

FREEZING RESISTANCE OF ARCTIC TUNDRA PLANTS ON SVALBARD

by
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INTRODUCTION

Temperature largely determines the distribution of vascular plants in northern latitudes. Extreme seasonal variations are particularly limiting in the high arctic. Species native to these habitats are resistant to the low freezing temperature extremes in winter and an occasional freeze during summer. Plants may freeze without injury (Scholander et al. 1953).

Perennial herbaceous plants of the tundra communities, in contrast to woody perennials, maintain growth capability throughout winter. Herbaceous plants are vulnerable to freezing during the growing season, but the floral, leaf and shoot primordia become modified in the fall. These organs can then withstand exposure to otherwise lethal winter temperatures (Steponkus 1979, Kacperska 1983). Seasonal variation in freezing resistance has been investigated in alpine plants in Sapporo, Japan (44°N) (Sakai & Otsuka 1970) and in plants from West Greenland (69°N) (Biebl 1968), but never in a group of arctic tundra species tested directly from the "in situ" temperature regime as far north as Ny-Ålesund, Svalbard (79°N).

Investigation of summer and winter freeze-killing temperatures were conducted to determine freezing resistance of ridge-top and snowbed arctic species. In winter, plants are usually insulated from the severe climate by ice and/or snow cover, but occasionally such a cover is lacking. Simulation experiments representing a particularly cold and dry climate with and without snowcover could indicate the plants capacity to withstand a more severe climate than they do today. Ridge plants were chosen from exposed and dry habitat conditions that probably were more widespread during Weichselian times (Troitsky et al. 1979).

MATERIALS AND METHODS

Study site

Plants were growing at a tundra site called "Gåsebu" in Kongsfjorden on northwest Svalbard (Fig. 1). Monthly mean and mean monthly extreme maximum and mean monthly extreme minimum temperatures for Ny-Ålesund (1971-1980) were measured at 2 m above the ground in a meteorological hut (Figs. 2 and 3). Mean monthly temperatures for Ny-Ålesund (1971-1980) (Aune 1982) are shown with monthly maximum of 5°C in July and minimum of -13°C in February and March (Fig. 2). The monthly lows for April 1985 through March 1986 show July with the highest minimum temperature, 3°C and March with the lowest, -42°C (Fig. 3). Annual precipitation in Ny-Ålesund is 385 mm/year. The sun comes above the horizon on 23 March each year. Daylight is continuous from 17 April to 25 August (Aune 1982).

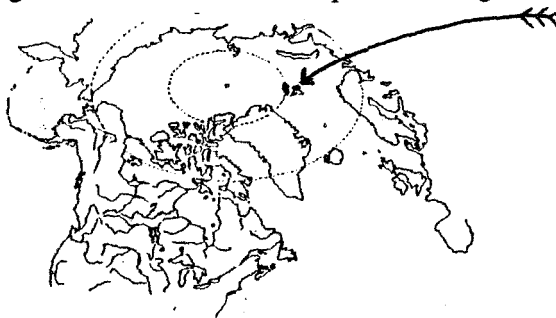


Figure 1. Location of Svalbard at 79°N latitude above the arctic circle.

Presented at the Western Snow Conference, April 17-19, 1990, Sacramento, California.

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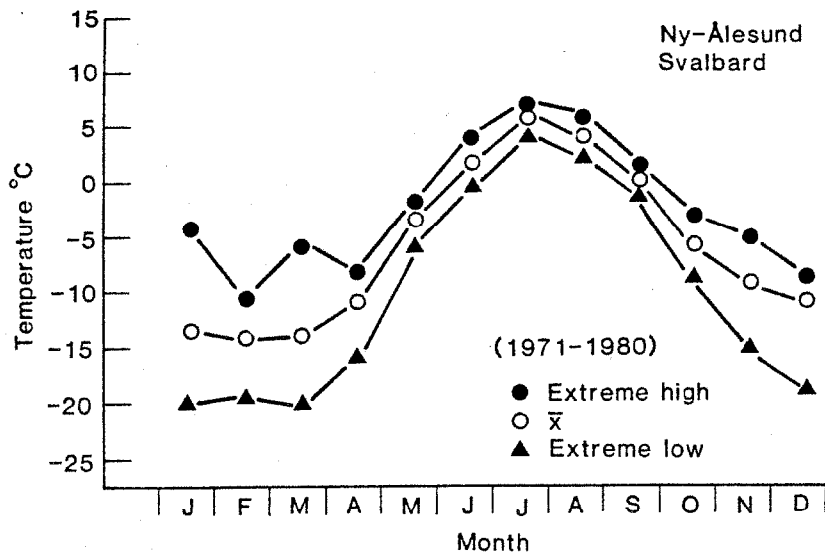


Figure 2. Monthly mean and mean monthly extreme maximum and mean monthly extreme minimum temperatures for Ny-Ålesund, Svalbard, 1971-1980.

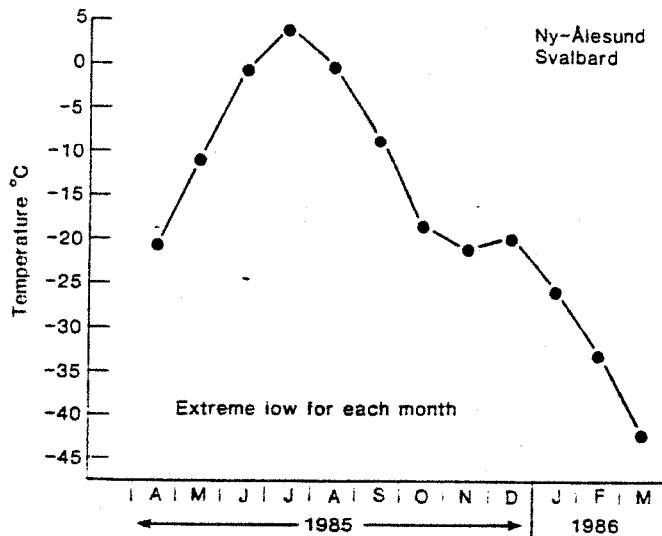


Figure 3. Extreme low monthly temperatures April 1985-March 1986.

Species investigated include:

- Carex misandra* R.Br.
- C. nardina* Fr.
- C. rupestris* All.
- Cassiope tetragona* (L.) D. Don
- Cerastium arcticum* L.
- Dryas octopetala* L.
- Equisetum variegatum* Schleich.
- Pedicularis hirsuta* L.
- Polygonum viviparum* L.
- Salix polaris* WG.
- Saxifraga aizoides* L.
- S. oppositifolia* L.
- Silene acaulis* (L.) Jacq.

Species have high arctic circumpolar distribution except *Saxifraga aizoides*, *Cerastium arcticum* and *Pedicularis hirsuta* which have a more restricted amphi-atlantic distribution, and *Salix polaris*, an amphi-pacific plant.

Vegetation

Plants were collected from soil on ridges rich in lime, in a vegetation complex named "Kobresio-Dryadion" alliance in phytosociological sense, comprising four "Dryadetum" associations sensu Rønning (1965). Carici rupestri-"Dryadetum" (Rønning 1965) is widespread on raised and well-drained surfaces in Svalbard. It has high cover of *Dryas octopetala* and *Carex rupestris*. *Silene acaulis*, *Saxifraga oppositifolia*, *S. aizoides*, *Pedicularis hirsuta*, *Polygonum viviparum*, *Carex misandra*, and *C. nardina* are also present. Carici nardino-"Dryadetum" and Cassiopo tetragonae-"Dryadetum" occur locally. Species comprising the *Dryas* communities are the most likely to have survived glaciations based on present day distribution and ecology (Rønning 1965, Funder 1979).

Temperature recording

Squirrel (Grants) and Delta (Delta-T Devices Ltd.) data-loggers recorded temperatures at vegetation level, within the canopy, 2 m above the ground and under the insulation of the snow. Thermocouples were shaded from direct sunlight. Data were logged hourly at the tundra site "Gåsebu" from 4 July to 10 August, 1986 at vegetation level and 2 m above the ground. During the period 20 March to 10 May, 1987 hourly temperatures were recorded at 1.5 m and on the tundra vegetation at Gåsebu and in a potted plant in the greenhouse from 20 March until 12 April.

Freezing experiments

Test 1. "Growing season".

Clumps of tundra vegetation, approximately 30 cm², with 1-6 species, from "Gåsebu" were wrapped in aluminium foil and packed in boxes with styrofoam chips on 19 July 1986. Clumps were cooled at 3 °C/hour to temperatures of -2 °C, -4 °C, and -23 °C in a "bio-freezer" at the Norwegian Polar Research Institute's Station in Ny-Ålesund, Svalbard. Temperatures in the plant canopies were monitored continually during the freezing tests with thermocouples and data loggers. This assured plant exposure to appropriate low temperatures. They were maintained at the cold temperature 10 hours before removal from freezing. Control samples, packed in the same way were maintained on the tundra.

Plants were then slowly thawed for 24 h while still wrapped in foil. They were placed outdoors after the tests and injury was scored each week as 1: normal plants, 2: injured and 3: dead, based on the extent of browning.

Test 2. "Midwinter".

Plants were collected during fall 1986 while soils were still thawed. Approximately 20 individuals of each species were collected in clumps of tundra from the "Gåsebu" site and placed in 10 cm diameter plastic pots: *Carex misandra*, *C. rupestris*, *Dryas octopetala*, *Pedicularis hirsuta*, *Polygonum viviparum*, *Saxifraga aizoides*, and *Silene acaulis*. Pots were placed on the tundra vegetation at "Gåsebu" where they experienced the natural tundra winter conditions.

Pots were excavated from the snow cover and taken from the field on 25-28 March, 1987 and cooled in a biofreezer at a rate of 3 °C/h to -20 °C, then 10 °C/h to -50 °C. Plants were removed after 10 h at -36 °C and -50 °C and thawed for 24 h while still packed in foil. Clumps were unpacked, placed at 18 °C in continuous light and watered at regular intervals. Survival was recorded after 3 weeks. Percent of each plant surviving was recorded as well as vitality on a scale of 1-5 (5 = most vital).

Test 3. "Continental climate".

Pots containing about 20 individuals of each test species were placed in the greenhouse in Ny-Ålesund, Svalbard fall 1986. Here they were not covered with snow and therefore experienced greater diurnal fluctuations than the snow-insulated plants at the "in situ" tundra site at "Gåsebu". This experiment simulated the probably more arid and hence, snow-free conditions, which may have existed during glacial times. The drying effects of wind were, however, not simulated. Freezing tests as in test 2 were conducted 2-4 April 1987 to temperatures of -31°C and -57°C . Freezing to exactly the same temperatures was not easily accomplished due to technical construction of the biofreezer.

RESULTS

Temperature measurements

Daily maximum and nightly minimum temperatures from the "Gåsebu" site ranged between almost 30°C and 1°C during the summer 1986 (Fig.4).

Air temperatures (1.5 m above ground level) at the "Gåsebu" site ranged from lows of almost -30°C in March to highs reaching above 0°C in mid to late April and May (Fig. 5). At vegetation level daily maximum and nightly minimum variation was rarely greater than 4 degrees. While in the greenhouse temperatures fluctuated daily as much as 26 degrees, for example in early April measurements of 18°C and -8°C were made within a 14 hour period (Fig.5).

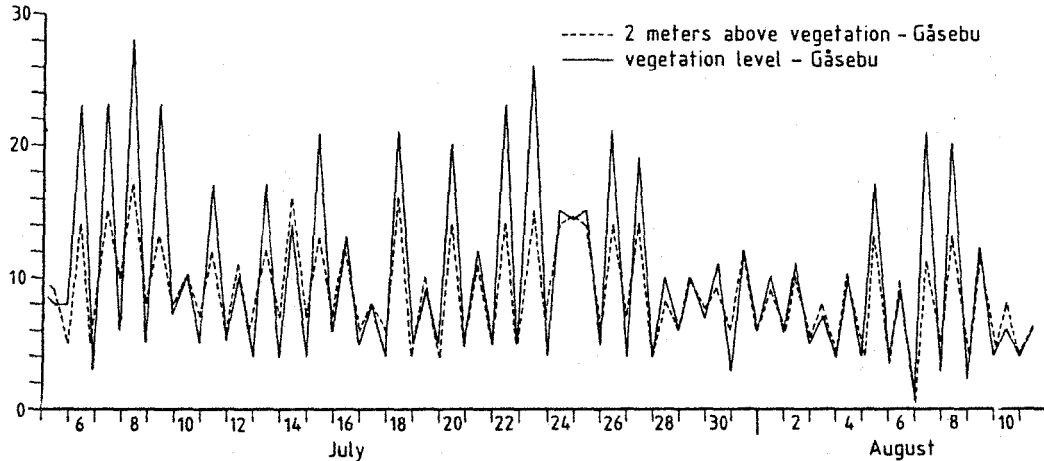


Figure 4. Daily maximum/nightly minimum extreme temperatures recorded 2 m above and at vegetation level at the "Gåsebu" site, summer 1986.

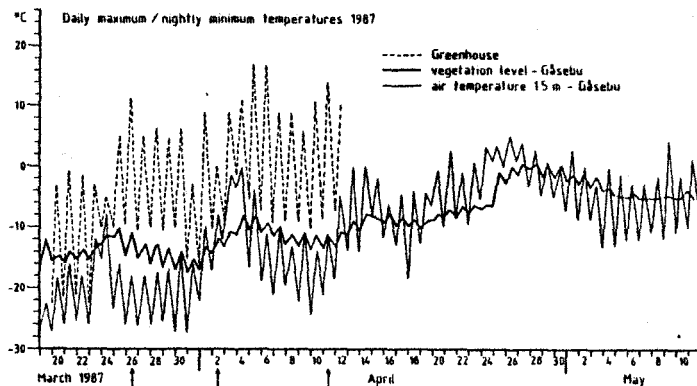


Figure 5. Daily maximum/nightly minimum extreme temperatures recorded 1.5 m above and below 30 cm snow on the 18 cm thick layer of ice on the experimental potted plants at the "Gåsebu" site and in the greenhouse, winter 1987. Arrows indicate dates of freeze testing.

Freezing experiments

The freezing resistance of plants varied considerably between July 1986 and March/April 1987. Plants surviving only -2°C to -4°C during the growing season had freeze-killing temperatures below extremes of -57°C in winter 1987 (Tables 1-3).

Polygonum viviparum, *Cassiope tetragona*, *Pedicularis hirsuta*, *Carex nardina*, *Carex rupestris* and *Salix polaris* survived only -4°C in summer (Table 1). All species were killed by exposure to -23°C. *Polygonum viviparum* and *Cassiope tetragona* showed sensitivity to injury at temperatures just below zero.

Species	Degree of freezing injury 1:normal; 2:injury; 3:dead				
	Gåsebu field site Treatment:	C	-2	-4	-23
<i>Polygonum viviparum</i>		1	3	3	3
<i>Cassiope tetragona</i>		1	2	3	3
<i>Pedicularis hirsuta</i>		1	nd	3	nd
<i>Carex nardina</i>		1	2	3	3
<i>Carex rupestris</i>		1	2	3	3
<i>Salix polaris</i>		1	2	3	3
<i>Dryas octopetala</i>		1	2	2	3
<i>Silene acaulis</i>		1	2	2	3
<i>Carex misandra</i>		1	1	2	3
<i>Saxifraga aizoides</i>		1	1	2	3
<i>S. oppositifolia</i>		1	1	2	3

Table 1. Freezing resistance of arctic dryadion plants in summer (July 19, 1986). Degree of freezing injury recorded (August 7, 1986) was expressed as follows; 1: normal plants; 2: injury; 3: dead. nd = no data.

All species of winter tests 2 "Midwinter" and 3 "Continental climate" survived freezing to -50°C (Tables 2 and 3) except *Pedicularis hirsuta*. Most individuals of *Dryas octopetala* died in the "in situ" field "Gåsebu" treatment. *Polygonum viviparum* flowered in the "in situ" field "Gåsebu" treatment, and *Saxifraga aizoides* formed buds in both tests. Tops of many of the cushion plants, *Silene acaulis* and *Saxifraga oppositifolia* were dried out, possibly due to water stress. However, when these species were surrounded and protected from exposure by other species, as *Carex misandra*, such injury was not observed.

Table 2. Freezing resistance of "snow-insulated" arctic tundra plants in Winter 1987 after 3 weeks recovery.

Species	Temperature °C			-50		
	No. of pots	mean proportion of living material $\bar{x} \pm$	Vitality (\bar{x})	No. of pots	mean proportion of living material $\bar{x} \pm$	Vitality (\bar{x})
<i>Saxifraga aizoides</i>	3	25.3 ± 30.1	5.0	4	23.8 ± 13.8	4.5
<i>S. oppositifolia</i>	7	34.3 ± 16.2	3.7	5	40.0 ± 12.3	4.0
<i>Silene acaulis</i>	4	26.2 ± 36.8	4.7(1d)	3	40.0 ± 17.3	4.0
<i>Dryas octopetala</i>	4	10.0 ± 14.1	5.0(2d)	5	6.8 ± 6.6	3.5(1d)
<i>Salix polaris</i>	6	80.0 ± 15.5	4.6	6	45.0 ± 10.5	4.2
<i>Carex misandra</i>	4	50.0 ± 11.6	4.5	3	16.7 ± 5.8	3.3
<i>Pedicularis hirsuta</i>	2	70.0 ± 14.1	4.5	2	0 ± 0	0 (2d)
<i>Equisetum variegatum</i>	5	76.0 ± 24.1	4.6	3	46.7 ± 35.1	4.3
<i>Carex rupestris</i>	7	49.3 ± 25.9	4.4	4	23.8 ± 11.1	4.3
<i>Polygonum viviparum</i>	6	60.0 ± 35.2	4.8	7	64.3 ± 27.0	4.0

(1) mean ± SD

(2) Vitality - 1-5 scale, where 5 is most vital

Table 3. Freezing resistance of "exposed" arctic tundra plants in Winter 1987 after 3 weeks recovery.

Species	Temperature °C			-57		
	No. of pots	mean proportion ⁽¹⁾ of living material	Vitality ⁽²⁾	No. of pots	mean proportion of living material	Vitality
<i>Saxifraga aizoides</i>	3	35.0 ± 13.2	4.7	4	32.5 ± 9.6	4.5
<i>S. oppositifolia</i>	11	44.1 ± 29.9	4.4	13	23.1 ± 16.4	4.2
<i>Silene acaulis</i>	6	32.5 ± 19.4	4.2	9	19.7 ± 27.4	4.1(2d)
<i>Dryas octopetala</i>	3	40.0 ± 10.0	4.7	4	28.8 ± 8.5	4.8
<i>Salix polaris</i>	6	61.7 ± 20.4	4.3	9	37.8 ± 22.8	3.9(1d)
<i>Carex polaris</i>	7	55.7 ± 18.1	4.3	8	40.0 ± 5.4	4.3
<i>Pedicularis hirsuta</i>	4	27.5 ± 32.0	4.5(2d)	7	0 ± 0	0 (7d)
<i>Equisetum variegatum</i>	2	65.0 ± 21.2	4.5	6	32.5 ± 28.2	4.0
<i>Carex rupestris</i>	9	56.7 ± 22.9	4.1	8	52.5 ± 11.7	4.3
<i>Polygonum viviparum</i>	8	70.0 ± 31.2	4.4	8	44.4 ± 10.5	3.9

(1) mean ± SD

(2) Vitality 1-5 scale, where 5 is most vital

DISCUSSION

Continuous sunlight warms up the surface of the soil and plants. These maintain higher temperatures for a longer period than the ambient air. This heating spreads to some extent above and below the ground level. The microclimate is most favorable as long as the sun shines. However, in cloudy weather the surface layer may remain cool and lag behind the warming air temperature. Wilson (1957) reports leaf temperatures are higher than the air in polar regions, but this is not always the case. At the tundra field site at "Gåsebu" early morning temperatures are coldest and on clear nights, temperatures at vegetation level do fall below that of the air (Fig. 4).

During active growth plants are more vulnerable to freezing temperatures than during winter, compare -4°C to under -57°C. Vitality after treatment differs between individuals within a species. Freeze-killing temperatures of Svalbard tundra species fall within the range of other arctic/alpine species. Frost resistance of *Rubus chamaemorus* was investigated in plants from a bog at Tromsø, Northern Norway (69°N, alt. 75m) and found to be -4°C in summer (Kaurin et al. 1981). Fast growing alpine plants from West Greenland (69°N) survived freezing to -5°C in summer (Biebl 1968).

Many of the arctic species show higher sensitivity to freezing summer temperatures than alpine species in humid, temperate regions. Species in this study did not tolerate summer freezing to below -4°C, while herbaceous plants in temperate mountains had lethal temperature of -6°C to -8°C (Sakai and Larcher 1987). Plants of the high temperate alpine climates also had freeze-killing temperatures of -5°C to -7°C (Sakai and Otsuka 1970) during the active growing season in summer. This may be an apparent adaptation to periodic lower freezing temperatures in the alpine during the growing season.

On Svalbard, in September and October mean monthly temperatures approached -10°C (Fig. 2) with extreme lows reaching -22°C in November (Fig. 3). Lows of -20°C are not uncommon in February and March and in 1986 they were -33°C and -42°C respectively. The primordia hardened in the fall and maintained growth capacity after freezing to below -50°C.

Sakai and Otsuka (1970) reported that shrub twigs acquire resistance to freezing without exposure to low temperatures right after cessation of annual shoot expansion. They hardened abruptly when exposed to low temperatures.

In early October, alpine plants on Mt. Kurodake (44°N, alt. 1,984 m) in Sapporo, Japan with mean air temperatures close to 0°C, increased resistance from -5°C to freezing at -15°C to -70°C. This rate of increase in freezing resistance varied considerably among species growing in the same locality (Sakai and Otsuka 1970). In another test, hardening increased in *Rubus chamaemorus* during the fall and in November -11.5°C was tolerated (Kaurin et al. 1981). A freezing experiment with ecotypes of *Salix polaris*, including plants collected from Svalbard (but tested in Tromsø) maintained growth capacity after a testing of exposure to -35°C, *Salix polaris* of this study even survived temperatures of -57°C with good vitality (Table 3). The lethal temperature for the Tromsø ecotype was between -25°C and -35°C (Paus and Kaurin pers. comm.). The frost hardiness of the perennating organs is decisive for plant survival.

Winter survival is a complex of interrelated events; in addition to cold, wind and dehydration are additional stress factors. Above-ground plant parts mediate the effect of severe climate by functioning as windbreaks, and by providing protection by insulating individuals growing nearby. Dense growth of species like *Carex misandra*, can reduce potential water stress conditions by increasing boundary layers of low-growing neighboring species like *Saxifraga oppositifolia* and *S. aizoides*. Even in snowbed sites overwintering buds are exposed to extreme ambient temperatures and wind desiccation before the insulating snow cover is established.

Exposed *Dryas* ridge sites may resemble Weichselian conditions and plants growing here are preadapted to a more pronounced continental climate: warm summer temperatures, colder winters and little precipitation. Of the predominating vegetation in the area, the *Dryas* ridge vegetation has the lowest average soil moisture content and the highest average summer temperature at ground surface and 2 cm depth (Sendstad and Sveum 1985). When wind-blown, such ridge vegetation is exposed to greater fluctuations of air temperature as opposed to below the protective snow-cover in winter and early spring.

Plant survival in the simulated "continental climate" conditions indicates that the tested tundra species may be adapted to withstand a more severe winter and desiccating climate than they do today. Hence, the persistence of many species of this ridge vegetation through recent glacial times (Weichselian and possibly earlier) in the suggested ice-free sites on Svalbard (Forman and Miller 1984) was probably not limited by low temperatures and/or desiccation.

Future research in the physiology of frost resistance in vascular plants should focus on the effects of decreased water potential. Such would explain the role of osmoregulatory mechanisms in cold acclimation of high arctic species.

ACKNOWLEDGEMENTS

The project was made possible by the support from the Norwegian-American Foundation Marshall Fund, NAVF, Norwegian Polar Institute and a NATO post-doctoral grant. I am grateful for field assistance from Erling Johan Solberg, Paal Johansen and Øystein Jolma. Logistic support from the Norwegian Polar Research Institute and Kings Bay Coal Company is appreciated. The manuscript benefitted from review by Åse Kaurin and by discussions with Eilif Dahl, Knut Asbjorn Solhaug and Olav Junttila.

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