Snowmelt timing affects short-term decomposition rates in an alpine snowbed

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Abstract. Alpine snowbed communities are characterized as having areas of longer lasting snow cover duration compared with the surrounding landscape. The predictable accumulation of deep and long-lasting snow on lee side ridges drives a unique ecology, providing stable microclimatic conditions under the snow through winter, supplying meltwater in spring, and controlling many biological processes. The timing and rate of plant litter decomposition are key controls on the nutrient balance of snowbed communities, and are thought to be strongly driven by snow dynamics. However, little is known about how the patterns and timing of snowmelt affect decomposition, nor how long these effects last into the growing season. We investigated the influence of snowmelt timing on decomposition rates across an alpine snowbed community by burying standardized plant litter (rooibos and green tea), at three incubation times (whole year, winter + spring, and summer), across three snowmelt zones. Decomposition rate (as percent mass loss of tea) was significantly higher in early-melting zones compared to late-melting zones, particularly for the recalcitrant litter (rooibos tea). Decomposition was also affected by the season(s) of incubation and was greatest where tea was buried for the whole year, or only over summer, with winter + spring only incubations decomposing the least. However, decomposition was more strongly influenced by litter quality (type of tea) than either the timing of snowmelt or seasonality. These results provide further understanding about how changes to the timing of snowmelt may in turn transform these rare and unique plant communities.

Key words: climate change; litter decomposition; snowbed community; snowmelt timing; tea bag index.

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INTRODUCTION

Snow cover is one of the defining characteristics of alpine ecosystems, but is highly susceptible to change as the climate warms (Wipf and Rixen 2010). The presence and absence of snow controls the energy balance throughout the year, reflecting approximately 90% of solar energy (Edwards et al. 2007), acting as a heat sink during snowmelt, and insulating soils sufficiently to decouple them from fluctuating air temperatures (Cline 1997). Snow cover duration determines the amount, phase, and availability of soil moisture, a critical determinant of above- and below-ground biological activity (Sierra et al. 2015). The duration of snow cover also determines the length of the growing season for plants (Bjorkman et al. 2015) and influences nutrient availability via controls on decomposition, thus shaping the structure and distribution of alpine plant species and communities, via their associated functional traits (Gavazov 2010). Understanding the relationships between snow cover duration, vegetation dynamics, and resulting ecosystem processes is thus important...
for predicting how alpine ecosystems will respond to climate change.

Decomposition is typically very slow in arctic and alpine environments, and may be negligible in winter due to low temperatures and an absence of liquid water (Douglas and Tedrow 1959, Bokhorst et al. 2013). Experimental deepening of snow, particularly in arctic landscapes, can increase winter soil temperatures sufficiently to thaw or increase the depth of the active soil layers in permafrost where it occurs (Nowinski et al. 2010, Natali et al. 2012), increase wintertime microbial activity and organic matter decomposition (Buckeridge and Grogan 2008), and increase overall mass loss (Blok et al. 2016). Experimentally induced earlier snowmelt (e.g., using open top chambers) may also be associated with lower decomposition rates due to the drying of the litter layer late in the season (Blok et al. 2016). In alpine and subalpine areas of naturally occurring deep and permanent snow, soil temperatures may also be better insulated than in areas of shallow snow, resulting in higher decomposition rates (Walker et al. 1999, Saccone et al. 2013), although changes in the frequency of freeze–thaw processes may disrupt and influence soil microbial processes (Edwards et al. 2007).

At landscape scales, the climate directly and indirectly influences decomposition through the distribution and growth of plant communities and their associated plant litter of various qualities. However, at smaller scales the timing of snowmelt can also influence plant litter decomposition rates due to the multiple interactions between vegetation communities, soils, temperature, litter quality, and nutrient availability (Fig. 1). Litter quality can explain up to 90% of variation in decomposition at the site scale (Berg et al. 1993) and may be the primary control on global decomposition rates (Cornwell et al. 2008). In alpine environments, a number of studies have found that litter quality explains more variation in decomposition rates than experimental treatments (Baptist et al. 2010, Wang et al. 2010, Carbognani et al. 2014 though see Saccone et al. 2013), while changes in plant community composition have been hypothesized to have a greater effect on decomposition rates than the direct microclimatic effects of climate change (Baptist et al. 2010). For example, the increase in the abundance of shrubs observed in many artic and alpine communities (Myers-Smith et al. 2011) may slow overall community decomposition rates, although this depends on the amount of litter being incorporated into the system (Cornellissen et al. 2007, DeMarco et al. 2014, Christiansen et al. 2018). Understanding the relative importance of litter quality compared to the environmental associations of snowmelt dynamics is thus critical for determining the rate, direction, and magnitude of future changes to decomposition rates in alpine ecosystems.

Winter snow in alpine environments is not uniformly distributed across the landscape because of a strong interaction between the prevailing winds and topography (Körner 2003). At landscape scales, snow accumulates mostly on the lee side of ridges and forms deep drifts that can persist for months after snow has melted elsewhere. These areas are known as snowbeds or snowpatches (Costin et al. 2000, Venn and Morgan 2007). Snowbed plant communities are highly specialized and restricted, occurring only in alpine areas where snow accumulates and persists on lee slopes for several months after adjacent areas have thawed. In these environments, snow can last well into summer or autumn (Kudo 1991, Costin et al. 2000, Venn and Morgan 2007, Green and Pickering 2009), substantially reducing the length of the growing season. As snow melts in mid-summer, the plant community experiences a rapid increase in soil and ambient temperatures, and there is abundant soil moisture that together act as a cue for many plants to flower and re-commence growth, and take advantage of the very short growing season (Bliss and Mark 1974, Inouye et al. 2002, Keller and Körner 2003). Across snowbeds, small-scale variations in snowmelt often drive patterns of plant species composition, the timing of phenological events, and biomass accumulation (Venn and Morgan 2007, Baptist et al. 2010, Venn et al. 2011).

The factors that drive decomposition in snowbed soils are unclear. On one hand, the very short, snow-free growing season might lead to snowbed communities having relatively low annual decomposition rates and low remobilization of nutrients from soil organic matter compared to adjacent areas, due to the overall shorter time period when temperatures are warm and soils are moist (Gavazov 2010). On the other hand, snowbed soils may have higher overall
decomposition rates compared with adjacent areas due to the long-lasting and insulating effects of snow, stable soil temperatures over winter, and the sustained provision of soil moisture (Carbognani et al. 2014).

In this study, we investigate the influence of snowmelt timing on decomposition rates across a late-lying snowbed community with a regular pattern of snowmelt. We use the tea bag index (Keuskamp et al. 2013), a globally consistent methodology which uses teabag leaf litter as a proxy for soil organic matter, to determine (1) how the regular timing of snowmelt across a snowbed community affects decomposition rates; (2) whether the influence of snowmelt is seasonal or pervades throughout the year; and (3) the relative importance of the snowmelt gradient compared with litter quality in determining decomposition rates. We predict that teabag mass loss of litter will increase in areas with longer lasting snow, particularly for winter incubations, and therefore that decomposition rates will be greatest in areas with later snowmelt in this snowbed ecosystem. We also expect litter quality will explain at least as much variation in decomposition rates as snowmelt timing, indicating that vegetation change will be a critical determinant of future decomposition rates.

**METHODS**

**Study site**

The study was conducted at the Warby Corner snowbed (~36°50’00” S, 147°19’48” E; 1840 m asl), close to Mt Nelse on the Bogong High Plains, approximately 320 km northeast of Melbourne, Victoria, Australia. The region is characterized by low mean annual minimum and maximum temperatures (2.7–9.5°C, respectively), frequent frosts (>100 per annum, occurring at any time of year), and high annual mean precipitation (>1273 mm/yr), much of which falls as snow between June and September (mean June precipitation is 139.3 mm; Bureau of Meteorology 2019). The snowbed community occurs on an approximately 33° slope with an aspect of 160° and covers an area approximately 150 m long and 80 m wide. It consists of outcropping rock and a mosaic of low (<0.4 m) shrub, forb, sedge, and grass-dominated patches which are strongly structured according to the regular pattern of snowmelt across the snowbed, previously defined and mapped in Venn and Morgan (2007) as early, mid, and late snowmelt zones. Shrubs (Lamiaceae, Proteaceae, and Ericaceae) are found mostly around the edges of the community.
Where snow melts the earliest, a mixed community composition with graminoid (Poaceae, Jucaceae, and Cyperaceae) and forb (mostly Asteraceae) species throughout the mid-snowmelt areas, and the late snowmelt areas dominated by the grass *Poa costiniana*. Across the snowbed, species phenology and biomass accumulation are also tightly controlled by the timing of snowmelt (Venn and Morgan 2007). The region is characterized by deep (10 to >40 cm) alpine humus soils which are rich in organic matter (Kirkpatrick et al. 2014). Soils in this region rarely freeze, and this happens only when bare soils (not protected by snow or vegetation) are exposed to overnight freezing temperatures (Venn et al. 2009). Australian snow is regarded as maritime (Green 1998) and is generally wet, easily becomes hardpacked, and increases in density throughout the season from approximately 0.25 to >0.45 g/cm³ (S. E. Venn 2016, unpublished data). In this region, predictable snowfalls and a lasting annual snowpack are already dwindling (Fiddes et al. 2015, Pepler et al. 2015), and a 30–70% decline in annual maximum snow depth relative to 1990 levels is projected for 2050 on the highest mountains in Victoria (under a low-emissions scenario; Fiddes et al. 2015). In this snowbed community, winter snow depths (>2 m in the deepest areas with strong south-east aspect and steep slopes) have little bearing on soil temperatures. Rather, the timing of snowmelt dramatically affects soil temperatures, from a gradual cooling down period at the first snowfall of the season, to being stable throughout winter for many months, between 0.1°C and 0.5°C (S. E. Venn 2019, unpublished data; Appendix S1: Fig. S1), to immediately fluctuating according to ambient daily conditions upon release from snow (Edwards et al. 2007, Venn et al. 2014).

**Litter decomposition experiment**

We used the tea bag index (Keuskamp et al. 2013) to measure decomposition rates in the early, mid-, and late snowmelt zones of the snowbed. The tea bag index replicates standard litterbag methods and uses two types of commercially produced tea as the litter medium in 0.25-mm synthetic mesh. By using two tea types of differing quality (labile green tea vs. recalcitrant rooibos tea), we can construct a decomposition curve using a single measurement in time, indicating the total, rate (TBI k), and stabilization factor (TBI S) of mass loss. Differences between tea types also allow for comparison of the importance of litter quality in relation to other influences on decomposition rates.

Well-defined snowmelt zones are a feature of the snowbed, and while the number of snowdays varies from year to year, the pattern of snowmelt is very regular. The snowmelt zones were mapped and defined by Venn and Morgan (2007) with permanent markers in 2000. The snowmelt zones are defined as early, with approximately 155–176 d of snow, mid with approximately 177–195 d of snow, and late with approximately 196–214 d of snow. To examine the effect of snowmelt timing on litter mass loss, we established two 2 m transects in each of the early, mid, and late snowmelt zones at the Warby Corner site. Along these transects at 15 cm intervals, we buried 12 air-dried teabags of each type (mass recorded prior to burial) in each plot at 5 cm depth in mid-December 2015 (snow-free season, mid-summer). The transects were positioned in representative vegetation of each snowmelt zone, while avoiding the canopies of shrubs. We buried a further six teabags of each tea type into each snowmelt zone in mid-March 2016 to capture winter + spring decomposition over the 2016 snow season. A total of 216 teabags were buried at the site. To examine differences in seasonality and incubation length, we recovered tea bags at three time periods: 92 d after spring burial, representing summer decomposition, 214 d after spring burial, representing annual decomposition, and 293 d after autumn burial, representing winter + spring decomposition (Fig. 2).

Upon recovery, we dried the teabags at 70°C for 48 h, removed soil using a small soft-bristled brush, and carefully removed ingrown root material with tweezers. Teabags were reweighed to determine their final mass. We calculated the mass loss of tea material by subtracting the mass of the synthetic bag and label from initial and final weights and corrected for any loss of material during transit using control teabags. The actual number of snow days in each snowmelt zone was determined from the first day that snow settled on the study site for the season (21st June 2016), and remaining snow was

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**Notes:**

- **Figure 2:**
- **Appendix S1: Fig. S1:**
- **Unpublished data:**
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mapped and visually assessed twice-weekly during the snowmelt period the following summer.

**Data analysis**

We calculated three indices of decomposition: (1) total mass loss (final divided by initial mass), (2) the stabilization factor (TBI S), which describes the proportion of potentially decomposable compounds (the hydrolysable or acid-digestible fraction, \( H \)) remaining upon stabilization of decomposition, according to Keuskamp et al. (2013). TBI S is calculated using green tea, for which mass loss is assumed to stabilize within three months of burial:

\[
TBI \ S = 1 - \left( \frac{a_g}{H_g} \right)
\]

where \( a_g \) is the decomposable fraction (mass loss) of green tea and \( H_g \) is the hydrolysable fraction of green tea, and (3) the decomposition rate (TBI k), which represents the rate at which decomposable compounds are lost during decomposition. This two-pool model accounts for the multiple chemical components of plant litter (Wieder and Lang 1982, Harmon et al. 2009) and is calculated using rooibos tea, for which decomposition has not yet stabilized during the incubation periods covered by this analysis:

\[
TBI \ k = \ln \left( \frac{a_r}{M_{(t)} - a_r} \right) \times \frac{1}{t}
\]

\( M \) is equal to the mass of rooibos tea at time point \( t \) (days), and \( a_r \) is the decomposable fraction of rooibos tea. \( a_r \) is calculated from the hydrolyzable fraction of rooibos tea (\( H_r \)) and stabilization factor (TBI S), whereby \( a_r = H_r (1 - TBI \ S) \).

**Statistical analysis**

To test how decomposition variables changed with date of snowmelt, we fitted linear mixed models with random intercepts using the package lme4 (Bates 2010). We did not use random slope models due to non-convergence. We treated tea type and length of snow cover duration as fixed effects and site as a random effect. Where we modeled relationships across all incubation periods to test for the significance of snowmelt timing and litter quality, we also treated incubation period as a random effect. To test the significance of differences in decomposition variables across snowmelt zones, seasons, and litter types, we conducted pairwise \( t \) tests using the Bonferroni adjustment. All data analysis was performed using R statistical software, version 1.0.136 (R Core Team 2017). All data and code are archived at github.com/hjdthomas/snowbed_tea.

**RESULTS**

**Effect of snowmelt timing on decomposition rates**

Mass loss decreased with snow cover duration for both tea types during winter+spring, that is, during the time in which snow is present in this landscape (Fig. 3b; green tea, slope = \(-3.03e-03 \pm 4.44e-04\); rooibos tea, slope = \(-3.61e-03 \pm 5.76e-04\)). Mass loss also decreased for rooibos tea with snow cover duration for year-long incubations and across all seasons combined (Fig. 3a, d; full year, slope = \(-3.97e-03 \pm 1.72e-03\); all seasons, slope = \(-2.38e-03 \pm 7.02e-04\)). We found no significant relationship between snowmelt timing and mass loss during the summer (Fig. 3c) or for labile green tea over the full year. The
decomposition rate (TBI k) non-significantly increased and the stabilization factor (TBI S) significantly decreased (Appendix S1: Fig. S2) with earlier snowmelt, indicating lower storage of carbon and other nutrients in undecomposed litter material. The mean mass loss of tea from handling (non-buried controls which were only transported to and from the field site) was negligible, approximately 0.26 g for both tea types.

Differences in mass loss across seasons

Differences in mass loss between melt zones were only significant during the winter + spring seasonal incubation (pairwise t tests, P < 0.01; Fig. 4a–c), except for between early and mid-melt zones for rooibos tea. We found significant differences in mass loss across seasons (pairwise t tests, P < 0.001; Fig. 3d), with the highest mass loss during the full-year incubation, and lowest mass loss during the winter + spring incubation. However, for the more recalcitrant rooibos tea, there was no significant difference in mass loss between the winter–spring and summer incubations. Both decomposition rate (TBI k) and the stabilization factor also displayed the strongest differences among snowmelt zones during winter–spring, while decomposition rates were significantly slower and stabilization significantly higher during winter (Appendix S1: Figs. S3, S4). Differences did not solely correspond to incubation length, with the summer incubation (92 d) shorter than the winter–spring incubation (293 d).

Fig. 3. Mass loss across snowbed melt zones for (a) all seasons and incubations, (b) winter + spring incubations, (c) summer incubations, and (d) full year incubations in relation to snow cover duration (measured in days). Colors indicate tea type (green is green tea; red is rooibos tea). Points indicate individual tea bag mass loss. Lines indicate linear mixed model fit, and shading indicates 95% confidence intervals. Modeled slope fit and standard error for each tea type indicated; significant models are highlighted in bold.
Differences in mass loss across litter types

Differences in mass loss between tea types were highly significant \( (P < 0.001) \) across all snowmelt zones and seasons, and accounted for the largest differences in mass loss regardless of experimental treatment. Mass loss of tea bags has previously been found to be representative of mass loss of local plant litter in alpine environments (H. Thomas, *unpublished data*) but was not tested in this study.

**DISCUSSION**

Our study investigating the decomposition rates of a standardized plant litter (green and rooibos tea) across a snowmelt gradient in an alpine snowbed revealed that snow cover duration is a significant factor determining the mass loss of litter. In particular, we found a negative relationship between litter decomposition and the number of snow days for both litter types (an overall decrease in mass loss with longer snow cover duration), with a stronger effect found in the winter + spring incubations for the recalcitrant rooibos tea. In addition, the differences in decomposition rates between snowmelt zones were significant during the winter + spring incubations and across seasons for both litter types, and between litter types, with decomposition rates being significantly higher in the early
snowmelt zone, compared to the mid- and late snowmelt zones. Importantly, decomposition rates were highest for tea buried over the whole year or only over summer, with winter + spring incubations decomposing the least.

Our results do not demonstrate that a longer snow cover duration increases decomposition rates, which has been demonstrated elsewhere and is most likely due to the insulative effects of the snowpack (Walker et al. 1999, Natali et al. 2012, Saccone et al. 2013). Rather, our results indicate significantly higher decomposition rates in the early snowmelt areas, particularly for winter + spring only incubations, possibly due to the favorable warm spring temperatures that occur immediately after snowmelt, and a longer time in these conditions for decomposition to occur. The litter incubations in early snowmelt areas during the course of this study had 17 and 28 extra days post-snowmelt compared with the mid and late snowmelt, respectively. The relatively high spring temperatures in this region (daily maximums between 12.0°C and 20.0°C and daily minimums between 0.0°C and 2.5°C from September to November; Bureau of Meteorology 2019) may contribute to the early snowmelt zones experiencing higher decomposition rates if temperature fluctuations such as these activate soil microbes sufficiently (Gavazov 2010). In this snowbed system, the soil temperatures remain stable until the snow has melted (Appendix S1: Fig. S1), resulting in reduced time for soils in late snowmelt sites to experience warmer and fluctuating temperatures in combination with abundant soil moisture. The late snowmelt zone (also the last patch of snow remaining in the landscape) consequently experiences a rapid transition to mid-summer temperatures immediately upon snowmelt, with presumably far less soil moisture available during the snow-free months. Over the course of a whole year, however, the differences in mass loss of litter between snowmelt zones diminishes (Fig. 4a). Spring temperatures above freezing may also increase the availability of liquid water in early melt zones, which is known to be an important driver of decomposition, especially in arctic sites where soils may dry out substantially later in the season (Hicks Pries et al. 2013, Blok et al. 2016). Decomposition in early melt zones may be further enhanced by physical processes such as freeze–thaw action (Wang et al. 2012, Bokhorst et al. 2013), or by differences in microbial communities among melt zones (García-Palacios et al. 2013). As a consequence, the predicted climate change induced reductions in snow cover duration, and warmer temperatures in spring and summer (unless a cold spell occurs in spring), may lead to an overall increase in decomposition in snowbed systems similar to this one, demonstrating that the realized impacts of climate warming are strongly dependent on the environmental context.

In this study, we found that snowmelt timing had no significant effect on summer decomposition contrary to previous studies (Bokhorst et al. 2013), suggesting that the impacts of snowmelt timing on decomposition are short term and primarily affect nutrient availability during spring. Differences between melt zones were more pronounced in the recalcitrant rooibos tea compared to the labile green tea; a likely explanation being that the most easily decomposed material decomposes first and then overall decay rates slow down. Several previous studies have suggested that decomposition rates in recalcitrant litters and lower quality organic matter are more sensitive to changes in temperature and moisture than more labile litters, likely due to initial leaching (Conant et al. 2008, Bokhorst et al. 2013, Susela et al. 2013, Djukic et al. 2018). Our findings support this hypothesis, but we suggest the differences are less important over longer time periods. We also observed significantly higher decomposition over the summer months than winter months for green tea, with faster decomposition rates and greater mass loss before stabilization, despite a shorter incubation period. Although some studies have suggested that substantial decomposition continues to occur under snow during winter (Baptist et al. 2010, Saccone et al. 2013), the three decomposition variables examined in this study support the view that winter decomposition of fresh litter is low (Bokhorst et al. 2013). Indeed, it is likely that the majority of mass loss occurred during spring thaw, rather than under snow during winter, evidenced by significantly greater mass loss in early snowmelt zones.

Overall, we found that litter quality was the greatest determinant of decomposition, with clear differences in mass loss between tea types.
across all treatments, seasons, and incubation periods. Although some studies have found little effect of litter quality under some snow cover duration regimes (Saccone et al. 2013), our results align with evidence that litter quality is the greatest driver of decomposition in alpine environments (Saleska et al. 2002, Cornwell et al. 2008, Baptist et al. 2010, Djukic et al. 2018). If changes in snowmelt timing or other environmental variables alter the composition of snowbed vegetation communities sufficiently, and thus litter quality, this could potentially produce large feedbacks to nutrient cycling (Aerts 2006, Gavazov 2010, though see Rinnan et al. 2008, Baptist et al. 2010, Blok et al. 2016). A likely scenario for snowbeds in this particular region is the encroachment and an increase in the abundance of alpine shrubs due to overall climate warming and earlier melting snow (Williams et al. 2015). Shrubs encroaching into snowbeds could also affect overall decomposition rates due to their stature and shading effects, thus altering the microclimate, their ability to affect snow drifting patterns and trap wind-blown snow (McLaren and Turkington 2010, Myers-Smith and Hik 2013). Shrubs may also interact with warmer soils which could potentially lead to greater litter inputs (Christiansen et al. 2018). Shrub-specific decomposition-related plant traits such as specific leaf area and leaf nitrogen have also been shown to have strong relationships with temperature and moisture in alpine environments (Venn et al. 2011, Bjorkman et al. 2018).

Together, our results indicate that decomposition in this alpine snowbed is strongly influenced by both snowmelt timing and litter quality traits. The predicted declines in snowfall in coming decades for this region (Fiddes et al. 2015, Pepler et al. 2015) are thus likely to have multiple flow-on effects relating to the timing of soil nutrient availability and nutrient cycling, which in turn may produce feedbacks by altering vegetation communities. Without lasting snow and the regular patterns of snowmelt across the landscape, snowbed communities, like the one we studied, face an unprecedented level environmental change, as do the downslope plant communities that rely on the moist conditions provided by slowly melting snow. A better understanding of the interactions between plant community composition, local litter decomposition rates, and soil nutrient cycling will therefore be necessary to fully determine the important and unique role that snowbeds play in alpine landscapes.

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