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Late winter light exposure increases summer growth in the grass *Poa pratensis*: Implications for snow removal experiments and winter melt events

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ABSTRACT

Reductions in snow cover over winter can increase frost exposure in herbaceous plants. Nevertheless, increased exposure to light can potentially increase plant carbon gain during periods of reduced snow cover. We used a combined field and growth chamber experiment to examine how variation in the timing and cumulative duration of light exposure over winter (from one to four 1-week incubation periods at 5 °C) affected subsequent summer growth in the grass *Poa pratensis*. We also measured net photosynthetic rates, dark respiration and chlorophyll fluorescence both 48 h and 120 h after the start of each winter light exposure period. Summer biomass increased by up to 50% for tillers exposed to light during the final winter incubation period (mid-late February), and the timing of light exposure, not the cumulative duration, was the most influential factor in increasing biomass. In contrast, for tillers incubated in the dark, multiple weeks of incubation at 5 °C resulted in the largest reductions in summer biomass. Leaf-level net photosynthetic rates were highest for the earliest and latest light exposure periods over winter, whereas dark respiration rates were highest in early winter and lowest in late winter. Thus, the gas exchange and biomass results were consistent in revealing that the last period of light exposure promoted the highest carbon gain. Overall, our results reveal that naturally occurring periods of snow melt over winter, or scenarios where snow is removed or melted as an experimental treatment, have the potential to benefit plant growth substantially, as opposed to simply rendering plants vulnerable to frost damage.

1. Introduction

Snow cover plays a key role in the stress physiology of herbaceous plants in seasonally-frozen regions. Due to its insulative properties, snow buffers overwintering plants from cold air temperatures and freeze-thaw cycles (Henry 2008). The influence of snow cover on soil temperatures is sufficiently strong that reduced snow cover in warm years can paradoxically result in colder soils over winter (Groffman et al., 2001). Despite the potential for thick snow cover to benefit overwintering plants by protecting them from frost damage, a persistent snow pack in early spring can delay the onset of plant growth, thus reducing annual biomass production (Henry et al., 2015). Moreover, the effects of pathogens (*e.g.* snow molds), ice encasement and increased subnivian herbivore activity, which can be associated with snow cover, can reduce subsequent plant growth (Gaudet 1994; Rapacz et al., 2014), and the timing and extent of snow melt can influence subsequent plant water availability over summer. Therefore, the overall effects of snow cover on plant stress physiology and plant growth are multi-faceted (Fig. 1), and can vary substantially depending on the timing and depth of snow cover, and on plant community type (Kreyling et al., 2008, 2010, 2011).

In addition to the important observations that have been obtained from studying naturally-occurring variation in snow cover, snow removal experiments have been employed to examine the effects of soil frost on plants *in situ* (Comerford et al., 2013; Vankoughnett and Henry, 2014). The rationale for such experiments has typically been that the effects of snow removal on subsequent plant growth over summer can be attributed to frost damage, provided that snow removal effects on spring melt water recharge are controlled for (*e.g.* by ceasing the snow removal before the end of winter, allowing snow to accumulate in the plots prior to spring melt). Likewise, warming experiments using overhead infrared heaters and heated soil cables have been used to simulate

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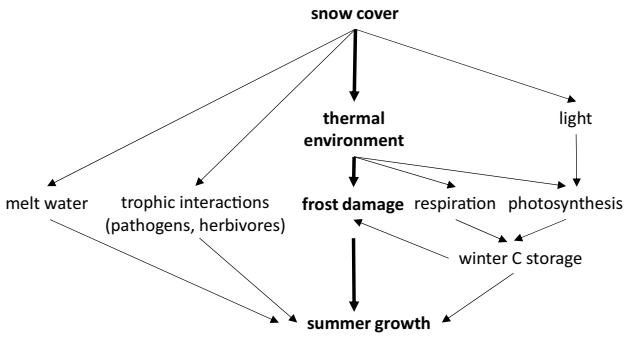

Fig. 1. Conceptual diagram of how variability in snow cover can influence plant growth over the following summer. While there has been a focus on how changes in snow cover can alter the thermal environment, thus increasing frost damage (bold arrows), changes in water availability, trophic interactions and light exposure caused by variation in snow cover (thin arrows) can also affect summer plant growth.

the effects of increased frost stress associated with mid-winter melt events (*e.g.* Bokhorst et al., 2009). However, for overwintering herbaceous plants, while snow removal and mid-winter heating can modify the plant thermal environment, these treatments also increase plant exposure to light. To what extent might the latter also affect the physiological responses of plants to changes in snow cover?

Contrary to the perception that plants remain dormant over winter, measureable plant activity can occur at this time (Andresen and Michelsen, 2005; Campbell et al., 2005). Respiration by cold-acclimated plants under the snowpack can be substantial (Nobrega and Grogan, 2007), but many cold-adapted plants can continue to photosynthesize down to temperatures at or below 0 °C during the winter (Day et al., 1989; Starr and Oberbauer, 2003; Skinner, 2007; Tuba et al., 2008; Höglind et al., 2011; Bjerke et al., 2013). Therefore, when sufficient light is available for photosynthetic carbon gain in winter, it can allow plants to replenish carbohydrate reserves lost through respiration. Moreover, plants exposed to warm periods over winter can quickly up-regulate photosynthesis within hours to days (Höglind et al., 2011; Saarinen et al., 2011), which provides them with a further opportunity to replenish carbohydrates pools. These reserves can be used to promote cold tolerance (Huner et al., 1993; Kalberer et al., 2006), and stored carbohydrates can also accelerate plant growth in the spring (Bannister 1980; Busso et al., 1990; Frankow-Lindberg 2001; Luscher et al., 2001; Dhont et al., 2002; Acuna-Maldonado and Pritts, 2008). While plant biomass accumulation at near-freezing temperatures appears to be minimal in most cases (particularly in grasses, where low temperatures generally limit growth more than photosynthesis – Pollock et al., 1983; Hjelm and Ögren, 2003), it is conceivable that small gains in carbon storage (or reductions in carbon losses) at this time could reap disproportionate benefits over the growing season during periods of exponential or near-exponential growth. Nevertheless, it remains unclear to what extent short periods of increased light availability over winter may benefit plants during the subsequent growing season.

We conducted a combined field/growth chamber experiment to examine the ability of the grass *Poa pratensis* to exploit increased light availability over winter. Tillers contained in mesocosms were incubated outdoors during the winter, but temporarily transferred to growth chambers at 5 °C in either the light or dark for 7 days at a time for 1–4 weeks, such that the effects of the timing and cumulative duration of light exposure could also be examined. Leaf gas exchange and chlorophyll fluorescence were measured during the warming periods, and biomass production was assessed over the following growing season. We predicted that increased light availability at cold temperatures over winter would increase plant carbon gain (as estimated through leaf gas exchange measurements) and subsequent growth. We were particularly interested in documenting the magnitude of the latter (*i.e.* to examine the biological/ecological relevance of the effect), and examining how these effects might be modulated by the timing and overall duration of light exposure.

2. Methods

We selected the common grass *Poa pratensis* as a study species given that it has a low stature (*i.e.* it experiences a sub-nivean habitat when snow cover is present) and it overwinters with a partially green leaf canopy (Chabot and Hicks 1982). In early fall, we used 10 cm diameter × 10 cm deep sections of PVC pipe to collect intact plant-soil mesocosms containing predominately *Poa pratentsis* from a grass-dominated temperate old field located at the Agriculture and Agri-Food Canada Southern Crop Protection and Food Research Centre in London, Ontario, Canada (43°0146 N, 81°1252 W). The mesocosms were selected by visual inspection to contain uniform grass cover and tiller size, and other species were weeded out by hand. We placed the mesocosms in a common garden with their soil surfaces level with the surrounding soil and watered them 1–2 times per week as needed to maintain a moist soil for the remainder of the fall. Four temperature loggers (Ibutton DS1922L-F5, Maxim Integrated, San Jose, CA, USA) were placed at 2 cm depth in the soil surrounding the mesocosms.

We removed subsets of the mesocosms on 7 Jan., 21 Jan., 4 Feb. and 18 Feb. and placed them in high light intensity, low temperature growth chambers (Model M18SI, Environmental Growth Chambers, Chagrin Falls, OH, U.S.A.) at 5 °C and relative humidity between 50–60% for 7 days before returning them to the common garden and re-covering them with snow (for the mesocosms that had remained outdoors, the snow was also removed and replaced, to ensure uniform snow cover among all mesocosms). The mesocosms were removed for 1–4 weeks each, with 10 different combinations of number of weeks and first week of freezing examined (n = 8 for each treatment combination; combinations of weeks tested were: (1), (2), (3), (4), (1,2), (2,3), (3,4), (1, 2, 3), (2, 3, 4) and (1, 2, 3, 4)). A further subset of control mesocosms (n = 10) was left outdoors for the entire winter. Once placed in the chambers, half of the replicates in each chamber were placed under cardboard boxes covered with aluminium foil to prevent light penetration (there was no significant effect on air temperature), while the other half were exposed to light (photosynthetically active radiation (PAR): 200 μmol photons $m^{-2} s^{-1}$ from 0730 to 0900, 400 μmol photons $m^{-2} s^{-1}$ from 0900 to 1030, 800 μmol photons $m^{-2} s^{-1}$ from 1030 to 1430, 400 μmol photons $m^{-2} s^{-1}$ from 1430 to 1600, 200 μmol photons $m^{-2} s^{-1}$ from 1600 to 1730).

At 48 and 120 h after placing the mesocosms in the chambers, we measured rates of net photosynthesis and dark respiration per unit leaf area on the green leaves closest to the center of the light-exposed mesocosms using a LI-6400 XRT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE, USA) with a 6400-40 Leaf Chamber. We only examined the mesocosms that were exposed to light and 5 °C for a single week, and only 6 of the 8 possible replicates were examined. Net photosynthesis and dark respiration were characterized at PAR values of 800 (the maximum chamber light level) and 0 μmol photons $m^{-2} s^{-1}$, respectively, and all measurements were collected between the hours of 1030–1430 in the chambers at a leaf temperature of 5 °C, a CO_2 concentration of 400 ppm and a relative humidity of 49–53%. Dark respiration was measured following a 20 min dark acclimation period. The photosynthetic light saturation point, calculated from photosynthetic light response curves (data not shown) was 893 μmol