2015-06-01

Environmental and Adaptive Buffers that Mediate the Response of Subalpine Ecosystems to Environmental Change

Lafe G. Conner
Brigham Young University - Provo

BYU ScholarsArchive Citation

Conner, Lafe G., "Environmental and Adaptive Buffers that Mediate the Response of Subalpine Ecosystems to Environmental Change" (2015). *All Theses and Dissertations*. 5913.
https://scholarsarchive.byu.edu/etd/5913

Environmental and Adaptive Buffers that Mediate the Response of Subalpine Ecosystems to Environmental Change

Lafe G. Conner

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Richard A. Gill, Chair
Zachary T. Aanderud
Jayne Belnap
David R. Bowling
Roger T. Koide
Samuel B. St. Clair

Department of Biology

Brigham Young University

June 2015

ABSTRACT

Environmental and Adaptive Buffers that Mediate the Response of Subalpine Ecosystems to Environmental Change

Lafe G. Conner
Department of Biology, BYU
Doctor of Philosophy

This document reports the results of 4 studies of subalpine ecosystem ecology, describing ways that spatial heterogeneity in soils and plant communities mediate ecosystem responses to environmental change. Ecosystem responses to environmental change are also mediated by regional climate patterns and interannual variability in weather. In the first chapter we report the results of an experiment to test for the mediating effects of associational resistance in a forest community that experienced wide-spread beetle kill. We found that Engelmann spruce were more likely to survive a beetle outbreak when growing in low densities (host dilution) and not through other types of associational resistance that relate to higher tree-species richness or greater phylogenetic diversity of the forest community. In the second chapter we report the effects of early snowmelt on soil moisture in subalpine meadow and aspen communities. We found that soil organic matter, soil texture, and forest cover mediated the effects of early snowmelt and were more important drivers of growing-season soil moisture than was snow-free date. In the third chapter we report the effect of early snowmelt on growth and seed production of early-season and midsummer herbaceous species. We found that the primary effect that snowmelt timing had on plant growth was through its effect on species distribution. Changes in the timing of snowmelt had limited effect on the growth, flowering, and seed count of species after they were established. In the final chapter, we report the effect of early snowmelt on soil respiration, microbial biomass, dissolved organic carbon and soil organic carbon. We found that early snowmelt resulted in warmer soil temperatures compared to neighboring snow-cover plots, and that microbial biomass and soil respiration showed no signs of a snowmelt legacy effect during the growing season. Soil organic carbon in rapid and slow-turnover pools was affected more by plant community than by snowmelt timing, and the primary drivers of soil respiration during the snow-free period were first soil organic matter and second soil temperature. Taken together, this dissertation reports our findings that subalpine ecosystems are resilient to environmental change in part because organisms in these systems are adapted to environmental conditions that are highly variable between sites, seasons, and years.

Keywords: aspen, associational resistance, biodiversity, climate change, carbon sequestration, Engelmann spruce, microbial biomass, phenology, plant growth, seed count, snow, snowmelt, soil moisture, soil organic matter, soil respiration, subalpine

ACKNOWLEDGEMENTS

I would like first to thank my committee chair, Richard Gill, for providing me the opportunity to conduct this research and for his continuing advisement and support of the research through many revisions and changed directions. Next, I would like to thank Jayne Belnap and David Bowling who each played an instrumental part in the initial idea and refining design of the snow manipulation experiment. I would like to acknowledge and thank the other members of my committee. Sam St. Clair provided encouragement and modeled excellent research in forest and plant physiological ecology and opened his lab for me to complete the nitrogen analyses and measure plant water potentials. Zach Aanderud provided guidance in measuring microbial biomass, dissolved organic carbon, and soil nitrogen. Roger Koide provided encouragement when I was discouraged and needing direction. I would also like to thank Leigh Johnson for the encouragement and guidance he provided during his time on the committee.

Funding for this dissertation research was provided by the GA Harris Graduate Research Instrumentation Fellowship (2010) from Decagon Devices, Inc. (Pullman, WA), BYU Graduate Studies Graduate Research Fellowship (2011-2012), Rocky Mountain NASA Space Grant Consortium Fellowship (2012-2013), and a Charles Redd Center for Western Studies Summer Research Fellowship (2014).

I would like to thank several graduate student colleagues who have assisted this research by sharing their expertise. Greg Maurer showed me how to manipulate snowmelt with dust and provided valuable feedback on the soil moisture chapter. Debbie Rigby showed me how to measure ammonium, nitrate, and dissolved organic carbon. Rachel Buck, at the BYU Environmental Analytics Lab, helped with a number of procedures and offered support with instruments. Eric Billman taught me the mixed-effects linear regression analysis that became a

central part of the statistical analysis of the dissertation. Spencer Ingley was a great office mate and helped me learn structural equation modeling. Other BYU faculty members offered expertise in completing this research, and I would like to thank Randy Larsen for his expertise in survival analysis and model selection and Steve Peterson for his expertise in landscape ecology and GIS. Thanks also to Daniel P. Ames for expertise in data management and for sharing HydroServer Lite with the Gill Lab.

I would like to acknowledge and thank my undergraduate research partners Michael Bunnell and Joshua Harvey. Mike and his field team over two summers collected the data for the analysis of spruce resistance to bark beetles and was instrumental in completing the manuscript for that paper. Mike has also been a great friend and colleague as a graduate student in the Gill Lab. Josh collected the soil respiration data in 2013 and collaborated with me in analysis and writing of the soil carbon chapter.

My family offered constant support throughout the research and writing of this dissertation. Thanks to Diane and to our children, Jensen, Abram, Ethan, and Maren, for following me into the field and for being fantastic companions. Thanks to my parents, Delose and Janice Conner, from whom I inherited a love for learning and for life.

To my own mountain home.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

PREFACE

In his *Letters to a Young Scientist*, E.O. Wilson describes two pathways leading to original scientific research. Through the first, the researcher begins with a problem or question and then seeks out a natural system, usually a model organism, particularly suited to addressing that question. Through the second path, researchers begin with a particular organism or natural entity they want to study and then discover the questions that organism is uniquely suited to answer. In this research, I have followed the latter path, and as a result this dissertation represents a collection of studies unified by their common tie to the ecology of subalpine ecosystems more than by a common question or problem. The central questions in each of the chapters of this dissertation could stand alone and lead to much greater depth of investigation. However, as it stands, these chapters combined may provide a variety of insights into the ecology of a system that is highly diverse as well as economically, scientifically, and culturally valuable and interesting.

Subalpine, or montane, ecosystems stand between alpine environments, those above continuous tree line, and the forested environments at lower elevations (Körner 2003). Abrupt changes in topography and intermittent forest cover in the subalpine create spatially heterogeneous patterns of microenvironments and result in a high degree of species, soil, and community diversity over a fine spatial scale. One of the first questions to arise in our investigation of subalpine ecosystems was whether the diversity of tree species and variation in stand density, along with heterogeneous environmental conditions, influenced patterns of spruce resistance to a bark beetle outbreak. We found support for density-dependent resistance, though no support for resistance associated with typical measures of community diversity such as species richness and evenness or associated with the phylogenetic distance between neighboring tree species. In researching other aspects of subalpine ecology and hydrology, we found that spatial patterns in forests, understory vegetation, and soils drive ecosystem processes such as the cycling of C (chapter 4), N (chapter 3), and water (chapter 2) and significantly mediate the response of these processes to environmental change.

Subalpine ecosystems experience a wide range of environmental conditions on seasonal and daily time-scales. The range of environmental conditions varies across regions and continents. The climate of tropical subalpine systems may differ dramatically from more temperate regions, and Mediterranean climates differ from continental. For example, we found that spring rain following snowmelt made an important contribution to growing season soil moisture in our continental climate in the western Rockies, but in similar research done in subalpine environments in the Sierra Nevada, a Mediterranean climate region, there were no spring rains and snowmelt was the only source of soil moisture for much of the growing season. A common feature of temperate subalpine environments may exist in seasonally-persistent snow cover and growing seasons limited both by the presence of snow and by cold temperatures following snowmelt (Inouye and Wielgolaski 2003).

Between-year variability in the amount of snow and the timing of snowmelt in subalpine environments can be dramatic. Maximum yearly snow depth at our lower elevation sites in Fairview Canyon, Utah, has ranged between 241 and 929 mm in the past 30 years, and the first snow-free date of the season has occurred as early as 23 April and as late as 19 June during the same time period. This inter-annual variability in snow cover and melt date and the accompanying range in temperature and day length represented by a 57-day window of time may have its own stabilizing effects on subalpine ecosystems through a variety of biotic adaptations.

Plant and microbial species have adapted to this variable and uncertain environment primarily though the timing of seasonal dormancy and active growth. During the summer growing season, it is common to find complete turnover in herbaceous plant species from spring ephemeral to midsummer and late-summer species. Microbial communities show similar seasonal turnover between species favoring winter conditions beneath the snowpack and others that are more abundant at warmer temperatures in the absence of snow (Lipson et al. 2002).

Global climate warming is affecting seasonally snow-covered environments by advancing snowmelt and reducing peak spring snowpack (Cayan et al. 2001, Pederson et al. 2010). Ironically, one effect of early snowmelt in a warmer world may be exposure of montane soils and vegetation to colder temperatures (Groffman et al. 2001). This occurs because snow insulates the soil from changes in atmospheric conditions and because snow cover delays the onset of growth and flowering, causing plants to avoid the colder times of year (Inouye 2008). At the onset of this project, we expected that exposure to colder temperatures following early snowmelt would affect plant growth and flowering and influence rates of C and N cycling in subalpine ecosystems under aspen canopy and in open meadows. We also expected that early snowmelt would extend the summer dry period and increase the drying of soils during the growing season, with potential cascading effects on plant growth and microbial activity. Instead we found that soil moisture, plant growth and flowering, and microbial biomass and activity were buffered against changes in snowmelt timing of 1 to 3 weeks in years of average or lower-than-average snowpack in our study sites. Though we were initially surprised by these results we have found that they agree with some of the results of other researchers (Jonas et al. 2008, Haei et al. 2011, Smith et al. 2011). This caused us to rethink some of the initial assumptions and predictions we made about the vulnerability of subalpine ecosystems to climate change. First, it has caused us to question whether studies done in other seasonally snow-covered environments in the alpine and arctic apply to lower latitude and lower elevation ecosystems. One of our initial assumptions, that early snowmelt would lead to increased freezing and more freeze-thaw cycles in subalpine soils, may be true at higher elevations and latitudes, but in our sites we found that soils at 5 cm were generally warmer in the early-snowmelt plots than in paired control plots still under snow. Our other primary prediction, that early snowmelt would lead to increased drying of soils and prolonged drought conditions, was not supported primarily because of the mediating effects of soil texture, soil organic matter, and forest cover. These other site factors exerted greater influence over soil moisture than did snowmelt timing generally or the treatment-induced early snowmelt specifically. We also found that the influence of snowpack on soil moisture diminished rather than increased as the growing season progressed.

As I have considered the difference between my initial predictions and the observed results of this research, it has become apparent to me that at the outset I was disposed to expect the worst possible outcome in this ecosystem's response to simulated climate change. Specifically, I expected dramatic and observable impacts on ecosystem processes and biotic communities to follow early snowmelt, and that the ecosystem that would be highly vulnerable to early snowmelt. Part of this assumption reveals my own ecological naiveté, but it may also reveal something about the process through which I was conducting global-change research. I suspect that I am not unique among researchers of global-change in my initial bias to search for dramatic examples of ecosystem and biotic vulnerability. My bias influenced my choice of topic, the design of my experiment, and the choice of response variables I was looking for. As I conducted the research, I observed a change in my disposition toward the study. Instead of observing dramatic responses and vulnerability to early snowmelt, I saw that the subalpine ecosystem demonstrated stability and resilience to the early-snowmelt treatment. This later discovery may indicate that subalpine ecosystems, perhaps unlike arctic and alpine ecosystems, may be uniquely suited to provide insights into the environmental and biotic buffers to mediate the effects of climate change.

References

Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society **82**:399-415.

Groffman, P., C. Driscoll, T. Fahey, J. Hardy, R. Fitzhugh, and G. Tierney. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry **56**:135-150.

Haei, M., J. Rousk, U. Ilstedt, M. Öquist, E. Bååth, and H. Laudon. 2011. Effects of soil frost on growth, composition and respiration of the soil microbial decomposer community. Soil Biology and Biochemistry **43**:2069-2077.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance on montane wildflowers. Ecology **89**:353-362.

Inouye, D. W., and F. E. Wielgolaski. 2003. High altitude climates. Pages 195-214 *in* M. D. Schwartz, editor. Phenology: an integrative environmental science. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Jonas, T., C. Rixen, M. Sturm, and V. Stoeckli. 2008. How alpine plant growth is linked to snow cover and climate variability. Journal of Geophysical Research: Biogeosciences **113**:G03013.

Körner, C. 2003. Alpine Plant Life. 2 edition. Springer-Verlag, Berlin, D.E.

Lipson, D. A., C. W. Schadt, and S. K. Schmidt. 2002. Changes in Soil Microbial Community Structure and Function in an Alpine Dry Meadow Following Spring Snow Melt. Microbial Ecology **43**:307-314.

Pederson, G. T., S. T. Gray, T. Ault, W. Marsh, D. B. Fagre, A. G. Bunn, C. A. Woodhouse, and L. J. Graumlich. 2010. Climatic Controls on the Snowmelt Hydrology of the Northern Rocky Mountains. journal of climate **24**:1666-1687.

Smith, T. J., J. P. McNamara, A. N. Flores, M. M. Gribb, P. S. Aishlin, and S. G. Benner. 2011. Small soil storage capacity limits benefit of winter snowpack to upland vegetation. Hydrological Processes **25**:3858-3865.

CHAPTER 1

Forest diversity as a factor influencing Engelmann spruce resistance to beetle outbreaks

Lafe G. CONNER[1]*, Michael C. BUNNELL[1], Richard A. GILL[1]

1. Department of Biology, 401 WIDB, Brigham Young University, Provo, Utah 84602, connerlg@byu.edu, michaelcbunnell@gmail.com, richard_gill@byu.edu

*Corresponding Author: Lafe G. Conner, Department of Biology, 401 WIDB, Brigham Young University, Provo, Utah 84602, phone: 801-422-2175, fax: 801-422-0090, connerlg@byu.edu

(Published in the *Canadian Journal of Forest Research*, 2014, 44(1): 1369-1375, 10.1139/cjfr-2014-0236)

Abstract

Tree mortality due to beetle outbreaks has become substantial and widespread in conifer forests in western North America. A number of environmental and physiological factors influence patterns of mortality. Tree diversity may reduce the severity and extent of insect damage to host trees by providing associational resistance, but the existence and importance of associational resistance varies by forest type and by tree and insect species. We assessed whether plot-level tree diversity contributed to survival of Engelmann spruce (*Picea engelmannii*) following a spruce beetle (*Dendroctonus rufipennis*) epidemic. Our study plots were comprised of 2 to 5 tree species including Engelmann spruce, subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudostuga menziesii*), quaking aspen (*Populus tremuloides*), and white fir (*Abies concolor*). We used a model-selection analysis to compare the importance of tree diversity to other known factors that influence spruce survival. We found lower rates of spruce survival in stands where spruce was the dominant tree species (by percent of stand density index) and higher survival in stands where non-spruce conifers (Douglas-fir, subalpine and white fir) were dominant. We also found that tree diversity (Shannon index) did not show a positive correlation to spruce survival and that there was no additional benefit derived from the presence of aspen, which has higher phylogentic distance from Engelmann spruce than the other trees in this study. The relationship between diversity and survival is complicated by factors that naturally co-vary with diversity, such as elevation, aspect, and stand density of spruce. Our results best support an explanation that if associational resistance does increase spruce survival during a beetle epidemic it is due to host or resource dilution, which may be an indirect effect of higher stand diversity.

Key words: associational resistance, biodiversity, Engelmann spruce (*Picea Engelmannii*), host dilution, insect epidemic, Shannon index of diversity, spruce beetle (*Dendrotonus rufipennis*)

Introduction

Biodiversity is a central guiding value in resource management and conservation. This has led to a widespread search for connections between biological diversity and ecosystem functions (Hooper et al. 2005). In forest management there has been longstanding uncertainty about whether tree diversity reduces damage from insect pests, herbivores, and disease (Koricheva et al. 2006). The benefit that a host species derives from reduced herbivory due to diversity of neighboring trees has been broadly termed as associational resistance (Root 1973). In forest systems, the existence and importance of associational resistance varies widely depending upon the characteristics of the host and herbivore species as well as the characteristics of the other trees present in the community (Riihimäki et al. 2005; Vehviläinen et al. 2007; Vehviläinen et al.2008; Barbosa et al. 2009). Furthermore, patterns of tree damage during insect outbreaks are influenced by landscape and environmental characteristics that may confound and mask the true importance of tree diversity at the stand and plot scale (Cappuccino et al. 1998; Simard et al. 2012). For these reasons it is worthwhile to evaluate associational resistance for specific forest-pest systems, using analyses that include environmental and spatial covariates alongside measures of stand diversity.

There are several reasons why tree diversity may reduce pest damage in forests (reviewed in Jactel and Brockerhoff 2007). Insects may use chemical or visual cues to locate host trees, and therefore higher tree diversity may result in chemical or physical interference that prevents insects from locating host plants (Jactel et al. 2011). Similarly, if host trees are small-statured in relation to neighboring trees, there may be associational resistance by means of reduced plant apparency (Castagneyrol et al. 2013). Associational resistance may arise in forest communities where tree diversity increases the number of natural enemies of the insect pest (Jactel et al.

2005). Additionally, a reduction or dilution of host-plant densities may also result in less insect damage (Otway et al., 2005). This host-dilution effect may confound the true importance of tree diversity, because it can occur in stands with only two tree species or it may increase in positive correlation with species richness.

Although associational resistance varies across forest-pest systems, some patterns exist that may help to predict whether it will occur as a result of higher tree diversity. The most robust generalization appears to be that greater associational resistance occurs when insect herbivores demonstrate host specificity to a single species and when forests are composed of tree species that are not suitable as alternative hosts (Koricheva et al. 2006). Damage caused by specialist herbivores tends to increase in a positive relationship with the density of the host tree species. When the herbivore demonstrates host specificity it likely does not matter which other species are present, but for generalist herbivores associational resistance may increase when stands contain trees which are phylogenetically distant from the host, such as broadleaf species when the host is a conifer (Castagneyrol et al., 2014). In addition, researchers found that greater structural complexity in agricultural ecosystems yielded more complex food webs with more predatory species and greater associational resistance through natural enemies (Root 1973; Zhang and Adams 2011). However, in forest systems the increase of natural enemies is related more to the specific combination of tree species comprising the stand than to the increase in species diversity alone (Vehviläinen et al., 2008). Finally, there is a temporal pattern that may influence associational resistance, because factors that influence patterns of pest damage early in an insect outbreak may not be as apparent or as important at later stages of insect epidemics (DeRose and Long 2012).

Engelmann spruce and spruce beetles provide an appropriate system for assessing the importance of associational resistance in forests, because spruce beetles show a high specificity to their host tree and use chemical signaling for communicating host location. Chemical signaling has been elaborated in other beetle-conifer systems, including the southern bark beetle (*Dendroctonus frontalis*) and the European spruce beetle (*Ips typographus*). In these systems, the two primary sources of chemical signaling are pheromones produced by the beetles and volatile compounds produced by host and non-host trees; both chemical sources can act as attractants or antiattractants and play a distinct role in olfactory-mediated behavior (Dickens and Payne 1977, Andersson 2012). In European spruce beetle populations, male individuals navigate to host trees and release an aggregation pheromone after locating a suitable host tree (Andersson 2012). This is the main mechanism by which initial aggregation occurs. As beetles follow the aggregation pheromone, they may be deterred if they encounter an antiattractant along the way. Non-host volatiles, such as green leaf volatiles and bark alcohols, produced by angiosperms and other species of conifer are known to inhibit pheromone mediated aggregation by producing antiattractants (Dickens et al. 1992, Zhang et al. 1999, Zhang et al. 2000). If non-host species produce antiattractant compounds this would be a potentially important source of associational resistance in spruce-beetle systems (Zhang and Schlyter, 2004).

In recent decades, populations of Engelmann spruce (*Picea engelmannii*) across western North America have experienced widespread mortality as a result of spruce beetle (*Dendroctonus rufipennis*) epidemics (DeRose and Long 2007). Dymerski et al. (2001) detailed the outbreak of spruce beetle on the Wasatch Plateau in central Utah, USA, which occurred from 1987 to 1998. An extensive survey conducted toward the end of the outbreak found that on average spruce mortality, measured in basal area reduction, was 78% by 1996 and 90% in 1998.

Similarly, the number of live spruce trees per hectare was 240 prior to the outbreak, decreasing to 62 by 1998. In many parts of the plateau, the outbreak caused a shift in dominance by basal area from spruce to subalpine fir (*Abies lasiocarpa*).

Our primary objective in this analysis was to characterize patterns of spruce survival following a spruce-beetle epidemic in relation to forest diversity. The influences of stand density, tree size and age, and plot aspect on spruce mortality have been well assessed in Engelmann spruce systems (Hart et al., 2014). However, there has been little direct assessment of the occurrence or importance of associational resistance resulting from increased tree diversity at the plot scale in this system (DeRose and Long 2010). We explored whether spruce survival was higher in stands with greater tree diversity, which we measured by the combination of richness and evenness captured in the Shannon index of diversity (Magurran 1988). We expected that if tree diversity led to associational resistance, then spruce survival would be positively correlated to Shannon's index of diversity. We also hypothesized that spruce survival would vary depending upon the *type* of dominant tree species in the plots. Stands that include a large proportion of aspen (*Populus tremuloides*) might lead to associational resistance and higher spruce survival through mechanisms of increased natural enemies, host dilution, and chemical interference. Similarly, stands dominated by non-spruce conifers may present a chemical environment that inhibits beetles from locating spruce (Byers et al., 1984). While host dilution and chemical interference may result from increases in both aspen and non-spruce conifers, it has been suggested that the phylogenetic distance between tree species in mixed stands may be an important factor in determining the degree of associational resistance in forest systems (Castagneyrol et al., 2014). We therefore, made separate comparisons of spruce survival in stands with high and low density of aspen and comparisons between stands with high and low densities of spruce.

To address these objectives and explore these hypotheses, we used spruce mortality from forest inventory data that covered a wide range of forest types with varying stand densities and tree diversity. The data were collected approximately one decade after a beetle epidemic occurred in this area. We used a model selection analysis of individual survival estimates to compare multiple explanatory variables and assess the importance of tree diversity in relation to other environmental and spatial parameters. We also compared survival between stand types with the classification of stands being based on the relative stand density of spruce, aspen, and non-spruce conifers.

Methods

Site Description

The study was conducted within central Utah's Great Basin Experimental Range (GBER) and all data were collected from a 1,468 hectare area within the Ephraim Canyon watershed. The study area lies on the western slope of the Wasatch Plateau (39°19' N, 111°29' W) in central Utah (Fig. 1A). The GBER was established by the U.S. Forest Service in 1912 to study rangeland management. Average annual precipitation near the summit (3008 m) of the GBER is 642 mm and precipitation within a year peaks in spring (March-April) and fall (September-October). Mean annual temperature is 1.6^{o} C, average maximum daily temperature for the summer months (June, July, and August) is 17.4^{o} C , and average minimum daily temperature for the winter months (December, January, and February) is -11.5^{o} C (NRCS, 2013). Spruce trees occur at elevations ranging from 2095 m on the western edge of the study area to 3163 m at the eastern border. Topography is highly variable with slopes ranging from 0 to 38^{o}. Soils at the study sites, occurring from low to high elevation, are loam-gravely loam, silt loam, and clay-loam. Soil moisture and temperature regimes are xeric-mesic, xeric-frigid, and udic-cryic (NRCS 2012). The survey plots were randomly dispersed across the watershed and include forest associations comprised of combinations of Engelmann spruce, quaking aspen, Douglas-fir (*Pseudotsuga menziesii*), subalpine fir, white fir (*Abies concolor*), big tooth maple (*Acer grandidentatum*), and Utah and Rocky Mountain juniper (*Juniperus osteosperma* and *J. scopulorum*). Maple, juniper, aspen, Douglas-fir, and white fir occurred at lower elevations than subalpine fir and Engelmann spruce (Fig. 2A). The study included 185 individual spruce trees (63 dead and 122 living) found across 24 sites (table 1). The average number of spruce trees at each site was 7.5 (range 2 to 50). The stand density index (SDI) of spruce in the 24 sites ranged from 55 to 3440 and accounted for between 2% and 91% of SDI.

Field Data Collection

We followed the multi-resource inventory protocols outlined in the Phase 2 Forest Inventory and Analysis (FIA) program to assess forest structure (USFS, 2011). Macroplots were established throughout the study area at randomly selected GPS coordinate locations. Macroplots are comprised of four subplots, each 0.0176 ha in size with a radius of 7.32 m. We measured and recorded diameter at breast height (DBH), tree height, species, and tree status (live or dead). DBH was measured using a diameter tape and tree height was measured using a standard carpenter's tape or laser range finder, depending on tree size and stand characteristics. When the data were collected we had not yet conceived of this study. We, therefore, did not attempt to identify the cause of death for individual trees. Given the history of the area and the observation that beetle-killed trees are likely to be standing dead at these sites, we made the assumption that the primary cause of mortality for all standing-dead spruce was the beetle epidemic of the 1990s.

This assumption is reasonable given findings in similar studies of recent spruce beetle outbreaks (Derose and Long, 2012).

Individual survival analysis

We evaluated our hypothesis that higher stand diversity would correspond with increased spruce survival using model selection of generalized linear models that represented combinations of individual and plot level covariates. The individual covariates (DBH, height, heat load index, and elevation) are unique for each of the 185 trees, but the site-level covariates (quadratic mean diameter, stand density index, Shannon's index of diversity, evenness, and richness) are the same for all individuals found at that particular site. Trees were used as statistical units. We used linear mixed effects models (lmer function in the lme4 package in R, Bates et al. 2013), with the plot declared as random factor to account for pseudo-replication of trees within plots. Heat load index is a comparison of the relative amount of heat received at any location due to its aspect and latitude. We calculated the heat load index using equation 2 described in McCune and Keon (2002). We calculated quadratic mean diameter (QMD) following the equation given in Curtis and Marshall (2000). We calculated stand density index (SDI) following the summation method described in (Shaw 2000). We calculated the Shannon index of diversity and evenness following the equations given in Magurran (1988).

From the combination of these covariates we created seventeen linear models that represent various combinations of individual and plot-level parameters known or suspected to influence patterns of spruce survival. Nearly all of the models included DBH, heat load, and elevation because of the established influence of diameter and heat load, and because elevation may represent a variety of environmental conditions that may also be important to survival. We examined a correlation matrix of these covariates, and when we found combinations of covariates that exhibited a high degree of collinearity ($r > 0.6$) we eliminated one of the parameters in the combination from the model. Parameter combinations that we eliminated included diameter and height ($r = 0.865$), for which we eliminated height from all models. We chose to eliminate height because diameter is the parameter typically used in similar analyses. We also avoided all combinations of SDI parameters with %SDI parameters. The elevation parameter was highly correlated to Shannon diversity ($r = -0.697$, Fig. 2B) and richness ($r= -0.773$). We needed to have both elevation and Shannon diversity because elevation had a large influence on model fit and Shannon diversity was important to the hypothesis being tested. Therefore, in the case of elevation and Shannon diversity we ran models with and without the elevation parameter to observe its influence on the model estimates, as recommended by Zuur et al (2010).

Through comparison of these models we identified the parameters that appeared in the best fit models, as determined by Akaike's Information Criterion (AIC). We adjusted the AIC for small sample size and made comparisons using this AICc value and the AICc weight which is a measure of the goodness of fit of a model in relation to other models being tested. To obtain the best estimate of the coefficients for the parameters in the models we calculated the model-averaged coefficients using a full-model averaging method (Symonds and Moussalli, 2011). One result of model averaging is that parameters that occur in models for which there is little support (i.e. low AICc weight) the model-averaged coefficients become very close to zero. This can serve as an indication of the significance of individual parameters.

We addressed our first hypothesis, that tree diversity would be positively correlated to spruce survival, by observing the goodness of fit (AICc weight) and the sign of the model-averaged coefficients for Shannon's index of diversity and percent SDI of spruce, aspen, and non-spruce conifers. To address our second hypothesis, that spruce survival would be dependent upon the identity of dominant trees in the stand, we grouped the plots by dominant tree species, as described below, and made two comparisons using average survival as the response variable.

Group analysis

The group analysis was accomplished in two parts (Fig. 2). First we separated plots that had spruce as the dominant tree species (n = 6) from those where non-spruce conifers (Douglas-fir and white and subalpine fir) were the dominant species (n = 18). This comparison served as a test of the host dilution hypothesis and we expected that if host dilution played an important role in associational resistance, then survival would be higher in stands where non-spruce conifers were dominant. In the second part of the group survival analysis, we separated plots where aspen were present (n = 15) from plots where aspen were not present (n=9). The purpose of the second group survival comparison was to evaluate the influence of phylogenetic distance between host trees and surrounding species in mixed stands. We expected that if phylogenetic distance of surrounding trees had a positive influence on associational resistance, then spruce survival would be higher in plots where aspen were present. It is also possible that the amount of aspen in the plot could be important to associational resistance so we conducted this aspen comparison with groups split at 10% (n = 12 plots with aspen > 10%, n = 12 plots with aspen < 10%) and 20% SDI of aspen (n = 7 plots with aspen > 20%, n = 14 plots with aspen < 20%). All pairwise comparisons were made using the Tukey Honest Significant Difference test in the 'stats' version 2.15.1 package in R (R Core Development Team 2012). The response variable in the model used for these comparisons was the percent of trees in the plot that were living at the time of the census.

Results

Individual survival

The best models for estimating spruce survival included DBH, heat load index, elevation, percent SDI of non-spruce conifers, percent SDI of spruce, and Shannon's index of diversity. Although there was not one single model that greatly outperformed the others (AICc weights were all lower than 0.21), there was consistency in the best models to include these parameters (table 2). The model-averaged estimate of the coefficients of these parameters indicated that DBH had a negative influence on spruce survival (β = -0.0468, table 3), heat load had a positive influence (β = 1.8154), elevation was negatively correlated (β = -0.0091), percent SDI of non-spruce conifers had a positive influence on spruce survival (β = 1.7532, Fig. 2A), percent SDI of spruce had a negative influence (β = -0.6259, Fig. 2B), and Shannon diversity had a negative influence (β = -0.9707, Fig. 2C). Although Shannon diversity had a negative influence on survival estimates when averaged across models, when we removed elevation from the model the coefficient of Shannon diversity was positive (β = 4.7386 in model 14 and β = 4.3437 in model 13, table 2). The two models that did not include elevation had the poorest fit of any of the 17 models and therefore there is little support for a positive influence of Shannon diversity upon survival.

Group survival

The first group comparison indicated that there was no significant difference in spruce survival in plots with aspen compared to plots without aspen (difference = 0.115, p = 0.09, Fig. 3A). There was still no significant difference when plots were divided at 10% SDI of aspen (difference = 0.071, p = 0.31) and at 20% SDI of aspen (difference = 0.029, p = 0.72). The second group comparison between plots with spruce versus non-spruce conifer dominants indicated that there was a significant difference in spruce survival (difference = 0.188, p = 0.007, Fig 3B).

Discussion

The combined insight of the individual and group survival analysis point us to an understanding that low spruce density and potential the dominance of non-spruce conifers (Douglas-fir and white and subalpine fir) have the biggest influence on associational resistance in the Engelmann spruce and spruce and spruce beetle system. We did not find that phylogenetic distance between the host species and neighboring trees made any contribution to associational resistance when we compared plots with and without aspen or when we compared plots with increasingly higher percentages of aspen. This observation displays consistency with the emerging understanding that phylogenetic distance in mixed stands results in associational resistance more from generalist herbivores than from specialist herbivores, such as the spruce beetle (Castagneyrol et al. 2014). The primary mechanism for associational resistance from generalist herbivores in phylogenetically diverse stands results from the inability of herbivores to find suitable hosts. Castagneyrol et al. (2014) recognize that, phylogenetic distance is a special case of resource dilution that does not occur when herbivores can switch easily between host species in stands of trees that are more closely related. Therefore, while phylogenetic distance may be important in some herbivore-host relationships, it does not appear to be important in the Engelmann spruce and spruce beetle system, likely because of host specificity characteristic of this system.

We did find possible support for associational resistance in spruce growing in stands dominated by non-spruce conifers. There are two likely biological explanations for the observed pattern of higher spruce survival in conifer-dominant compared to spruce-dominant stands. The first, and most likely explanation, is host or resource dilution. We observed that higher %SDI of non-spruce conifers is highly correlated with lower SDI of spruce (r = -0.800), and the mean SDI of spruce in conifer-dominant stands is 369.7 (σ = 335.1) and 1428.6 (σ = 1075.1) in spruce-dominant stands. . The dramatically lower SDI of spruce in conifer stands may indicate that higher survival of spruce in these stands occurs because spruce are less common and therefore may be more difficult for beetles to find or that spruce resources in these stands are not sufficient to support feeding or breeding of spruce beetles.

The second and more speculative of the biological explanations is that spruce are harder for beetles to find in stands of dense conifers because of chemical interference through antiattractant volatile compounds (Andersson 2012). This hypothesis may be worthy of further investigation specifically regarding antiattractant compounds that may be produced by Douglas-fir or subalpine fir. Regardless of the underlying mechanism, resource dilution or chemical interference, these data and analysis suggest that the risk of spruce mortality is lower in stands where spruce are non-dominant, in this case SDI of spruce was less than 20% in plots where non-spruce conifers were dominant.

The primary value of these findings may be in the comparisons we were able to make because of the wide diversity of stand compositions surveyed. While we feel confident that these findings may apply broadly to Engelmann spruce and spruce beetle systems and to other forest systems involving specialist herbivores, there may be additional causes for the patterns of spruce survival that we cannot address with this study design, and we cannot eliminate the possibility that spatial heterogeneity and distance from spruce-dominated plots at coarser scales, such as between watersheds, may also be important to spruce survival.

In stands composed almost entirely of Engelmann spruce, DeRose and Long (2012) found that spruce mortality in early stages of a beetle epidemic was closely tied to stand density of spruce and site aspect, a corollary of heat and solar input. They reported that beetles first attacked stands with low overall stand density but with a high proportion of spruce, and then moved to higher-density stands that contained large- diameter spruce. Our results are consistent with these observations. DeRose and Long (2012) also reported that spruce trees growing on warmer sites were killed earlier in the outbreak, possibly due to temperature-mediated limitations of spruce beetles. Our results show the opposite relationship, but this may be due to the difference in scale between the two studies, as our study covered a broader range of elevations and environments, some of which included high survival rates with high heat loads. In our data, this is true specifically for the conifer sites with a high SDI of subalpine fir, in which spruce had a higher survival and higher heat load index than the spruce-dominated plots.

Taken as a whole, our findings suggests that spruce growing in stands dominated by non-spruce conifer species are more likely to survive a beetle epidemic. This pattern may be due to a combination of lower stand density of spruce (i.e. host dilution) and may be enhanced by associational resistance arising from chemical or physical interference in beetles attempting to find suitable hosts. Neither species richness and evenness, represented by Shannon's index of diversity, nor phylogenetic distance representative of the combination of broadleaf-deciduous (aspen) and coniferous species had a significant impact on survival. Therefore, it seems likely that neither stand diversity or phylogenetic distance contribute to associational resistance in this system, and assessments of the risk of spruce mortality will do best to rely on spruce density and stand dominance as measures of the concentration of host individuals and the resources necessary to support spruce beetles.

Acknowledgements

We would like to thank Tamara Watkins, Michael McCain, Daniel Tullis, and Katie Packer for work in data collection. Maryfaith Snyder and Darin Toone were also integral to the data collection process. Thanks to Mark Jackson for GIS support in mapping plot and tree locations from the data collection sheets. Thanks to Randy Larsen for support with the survival analysis. Thanks to Justin DeRose and two anonymous reviewers for comments on an earlier version of the manuscript. This research was funded by a joint venture agreement with the USDA Forest Service Rocky Mountain Research Station. Additional funding was provided by the Sant Foundation and a Brigham Young University Mentoring Environment Grant.

References

Andersson, M. N. 2012. Mechanisms of Odor Coding in Coniferous Bark Beetles: From Neuron to Behavior and Application. Psyche (Cambridge) **2012**:1-14. http://www.hindawi.com/journals/psyche/2012/149572/citations/.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. 2009. Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. Annual Review of Ecology, Evolution, and Systematics **40**: 1-20. doi:10.1146/annurev.ecolsys.110308.120242.

Bates, D., Bolker, B., Maechler M., & Walker S. 2013. Linear mixed-effects models using Eigen and S4. http://lme4.r-forge.r-project.org/.

Byers, J. A., Wood, D. L., Craig, J. & Hendry, L. B. (1984) Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition *Journal of Chemical Ecology,* **10**: 861-877. Available online at http://www.chemical-ecology.net/pdf/Byersetal1984.pdf [accessed 18 June 2014].

Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* **114:** 236-242. doi: 10.1007/s004420050441.

Castagneyrol, B., Giffard, B., Péré, C. & Jactel, H. 2013. Plant apparency, an overlooked driver of associational resistance to insect herbivory. Journal of Ecology **101:** 418-429. doi: 10.1111/1365-2745.12055.

Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E. G. & Koricheva, J. (2014) Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology,* **51**: 134-141. doi: 10.1111/1365-2664.12175.

Cooch, E. 1999. Program MARK: techniques for monitoring wildlife populations. International Wildlife Management Congress, Hungary, June 1999, 343-349. Available online at http://warnercnr.colostate.edu/~gwhite/fw663/Mark.html [accessed 16 April 2014].

Curtis, R. O. & Marshall, D. D. 2000. Technical Note: Why Quadratic Mean Diameter? Western Journal of Applied Forestry **15**: 137-139.

DeRose, R. J. & Long, J. N. 2007. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. Forest Ecology and Management **244**: 16-23. Available from http://dx.doi.org/10.1016/j.foreco.2007.03.065 [accessed 28 January 2014].

DeRose, R. J. & Long, J. N. 2010. Regeneration response and seedling bank dynamics on a Dendroctonus rufipennis-killed Picea engelmannii landscape. Journal of Vegetation Science **21**: 377-387. doi: 10.1111/j.1654-1103.2009.01150.x.

DeRose, R. J. & Long, J. N. 2012. Factors Influencing the Spatial and Temporal Dynamics of Engelmann Spruce Mortality during a Spruce Beetle Outbreak on the Markagunt Plateau, Utah. Forest Science, **58**: 1-14. doi: 10.1139/x2012-102.

Dickens, J. C., Billings R. F., and Payne, T.L. 1992. Green leaf volitiles interrupt aggregation pheromone response in bark beetles infesting southern pines. Experientia **48**: 523-524. doi: 10.1007/BF01928180.

Dickens, J. C., and Payne, T. L. 1977. Bark beetle olfaction: pheromone receptor system in *Dendroctontus frontalis*. Journal of Insect Physiology **23**: 481-489. http://dx.doi.org/10.1016/0022-1910(77)90258-X.

Dymerski, A. D., Anhold, J. A. & Munson, A. S. 2001. Spruce beetle (Dendroctonus rufipennis) outbreak in Engelmann spruce (Picea engelmannii) in central Utah, 1986-1998. Western North American Naturalist, **61**: 11-18.

Hart, S. J., Veblen, T. T., Kulakowski, D. 2014. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the 21st century? Forest Ecology and Management, **318**: 44-53. doi: 10.1016/j.foreco.2013.12.035.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J. & Wardle, D. A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs, **75**: 3-35. doi: 10.1890/04-0922.

Jactel, H., Birgersson, G., Andersson, S. & Schlyter, F. 2011. Non-host volatiles mediate associational resistance to the pine processionary moth. Oecologia, **166**: 703-711.

Jactel, H., Brockerhoff, E. & Duelli, P. 2005. A Test of the Biodiversity-Stability Theory: Meta-analysis of Tree Species Diversity Effects on Insect Pest Infestations, and Re-examination of Responsible Factors. Forest Diversity and Function (eds M. Scherer-Lorenzen, C. Körner & E.-D. Schulze), pp. 235-262. Springer Berlin Heidelberg. doi: 10.1007/3-540-26599-6_12.

Jactel, H. & Brockerhoff, E. G. 2007. Tree diversity reduces herbivory by forest insects. Ecology Letters, **10**: 835-848. doi: 10.1111/j.1461-0248.2007.01073.x.

Koricheva, J., Vehviläinen, H., Riihimäki, J., Ruohomäki, K., Kaitaniemi, P. & Ranta, H. 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality? *Canadian Journal of Forest Research,* **36**: 324-336. doi:10.1139/X05-172.

Long, J. N. & Daniel, T. W. 1990. Assessment of growing stock in uneven-aged stands. Western Journal of Applied Forestry, **5**: 93-96.

Magurran, A. E. 1988. *Ecological diversity and its measurement.* Princeton University Press, Princeton, New Jersey.

McCune, B. & Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science, **13**: 603-606. doi: 10.1111/j.1654-1103.2002.tb02087.x.

NRCS (Natural Resource Conservation Service). 2013. Utah Snotel Sites. National Weather and Climate Center. Available from http://www.wcc.nrcs.usda.gov/snotel/Utah/utah.html [accessed 9 April 2013].

Otway, S. J., Hector, A. & Lawton, J. H. 2005. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. Journal of Animal Ecology, **74**: 234-240. doi: 10.1111/j.1365-2656.2005.00913.x.

R Core Development Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Riihimäki, J., Kaitaniemi, P., Koricheva, J. & Vehviläinen, H. 2005. Testing the Enemies Hypothesis in Forest Stands: The Important Role of Tree Species Composition. Oecologia, **142**: 90-97. doi: 10.1007/s00442-004-1696-y.

Root, R. B. 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (Brassica Oleracea). Ecological Monographs, **43**: 95-124. doi: 10.2307/1942161.

Shaw, J. D. 2000, Application of stand density index to irregularly structured stands. Western Journal of Applied Forestry, **15**: 40-42.

Simard, M., Powell, E. N., Raffa, K. F. & Turner, M. G. 2012. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? *Global Ecology and Biogeography,* **21:** 556-567. doi: 10.1111/j.1466-8238.2011.00710.x.

Symonds, M. E. & Moussalli, A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology, **65**: 13-21. doi: 10.1007/s00265-010-1037-6.

USFS (United States Forest Service). 2011. Forest inventory and analysis national core field guide, version 5.1. Forest Inventory and Analysis National Office, Arlington, VA. Available online at http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/Complete%20FG%20Document/core_ver_5-1_10_2011.pdf [accessed 18 June 2014].

Vehviläinen, H., Koricheva, J. & Ruohomäki, K. 2007. Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. Oecologia, **152**: 287-298. doi: 10.1007/s00442-007-0673-7.

Vehviläinen, H., Koricheva, J. & Ruohomäki, K. 2008. Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos, **117**: 935-943. doi: 10.1111/j.0030-1299.2008.15972.x.

Wang, X.-Q., Tank, D. C. & Sang, T. 2000. Phylogeny and Divergence Times in Pinaceae: Evidence from Three Genomes. Molecular Biology and Evolution, **17**: 773-781.

White, J. A. & Whitham, T. G. 2000. Associational susceptibility of cottonwood to box elder herbivore. Ecology, **81**: 1795-1803. doi: 10.1890/0012-9658(2000)081[1795:ASOCTA]2.0.CO;2.

Zhang, Y. & Adams, J. 2011. Top-down control of herbivores varies with ecosystem types. Journal of Ecology, **99**: 370-372. doi: 10.1111/j.1365-2745.2010.01770.x.

Zhang, Q.-H. & Schlyter, F. 2004. Olfactory recognition and behavioral avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology,* **6**: 1-20. doi: 10.1111/j.1461-9555.2004.00202.x.

Zhang, Q. H., Schlyter, F., & Anderson, P. 1999. Green leaf volatiles interrupt pheromone response of spruce bark beetle, *Ips typographus*. Journal of Chemical Ecology, **25**: 2847-2861. doi: 10.1023/A:1020816011131.

Zhang, Q. H., Schlyter, F., & Birgersson, P. 2000. Bark volatiles from nonhost angiosperm trees of spruce bark beetle, Ips typographus (L.) (Coleoptera : Scolytidae): Chemical and electrophysiological analysis. Chemoecology, **10**: 69-80. doi: 10.1007/s000490050010.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1**: 3-14. doi: 10.1111/j.2041-210X.2009.00001.x

Table 1. Parameters used in the model selection analysis.

Parameter	Mean (range)
Individual tree variables (N = 185 trees)	
Diameter at Breast Height (cm)	28.9 (3.0 – 86.9)
Heat load index	0.53 (0.08 – 1.25)
Elevation (m)	2804 (2420 – 3100)
Plot-level variables (N = 24 plots)	
Quadratic mean diameter spruce (cm)	34.67 (14.74 – 55.37)
Stand density index (SDI) non-spruce conifers	1268.0 (159.3 – 4813.0)
SDI spruce	634.4 (55.37 – 3440.0)
SDI aspen	310.2 (0.0 – 877.5)
SDI all trees	2235.0 (354.6 – 5738.0)
Percent SDI non-spruce conifers (%)	56.3 (9.3 – 90.7)
Percent SDI spruce	29.8 (2.7 – 90.7)
Percent SDI aspen	19.4 (0.0 – 49.0)
Shannon index of diversity (H’)	0.911 (0.451 – 1.369)
Evenness (H’/lnS)	0.824 (0.596 – 0.962)
Species richness (S)	3.2 (2 – 5)
Spruce trees per plot	7.7 (1 – 50)

Table 2. Models ordered by lowest AICc.

Model	AICc	Delta AICc	AICc Weights
DBH + Heat load[†] + Elev + %SDIconifer[‡]	196.169	0	0.206079
DBH* + Heat load + Elev + %SDIconifer + ShannonDiv[§]	196.496	0.326919	0.175002
DBH + Heat load + Elev + SDIspruce	197.168	0.9994	0.12503
DBH + Heat load + Elev + %SDIspruce + ShannonDiv	198.087	1.917519	0.079004
DBH + Heat load + Elev + %SDIspruce	198.268	2.0991	0.072147
DBH + Heat load + Elev + SDIconifer	198.416	2.2465	0.067021
DBH + Heat load + Elev	198.444	2.274516	0.066089
DBH + Heat load + Elev + %SDIaspen	199.341	3.1722	0.042189
DBH + Heat load + Elev + SDIaspen	199.516	3.3468	0.038662
DBH + Heat load + Elev + SDIall	200.436	4.267	0.024404
DBH + Heat load + Elev + ShannonDiv	200.588	4.4189	0.022619
DBH + Heat load + Elev + Evenness	200.591	4.4216	0.022589
DBH + Heat load + Elev + Richness	200.79	4.6206	0.020449
DBH + Heat load + Elev + QMDspruce[‖]	200.874	4.7046	0.019608
DBH + Heat load + Elev + %SDIaspen + ShannonDiv	201.878	5.709319	0.011865
DBH + Heat load + ShannonDiv	203.911	7.741816	0.004295
DBH + Heat load + %SDIconifer + ShannonDiv	204.664	8.4949	0.002947

*Diameter at breast height, [†]Heat load index (McCune and Keon 2002), [‡] Stand density index (SDI), [§]Shannon's index of diversity, [‖]Quadratic mean diameter of spruce in the plot. Conifer refers to non-spruce conifers (Douglas-fir and white and subalpine fir).

Table 3. Model-averaged estimates of coefficients.

Parameter	Estimate
Intercept	28.4758
DBH*	-0.0468
Heat load[†]	1.8154
Elevation	-0.0091
SDIconifer[‡]	0.0000
SDIspruce	0.0000
SDIaspen	0.0000
SDIall	0.0000
%SDIconifer[‡]	1.7532
%SDIspruce	-0.6259
%SDIaspen	-0.2241
ShannonDiv[§]	-0.9707
Evenness	0.0000
Richness	0.0000
QMDspruce [‖]	0.0000

*Diameter at breast height, [†]Heat load index (McCune and Keon 2002), [‡] Stand density index (SDI), [§]Shannon's index of diversity, [‖]Quadratic mean diameter of spruce in the plot. Conifer refers to non-spruce conifers (Douglas-fir and white and subalpine fir).

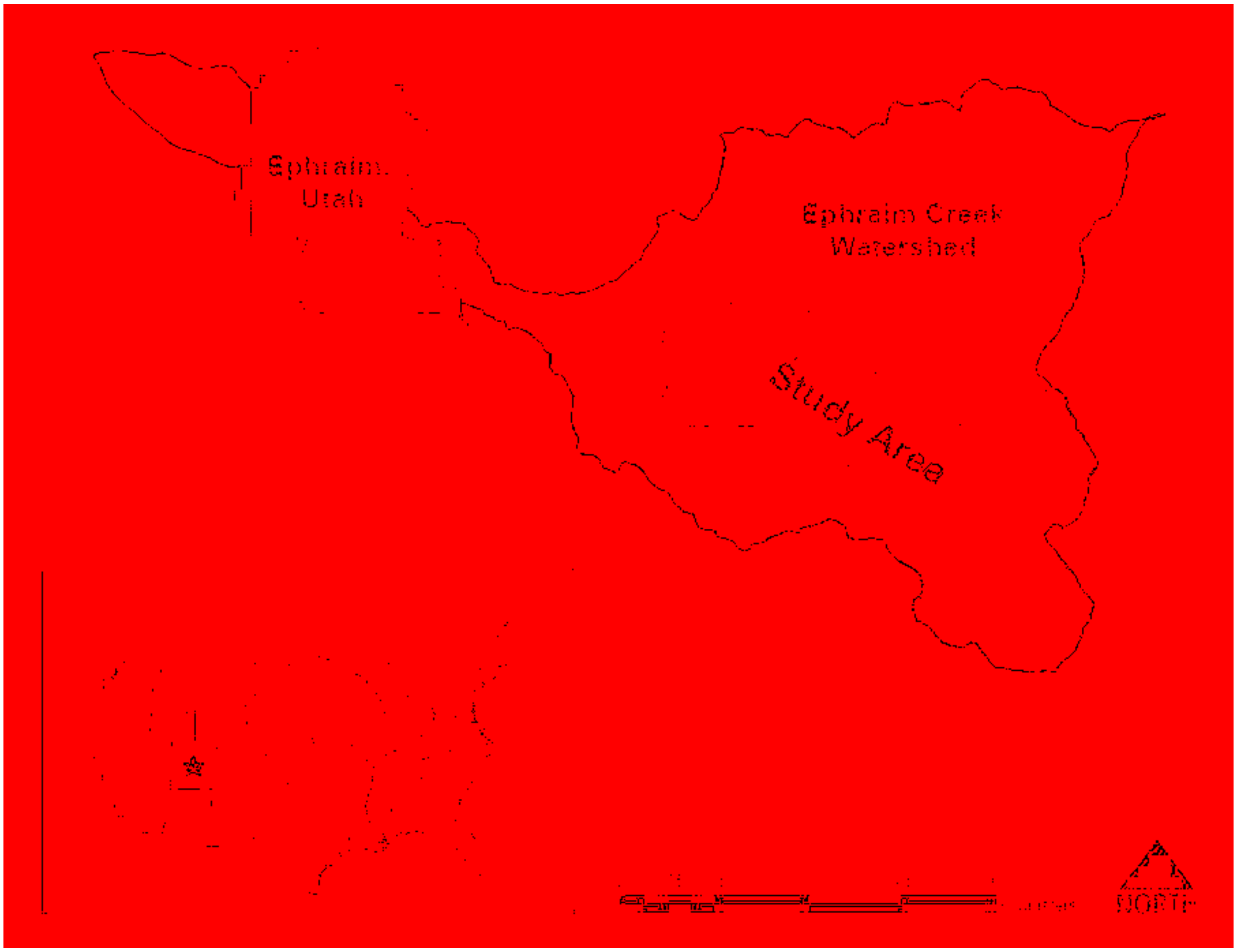


Fig. 1. Map of study area.

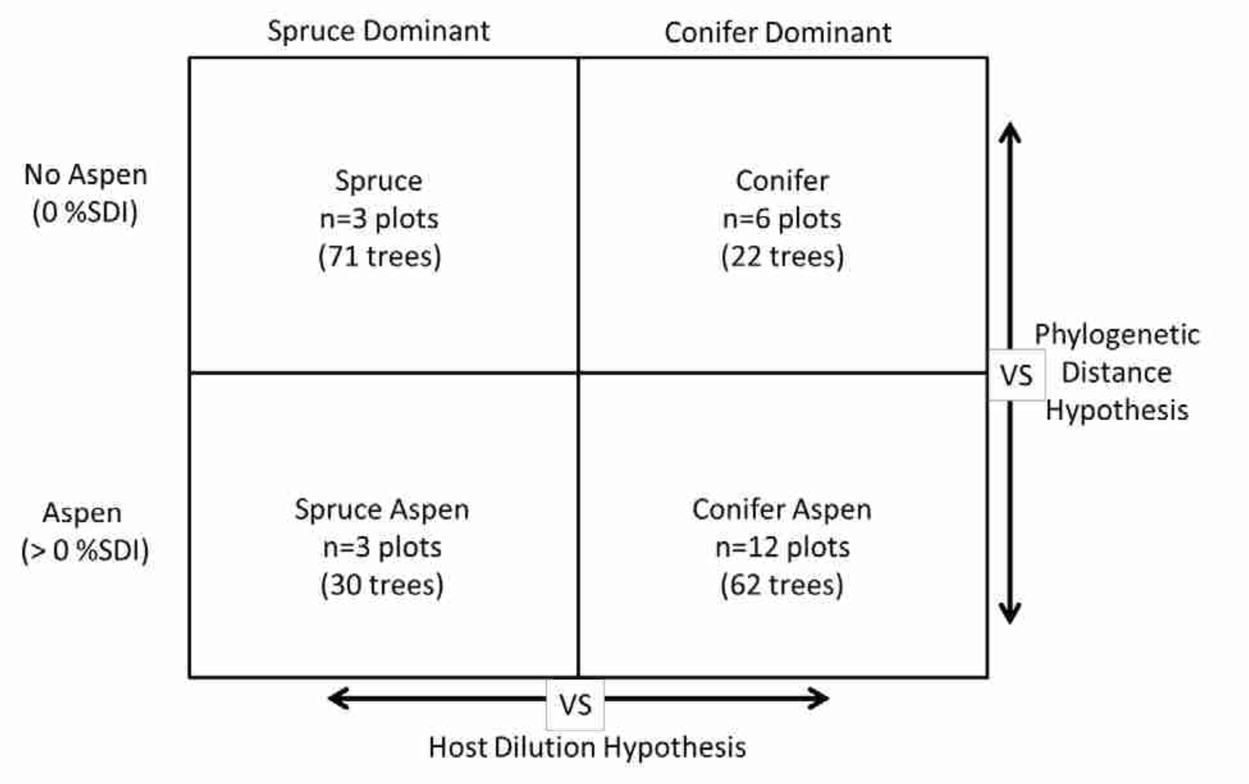


Fig. 2. Diagram of stand classifications used to make the group comparisons. The phylogenetic distance hypothesis is tested by comparing stands with and without aspen, while the host dilution hypothesis is tested by comparing stands where spruce is dominant to stands where non-spruce conifers (Douglas-fir and white and subalpine fir) are dominant.

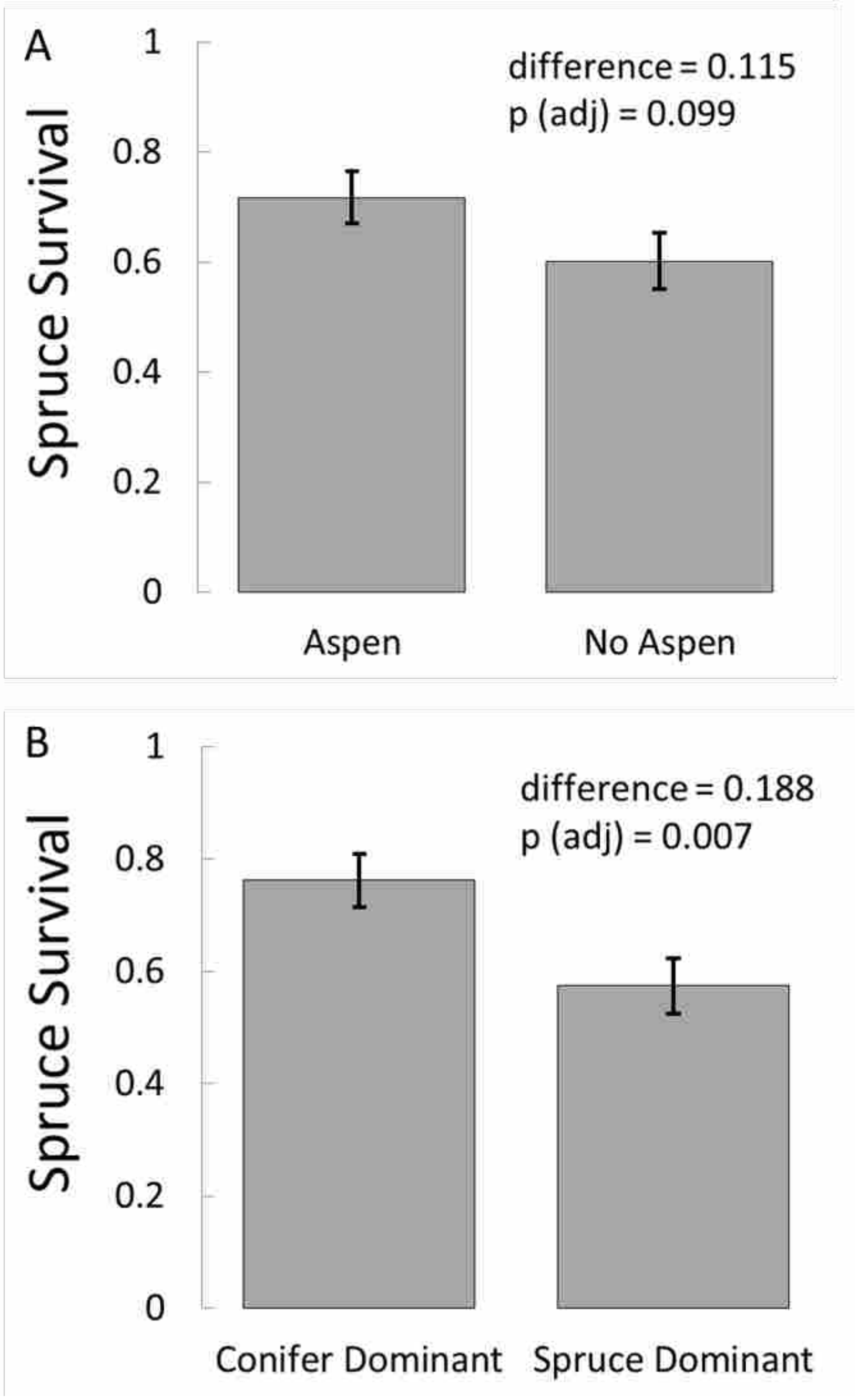


Fig. 3. Spruce survival estimates in stands with and without aspen (A) and spruce dominant and non-spruce conifer (Douglad-fir and white and subalpine fir) dominant stands (B).

CHAPTER 2

Soil moisture response to experimentally-altered snowmelt timing is mediated by soil, vegetation, and regional climate patterns

Lafe G. Conner[1*], Richard A. Gill[1], Jayne Belnap[2]

1. Department of Biology, Brigham Young University, 4102 LSB, Provo, UT 84602, USA

2. U.S. Geological Survey, Southwest Biological Science Center, Moab, UT 84532, USA

*corresponding author: connerlg@byu.edu, phone: 801-425-0911, fax: 801-422-0004

Abstract

Temporal dynamics of soil moisture in seasonally snow-covered environments can be divided into 5 soil moisture states by relative dryness and flux. Climate warming should advance the onset of the spring high-flux soil moisture state, lengthen the summer-dry state, and lead to drier soil conditions overall. The purpose of this study was to test for these responses in soil moisture and soil moisture states at different elevations in deciduous forest and meadow communities on the Wasatch Plateau in central Utah. We advanced snowmelt timing by an average of 14 days by adding dust to the snow surface during spring melt. We analyzed time series of volumetric water content at 5 cm (14 series) and 30 cm (8 series) for the 2013 and 2014 water years to determine transition dates. We found no consistent pattern of change in the onset or duration of soil moisture states as a function of experimentally manipulated snowmelt timing. We measured soil moisture (0-15 cm) gravimetrically at intervals across the growing seasons of 2012, 2013, and 2014. We found no significant differences in soil moisture between control and treatment plots, but rather that additional drivers of soil moisture, including soil organic matter and texture were significant mediators of the positive relationship between snowpack on soil moisture. The presence of forest cover had significant positive indirect effects on soil moisture. In addition to the mediating effects of soil and plant community, the relationship between snowpack and growing season soil moisture was moderated by late-spring precipitation.

Key word: climate change, soil moisture, soil moisture states, snowmelt, snowpack, subalpine

Introduction

Seasonal snowpack provides a primary water resource to montane environments in arid and semiarid regions of the world (Serreze et al. 1999, Service 2004, Hamlet et al. 2005). Climate warming and increased deposition of atmospheric dust on mountain snowpack can cause earlier snowmelt and may reduce growing season soil moisture in high elevation ecosystems and decrease water supply to the surrounding watersheds (Mote 2006, Westerling et al. 2006, Painter et al. 2007, Painter et al. 2010). Soil moisture mediates the relationship between snowpack and ecosystem processes during the snow-free season, because plants and microbes do not get water from snow directly but from liquid water in the soil (Smith et al. 2011). Soil moisture may affect C and N cycling by limiting primary productivity and altering the decomposition rates of organic matter (Berdanier and Klein 2011, Ernakovich et al. 2014). Furthermore, shallower snowpack and more frequent freeze-thaw events may increase nitrogen losses from seasonally-snow covered soils (Brooks et al. 1999, Brooks and Williams 1999, Schmidt et al. 2007). Given the expected changes in snowpack and the potential for cascading effects and climate feedbacks (Porporato et al. 2004), it is expedient to determine the mechanistic relationship between snowpack and soil moisture using a systematic approach that accounts for the multiple drivers of soil moisture and the spatial and temporal variability in soil moisture values and soil moisture states.

The positive relationship between snowpack and soil moisture in montane environments may be mediated by a number of direct and indirect effects related to the physical properties of the soil and characteristics of the plant community (Fig. S1). Most importantly, the contribution of winter snowpack to growing season soil moisture is limited by water storage capacity and soil depth (Smith et al. 2011), forest canopy structure (Molotch et al. 2009, Maurer and Bowling

2014a), and the summer precipitation regime that accompanies and follows snowmelt (Blankinship et al. 2014). The contribution that snowmelt water makes to growing-season soil moisture is further limited by soil physical and chemical properties, especially soil texture and organic matter that determine its moisture retention characteristics (Vereecken et al. 1989, Hudson 1994, Rodriguez-Iturbe and Porporato 2004, Smith et al. 2011). Therefore, growing-season soil moisture may display spatially heterogeneous patterns in which snowpack appears to play a secondary role in comparison to other features of the environment (Walker et al. 1994, Woodward 1998, Redding and Devito 2011).

The effect of precipitation on soil moisture varies by season. Seasonal soil moisture dynamics can be separated into wet and dry soil moisture states (Grayson et al. 1997). In seasonally snow-covered catchments wet-state soil moisture is influenced by fall rewetting before snow accumulates, the depth of snowpack and the duration of snow cover (Maurer and Bowling 2014b). Through most of the winter, soil moisture remains in a wet, low-flux state with very little evaporation or water addition, but as snows begin to melt in the spring, soils transition into a saturated, high-flux state that lasts until the soils become snow free (McNamara et al. 2005). Transitions between wet and dry states tend to occur rapidly and represent a relatively short window of time during the year (Grayson et al. 1997). With seasonal snow cover the transition from wet to dry states occurs shortly after soils become snow free. During the wet high-flux state and spring drying soil moisture dynamics result largely from non-local controls (topography) and horizontal fluxes, while during the ensuing summer dry state, soil moisture depends largely on the static properties of soil texture and depth and dynamic properties of precipitation, evapotranspiration, and antecedent soil moisture (Western et al. 1999, Williams et al. 2009).

These soil moisture states and transitions can be identified from time-series measurements of soil moisture (Fig. 1, Appendix A). During, the winter wet, low-flux state soil moisture remains generally stable and reflects the amount of water in the soil at the onset of persistent snow cover in the fall (Maurer and Bowling 2014b). Liquid water from snow melting in the spring infiltrates through the soil and initiates the spring wet, high-flux state, which appears in time series records of soil moisture as large and rapid changes in soil moisture. During the high-flux state, soils may obtain the hydraulic connectivity that allows for deep drainage and runoff, which also trigger spring peaks in stream flow (McNamara et al. 2005). The duration of the spring high-flux state depends on the volume of snowpack and the rate of melt (Sutinen et al. 2009). The late-spring drying appears in time series records as a consistent, almost linear, decline in soil moisture driven primarily by evaporation and the gravitational potential that transports water downward through the soil profile (McNamara et al. 2005). The rate of drying slows as soil moisture reaches the summer-dry state, during which time soil moisture remains relatively constant unless interrupted by the vertical flow of water following precipitation.

Because snowmelt contributes such a large proportion of water in semi-arid catchments with seasonal snow cover, earlier snowmelt is expected to have a significant effect on growing season soil moisture (Westerling et al. 2006). The actual influence of changes in snow amount and snowmelt timing on soil moisture remains unclear for a few reasons. First, snowpack can greatly exceed the water storage capacity of the soils in semi-arid catchments and therefore changes in the amount of snow water may have limited impact on soil water (Smith et al. 2011). In some alpine catchments, where snow accumulation exhibits large variation over short distances, snowmelt may have a strong influence over soil moisture at finer scales (Litaor et al. 2008, Williams et al. 2009). However, snow accumulation patterns can be highly correlated to other topographic variables that influence the lateral flow and accumulation of soil water (Körner 2003). This means that the effects of snowpack on soil moisture may be confounded by the influences of soil texture, topography, soil development, and vegetative community. Soil texture can be particularly important in mediating the effects of snowpack on dry-state soil moisture (Grant et al. 2004).

We expected early snowmelt would advance and potentially shorten the duration of the spring high-flux soil moisture state, lengthen the duration of the summer-dry state, and ultimately lead to drier soil conditions during the summer season. We manipulated snowmelt timing by adding dust to the snow surface during spring melt in forest and meadow communities at the upper and lower elevation limits in the zone of persistent snow cover in a semi-arid catchment between 2600 and 2900 m elevation. We observed soil moisture dynamics through time series of volumetric water content and compared soil moisture quantities through periodic measures of gravimetric water content. We also developed two structural, mechanistic models of the relationship between snowpack and soil moisture, one for the wet state following snowmelt and one for the summer-dry state. The structural equation models provided measures of the relative influence of individual factors of soil temperature, presence or absence of forest cover, percent soil organic matter, and soil texture. By comparing the strength of the direct effect between snowpack and soil moisture with and without these other factors, we were able to determine whether these other factors partially or fully mediated the direct effect between snowpack and soil moisture (Zhao et al. 2010). We expected that these structural equation models would help explain the patterns of sensitivity to early snowmelt across elevations and community types and would help resolve some of the uncertainty about the effect of early snowmelt on growing season soil moisture in semi-arid, seasonally snow-covered environments.

Materials and Methods

Study site and experimental design

The study was located in Fairview Canyon on the Wasatch Plateau in central Utah, USA. The experiment includes 12 treatment blocks with 3 treatments per block. The treatments were control, dust addition on snowpack, and dust-control, where dust was added directly following snowmelt as a control for fertilization and soil surface changes due to dust addition. There were six treatment blocks at lower elevation (39°41’N, 111°18’W, 2650 m) and six at higher elevation (39°37’N, 111°18’W, 2900 m) sites. Annual precipitation and mean annual temperature during the study varied by elevation and year (Table S1). The three years in this study included one of the years (2012) with the least snowpack and earliest snowmelt in recent decades and two years (2013 and 2014) of average snowpack and melt dates. The upper and lower elevation blocks were divided between aspen forest and subalpine meadow with 3 sites in each cover type at each elevation. The dominant herbaceous species and soil characteristics differed in each site type (Table 1). The Wasatch Plateau has been grazed seasonally by cattle and sheep for more than 150 years.

Each treatment plot was 5 X 5 m, and measurements were confined to a 4 X 4 m area in the center of the treatment plot (i.e. a 50 cm treatment buffer surrounded each plot). Plots were fenced after snowmelt to exclude livestock. Soil moisture and temperature sensors (EC-5, 5TM, 5TE, RT1, ECT; Decagon Devices, Inc., Pullman, WA) were installed at 5 cm and 30 cm depths in the control and dust plots. Measurements were taken every 30 seconds and averaged over 6 hours. We used the time-series data from these sensors to determine the transition dates and duration of the spring high-flux, spring drying, and summer dry soil moisture states (McNamara et al. 2005); Appendix A). Soil cores 1.6 cm diameter of 0-15 cm were collected periodically and a homogenized subsample (4 g) of soil was oven dried (105 °C) for at least 24 hours to obtain gravimetric water content.

Soil organic matter was determined by the method of Walkley and Black (1934). For SOM, we combined all of the remaining soils from samples taken in 2014. These soils were air dried and ground. Soil texture was determined by hydrometer (Day, 1965). Forest canopy was a binary presence or absence of aspen cover. Soil temperature was the average temperature at 5 cm depth during May, June, and July. Missing data for soil temperature were filled in with the closest match within the same site type and treatment (i.e., dust-control matched with control). We measured SWE at approximately weekly intervals from 15 March to the end of snow cover. SWE measurements were made at 3 points with spacing of 1 m along the western edge of each plot using a Federal aluminum tube snow sample (Union Forge, Yakima, WA). Dust was collected from a playa near the town of Kanosh, Utah (38°48’ N, 112°37’ W, 1776 m), which was identified by local land managers as a common dust source for the region (Jeff Gardiner, BLM, personal communication). The dust was sifted (50 µm) and autoclaved to avoid transport of living seeds and microorganisms. We applied dust by hand over the treatment plots after major snow events starting the second week of March until sites were snow-free for a total of 4 or 5 treatments per year. We applied an amount of dust sufficient to cover the area at a rate of 50 g m^{-2}. We chose this rate to maximize the treatment effect and not to reflect background deposition rates.

Statistical analyses

For the statistical analysis of differences in the onset and duration of soil moisture states, we used a repeated measures ANOVA of transition dates with treatment and sensor depth as factors and with plot as the subject (base package R version 3.1.1, R Core Development Team, 2014). We wanted to describe the relationship of average differences between paired plots, so we conducted paired t-tests for each transition date and depth. These analyses were performed in R (base package R version 3.1.1, R Core Development Team, 2014). There were 14 time series at 5 cm and 8 time series at 30 cm that were complete enough to make the paired comparison between dust and control for the onset and duration of soil moisture states. For the analysis of differences in gravimetric water content (0-15 cm) we used a repeated measures ANOVA of treatment, cover, elevation, and sampling date, with the subject in this analysis being the individual treatment plots in each site (R Core Development Team 2014). The raw time series data are archived in the Gill Lab HydroServer and are accessible through the Consortium of Universities for the Advancement of Hydrologic Science, Inc. (CUAHSI) Hydrological Information System (Conner et al. 2013). All other data, including gravimetric water content and the individual site covariates of SOM, soil texture, and average temperature are archived in the Dryad Digital Repository (source citation contingent on publication).

The structural equation model (SEM) represents hypothesized relationships between factors that influence soil moisture (Fig. S1). The individual site covariates used in the structural equation models represent percent soil organic matter (SOM), percent sand and percent clay, forest canopy, average soil temperature at 5 cm during May, June, and July, and maximum snow water equivalent (max SWE). The soil moisture responses used in these models were the maximum and minimum gravimetric water content measurements for each plot in the years 2012-2014 (n=108 maximum and 108 minimum soil moisture measurements). In the SEM, each arrow represents a regression analysis between the connected factors. The outputs of the model include estimates of the coefficients for each factor, standardized regression weights comparing the strength of effects, and an estimate of the standardized indirect effects between factors that are connected through one or more intermediate factor (Byrne 2001, Pugesek et al. 2003). We used SEM to test for direct and indirect effects and to test for mediation of the direct effect of snowpack on maximum and minimum soil moisture. The models we tested were determined *a priori* and included SOM, percent sand, percent clay, soil temperature, forest cover, and dust treatment. We chose these variables because they are known to influence soil moisture. We expected soil moisture to be mediated by static factors of soil texture and SOM and by the dynamic process of evaporation, so as mediators of the relationship between snowpack and soil moisture we included SOM, percent sand, percent clay, and average soil temperature. Mediation was determined by modeling the direct effect without the mediators and comparing it to the direct effects modeled with the mediators. Sobel's test statistic is used to determine the significance of mediation (Sobel 1982, 1986). Sobel's statistic was calculated using an online statistical calculation tool (Soper 2006-2014). For the structural equation modeling we used IBM SPSS Amos 22.0 (Arbuckle 2006).

Results

Snowpack and soil moisture

The dust addition treatment reduced snow water equivalent (SWE) in treatment plots by 21 to 50 % of the maximum and advanced the first snow-free date by 4 to 22 days ($F_{1,250} = 6.308$, $P < 0.001$; Table 2). Although we expected the dust addition treatment to advance the onset of spring high flux, late-spring drying, and summer dry soil moisture states, we found no differences between the timing of the transition dates between dust and control treatments in the repeated measures ANOVA analysis ($F_{1,4} = 0.834$, $p = 0.51$; see Fig. 2). We also expected that the dust addition treatment would change the duration of the spring high-flux and the summer dry states, but we found no difference in the duration of either state ($F_{1,2} = 0.528$, $p = 0.59$; Table

S2). The first dust addition treatments were applied in March, an average of 15 days prior to the onset of the spring high- flux state (Table 3).

We expected early snowmelt in the dust treatment plots to result in drier soil conditions by mid-summer in the dust treatment compared to the control plots. We found that there was no difference in gravimetric water content (GWC) 0-15 cm when plots were grouped by site type (elevation and cover) on any of the dates that soil cores were collected ($F_{2,105} = 0.915$, p = 0.702). GWC was different on different collection dates ($F_{2,68} = 19.323$, $P < 0.001$) and in different site types ($F_{2,3} = 144.734$, $P < 0.001$). Average GWC across all collection dates was higher in the upper elevation sites and greatest in the upper aspen sites (Table S3; Fig. 3).

Factors influencing spatial patterns of soil moisture (SEM results)

The most important factors with positive direct effects on gravimetric water content shortly after snowmelt were soil organic matter (SOM) and maximum SWE (Fig. 4A; estimates, standard errors, and p-values given in Table S4). Soil temperature had a direct negative effect on soil moisture shortly after snowmelt. The presence of forest cover had a positive indirect effect on soil moisture (standardized indirect effect estimate = 0.659). This indirect effect was the result of increased SOM, increased maximum SWE, and decreased soil temperature in forested sites. The dust treatment did not have a significant effect on soil moisture following snowmelt, as has been shown in the results of the soil moisture analyses described above.

Dry-state soil moisture was influenced most strongly by SOM (positive effect) and percent sand (negative effect; Fig. 4B; Table S4). Forest canopy had a significant indirect positive effect on dry-state soil moisture (standardized indirect effect = 0.345), which appears to be dominated by the higher SOM at forest sites compared to meadow sites. Maximum SWE had a negative effect on soil moisture, seeming to indicate that sites with higher SWE became drier in midsummer.

We found a significant positive direct effect of maximum SWE on soil moisture in wet and dry soil moisture states. The direct effect of maximum SWE on soil moisture was more important in the wet state than the dry state (table 7). In the wet state, shortly after snowmelt, SOM partially mediated the direct positive effect of snowpack on soil moisture, while in the dry state, SOM and percent sand fully mediated the positive effect of snowpack on soil moisture. The mediation of the effect of snowpack on soil moisture during the wet state was partial mediation, because the effect of snowpack remained significant when we included the mediating factors. The mediation of the effect of snowpack on soil moisture during the dry state was full mediation, because the direct effect of snowpack was no longer significant when we included the mediating factors.

Discussion

Early snowmelt, soil moisture states, and soil moisture differences

Changes in the timing of snowmelt are expected to have significant impacts on ecosystem processes (Lipson and Monson 1998, Brooks and Williams 1999, Steltzer et al. 2009, Blankinship and Hart 2012). In part, the effects of early snowmelt on seasonally snow-covered ecosystems are expected to result from decreased soil moisture (Berdanier and Klein 2011, Blankinship et al. 2014, Ernakovich et al. 2014, Parida and Buermann 2014). We expected early snowmelt to affect the transition dates and duration of soil moisture states in our treatment plots, and we did observe a difference in snow water equivalent and snow free date associated with the dust addition treatment. However, we found no differences in the transition dates or the duration of individual states, and we saw no treatment-caused difference in soil moisture in the upper 15 cm of the soil.

We expected that adding dust to the snow surface would advance the onset of the spring high-flux soil moisture state. In most instances this was not borne out in our time series data at either 5 cm or 30 cm depths. This indicates that melt water from our first dust treatment did not reach the sensors any sooner than melt water in the control plots. It is interesting that melt water from the initial dust addition did not reach the sensors at 5 cm. Some of the water may have evaporated as the temperature of the snowpack increased through radiative forcing and water that percolated downward may have been recaptured lower in the snow profile or near the soil surface. We also expected early snowmelt would advance the onset of spring drying and lengthen the summer-dry state. However, we saw no difference in the onset of drying or in the duration of the summer-dry state. We suspect that environmental conditions during snowmelt may partially explain this result. Following melt, soils in a wet state exhibit hydraulic connectivity and lateral flow. Topography and upslope conditions influence soil moisture in this state. Following snowmelt the soils transition from saturate to unsaturated flow and there is a transition from horizontal to vertical control (McNamara 2005). We expect that lateral flow did not have a significant impact on soil moisture toward the center of our plots where instruments were located. However, late-spring precipitation occurred during this treatment-induced snow-free window in almost every case (see table 5) and may have effectively reset drying that had already taken place near the soil surface. This result highlights the importance of late-spring precipitation as a factor influencing soil moisture dynamics in seasonally snow-covered systems, but this is certainly a regionally specific phenomenon and depends on summer precipitation regime (Blankinship et al. 2014).

We expected early snowmelt would cause the soils in our treatment plot to be drier during the growing season. However, we did not see a significant difference between gravimetric water content at 0-15 cm in any of the site types. We did find significant spatial patterns in soil moisture, such that high elevation and forested sites tended to have higher soil moisture than low elevation non-forested sites. Site differences related to soil organic matter, soil texture, and soil temperature were the major drivers of these patterns of soil moisture. Compared to these static controls of soil moisture, the dynamic controls (snowpack and temperature) had much less influence on growing season soil moisture. Though there was a direct positive relationship between maximum snowpack and soil moisture shortly after snowmelt, this positive relationship was partially mediated by SOM and reflects a relationship between forest cover, which increases SOM and maximum snow accumulation, in a positive feedback that increases SOM and soil moisture retention. Though the relationship between SOM and soil moisture may be under-appreciated in the literature of soil physics (see Hudson 1994), but there is sufficient evidence that SOM increases water retention especially at less negative water potentials, such as those found near field capacity, and the effect is more pronounced when comparing soils with a range of SOM content variation on the order we observed across our sites (Hudson 1994, Rawls et al. 2003).

In the summer dry phase, we found a decrease in the positive relationship between snowpack and soil moisture. We found that this relationship was fully mediated by SOM and percent sand. The critical physical water retention properties of the soil explained soil moisture better than the amount of snowpack. When we included the mediating factors in the structural equation model, we found a negative relationship between snowpack and soil moisture. Körner (2003) suggested that this type of relationship might be common when soils beneath the deepest snowpack are less developed than soils that experience a longer snow-free period. The finding that dry-state soil moisture is fully mediated by soil physical properties supports the conclusions from similar studies of semi-arid catchments, specifically that the influence of snowmelt water on growing season soil moisture is limited by the water holding capacity of the soil (Grant et al. 2004, Smith et al. 2011). This finding does not apply to all regions and may not apply at all spatial scales (Litaor et al. 2008, Williams et al. 2009).

We found that snowpack was a secondary driver of soil moisture and that the major drivers of soil moisture were the physical characteristics of the soil, as discussed above and the decrease in soil temperature below forest cover compared to the meadows. These findings match those observed in a similar experiment. Maurer and Bowling (2014a) found that dust-caused early snowmelt were secondary to the effects of forest canopy in determining growing season soil moisture dynamics (Maurer and Bowling 2014a). However, in their study, Maurer and Bowling examined the effects of forest canopy and did not examine the effects of soil physical properties. The results of their study and our current study indicate that forest cover, which has expanded in some high elevation environments and contracted in other, will have significant direct and indirect effects on the spatial pattern and temporal dynamics of soil moisture (Gehrig-Fasel et al. 2007). At these subalpine transitions from forest to meadow, soil properties are discontinuous and tightly coupled with vegetation cover with forest soils being cooler, wetter, and typically having higher OM contents. Therefore, forest canopy has a direct physical effect increasing snow accumulation and slowing snowmelt and also an indirect effect on soil development that fosters water retention. The western United States has experienced extensive forest die off in recent decades due to beetle kill, increased fire frequency and magnitude, and other climate related phenomena (Westerling et al. 2006, DeRose and Long 2012). These types of forest dynamics can have significant cascading effects on soil moisture that may be significantly greater than the effects of warming and early snowmelt alone.

Late-spring precipitation, which commonly occurred after the first snow-free date in the dust treatment plots, also contributed to the patterns of soil moisture we observed. It was common for late-spring snow and rain to rewet the soil in both the upper and lower elevation sites. Differences in soil moisture due to early snowmelt are therefore likely to be limited to locations where late-spring precipitation is uncommon, such as the Sierra Nevada and southwestern US (Blankinship et al. 2014), and in places like the Rockies, to years when late-spring precipitation is reduced or does not occur. With climate warming, we expect that the lower-elevation boundary of persistent snowpack will move upslope. That shift in persistent snowpack could mean that late-spring precipitation would fall more often on bare ground and may play an increasingly important role in soil moisture dynamics during spring drying (Hamlet et al. 2005, Knowles et al. 2006).

In the context of understanding soil moisture responses to climate warming, the results of this study align with results from similar experiments, specifically that early snowmelt acts as a secondary driver of soil moisture and is limited or mediated by soil properties and other site characteristics (Smith et al. 2011, Blankinship et al. 2014, Maurer and Bowling 2014a). These results do not, however, preclude the effect that warmer temperatures in the future may have on soil moisture due to increased evapotranspiration (Harte et al. 1995). In our study, warmer soil temperatures following snowmelt did have a significant negative correlation to soil moisture. The effect was strongest when soils were wet, perhaps suggesting that warmer temperatures in spring and early summer may lead to more rapid drying of soils following snowmelt and ultimately an extension of summer drought conditions. However, we still expect that changes in soil moisture or in drying rates due to warming will be mediated by soil physical properties, forest cover, and spring precipitation regimes.

Acknowledgements

The authors wish to thank to Greg Maurer for insight into experimental methods and comments on an earlier draft of the paper and David Bowling for insight and helpful critique of the project at various stages of the research. Thanks also to Michael McQueen, Joshua Harvey, Desiree Lindley for help with data collection; Rohit Katthar, Dan Ames, and Jiří Kadlec for help with data management and HydroServer Lite; Randy Beckstrand (BLM) for help sourcing the dust used for the experiment; and Jeff Gardiner and Robert Davidson (USFS) for review of proposal to locate study sites in Manti-La Sal National Forest. Thanks to Roger Koide and Samuel St. Clair for comments on an earlier version of the manuscript. This research was supported in part by the G.A. Harris Graduate Research Instrumentation Fellowship from Decagon Devices, Inc.; BYU Graduate Studies Research Fellowship; Rocky Mountain Space Grant Consortium Research Fellowship; and Summer Research Fellowship from the Charles Redd Center for Western Studies. JB was supported by the USGS Ecosystems and Climate and Land Use programs. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Berdanier, A., and J. Klein. 2011. Growing Season Length and Soil Moisture Interactively Constrain High Elevation Aboveground Net Primary Production. Ecosystems **14**:963-974. DOI: 10.1007/s10021-011-9459-1.

Blankinship, J. C., and S. C. Hart. 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere **3**:art1. http://dx.doi.org/10.1890/ES11-00225.1.

Blankinship, J. C., M. W. Meadows, R. G. Lucas, and S. C. Hart. 2014. Snowmelt timing alters shallow but not deep soil moisture in the Sierra Nevada. Water Resources Research **50**:1448-1456. DOI: 10.1002/2013WR014541.

Brooks, P. D., D. H. Campbell, K. A. Tonnessen, and K. Heuer. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. Hydrological Processes **13**:2191-2201. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2191::AID-HYP849>3.0.CO;2-L.

Brooks, P. D., and M. W. Williams. 1999. Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. Hydrological Processes **13**:2177-2190. DOI: 10.1002/(SICI)1099-1085(199910)13:14/15<2177::AID-HYP850>3.0.CO;2-V.

Day P.R. Particle fractionation and particle-size analysis. pp. 562-566. In: C.A. Black (ed.), Methods of Soil Analysis Part 1. 1965. American Society of Agronomy, Inc. Madison, WI.

DeRose, R. J., and J. N. Long. 2012. Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **42**:1649-1660. DOI: 10.1139/x2012-102.

Ernakovich, J. G., K. A. Hopping, A. B. Berdanier, R. T. Simpson, E. J. Kachergis, H. Steltzer, and M. D. Wallenstein. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology **20**:3256-3269. DOI: 10.1111/gcb.12568.

Gehrig-Fasel, J., A. Guisan, and E. N. Zimmermann. 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science **18**:571-582. DOI: 10.1111/j.1654-1103.2007.tb02571.x.

Grant, L., M. Seyfried, and J. McNamara. 2004. Spatial variation and temporal stability of soil water in a snow-dominated, mountain catchment. Hydrological Processes **18**:3493-3511. DOI: 10.1002/hyp.5798.

Grayson, R. B., A. W. Western, F. H. S. Chiew, and G. Blöschl. 1997. Preferred states in spatial soil moisture patterns: Local and nonlocal controls. Water Resources Research **33**:2897-2908. DOI: 10.1029/97WR02174.

Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2005. Effects of Temperature and Precipitation Variability on Snowpack Trends in the Western United States*. Journal of Climate **18**:4545-4561. DOI: http://dx.doi.org/10.1175/JCLI3538.1.

Harte, J., M. S. Torn, F.-R. Chang, B. Feifarek, A. P. Kinzig, R. Shaw, and K. Shen. 1995. Global Warming and Soil Microclimate: Results from a Meadow-Warming Experiment. Ecological Applications **5**:132-150. Stable URL: http://www.jstor.org/stable/1942058.

Hudson, B. D. 1994. Soil organic matter and available water capacity. Journal of Soil and Water Conservation **49**:189-194.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2006. Trends in snowfall versus rainfall in the Western United States. Journal of Climate **19**:4545-4559. DOI: http://dx.doi.org/10.1175/JCLI3850.1.

Körner, C. 2003. Alpine Plant Life. 2 edition. Springer-Verlag, Berlin, D.E.

Lipson, D. A., and R. K. Monson. 1998. Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze-thaw and dry-rewet events. Oecologia **113**:406-414. DOI: 10.1007/s004420050393.

Litaor, M. I., M. Williams, and T. R. Seastedt. 2008. Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. Journal of Geophysical Research: Biogeosciences **113**:G02008. DOI: 10.1029/2007JG000419.

Maurer, G. E., and D. R. Bowling. 2014a. Dust effects on snowpack melt and related ecosystem processes are secondary to those of forest canopy structure and interannual snowpack variability. Ecohydrology:n/a-n/a. DOI: 10.1002/eco.1558.

Maurer, G. E., and D. R. Bowling. 2014b. Seasonal snowpack characteristics influence soil temperature and water content at multiple scales in interior western U.S. mountain ecosystems. Water Resources Research **50**:5216-5234. DOI: 10.1002/2013WR014452.

McNamara, J. P., D. Chandler, M. Seyfried, and S. Achet. 2005. Soil moisture states, lateral flow, and streamflow generation in a semi-arid, snowmelt-driven catchment. Hydrological Processes **19**:4023-4038. DOI: 10.1002/hyp.5869.

Molotch, N. P., P. D. Brooks, S. P. Burns, M. Litvak, R. K. Monson, J. R. McConnell, and K. Musselman. 2009. Ecohydrological controls on snowmelt partitioning in mixed-conifer sub-alpine forests. Ecohydrology **2**:129-142. DOI: 10.1002/eco.48.

Mote, P. W. 2006. Climate-driven variability and trends in mountain snowpack in western North America*. Journal of Climate **19**:6209-6220. DOI: http://dx.doi.org/10.1175/JCLI3971.1.

Painter, T. H., A. P. Barrett, C. C. Landry, J. C. Neff, M. P. Cassidy, C. R. Lawrence, K. E. McBride, and G. L. Farmer. 2007. Impact of disturbed desert soils on duration of mountain snow cover. Geophys. Res. Lett. **34**:L12502. DOI: 10.1029/2007GL030284.

Painter, T. H., J. S. Deems, J. Belnap, A. F. Hamlet, C. C. Landry, and B. Udall. 2010. Response of Colorado River runoff to dust radiative forcing in snow. Proceedings of the National Academy of Sciences **107**:17125-17130. DOI: 10.1073/pnas.0913139107.

Parida, B. R., and W. Buermann. 2014. Increasing summer drying in North American ecosystems in response to longer nonfrozen periods. Geophysical Research Letters **41**:2014GL060495. DOI: 10.1002/2014GL060495.

Porporato, A., E. Daly, and I. Rodriguez-Iturbe. 2004. Soil water balance and ecosystem response to climate change. American Naturalist **164**:625-632. DOI:10.1086/424970.

Rawls, W. J., Y. A. Pachepsky, J. C. Ritchie, T. M. Sobecki, and H. Bloodworth. 2003. Effect of soil organic carbon on soil water retention. Geoderma **116**:61-76. DOI: 10.1016/S0016-7061(03)00094-6.

Redding, T., and K. Devito. 2011. Aspect and soil texture controls on snowmelt runoff on forested boreal plain hillslopes. Hydrology Research **42**:250-267. DOI: 10.2166/nh.2011.162.

Rodriguez-Iturbe, I., and A. Porporato. 2004. Ecohydrology of water-controlled ecosystems. Cambridge University Press, Cambridge.

Schmidt, S. K., E. K. Costello, D. R. Nemergut, C. C. Cleveland, S. C. Reed, M. N. Weintraub, A. F. Meyer, and A. M. Martin. 2007. Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. Ecology **88**:1379-1385. http://dx.doi.org/10.1890/06-0164.

Serreze, M. C., M. P. Clark, R. L. Armstrsong, D. A. McGinnis, and R. S. Pulwarty. 1999. Characteristics of the western United States snowpack from snowpack telemetry (SNOTEL) data. Water Resources Research **35**:2145-2160. DOI: 10.1029/1999WR900090.

Service, R. F. 2004. As the West Goes Dry. Science **303**:1124-1127. DOI: 10.1126/science.303.5661.1124.

Smith, T. J., J. P. McNamara, A. N. Flores, M. M. Gribb, P. S. Aishlin, and S. G. Benner. 2011. Small soil storage capacity limits benefit of winter snowpack to upland vegetation. Hydrological Processes **25**:3858-3865. DOI: 10.1002/hyp.8340.

Soper, D. 2006-2014. Sobel test calculator for the significance of mediation. [Available online at http://www.danielsoper.com/statcalc3/calc.aspx?id=31]. (Accessed 13 December 2014).

Steltzer, H., C. Landry, T. H. Painter, J. Anderson, and E. Ayres. 2009. Biological consequences of earlier snowmelt from desert dust deposition in alpine landscapes. Proceedings of the National Academy of Sciences **106**:11629-11634. DOI: 10.1073/pnas.0900758106.

Vereecken, H., J. Maes, J. Feyen, and P. Darius. 1989. Estimating the soil moisture retention characteristic from texture, bulk density, and carbon content. Soil Science **148**:389-403.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of Interannual Climate Variation on Aboveground Phytomass in Alpine Vegetation. Ecology **75**:393-408. http://dx.doi.org/10.2307/1939543.

Walkley, A., and I.A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Science 37:29-38.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science **313**:940-943. DOI: 10.1126/science.1128834.

Western, A. W., R. B. Grayson, G. Blöschl, G. R. Willgoose, and T. A. McMahon. 1999. Observed spatial organization of soil moisture and its relation to terrain indices. Water Resources Research **35**:797-810. DOI: 10.1029/1998WR900065.

Williams, C. J., J. P. McNamara, and D. G. Chandler. 2009. Controls on the temporal and spatial variability of soil moisture in a mountainous landscape: the signature of snow and complex terrain. Hydrol. Earth Syst. Sci. **13**:1325-1336. DOI:10.5194/hess-13-1325-2009.

Woodward, A. 1998. Relationships among environmental variables and distribution of tree species at high elevation in the Olympic Mountains. Northwest Science **72**:10-22. URL: http://hdl.handle.net/2376/1224.

Table S1. Climate characteristics of upper and lower elevation sites.

	Elevation (m)	Water year	Precip (mm)	MAT (°C)	Max SWE (mm)	SNOTEL site*
Upper	2900	2012	---	---	---	Huntington Horse (1216)
		2013	353	3.6	389	
		2014	400	2.7	503	
Lower	2650	2012	298	4.9	279	Mammoth-Cottonwood (612)
		2013	312	4.1	356	
		2014	282	3.3	414	

* USDA Natural Resource Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) [available online at http://www.wcc.nrcs.usda.gov/snow/].

Note: Mean annual temperature (MAT). Snow water equivalent (SWE).

Table 1. Comparison of site characteristics.

Site type	Sand (%)	Clay (%)	SOM (%)	Dominant understory vegetation
Lower aspen	77.5	4.6	5.7	*Latharus lanszwertii, Hackelia micrantha, Viola praemorsa, Claytonia lanceolata, Delphinium nuttallianum*
Lower meadow	70.3	6.3	3.8	*Artemisia tridentate, Ranunculus jovis, C. lanceolata, D. nuttallianum*, *Penstemon spp., L. lanszwertii, V. praemorsa*
Upper aspen	63.2	13.6	9.5	*H. micrantha, Thalictrum fendleri, C. lanceolata, Erythronium grandiflorum, Mertensia ciliata*, *Delphinium occidentale*, *Sambucus racemosa*, and *Ribes viscossimum*
Upper meadow	59.0	13.6	4.8	*H. micrantha, T. fendleri, Polemonium foliossimum, C. lanceolata, Potentilla spp.*, and *E. grandiflorum*

Note: Soil organic matter (SOM).

Table 2. Dust addition effects on snow water equivalent (SWE) and snow-free date.

	April 1 SWE (cm)	SWE max difference (cm) (control-dust)	Dust 1st snow-free date	Control 1st snow-free date	Treatment-induced snow-free interval (d)
2012					
Lower aspen	16.5	12.7	5 April	23 April	18
Lower meadow	19	14.1	5 April	23 April	18
Upper aspen	39.5	20.8	27 April	11 May	14
Upper meadow	25.5	15.4	27 April	3 May	6
2013					
Lower aspen	19	16.1	29 April	3 May	4
Lower meadow	21	17.8	22 April	14 May	22
Upper aspen	43	23.7	14 May	29 May	15
Upper meadow	30.5	20.5	3 May	17 May	14
2014					
Lower aspen	38.5	14.7	21 April	5 May	14
Lower meadow	38.5	14.7	21 April	13 May	22
Upper aspen	57	23.0	20 May	29 May	9
Upper meadow	45	19.6	5 May	20 May	15

Note: April 1 SWE is the average SWE by site type. Maximum SWE in all years occurred around the first week of April. SWE max difference is the maximum of the average difference between treatments by site type.

Table S2. Soil moisture states transition dates and duration results of paired t-tests.

	Mean dates and durations	mean difference (days)	t	df	p-value	lower 95%	upper 95%
Transition dates 5 cm							
Spring high-flux	5 Apr (7.1)	1.5	0.4104	7	0.69	-7.1	10.1
Late-spring drying	22 May (5.3)	1.5	0.8684	9	0.41	-2.4	5.4
Inflection point	6 Jun (8.8)	-0.09	-0.0418	10	0.97	-4.9	4.8
Summer dry	17 Jun (13.2)	1.3	0.4353	11	0.67	-5.4	8.1
Summer monsoon	19 Jul (15.8)	-3.9	-0.9305	12	0.37	-13.1	5.3
Transition dates 30 cm							
Spring high-flux	27 Mar (11.0)	5.6	1.3615	7	0.22	-4.1	15.4
Late-spring drying	19 May (8.3)	2.5	0.9172	7	0.39	-3.9	8.9
Inflection point	18 Jun (7.9)	-0.6	-0.1969	6	0.85	-7.7	6.5
Summer dry	28 Jun (7.5)	1.6	0.4741	7	0.65	-6.5	9.7
Summer monsoon	8 Aug (25.9)	13.2	0.96	4	0.39	-24.9	51.3
Duration 5 cm							
Spring high-flux	29.7 (13.3)	0.1	0.037	7	0.97	-7.9	8.1
Late-spring drying	46.4 (7.1)	-1.4	-0.3478	9	0.74	-10.5	7.7
Summer dry	31.5 (18.5)	-5.2	-0.8781	11	0.40	-18.1	7.8
Duration 30 cm							
Spring high-flux	38.1 (9.2)	-3.1	-0.6335	7	0.55	-14.8	8.5
Late-spring drying	52.6 (9.9)	0.7	0.1711	5	0.87	-9.3	10.7
Summer dry	37.3 (24.5)	8.6	0.7298	4	0.51	-24.1	41.3

Note: Mean dates and durations include (±SD) given in days. Mean difference was calculated as the average of the control day of year minus the dust day of year for the transition date in each time series.

Table 3. Dust addition and transition dates.

	1st Dust addition	Spring high-flux	Spring drying	Summer dry	Precipitation during snow-free interval (mm)
2012					
Lower aspen	10 Mar	--	--	--	22
Lower meadow	10 Mar	--	--	--	22
Upper aspen	10 Mar	29 Mar (4.9)	16 May (3.3)	29 Jun (7.9)	--
Upper meadow	10 Mar	29 Mar (15.6)	12 May (5.2)	17 Jun (11.9)	--
2013					
Lower aspen	12 Mar	14 Mar (1.4)	9 May (14.8)	22 Jun (10.7)	0
Lower meadow	12 Mar	25 Mar (7.2)	20 May (2.2)	13 Jun (7.9)	28
Upper aspen	12 Mar	28 Mar (0.7)	29 May (2.6)	25 Jun (8.1)	43
Upper meadow	12 Mar	--	--	12 Jun (--)	36
2014					
Lower aspen	18 Mar	4 Apr (13.6)	16 May (5.7)	21 Jun (10.2)	23
Lower meadow	18 Mar	28 Mar (8.1)	21 May (3.9)	13 Jun (10.8)	51
Upper aspen	18 Mar	9 Apr (1.5)	26 May (3.4)	10 Jul (13.5)	8
Upper meadow	18 Mar	4 Apr (7.4)	24 May (5.0)	7 Jun (2.1)	36

Note: transition dates are averaged across treatments, depths, and sites within each site type. The values in parentheses represent 1 standard deviation. Precipitation measurements were taken from the Mammoth-cottonwood SNOTEL site for lower elevation sites and from the Huntington-horse site for upper elevation sites. Huntington-horse was established in July 2012.

Table S3. Pairwise comparison of gravimetric water content 0-15 cm by site type.

	Lower aspen	Lower meadow	Upper aspen
Lower meadow	0.322	-	-
Upper aspen	< 0.001	< 0.001	-
Upper meadow	0.200	0.027	< 0.001

Notes: We used the Holm method of p-value adjustment for multiple pairwise comparisons of paired data.

Table S4. Parameter estimates for structural equation models of soil moisture.

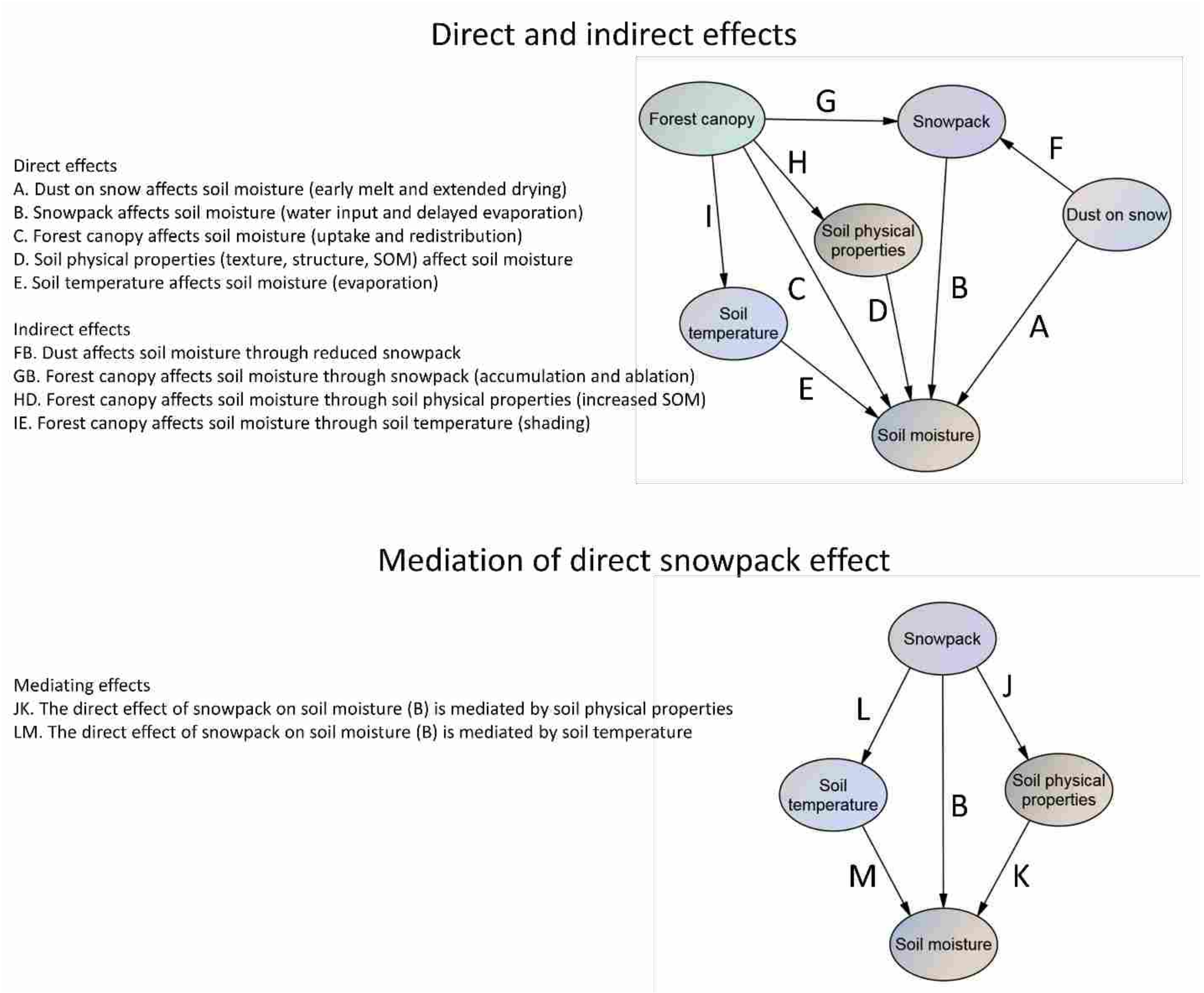
Path			Estimate	Standard error	P	Standardized Regression Weight
Model for maximum soil moisture						
MaxSWE	←	Canopy	5.166	2.810	0.066	0.175
Soil temp	←	Canopy	-2.740	0.305	***	-0.657
SOM	←	Canopy	3.325	0.412	***	0.616
GWC15cmMax	←	Canopy	-0.065	0.017	***	-0.355
GWC15cmMax	←	Percent Sand	0.000	0.001	0.730	0.033
GWC15cmMax	←	MaxSWE	0.001	0.000	***	0.228
GWC15cmMax	←	Soil Temp	-0.007	0.004	0.051	-0.160
GWC15cmMax	←	SOM	0.028	0.003	***	0.834
GWC15cmMax	←	Percent Clay	-0.001	0.001	0.730	-0.033
GWC15cmMax	←	Dust treatment	0.003	0.012	0.825	0.014
Model for minimum soil moisture						
MaxSWE	←	Canopy	5.166	2.810	0.066	0.175
Soil temp	←	Canopy	-2.740	0.305	***	-0.657
SOM	←	Canopy	3.325	0.412	***	0.616
GWC15cmMin	←	Canopy	0.020	0.010	0.052	0.174
GWC15cmMin	←	Percent Sand	-0.001	0.001	0.018	-0.211
GWC15cmMin	←	MaxSWE	-0.001	0.000	0.012	-0.148
GWC15cmMin	←	Soil Temp	0.001	0.002	0.524	0.049
GWC15cmMin	←	SOM	0.014	0.002	***	0.654
GWC15cmMin	←	Percent Clay	0.001	0.001	0.454	0.067
GWC15cmMin	←	Dust treatment	-0.014	0.007	0.044	-0.117

Note: Maximum snow water equivalent (MaxSWE), presence/absence forest canopy (Canopy), average soil temperature at 5 cm (SoilTempAvg5cm), soil organic matter (SOM), gravimetric water content 0-15 cm (GWC15cm). P of *** > 0.000.

Table 4. Mediation of the direct effects of snowmelt on wet and dry-state soil moisture.

		Standardized regression weight	Estimate	Standard error	p-value	Sobel's Z	p-value mediation
Wet state							
Direct effect (no mediation)		**0.45**	**0.003**	**0.001**	**< 0.001**		
Direct effect (with mediation)		**0.25**	**0.002**	**0.001**	**0.006**		
Wet-state mediation							
SOM	**(maxSWE → SOM)**	**0.30**	**0.055**	**0.17**	**0.001**	**3.13**	**0.002**
	(SOM → GWC)	**0.67**	**0.025**	**.002**	**<0.001**		
Soil temp	(maxSWE → Soil temp)	-0.58	-0.082	0.11	<0.001	-0.66	0.51
	(Soil temp → GWC)	0.04	0.002	0.003	0.546		
%Sand	(maxSWE → %Sand)	-0.45	-0.295	0.057	<0.001	0.98	0.33
	(%Sand → GWC)	-0.12	-0.001	0.001	0.072		
%Clay	(maxSWE → %Clay)	0.55	0.221	0.033	<0.001	0.98	0.32
	(%Clay → GWC)	-0.07	-0.001	0.001	0.320		
Dry state							
Direct effect (no mediation)		**0.22**	**0.001**	**0.000**	**0.021**		
Direct effect (with mediation)		-0.17	-0.001	0.000	0.074		
Dry-state mediation							
SOM	**(maxSWE → SOM)**	**0.30**	**0.055**	**0.017**	**0.001**	**3.15**	**0.002**
	(SOM → GWC)	**0.72**	**0.014**	**0.001**	**<0.001**		
Soil temp	(maxSWE → Soil temp)	-0.58	-0.082	0.11	<0.001	1.47	0.14
	(Soil temp → GWC)	-0.10	-0.003	0.002	0.195		
%Sand	**(maxSWE → %Sand)**	**-0.45**	**-0.295**	**0.057**	**<0.001**	**4.60**	**<0.001**
	(%Sand → GWC)	**-0.13**	**-0.001**	**0.000**	**0.064**		
%Clay	(maxSWE → %Clay)	0.55	0.221	0.033	<0.001	0.99	0.32
	(%Clay → GWC)	0.12	0.001	0.001	0.135		

Notes: Soil organic matter (SOM), maximum snow water equivalent (maxSWE), gravimetric water content 0-15 cm (GWC), average soil temperature at 5 cm (Soil temp).



Direct and indirect effects

Direct effects
A. Dust on snow affects soil moisture (early melt and extended drying)
B. Snowpack affects soil moisture (water input and delayed evaporation)
C. Forest canopy affects soil moisture (uptake and redistribution)
D. Soil physical properties (texture, structure, SOM) affect soil moisture
E. Soil temperature affects soil moisture (evaporation)

Indirect effects
FB. Dust affects soil moisture through reduced snowpack
GB. Forest canopy affects soil moisture through snowpack (accumulation and ablation)
HD. Forest canopy affects soil moisture through soil physical properties (increased SOM)
IE. Forest canopy affects soil moisture through soil temperature (shading)

Mediation of direct snowpack effect

Mediating effects
JK. The direct effect of snowpack on soil moisture (B) is mediated by soil physical properties
LM. The direct effect of snowpack on soil moisture (B) is mediated by soil temperature

Fig. S1. Conceptual model of the direct, indirect, and mediating factors that influence soil moisture.

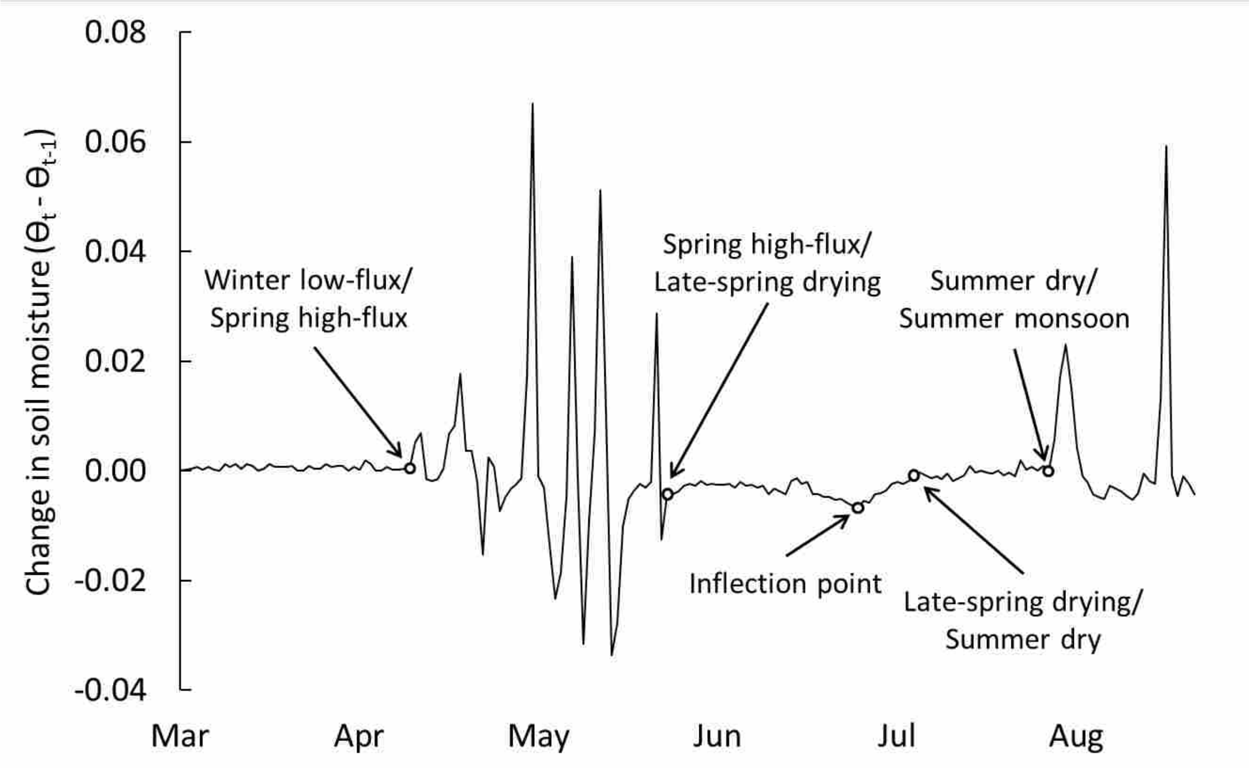


Fig. 1. Conceptual models of soil moisture states and transition dates derived from change in soil moisture. Open circles indicate transition dates between soil moisture states.

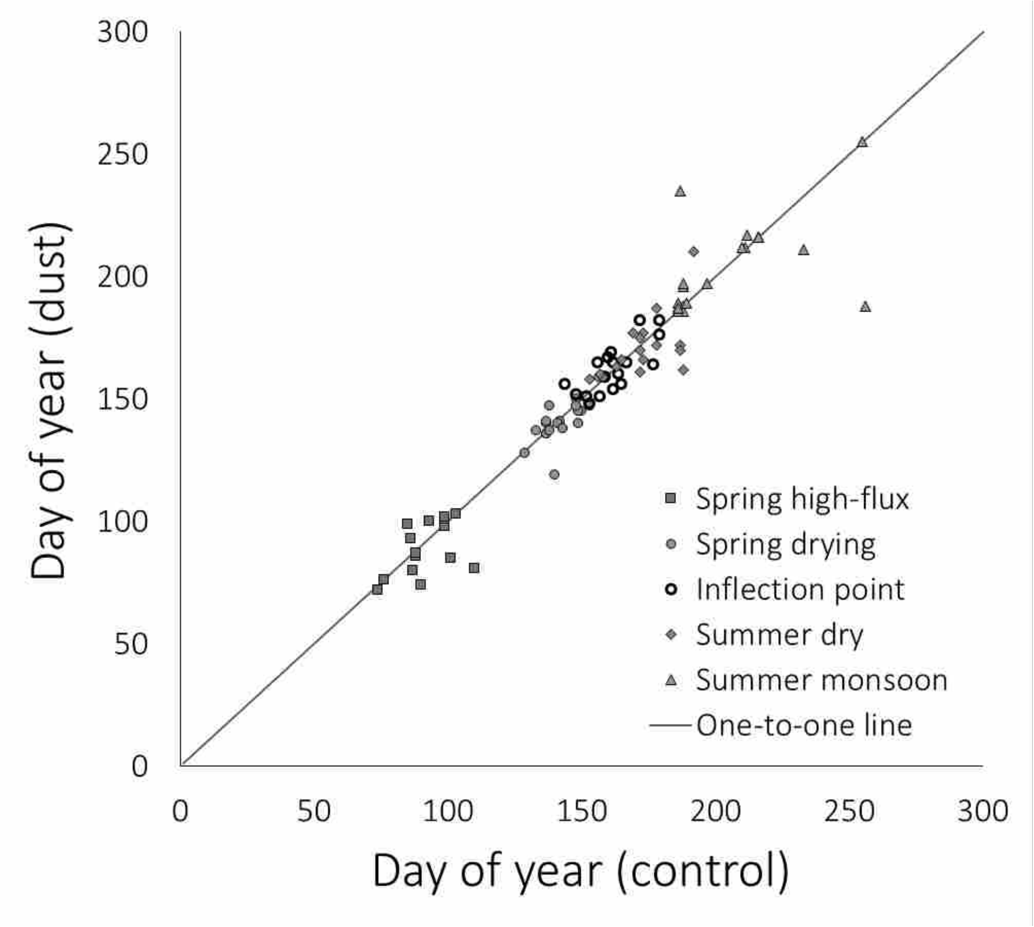


Fig. 2. Soil moisture state transition dates comparison between control and dust addition treatments by plot pair. The one-to-one line represents no difference, values falling below the line represent earlier transition dates in the dust treatment plot, and values above the line represent earlier transition dates in the control plot.

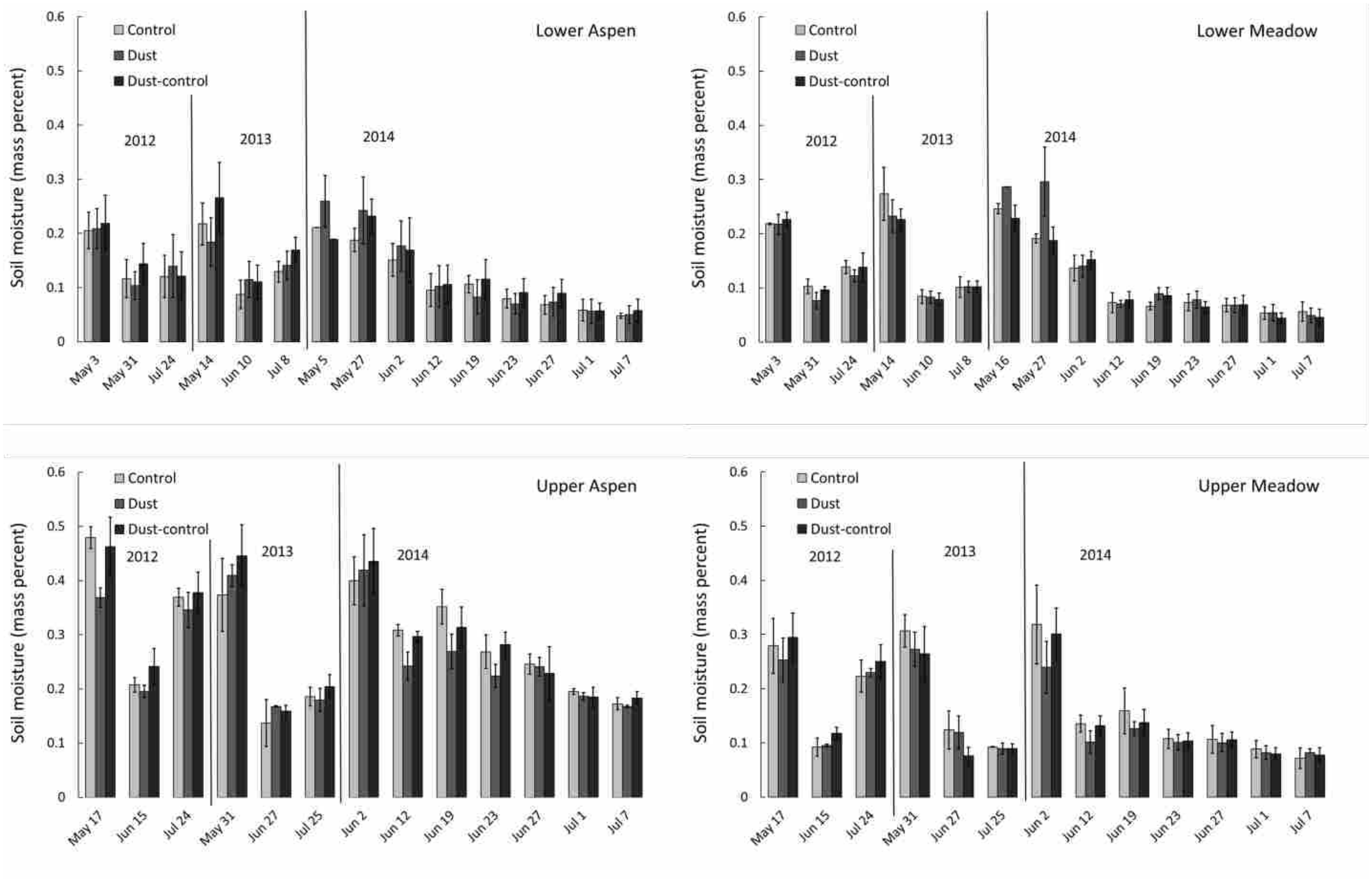


Fig. 3. Comparison of gravimetric water content (0-15 cm) by site type, treatment, and date. There were no significant differences in GWC between any of the treatments for any of the dates, though there were significant differences in GWC between dates and between site types. On average, GWC was highest in the upper aspen sites and lowest in the lower elevation sites.

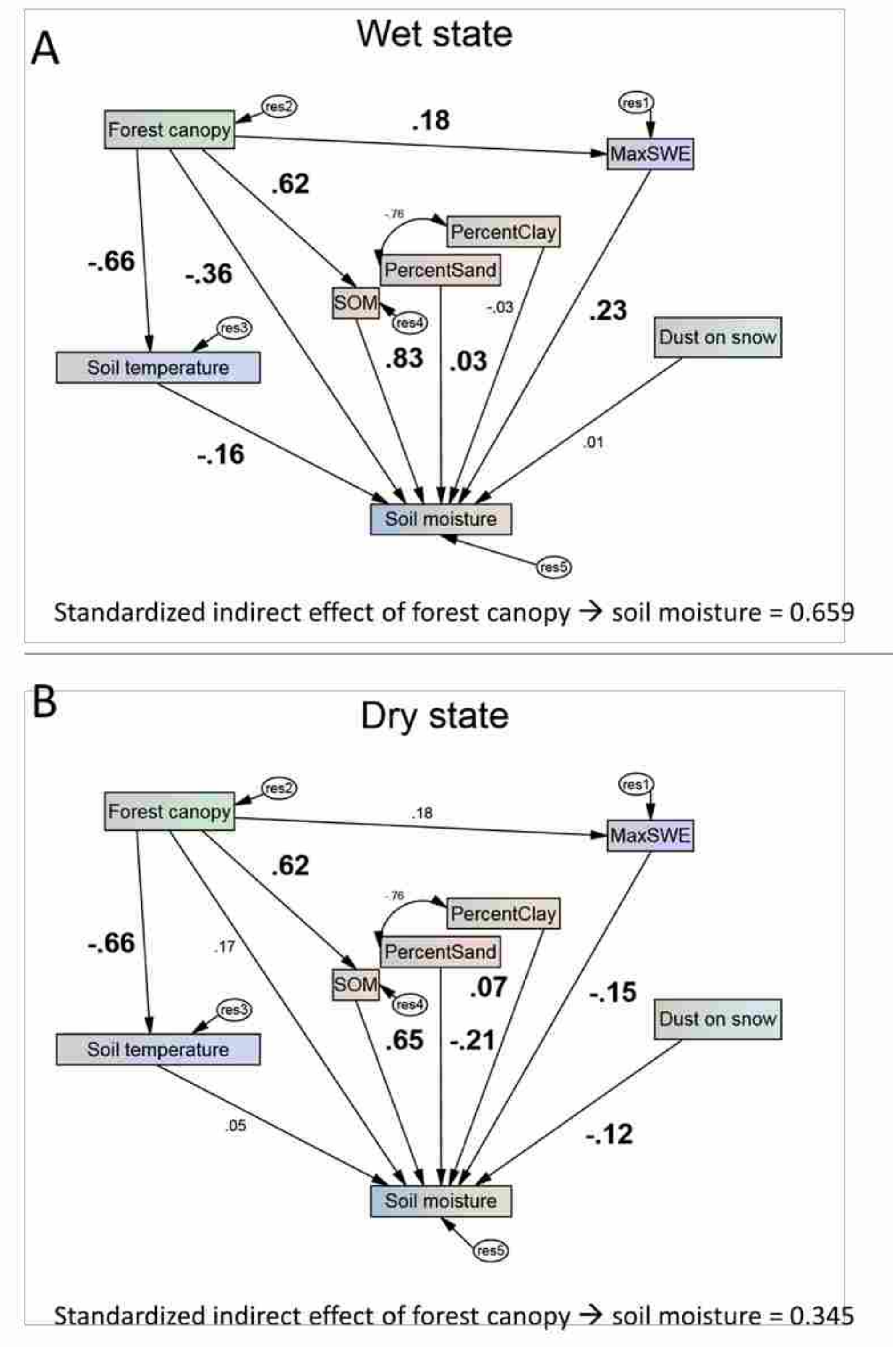


Fig. 4. Measurement models for factors affecting soil moisture following snowmelt (A) and during the summer-dry soil moisture state (B). Numbers represent standardized regression weights. Bold and enlarged numbers represent significant path coefficients. MaxSWE is maximum snow water equivalent. SOM is percent soil organic matter.

Appendix A

Identifying transition dates and duration of soil moisture states

McNamara et al. (2005) identified 5 soil moisture states that occur in a semi-arid, seasonally snow-covered environment in Idaho. Rather than being associated with absolute soil moisture values, the transition points between soil moisture states relate to the dynamic behavior of soil moisture (Fig. 1 also described in the introduction). Our study system receives summer monsoon rains that frequently rewet the soil at the 5 and 30 cm depths of our instrumentation. Therefore, we modified the summer dry period into summer-dry and summer monsoon, which took the place of fall rewetting in our analyses. We used the continuous measurements of volumetric water content (Θ) at 5 and 30 cm to detect changes in soil moisture. We used the change in daily average soil moisture (${}_{\Delta}\Theta$) to identify the transition dates and calculate the duration of soil moisture states. During the spring drying state, there was an inflection point when the rate of change in soil moisture reached its maximum absolute value, after which there was less change in daily soil moisture as soils approached the summer-dry state.

The steps of the calculation were first, visual examination of the soil moisture time series data and removal of data values that were obviously wrong. Such values occurred when sensors went offline, or were damaged. Second, calculate the daily average soil moisture from the 4 daily measurements of average soil moisture in 6 hour intervals. Third, identify the key transition dates using the following criteria: spring high-flux began after March 1 when ${}_{\Delta}\Theta \geq 0.01$. During the winter low-flux state, ${}_{\Delta}\Theta$ values range between -0.006 and 0.004. Spring high-flux ended and late-spring drying began when the soil surface became snow free and ${}_{\Delta}\Theta < 0$ for several consecutive days. The inflection point was the lowest value of ${}_{\Delta}\Theta$ after the spring drying transition. Spring drying ended and summer dry began when the absolute value of ${}_{\Delta}\Theta$ leveled off and was consistently less than one-third of the value near the inflection point. Summer dry ended and summer monsoon began when Θ increased by > 0.01 in one time step. Occasionally the summer monsoons began before soils reached the summer dry state. To provide a transition date in these instances we marked the onset of the summer dry state as the day before the monsoonal spike in soil moisture when soil moisture was at its lowest value during spring drying. We calculated the duration of soil moisture states as the number of days between the transition dates for periods representing spring high-flux, late-spring drying, and summer dry.

CHAPTER 3

Environmental and adaptive constraints limit growth response of subalpine snowbank and midsummer herbaceous species in longer growing seasons

Lafe G. Conner[1,2] and Richard A. Gill[1]

[1]Department of Biology, Brigham Young University, Provo, Utah 84602, USA

[2]E-mail: connerlg@byu.edu

Abstract

Snowmelt has come earlier to montane environments in western North America in recent decades and may arrive earlier still in the future. While longer and warmer growing seasons may increase plant growth in cold and snow limited systems, vegetation responses are constrained by environmental buffers, including soil water potential, temperature, nutrient availability and day length, and by adaptive buffers such as a fixed duration of active growth or developmental responses that are cued by environmental factors, such as day length, which do not change. We advanced snowmelt by 4 to 22 days by reducing snow albedo through dust addition. We observed responses in two spring ephemeral (*Erythronium grandiflorum* and *Ranunculus jovis*) and four midsummer species (*Delphinium nuttallianum*, *Hackelia micrantha, Latharus lanszwertii,* and *Mertensia* ciliata). To understand the ability of subalpine herbaceous species to respond vegetatively and reproductively to extended growing season caused by early snowmelt, we compared growth and seed counts as a function of snow melt timing. To identify the underlying mechanism controlling plant responses to snowmelt timing, we developed models of plant growth as a function of soil water potential, temperature after snowmelt, inorganic N and net N mineralization, and the snow-free and first-flowering dates to determine which mechanism limited growth and seed production in these plant species. We found no difference in plant responses between treatment and control plots, but we did find that snow-free date, water potential, and N mineralization were correlated with dry mass and seed count across community types and species.

Key words: climate change; environmental buffering; flowering; plant growth; snowmelt; subalpine

Running Head: Limited growth response to early snowmelt

Introduction

High elevation and high latitude ecosystems with seasonal snow cover and cold temperatures may be highly vulnerable to rapid climate change (Ernakovich et al. 2014). Since the 1950s, warming of cold and snow-limited ecosystems has lengthened the active growing season in the northern hemisphere (Myneni et al. 1997, Barichivich et al. 2013). Peak winter snowpack in mountainous areas of western North America has declined in the past several decades and spring runoff has come earlier as temperatures have warmed (Hamlet et al. 2005, Mote 2006, Pederson et al. 2010). These trends will likely continue into the future with additional spring warming, more frequent rain-on-snow events, and increased deposition of dust and black carbon on mountain snowpack (Cayan et al. 2001, Marks et al. 2001, Painter et al. 2007, Neff et al. 2008). The potential increase in plant growth in longer growing seasons and the resulting ecosystem carbon gains may be offset by environmental and adaptive constraints that prevent vegetation from taking full advantage of the increased opportunity to grow (Hu et al. 2010) unless there is a wholesale change in plant community composition (Chapin and Shaver 1985). Four constraints that might minimize plant responses to early snowmelt include low-temperature damage, reduced soil moisture, reduced N-availability, and fixed plant phenology. Low-temperature damage occurs if there is increased exposure of plants and flowers to freezing and frost damage with earlier snowmelt (Groffman et al. 2001, Inouye 2008). Decreased soil moisture can result from longer snow-free and unfrozen periods (Angert et al. 2005, Hu et al. 2010, Parida and Buermann 2014). Reduced nutrient availability and nutrient uptake can occur in drier soils even if plants have access to deeper soil water reserves and are not moisture limited (Körner 2003, Berdanier and Klein 2011). Finally, a fixed duration of growth and flowering determined be by photoperiod or minimum chilling requirements or growth stages cued by successful pollination, fruit, and seed development may limit vegetation responses to longer growing seasons (Körner 2006, Jonas et al. 2008, Iler et al. 2013, CaraDonna et al. 2014).

Because species respond individualistically to warming and early snowmelt, these environmental changes can have significant impacts on herbaceous plant communities and species interactions between plants and between plants and pollinators (Chapin and Shaver 1985, Galen and Stanton 1995, Arft et al. 1999). The composition of vegetative communities can change over several years to decades in response to altered growing season length (Walther et al. 2002, DeMarco et al. 2014, Rudgers et al. 2014). Within a single growing season, snowmelt timing and spring warming can affect co-flowering relationships as some species have higher developmental plasticity and respond more sensitively to environmental changes (Forrest et al. 2010, CaraDonna et al. 2014). A change in flowering time can alter resource availability for species that depend on floral resources in cold and snow limited environments (Aldridge et al. 2011, McKinney et al. 2012).

The consequences of early snowmelt differ for spring ephemeral and midsummer species. Spring ephemeral species emerge and flower within days following snowmelt and show higher sensitivity to changes in snowmelt timing than later-flowering species (CaraDonna et al. 2014). Changes in flowering time for spring ephemeral species may reduce pollination success, especially for early flowering cohorts of bee-pollinated species (Kudo et al. 2004, Thomson 2010, Kudo and Ida 2013). However, successful pollination in early flowering cohorts may result in more time to develop and ultimately larger seeds for some spring ephemerals (Galen and Stanton 1991). Spring ephemeral species may be constrained by a fixed duration of growth which can end when successfully pollinated flowers develop into seeds and fruit and as soils dry and late-flowering species grow over and shade the smaller ephemeral plants (Jackson and Bliss

1984). The growth and flowering response in midsummer species may be less limited by these adaptive constraints, but increased growth in longer growing seasons may be offset by drier soil conditions and the consequently reduced nutrient acquisition that result from earlier snowmelt and warmer summer temperatures (Walker et al. 1994, Kennedy and Peay 2007, Dijkstra and Cheng 2008, Berdanier and Klein 2011, Blankinship et al. 2014).

The objective of this study was to determine how early snowmelt influences plant growth in subalpine herbaceous species. We also wanted to determine which of the potential growth-limiting mechanisms affected early and midseason species. As a conceptual framework for this study, we developed five growth-limiting scenarios that represent these different growth constraining factors (Fig 1.) The snow-cover-limited scenario applies to vegetation growth limited by the presence of seasonal snow cover. In a warmer world with earlier snowmelt, the primary response of vegetation in this scenario is increased growth through an extended growing season. Under this scenario, we also expect the ranges and distributions of species to shift, especially for non-cold adapted species that may benefit more from increased growing season length than cold-hardy species (Körner 2006).

The temperature-limited scenario applies primarily to situations in which snow-cover duration is decoupled from seasonal or climate warming. There are multiple conditions that could result in decoupling of snowmelt from warming temperatures. One cause may be reduced snowfall and a period of spring snow melt that does not last very long. Another cause could be weather fluctuation, when a warm spring period could be followed by a sharp decline in later-spring temperatures. Another cause may be deposition of dust and black carbon on the snow surface which can sped snowmelt in disjunction with temperature (Painter et al. 2007, Steltzer et al. 2009). In the temperature-limited scenario, the response of vegetation to a longer growing season is limited by a window of cold-induced restriction to growth or by an increase in frost damage to plant and floral tissue. Although photosynthesis in cold-hardy species commonly occurs at near-freezing temperatures, growth of plant tissue is restricted at temperatures below 6 °C (Körner and Paulsen 2004, Körner 2006). While many montane herbaceous species escape freezing damage through dormancy and structural architecture (Körner 2003), freezing and loss of plant tissue does occur and may be more likely under elevated CO_2 (Martin et al. 2010) and earlier onset of growth and flowering (Inouye and McGuire 1991). The temperature-limited scenario also considers that increased freeze-thaw cycles can reduce soil N retention, which may limit plant growth over longer time scales (Brooks et al. 1999, Groffman et al. 2001, Schimel et al. 2007).

The fixed-growth scenario applies to vegetation for which the period of active growth shifts in step with earlier snowmelt and is not lengthened. Alternatively, a fixed signal to begin growth, such as photoperiod, could also apply under this scenario. The effects of the fixed-growth scenario include limited change in plant growth for constrained species, but range shifts for species that can respond to longer growing season.

Two additional scenarios for limited plant growth are the soil moisture and reduced nutrient scenarios. Soil moisture responses to early snowmelt can limit plant growth directly through a deepening and lengthening of midsummer drought. Low soil moisture can also limit plant growth indirectly through reduced nutrient acquisition which results both from lower nutrient availability in drier soils, as nutrients must pass through water, and the decrease in plant ability to acquire those nutrients because of reduced efficiency of mycorrhizal associations, although in more arid environments species with mycorrhizal associations tend to do better than those without the benefit of these associations (Kennedy and Peay 2007, Dijkstra and Cheng 2008).

We wanted to determine which of these scenarios, alone or in combination, affected plant growth response in a seasonally snow-covered environment exposed to early snowmelt. We applied dust to the snow surface to reduce snow albedo and advanced the snow-free date by an average of 14 days in 2012 and 2013 and 15 days in 2014. We measured growth response as the dry weight of aboveground biomass and the number of seeds g^{-1} of plant dry mass. During peak flowering, we counted the number of flowers $plant^{-1}$ and measured the height of midsummer species. For spring ephemeral species, we expected that early snowmelt would increase plant dry mass if species were growing-season limited, but that early snowmelt could reduce growth, flowering, and seeds through cold-limitation, frost damage, and decreased pollination success. We assessed cold temperature exposure by comparing air temperatures in the two weeks following snowmelt for early-snowmelt and control plots. For midsummer species, we expected that longer growing season would increase plant growth, but that this result could be constrained by drier soil conditions through water or nutrient limitation. For midsummer species, we measured predawn and midday leaf water potential and $\delta^{13}C$ and C:N ratios in leaf tissue to assess plant water relations and nutrient status prior to and during peak flowering. We expected plants that experienced increased water stress during growth would be enriched in ^{13}C (Farquhar et al. 1982), while plants that were nutrient limited would have reduced growth with no difference in $\delta^{13}C$ and may have reduced leaf N (Berdanier and Klein 2011). We also expected that growth limitation could result in lower floral and seed counts in midsummer species. We tested for growth responses to early snowmelt using paired treatment plots at the upper and lower limits of the subalpine and we assessed the factors of growth limitation by comparing temperature, soil water potential, initial soil inorganic N pool and net inorganic N flux, and snow-free and first-flowering dates to plant growth and seeds g^{-1} across species, plots, and years.

Methods

Study system

We conducted the snow manipulation experiment on the Wasatch Plateau in Fairview Canyon, Utah at a lower-elevation (39°41'N, 111°18'W, 2650 m) and higher-elevation site (39°37'N, 111°18'W, 2900 m). There were six treatment blocks at each elevation, three blocks located in open meadows and three within aspen (*Populus tremuloides*) stands. Soil texture and dominant vegetation varied by site type (table 1). The Wasatch Plateau is grazed by sheep and cattle during summer months, and we fenced each plot during the summer to exclude livestock. Each treatment block consisted of three 5X5 m treatment plots. The three treatment included dust addition (dust), dust-control, and control. In the dust plots, we applied dust by hand to the snow surface at a rate of approximately 50 g m^{-2} following major snow events from the second week of March until the end of snowmelt, a total of 4 or 5 applications of dust each year. In the dust-control plots, we added the equivalent of 4 or 5 dust treatments to the plot following snowmelt to control for effects of dust fertilization and changes to the soil surface resulting from dust addition. We collected the dust for this experiment from a playa near the town of Kanosh, Utah (38°48' N, 112°37' W, 1776 m). The dust was sifted (50 μm) and autoclaved to avoid transport of living seeds and microorganisms. We analyzed the dust for texture (Day 1965), organic matter (Walkley-Black 1934), pH (Rhodes 1982), total N by combustion using LECO TruSpec CN Determinator (LECO Instruments, St. Joseph, MI), sodium-bicarbonate extractable P (Olsen 1954) and K (Schoenau and Karamonos 1993), and trace elements (EPA method 3051A). Results of dust analysis are reported in the supplementary material (table S1).

We compared snowpack in our study years to the long-term average using daily snow water equivalent measurements from the Mammoth-cottonwood Snowpack Telemetry (SNOTEL) station (site number 612; 39°41'N, 111°19'W, 2660 m a.s.l.; NRCS 2014a). This station is located approximately 1 km from the lower elevation sites and has been in operation since 1980. We obtained temperature and precipitation data from Mammoth-cottonwood and Huntington Horse SNOTEL stations (site number 1216 39°37'N, 111°18'W, 2943 m a.s.l.; NRCS 2014b) for use in regression analysis and interpretation of treatment effects. The Huntington Horse station is approximately 1 km from the upper sites and opened in July 2012.

Data collection

We collected snow, soil, and vegetation data from March 2012 to July 2014. Beginning in March of each year, we visited the sites every 7 to 10 days to measure the snow depth and snow water equivalent on the dust and control plots. Using a Federal aluminum tube snow sample (Union Forge, Yakima, WA), we made three snow measurements at 1 m intervals along the western edge of each plot. Following snowmelt, we collected soil samples 0-15 cm (1.6 cm diameter) at periodic intervals to measure inorganic N and gravimetric water content. Gravimetric water content was determined by oven drying a 4 g homogenized sample at 105 °C for 48 hrs. Inorganic nitrogen was extracted in 0.5 M K_2SO_4, and NH_4 and NO_3 concentrations were determine through colorimetric analysis of samples in 96 well microplates (SpectraMax Plus 384, Molecular Devices, Sunnyvale, CA). NH_4 was determined following Forster (1995) and NO_3 following Miranda et al. (2001). During the summers of 2013 and 2014, we measured net N mineralization using buried open-top soil cores encased in 15 cm (4.5 cm diameter) clear pvc sleeves (Raison et al. 1987, Khanna and Raison 2013), using the inorganic N analysis methods described above.

We collected a variety of data for spring ephemeral (*Erythronium grandiflorum,* and *Ranunculus jovis*) and midsummer species (*Delphium nuttallianum, Hackelia micrantha, Latharus lanszwertii,* and *Mertenia ciliata*). We visited the sites every 3 to 4 days following snowmelt until midsummer species passed peak flowering, typically about the second week of July. We recorded the first flowering date of each species by plot. We counted the number of flowers per plant for *R. jovis* when plants were harvested and we counted the number of flowers plant^{-1} for *E. grandiflorum* by dividing each plot where the species occurred (N=12) into 4 subplots and counting the total number of plants and total number of flowers in each subplot. During peak flowering, we measured the plant height and counted the number of flowers per plant for midsummer species and measured predawn and midday leaf water potential (1505D-EXP pressure chamber, PMS Instrument Company, Albany, OR) for the midsummer species except *D. nuttallianum*. After fruits ripened in 2013 and 2014, we collected the aboveground portion of 2 to 10 individual plants of each species in plots where the species occurred (table 1). Plant materials were dried at 105°C for 24 hrs. We recorded the dry mass of each whole plant and each individual fruit before dissecting each fruit and counting and weighing the seeds. During peak flowering in 2012, we collected leaf tissues samples from axillary leaves at similar heights on midsummer plants in each type of treatment plot: *L. lanszwertii* (N=9), *M. ciliata* (N=9)*, H. micrantha* (N=17). These samples were analyzed for δ^{13}C and C:N ratio using an elemental analyzer and isotope ratio mass spectrometry (SIRFER Lab, Salt Lake City, UT).

Statistical Analysis

Our primary tool for statistical analysis between treatment plots was the mixed-effects linear model regression (lmer) in the lme4 package in R (Bates et al. 2014) with treatment as a fixed effect and year and plot as random effects. We also used two-way repeated measures

ANOVA (aov) in the R base package (R Core Development Team 2014) with treatment and year as factors and plot as subject. We used a paired t-test to compare differences in first-flowering and post-snow-free temperatures between plots. To control for the effect of plant size on seed number, we analyzed seed counts in linear mixed-effects regression with plant dry mass and treatment and as fixed effects and plot and year as random effects. The linear mixed-effects model provides estimates of the coefficient, standard error, and t-value, but not a p-value for parameters. P-values are reported for ANOVA, post-hoc pairwise comparisons, and paired t-tests. To determine which predictor variables best fit the response of plant growth we conducted model selection analysis of mixed-effects linear models with plot, year, and species as random effects and models that combined the fixed effects to represent different growth-limiting scenarios (table 2). We conducted similar model selection analyses for the response variable seeds g^{-1} but we divided species into k-selected (*D. nuttallianum, E. grandiflorum,* and *H. micrantha*) and r-selected (*R. jovis*) species. The k-selected species had significantly fewer seeds g^{-1} than r-selected species, resulting in a bimodal distribution of the combined response variable (model parameters reported in table S2 and S3). We compared model fit using the parameter-number adjusted AIC value, and we determined the model-averaged coefficients for each parameter and interaction (Symonds and Moussalli 2011). Using the model-averaged estimates of the parameter coefficients, we estimated the attributable change in plant growth and seeds g^{-1} by solving the regression equation for the highest and lowest observed value for each individual parameter, while holding all other parameter values constant at the mean value. The attributable change estimate is a useful way of deciphering the estimates of the coefficients when the parameters have been transformed, making the β values difficult to interpret.

Results

Snowmelt timing and early season temperature

The dust treatment advanced the first snow-free date by 4 to 22 days, with significant differences by site and year (table 2). Snowmelt occurred an average of 18 d earlier at the low elevation than at the high elevation sites. We compared temperature and precipitation in the two weeks following snowmelt. Two weeks is the average length of the treatment-induced snow-free interval. The average difference between minimum temperatures following snowmelt in dust and control plots was -3.1 °C ($t = -5.0081$, $df = 11$, $p < 0.001$). Minimum temperatures were on average 3.8 °C lower following snowmelt in the dust plots than the control plots ($t = -4.3053$, $df = 11$, $p = 0.001$). The treatment-caused difference in minimum temperatures after snowmelt was less than the elevation-caused difference, with minimum temperatures at the lower elevation sites being on average 5.2 °C colder than those at high elevation sites in the 2 weeks following snowmelt. Thawing degree days, the sum of average daily temperature for each day with temperatures > 0 °C, accumulated more quickly in control plots following later melt out than in dust plots following early snowmelt, with an average difference of -39.85 degree days ($t = -5.2563$, $df = 11$, $p < 0.001$). This difference in TDD between treatments was similar to the difference in TDD between elevations, with lower elevation sites accumulating and average 39.4 fewer degree days in the two weeks following snowmelt than the high elevation sites. During the 2012 water year, winter snowpack at the Mammoth-cottonwood SNOTEL site was one of the lowest on record (1980-2014), while the 2013 and 2014 water years were much closer to the long-term average and similar to each other in snow accumulation and timing of melt (Fig. S1).

First flowering dates

The average difference between first flowering dates between treatments was 6 days, which was not significantly different from the individual between-year differences for control (mean = 6 days, $p = 0.96$) or dust (mean = 7 days, $p = 0.45$) plots. The between-treatment difference in first-flowering dates was greater for *R. jovis* than for other species (table 4).

Soil moisture, net N mineralization, and soil inorganic N

The effect of early snowmelt on soil moisture was not significant across sites (Conner and Gill, soil moisture chapter). Soil characteristics that affect water holding capacity were more important in determining soil moisture than melt dates, and late spring precipitation that occurred during the treatment-induced snow-free interval (see table 2) rewet the soils and buffered soil moisture from the effects of early snowmelt. We observed net N-mineralization rates ranging between -0.21 and 0.33 $\mu g\ N\ g^{-1}$ soil d^{-1}. We expected drier soil conditions in dust plots to limit nitrogen mineralization compared to control plots, but we observed no difference in soil moisture and no difference in net N mineralization between dust and control treatments ($\beta = 0.04$, SE = 0.13, $t = 0.297$). We did see significantly lower mineralization in the dust-control plots where we added dust after snowmelt ($\beta = -0.28$, SE = 0.14, $t = -2.027$; Fig. 2A and 2B). This drop in net N mineralization in the dust-control plots occurred in the high meadow at the end of summer 2013 and in the low aspen at the beginning of summer 2014. The interaction between treatment and cover type (aspen or meadow) was significant ($\beta = 0.46$, SE = 0.19, $t = 2.352$) and net N mineralization was greater at the high elevation sites that the low elevation sites ($\beta = 0.46$, SE = 0.13, $t = 3.523$). Net N mineralization declined from early to later in the summer at the upper elevation sites in both aspen and meadow during both years ($\beta = -0.25$, SE = 0.07, $t = 3.661$). The initial soil inorganic N, the sum of NH_4 and NO_3 following snowmelt, was higher in 2013 than 2014 (β = -2.73, SE = 1.28, t = -2.138; Fig. 2C and 2D) and was greater in the upper elevation than the lower elevation sites (β = 6.4, SE = 2.95, t = 2.167). The interaction between year and elevation was significant (β = -2.75, SE = 1.8, t = -1.525). The differences in inorganic N pools between cover types were not significant (β = -0.06, SE = 0.13, t = -0.439).

Spring ephemeral flowers, growth, and seeds between years and treatments

For *R. jovis*, we counted the number of flowers when we collected the plants and found an average of 2.7 and 3.3 flowers plant^{-1} in 2013 and 2014 respectively (β = 1.6, SE = 7.6, t = 2.131). There were no differences in flowers plant^{-1} between control and dust treatments (β = -0.17, SE = 0.29, t = -0.606). For *E. grandiflorum*, the average number of flowers plant^{-1} was 1.2, and there was no difference in flowers plant^{-1} between control and dust treatments (β = 1.2, SE = 1.8, t = 0.685). For *R. jovis* plant dry mass was significantly higher in 2014 than 2013 (t = -2.22, df = 25.74, p = 0.03; Fig 3A) with no difference between treatments in either year ($F_{2,71}$ = 0.476, p = 0.62). For *E. grandiflorum* plant dry mass was also significantly higher in 2014 (t = -2.89, df = 70.96, p = 0.005; Fig. 3B) with no difference between treatments in either year ($F_{2,67}$ = 0.308, p = 0.73). For *R. jovis* there was a significant correlation between plant mass (mg) and seed count (β = 1.1, SE = 0.13, t = 8.336), but no difference in seeds mg^{-1} between treatments ($F_{2,71}$ = 0.851, p = 0.43; Fig. 3C). For *E.* grandiflorum, there was also a significant correlation between plant size and seed count (β = 0.06, SE = 0.007, t = 8.751) but no difference in seeds g^{-1} between treatments ($F_{2,67}$ = 0.383, p = 0.68; Fig. 3D).

Midsummer species growth and flower counts between treatments

Midsummer plants differed in height between species ($F_{3,333} = 228.8$, $p < 0.0001$) but not between years within species ($F_{3,333} = 1.463$, $p = 0.22$) nor between treatments in either year ($F_{6,333} = 1.093$, $p = 0.37$; Fig. 4A). The dry mass of individual plants differed between species ($F_{3,69} = 51.447$, $p < 0.0001$) and between years within species ($F_{2,69} = 19.913$, $p < 0.0001$) but not between treatments for any species in either year ($F_{4,69} = 0.231$, $p = 0.92$; Fig. 4B). We expected that growth responses to early snowmelt might influence the number of inflorescences and flowers plant^{-1}. There were significant differences in the average number of inflorescences plant^{-1} between species ($F_{3,333} = 283.6$, $p < 0.0001$) but not between years within any of the species ($F_{3,333} = 1.198$, $p = 0.31$) nor between treatments for any of the midsummer species in either year ($F_{6,333} = 0.456$, $p = 0.85$; Fig. S4A). Neither were there differences in flowers inflorescence^{-1} nor flowers plant^{-1} between treatments (Fig. S4B-C).

Plant water relations in midsummer species

We observed a statistically significant difference in predawn leaf water potential for *M. ciliata* on the first sampling date in 2013 ($F_{2,18} = 3.853$, $p = 0.04$; Fig. S5), but no difference when we sampled two weeks later. There were differences in predawn leaf water potential between years ($F_{1,86} = 22.257$, $p < 0.001$) and between species ($F_{2,86} = 3.529$, $p = 0.03$) but not between treatments ($F_{2,86} = 0.522$, $p = 0.59$). Leaves from midsummer species collected during peak flowering in 2012 showed no difference in δ^{13}C between treatments for *H. micrantha* ($F_{2,13} = 0.103$, 0.90), *L. lanszwertii* ($F_{2,6} = 0.35$, $p = 0.72$), or *M. ciliata* ($F_{2,6} = 0.092$, $p = 0.91$). We found no difference in percent leaf N or C:N ratios for any species.

Factors limiting plant growth

To determine which factors limited plant growth, we conducted model selection using the factors of snow-free date, temperature following snowmelt, growing season average soil water potential, nitrogen, and soil texture. These parameters were combined in multiple regression to represent different growth-limiting scenarios. Of the models tested, we found the best fitting models included snow-free date (which is roughly inverse to growing season length), temperature (thawing degree days in the 2 weeks following snowmelt), temperature plus water potential, snow cover plus water potential, and water potential alone. These models accounted for 98.5 % of the AICc model weight, with the largest weight accounted for in the models of snow-free date and temperature (table 5). The model-averaged coefficients indicate the estimate of the effect that snow-free date, temperature, and water potential had on plant growth and the estimated change in plant growth that may be statistically attributed to the parameter (table 6). Positive growth was associated with later snow-free date, more rapid accumulation of degree days, and water potentials closer to zero. This signifies that larger plants grew in the aspen sites compared to meadows and the largest plants grew in the high elevation aspen sites.

Factors limiting seed production

To determine which factors limited the production of seeds g^{-1} of plant dry we conducted two sets of model selection analyses, one for k-selected species with relatively few (mean = 89.4) seeds g^{-1} (*E. grandiflorum, D. nuttallianum,* and *H. micrantha*) and the other for an r-selected species (*R. jovis*) which was much smaller and produced many more seeds g^{-1} (mean = 1541). In both cases, snow-free date and first-flowering date were the best fit models and parameters to explain changes in seed count (Table 7). These two parameters accounted for 78.2 and 88.8 % of the model weight in k-selected and r-selected species, respectively. Snow-free date and first-flowering date were negatively correlated to seeds g^{-1} in k-selected species and positively correlated to seeds mg^{-1} in *R. jovis* (table 8). Net N mineralization was the parameter with the next largest effect on seed counts in both species groups, and the relationship was positive in both cases (table 8). Water potential and temperature sum had minor effects (table 8).

Discussion

The timing of spring snowmelt in subalpine environments has advanced in western North America in the past several decades and is expected to continue in the future (Cayan et al. 2001, Hamlet et al. 2005, Mote 2006, Pederson et al. 2010). We expect that plant species will respond to these changes individualistically and that those responses will be buffered by environmental and adaptive constraints, including soil water potential, temperature, nutrient acquisition, and fixed duration of growth. In this study, we found that the most important controls over subalpine plant growth across ephemeral and midsummer species were growing season length, determined by the first snow-free and the first flowering dates. We also found that net N mineralization rates were correlated with seed count but not growth. Temperature and water potential had stronger effects on growth than on seed counts and growth was positively correlated to warmer temperatures and less negative water potentials. These results support previous research in suggesting that plant growth is interactively constrained by the opportunity to grow (growing season length) and the favorable conditions to that support growth (Berdanier and Klein 2011).

We presented a growing-season limited scenario, in which vegetation responds to lengthened growing season with increased growth, but in this study we found the opposite response in the subalpine herbaceous species we observed. Specifically, we found that plant dry mass was positively correlated with later snow-free dates. This observation matches spatial patterns in species distribution, in which larger species (*M. ciliata*, *H. micrantha,* and *L. lanszwertii*) occur in sites with later snow-free dates and smaller species occur across the range of snow-free dates. This result suggests that the sheltering effect of snow, which delays growth until spring temperatures become more favorable, is a major driver of plant growth across the landscape (Körner 2006). Rather than finding support for a benefit of early snowmelt and longer growing season, we found that the difference of 1 to 2 weeks induced by our dust treatment made no difference in plant dry mass. We interpret this to mean that plants that have survived the environmental filters, such as temperature and water potential, and have become established in a given location can grow efficiently within the range of conditions associated with a 1 to 2 week difference in snowmelt timing.

The process of filtering species through microclimate and snow-cover distribution may be sensitive to changes snowmelt and may result in range shifts and change plant distributions and plant community composition. Where cold and snow interactively limit plant growth, we expect that larger herbaceous plant will continue to persist in more sheltered sites. Early season temperature may constrain plant growth for herbaceous species by delaying initial growth (Steltzer et al. 2009) or by frost damage to plant and floral tissues (Inouye 2008). Small-statured plants, such as *R. jovis*, take advantage of soil heating and have a structural architecture through which they avoid exposure to the coldest temperatures (Körner 2003). These adaptations permit them to grow on sites with early snowmelt and exposure to colder temperatures. The midsummer species we observed have similar adaptations in the initial stages of growth. *D. nuttallianum, H. micrantha,* and *M. ciliata* begin growth with a cluster of short leaves with a pink or purple color, and for *H. micrantha* and *M. ciliata*, these initial leaves have a downy covering of trichomes. These adaptations likely protect plant tissue through occasional periods of cold that may occur at the beginning of the growing seasons with early snowmelt. However, it is apparent that later snow-free dates offer additional protection to plants that has a greater benefit for growth than the potential for earlier growth in a longer growing season.

We presented alternative growth-limiting scenarios in which temperature, soil moisture, nutrient acquisition, and fixed growth periods limit the benefit plants may obtain from a longer growing season. Our results suggest that temperature limits may be important as a limit to plant distributions and that the rate of accumulation of temperature following snowmelt may have effects on plant growth of about 0.001 g dry mass degree day^{-1}. We also observed that soil water potential limited plant growth with most of the effect being in the water potential range of -0.5 to -0.1 MPa. Plant growth was not N limited but seed counts were. Net N mineralization was positively correlated with soil water potential and mineralization rates declined during the growing season. Other researches have demonstrated that the decline in N mineralization associated with soil drying results from reduced microbial activity and from the accumulation of nitrogen containing solutes in microbial cells as a means of balancing their internal osmotic potential with the increased pull on water from outside the cell in drier soils (Stark and Firestone 1995, Schimel et al. 2007, Schmidt et al. 2007). All of the species we observed demonstrated earlier first flowering dates in association with earlier snow-free dates. This shift indicates that the onset of growth and flowering for these species was not limited by a fixed seasonal cue, such as photoperiod, or that the shift in photoperiod associated with the earlier snow-free and first flowering dates was not less than the required photoperiod (Iler et al. 2013). We harvested plants after fruits ripened and leaves began to senesce. For all the herbaceous species we observed, senesce occurred in early or midsummer. This suggests that, although they may not be limited by a fixed onset of growth, they may be limited by a fixed duration of growth that can shift earlier or later without becoming significantly longer.

The purpose of this study was to determine the effect of early snowmelt on spring ephemeral and midsummer species and we found that across the landscape snowmelt timing and temperature following snowmelt act as important filters for plant species, limiting the distribution of larger species to more sheltered sites with more persistent snow cover. We also found that established species are buffered against changes in growing season length so that they are not significantly hampered nor significantly benefited by a shift in snowmelt timing of about two weeks in years of average snowpack.

Acknowledgements

The authors thank Michael McQueen, Joshua Harvey, Desiree Lindley, and Katie Larson for help with data collection. Funding and research assistance for this project were provided by Decagon Devices Inc. (GA Harris Graduate Research Instrumentation Fellowship 2010), BYU Graduate Studies (Graduate Research Fellowship 2011-2012), Rocky Mountain NASA Space Grant Consortium (Graduate Research Fellowship 2012-2013), and the Charles Redd Center for Western Studies (Summer Graduate Research Fellowship 2014).

References

Aldridge, G., D. W. Inouye, J. R. K. Forrest, W. A. Barr, and A. J. Miller-Rushing. 2011. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. Journal of Ecology **99**:905-913.

Angert, A., S. Biraud, C. Bonfils, C. C. Henning, W. Buermann, J. Pinzon, C. J. Tucker, and I. Fung. 2005. Drier summers cancel out the CO2 uptake enhancement induced by warmer springs. Proc Natl Acad Sci U S A **102**:10823-10827.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenström, Ø. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Response of tundra plants to experimental warming meta-analysis of the International Tundra Experiement. Ecological Monographs **69**:491-511.

Barichivich, J., K. R. Briffa, R. B. Myneni, T. J. Osborn, T. M. Melvin, P. Ciais, S. Piao, and C. Tucker. 2013. Large-scale variations in the vegetation growing season and annual cycle of atmospheric CO2 at high northern latitudes from 1950 to 2011. Glob Chang Biol **19**:3167-3183.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. Linear mixed-effects models using Eigen and S4.

Berdanier, A., and J. Klein. 2011. Growing Season Length and Soil Moisture Interactively Constrain High Elevation Aboveground Net Primary Production. Ecosystems **14**:963-974.

Blankinship, J. C., M. W. Meadows, R. G. Lucas, and S. C. Hart. 2014. Snowmelt timing alters shallow but not deep soil moisture in the Sierra Nevada. Water Resources Research **50**:1448-1456.

Brooks, P. D., D. H. Campbell, K. A. Tonnessen, and K. Heuer. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. Hydrological Processes **13**:2191-2201.

CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. Shifts in flowering phenology reshape a subalpine plant community. Proceedings of the National Academy of Sciences **111**:4916-4921.

Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society **82**:399-415.

Chapin, F. S., and G. R. Shaver. 1985. Individualistic Growth Response of Tundra Plant Species to Environmental Manipulations in the Field. Ecology **66**:564-576.

Day P.R. Particle fractionation and particle-size analysis. pp. 562-566. In: C.A. Black (ed.), Methods of Soil Analysis Part 1. 1965. American Society of Agronomy, Inc. Madison, WI.

DeMarco, J., M. C. Mack, M. S. Bret-Harte, M. Burton, and G. R. Shaver. 2014. Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. Ecosphere **5**:art72.

Dijkstra, F., and W. Cheng. 2008. Increased soil moisture content increases plant N uptake and the abundance of 15N in plant biomass. Plant and Soil **302**:263-271.

EPA (Environmental Protection Agency). 2007. Microwave assisted acid digestion of sediments, sludges, soils, and oils. Method 3051a. Available online at http://www.epa.gov/solidwaste/hazard/testmethods/sw846/pdfs/3051a.pdf. [accessed 27 Jan 2015].

Ernakovich, J. G., K. A. Hopping, A. B. Berdanier, R. T. Simpson, E. J. Kachergis, H. Steltzer, and M. D. Wallenstein. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology **20**:3256-3269.

Farquhar, G., M. O'Leary, and J. Berry. 1982. On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. Functional Plant Biology **9**:121-137.

Forrest, J., D. W. Inouye, and J. D. Thomson. 2010. Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? Ecology **91**:431-440.

Forster, J. C. 1995. Soil nitrogen. Pages 79-87 *in* K. Alef and P. Nannipieri, editors. Methods in Applied Soil Microbiology and Biochemistry. Academic Press, San Diego.

Galen, C., and M. L. Stanton. 1991. Consequences of Emergence Phenology for Reproductive Success in Ranunculus adoneus (Ranunculaceae). American Journal of Botany **78**:978-988.

Galen, C., and M. L. Stanton. 1995. Responses of Snowbed Plant Species to Changes in Growing-Season Length. Ecology **76**:1546-1557.

Groffman, P., C. Driscoll, T. Fahey, J. Hardy, R. Fitzhugh, and G. Tierney. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry **56**:135-150.

Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2005. Effects of Temperature and Precipitation Variability on Snowpack Trends in the Western United States*. journal of climate **18**:4545-4561.

Hu, J. I. A., D. J. P. Moore, S. P. Burns, and R. K. Monson. 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. Global Change Biology **16**:771-783.

Iler, A. M., T. T. Høye, D. W. Inouye, and N. M. Schmidt. 2013. Nonlinear flowering responses to climate: are species approaching their limits of phenological change?

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance on montane wildflowers. Ecology **89**:353-362.

Inouye, D. W., and A. D. McGuire. 1991. Effects of Snowpack on Timing and Abundance of Flowering in Delphinium nelsonii (Ranunculaceae): Implications for Climate Change. American Journal of Botany **78**:997-1001.

Jackson, L. E., and L. C. Bliss. 1984. Phenology and Water Relations of Three Plant Life Forms in a Dry Tree-Line Meadow. Ecology **65**:1302-1314.

Jonas, T., C. Rixen, M. Sturm, and V. Stoeckli. 2008. How alpine plant growth is linked to snow cover and climate variability. Journal of Geophysical Research: Biogeosciences **113**:G03013.

Kennedy, P., and K. Peay. 2007. Different soil moisture conditions change the outcome of the ectomycorrhizal symbiosis between Rhizopogon species and Pinus muricata. Plant and Soil **291**:155-165.

Khanna, P. K., and R. J. Raison. 2013. In situ core methods for estimating soil mineral-N fluxes: Re-evaluation based on 25 years of application and experience. Soil Biology and Biochemistry **64**:203-210.

Körner, C. 2003. Alpine Plant Life. 2 edition. Springer-Verlag, Berlin, D.E.

Körner, C. 2006. Significance of temperature in plant life. Pages 48-66 *in* J. I. L. Morison and M. D. Morecroft, editors. Plant growth and climate change. Blackwell Publishing, Ames, Iowa.

Körner, C., and J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. Journal of Biogeography **31**:713-732.

Kudo, G., and T. Y. Ida. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. Ecology **94**:2311-2320.

Kudo, G., Y. Nishikawa, T. Kasagi, and S. Kosuge. 2004. Does seed production of spring ephemerals decrease when spring comes early? Ecological Research **19**:255-259.

Marks, D., T. Link, A. Winstral, and D. Garen. 2001. Simulating snowmelt processes during rain-on-snow over a semi-arid mountain basin. Annals of Glaciology **32**:195-202.

Martin, M., K. Gavazov, C. Korner, S. Hattenschwiler, and C. Rixen. 2010. Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO2. Global Change Biology **16**:1057-1070.

McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. Ecology **93**:1987-1993.

Miranda, K. M., M. G. Espey, and D. A. Wink. 2001. A Rapid, Simple Spectrophotometric Method for Simultaneous Detection of Nitrate and Nitrite. Nitric Oxide **5**:62-71.

Mote, P. W. 2006. Climate-Driven Variability and Trends in Mountain Snowpack in Western North America*. journal of climate **19**:6209-6220.

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature **386**:698-702.

Neff, J. C., A. P. Ballantyne, G. L. Farmer, N. M. Mahowald, J. L. Conroy, C. C. Landry, J. T. Overpeck, T. H. Painter, C. R. Lawrence, and R. L. Reynolds. 2008. Increasing eolian dust deposition in the western United States linked to human activity. Nature Geosci **1**:189-195.

Olsen, S.R., C.V. Cole, F.S. Watanabe, and L.A. Dean. 1954. Estimation of available phosphorus in soil by extraction with sodium bicarbonate. USDA Cir. No. 939.

Painter, T. H., A. P. Barrett, C. C. Landry, J. C. Neff, M. P. Cassidy, C. R. Lawrence, K. E. McBride, and G. L. Farmer. 2007. Impact of disturbed desert soils on duration of mountain snow cover. Geophys. Res. Lett. **34**:L12502.

Parida, B. R., and W. Buermann. 2014. Increasing summer drying in North American ecosystems in response to longer nonfrozen periods. Geophysical Research Letters **41**:2014GL060495.

Pederson, G. T., S. T. Gray, T. Ault, W. Marsh, D. B. Fagre, A. G. Bunn, C. A. Woodhouse, and L. J. Graumlich. 2010. Climatic Controls on the Snowmelt Hydrology of the Northern Rocky Mountains. journal of climate **24**:1666-1687.

R Core Development Team. 2014. R: A language and environment for statistical computing.*in* R Foundation for Statistical Computing, editor., Vienna, Austria.

Raison, R. J., M. J. Connell, and P. K. Khanna. 1987. Methodology for studying fluxes of soil mineral-N in situ. Soil Biology and Biochemistry **19**:521-530.

Rhodes, J.D. Soluble Salts, pp. 167-179. In: A.L. Page (ed), Methods of Soil Analysis Part 2. 1982. American Society of Agronomy, Inc. Madison, WI.

Rudgers, J. A., S. N. Kivlin, K. D. Whitney, M. V. Price, N. M. Waser, and J. Harte. 2014. Responses of high-altitude graminoids and soil fungi to 20 years of experimental warming. Ecology **95**:1918-1928.

Schimel, J., T. C. Balser, and M. Wallenstein. 2007. MICROBIAL STRESS-RESPONSE PHYSIOLOGY AND ITS IMPLICATIONS FOR ECOSYSTEM FUNCTION. Ecology **88**:1386-1394.

Schmidt, S. K., E. K. Costello, D. R. Nemergut, C. C. Cleveland, S. C. Reed, M. N. Weintraub, A. F. Meyer, and A. M. Martin. 2007. BIOGEOCHEMICAL CONSEQUENCES OF RAPID MICROBIAL TURNOVER AND SEASONAL SUCCESSION IN SOIL. Ecology **88**:1379-1385.

Schoenau, J.J., and R.E. Karamonos. Sodium Bicarbonate Extractable P, K, and N. pp. 51-58. In: M.R. Carter (ed.), Soil Sampling and Methods of Analysis. 1993. Canadian Society of Soil Science. Ottawa, Ontario, Canada.

Stark, J. M., and M. K. Firestone. 1995. Factors for soil moisture effects on activity of nitrifying bacteria. Applied and Environmental Microbiology **61**:218-221.

Steltzer, H., C. Landry, T. H. Painter, J. Anderson, and E. Ayres. 2009. Biological consequences of earlier snowmelt from desert dust deposition in alpine landscapes. Proceedings of the National Academy of Sciences **106**:11629-11634.

Symonds, M. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology **65**:13-21.

Thomson, J. D. 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte.

Walkley, A., and I.A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Science 37:29-38.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of Interannual Climate Variation on Aboveground Phytomass in Alpine Vegetation. Ecology **75**:393-408.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Table S1. Results of dust analysis, physical characteristics, major elements, and trace elements.

Characteristic		**Trace elements**	**µg g^{-1}**
%Sand	72.9	Cu	16.8
%Clay	11.8	Fe	22924
%Silt	15.3	Mg	8678.9
%OM	1.6	Mn	887.3
pH	7.4	S	204.8
		Zn	28.3
Major elements	**µg g^{-1}**	As	1.2
P	27.9	Ba	454.9
K-av	686.7	Cd	3.3
Ca-EX	3146.0	Co	8.8
Mg-EX	169.7	Cr	19.2
K-EX	839.8	Mo	0
Na-EX	21.1	Ni	4.9
total N	893.6	Pb	15
		Se	0
		Si	1834.3
		Sr	251.7
		Ti	2995.1
		V	0

Table 1. Site characteristics and species sampled.

Site type	Sand (%)	Clay (%)	Average θ (%)	SOM (%)	Species sampled
Lower aspen	77.5	4.6	0.143 (0.046)	5.7	*L. lanszwertii* (3 blocks)*, H. micrantha* (3)*, D. nuttallianum* (1)
Lower meadow	70.3	6.3	0.130 (0.029)	3.8	*R. jovis* (2)*, D. nuttallianum* (1), *L. lanszwertii* (1)
Upper aspen	63.2	13.6	0.260 (0.036)	9.5	*H. micrantha* (1)*, Erythronium grandiflorum* (3)*, Mertensia ciliata* (3)
Upper meadow	59.0	13.6	0.153 (0.029)	4.8	*H. micrantha* (1) and *E. grandiflorum* (1)

Note: Gravimetric water content (θ). Soil organic matter (SOM). Plants were sampled in blocks of three treatment plots.

Table 2. Growth limiting scenarios and model parameters for mixed-effects model regression.

Growth-limiting scenario	Model parameters (Fixed effects)	Range of values	Units
Growing season	Snow free day of year	122.5 (11.4) (2-May)	days
Temperature	TDD 14 days	122.3 (37.6)	°C
Soil moisture	Soil water potential	-0.55 (0.59)	MPa
	Soil organic matter	5.9 (2.8)	Percent
	Sand	67.5 (9)	Percent
Nutrient acquisition	Inorganic N	3.1 (1.7)	µg N g^{-1} soil
	Net N mineralization	0.12 (0.09)	µg N g^{-1} soil d^{-1}
Observations	**Random effects**	**Number of Groups**	
240	Species	6	
	Plots	33	
	Years	2	

Note: Thawing degree days (TDD) calculated as the cumulative sum of daily average temperature > 0 °C in the 14 days following the first snow-free date.

Table S2. Growth-limiting scenarios and model parameters for linear mixed-effects regression of seeds g-1 for k-selected species (*D. nuttallianum, E. grandiflorum, H. micrantha*).

Growth-limiting scenario	Model parameters (Fixed effects)	Mean parameter value	Units
Growing season limited	Snow free day of year	140.3 (10.4) (20-May)	days
	First flowering day of year	154.9 (6.5) (4-Jun)	days
Temperature limited	TDD 14 days	134.7 (36.8)	Deg. days
	MinTmin 14 days	-0.68 (4.2)	°C
Soil moisture limited	Soil water potential	-0.63 (0.65)	MPa
Nutrient limited	Inorganic N	3.2 (1.9)	µg N g^{-1} soil
	Net N mineralization	0.13 (0.09)	µg N g^{-1} soil d^{-1}
Control variables	Plant dry mass	1.42 (2.2)	g
Observations	Random effects	Number of Groups	
127	Species	3	
	Plots	27	
	Years	2	

Note: Thawing degree days (TDD) calculated as the cumulative sum of daily average temperature > 0 °C in the 14 days following the first snow-free date. The lowest minimum daily temperature (MinTmin) was the lowest recorded temperature during the 14 days following the first snow free date, which varied by plot.

Table S3. Growth-limiting scenarios and model parameters for linear mixed-effects regression of seeds g-1 for r-selected species (*R. jovis*).

Growth-limiting scenario	Model parameters (Fixed effects)	Mean parameter value	Units
Growing season limited	Snow free day of year	127.6 (8.7) (7-May)	days
	First flowering day of year	128.9 (7.9) (8-May)	days
Temperature limited	TDD 14 days	105.3 (30.0)	Deg. days
	MinTmin 14 days	-2.4 (4.2)	°C
Soil moisture limited	Soil water potential	-0.40 (0.30)	MPa
Nutrient limited	Inorganic N	2.7 (1.3)	µg N g^{-1} soil
	Net N mineralization	0.11 (0.08)	µg N g^{-1} soil d^{-1}
Control variables	Plant dry mass	51.9 (40.6)	mg
Observations	**Random effects**	**Number of Groups**	
69	Plots	7	
	Years	2	

Note: Thawing degree days (TDD) calculated as the cumulative sum of daily average temperature > 0 °C in the 14 days following the first snow-free date. The lowest minimum daily temperature (MinTmin) was the lowest recorded temperature during the 14 days following the first snow free date, which varied by plot.

Table 3. Snow-free dates and precipitation and temperature following snowmelt.

	April 1 SWE (cm)	Dust 1st snow-free date	Control 1st snow-free date	Treatment-induced snow-free interval (days)	Precip during snow-free interval (mm)	Dust 14-day Tmin (°C)	Control 14-day Tmin (°C)	Dust TDD (°C)	Control TDD (°C)	Dust FDD (°C)	Control FDD (°C)
2012											
Lower aspen	16.5	5 April	23 April	18	22	-3.8 (-11.8)	0.54 (-5.7)	38.5	94.9	-10.3	-0.7
Lower meadow	19	5 April	23 April	18	22	-3.8 (-11.8)	0.54 (-5.7)	38.5	94.9	-10.3	-0.7
Upper aspen	39.5	27 April	11 May	14	*13	*-0.1 (-5.7)	1.5 (-2)	88	128.6	-0.7	0
Upper meadow	25.5	27 April	3 May	6	*13	*-0.1 (-5.7)	0.7 (-5.7)	88	110.2	-0.7	0
2013											
Lower aspen	19	29 April	3 May	4	0	-1.4 (-8.9)	1.3 (-4.4)	71.8	105.1	-3.2	0
Lower meadow	21	22 April	14 May	22	28	-3.0 (-8.9)	2.8 (-1.1)	58.7	122	-5.5	0
Upper aspen	43	14 May	29 May	15	43	3.3 (-0.5)	6.6 (-0.5)	101.1	151.2	0	0
Upper meadow	30.5	3 May	17 May	14	36	3.0 (-2.9)	1.8 (-0.5)	97.1	76.6	0	0
2014											
Lower aspen	38.5	21 April	5 May	14	23	-3.0 (-10.9)	-0.7 (-9.1)	58.3	71.1	-10.6	-4.4
Lower meadow	38.5	21 April	13 May	22	51	-3.0 (-10.9)	1.5 (-8.4)	58.3	114.7	-10.6	0
Upper aspen	57	20 May	29 May	9	8	5.6 (1.6)	7.7 (2.6)	133.6	164.8	0	0
Upper meadow	45	5 May	20 May	15	36	-0.5 (-7.6)	5.6 (1.6)	57.6	133.6	-9	0

*Precipitation and air temperature measurements taken from the Mammoth-cottonwood SNOTEL site for lower elevation sites and upper elevation 2012. The Huntington-horse site was established in July 2012 and provided temperature values for upper elevation sites for 2013 and 2014. Temperature values are given as the average with the lowest minimum temperature in parentheses. Thawing degree days (TDD) calculated as the sum of daily average temperatures greater than 0 °C. Freezing degree days (FDD) calculated as the sum of daily average temperatures less than 0 °C.

Table 4. First flowering date and days after snowmelt.

	Control first flowering date	Dust first flowering date	Dust-control first flowering date	Number of plots observed	Between-treatment difference (d)	Control between-year difference (d)	Dust between-year difference (d)
2012					Control-Dust	2012-2013	2012-2013
R. jovis	--	--	--	--	--	--	--
E. grandiflorum	26-May	18-May	26-May	12	8	8*	3
D. nuttallianum	5-Jun	31-May	3-Jun	6	5	6	6
H. micrantha	3-Jun	30-May	3-Jun	18	4	9	8
L. lanszwertii	8-Jun	31-May	4-Jun	6	8	5	15
M. ciliata	11-Jun	2-Jun	11-Jun	9	9	8	8
2013					Control-Dust	2013-2014	2013-2014
R. jovis	14-May	29-Apr	11-May	6	15	2	4
E. grandiflorum	3-Jun	21-May	4-Jun	12	12	1	6
D. nuttallianum	11-Jun	6-Jun	10-Jun	6	5	3	2
H. micrantha	11-Jun	7-Jun	12-Jun	21	4	4	3
L. lanszwertii	13-Jun	15-Jun	17-Jun	9	-2	2	0
M. ciliata	18-Jun	10-Jun	17-Jun	9	8	3	6
2014					Control-Dust	2014-2012	2014-2012
R. jovis	16-May	25-Apr	16-May	6	21	--	--
E. grandiflorum	4-Jun	27-May	4-Jun	12	7	9	9
D. nuttallianum	14-Jun	9-Jun	17-Jun	9	5	9	8
H. micrantha	15-Jun	10-Jun	14-Jun	24	5	13	11
L. lanszwertii	15-Jun	15-Jun	15-Jun	12	0	7	15
M. ciliata	22-Jun	17-Jun	24-Jun	9	5	11	14

*Between-year difference in first flowering dates are given as the average absolute value of the difference between years.

Table 5. Results of model selection for plant growth measured as dry weight of aboveground biomass.

	Num. Par*	AIC	AICc	Delta AICc	AICc Weights
Snow cover	2	456.66	456.90	0.00	0.478
Temperature	2	456.711	456.96	0.05	0.465
Temperature + Water potential (WP)	3	462.979	463.48	6.58	0.018
Snow cover + WP	4	462.98	463.83	6.93	0.015
WP	2	464.65	464.89	7.99	0.009
Snow cover + Nitrogen	4	465.32	466.17	9.26	0.005
Temperature + Nitrogen	4	465.403	466.25	9.35	0.004
Snow cover + WP + Interaction (Int)	3	466.12	466.62	9.71	0.004
Nitrogen (Nminz + InN)	3	467.72	468.22	11.32	0.002
Nitrogen + Int (Nminz * InN)	4	469.97	470.82	13.92	0.000
Temperature + WP + Nitrogen	5	471.557	472.86	15.96	0.000
Nitrogen + WP	4	473.03	473.88	16.97	0.000
Soil texture (Sand + SOM)	3	476.04	476.54	19.64	0.000
Soil texture + Int (Sand * SOM)	4	488.82	489.68	32.77	0.000
Full model	8	488.963	492.31	35.41	0.000

*Number of parameters used to calculate the adjusted AIC (AICc).

Notes: Snow cover represents the square root of the snow free day of year. Temperature represents square root of thawing degree days (TDD) for the 14 days following snowmelt. Water potential represents log(WP * -1), where water potential is the growing season average at 0-15 cm. Initial inorganic nitrogen (InN) is the sum of NH_4-N and NO_3-N following snowmelt. Net N mineralization (Nminz) is the average daily N mineralization rate for the growing season. Texture represents percent sand (Sand) and percent soil organic matter (SOM).

Table 6. Model-averaged parameter estimates from mixed-effects linear model regression of dry mass.

Parameter	Estimate	Observed parameter range	Attributable Δ plant mass
Intercept (log(Dry mass))	-2.8382	0.003 – 11.6 (g)	--
sqrt(Snow free day of year)	0.1592	111 – 155 (d)	0.004 g d^{-1}
sqrt(Thawing degree days)	0.04	56.6 – 175.3 (deg. d)	0.001 g deg. d^{-1}
log(Water potential * -1)	-0.004	-3.09 – -0.01 (MPa)	-0.002 g MPa^{-1}
% Sand	0	--	--
% Soil organic matter	0	--	--
Net N mineralization	0	--	--
Initial N ($NH_4 + NO_3$)	0	--	--

Note: Parameter estimates were used to determine the average change in plant dry mass (Δ plant mass) for each unit of change in the parameter over the range of observed values for that parameter. These calculations were made while holding all other parameters constant at their mean value.

Table 7. Results of model selection for seed g-1 for k-selected species (*D. nuttallianum, E. grandiflorum, H. micrantha*) and seeds mg-1 for r-selected species (*R. jovis*).

k-selected species					
Model	Num. Par	AIC	AICc	Delta AICc	AICc Weights
First flowering date	2	264.633	264.88	0.00	0.476
Snow-free date	2	265.519	265.76	0.89	0.306
Temperature (TDD14days)	2	268.829	269.07	4.20	0.058
Water potential (WP)	2	268.858	269.10	4.22	0.058
Nitrogen (InN + Nminz)	3	270.223	270.72	5.85	0.026
Flowering date + TDD14days	3	270.252	270.75	5.87	0.025
Lowest Tmin	2	270.918	271.16	6.28	0.021
Flowering date + WP	3	270.749	271.25	6.37	0.020
Flowering date + Nitrogen	4	271.888	272.74	7.86	0.009
Nitrogen + WP	4	276.261	277.11	12.23	0.001
Flowering + Nitrogen + WP	5	277.96	279.26	14.39	0.000
Full model	6	283.299	285.17	20.29	0.000
r-selected species					
Model	Num. Par	AIC	AICc	Delta AICc	AICc Weights
Snow-free date	2	35.2517	35.50	0.00	0.726
First flowering date (Flowering)	2	38.2491	38.49	3.00	0.162
Temperature (TDD14days)	2	41.2186	41.46	5.97	0.037
Water potential (WP)	2	41.4345	41.68	6.18	0.033
Flowering + WP	3	42.8806	43.38	7.88	0.014
Flowering + Temperature	3	43.3541	43.85	8.36	0.011
Nitrogen (InN + Nminz)	3	43.8646	44.36	8.87	0.009
Lowest Tmin	2	45.335	45.58	10.08	0.005
Flowering + (Nitrogen)	4	46.0293	46.88	11.38	0.002
Nitrogen + WP	4	48.1993	49.05	13.55	0.001
Flowering + Nitrogen + WP	5	50.0389	51.34	15.85	0.000
Full model	6	54.5982	56.46	20.97	0.000

Notes: The sum of average daily temperatures for days with T > 0 °C in the 14 days following the first snow-free date (TDD14days). The lowest recorded minimum temperature value in the 14 days following snowmelt (lowest Tmin). Initial inorganic N ($NH_4 + NO_3$) (InN) and net N mineralization (Nminz).

Table 8. Model-averaged parameter estimates from mixed-effects linear model regression of seeds g-1 for k-selected species (*D. nuttallianum, E. grandiflorum, H. micrantha*) and seeds mg-1 for r-selected species (*R. jovis*).

k-selected species

Parameter	Estimate	Observed parameter range	Attributable Δ seeds g^{-1}
Intercept (log(Seed g^{-1}))	6.37	1.2 – 341 (seeds g^{-1})	--
sqrt(First flowering day of year)	-0.14	142 – 174 (22-May – 23-Jun)	-0.3 seeds g^{-1} d^{-1}
sqrt(Snow free day of year)	-0.05	111 – 155 (21-Apr – 4-Jun)	-0.12 seeds g^{-1} d^{-1}
Net N mineralization	0.018	-0.21 – 0.29 (µg g^{-1} d^{-1})	1.01 seeds g^{-1} (µg g^{-1} d^{-1})$^{-1}$
log(WP * -1)	-0.002	-3.09 – -0.01 (MPa)	0.09 seeds g^{-1} MPa^{-1}
sqrt(Thawing degree days)	-0.002	56.6 – 175.3 (degree days)	-0.004 seeds g^{-1} deg. d^{-1}
Initial N ($NH_4 + NO_3$)	0	0.82 – 7.4 (µg g^{-1})	--
Lowest Tmin	0	-10.9 – 2.8 (°C)	--

r-selected species

Parameter	Estimate	Observed parameter range	Attributable Δ seeds mg^{-1}
Intercept (log(Seed g^{-1}))	-1.95	0.12 – 3.4 (seeds mg^{-1})	--
sqrt(Snow free day of year)	0.23	111 – 136 (21-Apr – 16-May)	0.03 seeds mg^{-1} d^{-1}
sqrt(First flowering day of year)	0.04	115 – 136 (25-May – 16-May)	0.006 seeds mg^{-1} d^{-1}
Net N mineralization	0.004	0.02 – 0.32 (µg g^{-1} d^{-1})	0.01 seeds mg^{-1} (µg g^{-1} d^{-1})$^{-1}$
sqrt(Thawing degree days)	0.002	58.3 – 145.0 (degree days)	0.0004 seeds mg^{-1} deg. d^{-1}
log(WP * -1)	-0.001	-1.3 – -0.11 (MPa)	0.004 seeds mg^{-1} MPa^{-1}
Initial N ($NH_4 + NO_3$)	0	0.96 – 6.4 (µg g^{-1})	--
Lowest Tmin	0	-10.9 – 2.8 (°C)	--

Note: Parameter estimates were used to determine the average change in plant dry mass (Δ plant mass) for each unit of change in the parameter over the range of observed values for that parameter. These calculations were made while holding all other parameters constant at their mean value. Average seeds g^{-1} was 84.9 for k-selected species and 1541 for r-selected species, equivalent to (1.541 seeds mg^{-1}).

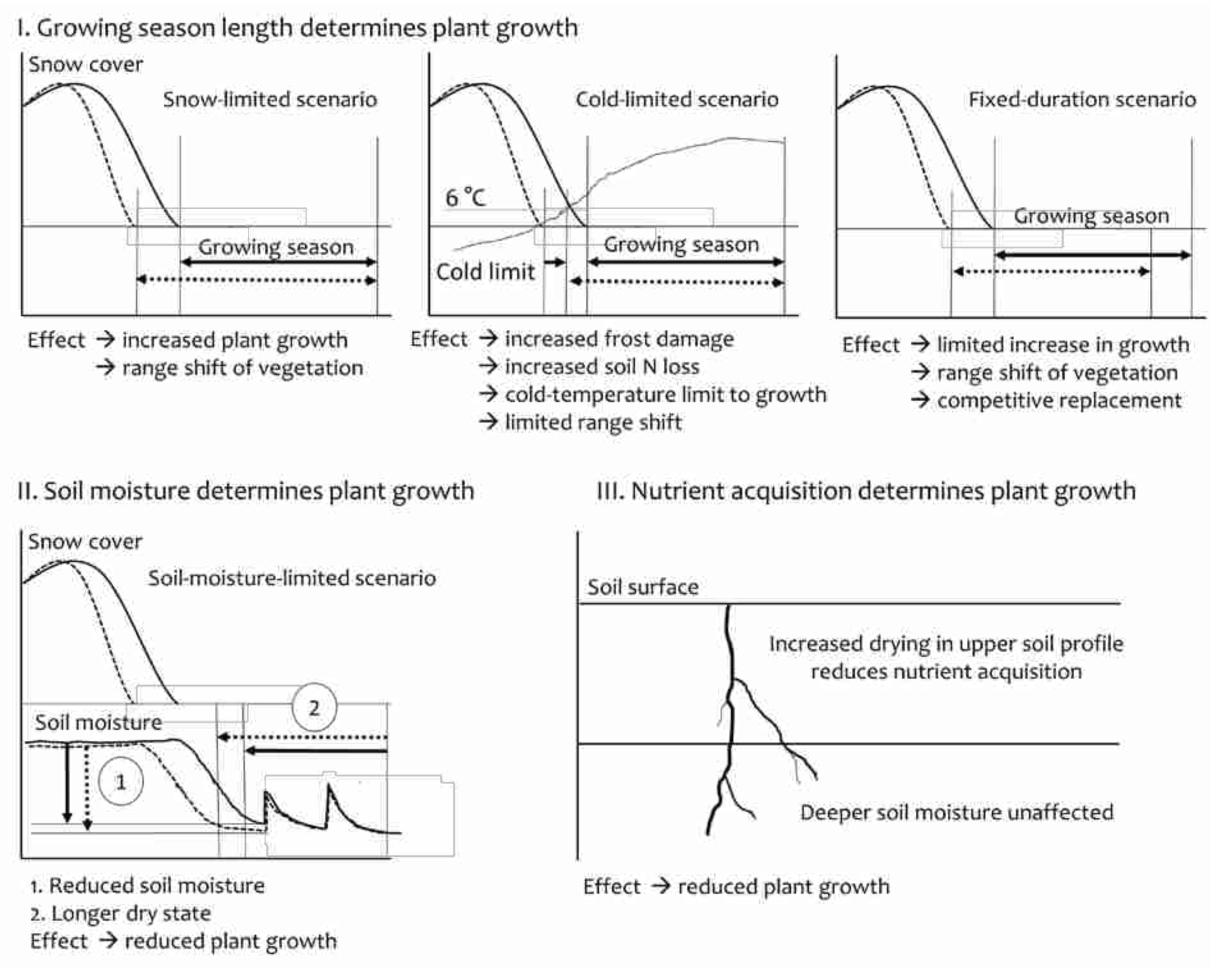


Fig. 1. Growth-limiting scenarios. Three scenarios represent plant growth limited by growing season length (I). In the snow-limited scenario, growing season length is determined by the absence of snow cover alone. In the temperature-limited scenario growth is limited by cold temperature following snowmelt. The limit may be either through a cold-temperature threshold for growth, which averages approximately 6 °C across growth forms, by tissue damaged from freezing, or through the loss of N due to increased mobilization and leaching during snowmelt. In the fixed duration scenario, growing season is limited by a fixed cue, such as photoperiod, or the growing season has a fixed duration that shifts in response to early snowmelt but is not lengthened. In the two alternative scenarios, growth is limited by soil moisture or by nutrient acquisition.

Fig. S1. Study species. These species include spring ephemeral and midsummer species. Spring ephemeral species have reduced vegetative growth and flower number and flower within days of snowmelt. Midsummer species have more vegetative growth, higher flower counts, and flower within weeks after snowmelt.

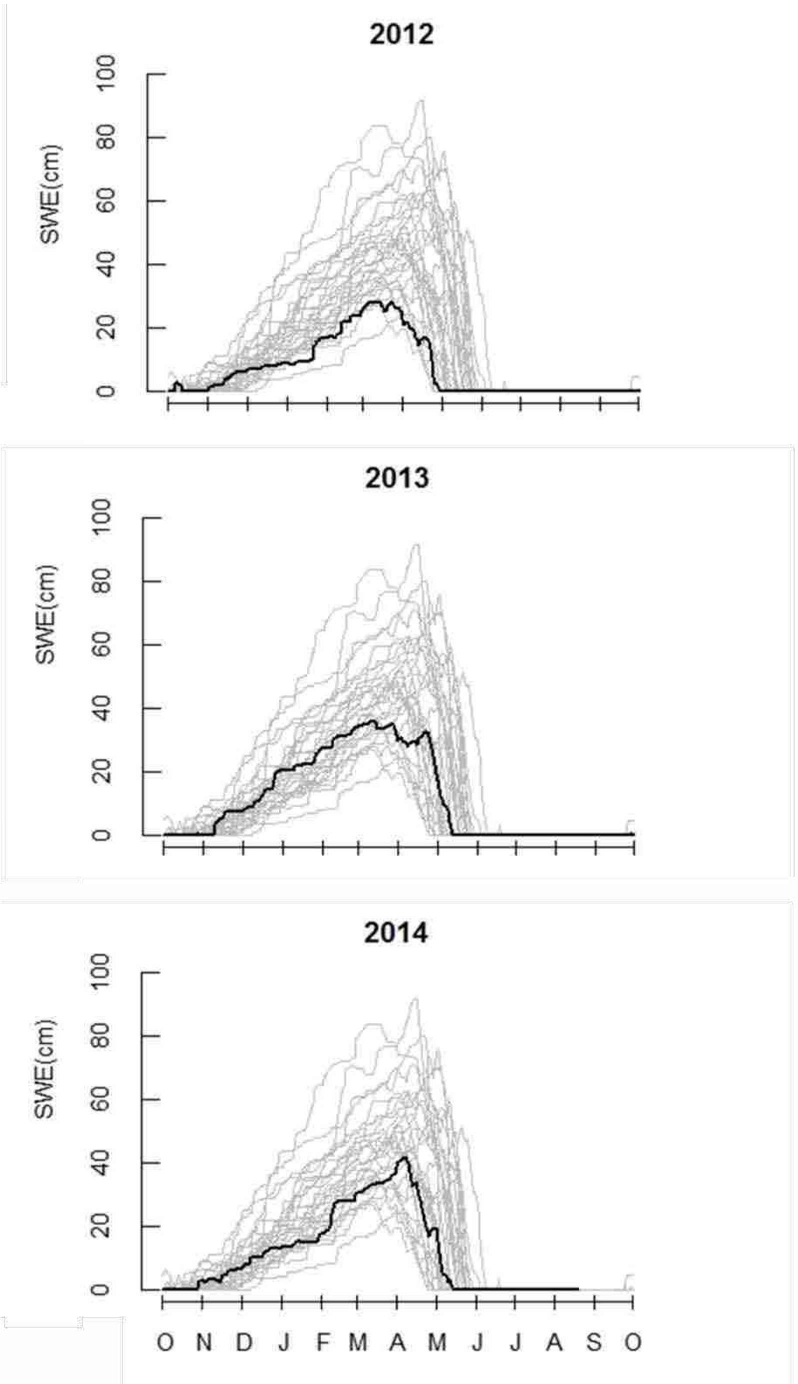


Fig. S2. Snow water equivalent (SWE) in study years (black lines) compared to observed snowpack in years on record (1980-2014) for the NRCS Snowpack Telemetry (SNOTEL) site at Mammoth-cottonwood, approximately 1 km from the lower elevation study sites.

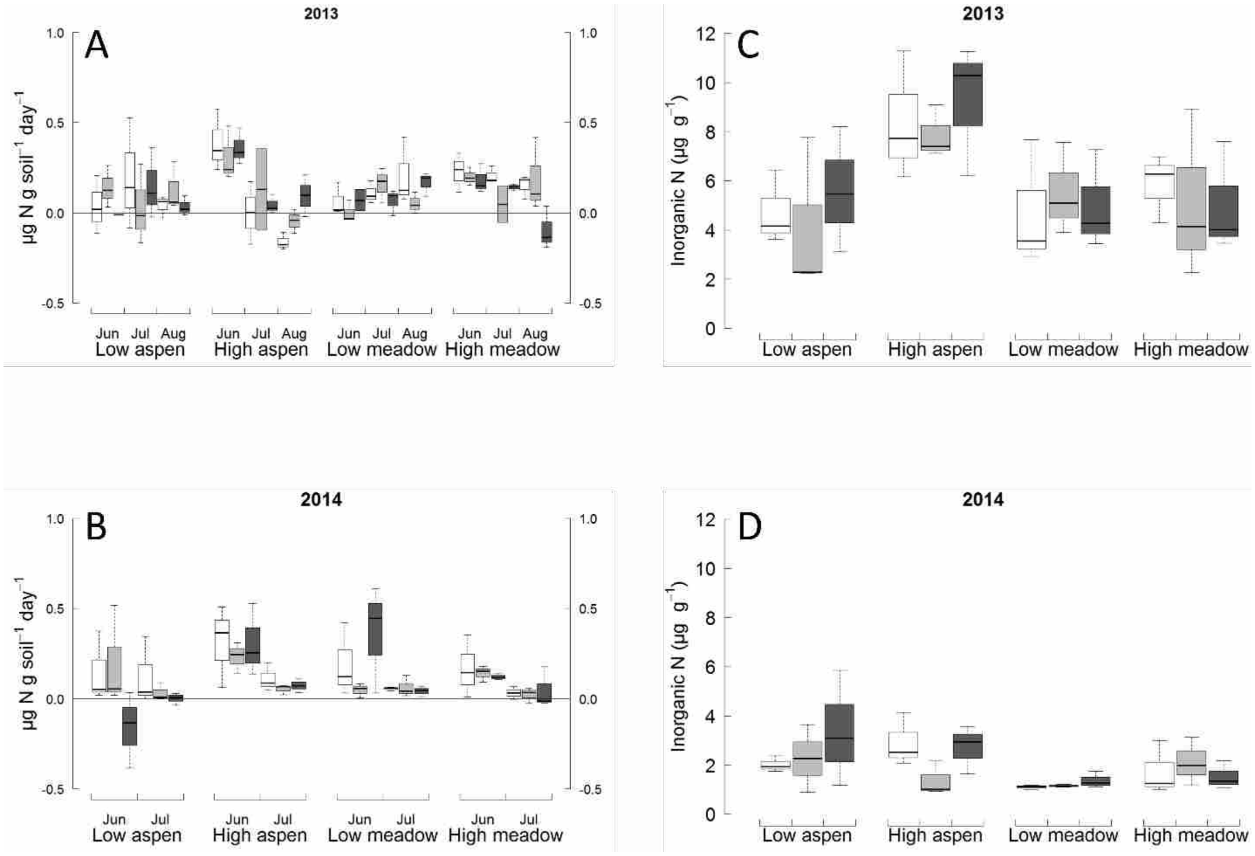


Fig. 2. Net N mineralization (Nminz) for June, July, and August 2013 (A) and June and July 2014 (B), initial inorganic N (InN), the sum of NH_4 and NO_3 following snowmelt in 2013 (C), and 2014 (D). Significant differences were found between sampling dates and year for Nminz and InN. Nminz decreased during the growing season within site types. Dust-control plots had significantly lower Nminz in upper meadow at the end of 2013 and in the lower aspen at the beginning of 2014. Differences between treatments were not significant. InN was higher in the upper elevation sites, but not difference between cover types of treatments.

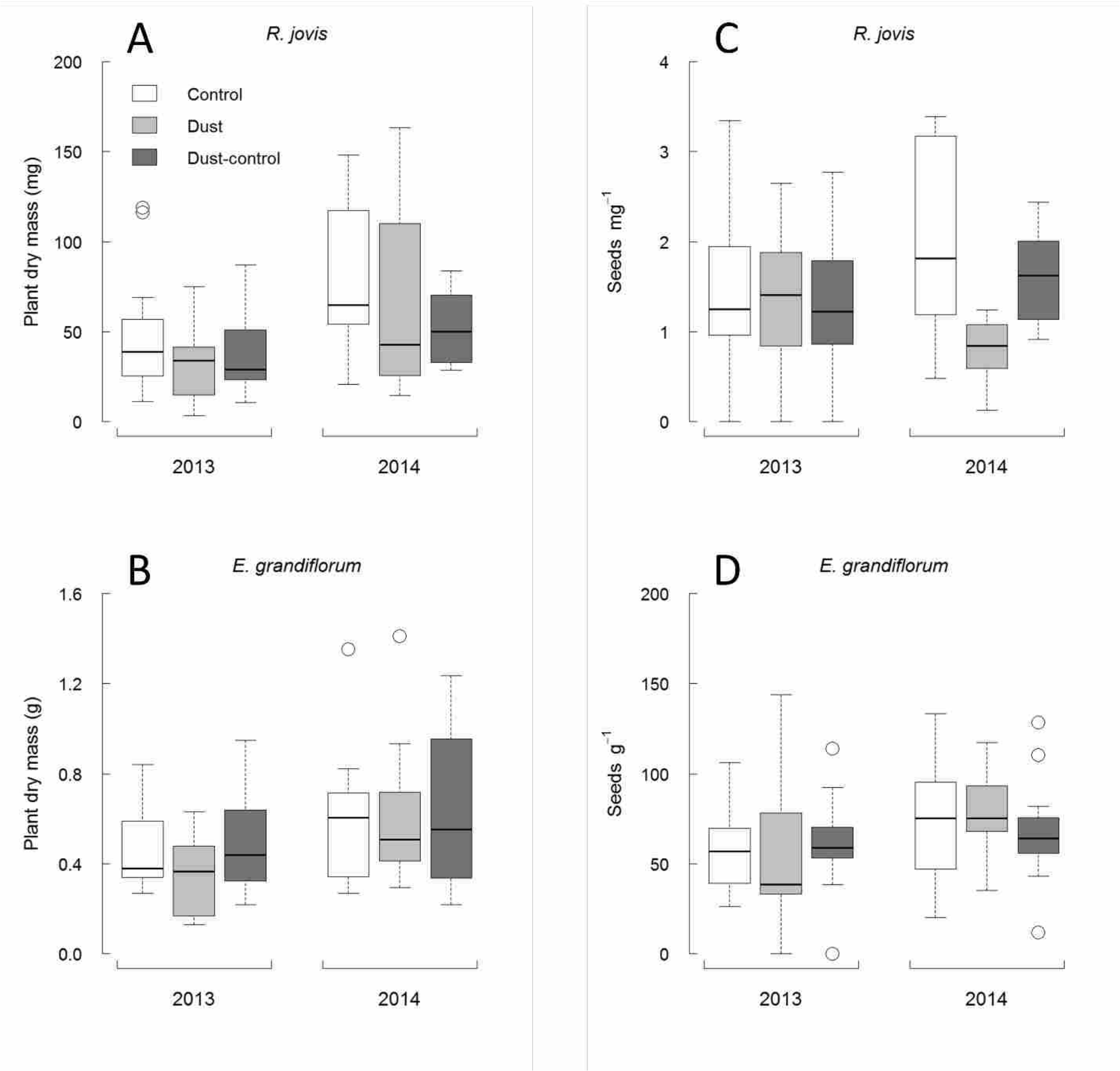


Fig. 3. Between-treatment and between-year comparisons of plant dry mass and seeds g^{-1} for spring ephemeral species *R. jovis* (A and C) and *E. grandiflorum* (B and D). Plant dry mass was significantly higher in 2014 than 2013 for both species. There was no difference in mass or seed counts between treatments.

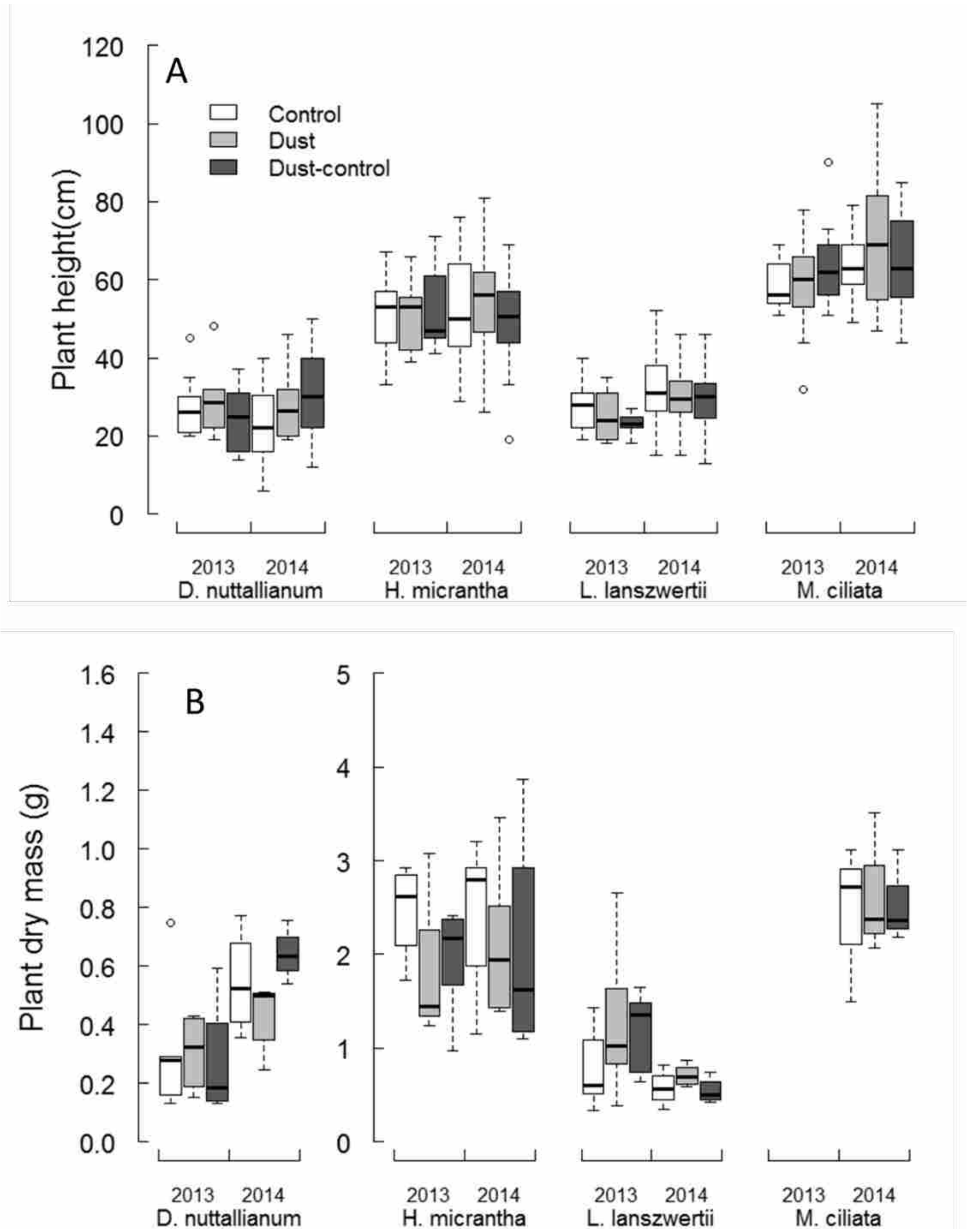


Fig. 4. Between-treatment and between-year comparisons of plant height (A) and plant dry mass (B) for midsummer species. Height and mass were different between species but not between treatments. Height was not different between years though dry mass was.

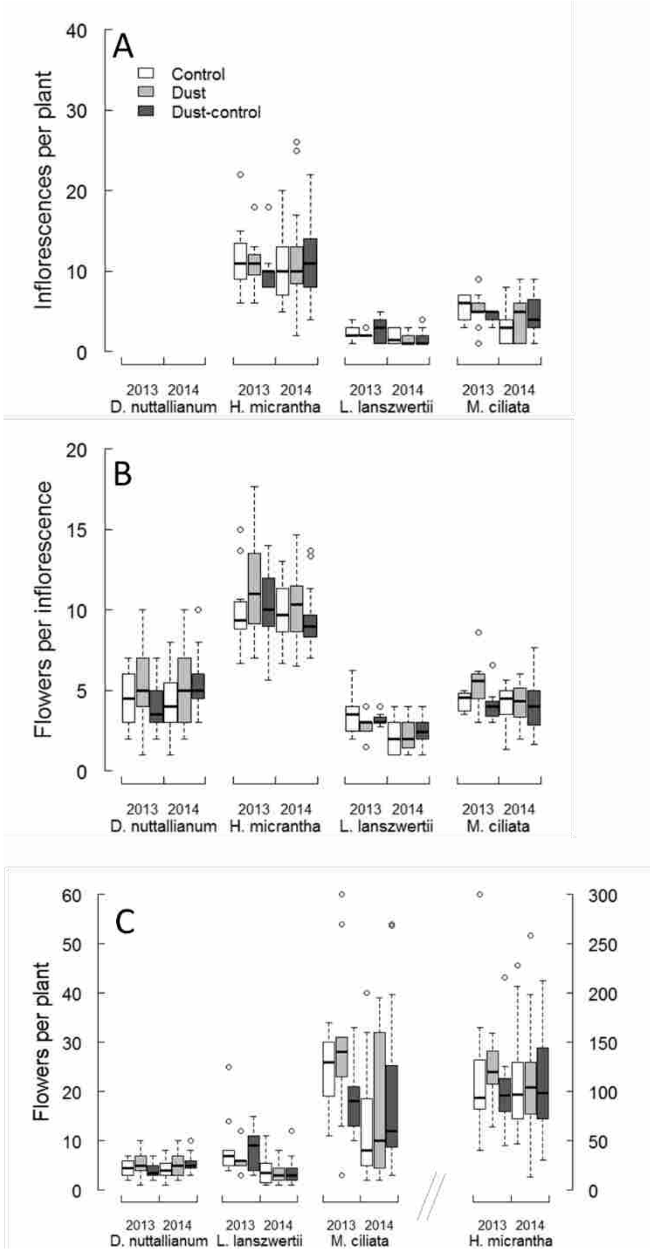


Fig. S4. Between-treatment and between-year comparison of inflorescences plant^{-1} (A), flowers inflorescence^{-1} (B), and flowers plant^{-1} (C). In the inflorescence plant^{-1} figure *D. nuttallianum* is omitted because each plant contains only 1 inflorescence. There were not significant differences between treatments or years.

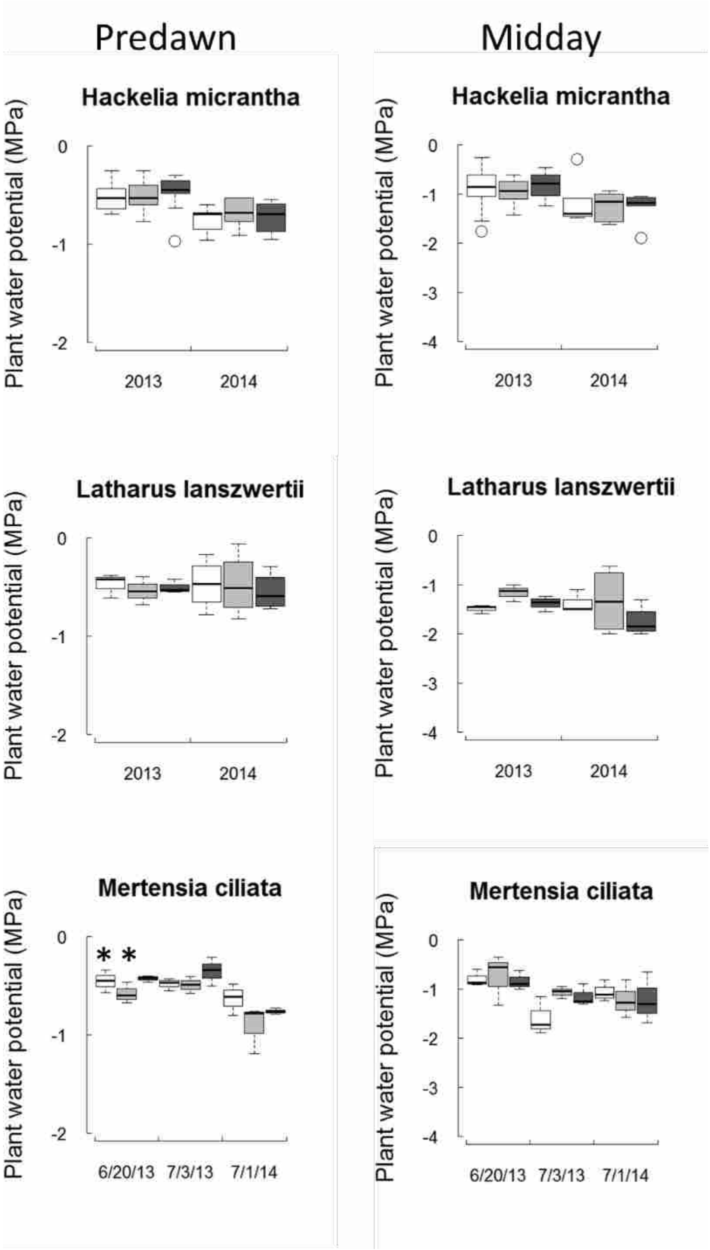


Fig. 5. Between-treatment and between-year comparison of predawn and midday leaf water potential. (*) indicates significant difference at 0.05 level. There were differences between years.

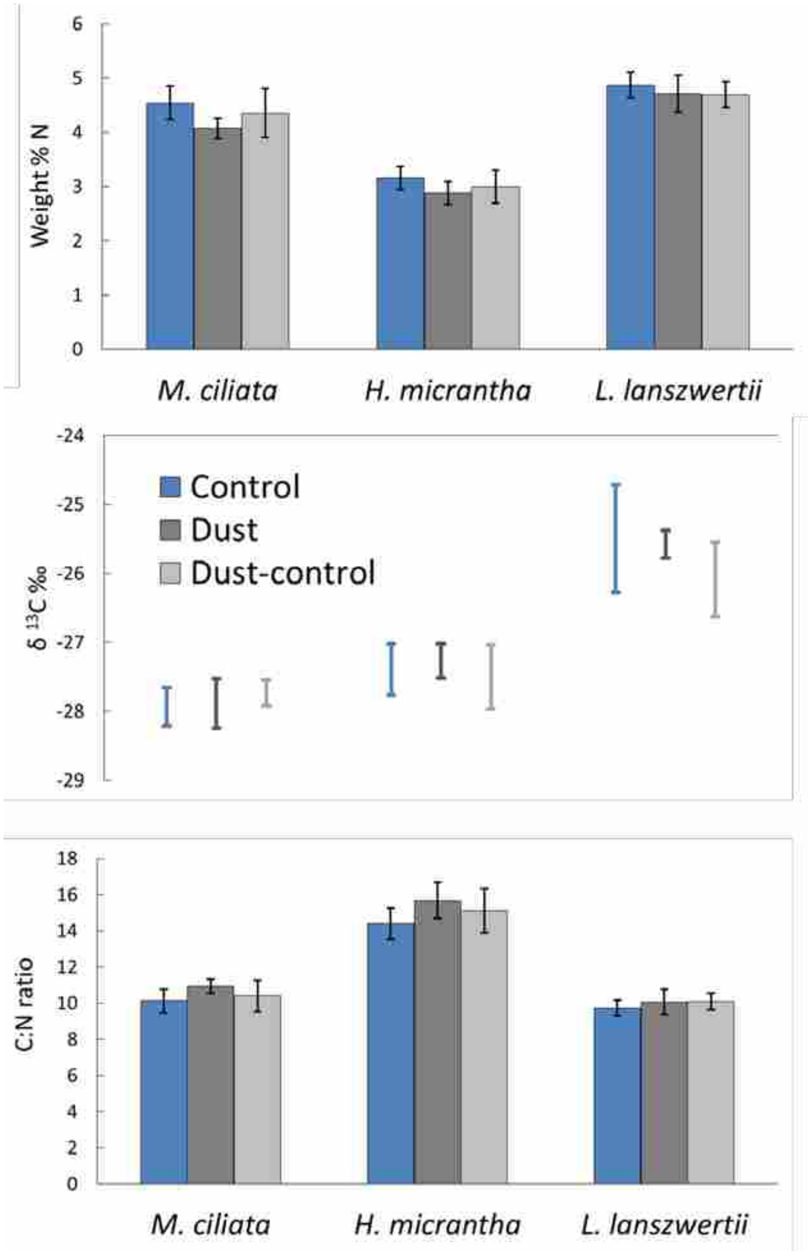


Fig. S5. Percent N, δ^{13}C, and C:N ratio in bulk leaf tissue for midsummer species collected in 2012.

CHAPTER 4

Early snowmelt leads to warmer spring soil temperatures in mid-latitude aspen forest and subalpine meadow: implications for soil carbon cycling

Lafe G. Conner[a], Richard A. Gill[a], Joshua T. Harvey[a]

a. Department of Biology, Brigham Young University, 4102 Life Science Building, Provo, UT 84602, USA

Corresponding author: connerlg@gmail.com

Abstract

Seasonal snow cover influences soil respiration (R_s), microbial biomass, and ecosystem C retention. Many seasonally snow-covered environments have experienced reduced spring snowpack and advance in the timing of spring snowmelt and this trend is expected to continue into the future. Short-term responses to early snowmelt, including bursts in CO_2 flux following freeze-thaw cycles, have been observed, but the effect of these short-term responses on net C storage remains unclear. We present and test three possible alternative early-snowmelt scenarios: warm spring enhanced mineralization, cold spring enhanced mineralization, and cold spring reduced mineralization. We added dust to the snow surface during spring ablation and advanced the timing of snowmelt by an average of 14 days over 3 consecutive years in subalpine meadows and aspen forests in central Utah, USA. We expected early-snowmelt plots to experience deeper freezing and more freeze-thaw cycles than control plots (cold-spring scenarios), but we found early-snowmelt soils were significantly warmer following snowmelt (warm-spring scenario) than neighboring snow-covered soils. We tested for cumulative effects of early snowmelt on ecosystem C stocks including DOC, microbial biomass, and SOC after 3 years. We also observed soil respiration (R_s) during the snow-free period to test for legacy effects of early snowmelt. We found that soil temperature and SOC, in combination, were the best predictors of R_s across all sites, and we did not find evidence of an early snowmelt legacy effect in R_s. We found that microbial biomass, DOC, and SOC remained similar between treatments in the weeks following snowmelt and after 3 years of the study. We conclude that in mid-latitude subalpine ecosystems, early snowmelt is likely to increase R_s compared to snow-covered conditions due primarily to longer snow-free, warm soil conditions but may have limited impact on soil C stocks because plant growth initiation may also respond to warmer spring temperatures.

Keywords

Carbon sequestration, climate change, microbial biomass, snowmelt, soil organic carbon, soil respiration, subalpine

1. Introduction

In seasonally snow-covered ecosystems, the depth and duration of snow cover can significantly influence soil C dynamics and soil CO_2 flux (Blankinship and Hart 2012). The timing of snowmelt and the initiation of the snow-free period in alpine and subalpine environments affect soil moisture and thermal conditions that provide dominant controls over soil C processes (Parton et al. 1987, Neff and Asner 2001, Miller et al. 2007, Lawrence et al. 2009, Fan et al. 2010). After long periods of stable temperature and soil moisture, the initiation of snowmelt creates high-variance conditions for soil moisture with high rates of water flow through the soil profile (McNamara et al. 2005, Maurer and Bowling 2014a). These high flux conditions influence both the amount and the reactivity of the dissolved organic matter pool in soils (Neff and Asner 2001) and influence the osmotic stresses faced by microbes (Schimel et al. 2007, Lawrence et al. 2009, Jefferies et al. 2010). In subalpine environments, soils become snow-free within weeks after the initiation of snowmelt. The rapid change from snow-covered to snow-free soils exposes soil organisms to highly variable diurnal temperatures, while prior to melt the soil temperatures may remain highly stable and near 0 °C (Maurer and Bowling 2014a). The exposure of these soils to freeze-thaw cycles and directional warming as seasons change influences the physiology and metabolism in microbial communities and changes community structure (Miller et al. 2007, Miller et al. 2009, Carbone et al. 2011, Schimel and Schaeffer 2012). For seasonally snow-covered ecosystems, the processes that occur at snowmelt are fundamental to soil C loss and storage, and understanding of these processes and responses is critical as many snow-covered ecosystems are experiencing earlier snowmelt and a decrease in the snow-covered period due to climate change and dust deposition (Painter et al. 2007, Neff et al. 2008, Pederson et al. 2010, Ernakovich et al. 2014, Lawrence et al. 2015).

For decades soil scientists have understood that soil C dynamics are complex processes regulated by physical and biological processes operating on a highly heterogeneous substrate (Parton et al. 1987). To simplify some of this complexity soils are often modeled using multiple interacting pools of C defined by the decay characteristics of the individual pools, presumably due to the physical protection or chemical characteristics of the C in these pools. Most models include one pool that experiences rapid cycling either because it is physically accessible or chemically available for microbial mineralization (Parton et al. 1987, Lawrence et al. 2009). Additional pools include slowly-cycling C, with year to decade-scale turnover times and passive C that is relatively inert. In an effort to better understand controls over C balance, soil C models are beginning to add additional mechanistic understanding of soil C pools and fluxes that separate the active pool in particular into quantifiable pools that are mechanistically important. These models have focused on C pools such as extracellular enzymes (Kelley et al. 2011, Puissant et al. 2015) or on dissolved organic carbon and microbial biomass (Lawrence et al. 2009). With additional information about the structure and dynamics of specific, microbially-relevant pools of C it is hoped that we can better understand the loss or sequestration of C from ecosystems through soil respiration (R_s) or leaching as affected by changes in snowmelt dynamics (Neff and Asner 2001, Fan et al. 2010, Fan et al. 2015).

Snow cover provides insulation from winter freezing and creates an environment in which microorganism remain active (Brooks et al. 1996, Edwards et al. 2007). Winter-time R_s accounts for up to 17% of annual R_s across a variety of high-elevation, temperate sites (McDowell et al. 2000, Brooks et al. 2005, Hirano 2005, Monson et al. 2006, Wang et al. 2010, Warren and Taranto 2011, Wang et al. 2013). The depth of snow determines the degree of insulation, and the removal or reduction of winter snowpack results in colder soil temperatures and deeper freezing in the soil profile (Groffman et al. 2001, Jones et al. 2001, Groffman et al. 2011). Reduced soil temperature associated with snow cover removal can affect the behavior and reduce the abundance of soil arthropods and some types of bacteria and may reduce winter-time R_s by as much as 47% (Edwards et al. 2007, Haei et al. 2011, Aanderud et al. 2013, Bokhorst et al. 2013). Furthermore, changes in winter snow cover may have legacy effects that continue to influence R_s during the spring and summer seasons. In a synthesis of snow manipulation studies, Blankinship and Hart (2012) found that treatments of reduced winter snowpack had limited effect on springtime R_s but reduced summertime R_s by 35%. The reduced summer-time R_s associated with snow removal has been variously attributed to soil moisture limitations from less water input (Blankinship and Hart 2012) and to soil C limitations (Lipson et al. 2000).

Reduced snow cover may increase soil exposure to freeze-thaw cycles (Schimel et al. 2007). Soil freezing lowers the osmotic potential in films of unfrozen water and microbes accumulate compatible solutes within their cells and may alter the structure of their membranes to avoid desiccation during freezing events (Jefferies et al. 2010). Upon thawing, microbes quickly metabolize or expel those solutes, creating the burst of CO_2 that represents both the adjustment of the soil microbial community to changes in osmotic potential and the release of CO_2 temporarily trapped in frozen pockets of soil (Schimel et al. 2007, Jefferies et al. 2010). The magnitude of these temporary bursts of CO_2 decreases after the first FTC. Freezing may also damage fine roots or lyse microbial cells and so increase the substrate, typically in the form of DOC, available to the remaining microbial community (Groffman et al. 2001, Edwards et al. 2007, Haei et al. 2011). The metabolism of this substrate may further increase R_s.

Snow cover may also affect seasonal dynamics in soil microbial biomass (Lipson et al. 2000, Lipson et al. 2002). Beneath the insulating cover of snow, microbial communities in alpine and arctic sites reach a late-winter peak in biomass, which then declines through spring melt as temperatures rise above 0 °C (Brooks et al. 1998, Lipson et al. 2000, Larsen et al. 2007). The spring-time decline in biomass of the microbial community accompanies a shift from a winter community in which fungi greatly outnumber bacteria (4.3:1 fungal:bacterial ratio) to a relatively more even community (1.6:1 summer ratio; (Lipson et al. 2002, Buckeridge and Grogan 2008, Jefferies et al. 2010). Researchers have observed contrasting results of microbial biomass responses to FTCs (Henry 2007) with some studies (Larsen et al. 2002, Larsen et al. 2007) reporting a 30 – 43% reduction in microbial biomass following FTCs, while other studies report that FTCs had no significant impact on miocrobial biomass nor on microbial communities (Koponen et al. 2006, Haei et al. 2011, Aanderud et al. 2013, Wang et al. 2013). The contrasting results reflect differences in methodology and also perhaps differences in freeze thaw tolerance of the microbiota (Walker et al. 2006, Henry 2007).

If reduced snow cover increases freeze-thaw cycles, then the expected result may be a reduction in soil C stocks. However, in a review of several freeze-thaw experiments, Matzner and Borken (2008) concluded instead that greater soil C loss may accompany milder winters with fewer freeze-thaw cycles, while increased freeze-thaw cycles may have on effect or perhaps even a positive effect on ecosystem C storage in spite of the transient bursts of CO_2 that accompany thawing. One of the factors that might make up the difference between net C losses and net C storage are the legacy effects of reduced winter snowpack on summer R_s (ÖQuist and Laudon 2008, Blankinship and Hart 2012).

We had two purposes in this study. First, to determine the net effect of reduced snow cover on the key active C pools of dissolved organic C and microbial biomass, with their integrated impacts on total soil organic carbon. Second, to test for a snow-melt legacy in soil microbial biomass and growing season R_s and determine which site factors were potentially the most important mediators of snow-melt legacy effects. We added dust to the snow surface during spring ablation to reduce the snow albedo and cause more rapid melt, thus advancing the timing of the snow-free date without significantly altering the amount of water added to the system (Maurer and Bowling 2014b). We situated our study at the upper and lower boundaries of aspen (*Populus tremuloides*) in a subalpine watershed in the western Rocky Mountains and included meadow and aspen replicates so that we would have a broad range of site variables to study the factors that mediate snow-cover legacy effects. Matzner and Borken (2008) proposed three alternative hypotheses to characterize the possible responses of soil C to increased freeze-thaw exposure. These hypothetical responses can be characterized by two temperature scenarios and two difference responses to colder temperatures (Fig. 1). Following snowmelt soils may be either warmer or colder than the snow-covered control plots. If soils are warmer in the snow-free treatment plots than in the snow-covered controls, then R_s should be higher in the treatment plots and soil C loss may be enhanced (Warren and Taranto 2011). We named this the warm-spring scenario. The alternative temperature scenario is that soils in the snow-free treatment plots may be colder than the snow-covered control plots. We named this the cold-spring scenario and divided into enhanced and reduced soil respiration scenarios. In the cold-spring enhanced R_s scenario, increased freeze-thaw cycles free additional C substrate and result in greater loss of soil C compared to the control, while in the cold-spring reduced R_s scenario, colder soil temperatures relative to the control reduce overall soil respiration without freeing additional soil C, having the net effect of reduced R_s and greater C storage compared to the control.

2. Methods

2.1. Study area and treatment

We conducted the study in Fairview Canyon on the Wasatch Plateau in central Utah, USA. The experiment includes 12 treatment blocks with 3 treatments per block. Treatments included control, dust addition on snowpack, and dust addition after snowmelt (dust-control). We added dust after snowmelt in dust-control plots to account for effects of fertilization or changes in the soil surface related to the dust treatment but unrelated to snowmelt timing. Beginning in mid-March, we added dust following each major snowfall event at a rate of 50 g m^{-2}, with 4 to 5 applications each year. Dust was collected from an open playa near Kanosh, Utah at a site that land managers identified as a regional dust source (Jeff Gardiner, personal communication). After collection, dust was sieved 0.5 mm and autoclaved to avoid transporting live seeds or microorganisms. We measured the organic C content of the dust using the Walkley-Black method and found it contained 9.3 mg C g^{-1} of dust. Six treatment blocks were located at the lower elevation limit of aspen in the watershed (39°41'N, 111°18'W, 2650 m), and six blocks were located at the upper elevation limit of tree line (39°37'N, 111°18'W, 2900 m). We divided the treatment blocks at each elevation between aspen forest and subalpine meadow. The dominant herbaceous species and soil characteristics differed in each site type (Table 1). Annual precipitation and mean annual temperature during the study varied by elevation and year (Table 2). The 2012 snowpack was one of the lowest since 1981, while 2013 and 2014 were average years for snowpack and snow-free date. The Wasatch Plateau has been grazed seasonally by cattle and sheep for more than 150 years, and we fenced each 5 X 5 m plot to exclude livestock.

2.2. Data Collection

We installed temperature sensors (EC-5, 5TM, 5TE, RT1, ECT; Decagon Devices, Inc., Pullman, WA) at 5 cm depths in at least 1 pair of control and dust plots for each site type and elevation. Sensor readings taken every 30 seconds were averaged over 6 hour intervals. We collected 3 soil cores (1.6 cm diameter X 15 cm depth) from each plot within a few days following snowmelt in 2013 and 2014. In 2014, we collected additional samples at 2 – 3 weeks and 4 – 6 weeks following snowmelt. The core samples from each plot were homogenized. One sample was immediately extracted with Nanopure water in 1:2 weight (g):volume (mL) ratio and a second sample was chloroform fumigated for 5 days and then extracted (Brookes et al. 1985). We filtered the soil solution and two blanks through standard filter paper (VWR Filter quality 413, VWR International, Randor, PA) and stored the filtrate at -20 °C. Prior to analysis, we thawed the samples and filtered them again using 0.45 µm Whatman polyamide membrane filters (Sigma-Aldrich, steinheim, Germany). We added a drop of 6 N HCl to the filtrate, bringing the pH of the solution close to 3. We stored the samples at 4 °C before analyzing them on the Shimadzu TOC-L (Shimadzu Scientific Instruments Inc., Columbia, MD). Soil cores 0-15 cm were collected at weekly intervals during the summer of 2014 to measure gravimetric water content, at the end of the summer the remaining samples were combined, air dried, and ground before analyzing total soil organic carbon by the Walkley-Black method (Walkley and Black, 1934). We measured soil respiration (R_s) in 2012 and the first part of 2013 using an EGM-4 Environmental Gas Analyzer for CO_2 with a soil respiration chamber (PP Systems, Amesbury, MA). In June 2013, we began measuring R_s using the Li-Cor 8100 soil chamber system (Li-Cor Inc., Lincoln, Nebraska) attached to a 20 cm PVC collar. The PVC collars were 10 cm deep and were inserted into wet soil following snowmelt in 2013 and remained in place for the remainder of the experiment. To compare measurements between the EGM-4 and Li-Cor systems we measured respiration in 15 plots with each system with approximately 3 - 4 minutes between measurements and placing the EGM 4 soil chamber in the center of the 20 cm PVC collar. We compared the resulting measurements and found them to be highly correlated (r = 0.91). We found that EGM 4 measurements > 6 µmol m^{-2} s^{-1} were not correlated with the comparison Li-Cor measurements, so we dropped EGM 4 data points > 6 from the analysis (n=4). Removing these 4 data points did not change the estimates of the linear mixed-effects regression.

2.3. Statistical analyses

To make comparisons between means across factors of elevation, cover, date, and treatment we used a linear mixed-effects regression model (lmer) from the lme4 package in R (Bates et al. 2014). We included plot as a random factor to account for repeated sampling of the same plot; this model construction is similar to a repeated measures ANOVA. The outputs of the lmer include estimates of the coefficients, standard errors, and a t value. To obtain a p value with the mixed-effects model we creates an object of the lmer and ran it through the anova command in the stats package (R Core Development Team 2014), which provides degrees of freedom and an F statistic, and through the Anova command in the car package (Fox and Weisberg 2011), which provides a Chisquare estimate of the type II Wald Chisquare test and a p value. We used this combination of statistical analyses to determine significant differences in the response between factors and significant interactions between factors, and we report these results in table form. To isolate individual differences between means, we used individual pair-wise comparisons of paired t-tests and the Holm adjustment method for calculating p value with multiple comparisons (Holm 1979).

Using the soil respiration data, we constructed a series of linear mixed-effects regression models. The first set of models included singular and multiple regression models comprised of the parameters *cover, elevation, temperature, log(water potential), SOC, DOC, days snow free,* and *treatment*. We included models with and without the interaction terms. Both cover and elevation were included as binary factors, meadow or aspen and upper or lower. We used the log(R_s) as the response variable. We used the AICc values to identify best-fitting models and calculated the model-averaged coefficients (Symonds and Moussalli 2011) to determine the model that provided the best prediction of observed R_s. Taking the model-averaged coefficients, we calculated the exponential regression function for the effect of temperature and SOC on R_s. These calculations were made by varying temperature and SOC values across the range of observed values while keeping all other model parameters constant at the mean observed value.

3. Results

3.1. Soil temperature

We compared soil temperature at 5 cm depth in paired time series from dust and control plots. In all cases we found the soils were warmer in the snow-free plots than in the snow covered plots during the treatment-induced snow-free interval (TSI), even though above ground air temperatures often fell below 0 °C during the TSI (Table 3). The number of days with above ground air temperatures falling below 0 °C decreased when melt occurred in later in the season (May versus April melt). At 5 cm depth, the average minimum temperature reached at a site during the snow-free interval was 0.4 °C warmer in the snow-free plots than in adjacent snow-covered plots, while the average maximum temperature reached at a site was 11.6 °C warmer (Table 4). The sum of average daily temperature during the TSI was greater in the snow-free plots than the snow-covered plots by 56.1 degree days.

3.2. Soil Respiration

We compared R_s between treatments using a linear mixed-effects model regression with fixed effects of treatment, cover, elevation, and date and with plot as a random effect. We observed significant differences in R_s between cover types (aspen = 2.99 (±1.2) μ mol C m^{-2} s^{-1}, meadow = 2.14 (±1.2)) and between dates but not between treatments or between upper and lower elevations (Table 5). The linear mixed-effects regression model comprised of temperature and SOC provided the best fit to the observed R_s data and accounted for 72.6 % of the model weight (Table 6). The model with cover, temperature, and SOC accounted for 21.5 % of the model weight, and all of the remaining model combinations accounted for only 5.9 % of the model weight. We used the model averaged estimates (Table 7) to determine the individual effects of temperature and soil organic carbon on R_s (Fig. 2). The effect of temperature on R_s represents a Q_{10} temperature coefficient of 1.18 for soil temperature measured at 0 – 5 cm. By comparison, the rate of increase in R_s with increasing SOC between sites had an effect on R_s that was nearly 4 times greater than the temperature effect.

3.3. DOC and microbial biomass

We compared microbial biomass C (MBC) and water-extractable, non-purgeable organic C (DOC) between treatments, elevations, and cover types at three 2-week intervals following snowmelt in 2014. We found significant differences ($p < 0.001$) in MBC between aspen (31.1 ± 11.5 µmol C g^{-1} soil) and meadow (14.7 ± 8.3 µmol C g^{-1} soil; Fig. 3A), and MBC was significantly different across sampling dates (Fig. 3B). The two-way interaction between elevation and date was significant as were the three-way interactions between treatment, date, and elevation and between treatment, date, and cover and the four-way interaction between treatment, date, elevation, and cover (Table 8). We used individual pairwise comparisons of paired t-tests to determine significant differences in mean MBC and DOC between treatments and dates within each elevation-cover type. DOC was higher ($p = 0.002$) in aspen (3.89 ± 1.2 µmol C g^{-1} soil) than in meadow (3.24 ± 1.3 µmol C g^{-1} soil), but there were no differences in DOC between elevations, treatments, or sampling dates (Fig. 3CD).

3.4. Soil organic C final

We compared final SOC at the end of the 3-year experiment. SOC was significantly different between cover type ($F_{1,24} = 22.088$, $p < 0.001$) and between elevations ($F_{1,24} = 8.407$, $p = 0.008$) but not between treatments ($F_{2,24} = 1.187$, $p = 0.322$; Fig. 4). We observed an average of 5.5 (± 1.7) kg C m^{-2} in the aspen soils and 3.8 (± 0.9) kg C m^{-2} in the meadow. The upper elevation sites had 5.2 (± 1.6) kg C m^{-2} compared to 4.1 (± 1.4) kg C m^{-2} in the lower elevation.

4. Discussion

To date, much of the emphasis in research of ecosystem effects of early snowmelt have emphasized the exposure of seasonally snow-covered ecosystems to colder temperatures and more frequent and severe freeze-thaw events (Groffman et al. 2001, Matzner and Borken 2008, Groffman et al. 2011, Durán et al. 2014). The paradoxical occurrence of colder soils in a warmer world (Groffman et al. 2001) can affect ecosystem C cycling and result in either more or less soil C storage (Matzner and Borken 2008). In this experiment we tested for the effects of early snowmelt on total soil organic C, post-snowmelt microbial biomass, dissolved organic carbon, and soil respiration. We found that R_s and microbial biomass varied by sampling date, confirming that both measurements responded to short-term changes in the environment or substrate. The highest microbial biomass was observed directly following snowmelt and declined later in the summer. We found that DOC, for the most part, remained similar across sampling dates and between treatments in any given site type. After 3 years of the experiment, there were no differences in DOC or SOC between treatments.

Soil respiration has been shown to account for a significant fraction of annual R_s in seasonally snow-covered ecosystems, and R_s has been observed to peak in the growing season when plant activity is greatest and temperatures are warmest (Wang et al. 2010, Wang et al. 2013). ÖQuist and Laudon (2008) reported that shallow snow cover during the winter led to reduced respiration during the growing season in a Norway spruce stand in Sweden. They found that growing-season respiration decreased with maximum soil frost depth during the previous winter. We expected our temperature time-series data to show colder temperatures and more frequent freezing in early-snowmelt compared to control plots. However, we found that early snowmelt led to warmer temperatures in early-snowmelt plots across site types and years, while extended snow cover in control plots chilled soils longer and possibly delayed the growing season increase in R_s. We found no evidence of a snow-melt legacy effect on soil respiration during the snow free period (i.e., no difference in R_s between treatments), though we did not measure or estimate cumulative R_s and we did not measure R_s beneath snow. The cumulative effect of early snowmelt in our study was likely to be increased C mineralization due to significantly more days with warmer temperature in early-snowmelt compared to control plots. We saw no snowmelt legacy effect on microbial biomass following snowmelt, and multiple snow-removal studies report that summer microbial biomass can fully recover from reduced winter snow cover (Groffman et al. 2001, Aanderud et al. 2013). Our sites did not experience increased freeze-thaw cycles due to early snowmelt, and freeze-thaw experiments are beginning to show that some microbial biomass and microbial communities are resistant or resilient to FTCs (Haei et al. 2011).

We did find that summer R_s was most sensitive to changes in temperature and to plot-level differences in SOC. This finding supports similar conclusions about the primary drivers of R_s in forested montane ecosystems (Buchmann 2000, Raich et al. 2002, Lavigne et al. 2004, Scott-Denton et al. 2006). We also found that R_s over the summer season was not well explained by soil water potential, which may be in line with Blankinship and Hart (2014) who found that water potential was not a good predictor of CO_2 flux across a soil moisture gradient in a subalpine meadow and that SOC concentration and plant species richness were the primary drivers of R_s. In our experiment, the highest R_s rates occurred in high elevation aspen sites. These sites experience prolonged snow cover compared to lower elevation and meadow sites and have higher SOC concentrations.

We began the study with three conceptual ecosystem C responses to early snowmelt. Our temperature data point toward the warm-spring scenario and do not support either the cold-spring scenario. Thought we did not measure the cumulative R_s nor compare R_s beneath snow cover to R_s in exposed sites, we did measure the difference in rapid-turnover and slow-turnover C stocks. Early snowmelt did not change the concentration of DOC or SOC after 3 years of the experiment. This result may indicate that enhanced C mineralization resulting from a warm-spring scenario was compensated for by microbial activity under the reference snowmelt regime. We would expect this compensation to occur if microbial activity in late winter and early spring was substrate limited, which some researchers have suggested it may be (Lipson et al. 2000).

Through this study we observed the effects of climate change on a temperate subalpine ecosystem with a continental climate regime. Expected early snowmelt would influence ecosystem C storage though enhanced or reduced C mineralization. The differences in C cycling and storage that we did see where predominantly through spatial variation in SOC related to plant community. In meadows, with lower SOC, greater exposure, less herbaceous vegetation, we found consistently lower R_s than aspen communities. Ultimately, if climate change is going to have a substantial influence on subalpine C stocks it will likely be through extending the period of warm soil temperatures and shifting vegetation. It is somewhat counterintuitive that the highest respiration is found on the sites with greatest C stocks, but this could be because they because had a higher net primary production, a shorter snow-free period, and remained wet through much of the growing season.

The results of this study contribute to the resolution of an apparent discrepancy between short-term and long-term ecosystem C responses to early snowmelt. Short-term responses, including enhanced mineralization due to greater accumulation of warm temperature days or perhaps due to increased FTCs, may be compensated for through longer-term ecosystem activity, the result of this compensation being a neutral effect of early snowmelt on DOC and SOC pools. We expect that these findings may apply to ecosystems that experience substrate limited R_s during winter-spring transition and should be tested in other ecosystems and with C additions to determine the extent of substrate limitation and the potential for microbial activity to compensate for short-term differences in C mineralization.

Acknowledgements

The authors wish to thank Michael McQueen, Desiree Lindley, and MacKenzie Mayo for help collecting data and analyzing soil samples, Rachel Buck and the BYU Environmental Analytics lab for consultation and use of instruments, Debbie Rigby and Zach Anderud for help with analysis methods, and Jayne Belnap, David Bowling, Samuel St. Clair, and Roger Koide for consultation on the design of the snow manipulation experiment. We would like to thank Jeff Gardiner (BLM) for help locating the dust source and for permission to collect dust and the Manti-La Sal National Forest for permission to conduct research in Fairview Canyon. Funding for this research was provided by the GA Harris Graduate Research Instrumentation Fellowship (Decagon Devices, Inc.), Brigham Young University Graduate Studies Research Fellowship, Brigham Young University Mentoring Environment Grants, NASA Rocky Mountain Space

Grant Consortium Graduate Research Fellowship, and the Charles Redd Center for Western Studies Summer Research Fellowship.

References

Aanderud, Z. T., S. E. Jones, D. R. Schoolmaster Jr, N. Fierer, and J. T. Lennon. 2013. Sensitivity of soil respiration and microbial communities to altered snowfall. Soil Biology and Biochemistry **57**:217-227.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. Linear mixed-effects models using Eigen and S4.

Blankinship, J. C., and S. C. Hart. 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere **3**:art1.

Blankinship, J. C., and S. C. Hart. 2014. Hydrological Control of Greenhouse Gas Fluxes in a Sierra Nevada Subalpine Meadow. Arctic, Antarctic, and Alpine Research **46**:355-364.

Bokhorst, S., D. B. Metcalfe, and D. A. Wardle. 2013. Reduction in snow depth negatively affects decomposers but impact on decomposition rates is substrate dependent. Soil Biology and Biochemistry **62**:157-164.

Brookes, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry **17**:837-842.

Brooks, P., M. Williams, and S. Schmidt. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. Biogeochemistry **32**:93-113.

Brooks, P. D., D. McKnight, and K. Elder. 2005. Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. Global Change Biology **11**:231-238.

Brooks, P. D., M. W. Williams, and S. K. Schmidt. 1998. Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. Biogeochemistry **43**:1-15.

Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in Picea abies stands. Soil Biology and Biochemistry **32**:1625-1635.

Buckeridge, K. M., and P. Grogan. 2008. Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. Applied Soil Ecology **39**:210-222.

Carbone, M. S., C. J. Still, A. R. Ambrose, T. E. Dawson, A. P. Williams, C. M. Boot, S. M. Schaeffer, and J. P. Schimel. 2011. Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration. Oecologia **167**:265-278.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, M. J. Mitchell, and P. H. Templer. 2014. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Global Change Biology **20**:3568-3577.

Edwards, A. C., R. Scalenghe, and M. Freppaz. 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. Quaternary International **162–163**:172-181.

Ernakovich, J. G., K. A. Hopping, A. B. Berdanier, R. T. Simpson, E. J. Kachergis, H. Steltzer, and M. D. Wallenstein. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biology **20**:3256-3269.

Fan, Z. S., J. C. Neff, and N. P. Hanan. 2015. Modeling pulsed soil respiration in an African savanna ecosystem. Agricultural and Forest Meteorology **200**:282-292.

Fan, Z. S., J. C. Neff, and K. P. Wickland. 2010. Modeling the Production, Decomposition, and Transport of Dissolved Organic Carbon in Boreal Soils. Soil Science **175**:223-232.

Fox, J., and S. Weisberg. 2011. An {R} Companion to Applied Regression, Second Edition. Sage, Thousand Oaks, CA.

Groffman, P., C. Driscoll, T. Fahey, J. Hardy, R. Fitzhugh, and G. Tierney. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry **56**:135-150.

Groffman, P., J. Hardy, S. Fashu-Kanu, C. Driscoll, N. Cleavitt, T. Fahey, and M. Fisk. 2011. Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape. Biogeochemistry **102**:223-238.

Haei, M., J. Rousk, U. Ilstedt, M. Öquist, E. Bååth, and H. Laudon. 2011. Effects of soil frost on growth, composition and respiration of the soil microbial decomposer community. Soil Biology and Biochemistry **43**:2069-2077.

Hirano, T. 2005. Seasonal and diurnal variations in topsoil and subsoil respiration under snowpack in a temperate deciduous forest. Global Biogeochemical Cycles **19**:GB2011.

Holm, S. 1979. A Simple Sequentially Rejective Multiple Test Procedure. Scandinavian Journal of Statistics **6**:65-70.

Jefferies, R. L., N. A. Walker, K. A. Edwards, and J. Dainty. 2010. Is the decline of soil microbial biomass in late winter coupled to changes in the physical state of cold soils? Soil Biology and Biochemistry **42**:129-135.

Jones, H. G., J. W. Pomeroy, D. A. Walker, and R. W. Hoham, editors. 2001. Snow ecology: An interdisciplinary examination of snow-covered ecosystems. Cambridge University Press, Cambridge.

Kelley, A. M., P. A. Fay, H. W. Polley, R. A. Gill, and R. B. Jackson. 2011. Atmospheric CO2 and soil extracellular enzyme activity: a meta-analysis and CO2 gradient experiment. Ecosphere **2**.

Larsen, K., P. Grogan, S. Jonasson, and A. Michelsen. 2007. Respiration and Microbial Dynamics in Two Subarctic Ecosystems during Winter and Spring Thaw: Effects of Increased Snow Depth. Arctic, Antarctic, and Alpine Research **39**:268-276.

Lavigne, M. B., R. J. Foster, and G. Goodine. 2004. Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. Tree Physiol **24**:415-424.

Lawrence, C. R., J. W. Harden, X. M. Xu, M. S. Schulz, and S. E. Trumbore. 2015. Long-term controls on soil organic carbon with depth and time: A case study from the Cowlitz River Chronosequence, WA USA. Geoderma **247**:73-87.

Lawrence, C. R., J. C. Neff, and J. P. Schimel. 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. Soil Biology & Biochemistry **41**:1923-1934.

Lipson, D. A., C. W. Schadt, and S. K. Schmidt. 2002. Changes in Soil Microbial Community Structure and Function in an Alpine Dry Meadow Following Spring Snow Melt. Microbial Ecology **43**:307-314.

Lipson, D. A., S. K. Schmidt, and R. K. Monson. 2000. Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. Soil Biology and Biochemistry **32**:441-448.

Matzner, E., and W. Borken. 2008. Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. European Journal of Soil Science **59**:274-284.

Maurer, G. E., and D. R. Bowling. 2014a. Seasonal snowpack characteristics influence soil temperature and water content at multiple scales in interior western U.S. mountain ecosystems. Water Resources Research **50**:5216-5234.

Maurer, G. E., and D. R. Bowling. 2014b. Dust effects on snowpack melt and related ecosystem processes are secondary to those of forest canopy structure and interannual snowpack variability. Ecohydrology:n/a-n/a.

McDowell, N. G., J. D. Marshall, T. D. Hooker, and R. Musselman. 2000. Estimating CO2 flux from snowpacks at three sites in the Rocky Mountains. Tree Physiology **20**:745-753.

McNamara, J. P., D. Chandler, M. Seyfried, and S. Achet. 2005. Soil moisture states, lateral flow, and streamflow generation in a semi-arid, snowmelt-driven catchment. Hydrological Processes **19**:4023-4038.

Miller, A. E., J. P. Schimel, J. O. Sickman, T. Meixner, A. P. Doyle, and J. M. Melack. 2007. Mineralization responses at near-zero temperatures in three alpine soils. Biogeochemistry **84**:233-245.

Miller, A. E., J. P. Schimel, J. O. Sickman, K. Skeen, T. Meixner, and J. M. Melack. 2009. Seasonal variation in nitrogen uptake and turnover in two high-elevation soils: mineralization responses are site-dependent. Biogeochemistry **93**:253-270.

Monson, R. K., S. P. Burns, M. W. Williams, A. C. Delany, M. Weintraub, and D. A. Lipson. 2006. The contribution of beneath-snow soil respiration to total ecosystem respiration in a high-elevation, subalpine forest. Global Biogeochemical Cycles **20**:GB3030.

Neff, J. C., and G. P. Asner. 2001. Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model. Ecosystems **4**:29-48.

Neff, J. C., A. P. Ballantyne, G. L. Farmer, N. M. Mahowald, J. L. Conroy, C. C. Landry, J. T. Overpeck, T. H. Painter, C. R. Lawrence, and R. L. Reynolds. 2008. Increasing eolian dust deposition in the western United States linked to human activity. Nature Geoscience **1**:189-195.

ÖQuist, M. G., and H. Laudon. 2008. Winter soil frost conditions in boreal forests control growing season soil CO2 concentration and its atmospheric exchange. Global Change Biology **14**:2839-2847.

Painter, T. H., A. P. Barrett, C. C. Landry, J. C. Neff, M. P. Cassidy, C. R. Lawrence, K. E. McBride, and G. L. Farmer. 2007. Impact of disturbed desert soils on duration of mountain snow cover. Geophysical Research Letters **34**.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. ANALYSIS OF FACTORS CONTROLLING SOIL ORGANIC-MATTER LEVELS IN GREAT-PLAINS GRASSLANDS. Soil Science Society of America Journal **51**:1173-1179.

Pederson, G. T., S. T. Gray, T. Ault, W. Marsh, D. B. Fagre, A. G. Bunn, C. A. Woodhouse, and L. J. Graumlich. 2010. Climatic Controls on the Snowmelt Hydrology of the Northern Rocky Mountains. journal of climate **24**:1666-1687.

Puissant, J., L. Cecillon, R. T. E. Mills, B. J. M. Robroek, K. Gavazov, S. De Danieli, T. Spiegelberger, A. Buttler, and J. J. Brun. 2015. Seasonal influence of climate manipulation on microbial community structure and function in mountain soils. Soil Biology & Biochemistry **80**:296-305.

R Core Development Team. 2014. R: A language and environment for statistical computing.*in* R Foundation for Statistical Computing, editor., Vienna, Austria.

Raich, J. W., C. S. Potter, and D. Bhagawati. 2002. Interannual variability in global soil respiration, 1980–94. Global Change Biology **8**:800-812.

Reichstein, M., J.-A. Subke, A. C. Angeli, and J. D. Tenhunen. 2005. Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? Global Change Biology **11**:1754-1767.

Schimel, J., T. C. Balser, and M. Wallenstein. 2007. MICROBIAL STRESS-RESPONSE PHYSIOLOGY AND ITS IMPLICATIONS FOR ECOSYSTEM FUNCTION. Ecology **88**:1386-1394.

Schimel, J. P., and S. M. Schaeffer. 2012. Microbial control over carbon cycling in soil. Frontiers in Microbiology **3**.

Scott-Denton, L. E., T. N. Rosenstiel, and R. K. Monson. 2006. Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. Global Change Biology **12**:205-216.

Symonds, M. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. Behavioral Ecology and Sociobiology **65**:13-21.

Wang, C., Y. Han, J. Chen, X. Wang, Q. Zhang, and B. Bond-Lamberty. 2013. Seasonality of soil CO2 efflux in a temperate forest: Biophysical effects of snowpack and spring freeze–thaw cycles. Agricultural and Forest Meteorology **177**:83-92.

Wang, W., S. Peng, T. Wang, and J. Fang. 2010. Winter soil CO2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. Soil Biology and Biochemistry **42**:451-458.

Warren, C. R., and M. T. Taranto. 2011. Ecosystem Respiration in a Seasonally Snow-Covered Subalpine Grassland. Arctic, Antarctic, and Alpine Research **43**:137-146.

Table 1. Comparison of site characteristics.

Site type	Sand (%)	Clay (%)	SOM (%)	ρb	Dominant understory vegetation
Lower aspen	77.5	4.6	5.7	1.01	*Latharus lanszwertii, Hackelia micrantha, Viola praemorsa, Claytonia virginica, Delphinium nuttallianum*
Lower meadow	70.3	6.3	3.8	1.07	*Artemisia tridentate, Ranunculus jovis, C. virginica, D. nuttallianum*, *Penstemon spp., L. lanszwertii, V. praemorsa*
Upper aspen	63.2	13.6	9.5	0.77	*H. micrantha, Thalictrum fendleri, C. virginica, Erythronium grandiflorum, Mertensia ciliata*, *Delphinium occidentale*, *Sambucus racemosa*, and *Ribes viscossimum*
Upper meadow	59.0	13.6	4.8	0.99	*H. micrantha, T. fendleri, Polemonium foliossimum, C. virginica, Potentilla spp.*, and *E. grandiflorum*

Note: Soil organic matter (SOM). Bulk density (ρb) g soil cm^{-3}.

Table 2. Climate characteristics of upper and lower elevation sites.

	Elevation (m)	Water year	Precip (mm)	MAT (°C)	Max SWE (mm)	SNOTEL site*
Upper	2900	2012	---	---	---	Huntington Horse (1216)
		2013	353	3.6	389	
		2014	400	2.7	503	
Lower	26500	2012	298	4.9	279	Mammoth-Cottonwood (612)
		2013	312	4.1	356	
		2014	282	3.3	414	

* USDA Natural Resource Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) [available online at http://www.wcc.nrcs.usda.gov/snow/].

Note: Mean annual temperature (MAT). Snow water equivalent (SWE).

Table 3. Soil temperature at 5 cm during the treatment-induced snow-free interval (TSI).

	Mean difference*	Dust mean	Control mean	t	df	p
Interval Tmin	0.4	0.675	0.25	-2.567	7	0.04
Interval Tmax	11.6	12.2	0.6	-8.2447	7	< 0.001
Interval daily sum	56.1	59.1	3.1	-5.526	7	< 0.001

*Absolute value of Control – Dust.

Notes: Minimum (Tmin) and maximum (Tmax) temperature recorded for any six hour period during the TSI, when dust plots were snowfree and the control plots were not. Interval daily sum is the sum of average daily temperature during the TSI.

Table 4. Above-ground air temperatures during the treatment-induced snow-free interval (TSI).

SNOTEL Measurement Location	Year	Cover type	TSI Dates	TSI length (days)	Average TSI maximum temperature	Average TSI minimum temperature	Total TSI days with below zero temperatures	TSI maximum temperature	TSI minimum temperature
Huntington Horse (upper elevation sites)	2012	Aspen	27 Apr - 11 May	14	--	--	--	--	--
		Meadow	27 Apr - 3 May	6	--	--	--	--	--
	2013	Aspen	14 May - 29 May	15	10.34	2.87	3	16.4	-0.5
		Meadow	3 May - 17 May	14	12.14	2.85	4	19.1	-2.9
	2014	Aspen	20 May - 29 May	9	12.5	4.82	0	1.6	18.2
		Meadow	5 May - 20 May	15	8.47	0.0375	9	-7.6	13.7
Mammoth-Cottonwood (lower elevation sites)	2012	Aspen	5 Apr - 23 Apr	18	10.29	-2.56	0	-11.8	20.3
		Meadow	5 Apr - 23 Apr	18	10.29	-2.56	0	-11.8	20.3
	2013	Aspen	29 Apr - 3 May	4	9.66	-4.06	4	-8.9	13.6
		Meadow	22 Apr - 14 May	22	11.71	-1.28	14	19.3	-8.9
	2014	Aspen	21 Apr - 5 May	14	9.33	-2.32	11	15.8	-10.9
		Meadow	21 Apr - 13 May	22	8.35	-2.77	18	15.8	-10.9

Table 5. Analysis of variance results for soil respiration (R_s).

Response: R_s (2012 – 2014)	Df	F value	Chisq	Pr(>Chisq)	
Treatment	2	0.658	1.197	0.550	
Cover	1	24.818	27.566	0.000	***
Elevation	1	6.664	0.427	0.513	
Date	30	12.852	385.165	0.000	***
Treatment:Cover	2	0.279	0.162	0.922	
Treatment:Elevation	2	0.206	0.633	0.729	
Cover:Elevation	1	0.083	0.485	0.486	
Treatment:Date	58	1.222	64.590	0.257	
Cover:Date	28	4.152	120.602	0.000	***
Elevation:Date	16	3.400	53.085	0.000	***
Treatment:Cover:Elevation	2	0.783	0.663	0.718	
Treatment:Cover:Date	56	0.880	47.398	0.787	
Treatment:Elevation:Date	32	1.057	32.788	0.428	
Cover:Elevation:Date	15	0.970	14.549	0.484	
Treatment:Cover:Elevation:Date	24	1.402	33.648	0.091	.

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 6. Model selection results for factors influencing soil respiration (*R_s*).

Model	Num. Par	AICc	Delta AICc	AICc Weights
Temp + SOC	3	557.51	0.00	0.726
Cover + Temp + SOC	4	559.95	2.43	0.215
Elevation + Temp + SOC	4	562.84	5.32	0.051
Treatment + Temp + SOC	5	567.40	9.88	0.005
Temp*SOC	4	570.53	13.02	0.001
Temp + SOC + Days snow free	4	570.82	13.30	0.001
Cover + Temp	3	571.30	13.78	0.001

Notes: Soil temperature 0-5 cm (Temp), soil organic carbon (SOC), cover refers to aspen or meadow, elevation refers to upper or lower.

Table 7. Model averaged estimates of coefficients for factors influencing soil respiration (R_s).

Parameter	Estimate	Mean value	Observed range
Intercept	-0.3569	--	
SOC	0.1627	4.59 kg C m^{-2}	1.99 – 7.9
Temp	0.0148	24.5 °C	0.5 – 44.7
Cover (meadow)	-0.0328	Binary	Aspen or meadow
Elevation (upper)	-0.0016	Binary	Lower or upper
DOC	0	2.8 µmol C g^{-1} soil	1.57 – 4.58
WP	0	-0.697 MPa	-8.05 – - 0.001
Days snow free	0	36.7	0 – 122
Treatment (dust)	0	Factor	Control, Dust, Dust control
Treatment (dust control)	0	Factor	Control, Dust, Dust control

Notes: The response variable, soil respiration (R_s µmol C m^{-2} s^{-1}), was log transformed. Water potential (WP) was also log transformed. Soil organic carbon (SOC) and dissolved organic carbon (DOC) were included as plot-level variables, and plot was included as a random factor in the linear mixed-effects model regression.

Table 8. Analysis of variance results for microbial biomass C and DOC.

Response: Microbial Biomass C (2014 data only)	Df	F value	Chisq	Pr(>Chisq)	
Treatment	2	0.046	0.086	0.958	
Date	1	12.135	17.277	0.000	***
Elevation	1	3.194	6.154	0.013	*
Cover	1	43.631	40.407	0.000	***
Treatment:Date	2	0.042	0.008	0.996	
Treatment:Elevation	2	1.805	3.090	0.213	
Date:Elevation	1	4.570	0.627	0.428	
Treatment:Cover	2	0.190	0.316	0.854	
Date:Cover	1	17.285	17.886	0.000	***
Elevation:Cover	1	0.561	0.569	0.451	
Treatment:Date:Elevation	2	0.607	0.712	0.701	
Treatment:Date:Cover	2	0.908	1.469	0.480	
Treatment:Elevation:Cover	2	0.844	1.686	0.430	
Date:Elevation:Cover	1	0.678	0.678	0.410	
Treatment:Date:Elevation:Cover	2	0.294	0.588	0.745	

Response: DOC (2013 and 2014 data)	Df	F value	Chisq	Pr(>Chisq)	
Treatment	2	0.938	1.860	0.394	
Date	1	8.137	8.140	0.004	**
Elevation	1	1.133	1.137	0.286	
Cover	1	7.794	7.807	0.005	**
Treatment:Date	2	0.359	0.717	0.699	
Treatment:Elevation	2	1.979	3.957	0.138	
Date:Elevation	1	5.821	5.814	0.016	*
Treatment:Cover	2	1.642	3.286	0.193	
Date:Cover	1	2.864	2.862	0.091	.
Elevation:Cover	1	1.163	1.163	0.281	
Treatment:Date:Elevation	2	0.028	0.056	0.973	
Treatment:Date:Cover	2	0.284	0.568	0.753	
Treatment:Elevation:Cover	2	1.175	2.349	0.309	
Date:Elevation:Cover	1	0.958	0.958	0.328	
Treatment:Date:Elevation:Cover	2	0.371	0.743	0.690	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 9. Results of ANOVA for final SOC.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Treatment	2	2.942	1.471	1.187	0.323	
Cover	1	27.376	27.376	22.088	0.000	***
Elevation	1	10.420	10.420	8.407	0.008	**
Treatment:Cover	2	1.729	0.865	0.698	0.508	
Treatment:Elevation	2	4.553	2.277	1.837	0.181	
Cover:Elevation	1	3.531	3.531	2.849	0.104	
Treatment:Cover:Elevation	2	6.607	3.304	2.666	0.090	.
Residuals	24	29.746	1.239			

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

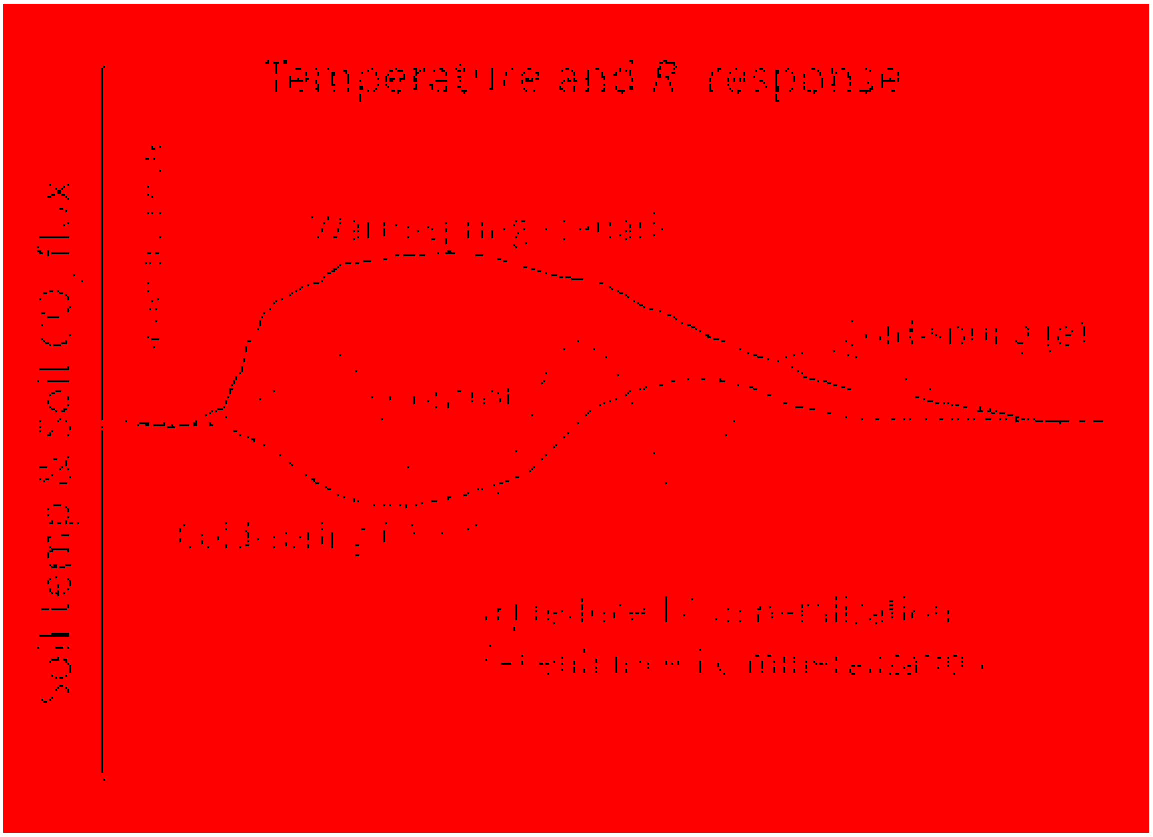


Fig. 1. Conceptual diagram representing alternative scenarios for responses of soil C mineralization to early snowmelt. These scenarios represent the change in soil respiration (R_s) in early snowmelt plots in reference to control plots.

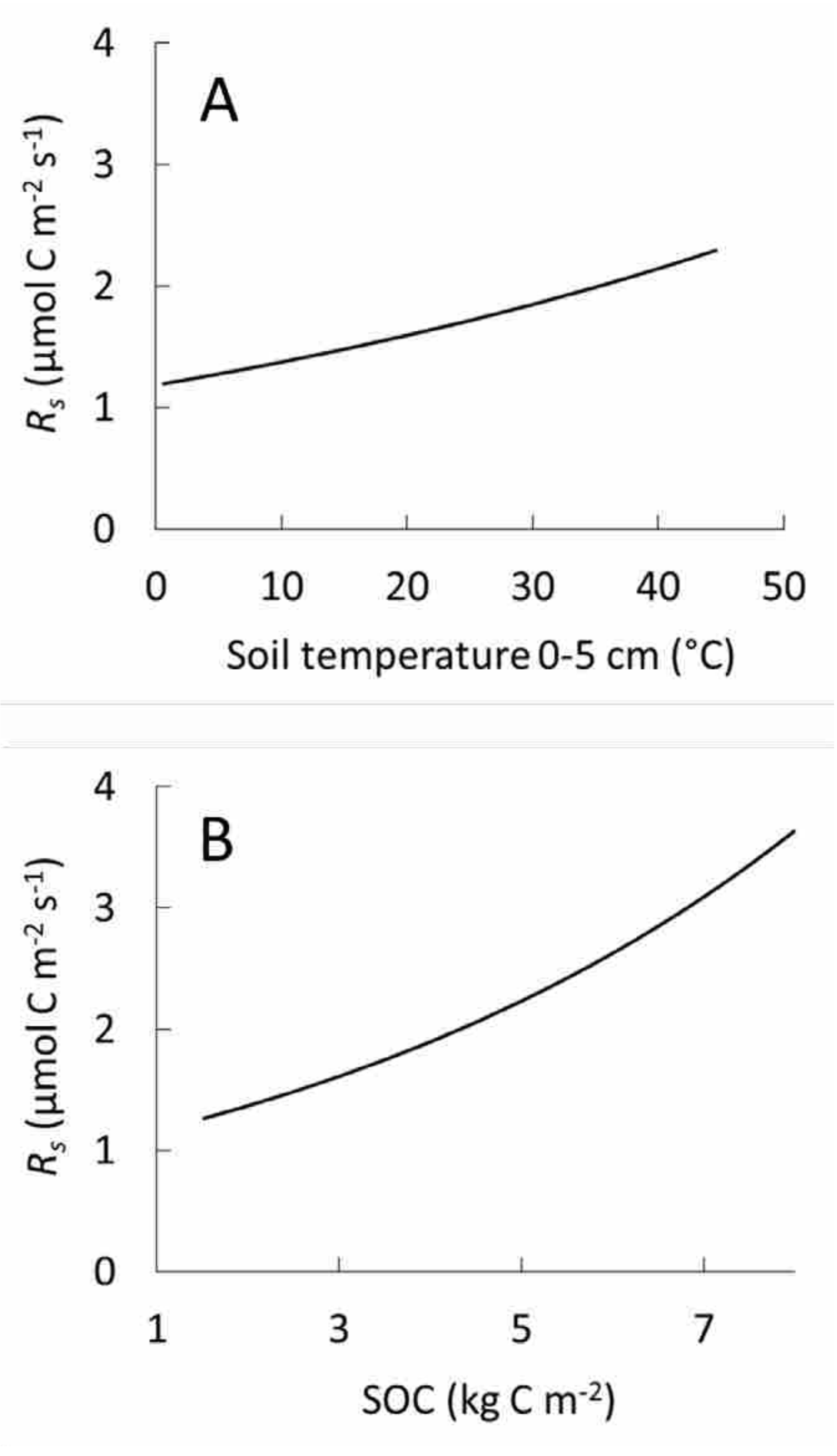


Fig. 2. Sensitivity of summer-time soil respiration (Rs) to soil temperature at 0 – 5 cm (A) and to soil organic matter (SOC) at 0 – 15 cm (B). These curves represent the model-averaged parameter estimates from the best-fit models that included soil temperature, water potential, SOC, dissolved organic C, cover and elevation as binary factors, days snow free, and treatment.

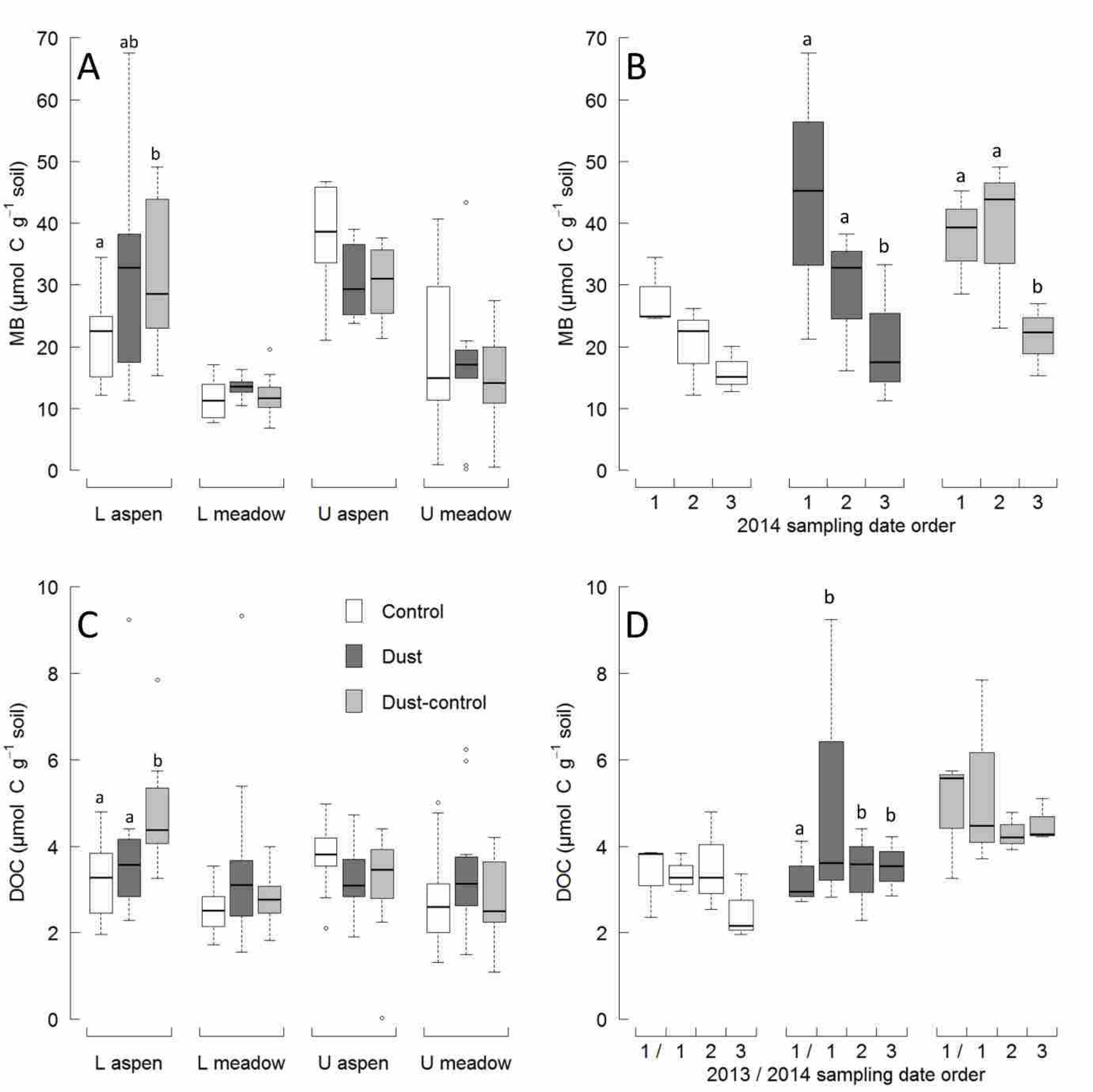


Fig. 3. Comparison of microbial biomass C (MB) and dissolved organic C (DOC) between treatments by site type (A) and by order of sampling date (B) and comparison of DOC between treatments by site type (C) and by sampling date order (D). Sampling occurred in the week following snowmelt (1), 2-4 weeks after snowmelt (2), and 4 to 6 weeks after snowmelt (3). Letters indicate statistically significant differences of pairwise comparisons within site types (α = 0.05).

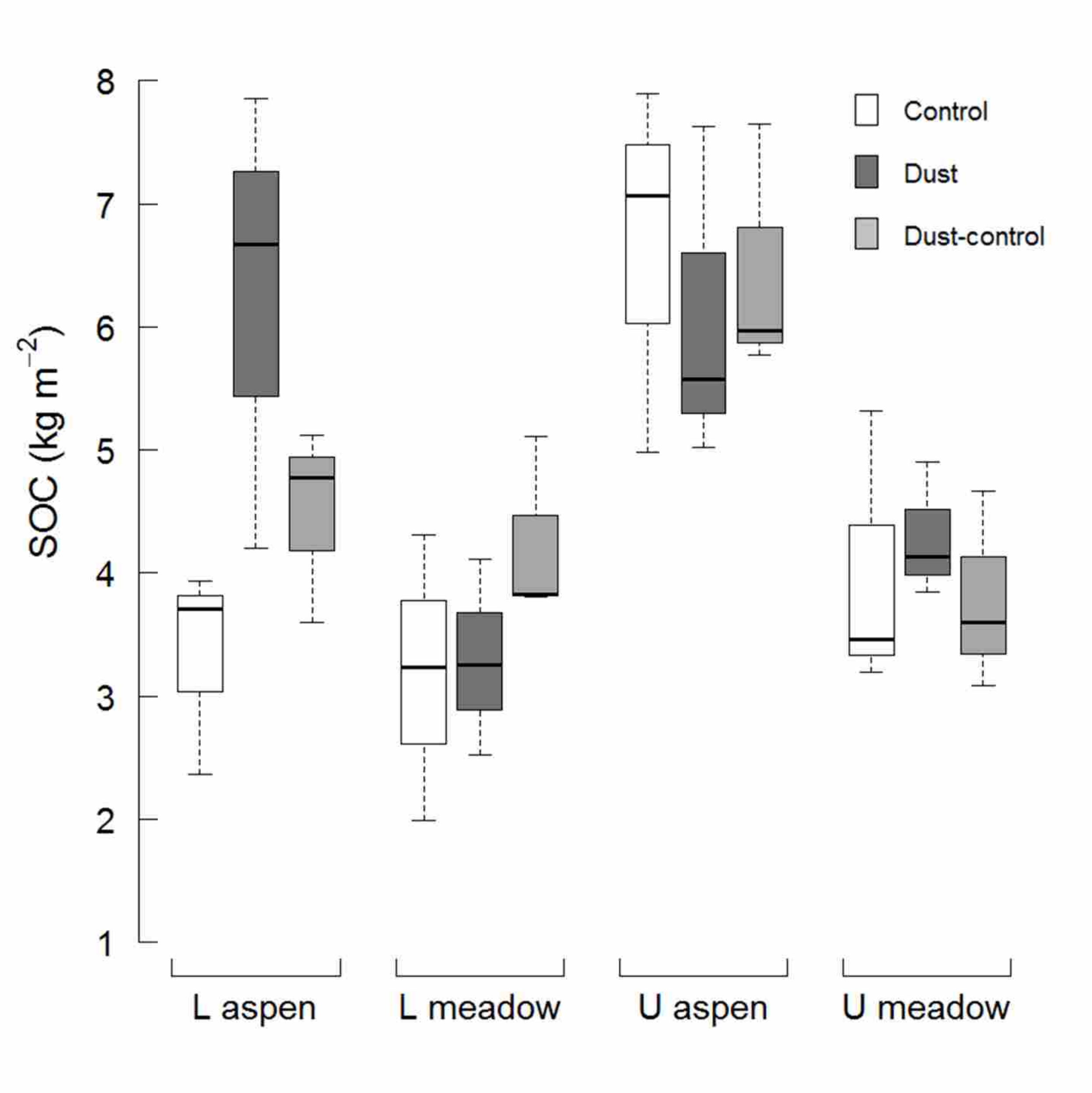


Fig. 4. Comparison of final SOC by treatment and site type. Differences between cover type and elevation are statistically significant, while differences between treatments within elevation and cover type are not statistically significant.