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Key Points:
- Earlier snowmelt aligns with colder periods of the seasonal air temperature cycle
- Lower air temperatures reduce net carbon uptake during the annual snow ablation period
- Under a warming scenario we expect decreased carbon uptake during the annual snow ablation period

Supporting Information:
- Figure S2
- Figure S1
- Supporting Information S1

Correspondence to:
T. S. Winchell,
taylor.winchell@colorado.edu

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Earlier snowmelt reduces atmospheric carbon uptake in midlatitude subalpine forests

Taylor S. Winchell[1,2], David M. Barnard[1], Russell K. Monson[3], Sean P. Burns[4,5], and Noah P. Molotch[1,4,6]

[1]Institute of Alpine and Arctic Research, University of Colorado Boulder, Boulder, Colorado, USA, [2]Department of Civil, Environmental, and Architectural Engineering, University of Colorado, Boulder, Colorado, USA, [3]Department of Ecology and Evolutionary Biology and Laboratory for Tree Ring Research, University of Arizona, Tucson, Arizona, USA, [4]Department of Geography, University of Colorado Boulder, Boulder, Colorado, USA, [5]National Center for Atmospheric Research, Boulder, Colorado, USA, [6]Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California, USA

Abstract Previous work demonstrates conflicting evidence regarding the influence of snowmelt timing on forest net ecosystem exchange (NEE). Based on 15 years of eddy covariance measurements in Colorado, years with earlier snowmelt exhibited less net carbon uptake during the snow ablation period, which is a period of high potential for productivity. Earlier snowmelt aligned with colder periods of the seasonal air temperature cycle relative to later snowmelt. We found that the colder ablation-period air temperatures during these early snowmelt years lead to reduced rates of daily NEE. Hence, earlier snowmelt associated with climate warming, counterintuitively, leads to colder atmospheric temperatures during the snow ablation period and concomitantly reduced rates of net carbon uptake. Using a multilinear-regression ($R^2 = 0.79$, $P < 0.001$) relating snow ablation period mean air temperature and peak snow water equivalent (SWE) to ablation-period NEE, we predict that earlier snowmelt and decreased SWE may cause a 45% reduction in midcentury ablation-period net carbon uptake.

1. Introduction

Globally, forests represent a large and persistent terrestrial carbon sink that regulates atmospheric CO_2 concentration [*Pan et al*., 2011]. Forty percent of these forests reside in seasonally snow-covered environments, which are particularly sensitive to climate change due to the temperature dependence of precipitation phase [*Barnett et al*., 2005; *Flanner et al*., 2011]. Seasonally snow-covered forests represent a key terrestrial carbon sink in both mountainous [*Schimel et al*., 2002] and boreal ecosystems [*Bernhardt and Schlesinger*, 2013]. Evaluating the climate sensitivity of these forests is critical as winter temperatures are increasing [*Baldwin et al*., 2003; *Bradley*, 2004; *Nogués-Bravo et al*., 2007], causing reductions in snow accumulation [*Hamlet et al*., 2005; *Mote*, 2006; *Clow*, 2010] and shifting snowmelt earlier in the year [*Stewart et al*., 2004; *Clow*, 2010].

The snow ablation period, which provides a sustained soil water input, is a time of great potential for carbon uptake in seasonally snow-covered environments [*Monson et al*., 2005; *Harpold and Molotch*, 2015]. In evergreen mountain forests, where carbon uptake is biophysically restrained during the winter, the snow ablation period is when the ecosystem begins to assimilate carbon through photosynthesis and relatively low soil temperatures diminish carbon loss from soil respiration [*Monson et al*., 2005]. As a result, carbon uptake during the snow ablation period can account for a significant component of growing season NEE (up to 42% [*Monson et al*., 2005]). However, varying meteorological conditions can impact carbon uptake rates during this time [*Huxman et al*., 2003].

Synthesis studies of atmospheric carbon uptake in forested ecosystems, including those from mountain and high-latitude sites, have predicted that earlier springs and later autumns, due to climate warming, will result in increased carbon sequestration [*Richardson et al*., 2010]. However, several reports have blurred our understanding of the direction (source or sink) and magnitude of forest-atmosphere CO_2 exchange in the face of climate variation. Some studies of high-latitude forests have revealed increased [*Black et al*., 2000], decreased [*Goulden*, 1998], or no effect [*Dunn et al*., 2007] of earlier spring snow melt on total seasonal forest carbon uptake. *Piao et al.* [2008] and *Wu et al.* [2013] have shown that the effects of earlier spring warming and snowmelt on high-latitude forest net carbon exchange are dictated by the relative magnitudes of increased seasonal photosynthetic uptake versus increased autumn respiration. Similar photosynthesis-respiration trade-offs are at play in subalpine forests, as some studies show that longer growing seasons lead to less carbon uptake [*Sacks et al*., 2007; *Hu et al*., 2010], while others indicate the contrary [*Scott-Denton et al*., 2013; *Mitchell et al*., 2015]. We note that these seasonally snow-covered high-latitude and subalpine forests share similar dependencies on snowmelt as a water source and both have a general energy limitation during the winter; however, they differ in their species compositions and meteorological conditions (e.g., given latitudinal gradients in solar radiation).

Given the lack of consensus regarding the carbon balance response to changing snowmelt timing, it is important to determine whether seasonally snow-covered forest carbon sinks are strengthened or weakened in response to climate warming. We examined relationships between net ecosystem exchange (NEE) eddy covariance measurements and observed snow water equivalent (SWE) in a midlatitude subalpine forest. Our objective is to characterize the productivity response of subalpine forest ecosystems to hydrometeorological conditions during the snow ablation period and to predict future productivity given changes in snowmelt timing and accumulation associated with climate warming.

2. Data and Methods

2.1. Site Description

This study was conducted at the Niwot Ridge AmeriFlux site US-NR1, a subalpine forest in the Colorado Rocky Mountains at an elevation of 3050 m located 8 km east of the Continental Divide (40°1′58″N–105°32′47″W). The subalpine forest ecosystem (LAI = 4.2 m^2/m^2; canopy height = 11.5 m) is dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Mean-annual precipitation is approximately 800 mm, with about 65% in the form of snow. Mean-annual temperature is 1.5°C. Descriptions of the physical and meteorological characteristics of the site can be found in previous studies [*Monson et al*., 2002, 2005; *Turnipseed et al*., 2002, 2003].

2.2. Eddy Covariance and Snow Water Equivalence (SWE) Measurements

NEE has been continuously measured at 30 min intervals from the 26 m Niwot Ridge AmeriFlux tower since November 1998. We used 15 years (1999–2013) of AmeriFlux friction-velocity-filtered NEE, gap-filled measurements (ver.2014.12.02). This version includes a correction to an error in the data set where a water vapor correction was applied twice during the closed-path infrared gas analyzer (IRGA) CO_2 flux calculation [*Burns et al*., 2015]. Full descriptions of the eddy covariance method used to measure NEE have been previously presented [*Monson et al*., 2002]. Further information on the turbulent flux gap-filling procedures can be found at http://urquell.colorado.edu/data_ameriflux/.

Daily SWE measurements were obtained from the Niwot snowpack telemetry station, located within 500 m of the flux tower (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=663). We defined both the date and magnitude of peak SWE by the final local maxima in the SWE time series in which the SWE magnitude is within 95% of the global SWE maxima. Subsequently, we defined the ablation period as the peak SWE date to the day of snow disappearance (SWE = 0 m) and analyzed ablation-period daily NEE (cumulative ablation period NEE divided by the length of the ablation period) in relation to the ablation-period mean air temperature (21.5 m). In this study "daytime" is defined as any period of the day that the photosynthetic photon flux density (PPFD) is greater than 20 $\mu mol/m^2/s$. We defined the nonablation period as the date of snow disappearance to the day that the 13 day moving average of NEE switches from negative to positive at the end of the season, indicating a transition from net carbon uptake to net carbon loss. We thus defined a "full season" from the date of peak SWE to the last day of the nonablation period.

2.3. Statistical Methods and Ablation-Period NEE Model

Previous work in subalpine forests has illustrated NEE sensitivity to air temperature [*Huxman et al*., 2003; *Monson et al*., 2005], with maximum light saturated CO_2 uptake occurring at approximately 11°C [*Huxman et al*., 2003]. A shift in the timing of snowmelt may have large impacts on air temperature during the early part of the growing season—which generally begins at the onset of snowmelt [*Monson et al*., 2005]. To explore the relationship between the change in the timing of snowmelt and air temperature during the ablation period, we used a linear regression relating the date of peak SWE and ablation-period mean air temperature. We then explored the relationship between ablation-period mean air temperature and ablation-period daily NEE, as well as the relationship between the date of peak SWE and the ratio of ablation-period cumulative NEE to full-season cumulative NEE. We used the relationship between date of peak SWE and

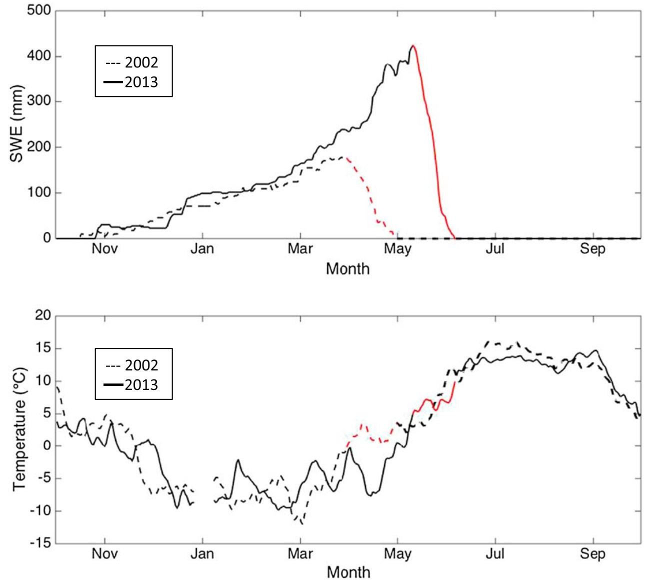

Figure 1. (a) Snow water equivalent seasonal cycles for an early (WY-2002) and late (WY-2013) ablation period. Red lines distinguish the ablation period. (b) Corresponding air temperature seasonal cycles for WY-2002 and WY-2013. Plotted as the 13 day moving average of daily temperatures. Red lines distinguish the temperatures during the ablation period.

ablation-period mean air temperature to produce a linear regression equation which uses the date of peak SWE as a predictor of ablation-period mean air temperature.

To evaluate the processes influencing the range in total ablation-period NEE, we performed a multiple linear regression analysis with ablation-period mean air temperature and peak SWE magnitude as physical predictors to explain the variation in total ablation-period NEE. These predictor variables were chosen for the multiple linear regression analysis both because of their individual correlations with ablation-period NEE and our ability to project future trends of these variables based on current literature. We used the resulting multiple linear regression equation as a model to demonstrate potential current and future scenarios of ablation-period NEE. To obtain the range of temperature values used as model input, we first inputted a range of day of peak SWE values into the linear regression equation established between day of peak SWE and ablation-period mean air temperature. Day of peak SWE inputs ranged from day of year (DOY) 65 to DOY 145, as the minimum DOY of peak SWE from the observed record was 73 and the maximum DOY of peak SWE was 144. We then took the resulting temperature range, along with a peak SWE magnitude range of 0.17 m–0.50 m (15 year observed record ranged from 175.3 mm to 454.7 mm), as model inputs to generate a range of potential ablation-period NEE values.

3. Results

The maximum ablation-period length was 55 days (2003) and the minimum was 17 days (2010) (Table S1). The latest date of peak SWE was 24 May 2011 and the earliest was 13 March 2012, resulting in a substantial range in the date of peak SWE (71 days). Figure 1 demonstrates that the timing of peak SWE determined the alignment of the ablation period with the seasonal air temperature cycle: an early ablation period (e.g., 2002) occurred during a colder period (mean temperature = 1.9°C) of the seasonal air temperature cycle relative to a later ablation period (e.g., 2013) that occurred during a warmer period (mean temperature = 6.7°C). Thus, we next explored the phenological implications of the ablation timing/temperature alignment for ablation-period NEE.

We found that the range in the date of peak SWE resulted in a vast range of ablation-period mean air temperatures (1.9–7.9°C). Figure 2a displays a significant positive correlation ($R^2 = 0.72$, $P < 0.001$) between the date of peak SWE and the ablation-period mean air temperature. This relationship produced the following linear regression equation:

$$T = -4.1662 + 0.07881*(D) \tag{1}$$

where D is the day of year (DOY) of peak SWE. Equation (1) demonstrates that as snow melts earlier, the ablation period experiences mean air temperatures progressively less than the maximum CO_2 uptake rate temperature of 11°C [*Huxman et al.*, 2003], effectively misaligning the period of sustained soil water input from the timing of the optimum net uptake temperature.

We found a significant negative correlation ($R^2 = 0.87$, $P < 0.001$) between ablation-period daily NEE and ablation-period mean air temperature (Figure 2b). Lower mean air temperatures corresponded with reduced

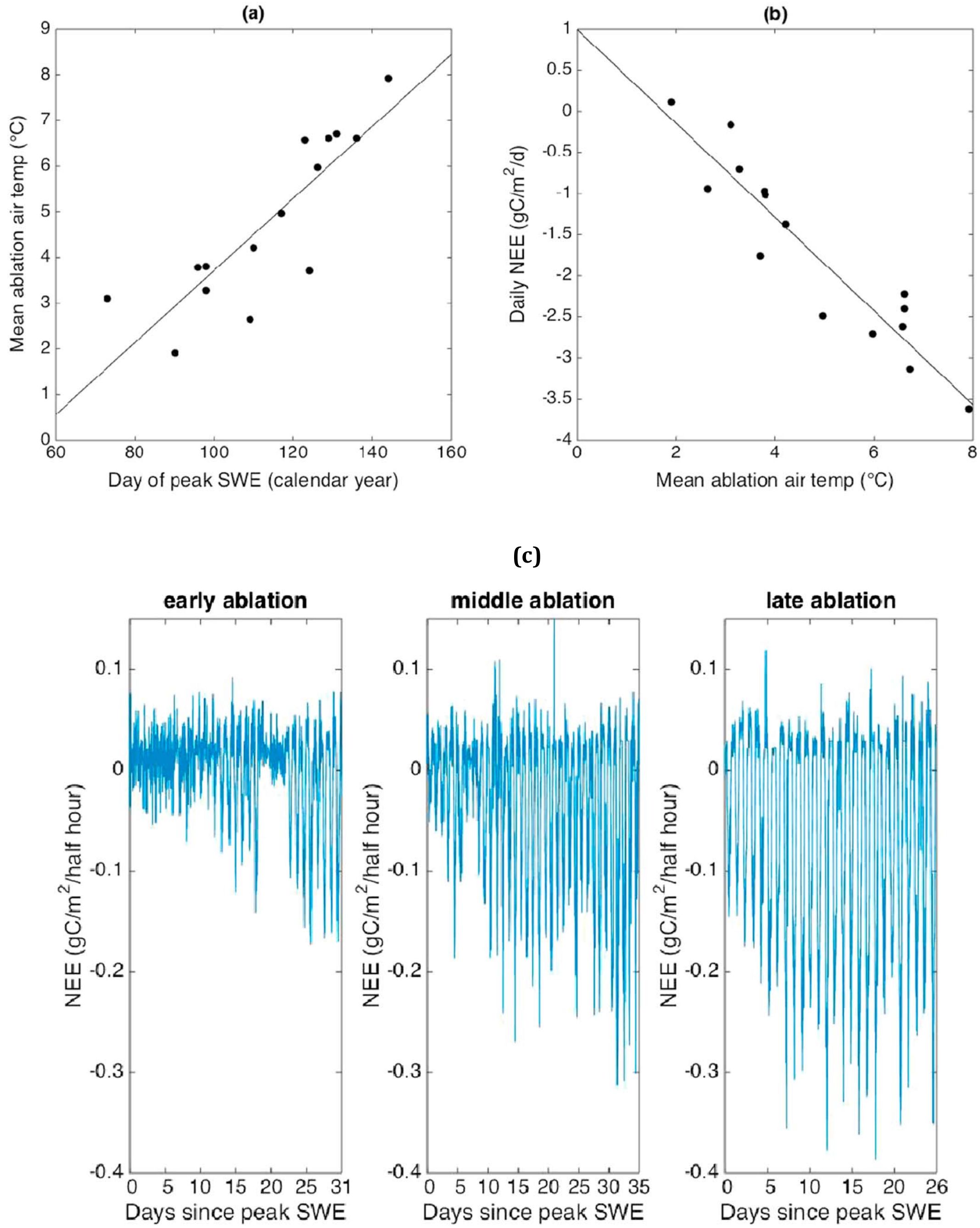

Figure 2. (a) Relationship between date of peak SWE (horizontal axis) and mean air temperature during the ablation period (vertical axis) ($R^2 = 0.72$, $P < 0.001$). (b) Relationship between mean air temperature during the ablation period (horizontal axis) and ablation-period daily NEE (vertical axis)($R^2 = 0.87$, $P < 0.001$). (c) Half-hourly NEE for the 2002 ablation period that began on 31 March (early ablation) 2009 ablation period that began on 20 April (middle ablation) 2013 ablation period that began on 22 May (late ablation).

ablation-period daily NEE. The variation in ablation-period daily NEE was driven by ablation-period daytime NEE, as daytime NEE had a range of 3.78 gC/m^2/d, whereas nighttime NEE had a range of only 0.16 gC/m^2/d. Example half-hourly data illustrate the NEE sensitivity to snowmelt timing and air temperature whereby NEE rates are shown to increase dramatically from early to late snowmelt (Figure 2c). In comparing NEE between an early ablation period (2002) and the same period during a year with late melt (2013), the daytime NEE rate during the 2002 ablation period (31 March to 1 May) was $-$ 0.42 gC/m^2/d, while the same time

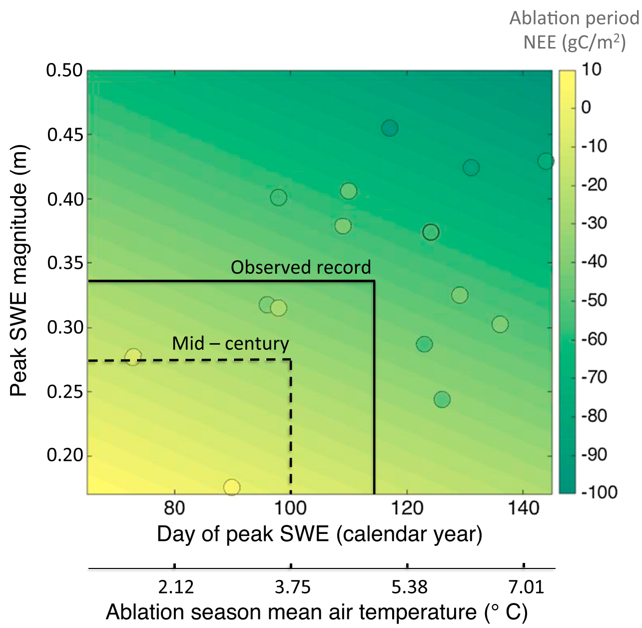

Figure 3. Model output results from equations (1) and (2) demonstrating the range of potential ablation-period total NEE. Each scatter point is an ablation period from the observed record. The solid lines represent the mean day of peak SWE and peak SWE magnitude from the observed record and the dotted lines represent the projected midcentury scenario.

period for late ablation year of 2013 (31 March to 1 May, before 2013 ablation period begins) reported a daytime NEE rate of 0.29 gC/m^2/d. The sign difference in these two daytime NEE quantities indicates that the forest was active during the melt period in 2002 but not during the same time period in 2013 when melt was not occurring. The early ablation example in Figure 2c further demonstrates the sensitivity of forest NEE to early snow ablation, as we see that there was a sudden reduction in NEE for an approximate 4 day stretch associated with air temperatures below 0°C; these rapid drops in air temperature are less likely to occur later in the year. We note that we did not find a significant relationship between ablation-period daily NEE and ablation-period mean daytime PPFD ($R^2 = 0.11$, $P = 0.23$, supporting information Figure S1).

The range in ablation-period NEE was 95.4 gC/m^2. In 2002 we observed a positive ablation-period NEE (3.36 gC/m^2); the ablation-period mean air temperature (1.9°C) and the peak SWE magnitude (175.3 mm) for 2002 were the respective variable minimums for the 15 year record. Additionally, the 2002 ablation-season mean daytime uptake rate (−0.42 gC/m^2) was the minimum for the period of record. The mean nighttime respiration (0.53 gC/m^2) during this same period was enough to overwhelm the small daytime uptake rate and result in a net loss of carbon. All other years demonstrated a negative NEE during the ablation period, indicating net carbon uptake, with the greatest in magnitude being − 92.02 gC/m^2 occurring in 2007; a year with an ablation-period average temperature of 5.0°C and the maximum peak SWE magnitude (454.7 mm) for the period of record.

There was a significant negative correlation between total ablation-period carbon uptake (dependent variable) and ablation-period mean air temperature and peak SWE magnitude (independent variables; $R^2 = 0.79$, $P < 0.001$) that produced the following multiple linear regression equation:

$$\mathrm{NEE} = 54.956 - (5.4992 \times T) - (222.9 \times \mathrm{SWE}) \tag{2}$$

where NEE is the total ablation-period NEE (gC/m^2), T is the ablation-period mean air temperature (°C), and SWE is peak SWE (m). The range in the observed NEE that was fit with equation (2) demonstrates that early season NEE is strongly coupled with snowpack dynamics. We note that ablation-period mean air temperature and peak SWE magnitude did not exhibit collinearity for the observed record (variable inflation factor = 1.09) and that SWE had a greater influence than temperature in predicting total ablation-period NEE. We use equation (2) to demonstrate potential current and future scenarios of ablation-period NEE under various temperature-SWE magnitude scenarios. Figure 3 displays the range of model results overlaid with the observed data. For an example future scenario corresponding to midcentury Western U.S. projected SWE reductions of 20% percent [*Leung et al.*, 2004] and snowmelt timing shift of 2 weeks earlier [*Stewart et al.*, 2004; *Clow*, 2010], the mean ablation-period NEE is predicted to decline by approximately 45% compared with the observed record.

In Figure 4, we analyzed the contribution of the ablation-period NEE to the full-season NEE (cumulative NEE from the date of peak SWE to the end of the previously defined nonablation period). Figure 4a shows a significant positive correlation ($R^2 = 0.42$, $P < 0.01$) between the ratio of ablation-period NEE to full-season NEE and the date of peak SWE, indicating that when peak SWE occurred later in the year, the relative uptake

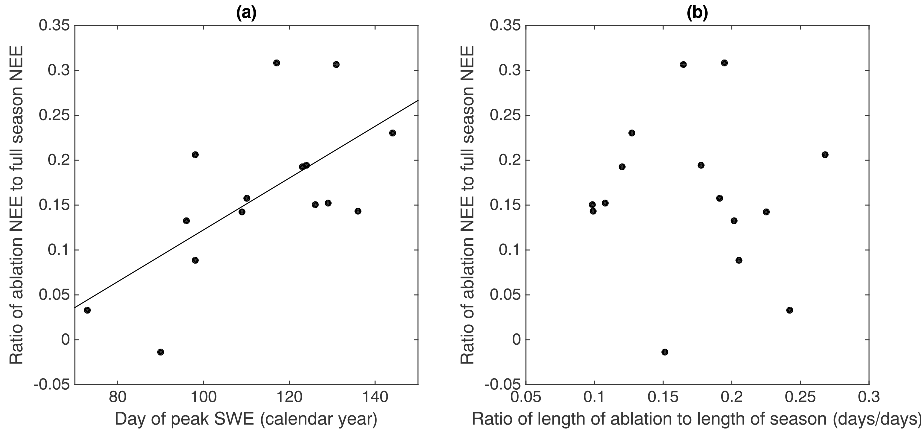

Figure 4. (a) Relationship between the date of peak SWE (horizontal axis) and the ratio of ablation-period NEE to full-season NEE (vertical axis) ($R^2 = 0.42$, $P < 0.01$). (b) Relationship between the ratio of the length of the ablation season to length of the full season (horizontal axis) and the ratio of ablation period NEE to full-season NEE (vertical axis).

contribution of the ablation period increased. Two years (2007 and 2013) had a ratio of approximately 0.31, demonstrating that the ablation-period NEE can comprise >30% of full-season NEE. However, as the date of peak SWE shifted to earlier in the year, the relative uptake contribution from the ablation period approached zero. Therefore, as the ablation period continues to shift earlier in the year under climate warming, the resulting seasonal net carbon uptake will be more dependent upon the dynamics of the nonablation period. Figure 4b shows that there was no significant relationship between the ratios of ablation NEE/full-season NEE and ablation-period length/full-season length; therefore, seasons with a relatively high ratio of ablation-period NEE/full-season NEE can occur during years in which the ablation-period length constitutes either a high or a low proportion of the full-season length. Finally, we note that we did not find a significant relationship between date of peak SWE and full-season NEE ($R^2 = 0.06$, $P = 0.39$, supporting information Figure S2).

4. Discussion

In the 21st century the Rocky Mountain region is projected to experience a 2.0–3.5°C temperature increase in mean-annual temperatures relative to the end of the 20th century [*Baldwin et al.*, 2003]. By the nature of the precipitation phase dependence on temperature, warming has vast implications for snowpack accumulation and melting patterns. For example, snow melts earlier under warming scenarios [*Stewart et al.*, 2004; *Clow*, 2010] due to increases in incident thermal radiation and sensible heat flux. Additionally, warmer air temperatures reduce snowpack cooling in the winter period which, in addition to reduced SWE accumulation, reduces the energy required to bring the snowpack to 0°C and initiate snowmelt. The influence of warming on ablation timing can be exacerbated by the effects of decreased snowpack albedo brought about by snowpack dust loading [*Painter et al.*, 2012].

Our results indicate that the timing of snowmelt determines the alignment of the ablation period with the seasonal temperature cycle, whereby early melt occurs during colder periods of the seasonal temperature cycle. The magnitudes of ablation-period daily NEE rates were shown to decrease under colder temperature conditions. Thus, as ablation shifts earlier under climate warming and aligns with the colder periods of the seasonal temperature cycle, ablation-period NEE trends to decrease. This concept presents a notable paradox: as global temperatures slowly rise, midlatitude subalpine forests are likely to experience colder temperatures during the ablation season as a result of the shift in snowmelt timing with respect to the seasonal air temperature cycle. Therefore, warming temperatures will likely lead to less CO_2 uptake during the annual ablation period. Additionally, it is predicted that future warming will cause a larger fraction of winter precipitation to fall as rain, rather than snow [*Scott-Denton et al.*, 2013]. This phenomenon is a contributing factor in decreasing SWE magnitude. Declines in peak SWE will further contribute to a decreasing trend in ablation period carbon uptake.

It is perhaps surprising that we did not observe a significant relationship between daily NEE and PPFD. Importantly, the results of this study demonstrate that ablation-period air temperature has a much stronger seasonal-phenological influence on ablation-period daily NEE compared with PPFD. Additionally, we note that this ablation-period temperature influence acts primarily on the process of forest carbon uptake, as we observed a substantially greater range in daytime NEE (when photosynthesis is actively occurring) opposed to nighttime NEE when respiration is the dominant process. Regarding the greater influence of SWE compared with air temperature in predicting total ablation-period NEE, we suggest that this may be a result of varying ablation period lengths and/or a limitation of the 15 year length of the data set. We find it imperative to emphasize that as shown in Figure 2b, air temperature strongly influences daily NEE during the ablation period, which contributes a deeper understanding of forest phenological processes during the ablation period. In predicting total ablation-period NEE, temperature and SWE magnitude are both important and allow us to generate future ablation-period NEE scenarios, thus contributing to our understanding of carbon uptake trends under a warming scenario in seasonally snow-covered environments.

Our analysis used gap-filled data to develop the best estimate of cumulative NEE during the ablation period. The specific gap-filling technique was based on a model that uses net radiation, temperature, and wind speed to produce half-hourly NEE values. The median percentage of model gap-filled data per ablation period was 8.13%. There were three years that had gap-filled percentages greater than 20% (2003—21%; 2006—35%; 2009—35%). If we remove these three high gap fraction years from our analysis, the relationships were rather unaffected, implying that these higher percentage gap-filled years were not having undue influence on the results. The coefficient of determination of the date of peak SWE versus ablation-period mean air temperature relationship decreased only slightly from $R^2 = 0.72$ for all years to $R^2 = 0.70$ when excluding the three high gap fraction years. Additionally, the coefficient of determination of the ablation-period mean air temperature versus daily NEE decreased only slightly from $R^2 = 0.87$ for all years to $R^2 = 0.86$ when excluding the three high gap fraction years.

In developing a complete understanding of the annual carbon budget it is important to also consider the NEE trends during the times preceding and following the ablation period. It has been demonstrated that shallower winter snowpacks result in colder soil temperatures and thus less soil respiration during the snow cover period (accumulation + ablation) [*Monson et al.*, 2006]. This reduction in wintertime respiration (less carbon release) acts in opposition to the potential reduction in ablation-period carbon uptake proposed in this study. The fact that ablation-period NEE, which represents the sum of opposing photosynthesis and respiration CO_2 fluxes, decreases in seasons with earlier and colder snowmelt is consistent with the conclusion that lower temperatures during snowmelt inhibits photosynthesis to a greater degree than respiration.

While we have a firm understanding as to how the NEE trends will progress during the periods of snow accumulation and snowmelt under changing snowpack dynamics, it is less clear as to how the respiration-uptake balance during the snow-free period will respond as future trends in summer precipitation and soil water availability are uncertain. The reported lack of correlation between the date of peak SWE and full-season NEE indicates that there is a decoupling in NEE processes between the ablation period and snow-free period. Thus, future work should focus on analyzing the factors that control NEE processes during the nonablation period of the growing season. That said, isotopic signatures of xylem water suggest that snowmelt, as opposed to summer rainfall, is the primary driver of forest water availability [*Hu et al.*, 2010]. Hence, the ablation-period NEE climate sensitivities reported here have important implications for developing robust predictions of future terrestrial carbon cycling in seasonally snow-covered forests.

5. Conclusion

Using 15 years of SWE and eddy covariance CO_2 measurements in Colorado, we showed that temperature is a strong phenological control on ablation-period daily NEE. Early ablation periods shifted melt to colder periods of the seasonal air temperature cycle, which resulted in lower magnitude daily NEE because of the strong phenological temperature influence on ablation-period NEE. These results represent an important paradox whereby climate warming shifts the timing of snowmelt to colder periods of the seasonal temperature cycle, which acts to decrease NEE. Projecting forward our multilinear-regression model to predict future ablation-period NEE scenarios, a 45% reduction in midcentury ablation-period NEE is estimated. In building our understanding of NEE processes during the growing season as a whole, it is important that we first develop a firm grasp on NEE processes during the two distinct periods that together compose the growing season (snow ablation period + snow-free period). This study provides evidence that snowpack dynamics are a strong control on forest carbon uptake during the snow ablation period. Future efforts should be directed toward an improved understanding of NEE processes during the snow-free period of the growing season, with a focus on how future precipitation and temperature scenarios will affect the balance between photosynthetic carbon uptake and ecosystem respiration.

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