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Overwintering stress of *Vaccinium vitis-idaea* in the absence of snow cover

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ABSTRACT

A snow manipulation experiment aimed to assess risks of direct freezing injury, freeze-induced dehydration and winter desiccation in the absence of snow cover on lingonberry (*Vaccinium vitis-idaea*). Frames with sheet-plastic sides and removable lids were used in this experiment for two purposes: to prevent accumulation of snow in mid-winter and to provide extra heat during early spring. Leaves were analyzed for frost hardiness, tissue water content and osmotic concentrations, and photoinhibition (Fv/Fm) during the period from the 10th of February to the 7th of April. The natural snow accumulation was low indicated by a minor difference in minimum temperatures between the frame treatment and naturally snow-covered plots. The heating effect of the frames started gradually at the end of February along with increasing solar elevation angles, and was highest at the beginning of April. Frost hardiness peaked in March as a consequence of cold periods, but it was practically lost by the beginning of April. Tissue water content decreased gradually at first, becoming greatly decreased later due to the extra heat. In accordance, the tissue osmotic concentrations increased first gradually, followed by a dramatic increase. Photoinhibition increased uniformly with increasing solar radiation, but at the end showed a sharp increment within a few days, obviously also indicating the effect of heating. It was concluded that neither lethal freezing stress nor significant freeze-induced dehydration occurred during the experiment. However, plants that overwintered without snow suffered from severe winter desiccation injuries due to the combination of solar heat and frozen soil. Although the desiccation stress was possibly a lethal factor, it was preceded by long-term and continued photoinhibition. It was concluded that during overwintering, chamaephyte species may suffer from both freezing and winter desiccation in the absence of protecting snow cover. However, during mild winters provided by climatic change scenarios, the risk of winter desiccation will be more probable. In relation to the future climate, it was concluded that winter desiccation and photoinhibition may develop gradually during a snowless winter and would, even if they did not reach a lethal level by themselves, possibly reduce frost hardiness.

1. Introduction

Snow cover is a specific ecological factor in the annual cycle of northern nature. Its thickness and duration depends on latitude and local climatic features such as altitude and oceanity, as well as annual variations. For example, in Northern Finland the thickness of snow cover has usually been above 50 cm, with snow cover usually lasting for more than 6 months of the year (e.g. Taulavuori et al., 2003; Jalkanen, 2007). Winter temperatures of Arctic areas are expected to elevate by 4–7 °C or more by the end of this century, which will shorten the snowy season and reduce the thickness of snow cover (ACIA, 2005). The decreases in areas covered with snow are projected to be greatest in spring (ACIA, 2005), but some recent winters (2006/07, 2007/08, 2008/09) have shown that the snowless time in autumn may extend until the turn of the year instead of its usual end around November.

Snow cover provides protection against extreme winter conditions for many plant species. The species that require snow cover to overwinter successfully are called chamaephytes in *Raunkier's* classification. It is seldom colder than −5 °C under a 50 cm snow layer, indicating that snow protects plants significantly from low temperatures (Salisbury, 1985). In addition to protection against freezing, snow protects also from excess dehydration, which is an avoidance mechanism against lethal intracellular freezing (Sakai and Larcher, 1987; Pearce, 2001). More over, snow provides protection against high light levels in spring and thereby against solar heat as well. Intense light may cause photoinhibition (e.g. Strand and Öquist, 1985) of the photosynthetic apparatus, while solar heat may result in a so-called winter desiccation phenomena, as the water held in ground frost cannot serve as compensation for transpired water (e.g. Herrick and Friedland, 1991; Larcher, 2003).

Lingonberry (*Vaccinium vitis-idaea* L.) is an ericaceous dwarf shrub and forms large clones in various habitats. Lingonberry is a

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typical field-layer species of boreal forests, especially in sub-mesic forest sites. The objective of this work was to assess overwintering of this chamaephyte species under experimental conditions without protective snow cover. For this purpose, plastic covered wooden frames were built to prevent accumulation of snowfall. The frames also warmed the plots by capturing solar heat, mimicing the spring-time temperature elevations, projected by climatic scenarios. It was hypothesized that the chamaephyte species would suffer from stress due to the lack of snow. However, it was unpredictable which of the three factors contribute most stress: (1) direct freezing injury at low temperatures (i.e. intracellular freezing), (2) freeze-induced dehydration under prolonged exposure to freezing conditions, or (3) winter desiccation caused by the combined effect of frozen ground and solar heat? The first point of view is based on the fact that a chamaephyte species obviously cannot develop a high degree of frost hardiness as they are adapted to overwinter below snow (e.g. Havas, 1971). Therefore they may be killed due to intracellular ice formation and consequent injuries in membranes, which occur soon after exposure to a sufficiently low temperature level. The second hypothesis would argue that since lingonberry is adapted to overwinter below snow, it is possible that they cannot tolerate (e.g. via synthesis of compatible solutes) high osmotic concentrations. High osmotic concentrations in plants are typical in winter (Sakai and Larcher, 1987), especially without snow cover (Havas, 1971). High osmotic concentrations result from cellular dehydration, driven by extracellular freezing (Taulavuori and Lűttge, 2007). It is assumed that this dehydration is not short-term damage, but rather develops gradually over time in winter. Winter desiccation is a consequence of transpiration during late winter and early spring, especially in parts of the plant directly exposed to solar radiation. To test these hypotheses, frost hardiness, water content, osmotic concentrations and photoinhibition were analyzed from the middle of February to the beginning of April. The data gives information about the risk of overwintering without snow as well as the mechanism behind possible damage.

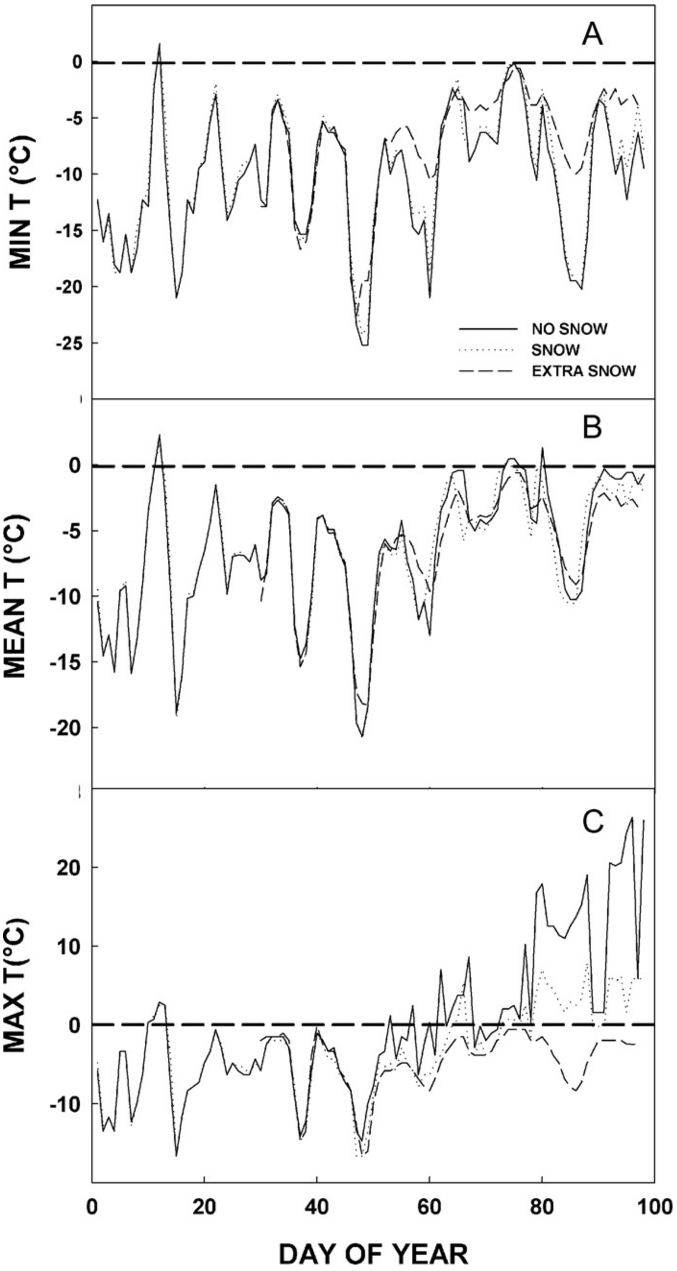

Fig. 1. Daily minimum (A), mean (B) and maximum (C) temperatures during the experiment. The time axis indicates days from the 1st of January. The dashed horizontal line at 0 °C is to make reading easier.

2. Materials and methods

The experiment was carried out in a small forest site in the vicinity of the University of Oulu, Northern Finland (65°N), during winter of 2008–2009. The site of the experiment was located approximately 50 m from the entrance to the laboratory, thus allowing analysis immediately after sampling, and ease management of the field. The studied species lingonberry (*V. vitis-idaea*) grows naturally in the field-layer of this habitat. The experiment was installed in December 2008, and sampling began at the beginning of February 2009. The last samples were taken in the middle of April. Six ($n = 6$) wooden frames of the size 0.5 m × 0.5 m × 0.5 m were built and covered with a plastic sheet, leaving the top and bottom open. Separate removable lids were also built using wood and plastic sheeting. The purpose of the frames was to prevent the accumulation of snowfall inside the frames, and the lids had dual functions: (1) removing the fallen snow covering the lids was simply done by just lifting up the lid and cleaning it away from the frames. (2) Temperature elevations inside the frames could be regulated by removing the lids during sunny days. Otherwise, when snow started to accumulate it was also removed from the outside of the frame sheets. In addition to the frames, there were two other treatments. Natural snow accumulation served as a control ($n = 6$ plots). Extra snow was collected to provide an increased snow effect, as the natural accumulation of snow was relatively shallow during the first weeks of the experiment. The extra snow was collected in one area, approximately 3 m × 5 m, in order to provide a wide sampling area having snow enough for thermal insulation in horizontal direction. Six samples were also collected from this area ($n = 6$). The treatments were thus: control plots with natural snow accumulation (S), plots covered by extra snow (E), and the frame plots with no snow (N). The experiment was established on a site where the sun shines over an 5–10 m wide open area from south-southeast (150°). This meant that the site received direct sunshine at around 11 a.m. local time (UTC +2). Data loggers (Hobo H08-004-02, Onset Computer Corporation, U.S.A.) were placed in each treatment to collect temperature data at 2 h intervals. The loggers were set in the no snow and natural snow treatments on the 15th of December 2008, and in the extra snow treatment on the 30th of January 2009 when the addition of snow was possible in practice. The loggers were mounted in a way that the probe (0.5 cm × 2.5 cm, stainless steel) of the temperature sensor (1.8 m grey cable) was attached to a stick at the height of average shoot tips of the ramets. The daily minimum, mean and maximum temperatures are shown in Fig. 1. Due to reflective properties of the temperature probe, it is probable that incoming radiation did not cause an overestimation of the