$ in June or $-5\text{ }^{\circ}\text{C}$ in July, at least once in a century, at the climatic conditions recorded so far. Most recently, the climate in Svalbard has warmed significantly, and most glaciers retreat (PRZYBYŁAK 2007). However, a warmer climate may not exclude/reduce the likelihood of such extreme events, but may accelerate spring development and thus, actually enhance the risk of plants becoming exposed to such conditions in June (the beginning of the growing season). It would thus be good to know how sensitive plant species actually are to summer time freezing events and whether such events could cause differential damage across species and thereby influence community composition. We explored this possibility in a small screening experiment, using fully developed, flowering plant individuals of 12 common species growing at 30 m above sea level, in Endalen 4 km east of Longyearbyen.



Fig. 1a



Fig. 1b

Methods

At least 5 mature leaves and 5 non-senescent, fully open inflorescences (except for *Saxifraga nivalis*) were collected for each of three treatments (see below) from randomly selected individuals around 6 p.m. on July 10, 2007 ($3 \times 5 = 15$ samples for 12 species). Samples were collected into and transported to the lab in 100 ml plastic vials and were exposed to the following three conditions by 8 p.m. the same day: a cool room at +5 °C (control), a freezer set at -18 °C (guaranteed freezing damage) and a freezer set to -7 °C. We had selected the -7 °C treatment because this temperature falls midway the known range of summer-time freezing damage in alpine plant species (KÖRNER 2003). All species analyzed here (Table 1) are widespread in Svalbard and classified as temperature indifferent species except *Dryas octopetala*, which is classified as weakly thermophilous, and *Petasites frigidus* and *Silene furcata*, which both are classified as distinctly thermophilous species (ELVEBAKK 1989). *Dryas octopetala* is common in the northern arctic tundra zone but does not grow in the polar desert zone. *Petasites frigidus* and *Silene furcata* are limited to the climatically more favorable inner fjord zone of Svalbard (www.svalbardflora.net).

The two groups of vials in the freezers were placed in insulating boxes, so that the lowest temperature was approached slowly (over several hours), persisted over several hours (until noon of July 11) and was slowly allowed to ramp back to +5 °C in the cool room. Temperatures were logged inside the boxes with one channel temperature loggers (± 0.2 K, Tidbit, Onset Corp., Bourne, USA). By 5 p.m. samples were removed from the cool room and immersed in distilled water in petri-dishes on white paper at room temperature (Fig. 1). The next morning (12 July) samples were inspected by eye for discoloration, turgor and/or smell and the immersion water was checked conductometrically for ion leaching (cell membrane collapse). Because the amount of tissue differed greatly (because of different leaf and flower sizes) the conductometric readings have only semi-quantitative value.

Fig. 1a and 1b: Assessment of tissue conditions after freezing treatment in petri-dishes filled with water.

Beurteilung des Gewebezustandes nach der Frostbehandlung in wassergefüllten Petrischalen.

Table 1: Ranking of examined plant species for freezing damage in leaves.

Rank	Plant species	Damage (%)	Conductivity (μS)
1	<i>Papaver dahlianum</i>	0	19
2	<i>Dryas octopetala</i>	2	17
3	<i>Petasites frigidus</i>	7	51
4	<i>Saxifraga nivalis</i>	10	54
5	<i>Salix polaris</i>	12	17
6	<i>Cerastium arcticum</i>	26	114 ^a
7	<i>Luzula confusa</i>	40	19
8	<i>Saxifraga caespitosa</i>	58	– ^b
9	<i>Oxyria digyna</i>	60	138
10	<i>Bistorta vivipara</i>	84	63 ^c
11	<i>Saxifraga cernua</i>	98	239
12	<i>Silene furcata</i>	100	383

^a Central, young part of rosette alive, outer and bigger part (older leaves) dead.

^b Some soil and dead leaf material attached to rosettes, i.e. odd reading.

^c Note, the small leaf area is causing a small signal despite large damage.

Table 2: Ranking of examined plant species by freezing damage in flowers^a.

10–30% survival, i.e. 70–90% damage	0% survival, i.e. 100% damage
<i>Oxyria digyna</i>	<i>Silene furcata</i>
<i>Dryas octopetala</i>	<i>Cerastium arcticum</i>
<i>Luzula confusa</i>	<i>Bistorta vivipara</i>
<i>Saxifraga caespitosa</i>	<i>Saxifraga cernua</i>
<i>Papaver dahlianum</i>	<i>Salix polaris</i>
<i>Saxifraga nivalis</i> ^b	

^a *Petasites frigidus* had no flowers.

^b Uncertain, flowers looked almost ok.

The visual inspection was repeated 24 hours later. In flowers we counted the number of damaged flowers, in leaves we estimated the % leaf area damaged per leaf, and calculated a mean.

Results and Discussion

The minimum temperatures recorded in the vicinity of the samples in the freezers were $-18.2\text{ }^{\circ}\text{C}$ and $-7.2\text{ }^{\circ}\text{C}$. All control tissue ($+5\text{ }^{\circ}\text{C}$) remained intact, freshly looking, and served as a reference. All -18° treated tissue was dead and served as a reference for how damaged tissue looks like. The $-7.2\text{ }^{\circ}\text{C}$ treated cohort exhibited a clearly species specific differentiation in damage, with some species/organ types completely damaged or undamaged or partially damaged (Table 1, Fig.2). Two species turned out to be difficult to assess. *Saxifraga nivalis* leaves largely looked fine, but there was significant ion leakage to the immersion water. *Luzula confusa* naturally has reddish and rigid leaves and flowers

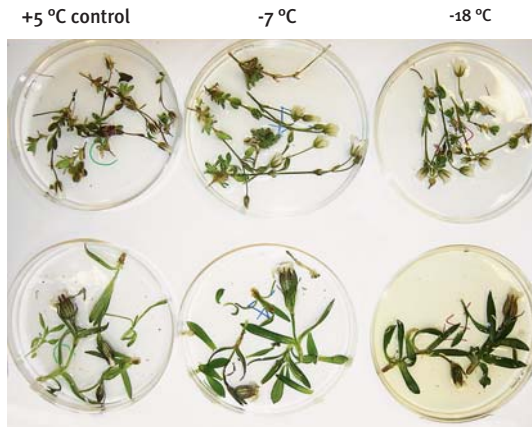
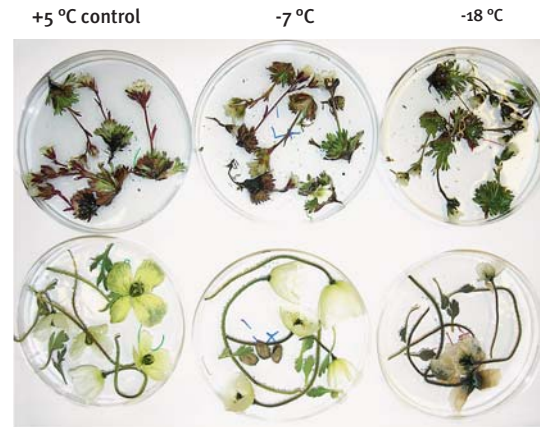
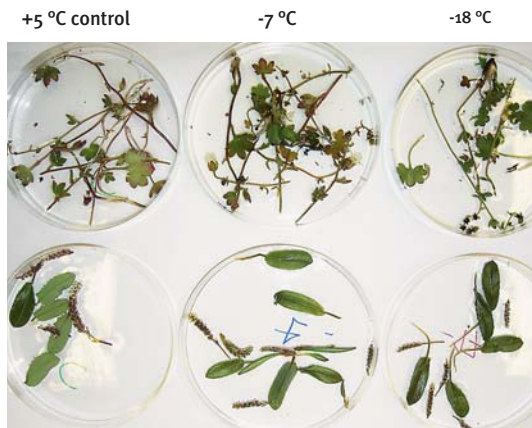
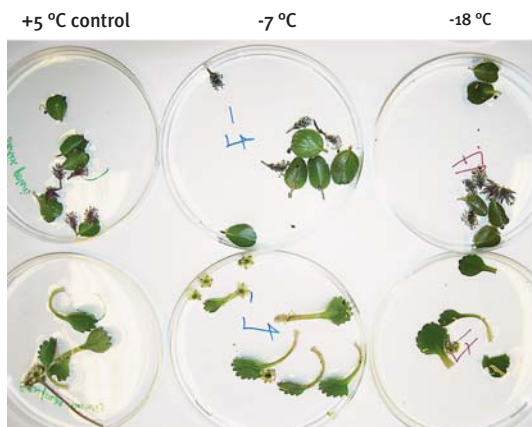
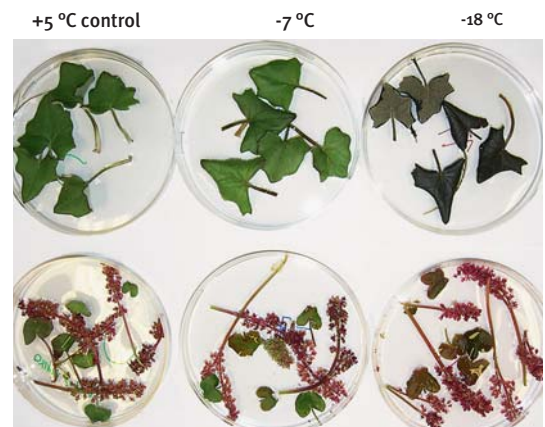
2a: *Cerastium arcticum* and *Silene furcata*2b: *Saxifraga caespitosa* and *Papaver dahlianum*2c: *Saxifraga cernua* and *Bistorta vivipara*2d: *Dryas octopetala* and *Luzula confusa*2e: *Salix polaris* and *Saxifraga nivalis*2f: *Petasites frigidus* and *Oxyria digyna*

Fig. 2a–f: Leaf and flower conditions 30 hours after thawing.
Blatt- und Blütenzustand 30 Stunden nach dem Auftauen.



Fig. 3a

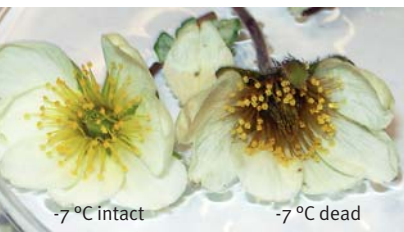


Fig. 3b

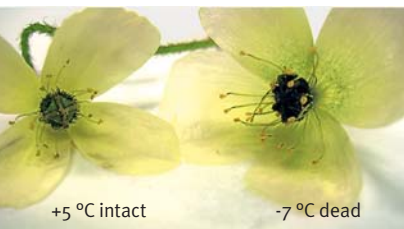


Fig. 3c

Fig. 3a–c: Close-up examples of flower conditions after the $-7\text{ }^{\circ}\text{C}$ treatment. Note the negative geotropic position of 2 *Saxifraga caespitosa* shoots after 30 hours (3a), flowers (one of each damaged at $-7\text{ }^{\circ}\text{C}$ and one undamaged at $-7\text{ }^{\circ}\text{C}$) of *Dryas octopetala* (3b) and *Papaver dahlianum* (3c).

Nahaufnahmen von Beispielen für den Zustand von Blüten nach $-7\text{ }^{\circ}\text{C}$ -Behandlung. Die Grossaufnahme von zwei *Saxifraga caespitosa*-Trieben zeigt aktiven Geotropismus nach 30 Stunden (3a), Blüten (je eine geschädigt bei $-7\text{ }^{\circ}\text{C}$ und eine ungeschädigt bei $-7\text{ }^{\circ}\text{C}$) von *Dryas octopetala* (3b) und *Papaver dahlianum* (3c).

and neither showed clear color changes nor turgor loss, nor was ion leakage obvious, but some leaves and flowers looked slightly altered. All other species/organs could be clearly judged. Damage in flowers was generally much greater, but our sample size was too small to rank species in a trustworthy manner. We thus, present two damage categories only for flowers (Table 2).

In summary, these data show that a $-7\text{ }^{\circ}\text{C}$ freezing event at that time of the year and/or developmental stage of plants, would have a dramatic impact on above ground structures of these plants in mid-summer. Yet, species known for their occurrence in the most extreme polar habitats, such as *Papaver dahlianum* showed not only no leaf damage, but even a fraction of the otherwise delicate looking, big flowers had survived (Fig. 3c). *Dryas octopetala* commonly ranked as weakly thermophilous (ELVEBAKK 1989), survived with almost 100% intact foliage, and even part of the flowers survived (Fig. 3b). Even more surprising, *Petasites frigidus*, ranked as distinctly thermophilous (ELVEBAKK 1989), showed over 90% survival. Thus, the distribution of these species is probably not limited by extreme low temperatures. Rather, other factors such as limited ability for sexual reproduction (BROCHMANN & STEEN 1999, RÖNNING 1996) may limit its distribution in Svalbard.

Of the 5 individuals (leaf rosette with inflorescence) of *Saxifraga caespitosa*, 2 individuals showed negative geotropism over night, i.e. they uprighted their fully intact flowering shoots from the flat position in the petri-dish (Fig. 3a). For half of the tested species, such a freezing event would eradicate the complete reproductive investment of that season, but in these species most or all leaves would also be killed.

Silene furcata, the other distinctly thermophilous species analysed here, emerged as the most sensitive species. Hence, it may serve as an indicator species of favourable site conditions, provided such selective freezing would occur. The plant genus does not seem to be of predictive value, given that *Saxifraga* exhibits particularly sensitive and robust representatives. *Silene acaulis* was found to be very robust against mid-summer freezing near Tromsø (surviving -8.5 to $-9\text{ }^{\circ}\text{C}$; JUNTILA & ROBBERECHT 1993). The latter authors had confirmed earlier evidence that growth temperatures have a strong influence on actual freezing resistance. It was thus considered that repeated warm episodes in the arctic could weaken freezing tolerance (MARCHAND et al. 2006). We sampled plants during a very warm period, with noon air temperatures of around $+12\text{ }^{\circ}\text{C}$, which could have sensitized our test plants.

The low freezing resistance of *Saxifraga cernua* was unexpected given that this species is common in the polar desert zone and is one of the species reaching highest up in the mountains in Svalbard ($>900\text{ m a.s.l.}$, SUNDING 1960). Also, some other hardy arctic species such as *Bistorta vivipara*, *Oxyria digyna* and *Saxifraga caespitosa* showed over 50% freezing damage. Common for all these species is their ability to produce viable seeds or bulbils

even at cold sites (COOPER et al. 2004). Recruitment from seed bank may therefore replace any lost individuals due to freezing events and thus secure long-time survival of these species even at the coldest sites in the Arctic.

It can be concluded that during the growing season, freezing temperatures of -7 °C or possible less, would damage a significant fraction of the arctic flora. Given that -10 °C had been recorded for air temperature in June, this means that earlier spring growth in the course of global warming at an otherwise unchanged likelihood of the occurrence of such an extreme events would lead to massive losses of tissue and above ground productivity. It would be interesting to know, whether low temperature extremes during the growing season had in fact become rarer as the overall means in temperatures rose in recent years. Our survey indicates the critical range of temperature to be explored in a more detailed assessment and that biodiversity (species identity) matters a lot. Overall, the data appear to match the summer freezing tolerance known for alpine plants of the temperate zone (KÖRNER 2003) and do not indicate a greater frost hardness for these high arctic plants as had been suggested from experiments with *Saxifraga oppositifolia* under controlled growth conditions (JUNTILA & ROBBERECHT 1992).

Acknowledgements

UNIS organized and financed this arctic plant ecology course in July 2007 and provided the needed infrastructure. The participating students contributed the practical work and are listed on the title page.

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