Soil Responses to Long-Term Climate Change

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Summary

General circulation model scenarios of future precipitation patterns are highly uncertain regarding patterns of snow depth and snow melt timing. Because snowfall provides the majority of annual soil water recharge in many western high-elevation North American ecosystems, this study tested hypotheses about the linkages of snow depth to soil water content, physiological performance, and carbon cycling for deeply-rooted shrubs at the ecotone between the Great Basin Desert shrub-steppe and Sierra Nevada conifer forest. Snow depth was manipulated using eight long-term snow fences near Mammoth Lakes, Mono County, California, USA. Snow depth, soil moisture content, water potential, whole-system gas exchange, and NPP were measured for Artemisia tridentata and Purshia tridentata in response to increased and decreased snow depth in the spring and summer following four winters that considerably differed in snowfall (2004 - 2007). Snow depth on increased-depth (“+snow”) plots was about twice that of ambient-depth plots in all years, and about 2.2 times of that for decreased-depth (“-snow”) plots. Soil water content on +snow plots was double that on ambient and -snow plots, except following the dry winter of 2006 - 2007. Plant water potential differed in some but not all years for the two shrub species across snow depth treatments. Whole-system fluxes of CO$_2$ and H$_2$O showed sensitivity to snow depth and soil moisture, with greater C inputs on wetter plots. Soil C and root biomass were generally higher under A. tridentata, whereas soil NO$_3^-$ was higher under the N-fixing species P. tridentata, particularly on +snow plots. There were no differences in litterfall and decomposition in 2005. We conclude that in some years snow depth and soil water availability affect plant water potential and C fluxes into biomass. Perhaps most important, water from heavy snowfall years can be used in subsequent low-snowfall years and helps to supplement plant water relations, carbon uptake and growth. Patterns of NPP, soil C and NO$_3^-$ suggest that over the 50-year history of snow depth forcing, soil water availability has affected C storage and N cycling.

Objectives

We addressed the following objectives: (1) linking variation in winter snow depth with soil water relations in the subsequent spring and summer; (2) measuring plant water potential, leaf-level CO$_2$ assimilation, and NPP for the dominant shrub species Artemisia tridentata and Purshia tridentata; (3) quantification of the relationship between seasonal soil and plant water relations with whole-system carbon fluxes, as an indicator of carbon input into this system; and (4) further quantification of carbon inputs into soil, in terms of snow depth and soil moisture effects on root biomass, soil organic matter, litterfall, decomposition, and C and N content under adult shrub canopies and in open microsites between shrubs.
Soil Responses to Long-Term Climate Change—Loik

Approach and Procedures

We have been using interannual snowfall variation, and spatial variation in snow depth caused by snow fences, to simulate different future scenarios of climate change on snow-fall characteristics. We have been using long-term (50 yr) snow fences to manipulate snow depth across a large spatial gradient (8 fences over 50 km of landscape). Soil moisture in ambient snow depth, +snow, and –snow plots associated with snow fences was measured from October 2004 to June 2007 using Decagon ECH2O dielectric probes at 5- to 25-cm depth. In 2006 and 2007, we sampled aboveground NPP for the two main shrub species (*Artemisia tridentata* and *Purshia tridentata*) and in 2006 for the two main grasses (*Carex* spp. and *Achnatherum* spp.). We collected soil samples in each of ambient, +snow, and –snow plots, and within each treatment we removed soil from open microsites between adult shrubs, as well as from under the canopy of *Artemisia tridentata* and *Purshia tridentata*. For each treatment × microsite combination, we also sampled at 0 – 20 cm and 20 – 40 cm depths. Soil samples were separated into rock, soil, root, and litter fractions by sieving and hand-picking. The resulting soil fractions were analyzed for C, N (as NO\textsubscript{3}\textsuperscript{-}), K, and P content at the DANR Analytical Lab at the University of California, Davis.

![Figure 1](image1.png)

Figure 1. Effects of snow fences on wind, snow, and soil moisture characteristics. Snow depth profile (*upper left*), wind speed on either side of the snow fences (*upper right*), snow depth in +snow and –snow plots as a function of ambient depth (*lower left*), and average snow depth forcing (relative to ambient depth; *lower right*).
Results

For all winters, snow depth in February on +snow plots was about two-fold that on ambient plots, and about 70% of ambient on –snow plots (fig. 1). Wind speed did not differ in summer on either side of the fences, and snow depth forcing was consistent across all levels of ambient snow depth (fig. 1). Average volumetric soil water content was about twice as high on +snow as on ambient depth plots at least for a small period of time during the snowmelt period (fig. 2), but the differences in soil water content on –snow vs. ambient plots were smaller and short-lived. Snow melted about two to three weeks earlier on –snow plots compared to +snow plots (data not shown). There was considerable complexity in the soil water signals, partly due to transient melting periods during winter. For the spring and summer of 2007, soil water content did not differ after the quite dry winter of 2006 – 2007, in which only 53 cm of snow fell (93rd frequency percentile for a mean of 136 cm and n = 79 years; fig. 3).

Figure 2. Volumetric soil moisture for 2004-2007 on ambient depth, +snow, and –snow plots. Data are means of Decagon ECH2O dielectric sensors at 5 to 25 cm depth at each of eight different snowfences.

Plant water potential was significantly affected by snow depth treatment for both species in 2004 and 2007 (fig. 4). Water potential was higher in general for A. tridentata compared to P. tridentata; for both species water potential was generally lowest on –snow plots, consistent with our overall hypothesis linking snow depth with soil moisture and plant water relations.

Leaf-level photosynthetic CO2 assimilation was significantly different across snow depth treatments only in 2004 for A. tridentata and in 2004 and marginally so in 2007 for P. tridentata (fig. 5). The lack of treatment differences in 2005 and 2006 may be due to the high amount of ambient snowfall in those two years. Although there were considerable differences in snow depth between ambient, +snow, and –snow plots in these years, the snow fence treatment may have been overwhelmed by the high snowfall.
Aboveground Net Primary Productivity (NPP) for the co-dominant shrub *Artemisia tridentata* was consistently higher across snow depth treatments in comparison to the other co-dominant shrub, *Purshia tridentata* (fig. 6). NPP was lowest on –snow plots for *A. tridentata*, and highest on +snow plots for *P. tridentata*. Whole-system CO\textsubscript{2} and water vapor fluxes were about two-fold higher on +snow vs. –snow plots in July 2006 (fig. 7).

**Figure 3.** A Historic snowfall for Mammoth Mountain, 1928 – 2007 (source: California Data Exchange Center). B Frequency histogram of annual snowfall totals for 79 years.

There are no shallow-rooted shrub species at this site, but we wanted to expand growth analyses to other species, so we examined in 2006 the two main grass species (*Carex* and *Achnatherum* spp.) and started preliminary measurements for the two main conifers at this site (*Pinus contorta* and *P. jeffreyi*). Although standing biomass and cover were higher for both grass species on +snow plots, NPP was not different, due to differences in plant basal area across snow depth treatments. Analyses of conifer gas exchange and annual ring growth trends for trees on ambient, +snow, and –snow plots are ongoing. Interestingly, the two main conifer species show different patterns of recruitment on ambient, +snow, and –snow plots (data not shown), which is now a focus of research supported by a NICCR award in 2007 to PI Loik. These differences in tree spatial patterns could lead to considerable effects of snow depth forcing on standing C stocks across treatments.

Root biomass was generally highest under *A. tridentata* compared to *P. tridentata*, and in open microsites, and values on +snow and –snow plots were lower than for ambient-depth plots.
Soil Responses to Long-Term Climate Change—Loik

(fig. 8). The patterns for roots, NO$_3^-$ and C are complex and not simply a clear function of snow depth or microhabitat. We speculate on some possible mechanisms for these patterns in the discussion below.

There were significant differences in NO$_3^-$, and organic C in soils from open microsites between shrubs, and from under the canopy of *Artemisia tridentata* and *Purshia tridentata* for ambient, +snow, and –snow plots (fig. 9). On ambient snow-depth plots, C was highest under *A. tridentata* canopies, yet on –snow plots C was highest under *P. tridentata* canopies. On ambient snow-depth plots, NO$_3^-$ was lowest in open microsites, but it was highest under *P. tridentata* (an N-fixer) on +snow and –snow plots. There also were differences in K, but not for P (data not shown).

![Figure 4](image)

**Figure 4.** Water potential from 2004 to 2007 on ambient, +snow, and –snow plots. Data are means ± 1 s.e. for five composited subsamples from each of n = 8 snowfences.

**Discussion**

Our Kearney-supported work from 2004 through 2007 showed differences in plant water potential and leaf-level photosynthetic gas exchange in response to snow depth forcing in some but not all years. The responses of plants to the typical snow-fall winter of 2003-2004 and the El Niño winter of 2004-2005 differed, and although 2005-2006 was a mild La Niña, there was considerable amount of snow at our site. By contrast, winter 2006-2007 was quite dry. Despite the lower amount of soil water in 2007, only *A. tridentata* had significantly different levels of water potential across snow-depth treatments, and leaf-level CO$_2$ exchange was not greater on +snow plots for either species. We hypothesize that (1) interannual patterns of snowfall help
explain the lack of differences between snow treatments, (2) high snowfall years help support plant water status and photosynthesis after dry winters (such as 2006 and 2007, respectively), and (3) there are details in the timing of snow-fall and snowmelt that are critical for the way that plants use the resultant meltwater (Loik et al. 2004). Nevertheless, the results are consistent with the importance of a snow depth threshold, above which there are no further increases in plant productivity in high-snowfall years (e.g., 2005 and 2006 in contrast to 2007). In other words, there is an upper threshold on carbon entering this system that is dependent on snow inputs to annual soil water content, and these effects can carry-over from one year to the next.

**Figure 5.** Leaf-level CO$_2$ assimilation for 2004 – 2007 on ambient, +snow, and –snow plots. Data are means ± 1 s.e. for five composited subsamples from each of n = 8 snowfences.

We found evidence for effects of snow depth on NPP for the deep-rooted shrubs *Artemisia tridentata* and *P. tridentata* in summer 2006. These differences are at least partially consistent with the effects of manipulated snow depth in winter and subsequent spring/summer soil moisture availability. Interestingly, for the two main native grasses at this site, increases in biomass were offset by cover increases, resulting in no net difference in NPP across snow depth treatments. It is important to note that our photosynthetic gas exchange measurements across years compare only May and June, and thus do not capture potential differences in other months. Although we expected the highest levels of photosynthesis after snowmelt in May and June, photosynthesis in 2005 continued to increase for both shrub species well into September.
Soil Responses to Long-Term Climate Change—Loik

Figure 6. Aboveground net primary productivity for *Artemisia tridentata* (Asteraceae) and *Purshia tridentata* (Rosaceae), measured after leaf-out in July 2006. Data are means ± 1 s.e. for one individual of each species sampled at n = 8 snowfences.

Given some logistical limitations, we were only able to conduct whole-system C and water vapor flux measurements on one day in summer 2006. Clearly it would be valuable to repeat them on several days throughout a growing season. These measurements were staff-intensive and were not repeated in other months or years. It would be valuable to expand the scope of these closed-chamber system measurements. Due to the nature of the snow treatments, eddy flux correlation techniques are not likely to detect signals from the 5-m wide × 100-m long plots. In 2006, we began preliminary measurements of soil CO$_2$ fluxes from under the snowpack, as some studies have suggested that this may be an important source of C loss from snow-dominated systems (Sturm et al. 2005; Monson et al. 2006). Our experiments continued in winter 2007, and early results show signs of dependence of soil C flux on soil temperature, which is affected by the insulating effect of snow depth. We have also conducted a limited amount of soil surface CO$_2$ flux measurements at various times of the year, but we do not have much confidence in the results due to the small number of sampling campaigns. New automated soil flux measurement systems would help to fill in the gaps in our data, but their performance within the snowpack is yet to be assessed. Due to the transient and rapid nature of snowmelt each year, it has been difficult to travel to the sites and measure CO$_2$ fluxes from the soil when they are likely to be highest (i.e., during the height of snowmelt).

As noted above and shown in figure 9, there is considerable complexity in the responses of soil C and NO$_3^-$ levels in response to snow depth treatment, microhabitat, and soil depth. Regarding soil C results, we hypothesize that snow depth imparts treatment-specific impacts. In particular we hypothesize that increased snow on +snow plots results in greater production and inputs into the soils via belowground litter production and root exudates. By contrast, reduced soil water availability limits respiration on –snow plots, thereby leading to less loss of soil C to the atmosphere. We measured aboveground litterfall and decomposition at the soil surface in 2005 and did not find any significant differences across snow depth treatments or shrub canopy vs. open microhabitat sites. We are currently repeating these experiments with slightly modified methods (e.g., decomposition bags have been partially buried to improve contact with soil microbes). However, our soil analysis results suggest fertile island development (Reynolds et al.)
Soil Responses to Long-Term Climate Change—Loik

1999) for this Great Basin Desert ecotone and potential differences in soil C storage over time under climate-change induced altered snow depth.

Figure 7. Whole-system CO$_2$ and H$_2$O$_v$ fluxes for A. tridentata and P. tridentata on +snow and –snow plots. Data are means ± 1 s.e. for three snowfences.

Water potential and whole-system carbon and water vapor fluxes were responsive to the snow fence-mediated changes in snow depth in 2006, further increasing the complexity of relationships between snow depth, soil water content and plant production measured in the typical snowfall year of 2003 – 2004, the El Niño year of 2004 – 2005, and the mild La Niña of 2005 – 2006. Moreover, water potential and leaf-level photosynthesis in the very dry spring and summer of 2007 were not that different from the prior wet years of 2005 and 2006. These results highlight the importance of surprises and non-linearities in ecological responses to physical forcing of the environment (Norby and Luo 2004). It is still far from clear whether and how the frequency and intensity of ENSO events will change under continued anthropogenic forcing of atmospheric radiative gas concentrations (Yeakley et al. 1994; Frei and Robinson 1999; Peterson et al. 2000; Frei et al. 2003; Groisman et al. 2004; Lee et al. 2004; Saito et al. 2004; Ashrit et al. 2005; Frei and Gong 2005). Despite uncertainties in future ENSO characteristics, research concerning ecological responses to climate change should consider impacts of ENSO and other episodic extreme events in addition to changes in average conditions.
Soil Responses to Long-Term Climate Change—Loik

**Figure 8.** Root biomass on ambient, +snow, and –snow plots for samples collected at 0-20 cm depth under *Artemisia tridentata* (Artr) or *Purshia tridentata* (Putr) canopies, or in open microsites between shrubs (Inter). Data are means ± 1 s.e. for five composited subsamples from each of n = 8 snowfences.

Complex patterns between snow depth, microhabitat (i.e., sampling under shrubs and in open microsites), soil water, and soils characteristics (e.g., root biomass, organic C, NO₃⁻, K, P) should probably not surprise us. In some cases, greater soil water availability may enhance aboveground plant production, but reduce root production based on optimal allocation of photosynthates above vs. belowground. By contrast, water may limit the amount of root production that can be sustained on –snow plots. At the same time, soil water availability may lead to enhanced soil respiration on +snow plots, and less on –snow plots, thereby explaining soil C results. Differences in N (as NO₃⁻) may depend on inputs from atmospheric deposition and N-fixation by the shrub *P. tridentata*. Finally, plant and ecosystem responses to snow depth are not simply a function of winter snowfall delivery at least for deep-rooted species, and interannual differences must be considered for their role in sustaining production in dry years.
Soil Responses to Long-Term Climate Change—Loik

Med blue = *A. tridentata* canopy, light blue = *P. tridentata* canopy, dark blue = open, intershrub microsites

![Bar chart showing soil carbon and NO$_3^-$ on ambient, +snow, and –snow plots. Soils were sampled at 0-20 and 20-40 cm depths (only data from 0-20 cm are shown) under the canopy of adult *A. tridentata*, *P. tridentata*, or in open microsites between adult shrubs. Within a treatment, bars are ordered: *A. tridentata* canopy, *P. tridentata* canopy, open intershrub microsite.](image)

**Figure 9.** Soil Carbon and NO$_3^-$ on ambient, +snow, and –snow plots. Soils were sampled at 0-20 and 20-40 cm depths (only data from 0-20 cm are shown) under the canopy of adult *A. tridentata*, *P. tridentata*, or in open microsites between adult shrubs. Within a treatment, bars are ordered: *A. tridentata* canopy, *P. tridentata* canopy, open intershrub microsite.

**Relation to the Kearney Mission**

This research contributes to the overall mission of the Kearney Foundation in the following ways: (1) We are providing a greater understanding of the mechanisms and processes governing the storage and flow of carbon pools in the coupled soil-plant-atmosphere system; (2) We are continuing to quantify impacts of anthropogenic changes in the inputs of water on transformations of carbon in ecosystems and soils; and (3) We are about to begin assessing the roles that soil moisture plays in affecting shrub and tree recruitment and resultant impacts on the carbon stored within the plant-soil system.

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Soil Responses to Long-Term Climate Change—Loik

References


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