Alpine garden plants from six continents show high vulnerability to ice encasement

Icy surfaces impose challenges for northern societies, wildlife and agriculture. However, the impacts of anoxic ground-ice on non-agricultural plants is poorly studied. During the winter of 2009/10, an extreme winter warming event led to thick ground-ice layer development in the World's northernmost botanical garden in the city of Tromsø in sub-Arctic Norway due to much rain on warm days intervening with cold dry days. After ice melt in late spring we undertook an assessment (not part of any monitoring programme) of plant mortality, testing whether certain growth forms, geographical origins, or terrain features were more vulnerable to stress. We found that mortality was negatively correlated with terrain slope, that cryptophytes (plants with resting buds beneath the surface of the ground) were most vulnerable, and that high soil drainage improved survival. Vegetation greenness (NDVI) reached an unprecedented minimum in the summer of 2010 and remained low for two more years. The results suggest that more investigations of the impacts of ground-ice are needed to understand better how alpine ecosystems will change with increasing climate change. This study shows that garden studies may be a valuable supplement to field studies, as plants of different origins can be studied under similar climatic conditions.

Keywords: *anoxia, extreme event, NDVI, plant mortality, winter warming*

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Introduction

Ongoing climate change has caused large reductions in the extent and duration of snow cover (Liston & Hiemstra 2011; Walsh et al. 2011). It also affects the properties of the snowpack in regions where snow still is common. Increasing frequency of warm spells in winter cause partial snowmelt, which lead to shallower snowpack, which, upon return to freezing, become compact with one or multiple ice layers (Johansson et al. 2011; Vikhamar-Schuler et al. 2016). Ice layers on the ground is a recurrent problem for alpine and Arctic mammals. Large grazers such as reindeer/caribou and muskoxen are not able to dig through a hermetic ice sheet (Forchhammer & Boertmann 1993; Riseth et al. 2011; Hansen et al. 2014). Starvation and population crashes are often the result. Small mammals such as lemming are dependent on air-filled spaces in their subnivean environment (the subnivium); hence, transformation of the basal snow into ice reduces the survival rate (Pauli et al. 2013).

The impacts of ground-ice on vegetation is much less known. Most knowledge is from northern agricultural grasslands in Canada, Iceland and Norway. The anoxic conditions under the ice sheet is detrimental to grasses due to toxifying accumulation of carbon dioxide, ethanol and lactic acid in the leaves (Andrews 1996; Höglind et al. 2010).

The conditions under an ice sheet are similar to the anoxic conditions during inundation. Hygrophytes survive inundation by transporting oxygen through their aerenchyma, while meadow grasses lack such tissues and are therefore more vulnerable to both inundation and ice encasement (Crawford 1978; Andersen 1986). Furthermore, plants with low respiration rates at cool temperatures have lower rates of accumulation of anoxic metabolites. Northern species or ecotypes tend to have lower rates than southern species or ecotypes and may therefore be more tolerant of ice encasement (Eagles 1967; Andersen 1986; Crawford et al. 1994; Höglind et al. 2010). Consequently, it has been proposed that high-Arctic species are the most tolerant plants to ice encasement (Crawford et al. 1994). However, experimental icing show that the Arctic-alpine snowbed forbs *Omalotheca supina* and *Sibbaldia procumbens* and the dwarf shrub *Cassiope tetragona* have very low tolerance of ice encasement (Gudleifsson 2009; Milner et al. 2016), while sub-Arctic ecotypes of *Empetrum nigrum* and *Vaccinium vitis-idaea* show reduced reproduction and increased electrolyte leakage under certain icing conditions (Preece & Phoenix 2014). Sub-Arctic lichens are intolerant of ice encapsulation at mild subfreezing temperatures (Bjerke 2011), but show no mortality after being encapsulated in ice at temperatures below −10 °C (Bjerke 2009). Overall, this shows that we are far from understanding the role of ground-ice in regulating primary productivity and ecosystem structure of boreal, alpine and Arctic ecosystems.

Winter climate at high northern latitudes will probably change drastically during the next decades (Vikhamar-Schuler et al. 2016). Higher average temperatures and higher frequency of warm spells will have strong impacts on the snowpack (Walsh et. al. 2011; Pauli et al. 2013). In areas without complete snowmelt, ground-ice will become more common and expose plants to a stress type to which they are not selected (Gudleifsson 2009). This will have unknown consequences on plant communities and trophic interactions and should therefore be elucidated in further detail (Bokhorst et al. 2016). In cases where little information is available from experimental studies, observations in the aftermath of real hazardous events may provide much added knowledge (Jentsch et al. 2007; Callaghan et al. 2013; Phoenix & Bjerke 2016).

We here report on results from such case study. We estimated damage ratios to a wide variety of primarily alpine plant species after an extreme icing event that took place in Tromsø Arctic-Alpine Botanic Garden, the World’s northernmost botanical garden, situated in Tromsø, North Norway, during the winter of 2009/10. In the aftermath of damage, we collected data to elucidate which growth forms and landscape features that were most strongly affected, and we studied the vegetation performance of the Garden area in the years before and after the event using remotely-sensed data. The primary objective of this study was to shed light on contrasting vulnerabilities to winter stress related to differences in growth form, geographical origin and microhabitat characters.

Materials and Methods

Observations of an extreme event

An extreme accumulation of ground-ice and soil frost took place in sub-Arctic Norway during the winter of 2009/10, which caused much nuisance to this northern society (Bjerke et al., 2014, 2015). That winter was characterized by large temperature fluctuations involving several freeze-thaw events (Fig. 1). Ten periods of one or several days with daily mean average temperature above 0 °C were recorded during the period from the first freezing event in November to the end of February. The freezing periods were mostly dry, while the thaw periods were associated with much rain; 72 % of the precipitation in January and February fell on days with daily mean temperature above 0 °C (black squares in Fig. 1b). The rain quickly froze during freezing periods, which led to an extreme build-up of ice on the ground (Bjerke et al. 2015). This winter had the lowest temperature sum on snow-free days of all winters between 1998 and 2014, thus the combination of lack of an insulating snow layer and long periods of freezing led to extremely deep soil frost (Bjerke et al. 2015). In the city of Tromsø, soil frost to at least 150 cm depth was reported from a nearby graveyard (Bjerke et al. 2014). Agricultural yields the following growing season were strongly reduced, because large areas of grasslands died from long-term ice encasement, and because spring farming was much delayed due to persistent soil frost (Bjerke et al. 2015).

Study area, plant material and mortality assessment

Tromsø Arctic-Alpine Botanic Garden is situated three latitudinal degrees north of the Arctic Circle in the boreal (sub-Arctic) part of Norway (Troms County, North Norway, 69°40’ N 18°58’ E). It opened in 1994 and became the World’s northernmost botanic garden (Elvebakk 2008). The Arctic and alpine species of the garden are mostly cultivated in hilly rock landscapes on well-drained soils dominated by mineral components between rocks and boulders, but partly also in flat to gently sloping terrains on more organic soils. The species grown in the Garden originate from cold areas from most parts of the world. Plants are partly grown in geographically defined collections, partly defined by plant families. Plant names follow the International Plant Name Index (2016). Weather data presented are from the station Holt in Tromsø (69°39’ N 18°54’ E), which is located 3.5 km SW at approximately the same altitude (12 m) as the botanic garden. Weather data were retrieved from an online database (NIBIO 2016).

During the winter of 2009/10, thick layers of ground-ice also accumulated in the Botanic Garden. Many plantings were recorded as dead shortly after ice melt in late spring. All major plantings affected were assessed for alive-to-dead shoot ratios. In the aftermath of damage, we had a strong focus on comparative analyses of contrasting terrain forms. Plant survival was recorded first in early summer, and again in late summer of 2010, by estimating a percentage-based survival rate. The percentage was based on numbers of individuals surviving, except for two genera (*Filipendula* and *Lilium*) cultivated as large and few individuals. For these, we instead estimated their area recovery relative to their state in 2009, prior to this event. Photographs from 2009 were used for comparison.

The plantings were defined as species and cultivars within one taxonomic group, as detailed below, and included either a few large and well-established individuals or a group of 30 to 300 individuals, generally comprising a restricted area less than 5 m^2. All these individuals, or more than 90 % in the case of large groups, had been established in the Garden and survived at least three years prior to the year of study, and surviving individuals also persisted during the three years that followed. In the case of large and long-established individuals, ‘survival’ does not include individuals remaining alive but with more than 90 % mortality of buds or branches.

In addition, terrain slope (in degrees), percentage of drainage-promoting mineral soil components and occurrence of convex or concave landforms were recorded. Mean values were recorded for many of these plantings, but only sites homogeneous with regard to soil properties and terrain slope were included. The same taxonomic groups were planted at several places in the Garden, in contrasting microhabitats. This made it possible to compare mortality within taxonomic groups (Table S1).

Similar detailed analyses of mortality rates are not available for any other years, but unpublished reports and notes from previous curators of the Garden, and our own observations, were used to evaluate the gravity of this event. Data on several species from a genus or a section of a genus were pooled, if their growth forms were identical and if their survival rates were nearly identical. Additional information on plantings and their origins is provided in the Supporting Information.

Statistics

We employed an automatic linear modelling analysis with forward stepwise model selection (SPSS Statistics version 22; IBM Co., Armonk, NY, USA) to explore the variation in mortality rates. This is an effective tool for linear modelling, compared to manual modelling procedures, as it accepts categorical, ordinal and numerical data in a single analysis, and allows for bootstrap aggregating to improve model stability, while at the same time providing multiple optimality statistics, including the Akaike's Information Criterion Corrected (AICC) (Yang 2013). The models are ranked according to accuracy (explanatory power) from 0 to 100 %. Predictors included in the best model are ranked according to their relative importance; i.e. the sum of relative importance of the selected predictors is 1. Parameters used were geographical origin (nominal), growth form (ordinal) according to Raunkiær (1934), leaf type (evergreen, semi-evergreen, herbaceous – ordinal), proportion of well-draining minerals in soil (scale), landscape relief (convex, sloping, flat, flat to slightly concave, concave -ordinal) and average terrain slope (scale). Growth forms included in the analysis were cryptophytes (including geophytes and helophytes), short overwintering shoots (i.e. chamaephytes and hemicryptophytes), and phanerophytes. Only the best model is presented in the Results.

Linear and non-linear curve fitting was analysed in Microsoft Excel using the add-on Xlfit ver. 5.3.1.3 (ID Business Solutions Ltd., Guildford, UK). Significance tests were run with SPSS.

Vegetation greenness

The Normalized Difference Vegetation Index (NDVI) is a radiometric measure of the amount of photosynthetically active radiation (~400 to 700 nm) absorbed by chlorophyll in the green leaves of vegetation and has proven to be a good surrogate for the photosynthetic capacity and hence energy absorption of plant canopies during the growing season (Tucker, 1979; Myneni et al., 1995). NDVI is defined as the ratio of the difference of the near-infrared

(NIR) and red reflectance (ρ) values, (ρNIR − ρred), divided by the sum of the red and NIR reflectance values (ρNIR + ρred) (Tucker 1979; Myneni et al. 1995). NDVI has shown to be a good proxy for reduced plant condition caused by extreme winter events and ground-icing (Bokhorst et al. 2009; Bjerke et al. 2014, 2015). To test if the observed mortality resulted in reduced primary productivity of the Garden area as a whole in 2010, time series on the satellite-based NDVI were retrieved from the Terra MODIS NDVI data, which is based on the MOD09Q1 250 m 8-d reflectance data product (see methods in Bjerke et al. 2014). This product is available from 2000 onwards. NDVI values were extracted from the Garden area, which covers two MODIS pixels, which also include fragments of urban areas and natural vegetation. We studied the time-integrated NDVI (TI-NDVI), which is an average of NDVI from day of year (DOY) 170 to DOY 193, which means from 19 June to 12 July in non-leap years. We also present early-season NDVI, i.e. for DOY 170-177.

Results

During the winter 2009/10, the hermetic ground-ice was measured to be between 5 and 40 cm thick in flat and weakly sloping areas of the Botanic Garden (Fig. 2). The ice started to accumulate in December 2009 and grew thicker until spring melt in May, in some shaded or north-facing areas persisting until June. This ice-accumulation trend was consistent with observations from elsewhere in the region. The thick ice layer shown in Fig. 2 was largely a result of the heavy rain in mid-January; from 9 January to 26 January, 60 mm of precipitation fell on days with mean average temperature above 0 °C (Fig. 1b). This precipitation froze to ice on the intervening cold days. The dieback was much more severe than during any other year in the Garden’s history, and plants originating from all parts of the world were affected, including plants proven to be bone-hardy during a long horticultural history in Tromsø.

The best model from the automatic linear modelling explains 61.6 % of the variation in mortality and includes four predictors. The most important is terrain slope, which has a relative importance of 0.60. The relative importance of the three additional predictors is 0.21 (geographical origin), 0.14 (proportion of well-draining minerals in soil), and 0.05 (Raunkiær growth forms). The model merged origin categories to maximize association with target. Plants from East Asia, Himalaya and New Zealand ('EAHNZ') were merged. Mortality of these plants was the double of the mortality of the other plants in the dataset (70 % ± 10 S.E. vs. 34 % ± 6 S.E.; $t = 3.05$, $P = 0.004$).

The relationship between terrain slope and mortality of the EAHNZ plants is best explained by a linear correlation (Fig. 3a), while the plants of other origins shows a decreasing concave relationship with terrain slope, i.e. a steep decrease from 0 to 20°, and thereafter levelling out (Fig. 3b).

The inclusion of mineral soil component in the best model is related to the EAHNZ plants; for these plants mortality and mineral soil component is inversely correlated (Fig. 3c). The correlation between these two parameters for plants of other origins is insignificant ($r = 0.186$, $P = 0.31$; not shown graphically).

The last predictor included in the best model was growth form. The inclusion of this predictor in the best model is due to the fact that all EAHNZ plants were cryptophytes (geophytes or helophytes), while plants of other origins also included other growth forms. Mortality of the EAHNZ cryptophytes was nearly the double than the mortality of cryptophytes from other regions (70 % vs. 36 %, $t = 2.71$, $P = 0.011$). Mortality of other growth forms (chamaephytes, hemicryptophytes and phanerophytes) also showed an inversely concave relationship with terrain slope, average mortality was 31 %, and high mortality rates was mostly restricted to weakly sloping terrain (Fig. 3d).

Of the 22 parallel recordings of taxa compared between strongly sloping vs. flat or weakly sloping terrain, 19 had much better survival rates in strongly sloping terrain (Table S1). In five of these (*Delosperma basuticum*, *Ephedra* spp., *Primula denticulata*, *Primula* Sect. *Sikkimenses,* and *Ranunculus carsei* and *R. insignis*), the garden populations in flat or almost flat terrains died off completely (Table S1), but had good or complete survival in strongly sloping terrain (*Sikkimenses* primulas: mortality between 0 and 30 %).

NDVI of the Garden area reached an unprecedented minimum level during the summer of 2010 (Fig. 4a). TI-NDVI in 2010 was 30.4 % lower than the average for the pre-event years from 2000 to 2009 (0.47 vs. 0.68). TI-NDVI increased in the following years, and after 5 years, TI-NDVI was slightly higher than the average of the pre-event years (2015: 0.68). Early-season NDVI shows a similar pattern as TI-NDVI, with the lowest value reached in 2010 (Fig. 4b), being 49.7 % lower than the average of the pre-event years (2010: 0.34; 2000-2009: 0.67). Early-season NDVI in 2004 was almost as low as in 2010. However, in contrast to the situation in 2010, NDVI quickly reached near-normal levels in 2004, as seen by the TI-NDVI for that year. Early-season NDVI increased slightly in the two years following the extreme event, but was in these years still well below the average of the pre-event years (Fig. 4b). After 2012, early-season NDVI increased considerably, in 2015 reaching a value 8.1 % higher than the pre-event average (2015: 0.72).

Discussion

High mortality rates were largely restricted to flat or gently sloping areas covered in thick ice, while plants in steeper terrain where ice did not accumulate, survived. Hence, this case study shows that the provided alpine plants from all continents are indeed intolerant of ice encasement. This is the first observations of ground-ice effects on a large number of alpine species, and it therefore provides added knowledge to the few previous studies on boreal, alpine and Arctic species (Bjerke 2009, 2011; Gudleifsson 2009; Preece et al. 2012; Preece & Phoenix 2013, 2014; Milner et al. 2016; Bjerke et al. 2017).

Except for the Arctic species of *Dryas*, the studied taxa are alpine or subalpine plants. The results are therefore not representative of Arctic plants. Nevertheless, recent observations from High-Arctic tundra plains indicate that *Dryas* in fact are intolerant of long-term ice encasement (Phoenix & Bjerke 2016; Bjerke et al. 2017).

The alpine/subalpine plants studied originate from high altitudes at rather low latitudes (30-50°) from North America, South America, Europe, South Africa, Asia and New Zealand. The EAHNZ plants tended to be more intolerant than plants from other regions. However, this may be due to the confounding factor that all EAHNZ plants were cryptophytes. In a planned experimental design, growth forms would be evenly distributed among geographical origins. However, in this unplanned observational study, we could not correct for this skewness. The inclusion of geographical origin can therefore not be taken as an indication that EAHNZ plants in general are more vulnerable to ice encasement than plants of other origins. However, the fact that mortality of EAHNZ cryptophytes was nearly the double of cryptophytes from other regions indicate region-specific differences in tolerance of cryptophytes to ground-ice.

The unprecedented low NDVI values in the following growing season clearly suggest that the icing event was highly unusual, supporting available information from previous curators of the garden that mortality of such extent had not occurred previously. The MODIS pixels are slightly larger than the Garden, and therefore also include some natural forest vegetation, which possibly also was set back by the icing event, as the entire region, including an agricultural grassland 3.5 km from the Garden, suffered from ice encasement (Bjerke et al. 2015).

The relatively low NDVI in 2011 and 2012 suggests that damage was persistent over several seasons. In the Garden, it took some time to replace all the dead plant areas with a new green cover. Overall, the widespread dieback and the multiyear reduction in NDVI indicate that icing events can have large impacts on ecosystem productivity and carbon budget. Other hazardous events during the winter 2011/12 and cool weather during the summer of 2012 may also have contributed to the low NDVI of the 2012 growing season, while the low NDVI of 2004 was probably due to an unusually cool spring and early summer (Turtiainen et al. 2011; Bjerke et al. 2014).

Icing damage may be a potential threat to these species in their natural environment, as most or all species are from areas with seasonal freezing. However, they may avoid being encased in ice by growing in sloping terrain where the risk for long-term ice accumulation is minor. Duration of ice exposure may be a factor of major importance. Experimental icing show that acclimated agricultural grasses and clover can sustain some weeks in ice, but survival starts to decrease quite considerably after ca. 7 days (Andersen 1986; Andrews 1996; Gudleifsson 2009). We here report on an extremely long period of ice encasement, lasting from December until May. This is much longer than what most of these alpine species from lower latitudes would experience in their natural environment. However, in the aftermath of this event, it is not possible to assess when mortality started to rise. It might be that most plants died during the first few weeks of ice encasement, like the plants studied experimentally.

The lack of reports of winter damage to these plants from their natural environment does not necessarily mean that winter-induced damage does not occur. An important issue raised in recent years is that events occurring in winter are hard to study (Pauli et al. 2013; Bokhorst et al. 2016; Phoenix & Bjerke 2016). The fact that winters are changing more than summers in many parts of the world has led to a stronger focus on potentially stressful events occurring in winter, but ground-based observations of impacts of extreme events on the snowpack are still limited (Bokhorst et al. 2016). Most recent reports are from high northern latitudes (e.g. Bokhorst et al. 2009; Bjerke et al. 2014, 2015, 2017; Phoenix and Bjerke 2016), but the impacts of subantarctic winter climate change has also recently received attention (e.g. Harsch et al. 2014).

Conclusion

Our report here of ice-related dieback to a high number of plants from a wide variety of geographical origins and growth forms is another clear indication that more studies of the impacts of events in winter are needed to understand better how alpine and other cryophilic ecosystems will change with increasing climate change. Furthermore, this study shows that garden studies using plants of different origins can be very useful, as such studies fill a gap between pure laboratory or climate chamber studies and field studies.

References

Andersen, I. L. 1986. Hva er isbrann? *Polarflokken* 10, 143–149.

Andrews, C.J. 1996. How do plants survive ice? *Annals of Botany* 78, 529–536.

Bjerke, J.W. 2009. Ice encapsulation rather protects than disturbs the freezing lichen. *Plant Biology* 11, 227–235.

Bjerke, J.W. 2011. Winter climate change: Ice encapsulation at mild subfreezing temperatures kills freeze-tolerant lichens. *Environmental and Experimental Botany* 72, 404–408.

Bjerke, J.W., Karlsen, S.R., Høgda, K.A., Malnes, E., Jepsen, J.U., Lovibond, S., Vikhamar-Schuler, D. & Tømmervik, H. 2014. Record-low primary productivity and high plant damage in the Nordic Arctic Region in 2012 caused by multiple weather events and pest outbreaks *Environmental Research Letters* 9, 084006.

Bjerke, J.W., Tømmervik, H., Zielke, M. & Jørgensen, M. 2015. Impacts of snow season on ground-ice accumulation, soil frost and primary productivity in a grassland of sub-Arctic Norway. *Environmental Research Letters* 10, 095007.

Bjerke, J.W., Treharne, R., Vikhamar-Schuler, D., Karlsen, S.R., Ravolainen, V., Bokhorst, S., Phoenix, G.K., Bochenek, Z. & Tømmervik, H. 2017. Understanding the drivers of extensive plant damage in boreal and Arctic ecosystems: Insights from field surveys in the aftermath of damage. *Science of the Total Environment* 599-600, 1965–1976.

Bokhorst, S.F., Bjerke, J.W., Tømmervik, H., Callaghan, T.V. & Phoenix, G.K. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology* 97, 1408–1415.

Bokhorst S., Pedersen, S.H., Brucker, L., Anisimov O., Bjerke J.W., Brown, R.D., Ehrich, D., Essery, R.L.H., Heilig, A., Ingvander, S., Johansson, C., Johansson, M., Jónsdóttir, I.S., Niila, I., Luojus, K., Macelloni, G., Mariash, H., McLennan, D., Rosqvist, G.N., Sato, A., Savela, H., Schneebeli, M., Sokolov, A., Sokratov, S.A., Terzago, S., Vikhamar-Schuler, D., Williamson, S.N., Qiu, Y. & Callaghan, T.V. 2016. Changing Arctic snow cover: a review of recent developments and assessment of future needs for observations, modelling and impacts. *Ambio* 45, 516–537.

Callaghan, T.V., Jonasson, C., Thierfelder, T., Zhenlin, Y., Hedenås, H., Johansson, M., Molau, U., van Bogaert, R., Michelsen, A., Olofsson, J., Gwynn-Jones, D., Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Tømmervik, H., Christensen, T.R., Hanna, E., Koller, E.K. & Sloan, V.L. 2013. Ecosystem change and stability over multiple decades in the Swedish sub-Arctic: complex processes and multiple drivers. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 368, 20120488.

Crawford, R.M.M. 1978. Biochemical and biological similarities in marsh plants and diving animals. *Naturwissenschaften* 65, 194–201.

Crawford, R.M.M., Chapman, H.M. & Hodge, H. 1994. Anoxia tolerance in high Arctic vegetation. *Arctic and Alpine Research* 26, 308–312.

Eagles, C.F. 1967. Apparent photosynthesis and respiration in populations of *Lolium perenne* from contrasting climatic regions. *Nature* 215, 557–560.

Elvebakk, A. 2008. Tromsø Arctic-Alpine Botanic Garden. *Rock Garden* 120, 40–63.

Forchhammer, M.C. & Boertmann, D. 1993. The muskoxen *Ovibos moschatus* in north and north-east Greenland: population trends and the influence of abiotic parameters on population dynamics. *Ecography* 16, 299–308.

Gudleifsson, B.E. 2009. Ice encasement damage on grass crops and alpine plants in Iceland – impact of climate change. Gusta, L., Wisniewski, M. & Tanino, K. (eds.) *Plant Cold Hardiness: From the Laboratory to the Field*, 163–172. CABI, Wallingford.

Hansen, B.B., Isaksen, K., Benestad, R.E., Kohler, J., Pedersen, Å.Ø., Loe, L.E., Coulson, S. J., Larsen, J.O. & Varpe, Ø. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters* 9, 114021.

Harsch, M.A., McGlone, M.S. & Wilmshurst, J.M. 2014. Winter climate limits Subantarctic low forest growth and establishment. *PLOS One* 9, e93241.

Höglind, M., Bakken, A.K., Jørgensen, M. & Østrem, L. 2010. Tolerance to frost and ice encasement in cultivars of timothy and perennial ryegrass during winter. *Grass and Forage Science* 65, 431–445.

International Plant Names Index 2015. *Plant Name Query*. Kew, Harvard, Canberra: The International Plant Names Index, [accessed 8 February 2017]. Available from: http://www.ipni.org/

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5, 365–374.

Johansson, C., Pohjola, V.A., Jonasson, C. & Callaghan, T.V. 2011. Multi-decadal changes in snow characteristics in sub-Arctic Sweden. *Ambio* 40, 566–574.

Liston, G.E. & Hiemstra, C.A. 2011. The changing cryosphere: pan-Arctic snow trends (1979-2009). *Journal of Climate* 24, 5691–5712.

Milner, J.M., Varpe, Ø., van der Wal, R. & Hansen, B.B. 2016. Experimental icing affects growth, mortality, and flowering in a high Arctic dwarf shrub. *Ecology and Evolution* 6, 2139–2148.

Myneni, R.B., Hall, F.G., Sellers, P.J. & Marshak, A.L. 1995. The interpretation of spectral vegetation indexes. *IEEE Transactions on Geoscience and Remote Sensing* 33, 481–486.

NIBIO 2016. *Landbruksmeteorologisk Tjeneste*. Ås: Norwegian Institute for Bioeconomy [accessed 8 February 2017]. Available from: http://lmt.bioforsk.no/

Pauli, J.N., Zuckerberg, B., Whiteman, J.P. & Porter, W. 2013. The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment* 11, 260–267.

Phoenix G.K. & Bjerke, J.W. 2016. Arctic browning: events and trends as drivers. *Global Change Biology* 22, 2960–2962.

Preece, C., Callaghan, T.V. & Phoenix, G.K. 2012. Impacts of winter icing events on the growth, phenology and physiology of sub-Arctic dwarf shrubs. *Physiologia Plantarum* 146, 460–472.

Preece, C. & Phoenix, G.K. 2013. Responses of sub-Arctic dwarf shrubs to low oxygen and high carbon dioxide conditions. *Environmental and Experimental Botany* 85, 7–15.

Preece C. & Phoenix, G.K. 2014. Impact of early and late winter icing events on sub-Arctic dwarf shrubs. *Plant Biology* 16, 125–132.

Raunkiær, C. 1934. *The Life Forms of Plants and Statistical Plant Geography, being the collected papers of C. Raunkiær*. Oxford University Press, Oxford.

Riseth, J.Å, Tømmervik, H., Helander-Renvall, E., Labba, N., Johansson, C., Malnes, E., Bjerke, J.W., Jonsson, C., Pohjola, V., Sarri, L.-E., Schanche, A. & Callaghan, T.V. 2011. Sámi traditional ecological knowledge as a guide to science: snow, ice and reindeer pasture facing climate change. *Polar Record* 47, 202–217.

Tucker, C.J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, 8, 127–150.

Turtiainen, M., Salo, K. & Saastamoinen, O. 2011. Variations of yield and utilization of bilberries (*Vaccinium myrtillus* L.) and cowberries (*V. vitis-idaea* L.) in Finland. *Silva Fennica* 45, 237–251.

Vikhamar-Schuler, D., Isaksen, K., Haugen, J.E., Tømmervik, H., Luks, B. & Bjerke, J.W. 2016. Changes in winter warm events in the Nordic Arctic Region. *Journal of Climate* 29, 6223–6244.

Walsh, J.E., Overland, J.E., Groisman, P.Y. & Rudolf, B. 2011. Arctic climate: recent variations. Symon, C., Thing, H., Pawlak, J. & Larson, T. (eds.) *Snow, Water, Ice and Permafrost in the Arctic (SWIPA): Climate Change and the Cryosphere,* chapter 3, 18 pp. Arctic Monitoring and Assessment Program, Oslo.

Yang, W. 2013. The case for being automatic: introducing the automatic linear modeling (LINEAR) procedure in SPSS statistics. *Multiple Linear Regression Viewpoints* 39, 27–37.

Figure captions

Fig. 1. Temperature (a) and precipitation (b) measured at the weather station Holt in Tromsø from 1 November 2009 to 1 March 2010. Black squares in (b) represent precipitation above 0 mm on days with daily average temperature above 0 °C.

Fig. 2. Extreme ground-ice formation. (a) In sloping terrain in the North-Norwegian Traditional Garden Plants and in the Succulent collections. (b) On and below large boulders in the Primulaceae collection. (c). In flat terrain around the pond. The photographs were taken 27 January 2010.

Fig. 3. Correlation with mortality in various groups of species for terrain slope or mineral soil component. (a) Terrain slope for plants from East Asia, Himalaya and New Zealand (EAHNZ); $r = 0.569$, $P = 0.027$. (b) Terrain slope for plants of other geographical origins; $r = 0.641$, $P = 0.001$. (c) Mineral soil component for EAHNZ plants; $r = 0.532$, $P = 0.041$. (d) Terrain slope for non-cryptophytes (i.e. hemicryptophytes, chamaephytes and phanerophytes); $r = 0.656$, $P = 0.023$. Dashed lines show 95 % confidence intervals.

Fig. 4. Vegetation greenness (NDVI) of the garden area. a. Time-integrated NDVI for the growing-season period from day-of year (DOY) 170 to 193 (i.e. 19 June to 12 July in non-leap years). b. Early-season NDVI (DOY 170-177).