

# Longer growing seasons lead to less carbon sequestration by a subalpine forest

JIA HU\*, DAVID J. P. MOORE†, SEAN P. BURNS\*‡ and RUSSELL K. MONSON\*§

\*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA, †Department of Geography, King's College London, Strand, London, WC2R 2LS, UK, ‡National Center for Atmospheric Research (NCAR), Boulder, CO 80307, USA, §Cooperative Institute for Research in Environmental Sciences (CIRES), University of Colorado, Boulder, CO 80309, USA

## Abstract

As global temperatures increase, the potential for longer growing seasons to enhance the terrestrial carbon sink has been proposed as a mechanism to reduce the rate of further warming. At the Niwot Ridge AmeriFlux site, a subalpine forest in the Colorado Rocky Mountains, we used a 9-year record (1999–2007) of continuous eddy flux observations to show that longer growing season length (GSL) actually resulted in less annual CO<sub>2</sub> uptake. Years with a longer GSL were correlated with a shallower snow pack, as measured using snow water equivalent (SWE). Furthermore, years with a lower SWE correlated with an earlier start of spring. For three years, 2005, 2006, and 2007, we used observations of stable hydrogen isotopes ( $\delta D$ ) of snow vs. rain, and extracted xylem water from the three dominant tree species, lodgepole pine, Engelmann spruce, and subalpine fir, to show that the trees relied heavily on snow melt water even late into the growing season. By mid-August, 57% to 68% of xylem water reflected the isotopic signature of snow melt. By coupling the isotopic water measurements with an ecosystem model, SIPNET, we found that annual forest carbon uptake was highly dependent on snow water, which decreases in abundance during years with longer growing seasons. Once again, for the 3 years 2005, 2006, and 2007, annual gross primary productivity, which was derived as an optimized parameter from the SIPNET model was estimated to be 67%, 77%, and 71% dependent on snow melt water, respectively. Past studies have shown that the mean winter snow pack in mountain ecosystems of the Western US has been declining for decades and is correlated with positive winter temperature anomalies. Since climate change models predict continuation of winter warming and reduced snow in mountains of the Western US, the strength of the forest carbon sink is likely to decline further.

*Keywords:* growing season length, isotope, net ecosystem productivity, SIPNET, subalpine forest

*Received 2 February 2009; revised version received 16 April 2009 and accepted 28 April 2009*

## Introduction

Human activities, such as the burning of fossil fuels and land use changes, have increased the atmospheric CO<sub>2</sub> concentration over the past century. The increase in CO<sub>2</sub> and other greenhouse gases is very likely to have caused climate warming at unprecedented rates (IPCC, 2007). While approximately half of the emitted anthropogenic CO<sub>2</sub> stays in the atmosphere, the remainder is assimilated into terrestrial and ocean ecosystems (Canadell *et al.*, 2007). These natural carbon sinks are vital for sequestering atmospheric CO<sub>2</sub>, and yet the strength

and longevity of these sinks may be diminishing (Cramer *et al.*, 2001; Canadell *et al.*, 2007). The tendency for ecosystem growing seasons to lengthen in response to climate warming (Myneni *et al.*, 1997; Cao & Woodward, 1998; Black *et al.*, 2000) may enhance the strength of the terrestrial carbon sink, and thus diminish the rate of atmospheric CO<sub>2</sub> buildup. An earlier spring, and associated longer growing season may increase the potential time for photosynthetic CO<sub>2</sub> uptake by terrestrial ecosystems.

Several recent studies have found longer growing seasons to increase net ecosystem productivity (NEP). Keeling *et al.* (1996) first used continuous measurements of CO<sub>2</sub> concentrations in Hawaii and the Arctic to show a general increase in northern hemisphere growing

Correspondence: Russell K. Monson, fax +303 492 8699, e-mail: russell.monson@colorado.edu

season length (GSL) since the mid 1960s. Using eddy flux data, Goulden *et al.* (1996) found longer GSL to correlate with an increase in NEP in an eastern deciduous forest; Black *et al.* (2000) and Griffis *et al.* (2003) also found a positive relationship between GSL and NEP in a boreal deciduous forest. In both of these studies, warmer springs and earlier leaf emergence were hypothesized to cause the higher observed rates of NEP. Analyzing 26 EUROFLUX network sites, Valentini *et al.* (2000) discovered a positive relationship between NEP and latitude, where latitude was used as a proxy for GSL, as well as radiation balance, frost events, and disturbance regimes. Finally, Churkina *et al.* (2005) used eddy flux measurements from 28 different sites, ranging from grasslands to forests and found a positive relationship between GSL and NEP. With the exception of Churkina *et al.* (2005), most of these studies focused on the relationship between GSL and NEP in deciduous forests, where warmer springs prompt an earlier bud break. Unlike deciduous forests, coniferous forests begin to photosynthesize before the onset of bud break, and therefore the mechanisms that couple ecosystem productivity to GSL may be fundamentally different than those in deciduous forests. For example, in the subalpine forests in the Western US, conifers can begin to photosynthesize almost 2 months before buds break (J. Hu, unpublished results). Therefore, although the effects of increasing GSL on NEP in coniferous forests remains relatively unknown, understanding this relationship is highly important for ecosystem–atmosphere carbon exchange models (White *et al.*, 1999).

Despite the relatively large body of literature showing a positive relationship between GSL and NEP, recently, Piao *et al.* (2008) found evidence for a hemisphere-scale relationship between GSL and lower rates of NEP due to higher rates of respiratory CO<sub>2</sub> loss during an extended, warmer autumn. Furthermore, Piao *et al.* (2008) found North America to be experiencing a larger warming in autumn than in spring, while Eurasia was experiencing a stronger spring warming than autumn. In mountain ecosystems of the Western US, however, autumns are relatively dry, and it is not clear that warmer temperatures will necessarily lead to higher soil respiration rates during years with a later start to winter. At the Niwot Ridge AmeriFlux site, for example, soil respiration rates were shown to be insensitive to warmer temperatures during drier growing seasons (Scott-Denton *et al.*, 2003).

NEP in mountain ecosystems of the Western US is controlled by precipitation, much of which falls in winter (Monson *et al.*, 2002; Hunter *et al.*, 2006). For example, high rates of carbon uptake occur in the Sierra Nevada and Rocky Mountains during years

of high precipitation [gross primary productivity (GPP)  $\approx 800 \text{ gC m}^{-2} \text{ yr}$ ], but rates of carbon uptake decrease during years of drought (Schimel *et al.*, 2000, 2002). These mountain ecosystems are also significant carbon sinks, with up to 70% of the Western US sink occurring at elevations above 750 m (Schimel *et al.*, 2002). Studies in the subalpine forest of the Colorado Rocky Mountains have found NEP and snow pack to be tightly linked. During the period of rapid snow melt in the early spring, forest–atmosphere CO<sub>2</sub> exchange rates switch from net ecosystem respiration to net ecosystem photosynthesis over the period of a few days or weeks (Monson *et al.*, 2002, 2005).

In our study of carbon and water dynamics in a subalpine forest, we used a 9-year record of eddy flux data to investigate the relationship between GSL and NEP. Furthermore, because both snow and rain can contribute to available water in subalpine forests, we used isotopic measurements to distinguish between these two precipitation sources. We coupled these measurements with an ecosystem model, the Simplified Photosynthesis and EvapoTranspiration (SIPNET) model, to quantify the importance of snow melt vs. summer monsoon rains on GPP. We hypothesized that photosynthetic CO<sub>2</sub> uptake was more dependent on snow water than summer rains. We also examined the effects of spring and autumn temperatures on NEP in order to see if the site was experiencing greater warming during spring or autumn.

## Methods

The study took place at the Niwot Ridge AmeriFlux site, a subalpine forest located in the Colorado Rocky Mountains at an elevation of 3050 m. The site receives about 800 mm of precipitation annually, with 60% in the form of snow and 40% in the form of rain (calculated from a 10-year average). Mean annual temperature is 1.5 °C. The forest is about 100 years old and has a mixture of trees, including *Pinus contorta* (lodgepole pine), *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), and *Pinus flexilis* (limber pine), and *Populus tremuloides* (quaking aspen), but the three dominant tree species and the ones we focused on were lodgepole pine, subalpine fir, and Engelmann spruce. For a more in depth description of the site, see Monson *et al.* (2002, 2005) and Turnipseed *et al.* (2003).

### Meteorological measurements

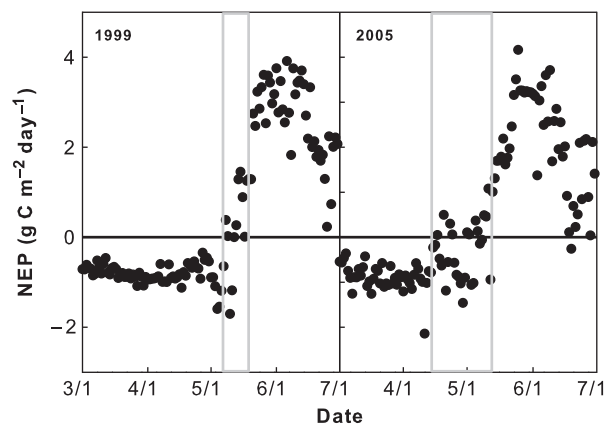
NEP was measured at 21.5 m at the main AmeriFlux tower (NR1) with an IRGA (model LI-6262, LI-COR Inc., Lincoln, NE, USA), and sonic anemometer (model csat-3, Campbell Scientific Inc., Logan, UT, USA). Raw CO<sub>2</sub> and

wind data were collected at 10 Hz frequency and NEP was calculated over 30-min time periods. Appropriate corrections for density fluctuations and sonic coordinate rotations were applied as described in Monson *et al.* (2002) and Turnipseed *et al.* (2002). NEP was summed for 9 years (1999–2007) using the gap-filled data record for 30-min averages. Methods for gap-filling and other details of data processing are available at the Niwot Ridge AmeriFlux web site ([http://urquell.colorado.edu/data\\_ameriflux/](http://urquell.colorado.edu/data_ameriflux/)) (Monson *et al.*, 2002, 2005; Turnipseed *et al.*, 2003). Uncertainty in NEE was estimated using the approach from Richardson *et al.* (2006), where we calculated random errors in the carbon flux measurements using the daily-difference approach. This analysis revealed that the error distribution was best described by a double-exponential probability distribution. Bootstrap pseudoreplicates were created using an original flux observation plus a random uncertainty term derived from the double-exponential distribution. These replicates were then used to estimate 95% confidence intervals around the mean flux. We found that the average uncertainty for each weekly integration of NEE for 9 years to be about 18% and applied this uncertainty to our annual NEP measurements.

Cumulative snow water equivalent (SWE) values for the Niwot Ridge LTER C1 site were obtained from the SNOTEL database (<http://www.co.nrcs.usda.gov/data/snow>) for all 9 years. For calculations of SWE, we chose to use 'water year' start and end dates (October–October). For example, for SWE of 2000, cumulative SWE was summed from October 1, 1999 through September 30, 2000. We chose to use cumulative SWE instead of peak SWE from April 1 because our site often experienced late spring storms that fell after the April 1 date, and we wanted to ensure that these storms were included in the analysis. Average temperatures during the first two weeks of spring (2 weeks after NEP became positive) and the last 2 weeks of autumn (2 weeks before negative NEP) were calculated for all 9 years to examine the relationship between temperature and NEP during the start and end of the growing season. We also calculated the average winter temperature (winter days were the days not included in the growing season days) for all 9 years. Precipitation was measured using a heated tipping bucket rain/snow gauge (model 385-L, Met One Inc., Grants Pass, OR, USA), and air temperature was measured with an aspirated sensor (model HMP35D, Vaisala Inc., Woburn, MA, USA). The uncertainty in SWE was estimated by assuming that all measurements had an error of 1% for SWE, which is the maximum observation error of the SNOTEL snow pillow instrument according to the manufacturer (Rickly Hydrological Company, Columbus, OH, USA).

### Calculating GSL

In other studies linking NEP and GSL, the start of the growing season was determined when positive daily cumulative NEP was first detected using eddy flux techniques (Churkina *et al.*, 2005), or when greening was detected in broadleaf forests (Goulden *et al.*, 1996; White *et al.*, 1999), and the growing season ended when daily cumulative NEP became negative or the leaves senesced. In some studies using eddy flux techniques, measurement of carbon uptake period was used instead of GSL because small amounts of CO<sub>2</sub> uptake were observed before daily cumulative NEP became positive (Baldocchi & Wilson, 2001; Churkina *et al.*, 2005). In contrast, in coniferous forests, NEP can become positive weeks or even months before buds break (J. Hu, unpublished results). During the transition from winter to spring, our site often experienced days when cumulative daily NEP oscillated between positive and negative during a weeklong period. After this initial oscillation period, cumulative daily NEP in some years remained positive (e.g. 2005), but relatively low for up to 3 weeks; in other years, cumulative daily NEP remained positive and began to increase quickly within 1 week (e.g. 1999) (Fig. 1). During years with a long spring turn on, cumulative daily NEP might be positive, but because daily NEP rates were so low, carbon uptake during the early spring was only a small fraction of the total annual NEP. However, during years with a short spring turn on, cumulative daily NEP rates were high, and carbon sequestration during this period was a significant fraction of the total annual NEP (Fig. 1). In our analysis, we took a different approach to determine the start and end of the growing season, which emphasized the kinetics



**Fig. 1** Daily NEP during springtime for years 1999 and 2005. In 1999, the period when NEP became and remained positive was short (4 days); in 2005, this same period was longer (20 days). The gray lines indicate the start and end of the period when NEP oscillates between negative and positive. NEP, net ecosystem productivity.

of spring and autumn response to seasonal climate. In order to account for this variation, we first calculated a regression between NEP and date, and we varied the number of days used in the regression from 3 to 9 days (analogous to the rate of change in daily NEP over a 3–9 day period). Ranging the number of days for our regression analysis allowed us to calculate the error associated with determining GSL. Using the different slopes of NEP for regressions between 3–9 days, we determined the start of the growing season as the day when the slope was the steepest. We believed this to be a better indicator of the start of the growing season because the method was informed by the rate *and* sign of the photosynthetic and respiratory responses to the beginning of the growing season, rather than the sign alone.

To determine the end of the growing season, we used the same regression approach, but instead we chose the day when the slope was the shallowest. We chose to use a shallow slope because unlike spring, daily NEP during the fall gradually became negative. In order to ensure that the days we determined to be the start and end of the growing season encompassed a period when most of the annual NEP occurred, we calculated the fraction of positive NEP between the start and end dates. Over the 9-year period, our definition of GSL captured more than 96% of the total NEP. Therefore, in our analysis, GSL is defined as the period when there was positive carbon uptake occurring in the forest between the start and end dates of the growing season.

#### *Collecting branches, soil, and water samples*

During the growing seasons of 2005, 2006, and 2007, branches of the three dominant tree species: lodgepole pine, subalpine fir, and Engelmann spruce, were collected every 2 weeks. The first collection began with the onset of snow melt and immediately (within 2–3 days) after the forest NEP became positive, indicating photosynthesis and net carbon uptake had been initiated by the forest. The last collection occurred in late August/early September, as nighttime temperatures began to fall. Eight branches from the three species were collected into a glass vial, sealed with Parafilm, and kept cool in an ice chest until they could be frozen in the laboratory (within the same day of collection). During the same time of branch collection, a soil pit was dug and soil samples were collected at 5-cm depth intervals. Due to the rocky nature of the site, soil pits were usually limited to 35 cm in total depth. Ground water (collected from a well), creek water, and rainwater were also collected during these dates. Rainwater was collected using a Nalgene container fitted with a funnel and screen. Mineral oil was poured into the rain container

to prevent evaporation of rainwater. The rainwater was collected every week or 2 weeks during the summer, depending on the amount of precipitation falling at the site.

In early April in 2005, 2006, and 2007, 10 snow pits were dug along a 240-m transect. A column of snow was collected using a capped PVC pipe. The 10 snow profiles were allowed to melt in the laboratory and the water was then collected in a glass vial, sealed with Parafilm and kept in a refrigerator until further analysis. During the spring of 2008, additional snow samples and corresponding soil samples were collected from one pit. From April 9 to May 29, a snow profile was collected from an existing snow pit every week to see if the snow pack oxygen and hydrogen isotopes changed as the snow pack melted. Soil from underneath the snow profile was also collected and water was extracted. A 'deuterium-excess' plot ( $\delta^{18}\text{O}$  vs.  $\delta\text{D}$ ) was used to check for enrichment of snow melt and rain water (Craig, 1961).

#### *Extracting water from branches and soils*

Branch and soil samples were extracted using cryogenic water distillation (Ehleringer *et al.*, 2000). Under vacuum conditions, the sample (branch or soil) was unsealed and placed into a glass tube and immersed in boiling water. The evaporated water from the branch or soil sample was then collected in another glass tube that was immersed in liquid nitrogen. In order to ensure that all the water was extracted from the soil or branch sample, the extracted samples were weighed and placed in a drying oven for 4 days before reweighing. We observed no difference in weight after drying. We also plotted a 'deuterium-excess' plot to check for enrichment in soil water below 10 cm, since upper soils tend to be enriched in  $^{18}\text{O}$  and  $^2\text{H}$  due to evaporative enrichment.

#### *Analysis of stable isotopes and construction of mixing model*

All water samples: snow, ground, creek, rain, extracted branch, and extracted soil samples were sent to the Stable Biogeochemistry Lab at the University of California at Berkeley for analysis. Both oxygen and hydrogen isotopes were analyzed on all the water samples. Because the results using both isotopes produced the same results, we present all the data using  $\delta\text{D}$ . Stable isotope ratios of hydrogen and oxygen were expressed using  $\delta$  notation (units of ‰):

$$\delta\text{D} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000, \quad (1)$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the molar ratios of D/H of the sample and standard water (V-SMOW), respectively.

The  $\delta D$  results of snow, rain, and ground water are shown in Table 2.

A two member mixing model was used to trace water use (Williams & Ehleringer, 2000). The model assumes two different compartments within the soil profile: the top soil reflecting rainwater and the deeper soils reflecting snow melt water:

$$\delta D_{\text{twig}} = \delta D_{\text{rain}}f + \delta D_{\text{snow}}(1 - f), \quad (2)$$

where  $\delta D_{\text{twig}}$ ,  $\delta D_{\text{rain}}$ , and  $\delta D_{\text{snow}}$  are the isotopic composition of the twig water, rainwater, and snow melt, respectively, and  $f$  is the fraction of rainwater in the twig. Rearranging Eqn (1), we can solve for the fraction of twig water from rain:

$$f = (\delta D_{\text{twig}} - \delta D_{\text{snow}}) / (\delta D_{\text{rain}} - \delta D_{\text{snow}}). \quad (3)$$

When constructing the mixing model, for the first end-member, we used the date of rainwater  $\delta D$  that most closely corresponded to the date of twig collection. We used snow melt as the second end-member. The values provided in Table 2 were used for the mixing models.

#### *Simplified Photosynthesis EvapoTranspiration (SIPNET) model*

The SIPNET model, based on the PnET (Photosynthesis-EvapoTranspiration) family of models (Aber & Federer, 1992; Aber *et al.*, 1995, 1996), was simplified to decrease the number of free parameters and run time (Braswell *et al.*, 2005; Sacks *et al.*, 2006, 2007). SIPNET contains two vegetation carbon pools and an aggregated soil carbon pool and simulates the carbon dynamics between these pools and the atmosphere. The vegetation pool is split into leaves and wood, where 'wood' refers to the combined pool of boles, branches, and roots. The model performs two time steps per day: day and night. The lengths of the day and night time steps in the model varied seasonally to account for changes in day length; fluxes were appropriately scaled for these changes in the length of the time steps.

Both NEP and ET (evapotranspiration) observations were used to parameterize the SIPNET model. Using the protocol and parameter starting values detailed in Moore *et al.* (2008), we estimated 17 of the 32 model parameters using a variation of the Metropolis algorithm (Metropolis *et al.*, 1953) modified by Hurtt & Armstrong (1996). The remaining 15 parameters were held constant at values estimated from the literature and from field studies at the Niwot Ridge site because they were difficult to estimate independently from the eddy flux data or because they had little or no effect on modeled NEE. The scheme used to assess the maximum likelihood outcomes of the model are discussed in detail

in Braswell *et al.* (2005), Sacks *et al.* (2006) and the parameter values used are listed in Moore *et al.* (2008).

The model was conditioned on half-daily NEP averages from the observed eddy flux data, to partition NEP into its photosynthetic (GPP) and respiratory components ( $R_E$ ). In this data assimilation and analysis, GPP was constrained by the entire NEP flux record from 1999 through 2007 through maximum likelihood parameter optimizations. We used the isotopic partitioning of rainwater vs. snow water for 2005 through 2007, presented in Fig. 5b, to calculate the fraction of annual GPP driven by rainwater vs. snow water.

#### *Statistical analysis*

For analysis of the relationship between GSL and NEP, GSL and SWE, and SWE and first day of the growing season, we first ran a Spearman's correlation analysis to generate  $R^2$ -values for these relationships. We then used a reduced major axis regression analysis following Ricker (1973) to account for the uncertainties in GSL, NEP, and SWE (Matlab R2008b). To test for differences in  $\delta D$  of xylem water between lodgepole pine, Engelmann spruce, and subalpine fir, we ran an ANOVA (PROC MIXED; SAS, The SAS Institute, Version 9.1, Cary, NC, USA) to test for the effects of species and day of year. *Post hoc* analysis was performed using Tukey's pairwise comparison (among species) and significance was found when  $P \leq 0.05$ .

## **Results**

### *Meteorological measurements*

For the 9 years of our NEP measurements, the precipitation pattern varied significantly from year to year (Table 1). For example, the SWE in 2007 (58.69 cm) was more than double the SWE in 2002 (27.18 cm), and summer precipitation in 2004 (39.98 cm) was almost double that of 2003 (21.34 cm). Furthermore, the length of the growing season also varied significantly year to year (Table 1). Interannual air temperatures during all 9 years, however, did not vary. For example, the spring air temperature during most years was between 6 and 7 °C, with the exception of 2002 and 2006. The average growing season temperature for all 9 years only ranged from 8.44 °C in 2004 to 10.70 °C in 2007.

The 3 years (2005, 2006, 2007) of hydrogen isotope collections were representative of hydrological dynamics observed during the entire 9 years in the analysis of Fig. 2. The mean cumulative SWE for the winters of 2005, 2006, and 2007 were 17% higher (57.4 cm), 10% lower (43.9 cm), and 22% higher (59.8 cm) than the 9-year mean (49.1 cm), respectively. Total summer rainfall

**Table 1** Climate patterns for the 9 years of net ecosystem exchange measurements

Year	Cumulative SWE (cm)	Maximum SWE (cm)	Date of maximum SWE	Dates of the growing season	Rain (cm)
1999	53.09	14.70	5/5	5/19–10/11	38.80
2000	40.64	11.60	3/23	4/25–10/22	30.55
2001	35.81	9.80	4/23	5/5–10/18	38.18
2002	27.18	7.00	3/27	4/25–10/21	29.19
2003	52.58	15.80	4/8	5/14–10/17	21.34
2004	51.31	11.60	4/26	5/6–10/14	39.98
2005	57.4	13.40	5/4	5/21–10/24	26.23
2006	43.94	12.80	4/3	4/28–10/11	24.03
2007	58.69	17.90	4/27	5/7–10/9	31.23

SWE, snow water equivalent.

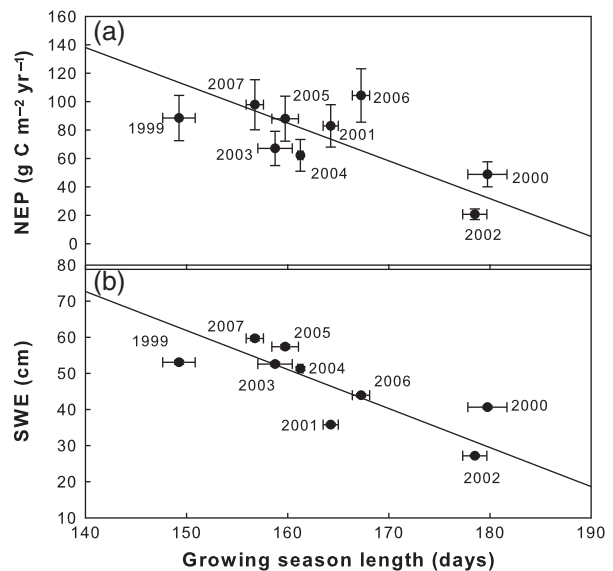
Year	Air <i>T</i> 2 weeks before snow melt	Spring air <i>T</i> (°C)	Growing season air <i>T</i> (°C)	Soil moisture June 1 (m <sup>3</sup> m <sup>-3</sup> )	Soil moisture July 15 (m <sup>3</sup> m <sup>-3</sup> )
1999	0.92	6.10	9.67	n/a	n/a
2000	1.89	6.24	9.71	n/a	n/a
2001	1.27	6.57	10.23	n/a	n/a
2002	1.08	3.75	9.54	0.16	0.08
2003	0.06	7.36	10.41	0.31	0.09
2004	1.36	6.05	8.44	0.22	0.12
2005	4.58	6.65	10.11	0.30	0.09
2006	1.66	2.08	9.83	0.16	0.13
2007	2.27	6.21	10.70	0.31	0.07

These patterns include: cumulative snow water equivalent (cum SWE), max SWE, date of max SWE, date of the growing season, total rain, average air temperature 2 weeks before snow melt, average spring air temperature, average growing season air temperature, soil moisture on June 1, and soil moisture on July 15. SWE, snow water equivalent.

amounts were 15% lower (26.2 cm), 22% lower (24 cm), and 1% higher (31.2 cm) than the 9-year mean (30.8 cm), respectively.

#### Relationship between GSL, NEP, and SWE

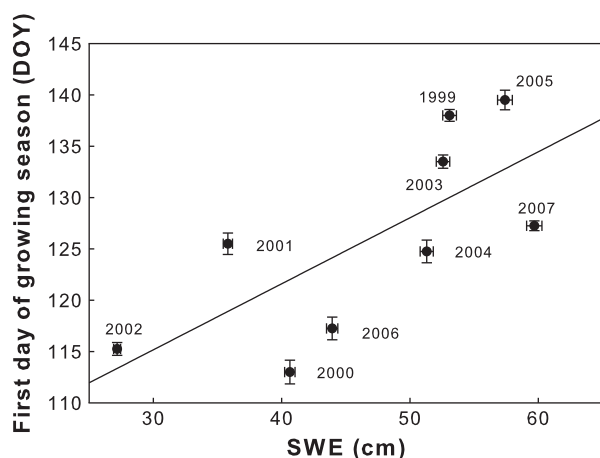
We found a significant negative correlation between GSL and NEP ( $P = 0.04$ ,  $R^2 = 0.42$ ,  $NEP = -2.66 \times GSL + 510.51$ ) for 9 years of eddy flux data, indicating that years with the longest growing seasons were correlated with the lowest annual rates of forest CO<sub>2</sub> uptake (Fig. 2a). Using the SWE data from the SNOTEL database, we also found a significant, negative correlation between SWE and GSL ( $P = 0.01$ ,  $R^2 = 0.61$ ,  $SWE = -1.08 \times GSL + 223.87$ ), suggesting that smaller winter snow pack occurred during years with a longer



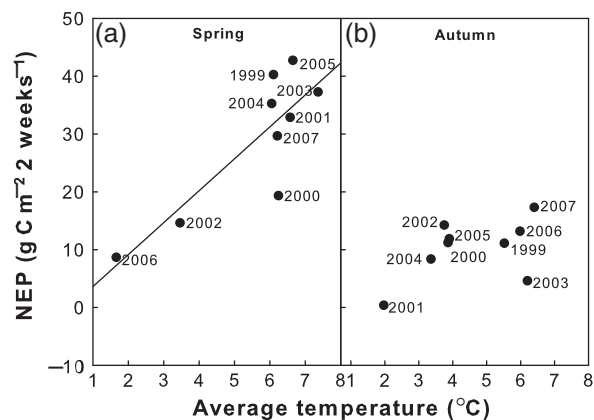
**Fig. 2** (a) Relationship between annual GSL and NEP for 9 years. A significant, negative relationship between GSL and NEP ( $P = 0.04$ ,  $R^2 = 0.47$ ,  $NEP = -2.66 \times GSL + 510.51$ ) demonstrate that longer growing seasons are correlated with lower annual rates of carbon sequestration by the forest. Vertical error bars correspond to 18% randomly generated NEP errors and horizontal error bars correspond to error in calculating the start and end of the growing season. (b) A significant, negative relationship between GSL and SWE ( $P = 0.01$ ,  $R^2 = 0.61$ ,  $SWE = -1.08 \times GSL + 223.87$ ) demonstrates that years with a longer growing season are correlated with less available snow melt water. Horizontal error bars correspond to 1% instrument error. NEP, net ecosystem productivity; GSL, growing season length; SWE, snow water equivalent.

GSL (Fig. 2b). For example, in 1999, a large snow pack delayed the onset of spring and reduced GSL to only 146 days, but annual NEP was one of the highest during the 9-year period. Contrary to 1999, in 2002, the snow pack melted earlier and extended the growing season to 179 days, but resulted in the lowest NEP during the observation period. Overall, we found a significant, positive relationship between SWE and the first day of the growing season ( $P = 0.03$ ,  $R^2 = 0.51$ ,  $DOY = 0.64 \times SWE + 95.87$ ); years with a later start of the growing season were correlated with a deeper winter snow pack (Fig. 3).

During the 9-year period, we found the lengthening of the growing season was more likely due to an earlier onset of spring than a later onset of winter. The end of the growing season date in the autumn varied by 2 weeks (October 9–October 24), but the beginning of the growing season date in the spring varied by nearly 4 weeks (April 25–May 21). We found there was no significant correlation between autumn temperature and NEP either in terms of absolute rate or percentage



**Fig. 3** Relationship between SWE and the first day of the growing season, expressed in day of year (DOY). The relationship is significant ( $P = 0.03$ ,  $R^2 = 0.51$ ,  $\text{DOY} = 0.64 \times \text{SWE} + 95.87$ ), and demonstrates that years with a large snow pack delayed the start of the growing season. Vertical error bars correspond to error associated with determining the start of the growing season and horizontal error bars correspond to 1% instrument error. SWE, snow water equivalent.



**Fig. 4** (a) The relationship between the average temperature during the first 2 weeks of spring and the first 2 weeks of spring NEP. There was a significant and positive relationship between spring temperature and spring NEP ( $P = 0.0048$ ,  $R^2 = 0.7$ ,  $\text{NEP} = 5.5 \times T - 1.91$ ). (b) The relationship between the average temperature during the last 2 weeks of autumn and the last 2 weeks of autumn NEP. There was no significant relationship between temperature and NEP ( $P = 0.18$ ). NEP, net ecosystem productivity.

of the annual cumulative NEP (Fig. 4b). We also found no relationship between mean winter temperature and cumulative winter NEP. However, we did find a significant relationship between average temperature and NEP during the first 2 weeks of the growing season ( $P = 0.0048$ ,  $R^2 = 0.7$ ) (Fig. 4a).

#### Hydrogen isotope ( $\delta D$ ) of water sources

The  $\delta D$  of snow melt water during the first week of April for all 3 years was:  $-146\text{‰}$  (2005),  $-149\text{‰}$  (2006), and  $-150\text{‰}$  (2007) (Table 2, Fig. 5a). The isotopic signature of ground water was slightly enriched compared with the snow melt water signature ( $-129 \pm 0.1\text{‰}$  mean for all 3 years), and remained constant through the entire growing season (Fig. 5a). The isotopic signature of collected rainwater varied through the season (Table 2, Fig. 5a). Soil water collected from 0 to 5 cm depth had an isotopic signature that most often tracked that of summer rain, except for the early summer in 2007 wherein the winter snow pack lingered well into June (Fig. 5a). The isotopic signature of soil water collected from 30 to 35 cm was most similar to ground water for the entire growing season. One exception to these patterns was in 2006, when a large rain event in early July caused soils at 35 cm to shift from a snow-like to a rain-like signature, relatively quickly. In 2008, the seven samples of snow pack collected at weekly intervals from April 9 to May 29 showed no enrichment of the snow pack during melt. The  $\delta D$  of snow melt ranged from  $-163\text{‰}$  to  $-158\text{‰}$  for April 9 and May 29, respectively, with an average value of  $-160 \pm 0.8$ . From the deuterium excess plot for snow melt, rain, and extracted soil water, we found that the slope of all three water sources were close to that of the meteoric water line (Fig. 6). The relationship between  $\delta^{18}\text{O}$  and  $\delta D$  for the three water sources were: snow melt  $\delta D = 5.48 \times \delta^{18}\text{O} - 40.54$ ,  $R^2 = 0.95$ , rain  $\delta D = 7.20 \times \delta^{18}\text{O} + 3.70$ ,  $R^2 = 0.98$ , and soil water  $\delta D = 8.52 \times \delta^{18}\text{O} + 7.06$ ,  $R^2 = 0.95$ .

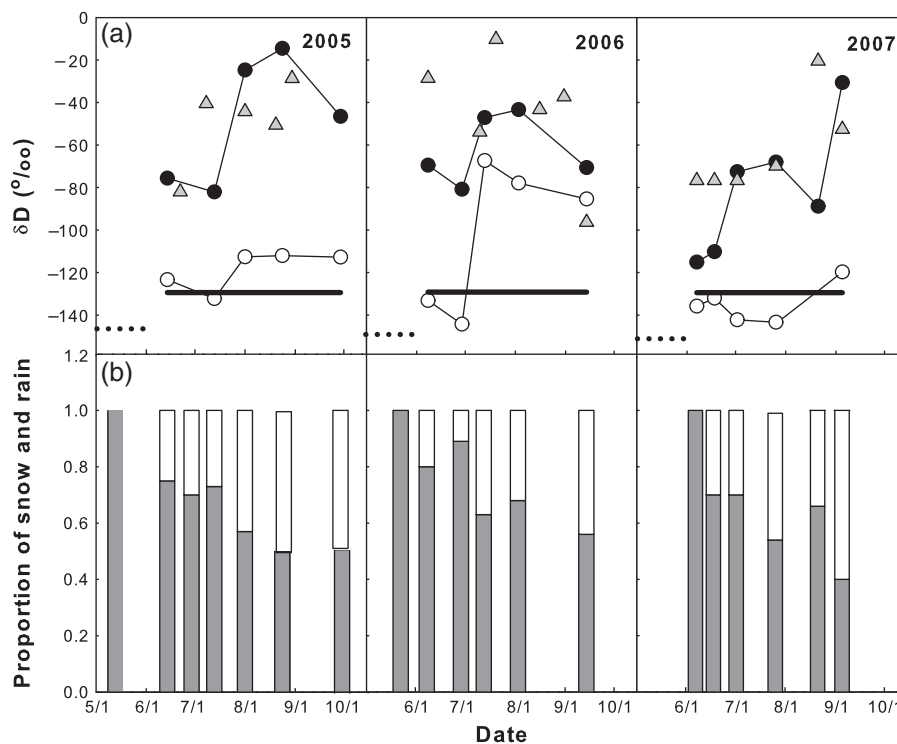
The  $\delta D$  of extracted xylem water for lodgepole pine, Engelmann spruce, and subalpine fir were not statistically different from one another throughout the growing season. Therefore, we binned the results of individual species  $\delta D$  into a 'conifer'  $\delta D$  value. In 2005, the xylem water  $\delta D$  ranged from  $-120 \pm 2\text{‰}$  to  $-85 \pm 4\text{‰}$ ; in 2006, the  $\delta D$  ranged from  $-135 \pm 1\text{‰}$  to  $-99 \pm 6\text{‰}$ ; and in 2007 the  $\delta D$  ranged from  $-133 \pm 2\text{‰}$  to  $-90 \pm 4\text{‰}$  (Table 2).

#### Mixing model and SIPNET

The results from the mixing model showed that all three dominant tree species relied heavily on snow melt water throughout the entire growing season (Fig. 5b). In all 3 years, at the start of the growing season, all the trees relied completely on snow melt water, and then began to use some rain during the middle to late growing season. In 2006, all tree species relied more on snow melt water, compared with 2005 or 2007. However, we found that in all 3 years, even late into

**Table 2**  $\delta D$  (‰) of snow melt, rain water, and xylem water for 2005, 2006, and 2007

Date	Snow melt ( $\delta D$ )	Date	Rain water ( $\delta D$ )	Date	Xylem water ( $\delta D$ )		
4/1/05	-146.18	6/22/05	-81.99	5/13/05	-120.24 $\pm$ 0.89		
		7/8/05	-40.46	6/14/05	-117.48 $\pm$ 4.38		
		8/1/05	-44.23	6/29/05	-111.19 $\pm$ 4.23		
		8/20/05	-50.57	7/13/05	-102.02 $\pm$ 4.11		
		8/30/05	-28.63	8/1/05	-92.51 $\pm$ 1.35		
		9/10/05	-12.88	8/24/05	-85.53 $\pm$ 3.337		
		9/30/05	-37.98	9/29/05	-94.35 $\pm$ 3.91		
		4/5/06	-149.0	6/8/06	-28.6	5/23/06	-135.38 $\pm$ 0.70
				7/10/06	-53.9	6/8/06	-123.30 $\pm$ 1.80
				7/20/06	-10.2	6/29/06	-115.29 $\pm$ 4.16
8/6/06	-43.3			7/13/06	-113.55 $\pm$ 6.76		
8/31/06	-37.3			8/3/06	-104.44 $\pm$ 4.76		
4/10/07	-150.5	9/16/06	-36.3	9/14/06	-98.98 $\pm$ 3.09		
		7/6/07	-76.7	6/7/07	-132.96 $\pm$ 0.50		
		7/26/07	-69.9	6/18/07	-128.20 $\pm$ 5.68		
		8/9/07	-72.8	7/2/07	-128.12 $\pm$ 2.73		
		8/21/07	-20.4	7/26/07	-113.94 $\pm$ 4.17		
		9/6/07	-52.6	8/21/07	-106.59 $\pm$ 2.38		
		9/27/07	-53.5	9/5/07	-89.46 $\pm$ 10.31		

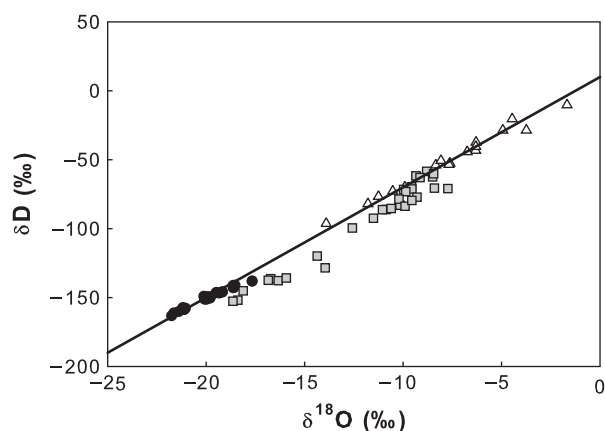


**Fig. 5** (a)  $\delta D$  of soil water profiles collected throughout a growing season in 2005, 2006, and 2007. Black circles are soil water samples collected from the top of the soil pit and white circles are soil water samples collected from 35 cm depth. Triangles represent the  $\delta D$  of rainwater, the black line represents ground water, and the dotted line represents snow melt. (b) Average percent snow (gray) vs. rain (white) water extracted from branch samples of the three dominant tree species: lodgepole pine, subalpine fir, and Engelmann spruce ( $n = 5$  for each species). A two point mixing model was used, with snow melt as one end member and different rain collections throughout the growing season as the second end member.

the growing season, 57–68% of the xylem water reflected the isotopic signature of snow water. Using SIPNET we found that in all 3 years, the highest rates of GPP occurred when the trees were using predominantly snow melt water (Fig. 7). For 2005, 2006, and 2007, annual GPP was 67% 77%, and 71% dependent on snow melt water respectively.

## Discussion

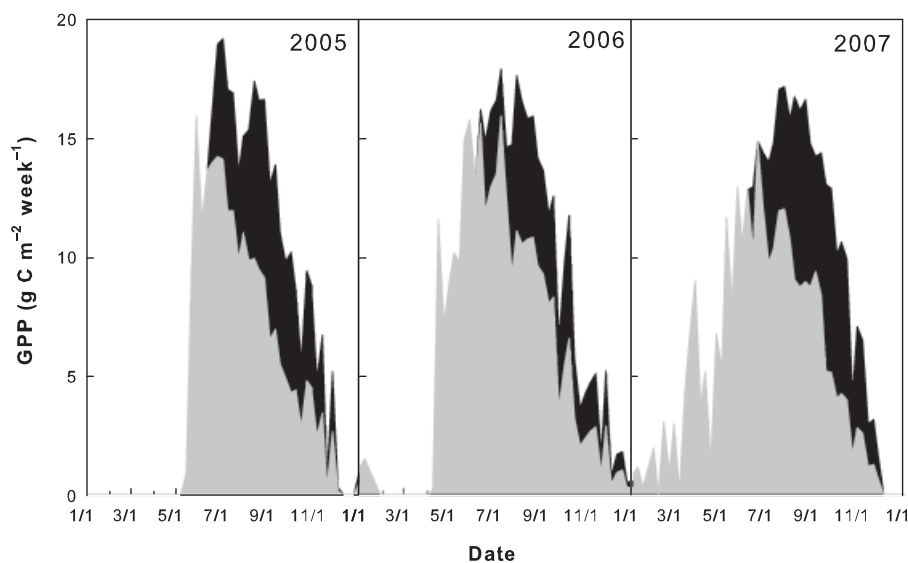
We found a negative relationship between GSL and NEP using 9 years of continuous eddy flux data. Furthermore, we discovered that the negative impact



**Fig. 6** The relationship between  $\delta^{18}\text{O}$  and  $\delta\text{D}$  for snow melt (solid circles), rain (open triangles), and extracted soil water below 10-cm depth (gray squares). The solid line represents the global meteoric water line.

of an earlier start of spring on annual NEP was due to the dependence of photosynthetic  $\text{CO}_2$  uptake on snow water through most of the growing season, and the failure of summer rains to compensate for years with earlier springs and shallower snow packs. Our isotopic results from the three dominant tree species combined with the SIPNET model provided additional evidence that highest rates of GPP occurred when the trees were using predominantly snow melt water.

Lower reliance on summer rain could be attributed to two reasons: (1) the trees were tapping into a deeper and more consistent water source during the growing season, and (2) rain events, although frequent during the summer, were too small to penetrate deeply into the soils. Previous studies have found subalpine conifers to possess a mat of shallow fine roots, and several forestry studies have shown that roots of lodgepole pine, one of the dominant species at the site, tend to grow more laterally than vertically (Bishop, 1962; Nicoll *et al.*, 2006). However, our results from the isotope sampling suggest that all three species were accessing water deeper than 35 cm. Rain events typically hydrated only the upper soils and rarely reached depths between 30 and 35 cm. The one exception was in 2006, when a large 3-day rain event occurred on July 6 and saturated the soils down to 35 cm. This large rain event brought 104 mm of rain in 3 days and was the largest rain in all 3 years (the next largest 5-day rain event in 2007 only brought 51 mm of rain). Reynolds & Knight (1973) found that in the subalpine forest, rain events <10 mm were either intercepted by the canopy, or absorbed by forest litter on the soil surface, and rarely penetrated to deep soil layers. In



**Fig. 7** Gross primary productivity (GPP) modeled using SIPNET for 2005, 2006, and 2007. Gray areas represent snow contributed GPP and black areas represent rain contributed GPP. Annual net ecosystem productivity (NEP) for each year is as follows: 2005 ( $88\text{ gC m}^{-2}\text{ yr}^{-1}$ ), 2006 ( $104\text{ gC m}^{-2}\text{ yr}^{-1}$ ), and 2007 ( $98\text{ gC m}^{-2}\text{ yr}^{-1}$ ).

**Table 3** Precipitation data for 2005 through 2007

Year	Days of rain	Average rain event (mm)	Percent of rain > 10 mm (%)	Average no. days between rain events	Total rain (mm)
2005	63	4.16 ± 0.69	7.90	3.30	262
2006	56	4.37 ± 1.25	10.70	3.90	240
2007	78	4.00 ± 0.54	10.20	2.58	312

Data are from May 1 to September 30. During the 3 years, the percentage of days with rain events > 10 mm was < 11%. The precipitation regime during the 2006 growing season was characterized by few, but larger rain events, while 2005 was characterized by more frequent, but smaller rain events. The growing season of 2007 experienced the most frequent rain events.

all 3 years of our study, 11% or less of all summer rain events were > 10 mm (Table 3). Reynolds & Knight (1973) also found that 60% of all water intercepted by the surface litter evaporated within 4 days, rendering it accessible to near-surface roots for only short periods of time. The average number of days between rain events for the 3 years of our study was 3.3 days. The relatively small and infrequent rain events may explain why the trees were not able to effectively utilize summer precipitation as a consistent water source.

The general pattern of CO<sub>2</sub> uptake by the Niwot Ridge forest reflects seasonal maximum rates during the initial few weeks of the growing season, with relatively low rates during the autumn (Sacks *et al.*, 2007). Thus, it is during the spring, not autumn, when changes in GSL are most likely to affect the annual rate of NEP. Furthermore, unlike Piao *et al.* (2008), we did not find a relationship between autumn temperatures and NEP. In fact, studies in the subalpine forest have found lodgepole pine to respond positively to warmer autumns by increasing productivity (Villalba *et al.*, 1994; Kueppers & Harte, 2005), which is opposite to the trend found by Piao *et al.* (2008). We did, however, find a positive, significant relationship between average temperature and NEP during the first 2 weeks of the growing season. Thus, while spring warming is clearly associated with longer GSL, it cannot explain the overall reduction in NEP during years with longer GSL.

In our study, the negative correlation between GSL and NEP stands in contrast to some previous studies. Using 28 different ecosystems, varying from grasslands to forest, Churkina *et al.* (2005) found GSL and NEP to be positively correlated. In this type of analysis, however, GSL was one of several spatially varying controls of ecosystem function, including aspects of community species composition, canopy structure, and deep historical influences on ecosystem formation and evolution. We focused on temporal (interannual) variation in GSL at a single site, keeping ecosystem type and history nearly constant. This allowed us to more clearly focus on GSL as a controlling variable. Our results also differed from some single-site studies conducted in

broadleaf forest ecosystems, where a positive relationship between GSL and NEP was observed (Goulden *et al.*, 1996; White *et al.*, 1999; Black *et al.*, 2000; Baldocchi & Wilson, 2001; White & Nemani, 2003). There may be a fundamental difference between broadleaf and needle leaf forests in their responses to climate change, especially those needle-leaf forests native to mountain ecosystems in the Western US. At the initiation of the seasonal spring warm up, western coniferous forests are able to reach maximum rates of CO<sub>2</sub> uptake quickly, and sustain those rates as long as snow melt water is available and temperatures are favorable (Monson *et al.*, 2005). Broadleaf forests, in contrast, reach maximum rates of CO<sub>2</sub> uptake during the middle of the summer (Wofsy *et al.*, 1993). An earlier spring warm-up may actually promote overall CO<sub>2</sub> uptake by broadleaf forests in allowing them to break their buds earlier and reach maximum canopy leaf area index earlier in the summer, effectively extending the mid-summer period of maximum CO<sub>2</sub> uptake. Thus, the annual rate of CO<sub>2</sub> uptake may be more tightly linked to mid-summer climate regimes in the case of broadleaf forests, and more tightly linked to spring climate regimes in the case of mountain coniferous forests.

Our observation that longer growing seasons were correlated with less annual carbon uptake in the subalpine forest also contrasts with observations made in boreal forest ecosystems. Generally, boreal forests assimilate carbon at higher rates in the face of earlier springs (Bergeron *et al.*, 2007). The differences in these observations may be due to the fact that boreal forests are less dependent on the spring snow pack to sustain annual GPP, and springtime GPP may be less important as an overall determinant of annual cumulative GPP, compared with our observations in the subalpine forest. In fact, the greatest influence of springtime climate on annual NEP in the boreal forests was temperature, and the mid-summer responses of ecosystem respiration to temperature and moisture were significant determinants of annual NEP (see also Angert *et al.*, 2005; Goetz *et al.*, 2005). Perhaps the largest difference between the subalpine and boreal forest is the lack of permafrost in

the subalpine forest. In some boreal forests, melting of permafrost during the summer can supply the trees with additional moisture (Bergeron *et al.*, 2007; Dunn *et al.*, 2007), potentially reducing the influence of winter snow pack on summer GPP.

Net primary productivity in mountainous regions of the Western US is susceptible to precipitation limitations due to reductions in snow pack and earlier spring snow melt (Monson *et al.*, 2005; Sacks *et al.*, 2006; Moore *et al.*, 2008). Recently studies of tree mortality across the Western US have proposed water deficit as one of the contributing factors (van Mantgem *et al.*, 2009). Snow packs and streamflows in the Western US have decreased in the past three-to-four decades due to warmer winter temperatures (Mote *et al.*, 2005; Kalra *et al.*, 2008), and the seasonality of snow melt has shifted to earlier in the spring (Aguado *et al.*, 1992; Dettinger & Cayan, 1995; Regonda *et al.*, 2005). Our analysis indicates that earlier spring warming and reduced winter snow pack, both of which occur with an increase in GSL, are associated with reductions in forest carbon sequestration. Future climate change in the Western US is likely to bring even warmer winters and further reductions in snow pack. Warmer summers may also bring more summer precipitation. In the Rocky Mountain region, future climate change is predicted to cause air temperatures to increase by 3.5 °C over the next century and, while snow fall is predicted to decrease by 50%, summer precipitation is predicted to increase by 54% to 184% (Baldwin *et al.*, 2003). Based on our results, however, it is not likely that this increase in summer precipitation will offset the decrease in carbon uptake that results from decreased snow fall. Although our study highlighted some of the uncertainties about the response of NEP to climate change in different ecosystems, we have provided evidence that increases in GSL for the subalpine forest ecosystem, one of the principal carbon sinks in the Western US, may not lead to higher rates of carbon sequestration.

## Conclusions

Using 9 years of eddy flux data, we found a negative relationship between GSL and NEP in a subalpine forest. This negative relationship was due to year-to-year variability in snow pack; years with a deeper snow pack resulted in shorter GSL, while years with shallower snow pack resulted in longer GSL. We also demonstrated that this negative relationship was due to the dependence of forest carbon uptake on snow melt water. Using SIPNET, we found that approximately 70% of the annual GPP was supported by snow melt water. The lack of summer rain use by the trees appears to be influenced largely by the size of precipitation events.

Since small and infrequent rain events could not penetrate the soil surface, the trees were forced into even greater dependence on snow melt water. If larger rain events were to increase in frequency in the future, or if spring snow storms were converted to spring rain storms with no overall loss in water content, some of the negative effects of the earlier spring on winter snow pack may be mitigated. In the absence of compensating rain, however, and with continued decreases in snow pack in the face of continued positive winter temperature anomalies, we predict that the strength of the current terrestrial carbon sink in high elevation forests of the Western US will be even further diminished.

## Acknowledgements

This research was supported with funds from the Western Section of the National Institute for Climate Change Research (NICCR) (Award MPC35TX-A2) administered by Northern Arizona University, and two grants from the US National Science Foundation (Biocomplexity Program; Grant EAR 0321918 and Doctoral Dissertation Improvement Program; Grant DEB 0709252). We would also like to thank our two anonymous reviewers and Michael White for providing helpful comments with this manuscript.

## References

- Aber JD, Federer CA (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*, **92**, 463–474.
- Aber JD, Ollinger SV, Federer CA *et al.* (1995) Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research*, **5**, 207–222.
- Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO<sub>2</sub> exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia*, **106**, 257–265.
- Aguado E, Cayan D, Riddle L, Roos M (1992) Climatic fluctuations and the timing of West-Coast streamflow. *Journal of Climate*, **5**, 1468–1483.
- Angert A, Biraud S, Bonfils C *et al.* (2005) Drier summers cancel out the CO<sub>2</sub> uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 10823–10827.
- Baldocchi DD, Wilson KB (2001) Modeling CO<sub>2</sub> and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. *Ecological Modelling*, **142**, 155–184.
- Baldwin C, Wagner F, Lall U (2003) Rocky mountain/great basin regional climate-change assessment report for the U.S. Global change research program. In: *Water Resources* (ed. Wagner F), pp. 79–112. Utah State University, Logan.
- Bergeron O, Margolis HA, Black TA, Coursolle C, Dunn AL, Barr AG, Wofsy SC (2007) Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada. *Global Change Biology*, **13**, 89–107.

- Bishop DM (1962) Lodgepole pine rooting habits in Blue Mountains of Northeastern Oregon. *Ecology*, **43**, 140–142.
- Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.
- Braswell BH, Sacks WJ, Linder E, Schimel DS (2005) Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology*, **11**, 335–355.
- Canadell JG, Le Quere C, Raupach MR *et al.* (2007) Contributions to accelerating atmospheric CO<sub>2</sub> growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866–18870.
- Cao MK, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Churkina G, Schimel D, Braswell BH, Xiao XM (2005) Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology*, **11**, 1777–1787.
- Craig H (1961) Isotopic variations in meteoric waters. *Science*, **133**, 1702–1703.
- Cramer W, Bondeau A, Woodward FI *et al.* (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Dettinger MD, Cayan DR (1995) Large-scale atmospheric forcing of recent trends toward early snowmelt runoff in California. *Journal of Climate*, **8**, 606–623.
- Dunn AL, Barford CC, Wofsy SC, Goulden ML, Daube BC (2007) A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends. *Global Change Biology*, **13**, 577–590.
- Ehleringer J, Roden J, Dawson T (2000) Assessing ecosystem-level water relations through stable isotope ratio analysis. In: *Methods in Ecosystem Science* (eds Sala O, Jackson R, Mooney H, Howarth R), pp. 181–198, Springer, New York City.
- Goetz SJ, Bunn AG, Fiske GJ, Houghton RA (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 13521–13525.
- Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC (1996) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science*, **271**, 1576–1578.
- Griffis TJ, Black TA, Morgenstern K *et al.* (2003) Ecophysiological controls on the carbon balances of three southern boreal forests. *Agricultural and Forest Meteorology*, **117**, 53–71.
- Hunter T, Tootle G, Piechota T (2006) Oceanic-atmospheric variability and western US snowfall. *Geophysical Research Letters*, **33**, L13706, doi: 10.1029/2006GL026600.
- Hurt GC, Armstrong RA (1996) A pelagic ecosystem model calibrated with BATS data. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **43**, 653–683.
- IPCC (2007) *IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), 966 pp. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Kalra A, Piechota TC, Davie SR, Tootle GA (2008) Changes in US streamflow and western US snowpack. *Journal of Hydrologic Engineering*, **13**, 156–163.
- Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. *Nature*, **382**, 146–149.
- Kueppers LM, Harte J (2005) Subalpine forest carbon cycling: short- and long-term influence of climate and species. *Ecological Applications*, **15**, 1984–1999.
- Metropolis N, Rosenbluth AW, Rosenbluth MN, Teller AH, Teller E (1953) Equation of state calculations by fast computing machines. *Journal of Chemical Physics*, **21**, 1087–1092.
- Monson RK, Sparks JP, Rosenstiel TN *et al.* (2005) Climatic influences on net ecosystem CO<sub>2</sub> exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest. *Oecologia*, **146**, 130–147.
- Monson RK, Turnipseed AA, Sparks JP, Harley PC, Scott-Denton LE, Sparks K, Huxman TE (2002) Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, **8**, 459–478.
- Moore DJP, Hu J, Sacks WJ, Schimel DS, Monson RK (2008) Estimating transpiration and the sensitivity of carbon uptake to water availability in a subalpine forest using a simple ecosystem process model informed by measured net CO<sub>2</sub> and H<sub>2</sub>O fluxes. *Agricultural and Forest Meteorology*, **148**, 1467–1477.
- Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in Western North America. *Bulletin of the American Meteorological Society*, **86**, 39–49.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Nicoll BC, Gardiner BA, Rayner B, Peace AJ (2006) Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **36**, 1871–1883.
- Piao SL, Ciais P, Friedlingstein P *et al.* (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, **451**, 49–52.
- Regonda SK, Rajagopalan B, Clark M, Pitlick J (2005) Seasonal cycle shifts in hydroclimatology over the western United States. *Journal of Climate*, **18**, 372–384.
- Reynolds J, Knight D (1973) The magnitude of snowmelt and rainfall interception by litter in lodgepole pine and spruce-fir forests in Wyoming. *Northwest Science*, **47**, 50–60.
- Richardson AD, Hollinger DY, Burba GG *et al.* (2006) A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology*, **136**, 1–18.
- Ricker WE (1973) Linear regressions in fishery research. *Journal of the Fisheries Research Board of Canada*, **30**, 409–434.
- Sacks WJ, Schimel DS, Monson RK (2007) Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. *Oecologia*, **151**, 54–68.

- Sacks WJ, Schimel DS, Monson RK, Braswell BH (2006) Model-data synthesis of diurnal and seasonal CO<sub>2</sub> fluxes at Niwot Ridge, Colorado. *Global Change Biology*, **12**, 240–259.
- Schimel D, Kittel T, Running S, Monson R, Turnipseed A, Anderson D (2002) Carbon sequestration studied in Western U. S. mountains. *Eos, Transactions, American Geophysical Union*, **83**, 445–449.
- Schimel D, Melillo J, Tian HQ *et al.* (2000) Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science*, **287**, 2004–2006.
- Scott-Denton LE, Sparks KL, Monson RK (2003) Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest. *Soil Biology and Biochemistry*, **35**, 525–534.
- Turnipseed AA, Anderson DE, Blanken PD, Baugh WM, Monson RK (2003) Airflows and turbulent flux measurements in mountainous terrain part 1. Canopy and local effects. *Agricultural and Forest Meteorology*, **119**, 1–21.
- Turnipseed AA, Blanken PD, Anderson DE, Monson RK (2002) Energy budget above a high-elevation subalpine forest in complex topography. *Agricultural and Forest Meteorology*, **110**, 177–201.
- Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.
- van Mantgem PJ, Stephenson NL, Byrne JC *et al.* (2009) Widespread increase of tree mortality rates in the Western United States. *Science*, **323**, 521–524.
- Villalba R, Veblen TT, Ogden J (1994) Climatic influences on the growth of sub-alpine trees in the Colorado front range. *Ecology*, **75**, 1450–1462.
- White MA, Nemani AR (2003) Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. *Global Change Biology*, **9**, 967–972.
- White MA, Running SW, Thornton PE (1999) The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, **42**, 139–145.
- Williams DG, Ehleringer JR (2000) Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs*, **70**, 517–537.
- Wofsy SC, Goulden ML, Munger JW *et al.* (1993) Net exchange of CO<sub>2</sub> in a midlatitude forest. *Science*, **260**, 1314–1317.