Research

Oikos 119: 1685–1689, 2010
doi: 10.1111/j.1600-0706.2010.18515.x

Subject Editor: Tiffany Knight. Accepted 26 March 2010

The effect of snow depth on overwinter survival in *Lobelia inflata*

Andrew M. Simons, Jillian M. Goulet and Karyne F. Bellehumeur

A. M. Simons (asimons@connect.carleton.ca), J. M. Goulet and K. F. Bellehumeur, Dept of Biology, Carleton Univ., 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada.

The snowpack in high altitude and latitude regions provides thermal insulation during the cold season. Recent climate change has resulted in a decrease in both the duration and the reliability of this snowpack and may thus affect overwinter survival of biota. Here we use a manipulation approach to ask how snow depth affects ground surface temperatures and how this in turn affects survival of the overwintering rosette stage in the monocarpic plant *Lobelia inflata*. A shallow but consistent insulation layer (R-value of 3) was sufficient to reduce temperature fluctuations and the accumulation of sub-zero degree-days substantially. For all treatments >R3 these measures were negligible. Survival results are consistent with a crucial role of thermal insulation to successful overwintering of *Lobelia inflata* rosettes: without a consistent snowpack survival was low (11%); with an insulation effect of R3 or greater survival increased dramatically (81%). The winter prior to the manipulation study was characterized by an anomalous absence of snow at the onset of cold temperatures. This resulted in substantially greater accumulation of sub-zero degree-days at the soil surface and almost 100% rosette mortality in the field. This study shows that inconsistent and reduced snowpack – a prediction of climate change – will have critical effects on plant survival because of increased temperature fluctuations and extreme temperatures experienced at the soil surface.

During the winter months at high latitudes and altitudes, a blanket of snow effectively insulates the belowground environment from ambient air temperatures. Climatic warming trends can have the seemingly paradoxical effect of increasing the biota's exposure to extreme cold (Groffman et al. 2001, Bokhorst et al. 2008, Inouye 2008); the thinning, absence or discontinuity of this layer increases exposure to temperature extremes, freeze-thaw events and other environmental insults (Bridgham et al. 1999, Inouye 2000, Groffman et al. 2001, Phoenix and Lee 2004, Campbell et al. 2005, Bokhorst et al. 2008).

Recent data indicate a warming trend that occurs predominantly in winter (Bonsal et al. 2001, Shabbar and Bonsal 2003, Groleau et al. 2007, IPCC 2007), reducing the duration and constancy of the snowpack (IPCC 2007) and its insulating effects. The frequency of extreme warming events in Canada increased over the second half of the 20th century (Shabbar and Bonsal 2003, Groleau et al. 2007) and anomalous January snowmelt has been increasing in frequency at 68°N in Sweden (Phoenix and Lee 2004). Given the potential importance of its effects, climate warming during winter months has been given inadequate attention (Inouye 2000, Phoenix and Lee 2004, Bokhorst et al. 2008).

Natural selection in response to predictable environmental changes – such as those associated with seasonality – have resulted in adaptations that allow survival through harsh periods. Winter quiescence and dormancy are considered to be finely tuned adaptations to seasonality but their initiation relies on appropriate photoperiod and temperature cues (Cleland et al. 2007). Maladaptation as a result of climate change may occur in different ways: a breakdown in the predictability of components of seasonality leads to a mismatch between the cues used by organisms and the environmental conditions they reflect (Dunne et al. 2003, Root et al. 2003, Aerts et al. 2004, Cleland et al. 2007, Visser 2008); second, even if cues for entering a dormant state are appropriate, survival of the organism in this dormant state may be reduced if conditions experienced are novel or more extreme than those under which the dormant state evolved. Study of success or viability under scenarios of climate change is necessary to provide a baseline for the extent of maladaptation expected. Maladaptation may be mitigated by population range shifts, phenotypic plasticity (Charmantier et al. 2008), the expression of evolved risk-averse strategies (Simons 2009), or through adaptive tracking (Bell and Collins 2008), or may result in extinction.

Altered phenology and allocation has been observed in perennial plants subjected to early warm episodes (Galen and Stanton 1995, Dunne et al. 2003, Root et al. 2003, Aerts et al. 2004, Schwartz et al. 2006, Bokhorst et al. 2008, Inouye 2008, Wipf et al. 2009), but it cannot be assumed that this plasticity is adaptive (Visser 2008). For example, perennial heathland shrubs exposed to artificial winter warming showed delayed bud development and reduced flower and berry production (Bokhorst et al. 2008); early snowmelt has led to increased incidence of frost damage to flower buds – and severely reduced reproductive success – in high altitude perennial wildflowers (Inouye 2008); and larvae of the freeze-tolerant gall fly, *Eurosta solidaginis*, show reduced survival when inhabiting broken goldenrod stems under an insulating snow cover because of maladaptive plasticity for increased energy expenditure (Irwin and Lee 2003). However, reductions in snow cover are responsible for frost injury and declines in yellow-cedar (Schaberg et al. 2008). Furthermore, differences among populations in phenology and life histories in rare arctic and alpine annuals (Simons and Wagner 2007, Wagner and Simons 2009) suggest that these characters may be adaptations to local harsh conditions.

The effects of exposure to extreme cold and increased frequency of freeze-thaw cycles are expected to be more severe for ephemeral monocarpic plant species because their allocation to vegetative structures including perennating organs is reduced relative to investment in reproduction (Roff 1992, de Jong and Klinkhamer 2005). Any benefit of a longer growing season cannot be realized if winter warming results in high mortality through increased exposure to cold temperatures (Wipf et al. 2009). Little direct evidence is available, however, on the effect of reduced snowpack on the survival of vulnerable monocarpic plants.

Here we employ a manipulation approach to ask whether the depth of an insulating layer influences mortality in the overwintering rosette stage of *Lobelia inflata* (Campanulaceae). *Lobelia inflata* germinates in the summer and must overwinter successfully in the form of a rosette prior to reproduction in a subsequent growing season. Furthermore, the life-history decision to 'bolt', or to enter the reproductive mode through the development of a flowering stalk, appears to be an adaptation that depends on reliable overwinter rosette survival (Simons and Johnston 2003). Although overwintering is also effected through seed dormancy, the seed bank in *L. inflata* is short lived and much variance in the timing of seed germination occurs within growing seasons, likely as an adaptation to unpredictable season length (Simons 2009). Thus, population persistence is expected to depend critically on overwinter rosette survival, making *L. inflata* an ideal organism with which to test the importance of snow cover.

Material and methods

Lobelia inflata is a monocarpic perennial inhabiting disturbed soils in eastern North America, from Nova Scotia in the northeast to as far south as Kentucky. This species rarely flowers in its first season in the northern part of its range (Simons and Johnston 2000), germinating throughout the growing season, and flowering only after overwintering at least once in the rosette stage.

From 8 to 19 November 2007, rosettes of *L. inflata* were transplanted from nearby field populations in the Laurentians (Québec) and Petawawa (Ontario) into individual cellpack inserts within Kord trays and transported to an outdoor experimental garden. A cell size of 5.5 cm was chosen to allow transplant of the intact root system of each rosette. The two field sites and the experimental garden are at similar latitudes (45°20' to 45°54') similar in overall exposure and snowfall characteristics. The trays were sunk into the soil and held until establishment of the manipulation treatments. Rosettes were measured and all individual insert cells were separated, but to reduce harmful transplant effects, rosettes were not removed from insert cells. No water or fertilizer was added at any time, but to allow free exchange of water and nutrients between the cell and surrounding soil, the cells were opened on the side by peeling off a 2 cm strip from top to bottom on two opposite sides of each cell, and rosettes were transplanted within these opened cells flush to the soil surface. Eighteen rosettes were allocated to two replicates within each of five insulation treatment plots, such that mean rosettes size (28.0 mm SE = 1.6 mm) did not differ among treatments (DF = 4, F = 0.293, p = 0.88) or replicates (DF = 5, F = 0.18, p = 0.97). Transplants to replicate A plots for all five treatments were performed on 26 to 28 November and for replicate B on 29 November to 4 December.

Wooden frames surrounded each of the ten 1.5 × 3 m plots to a height corresponding to the insulation treatment, both to contain the insulation and to provide a surface to guide snow clearing. Insulation, or thermal resistance, is given here in Imperial R-units ($ft^2\cdot°F\cdot h/Btu$; the standard unit used in the construction industry in North America, for example), and may easily be converted to SI units $m^2\cdot°C/W$. R1 Imperial = R0.175 SI, and is roughly the insulation value of 2.54 cm or 1 inch of untransformed snow. Treatments consisted of two replicates each of zero insulation (T0), one unit of vermiculite at a depth corresponding to R3 insulation value (T3), one unit of vermiculite plus R3 styrofoam board (T6), one unit of vermiculite plus two layers of R3 styrofoam board (T9) and a natural, undisturbed and uninsulated treatment from which snow was not cleared (TN). We used artificial insulation instead of natural snow in this manipulation study to maintain consistent insulation values (Discussion).

Temperature was recorded throughout the winter using iButtons, programmed to take readings every 144 minutes at the soil surface in all plots. Temperature was measured by three replicate iButtons per treatment: two iButtons in each replicate A plot and one in each replicate B plot. Two additional iButtons, attached at a height of 2 m on the north side of two posts, recorded air temperature also at a frequency of 144 min throughout the winter.

Snow was removed from all plots (except TN) as soon as possible after each snowfall event using shovels and an electric leaf blower. No attempt was made to remove ice coating from T0 rosettes. Removal followed 22 snowfall events during the 2007–2008 winter. For dates and snowfall amounts see Appendix 1.

To assess overwinter survival and spring rosette size, all plots were uncovered and rosettes were transferred into the greenhouse on 8 to 10 April 2008. Survival was gauged on an ordinal scale of 0 to 5 (0 = no rosette; 1 = black/brown rosette; 2 = some evidence of green tissue; 3 = <1 good leaf; 4 = >1 healthy leaves; 5 = healthy rosette) after two weeks in the greenhouse, and also as the length of the longest living leaf (LLL).

Results

Within each depth treatment, temperatures recorded by replicate iButtons were similar and averages of replicates were calculated for each 144 minute time period for clarity of presentation in subsequent figures. Temperatures recorded continuously throughout the winter reveal that soil surface temperature of the zero depth treatment follows air temperature extremes (Fig. 1a) more closely than any of the insulated treatments (Fig. 1b–e) and fluctuated between –17°C and 10°C. Reduced but substantial soil temperature fluctuation occurred for the T3 treatment (–10°C to +1.7°C), but under the T6 treatment remained between –1.2°C and 1.3°C and under the T9 and TN treatments between –0.5°C and +2.8°C throughout the period from 5 December 2007 to 1 April 2008, even when air temperatures reached –28°C. Mean temperatures were lower

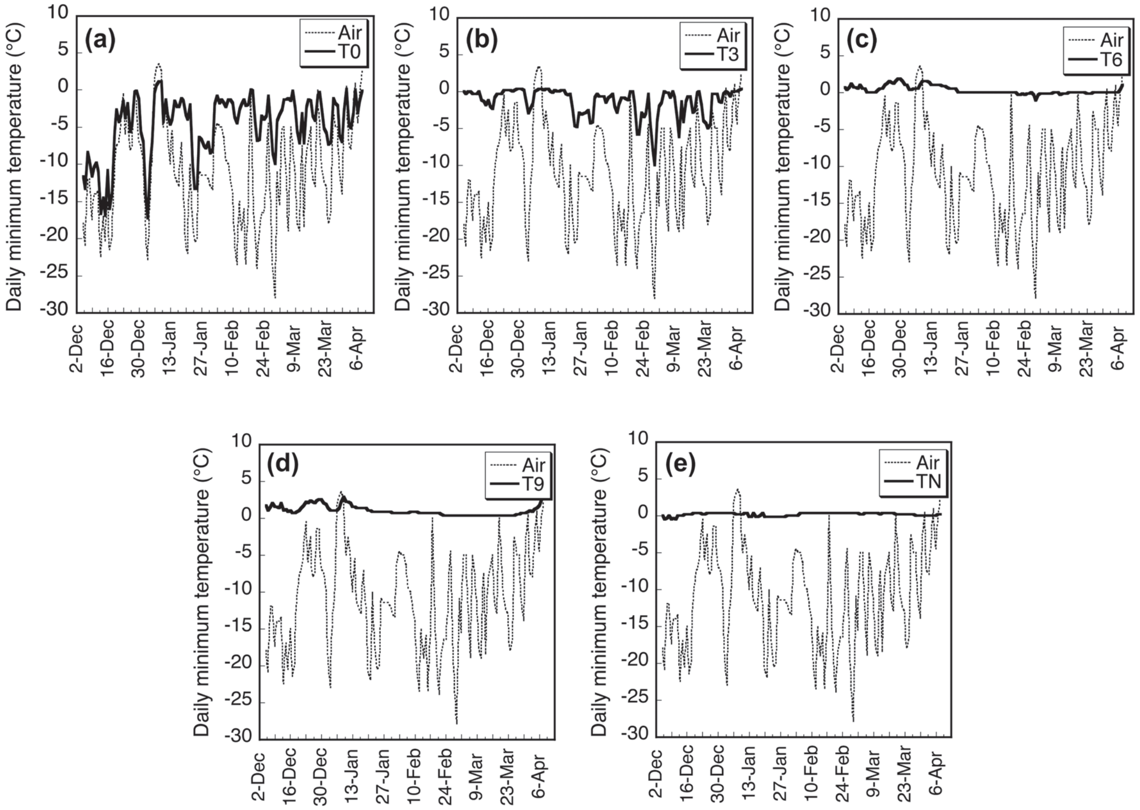

Figure 1. Minimum daily temperature at the soil surface throughout the winter of 2007–2008 under different insulation depth treatments. For clarity, air temperature is compared to a different depth insulation treatment in each panel: zero depth (a); T3 (b); T6 (c); T9 (d); and TN (e). Temperatures presented are based on averages of three replicate measurements from each depth treatment taken every 144 minutes using iButtons. See text for explanation of depth treatments.

and more variable for treatments with less insulation (Table 1) and the accumulation of sub-zero degree-days was over three times greater for the treatment without insulation compared to the T3 treatment and was negligible for the T6, T9 and TN treatments (Table 1).

Rosette survival in the absence of an insulating layer was 11% and, under an insulation layer of ⩾ R3 averaged 80.6%. To examine the effect of insulation on overwinter survival, an analysis of covariance was performed for both survival and spring LLL, with replicate depth treatment nested within depth treatment, including autumn LLL as a covariate to correct for original rosette size. The analysis of survival showed a significant effect of snow depth (Table 2a). There is no indication that survival was related to original rosette size (Table 2a).

The ANCOVA for final rosette size in the spring shows that this measure of overwintering success was also dependent on insulation depth (Table 2b) after correcting for the effect of original rosette size. A post-hoc Tukey test (not shown) indicates that the significant effect of depth in both survival and spring rosette size from the ANCOVAs is attributable solely to differences between zero depth treatment and all other depths.

Discussion

In regions with a winter season characterized by cold conditions adverse to growth and survival, a snow pack is known to moderate the physical environment at and below the soil surface. However, the effect of the moderating effects of snow on organismal survival is poorly studied. We find that the presence of an insulating layer during the winter is positively related to survival of rosettes of *Lobelia inflata*. Although thermal stability at the

Table 1. Summary thermal qualities of the insulation treatments. Air temperature was recorded at a height of 2 m and at the soil surface for all other treatments using miniature temperature loggers (iButtons) every 144 minutes from early December 2007 through early April 2008. D-d < 0°C is the degree-day accumulation of sub-zero temperatures over the entire measurement period, calculated as a weighted average of negative temperatures over each measurement period each day.

	Mean (SD)	Mean daily minimum (SD)	Mean daily maximum (SD)	D-d < 0°C
Air	–4.26 (7.82)	–11.03 (6.96)	3.69 (6.12)	704.2
T0	–2.04 (4.11)	–4.79 (4.26)	0.99 (4.93)	312.6
T3	–0.62 (1.56)	–1.36 (1.87)	0.16 (1.56)	97.9
T6	0.4 (0.63)	0.29 (0.55)	0.53 (0.71)	2.9
T9	1.1 (0.76)	0.98 (0.65)	1.26 (0.87)	0
TN	0.2 (0.2)	0.16 (0.21)	0.25 (0.24)	2.5

Table 2. The effect of insulation treatment on overwinter survival (a) and spring rosette size (b) in *Lobelia inflata*. Replicate insulation treatment blocks (Rep) were nested within insulation treatment (Depth), and original rosette size (LLL) was included as a covariate.

Source	MS	DF	F	p
(a) Survival				
LLL	1.111	1	0.522	0.472
Depth	30.499	4	15.708	0.005
Rep(Depth)	1.941	5	0.912	0.478
(b) Rosette size				
LLL	3714.57	1	30.144	<.0001
Depth	1954.97	4	17.974	0.004
Rep(Depth)	108.75	5	0.883	0.497

soil surface is not attained unless the insulation has an R-value of greater than 6, here an insulation layer of R3 was adequate to ensure rosette survival. It is important to note that high survival was observed under a completely invariable insulation layer and it would be erroneous to conclude from these results that a snow pack in the field averaging R3 but of variable depth through time would be sufficient to ensure rosette survival; rather, this should be interpreted as the minimum depth for rosette survival.

In a similar manner to previous studies of effects of snow depth, we used artificial insulation instead of natural snow. This is necessary because a lack of snow at any time during the season would prevent the maintenance of the nominal depth of treatments (see initial trial, below) and because the insulation value of a given snow depth is highly dependent on the type of initial precipitation, as well as on transformations that occur through time. The use of artificial insulation allows conclusions to be drawn about the specific effects of variation in thermal insulation while holding constant other factors, such as moisture that can affect biological processes (Grippa et al. 2005).

Although this manipulation allowed us to draw conclusions about the importance of insulation on a relative scale, the use of artificial insulation also makes it difficult to make quantitative extrapolations to effects of snow depth in nature. The effects of physical processes occurring within a natural snowpack that cannot be replicated under artificial insulation include those of air-flow exchange with the atmosphere, soil moisture content, and the latent heat of condensation and vaporization associated with phase changes. Therefore, an assumption we must make is that the trend observed (greater insulation leads to greater survival) is not a product of the absence of effects of physical processes not accounted for in our treatments. This is a problematic assumption only if these processes affect survival differently across different depths, and have the opposite effect of insulation.

The year prior to the study reported here, a preliminary manipulation experiment was conducted (winter 2006/2007). The intent in this initial trial was to manipulate snow depth by removal of natural snow to prescribed levels, rather than by the addition of artificial insulation. However, the winter of 2006/2007 turned out to be record setting in that the first substantial snowfall did not occur until late January, despite cold temperatures. Such an anomaly in fact provides the rationale for conducting studies of reduced snowpack on biota: it shows that rosettes may be exposed to extreme cold without snow insulation. However, this anomalous event prevented the establishment of different depth treatments through manipulation; lack of snow meant that all treatments were effectively zero depth, at least until the first snowfall in late January.

In an attempt to salvage this initial manipulation study, we added insulation in an identical manner to the subsequent experiment reported (except that R-values were 0, 3, 6, 12 and 24), but not until 14 January 2007. Early-winter soil frost resulting from lack of snow cover can be an important source of mortality, and soil may remain frozen for long periods even after snowfall has occurred (Goodrich 1982). Prior to the addition of insulation, soil surface temperatures dipped to −16°C and the accumulation of sub-zero degree-days $< 0°C$ had already averaged 79.8 across all (bare) treatment plots over the short period prior to 14 January 2007. Consequently, accumulation of sub-zero temperatures at the soil surface for the entire winter ($T0 = 619.9$, $T3 = 232.2$, $T6 = 184.2$, $T12 = 146.4$, $T24 = 157.0$, $TN = 188.1$ d.d. $< 0°C$) was higher in this initial experiment than that in the treatments showing high survival (i.e. T3, T6, T9 and TN) from the manipulation experiment reported (Table 1).

It is thus probable that severe and sustained freezing in the absence of snow cover was responsible for high mortality observed in this initial study: rosette survival in all treatments was very low. There were no surviving rosettes in either T0 replicate and only 0–2 rosettes survived in each of the insulated treatments. Furthermore, overwinter survival for a population of *L. inflata* rosettes monitored in Petawawa, Ontario averaged 88% for 2003/2004 through 2005/2006 (minimum 82%) but showed 0% survival over the anomalous 2006/2007 winter.

Climate change is being manifested not only in increased average temperatures, but increased environmental variability, predominantly during winter (Bonsal et al. 2001, Shabbar and Bonsal 2003, IPCC 2007). An expected consequence is a decrease in the reliability of an insulating snowpack (IPCC 2007), with increased January–Feburary precipitation in the form of rain (Groleau et al. 2007). Variance in physical characteristics at the soil surface as a result of variable snow depths has been studied extensively, but the relationship between these characteristics and survival is less well known. Every winter differs, and the effect of temperature fluctuations on survival is likely species-specific. However, this study shows that a consistent snowpack is critical to survival of the overwintering rosette stage of a monocarpic perennial plant and that survival is moderated by the effects of temperature fluctuations experienced at the soil surface. Our results suggest that the adverse effects of climate change during winter at high latitudes and altitudes may be underestimated, and merit further investigation.

Acknowledgements – We are grateful to P. Arbour and the Petawawa Research Forest (PRF) for access to long-term research sites and to D. Inouye for helpful comments. This work was supported by a Natural Sciences and Engineering Research Council (NSERC) of Canada Discovery Grant to AMS.

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Appendix 1. Dates of snowfall events, and amounts removed from insulated manipulation treatments T0, T3, T6 and T9.

Snow event no.	Snow clearing dates	Snowfall amount
1	30 November 2007	dusting
2	1 December	2 cm
3	3 December	20 cm
4	4 December	5 cm
5	5 December	dusting
6	7 December (a.m.)	dusting
7	7 December (p.m.)	dusting
8	12 December	8 cm
9	14 December	3 cm
10	17 December	37 cm
11	18 December	2 cm
12	21 December	4 cm
13	27 December	10 cm and ice
14	31 December	0.5 cm
15	2 January 2008	20 cm
16	23 January	10 cm
17	4–5 February	30 cm and ice
18	7 February	1 cm
19	10 February	0.5 cm
20	14 February	10 cm
21	17 February	2 cm
22	20 February	1 cm
23	27February	5 cm
24	2 March	10 cm
25	6 March	30 cm
26	9 March	57 cm