

2011

An interannual assessment of the relationship between the stable carbon isotopic composition of ecosystem respiration and climate in a high-elevation subalpine forest

Diego Andrés Riveros-Iregui
University of Nebraska - Lincoln, driveros2@unl.edu

Jia Hu
National Center for Atmospheric Research, Boulder, Colorado

Sean Burns
National Center for Atmospheric Research, Boulder, Colorado

David R. Bowling
University of Utah

Russell K. Monson
University of Utah

Follow this and additional works at: <http://digitalcommons.unl.edu/natrespapers>

 Part of the [Natural Resources and Conservation Commons](#)

Riveros-Iregui, Diego Andrés; Hu, Jia; Burns, Sean; Bowling, David R.; and Monson, Russell K., "An interannual assessment of the relationship between the stable carbon isotopic composition of ecosystem respiration and climate in a high-elevation subalpine forest" (2011). *Papers in Natural Resources*. 295.
<http://digitalcommons.unl.edu/natrespapers/295>

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

An interannual assessment of the relationship between the stable carbon isotopic composition of ecosystem respiration and climate in a high-elevation subalpine forest

Diego A. Riveros-Iregui,¹ Jia Hu,² Sean P. Burns,^{2,3} David R. Bowling,⁴ and Russell K. Monson^{3,5}

Received 23 September 2010; revised 28 January 2011; accepted 2 February 2011; published 22 April 2011.

[1] We measured the carbon isotopic composition ($\delta^{13}\text{C}$) of ecosystem respiration ($\delta^{13}\text{C}_R$) in a subalpine forest across four growing seasons to examine whether patterns in $\delta^{13}\text{C}_R$ were consistent with those expected based on leaf-level gas-exchange theory, and in agreement with past studies of the relation between $\delta^{13}\text{C}_R$ and climate conducted across broad geographic regions. Conventional trends (i.e., less negative $\delta^{13}\text{C}_R$ with increased vapor pressure deficit (VPD) and air temperature (T_{AIR}), and decreased soil moisture (θ)) were observed when we focused on the driest portions of average-wetness years and when $\delta^{13}\text{C}_R$ was positively correlated with nighttime ecosystem respiration (R_E). Nonconventional trends (i.e., more negative $\delta^{13}\text{C}_R$ with decreased θ , and increased VPD and T_{AIR}) were observed under specific climatic conditions (e.g., late snowmelt; extreme T_{AIR} late in the growing season), and when $\delta^{13}\text{C}_R$ was negatively correlated with R_E . These nonconventional trends were independently corroborated using $\delta^{13}\text{C}$ of extracted sugars from needles of dominant tree species at the site. Our results clearly demonstrate that the commonly reported relations between $\delta^{13}\text{C}_R$ and climate may break down depending on the interactions among environmental conditions. Efforts to model and predict the variability of $\delta^{13}\text{C}_R$ under changing climatic variables must characterize and parameterize the effects of unique combinations of weather conditions and variable hydrologic regimes, in combination with the susceptibility of photosynthetic isotope discrimination to extreme air temperatures.

Citation: Riveros-Iregui, D. A., J. Hu, S. P. Burns, D. R. Bowling, and R. K. Monson (2011), An interannual assessment of the relationship between the stable carbon isotopic composition of ecosystem respiration and climate in a high-elevation subalpine forest, *J. Geophys. Res.*, 116, G02005, doi:10.1029/2010JG001556.

1. Introduction

[2] Forests and forest soils are important stores of carbon and their capacity to retain carbon is of critical importance for regulating atmospheric CO_2 . Continuous measurements of net ecosystem exchange (NEE) at many temperate forests across the world [Baldocchi et al., 2001; Xiao et al., 2008] are reaching a temporal length useful for interpretation of the effects of mean changes in long-term climate and interannual climate variability on carbon uptake [e.g., Pereira et al., 2007; Chasmer et al., 2008], carbon loss [Misson et al., 2007; Knohl et al., 2008], and the resulting

net carbon balance [Wohlfahrt et al., 2008; Hu et al., 2010a]. Empirical relationships emerging between climate variation and ecosystem response are useful to enhance our knowledge of carbon cycling. However, the relationships that have been described to date tend to be site-specific and even year-specific, and this limits our ability to extrapolate and transfer knowledge to comparable sites and/or apply it across multiple years.

[3] One approach to extrapolating site-specific studies to regional and global scales involves “process modeling.” General ecosystem and global models of C cycling have been developed [e.g., Running and Gower, 1991; Amthor, 1994; Simon et al., 2005; Atkin et al., 2008] using knowledge obtained from observations at the scale of leaves or soil plots, combined with hierarchical scaling schemes that transfer process knowledge across multiple spatiotemporal scales [Jarvis, 1995]. An assumption that is inherent in this approach is that physiological and biochemical processes that control CO_2 and H_2O exchange at small scales (e.g., leaf or stand scale) transfer directly as controls over ecosystem exchange at larger scales. Tests of this assumption are rare. One measure of CO_2 exchange that is used across

¹School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska, USA.

²National Center for Atmospheric Research, Boulder, Colorado, USA.

³Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, Colorado, USA.

⁴Department of Biology, University of Utah, Salt Lake City, Utah, USA.

⁵Cooperative Institute for Research in Environmental Sciences, University of Colorado at Boulder, Boulder, Colorado, USA.

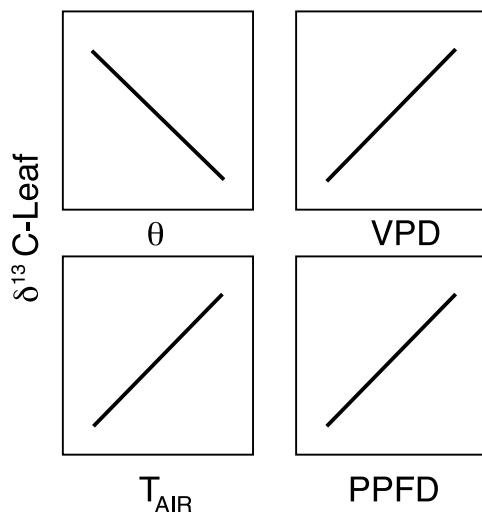


Figure 1. Expected correlations between $\delta^{13}\text{C}$ at the leaf level ($\delta^{13}\text{C}$ -Leaf) and various environmental variables (soil moisture (θ), atmospheric vapor pressure deficit (VPD), air temperature (T_{AIR}), and photosynthetic photon flux density (PPFD)). This illustration is based on process understanding of environmental effects at the leaf level according to *Farquhar et al.* [1982] and modified from *Alstad et al.* [2007].

scales to assess model validity is the $\delta^{13}\text{C}$ of atmospheric CO_2 . The isotopic ratio of atmospheric CO_2 is affected by photosynthetic and respiratory processes, as well as by physical processes associated with the transport of CO_2 across leaf or soil surfaces, all of which discriminate against $^{13}\text{CO}_2$ [Farquhar et al., 1982; Cerling et al., 1991]. Numerous studies have described fundamental relations that control the $\delta^{13}\text{C}$ of CO_2 exchanged at the leaf and plant levels [Farquhar et al., 1989; Dawson et al., 2002] (Figure 1), but fewer have attempted to test the degree to which those relationships can be used to predict processes at the ecosystem scale, or at even larger scales (see *Yakir and Sternberg* [2000] and *Bowling et al.* [2008] for reviews of those ecosystem-scale studies that have been conducted). A common assumption is that weather and climate effects on the $\delta^{13}\text{C}$ of recently respired CO_2 are a proxy for weather and climate effects on photosynthetic CO_2 discrimination of recently fixed photoassimilates [Ekblad and Hogberg, 2001; Bowling et al., 2002]. In fact, recent studies suggested that the correlations of $\delta^{13}\text{C}$ of soil and ecosystem respiration to environmental factors such as atmospheric vapor pressure deficit (VPD) and photosynthetic photon flux density (PPFD) may be used to estimate the time lag between photosynthesis and the CO_2 pulse of a respiratory flux [Kuzakov and Gavrichkova, 2010]. Yet these assumptions ignore effects imposed by other components of ecosystem respiration [Bowling et al., 2008], as well as asynchronous responses of different respiratory pools to changing environmental variables.

[4] At the leaf scale, it is well established that either decreased soil moisture or decreased atmospheric humidity may cause decreased discrimination against $^{13}\text{CO}_2$ in C_3 plants [Farquhar et al., 1989]. This effect has been attributed to reduced diffusivity in leaves, as stomatal conductance is reduced relative to net photosynthesis rate, and the

effect can be modeled as a function of the ratio of intercellular to ambient CO_2 concentration (c_i/c_a). The transfer of this effect to respiratory processes (i.e., less negative $\delta^{13}\text{C}$ of ecosystem-respired CO_2 with increased VPD and decreased soil moisture (θ)) has been detected when observations are compared for ecosystems distributed across broad geographic gradients in moisture availability [Bowling et al., 2002; Pataki et al., 2003; Knobl et al., 2005; Lai et al., 2005; Alstad et al., 2007]. These moisture effects have also been observed for a single growing season within the subalpine forest ecosystem of the current study (the Niwot Ridge AmeriFlux site) [Schaeffer et al., 2008a] and at a low-elevation maritime pine forest in France [Wingate et al., 2010]. To date, however, it remains uncertain whether these patterns are consistent across different seasonal states of moisture availability (i.e., early versus late growing season) or across multiple seasons.

[5] The objective of this paper is to assess whether stable carbon isotope correlations established at the leaf level (Figure 1) hold consistent when evaluated at the ecosystem scale and under a range of environmental variables and hydrologic conditions. We examined the $\delta^{13}\text{C}$ of atmospheric CO_2 at the Niwot Ridge subalpine forest across four growing seasons: 2006, 2007, 2008, and 2009. We also examined the $\delta^{13}\text{C}$ of sugars ($\delta^{13}\text{C}_{\text{NS}}$) extracted from leaves (needles) of the three dominant tree species for two of the growing seasons, 2006 and 2007, and investigated how the $\delta^{13}\text{C}_{\text{NS}}$ related to the $\delta^{13}\text{C}$ of ecosystem respiration ($\delta^{13}\text{C}_{\text{R}}$). We used $\delta^{13}\text{C}_{\text{R}}$ in combination with environmental variables (temperature (T_{AIR}), soil moisture (θ), atmospheric vapor pressure deficit (VPD), photosynthetic photon flux density (PPFD), and precipitation) to address the following questions: (1) Are patterns in $\delta^{13}\text{C}_{\text{R}}$ consistent with those predicted from general leaf-scale theory (i.e., less negative $\delta^{13}\text{C}_{\text{R}}$ with increased VPD and T_{AIR} , and less negative $\delta^{13}\text{C}_{\text{R}}$ with decreased θ)? (2) How consistent are these patterns across different hydrologic regimes (e.g., snowmelt, precipitation, drought) or in relation to previous studies reported for a single growing season at this site [e.g., Schaeffer et al., 2008a]? (3) Should process knowledge obtained at the leaf level be used to predict ecosystem level responses to environmental conditions?

2. Methods

2.1. Study Site

[6] The study site was the Niwot Ridge AmeriFlux Site in central Colorado, USA. ($40^\circ 1' 58''\text{N}$; $105^\circ 32' 47''\text{W}$, 3050 m elevation). Mean annual precipitation at the site is 846 mm (30 year average), and mean snow water equivalence (SWE) is 328 mm near peak (evaluated on 21 April for this site, Niwot SNOTEL, National Resources Conservation Service, <http://www.wcc.nrcs.usda.gov/snotel/>). Mean annual air temperature is 1.5°C . Snowpack accumulations typically last from early November through early June and peak snowmelt occurs between early May and early June. The forest is approximately 110 years old and the vegetation cover is composed mainly of *Pinus contorta* (lodgepole pine), *Abies lasiocarpa* (subalpine fir), and *Picea engelmannii* (Engelmann spruce) in the overstory, and *Vaccinium* spp. in the understory. The site is on a granitic moraine and soils are sandy with a thin (~ 6 cm) organic layer in most

Table 1. Pearson's Linear Correlation Coefficient (r) Between Environmental Variables (θ , VPD, T_{AIR} , and PPF) and $\delta^{13}\text{C}_{\text{R-WC}}$ (WC, From 0.1 to 11 m), $\delta^{13}\text{C}_{\text{R-UC}}$ (UC, From 5 to 11 m), and $\delta^{13}\text{C}_{\text{R-NG}}$ (NG, From 0.1 to 2 m), Across Different Hydrologic Phases and Across Four Growing Seasons^a

	Day Lag (d)	θ			VPD			T_{AIR}			PPFD		
		WC	UC	NG	WC	UC	NG	WC	UC	NG	WC	UC	NG
<i>2006</i>													
Snowmelt	0	-0.38			0.07			-0.05			0.11		
	1	-0.33			-0.37			-0.59			0.56		
	2	-0.16			-0.69			-0.58			0.42		
	3	0.04			-0.55			-0.16			-0.61		
	4	0.23			0.27			0.34			-0.08		
	5	0.24			0.72			0.68			0.08		
	6	0.07			0.44			0.18			0.38		
Drydown	7	0.05			-0.15			-0.34			0.23		
	0	0.20			-0.14			-0.28			0.27		
	1	0.20			-0.27			-0.30			0.05		
	2	0.20			-0.05			0.03			-0.23		
	3	0.19			0.11			0.18			-0.28		
	4	0.19			-0.01			-0.01			0.03		
	5	0.18			-0.04			0.00			0.14		
Late summer	6	0.18			0.17			0.20			0.13		
	7	0.18			0.29			0.29			0.05		
	0	-0.17	0.19	-0.34	-0.23	-0.34	-0.19	-0.28	-0.19	-0.07	0.02	-0.09	-0.44
	1	-0.19	0.23	-0.32	-0.26	-0.33	-0.22	-0.26	-0.22	-0.04	-0.30	-0.58	-0.55
	2	-0.20	-0.10	-0.35	-0.05	-0.04	-0.05	-0.07	-0.05	0.16	-0.27	-0.32	-0.21
	3	-0.23	-0.11	-0.39	0.14	-0.05	-0.03	0.12	-0.03	0.28	-0.04	-0.16	-0.42
	4	-0.23	-0.17	-0.38	0.26	0.05	0.29	0.15	0.29	0.41	0.18	-0.18	-0.27
5	-0.19	-0.20	-0.32	0.08	-0.34	-0.11	-0.09	-0.11	0.10	0.14	-0.01	-0.08	
6	-0.09	-0.20	-0.30	-0.07	0.04	-0.40	-0.18	-0.40	-0.07	0.18	-0.09	0.45	
7	-0.06	-0.16	-0.23	-0.07	0.12	-0.02	-0.13	-0.03	0.25	0.02	-0.29	-0.37	
<i>2007</i>													
Snowmelt	0	-0.32			0.22			0.41			-0.40		
	1	-0.35			0.49			0.67			-0.37		
	2	-0.41			0.61			0.66			-0.02		
	3	-0.50			0.21			0.31			0.13		
	4	-0.59			0.04			-0.03			0.36		
	5	-0.63			-0.37			-0.51			0.27		
	6	-0.59			-0.70			-0.82			-0.43		
Drydown	7	-0.50			-0.38			-0.56			-0.26		
	0	-0.49	-0.47	0.03	-0.02	0.00	-0.23	0.18	0.16	-0.06	-0.10	-0.02	-0.24
	1	-0.49	-0.47	0.03	0.24	0.24	-0.24	0.39	0.34	-0.05	-0.02	-0.02	-0.03
	2	-0.49	-0.46	0.04	0.35	0.24	0.22	0.47	0.35	0.20	0.13	0.52	0.58
	3	-0.48	-0.45	0.04	0.40	-0.02	0.01	0.55	0.20	0.15	0.16	-0.18	-0.04
	4	-0.47	-0.44	0.04	0.10	0.05	0.20	0.42	0.43	0.29	-0.23	-0.14	0.17
	5	-0.47	-0.44	0.04	-0.16	0.40	-0.04	0.24	0.56	0.13	-0.29	0.20	0.32
6	-0.47	-0.44	0.03	-0.29	0.09	-0.54	0.05	0.20	-0.28	-0.43	-0.24	-0.66	
Late summer	7	-0.47	-0.43	0.01	-0.07	0.19	-0.30	0.10	0.28	-0.15	-0.18	-0.21	-0.30
	0	0.02	0.06	0.07	-0.24	-0.26	-0.18	-0.37	-0.37	0.04	-0.09	-0.40	-0.27
	1	-0.03	0.01	0.08	-0.18	-0.41	-0.11	-0.35	-0.42	-0.01	-0.16	-0.39	-0.16
	2	-0.09	0.06	0.00	-0.15	-0.24	-0.12	-0.34	-0.42	-0.06	-0.22	-0.36	-0.11
	3	-0.11	0.22	0.10	-0.13	-0.08	-0.12	-0.34	-0.33	-0.13	-0.14	0.43	0.07
	4	-0.13	0.22	0.15	-0.13	-0.39	-0.02	-0.28	-0.54	0.12	0.05	-0.23	-0.13
	5	-0.17	0.16	0.17	-0.20	-0.35	0.02	-0.30	-0.39	0.24	-0.05	-0.36	0.03
6	-0.21	0.15	0.22	-0.08	-0.14	0.14	-0.21	-0.14	0.24	-0.06	-0.19	-0.19	
7	-0.27	0.10	0.24	-0.07	0.00	0.21	-0.18	-0.05	0.23	-0.11	0.21	0.11	
<i>2008</i>													
Snowmelt	0	0.59			0.51			0.51			0.46		
	1	0.55			-0.14			0.08			0.13		
	2	0.54			-0.20			-0.04			0.02		
	3	0.58			0.03			0.11			0.03		
	4	0.59			0.19			0.45			0.35		
	5	0.58			0.06			0.39			0.23		
	6	0.56			-0.19			0.17			-0.40		
Drydown	7	0.54			-0.34			-0.04			-0.44		
	0	-0.01	-0.39	-0.69	-0.13	0.45	-0.21	0.01	0.56	-0.35	-0.11	0.14	-0.52
	1	-0.03	-0.40	-0.70	-0.01	-0.39	-0.39	0.11	-0.31	-0.37	-0.18	-0.72	-0.69
	2	-0.08	-0.39	-0.70	0.05	-0.07	0.14	0.07	-0.04	0.25	-0.01	0.10	-0.22
	3	-0.13	-0.38	-0.70	0.03	-0.16	0.64	0.11	-0.05	0.60	-0.12	0.60	0.30
	4	-0.15	-0.37	-0.70	-0.02	0.24	0.03	0.02	0.45	0.21	0.25	0.60	0.71
	5	-0.18	-0.36	-0.69	0.08	0.50	0.16	0.08	0.33	0.05	0.07	0.17	0.23
6	-0.21	-0.37	-0.68	0.09	-0.45	-0.29	0.03	-0.29	-0.10	-0.01	-0.42	-0.55	

Table 1. (continued)

	Day Lag (<i>d</i>)	θ			VPD			T_{AIR}			PPFD		
		WC	UC	NG	WC	UC	NG	WC	UC	NG	WC	UC	NG
Late summer	7	-0.25	-0.38	-0.65	0.12	-0.07	0.15	0.21	0.10	0.16	0.03	0.17	-0.19
	0	-0.18	-0.03	-0.02	0.10	0.15	0.09	0.22	0.17	0.20	-0.10	-0.13	-0.36
	1	-0.18	0.03	0.04	0.21	0.13	0.37	0.31	0.10	0.36	-0.03	-0.08	-0.06
	2	-0.18	0.03	0.06	0.23	0.14	0.33	0.36	0.18	0.38	0.08	0.22	0.54
	3	-0.17	-0.01	0.03	0.14	0.13	0.11	0.29	0.18	0.21	-0.12	0.10	-0.20
	4	-0.19	0.02	0.10	0.21	-0.07	0.14	0.34	0.15	0.26	0.04	0.03	0.26
	5	-0.21	0.00	0.09	0.11	0.05	0.07	0.30	0.18	0.21	-0.18	-0.06	-0.14
	6	-0.25	-0.08	0.01	0.18	-0.06	0.11	0.36	0.14	0.28	-0.10	0.15	-0.04
7	-0.24	-0.13	-0.10	0.33	-0.03	0.22	0.41	0.11	0.31	0.16	-0.35	-0.41	
2009													
Snowmelt	0	0.53			-0.70			-0.51			0.16		
	1	0.53			-0.44			-0.29			-0.37		
	2	0.56			-0.42			-0.21			-0.02		
	3	0.53			-0.54			-0.31			0.34		
	4	0.45			0.16			0.38			0.31		
	5	0.35			0.00			0.22			0.14		
	6	0.30			-0.06			0.18			-0.06		
7	0.32			0.10			0.38			-0.36			
Drydown	0	-0.50	0.44	0.07	0.17	-0.21	-0.22	0.34	-0.38	-0.11	0.00	0.33	0.18
	1	-0.50	0.49	-0.07	0.16	-0.53	-0.19	0.33	-0.52	-0.15	-0.11	0.04	-0.25
	2	-0.40	0.54	-0.03	0.09	-0.46	0.16	0.24	-0.26	0.01	0.01	0.75	-0.20
	3	-0.28	0.57	0.33	0.28	-0.17	0.27	0.44	0.06	0.12	0.07	0.13	0.36
	4	-0.20	0.57	0.26	0.42	-0.18	0.06	0.56	0.00	0.06	0.16	-0.23	0.15
	5	-0.17	0.55	0.21	0.48	0.38	-0.04	0.53	0.38	0.02	0.10	-0.11	-0.20
	6	-0.21	0.52	0.26	0.46	0.35	0.09	0.46	0.19	0.11	0.12	0.03	-0.23
7	-0.21	0.53	0.29	0.57	0.35	0.22	0.49	0.13	0.16	0.16	0.12	-0.46	
Late summer	0	-0.49	-0.40	-0.73	-0.35	-0.01	-0.59	-0.46	-0.19	-0.55	-0.21	-0.11	-0.37
	1	-0.45	-0.39	-0.75	-0.33	0.01	-0.38	-0.44	0.20	-0.43	-0.04	-0.28	-0.47
	2	-0.51	-0.36	-0.77	-0.14	0.02	-0.33	-0.21	-0.06	-0.25	0.11	-0.21	-0.31
	3	-0.57	-0.21	-0.77	0.02	0.08	-0.23	0.01	0.11	-0.03	0.16	-0.32	0.22
	4	-0.59	-0.08	-0.66	0.10	0.30	0.23	0.05	0.31	0.26	0.10	0.31	0.13
	5	-0.55	-0.03	-0.47	0.15	0.35	0.28	0.05	0.32	0.37	0.00	0.03	-0.02
	6	-0.46	0.00	-0.35	0.12	0.09	0.23	-0.03	-0.05	0.29	0.11	0.10	0.01
7	-0.39	0.04	-0.29	0.12	0.19	0.42	-0.09	0.12	0.34	0.07	0.21	-0.03	

^aValues in bold denote significance at the 95% confidence level. Missing values denote fewer than four nightly intercepts. A lag analysis was performed using each environmental variable shifted in time by up to 7 days.

locations. Percent C content ranges from ~58% in the organic layer to ~10% in the mineral layer [Scott-Denton *et al.*, 2003]. Ongoing measurements of carbon, water, and energy fluxes over the canopy have been monitored with a 26 m flux tower since the autumn of 1998 [Monson *et al.*, 2002; Turnipseed *et al.*, 2002; Monson *et al.*, 2005].

2.2. Discharge and Hydrologic Phases of the Growing Season

[7] We divided each growing season into three different periods, using discharge measured at the outlet of the Niwot Ridge AmeriFlux site catchment (Como Creek) as a determinant of hydrologic phase, moisture availability for biological activity, and growing season stage. The three hydrologic phases were: (1) snowmelt, the period marked by the rapid and/or sustained increase in stream discharge; (2) drydown, the period marked by a gradual decrease in stream discharge; and (3) late summer, the period when stream discharge reached base flow conditions. Any pulse in discharge during the late summer period was in response to convective rain events. This three-phase separation allowed for comparison of forest dynamics across phases and across seasons on the basis of hydrologic conditions, rather than on the basis of specific dates.

2.3. Canopy Air CO₂, Climate Data, and Estimation of $\delta^{13}\text{C}_R$

[8] Measurements of canopy air CO₂ and $\delta^{13}\text{C}$ of CO₂ were made using a tunable diode laser absorption spectrometer (TGA100A, Campbell Scientific Inc., Logan, UT), adapted with a multiinlet sampling manifold that allowed for continuous sampling from 13 different inlets as follows: four inlets near the ground (NG; at 0.1, 0.5, 1, and 2 m); four inlets in the upper canopy (UC; at 5, 7, 9, 11 m); one inlet above canopy (at 21.5 m); and four inlets that sampled four calibration tanks. Each sampling cycle lasted 10 min and data were stored in 30 min means for each height using a data logger (CR5000, Campbell Scientific, Inc. Logan, Utah, USA; for 2008 and 2009 only the second half of each hour was recorded). Further details can be found in previous studies including instrument specifications [Bowling *et al.*, 2003], calibration and experimental setup at the site [Bowling *et al.*, 2005; Schaeffer *et al.*, 2008a], as well as forest CO₂ dynamics during single years [Schaeffer *et al.*, 2008a, 2008b; Bowling *et al.*, 2009]. The four calibration tanks contained CO₂-in-air mixtures that were filled with ambient air using a compressor system at the Stable Isotope Ratio Facility for Environmental Research (SIRFER), at the University of Utah. Above-ambient CO₂ molar fractions in

Table 2. Same as Table 1 but the Lag Analysis Was Performed Using Each Environmental Variable Averaged in Time Over 2–7 Days

	Averaged Lag (<i>d</i>)	θ			VPD			T_{AIR}			PPFD		
		WC	UC	NG	WC	UC	NG	WC	UC	NG	WC	UC	NG
<i>2006</i>													
Snowmelt	2	-0.36			-0.58			-0.61			0.49		
	3	0.31			-0.74			-0.50			0.70		
	4	-0.25			-0.51			-0.19			0.16		
	5	-0.16			-0.11			0.05			0.08		
	6	-0.10			0.14			0.08			0.11		
	7	-0.08			-0.27			-0.32			0.34		
	Drydown	2	0.20			-0.23			-0.26			0.24	
3		0.20			-0.16			-0.17			0.07		
4		0.19			-0.15			-0.15			-0.12		
5		0.19			-0.16			-0.13			-0.08		
6		0.19			-0.09			-0.06			-0.01		
7		0.19			0.02			0.04			0.07		
Late summer		2	-0.18	0.21	-0.34	-0.21	-0.28	-0.17	-0.22	-0.07	0.02	-0.17	-0.37
	3	-0.19	0.18	-0.35	-0.13	-0.22	-0.14	-0.14	-0.01	0.10	-0.25	-0.40	-0.52
	4	-0.21	0.10	-0.36	-0.05	-0.19	-0.06	-0.09	0.03	0.17	-0.22	-0.38	-0.57
	5	-0.22	0.04	-0.37	-0.03	-0.26	-0.08	-0.09	-0.01	0.18	-0.13	-0.36	-0.55
	6	-0.22	0.00	-0.37	-0.05	-0.26	-0.17	-0.11	-0.03	0.14	-0.08	-0.35	-0.54
	7	-0.20	-0.03	-0.37	-0.06	-0.23	-0.17	-0.11	-0.04	0.17	-0.02	-0.37	-0.42
	<i>2007</i>												
Snowmelt	2	-0.34			0.61			0.85			-0.52		
	3	-0.38			0.63			0.85			-0.50		
	4	-0.43			0.60			0.71			-0.33		
	5	-0.49			0.53			0.49			-0.12		
	6	-0.54			0.18			-0.03			-0.05		
	7	-0.56			-0.07			-0.36			-0.25		
	Drydown	2	-0.49	-0.47	0.03	0.25	-0.42	-0.25	0.43	-0.48	-0.12	-0.12	-0.05
3		-0.49	-0.47	0.03	0.44	-0.42	-0.26	0.58	-0.48	-0.12	-0.08	0.08	-0.06
4		-0.49	-0.46	0.04	0.66	-0.46	-0.22	0.72	-0.52	-0.06	-0.03	-0.01	-0.07
5		-0.49	-0.46	0.04	0.72	-0.45	-0.20	0.70	-0.49	0.00	-0.13	-0.07	-0.01
6		-0.48	-0.46	0.04	0.62	-0.47	-0.24	0.64	-0.48	0.00	-0.22	0.02	0.12
7		-0.48	-0.45	0.04	0.54	-0.45	-0.22	0.58	-0.45	0.01	-0.33	-0.06	-0.10
Late summer		2	-0.01	0.04	0.08	-0.25	-0.36	-0.16	-0.39	-0.44	-0.01	-0.16	-0.45
	3	-0.04	0.05	0.05	-0.27	-0.36	-0.20	-0.41	-0.47	-0.06	-0.23	-0.46	-0.21
	4	-0.06	0.10	0.07	-0.28	-0.45	-0.19	-0.40	-0.53	-0.02	-0.26	-0.23	-0.17
	5	-0.07	0.12	-0.09	-0.31	-0.50	-0.17	-0.41	-0.54	0.03	-0.21	-0.30	-0.21
	6	-0.09	0.14	0.10	-0.30	-0.51	-0.12	-0.40	-0.52	0.06	-0.21	-0.41	-0.18
	7	-0.11	0.14	0.13	-0.29	-0.48	-0.06	-0.39	-0.48	0.09	-0.17	-0.45	-0.24
	<i>2008</i>												
Snowmelt	2	0.58			0.10			0.22			0.38		
	3	0.57			0.09			0.20			0.32		
	4	0.57			0.13			0.29			0.30		
	5	0.58			0.14			0.35			0.39		
	6	0.58			0.09			0.39			0.44		
	7	0.58			-0.04			0.42			0.33		
	Drydown	2	-0.02	-0.40	-0.69	-0.05	0.03	-0.25	0.08	0.14	-0.20	-0.18	-0.35
3		-0.04	-0.40	-0.70	-0.02	0.04	0.05	0.10	0.09	0.05	-0.15	-0.23	-0.73
4		-0.06	-0.39	-0.70	-0.03	0.03	0.05	0.10	0.19	0.10	-0.18	0.03	-0.48
5		-0.08	-0.39	-0.70	0.00	0.18	0.10	0.10	0.27	0.10	-0.08	0.19	-0.29
6		-0.10	-0.38	-0.70	0.03	0.03	0.02	0.13	0.13	0.05	-0.04	0.21	-0.20
7		-0.12	-0.38	-0.69	0.06	0.05	0.07	0.17	0.14	0.07	-0.04	0.12	-0.31
Late summer		2	-0.18	0.00	-0.01	0.21	0.17	0.32	0.33	0.17	0.35	-0.09	-0.13
	3	-0.18	0.01	0.03	0.22	0.18	0.29	0.34	0.18	0.33	-0.03	0.05	0.07
	4	-0.19	0.01	0.03	0.24	0.12	0.29	0.35	0.18	0.33	-0.07	0.13	0.03
	5	-0.19	0.01	0.04	0.24	0.11	0.28	0.36	0.19	0.33	-0.06	0.10	0.16
	6	-0.20	0.01	0.06	0.25	0.09	0.29	0.38	0.19	0.34	-0.14	0.06	0.07
	7	-0.22	0.00	0.05	0.29	0.07	0.31	0.40	0.19	0.36	-0.16	0.11	0.06
	<i>2009</i>												
Snowmelt	2	0.59			-0.66			-0.42			0.03		
	3	0.59			-0.72			-0.46			0.04		
	4	0.58			-0.56			-0.25			0.08		
	5	0.56			-0.48			-0.15			0.26		
	6	0.54			-0.41			-0.10			0.77		
	7	0.52			-0.37			-0.01			0.52		
	Drydown	2	-0.52	-0.01	-0.44	0.17	-0.52	-0.09	0.33	-0.48	-0.08	0.05	0.44
3		-0.53	-0.02	-0.43	0.23	-0.55	0.00	0.37	-0.41	-0.04	0.00	0.47	-0.05
4		-0.54	-0.04	-0.43	0.30	-0.53	0.02	0.42	-0.34	-0.02	-0.01	0.36	0.02

Table 2. (continued)

	Averaged Lag (<i>d</i>)	θ			VPD			T_{AIR}			PPFD		
		WC	UC	NG	WC	UC	NG	WC	UC	NG	WC	UC	NG
Late summer	5	-0.54	-0.06	-0.42	0.37	-0.37	0.00	0.45	-0.20	-0.01	-0.16	0.43	-0.03
	6	-0.55	-0.08	-0.42	0.42	-0.25	0.03	0.46	-0.13	-0.01	-0.19	0.43	0.08
	7	-0.55	-0.10	-0.41	0.47	-0.13	0.08	0.47	-0.08	-0.04	-0.17	0.34	-0.02
	2	-0.54	-0.38	-0.75	-0.34	0.01	-0.54	-0.43	-0.20	-0.52	-0.16	-0.34	-0.69
	3	-0.57	-0.35	-0.78	-0.26	0.04	-0.51	-0.37	-0.14	-0.43	-0.08	-0.52	-0.59
	4	-0.60	-0.31	-0.79	-0.20	0.17	-0.37	-0.31	0.00	-0.28	-0.05	-0.51	-0.66
	5	-0.61	-0.29	-0.79	-0.14	0.29	-0.26	-0.26	0.11	-0.16	0.03	-0.18	-0.36
	6	-0.61	-0.27	-0.77	-0.10	0.27	-0.20	-0.24	0.08	-0.09	0.06	0.64	0.48
	7	-0.60	-0.25	-0.76	-0.06	0.29	-0.07	-0.24	0.10	0.01	-0.01	0.97	-0.56

the tanks was obtained by addition of pure CO_2 with $\delta^{13}\text{C}$ near -30‰ prior to filling. CO_2 molar fractions in the tanks ranged from 350 to 500 $\mu\text{mol mol}^{-1}$ (in 40–50 $\mu\text{mol mol}^{-1}$ increments) and the $\delta^{13}\text{C}$ of CO_2 in the tanks ranged from -8.5 to -14.5‰ , measured relative to the VPDB standard using isotope ratio mass spectrometry at the SIRFER facility. In this study we present data collected between 1 January 2006 and 31 December 2009 (with occasional gaps due to power outages), focusing on May–October periods to encompass the growing season. Additionally, the following variables were obtained or estimated from the Niwot Ridge AmeriFlux data archive (http://urquell.colorado.edu/data_ameriflux/): net ecosystem CO_2 exchange (21.5 m), air temperature (T_{AIR} ; 8 m), vapor pressure deficit (VPD; at 8 m), friction velocity (u^* ; at 21.5 m), precipitation (at canopy height), volumetric soil water content (θ ; at 5 cm depth), and photosynthetic photon flux density (PPFD; measured above the canopy).

[9] We calculated the nighttime carbon isotope composition of ecosystem respiration ($\delta^{13}\text{C}_R$) based on the Keeling plot approach [Keeling, 1958] using ordinary least squares regressions [Zobitz *et al.*, 2006]. For each night (2000–0430 MST), $\delta^{13}\text{C}_R$ was calculated as the intercept of a regression between the $\delta^{13}\text{C}$ of CO_2 and the inverse of the CO_2 mole fraction, including all eight heights within and below the canopy ($\delta^{13}\text{C}_{R\text{-WC}}$, 11, 9, 7, 5, 2, 1, 0.5, 0.1 m). Because the strength of the Keeling plot regression depends on the range of the mole fractions [Pataki *et al.*, 2003; Zobitz *et al.*, 2006], we only used nights with a CO_2 mole fraction range greater than 25 $\mu\text{mol mol}^{-1}$ across the eight heights ($\sim 72\%$ of nighttime periods). Nightly intercepts were removed from further analysis if the standard error of the intercept for any given night was greater than 1‰. After application of these quality criteria, available nightly intercepts for whole canopy $\delta^{13}\text{C}_{R\text{-WC}}$ were $n = 102, 117, 122,$ and 119 nights for 2006, 2007, 2008, and 2009, respectively. We also calculated separate $\delta^{13}\text{C}_R$ for upper-canopy inlets ($\delta^{13}\text{C}_{R\text{-UC}}$, 11, 9, 7, 5 m) and near-ground inlets ($\delta^{13}\text{C}_{R\text{-NG}}$, 2, 1, 0.5, 0.1 m). This separation into $\delta^{13}\text{C}_{R\text{-UC}}$ and $\delta^{13}\text{C}_{R\text{-NG}}$ was performed according to previous studies at this site [Bowling *et al.*, 2005; Schaeffer *et al.*, 2008a] and only for low-turbulence conditions ($u^* < 0.4 \text{ m s}^{-1}$) over periods longer than 4 h. Schaeffer *et al.* [2008a] demonstrated that for $u^* < 0.4 \text{ m s}^{-1}$ the canopy air is well stratified, thus this is an appropriate criterion to perform this separation. In doing so, however, nighttime Keeling plots can become less robust because there are fewer data points in each regression, thus only nights with standard error of the intercept smaller than

1‰ and simultaneous estimates for both $\delta^{13}\text{C}_{R\text{-UC}}$ and $\delta^{13}\text{C}_{R\text{-NG}}$ were considered. This resulted in a decrease in the number of nights used in each growing season ($n = 12, 32, 25,$ and 32 for each year from 2006 to 2009, respectively).

[10] Having estimated nightly Keeling-plot intercepts for whole canopy ($\delta^{13}\text{C}_{R\text{-WC}}$), upper canopy ($\delta^{13}\text{C}_{R\text{-UC}}$), and near ground ($\delta^{13}\text{C}_{R\text{-NG}}$) heights, we conducted an extensive correlation analysis using these Keeling intercepts as the dependent variable and various environmental variables (including daily mean values of θ , VPD, T_{AIR} , and daytime mean values of PPFD) as the independent variable, during each of the three hydrologic phases. We tested whether the addition of time lags systematically improved correlations, using two different lags: (1) a day lag, in which the estimated Keeling-plot intercept was regressed against each environmental variable shifted in time by up to 7 days; and (2) a time-averaged lag, in which the estimated Keeling-plot intercept was regressed against each environmental variable averaged in time over 2–7 days. Regressions and statistical analyses were performed using Matlab 7.7.0 (The MathWorks, Inc.). Pearson's linear correlation coefficients (r) for all correlations are reported in Tables 1 and 2.

2.4. Preevent Conditions and Effects of Nonlinearities in Vapor Pressure Deficit

[11] Changes in VPD can influence $\delta^{13}\text{C}_R$ at daily to weekly timescales [Bowling *et al.*, 2002; Knohl *et al.*, 2005; Lai *et al.*, 2005; Mortazavi *et al.*, 2005], but these influences can subsequently be affected by variable weather periods, particularly periods with rain. Therefore we investigated whether the effects of climatic variables on $\delta^{13}\text{C}_R$ differed between periods prior to or periods after precipitation. Using 30 min measurements of VPD, we calculated a 24 h running mean of atmospheric VPD for each of the late-summer stages and then separated periods of increasing VPD from periods of decreasing VPD (see auxiliary material).¹ This resulted in time intervals ranging from 2 to 7 days long. Increasing-VPD periods were considered “preevent conditions” and represented days that were progressively drier. Decreasing-VPD periods were considered “postevent periods” and were typically initiated by precipitation and subsequent reduction in VPD.

2.5. Needle Sugar $\delta^{13}\text{C}$ Values

[12] In order to assist us in interpreting seasonal and interannual trends in $\delta^{13}\text{C}_R$, we analyzed the $\delta^{13}\text{C}$ value of

¹Auxiliary materials are available in the HTML. doi:10.1029/2010JG001556.

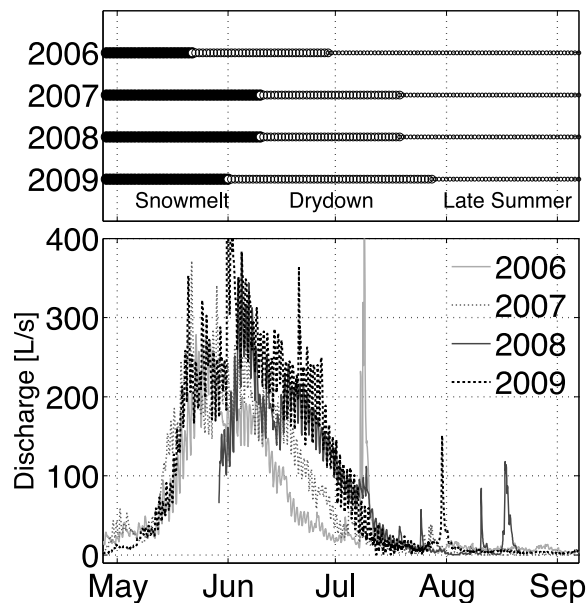


Figure 2. (top) Hydrologic phases for 2006–2009. (bottom) Stream discharge measured at the outlet of the Niwot Ridge AmeriFlux site catchment (Como Creek). Discharge data were used to determine the hydrologic phases and growing season stage shown in Figure 2 (top).

sugars in the needles ($\delta^{13}\text{C}_{\text{NS}}$) of all three of the dominant tree species at the site. Needles were collected every 14 days from six trees of each species during the growing seasons of 2006 and 2007 following protocols described by *Gessler et al.* [2004] and *Hu et al.* [2010b]. Selected trees were distributed broadly along a 100 m transect that ran east and west of the main flux tower and the same trees were used for collection on all dates. Needles were collected from the upper tree crown and immediately frozen in liquid nitrogen. Needles were collected between 1000 h and 1200 h during each collection to avoid any diel variability caused by changes in needle sugar or starch concentrations. Sugars were extracted from 150 mg of ground needle tissue using 150 mg of polyvinylpyrrolidone and 2 mL of distilled water combined in a vial, incubated at 10°C for 1 h and then boiled for 2 min. Samples were centrifuged at 12,000 G for 10 min; the supernatant was decanted and frozen at -20°C and it was later freeze-dried. This supernatant was considered as the soluble fraction, consisting mainly of sugars, but other water-soluble compounds such as organic acids and amino acids were also present. Samples were analyzed for $\delta^{13}\text{C}$ at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley.

3. Results

3.1. Discharge and Interannual Variability of Hydrologic Regimes

[13] In all years, stream discharge of Como Creek rose rapidly from ~ 30 L/s to a maximum between 250 and 400 L/s during snowmelt (Figure 2). No discharge data were collected in May 2008, but snow water equivalent measured at the Niwot SNOTEL site confirmed that for 2008 the major increase in stream discharge did not occur until 4 June (the

latest for the 4 years of the study), and discharge peaked at ~ 380 L/s. Stream discharge peaked earlier in 2006 and 2009 than in 2007 or 2008. Stream discharge reached base flow earlier during 2006 than in any of the other years, and further increases in discharge once base flow was reached were caused by precipitation. Precipitation varied in magnitude and timing across all growing seasons, and nearly 50% of the days in late summer did not receive precipitation. Summer precipitation was higher during 2006, 2007 and 2008, compared to 2003 (as reported by *Schaeffer et al.* [2008a]) and 2009 (Table 3). Based on the 30 year precipitation record for July–September periods, the driest summer on record was 2009. Conversely, summer precipitation in 2006, 2007 and 2008 was within one standard deviation of the 30 year mean, even though nearly 25% of the precipitation in 2006 was part of a single, 24 h event (Table 3). Late-summer precipitation in 2007 and 2008 was manifested in relatively frequent but small events. Thus, combined effects of snowmelt timing and summer precipitation frequency resulted in relatively drier conditions for 2006 and 2009, and wetter for 2007 and 2008.

3.2. Concentrations of Canopy CO_2 and $\delta^{13}\text{C}_\text{R}$

[14] Across each year, the diel range of CO_2 mole fractions across the canopy progressively increased from less than $20 \mu\text{mol mol}^{-1}$ during winter to over $100 \mu\text{mol mol}^{-1}$ by midsummer (data not shown). Diel CO_2 mole fractions and $\delta^{13}\text{C}$ of CO_2 were less variable during the growing season as height increased and in agreement with previous studies [*Bowling et al.*, 2005, 2009]. At 21m, for example, CO_2 mole fractions varied throughout the day by less than $10 \mu\text{mol mol}^{-1}$ and $\delta^{13}\text{C}$ of CO_2 varied by less than 1‰; however at 0.1m this variability was greater than $100 \mu\text{mol mol}^{-1}$ for mole fractions and 4 ‰ for $\delta^{13}\text{C}$ of CO_2 . Overall, observed growing season patterns of both mole fractions and isotopic compositions were consistent from year to year with those reported in the above studies, even though the absolute maximum values or the intraseasonal trends were different.

[15] In general, $\delta^{13}\text{C}_{\text{R-WC}}$ (where “WC” stands for whole-canopy and represents nightly Keeling intercepts calculated using all inlets in the canopy) varied between -23.5‰ and -27.5‰ , throughout the growing season (Figure 3), with seasonal means of -25.6 ± 0.7 , -25.8 ± 0.7 , -25.7 ± 0.8 , and $-25.9 \pm 0.6\text{‰}$, respectively, for each year from 2006 to 2009. In 2008 and 2009 $\delta^{13}\text{C}_{\text{R-WC}}$ values increased significantly ($p < 0.05$) as the season progressed from its wettest (early season) to its driest (late-season) periods (Figure 3); this trend is particularly evident by the monotonically

Table 3. Variability of Rainfall During the Late-Summer Hydrologic Phases^a

Late Summer	Cumulative Precipitation (mm)	Days With No Precipitation	Highest Single Daily Event (mm)
2006	222.6	51%	55.4
2007	143.3	42%	20.1
2008	167.2	62%	45.0
2009	88.7	56%	20.1
2003 ^b	120.8	62%	20.7

^aThirty year mean and standard deviation from 1 July to 30 September are 180.8 mm and 53.4 mm, respectively.

^bComparison with *Schaeffer et al.* [2008a].

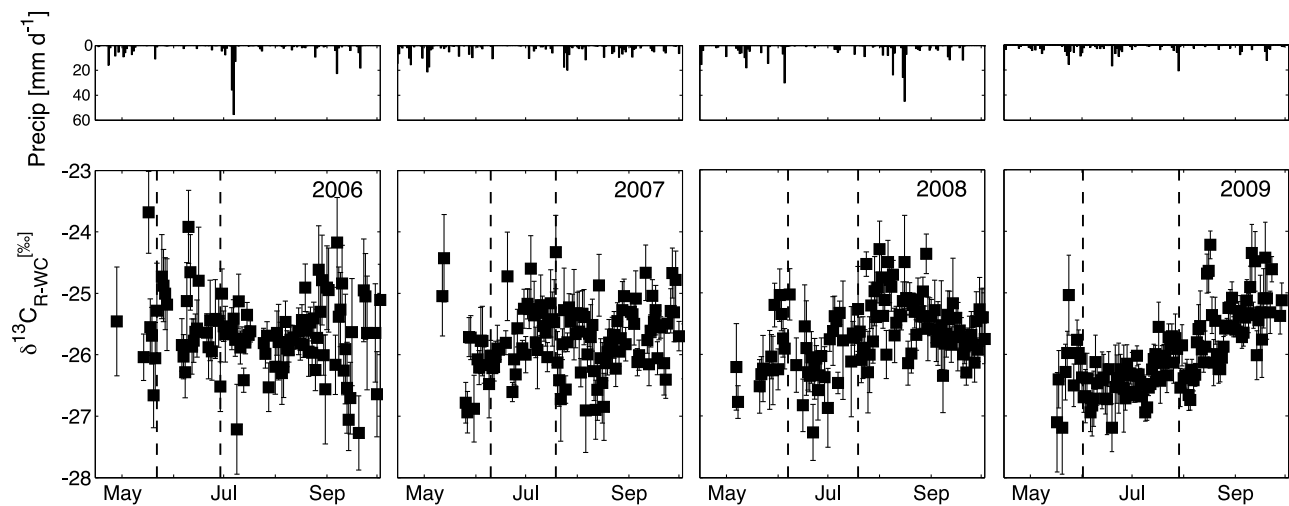


Figure 3. (top) Daily precipitation across four different growing seasons (2006–2009). (bottom) Nightly Keeling plot intercepts across the same seasons using all inlets within the canopy ($\delta^{13}\text{C}_{\text{R-WC}}$; 11, 9, 7, 5, 2, 1, 0.5, and 0.1 m). Each data point represents the intercept of an ordinary least squares regression using 30 min nighttime (2000–0430 h) measurements, and error bars denote standard error of each intercept. Intercepts were removed if they contained fewer than nine continuous observations or a standard error greater than 1‰ ($n = 102, 117, 122,$ and $119,$ for each year from 2006 to 2009, respectively). Vertical dashed lines denote separation among snowmelt, drydown, and late-summer hydrologic phases as described in Figure 2.

increasing $\delta^{13}\text{C}_{\text{R-WC}}$ values of 2009. Examination of upper-canopy (UC) and near-ground (NG) inlets separately demonstrated that seasonal medians of $\delta^{13}\text{C}_{\text{R-UC}}$ were significantly less negative than $\delta^{13}\text{C}_{\text{R-NG}}$ during 2008 and 2009, but not during 2006 or 2007 (Figure 4).

3.3. Hydrologic Phases, Environmental Variables, and $\delta^{13}\text{C}_{\text{R}}$

[16] The correlation between $\delta^{13}\text{C}_{\text{R}}$ and soil moisture content (θ) was not generally significant across the 4 years (Figure 5). In those three cases where it was significant, the correlation was positive during the snowmelt period (2008) and negative during the summer dry-down and late-summer

periods (2007 and 2009, respectively). After separating whole-canopy ecosystem respiration into $\delta^{13}\text{C}_{\text{R-UC}}$ and $\delta^{13}\text{C}_{\text{R-NG}}$ (as performed by Schaeffer *et al.* [2008a]), our analyses revealed a negative relation between $\delta^{13}\text{C}_{\text{R-NG}}$ and θ but only under dry conditions (e.g., 2009, the driest year of this study). Also during this time, a positive relation between $\delta^{13}\text{C}_{\text{R-UC}}$ and VPD was observed (Table 1). However, our analyses also revealed that separating $\delta^{13}\text{C}_{\text{R-WC}}$ into $\delta^{13}\text{C}_{\text{R-UC}}$ and $\delta^{13}\text{C}_{\text{R-NG}}$ did not systematically improve correlations with environmental variables across all times of the year (Tables 1 and 2), and correlations between $\delta^{13}\text{C}_{\text{R}}$ and environmental variables occurred more frequently when whole canopy was considered ($\delta^{13}\text{C}_{\text{R-WC}}$).

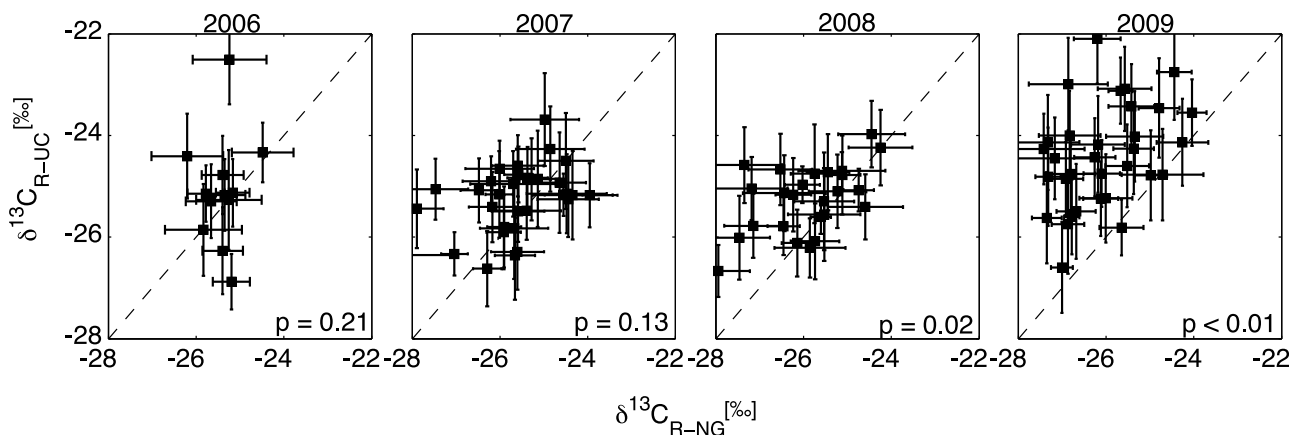


Figure 4. Nightly Keeling plot intercepts of upper-canopy ($\delta^{13}\text{C}_{\text{R-UC}}$) inlets and near-ground ($\delta^{13}\text{C}_{\text{R-NG}}$) inlets across four different growing seasons. Significant difference (Wilcoxon rank sum test, 95% significance level) between seasonal medians of $\delta^{13}\text{C}_{\text{R}}$ in upper-canopy and near-ground inlets was found in 2008 and 2009.

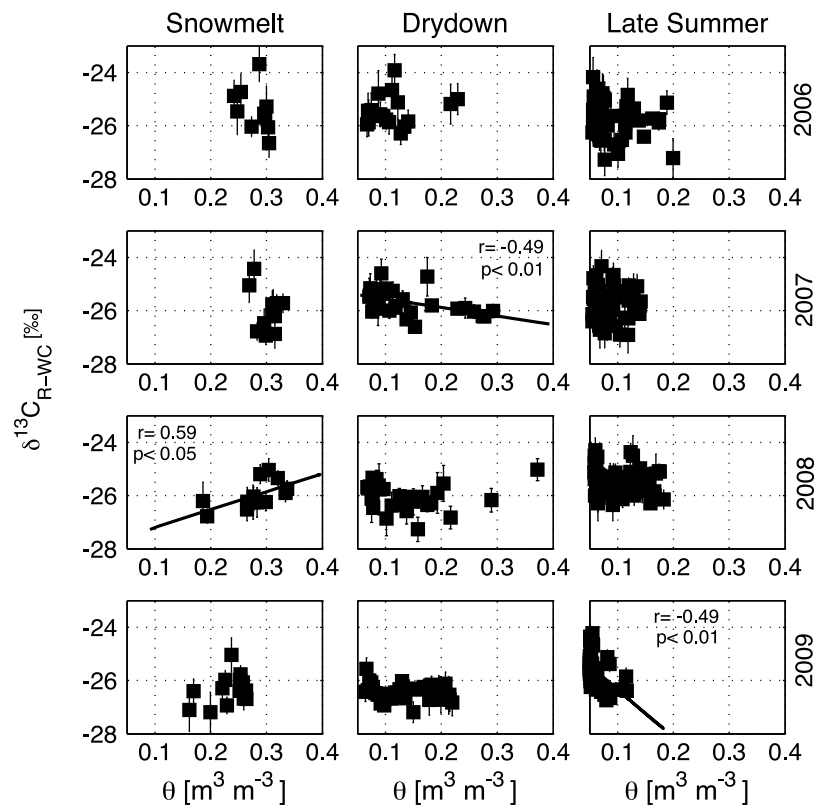


Figure 5. Relationship between nightly $\delta^{13}\text{C}_{\text{R-WC}}$ and soil water content (θ) across four growing seasons (2006–2009) and across three hydrologic phases in each season (snowmelt, drydown, and late summer). Pearson’s linear correlation coefficient (r), p value, and regression lines are shown for those relationships found significant at the 95% level.

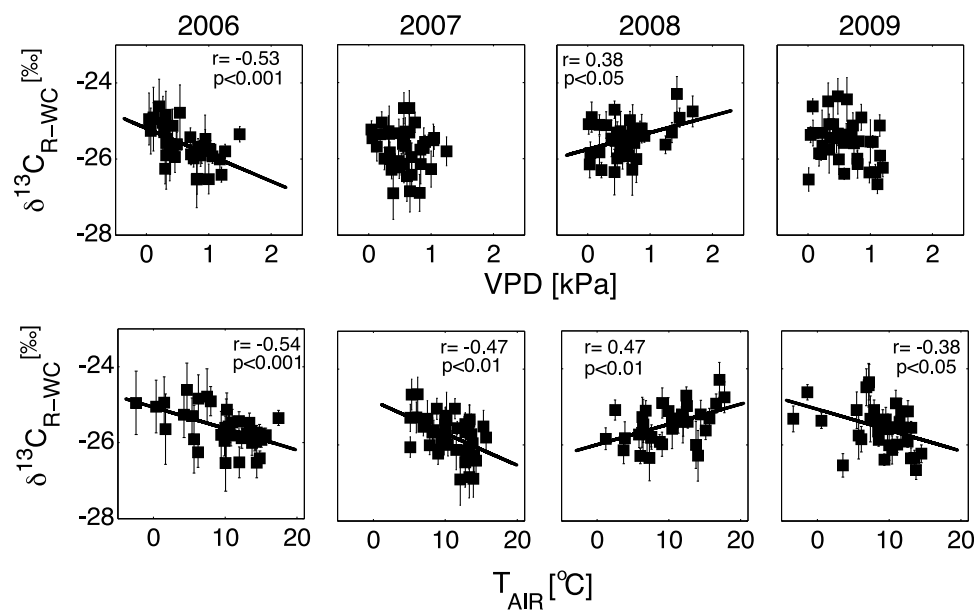


Figure 6. Relationship between nightly $\delta^{13}\text{C}_{\text{R-WC}}$ and environmental variables (VPD, T_{AIR}) during days prior to precipitation (preevent conditions) in the late-summer phases, from 2006 to 2009. Pearson’s linear correlation coefficient (r), p value, and regression lines are shown for those relationships found significant at the 95% level.

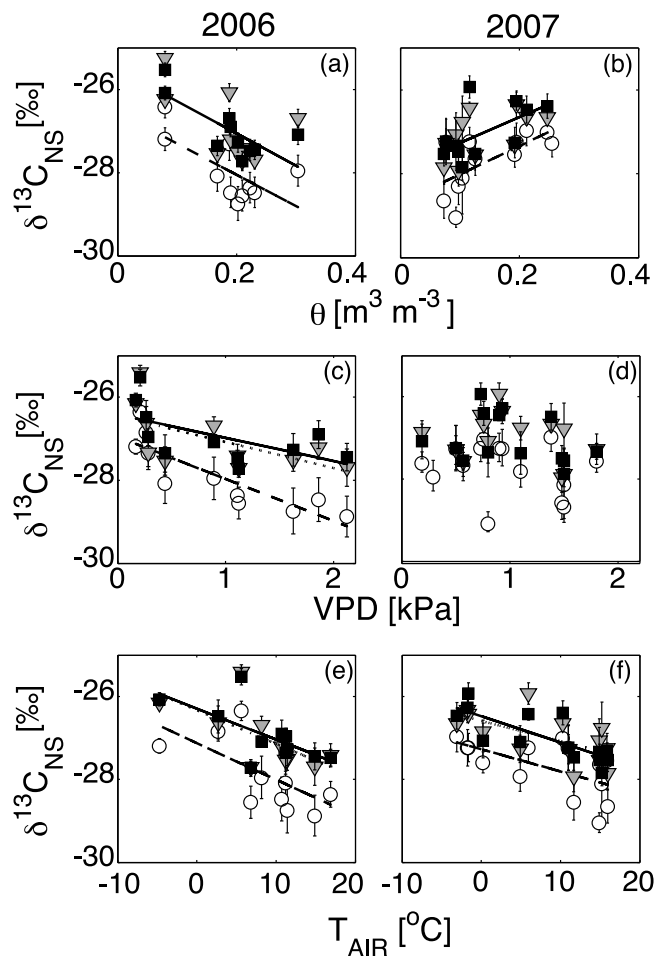


Figure 7. (a, b) The relationship between $\delta^{13}\text{C}$ of needle sugars ($\delta^{13}\text{C}_{\text{NS}}$) and θ for 2006 and 2007. (c, d) Same as Figures 7a and 7b but for VPD. (e, f) Same as Figures 7a and 7b but for T_{AIR} . Values of environmental variables (θ , VPD, and T_{AIR}) correspond to averages over the 3 days prior to needle collection. Fir data points are shown by open circles and a dashed line; pine are shaded triangles and a dotted line, and spruce are black squares and a solid line. All regression lines shown were significant at the 95% confidence level or above. See Table 4 for correlation coefficients.

[17] Examination of the effects of environmental variables such as air temperature (T_{AIR}) and atmospheric VPD on $\delta^{13}\text{C}_{\text{R-WC}}$ showed that significant correlations existed within single hydrologic phases (under various lag times), but these correlations (and associated lag times) were not consistently observed across multiple hydrologic phases or across years (Table 1). Despite the improvement in correlations when these environmental variables were averaged in time (Table 2), these correlations were not consistently observed across multiple hydrologic phases or across seasons. Thus we examined whether these relationships differed between days prior to (“preevent”) and days after (“postevent”) precipitation (see auxiliary material for an example of how “preevent” and “postevent” days were selected). We focused on preevent and postevent days during the late-summer hydrologic phases of each year (i.e., well after the period of melting snow),

because during these phases the soil was likely to be progressively drier prior to a rain event. We found no significant correlations between these two environmental variables and $\delta^{13}\text{C}_{\text{R-WC}}$ for any of the postevent periods (data not shown). However, during preevent periods, we found a significant correlation between VPD and $\delta^{13}\text{C}_{\text{R-WC}}$ for 2 of the 4 years (2006 and 2008; Figure 6). Also during preevent periods, we found significant correlations between air temperature (T_{AIR}) and $\delta^{13}\text{C}_{\text{R-WC}}$ in all 4 of the years. The correlations between $\delta^{13}\text{C}_{\text{R-WC}}$ and both VPD and T_{AIR} during 2008 occurred with opposite sign (i.e., positive) to those observed for 2006, 2007, or 2009. We found no systematic correlations between PPFD and $\delta^{13}\text{C}_{\text{R-WC}}$ for any of the 4 years.

3.4. Needle Sugar $\delta^{13}\text{C}$ Values, Nighttime Ecosystem Respiration, and $\delta^{13}\text{C}_{\text{R-WC}}$

[18] After excluding snowmelt periods, the relationship between $\delta^{13}\text{C}_{\text{NS}}$ and θ was significant for two of the three species, but differed in sign in 2006 and 2007 (Figure 7 and Table 4). The relationship between VPD averaged over 3 days prior to needle collection and $\delta^{13}\text{C}_{\text{NS}}$ was significant for each species during 2006, while the relationship between T_{AIR} and $\delta^{13}\text{C}_{\text{NS}}$ was significant for each species during 2006 as well as 2007.

[19] In regards to ecosystem respiration, we examined whether the opposite (positive) correlations between $\delta^{13}\text{C}_{\text{R-WC}}$ versus T_{AIR} and $\delta^{13}\text{C}_{\text{R-WC}}$ versus VPD observed in 2008 (Figure 6), were also observed when considering $\delta^{13}\text{C}_{\text{R-WC}}$ versus nighttime ecosystem respiration rate (R_{E}). No correlation was observed between $\delta^{13}\text{C}_{\text{R-WC}}$ and R_{E} when examined across entire growing seasons. However, when only periods of progressively decreasing atmospheric humidity were considered (i.e., preevent periods), significant relationships emerged for 3 of the 4 years (Figure 8). The relationship was negative during 2006 and 2007, which means that as R_{E} increased, the isotopic composition of respired CO_2 became more negative. During 2008, however, the opposite trend was observed, confirming that the opposite correlations observed during 2008 for T_{AIR} and VPD (Figure 6) also emerged in relation to R_{E} .

[20] To assess comparability of processes at the leaf and the canopy levels, we compared values of mean $\delta^{13}\text{C}_{\text{NS}}$ and $\delta^{13}\text{C}_{\text{R-WC}}$ during days surrounding the sampling of needle sugars. Upon evaluation of multiple lags ranging up to 15 days, the best correlation was found for $\delta^{13}\text{C}_{\text{R-WC}}$ values averaged in time over a period extending from 7 days prior

Table 4. Pearson’s Linear Correlation Coefficient (r) Between $\delta^{13}\text{C}_{\text{R-NS}}$ and Mean Values of θ , VPD, and T_{AIR} Averaged Over 3 Days Prior to Needle Collection, and for Three Different Tree Species^a

	Species	θ	VPD	T_{AIR}
$\delta^{13}\text{C}_{\text{R-NS}}$ (2006)	fir	-0.67	-0.86	-0.63
	pine	-0.57	-0.61	-0.66
	spruce	-0.76	-0.59	-0.67
$\delta^{13}\text{C}_{\text{R-NS}}$ (2007)	fir	0.67	-0.23	-0.59
	pine	0.55	-0.27	-0.61
	spruce	0.59	-0.29	-0.79

^aHere θ , soil moisture; VPD, vapor pressure deficit; T_{AIR} , air temperature. Values in bold represent significance at the 95% level.

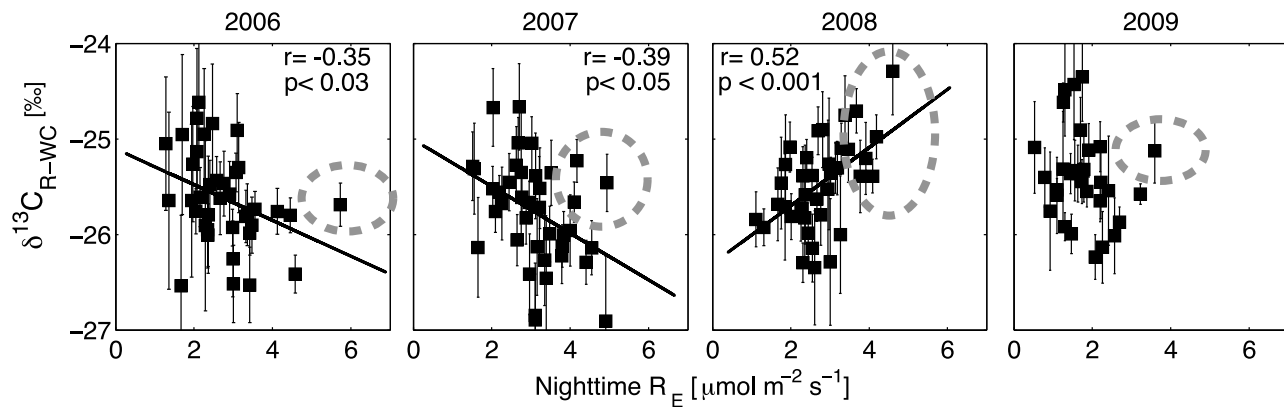


Figure 8. The relationship between nighttime ecosystem respiration (R_E) and $\delta^{13}\text{C}_{R-WC}$ during days prior to precipitation (preevent conditions) from 2006 to 2009. Dashed circles highlight late-summer days with combined relatively high T_{AIR} (daily mean $T_{AIR} \sim 20^\circ\text{C}$), high VPD (~ 2 kPa), and low soil moisture ($\sim 8\%$ or less).

to 3 days after the needle sugar sampling (Figure 9), and only for 2006 ($r = 0.702$; $p = 0.05$). For 2007, however, no correlation was found between mean $\delta^{13}\text{C}_{NS}$ and mean $\delta^{13}\text{C}_{R-WC}$ under any lag time.

4. Discussion

[21] Past studies have revealed that variation in $\delta^{13}\text{C}_R$ or in the $\delta^{13}\text{C}$ of soil respiration is correlated to variation in weather and climate in ways that are consistent with our understanding of leaf-scale controls over CO_2 and H_2O fluxes, and are consistent across broad geographic climate gradients [Ekblad and Hogberg, 2001; Bowling et al., 2002; Pataki et al., 2003; Ekblad et al., 2005; Knohl et al., 2005; Lai et al., 2005; Alstad et al., 2007; Schaeffer et al., 2008a]. In these studies, it was often hypothesized that at least some of the variation in $\delta^{13}\text{C}_R$ was due to the effect of moisture availability (soil and/or atmospheric moisture) on the $\delta^{13}\text{C}$ of photoassimilates via changes in leaf-level photosynthetic discrimination, and subsequent respiration by plants or root symbionts. If the relations among moisture availability and the $\delta^{13}\text{C}$ of recent photosynthate and $\delta^{13}\text{C}_R$ hold consistent (i.e., less negative $\delta^{13}\text{C}$ with increased VPD and decreased θ ; Figure 1), then these correlations should be observed within a single ecosystem across seasonal or interannual moisture variation. In fact, for one past study at Niwot Ridge, and for a portion of a single growing season, the negative correlation between $\delta^{13}\text{C}_R$ and θ , and the positive correlation between $\delta^{13}\text{C}_R$ and VPD were indeed observed [Schaeffer et al., 2008a]. However, in the present study, we only observed the correlation with θ in the drydown period of 2007 and during the summer of 2009 (Figure 5 and Tables 1 and 2); these were among the driest periods that we observed in the 4 years of our analysis (note that 2007 received only 1.1 mm of rain in 22 days during this drydown period, despite having a much wetter late summer; Figure 3).

[22] In agreement with previous studies [Andrews et al., 1999; Ekblad and Hogberg, 2001; Bowling et al., 2002], our findings demonstrate that time lags can range widely (0–

7 days in this study). However, our study also showed that significant correlations are more consistent within single hydrologic phases (under various lag times) and less consistent across multiple hydrologic phases or across years (Tables 1 and 2). We even observed opposite patterns when comparing similar hydrologic phases across the 4 years, and patterns that are opposite to those expected on the basis of leaf gas-exchange theory [e.g., Farquhar et al., 1989] (Figure 6). These opposing patterns did not appear to be an artifact of measuring $\delta^{13}\text{C}_{R-WC}$, rather than photosynthetic discrimination directly, because they were independently confirmed by the correlations between the $\delta^{13}\text{C}$ of needle sugars ($\delta^{13}\text{C}_{NS}$) and T_{AIR} or VPD (Figure 7). Our results demonstrate that the interactions among climate variables and the $\delta^{13}\text{C}$ of needle sugars and ecosystem-respired CO_2 can be more complex than previously shown, particularly as a result of variable precipitation frequencies and different

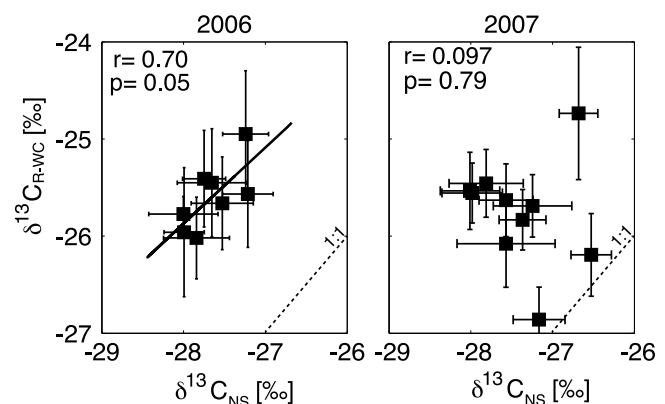


Figure 9. Comparison of mean $\delta^{13}\text{C}_{NS}$ and $\delta^{13}\text{C}_{R-WC}$ during periods surrounding the sampling of needle sugars. The relation with the highest correlation coefficient was found for averaged $\delta^{13}\text{C}_{R-WC}$ values within a combined time span of 3 days after and 7 days prior to needle sugar sampling, and significance occurred only during 2006. The 1:1 line is shown for context.

moisture regimes. In sections 4.1–4.3 we provide potential explanations for these results.

4.1. Variation in $\delta^{13}\text{C}_{\text{R-WC}}$ as a Function of Moisture Availability

[23] Despite the similarity of seasonal means of $\delta^{13}\text{C}_{\text{R-WC}}$ across the four growing seasons (-25.6 , -25.8 , -25.7 , and -25.9% , respectively, for each year from 2006 to 2009), the intraseasonal variability of $\delta^{13}\text{C}_{\text{R}}$ differed markedly from year to year. When analyzing the effect of soil water content on $\delta^{13}\text{C}_{\text{R-WC}}$ during snowmelt, we found a positive and significant correlation between $\delta^{13}\text{C}_{\text{R-WC}}$ and θ in one of the analysis years, 2008 (Figure 5 and Tables 1 and 2). During the snowmelt phase, soil moisture was correlated positively with higher $\delta^{13}\text{C}_{\text{R-WC}}$ in 2008, as opposed to negatively as has been commonly observed [Fessenden and Ehleringer, 2003; McDowell et al., 2004; Lai et al., 2005; Alstad et al., 2007; Schaeffer et al., 2008a]. On the basis of leaf-scale theory, it is expected that the ratio of stomatal conductance to net photosynthesis rate (g/A) would decrease at lower θ , thus causing less photosynthetic discrimination against $^{13}\text{CO}_2$ (resulting in less negative $\delta^{13}\text{C}_{\text{R}}$ values). In our study, the positive relationship observed in 2008 occurred after a late snowmelt (the latest among the 4 years of the study) that pushed the period of highest meltwater availability into mid-to-late June (a period when atmospheric VPD was also high). Thus, although soil moisture was high, atmospheric humidity was low, and this combination has the potential to force a reduction in stomatal conductance resulting in less photosynthetic discrimination against $^{13}\text{CO}_2$ during this part of the growing season. It remains to be addressed, however, how the spatiotemporal variability of soil moisture (a direct result of the lateral redistribution of soil water) might affect the temporal variability of $\delta^{13}\text{C}_{\text{R-WC}}$, or how differences in the spatial variability of sources of CO_2 (as demonstrated by Riveros-Iregui and McGlynn [2009] in subalpine ecosystems) in combination with tower footprint variability may affect our observations.

4.2. Preevent Periods, Postevent Periods, and $\delta^{13}\text{C}_{\text{R-WC}}$

[24] Analysis of the effects of environmental variables separately for preevent and postevent periods revealed significant relationships between $\delta^{13}\text{C}_{\text{R-WC}}$ and T_{AIR} during preevent periods in all 4 years, and between $\delta^{13}\text{C}_{\text{R-WC}}$ and VPD during preevent in 3 of the 4 years (Figure 6). The correlations with T_{AIR} were negative in late summer of 2006, 2007, and 2009, but positive in 2008. The negative correlations between T_{AIR} and $\delta^{13}\text{C}_{\text{R-WC}}$ are opposite to what has been observed between the $\delta^{13}\text{C}_{\text{R}}$ and soil temperature [McDowell et al., 2004]. As T_{AIR} increases, VPD also increases (exponentially so), potentially causing a decrease in c_i/c_a and the photosynthetic discrimination against $^{13}\text{CO}_2$ (driving a positive correlation; Figure 6). However, these negative correlations between $\delta^{13}\text{C}_{\text{R-WC}}$ and T_{AIR} in 2006 and 2007 were independently confirmed using carbon isotope ratio of needle sugars, and they appear to be highly influenced by cold periods early in the growing season (Figure 7). Many of the days with less negative $\delta^{13}\text{C}_{\text{R-WC}}$ also have mean daily temperatures well below 10°C , with accompanying low VPD. During these cold periods nighttime frosts are common. It is likely that the negative correlations of Figures 6 and 7 are due to stomatal limita-

tions, such as those previously reported following cold nights in conifer forests in the southern Rocky Mountains [Kaufmann, 1982; Smith et al., 1984] and the Pacific Northwest of the United States [Bowling et al., 2002]. Such stomatal limitations could also lead to a decrease in daily uptake and potentially nighttime ecosystem respiration (R_E), resulting in a negative correlation between $\delta^{13}\text{C}_{\text{R-WC}}$ and R_E (Figure 8).

[25] Contrastingly, the positive correlation between $\delta^{13}\text{C}_{\text{R-WC}}$ versus T_{AIR} and VPD during preevent periods of 2008 (Figure 6) was driven strongly by a few days of relatively high temperatures (daily mean T_{AIR} near 20°C) and high VPD (near 2 kPa). These effects (single, warm-and-dry days) on the $\delta^{13}\text{C}$ of both assimilated and respired carbon were further confirmed by the relationship between nighttime R_E and $\delta^{13}\text{C}_{\text{R-WC}}$ (Figure 8). It appears that the positive relationship between $\delta^{13}\text{C}_{\text{R-WC}}$ and R_E observed during preevent periods of 2008 was strongly driven by a few late-summer days (after 25 July) with high T_{AIR} , high VPD, and very low θ ($\sim 8\%$ or less). Similar periods of warm weather late in the summer also occurred, but were less common during 2006, 2007, or 2009 (Figure 8). Thus, these results show that the opposing trends among years, and trends that oppose those expected from past leaf and plot level studies [Farquhar et al., 1989; Dawson et al., 2002], may be due to unique combinations of weather conditions in each year, and the susceptibility of photosynthetic isotope discrimination in trees of this ecosystem to extreme air temperatures.

4.3. How Consistent Are These Patterns Across Growing Seasons?

[26] We investigated whether previous patterns observed at the Niwot Ridge forest (i.e., a strong, negative correlation between θ and $\delta^{13}\text{C}_{\text{R-NG}}$, emerging during the month of July and the first half of August 2003 [Schaeffer et al., 2008a]), emerged in the same manner and during the same periods from 2006 to 2009. We were able to identify similar patterns between θ and $\delta^{13}\text{C}_{\text{R-NG}}$ only during the late summer of 2009 (the driest July–September period on the 30 year record; see Tables 1 and 2). Our findings suggest that the contrasting differences across years are the result of the variable intraseasonal and interannual precipitation regimes observed during the 4 years of this study. Summer precipitation was higher during 2006, 2007 and 2008, compared to 2003 [Schaeffer et al., 2008a] and 2009 (Table 3), and this suggests that the low and less frequent precipitation of 2003 and 2009 may have played a role in revealing the emerging patterns between θ and $\delta^{13}\text{C}_{\text{R-NG}}$. These findings also imply a first-order control of moisture (including θ and atmospheric humidity) on ecosystem respiration, and systematic differences of these moisture controls on $\delta^{13}\text{C}_{\text{R-UC}}$ and $\delta^{13}\text{C}_{\text{R-NG}}$. These results are in agreement with previous studies that suggested that $\delta^{13}\text{C}_{\text{R-UC}}$ (including foliar respiration) varies in response to changes in VPD, while $\delta^{13}\text{C}_{\text{R-NG}}$ (including belowground autotrophic and heterotrophic respiration) varies in response to θ [Schaeffer et al., 2008a]; however our results also suggest that such differences may only emerge during drought when the strongest differences between $\delta^{13}\text{C}_{\text{R-UC}}$ and $\delta^{13}\text{C}_{\text{R-NG}}$ were also observed (e.g., during 2009; Figure 4). Low summer precipitation of 2009 resulted in progressively drier conditions and monotonically increasing $\delta^{13}\text{C}_{\text{R-WC}}$ values throughout

the summer (Figure 3); this was likely due to autotrophic activity responding to drier conditions and decreased contributions from other respiratory pools (e.g., microbial respiration). Future studies should specifically address how autotrophic and heterotrophic contributions to CO_2 in forest air vary across “wet” and “dry” periods of the year.

[27] This study offers an important opportunity to directly test the assumptions of previous studies in which $\delta^{13}\text{C}_{\text{R-WC}}$ is assumed to directly reflect $\delta^{13}\text{C}_{\text{NS}}$ (as shown in Figure 1). Our findings suggest that this assumption can hold true during the driest portions of the year; thus during this time photosynthetic effects at the leaf level may be transferable to the entire ecosystem. In fact, a direct comparison of $\delta^{13}\text{C}_{\text{NS}}$ and $\delta^{13}\text{C}_{\text{R-WC}}$ averaged over a 10 day span demonstrated that the strength of the correlation varied from one year to the next (Figure 9). During 2006, this correlation was positive ($r = 0.703$; $p = 0.05$), whereas 2007 showed no correlation ($r = -0.097$; $p = 0.79$). These differences may have resulted from different weather conditions during each growing season. The early spring of 2006 was the warmest across the 4 years, resulting in an early snowmelt, and summer precipitation was less frequent than 2007; the early spring of 2007 was cooler than that for 2006 and summer precipitation occurred more frequently. The cooler spring in 2007 may have resulted in smaller tree respiration rates (compared to 2006), and allowed sugar substrates assimilated during the winter and early spring period (which typically have less negative $\delta^{13}\text{C}_{\text{NS}}$ values), to last longer into the growing season and mix with sugars assimilated during the warmer summer period, obscuring any potential for close tracking between $\delta^{13}\text{C}_{\text{NS}}$ and seasonal climate. However, our results suggest that at a single site these patterns (i.e., leaf-canopy correlations) appear to be strongly dependent on moisture conditions and may “emerge” and “disappear” according to the wetness status of the system (strongest during the driest portions of the year and non-existent during wet periods). While in part our study does corroborate findings of previous studies [Bowling *et al.*, 2002; Schaeffer *et al.*, 2008a], our study also reports new observations and provides greater understanding for how environmental variables and weather events may influence the variability of $\delta^{13}\text{C}_{\text{R}}$. These findings are further supported by recent studies that demonstrate that the coupling between $\delta^{13}\text{C}$ of photosynthates and the $\delta^{13}\text{C}$ of soil-respired CO_2 may in fact be weakened (or anticorrelated) during cloudy and rainy conditions [Wingate *et al.*, 2010], highlighting the importance of understanding the effects that variable weather conditions and interannual hydrologic regimes may impose on whole ecosystem carbon cycling.

5. Conclusions

[28] Past studies have provided optimism that analyses of dynamics in $\delta^{13}\text{C}_{\text{R}}$ are informative about climate-photosynthesis relations at the ecosystem scale. The initial studies that provided this optimism were conducted on ecosystems in strongly contrasting climate regimes [Bowling *et al.*, 2002; Pataki *et al.*, 2003] and thus were most likely to reflect extreme contrasts in the relation between climate and $\delta^{13}\text{C}_{\text{R}}$. More recently, it has been suggested the correlations of $\delta^{13}\text{C}$ of soil and ecosystem respiration to environmental factors that affect ^{13}C discrimination during CO_2 fixation

may be used to estimate the time lag between photosynthesis and the CO_2 pulse of a respiratory flux [Kuzayakov and Gavrichkova, 2010]. We tested such correlations by studying a single ecosystem exposed to environmental variation within and between four growing seasons, and addressed three specific questions:

[29] 1. Are patterns in $\delta^{13}\text{C}_{\text{R}}$ consistent with those predicted from general leaf-scale theory (i.e., less negative $\delta^{13}\text{C}_{\text{R}}$ with increased VPD and T_{AIR} , and less negative $\delta^{13}\text{C}_{\text{R}}$ with decreased θ)? Our findings revealed that relations between $\delta^{13}\text{C}_{\text{R}}$ and climate are more complex and nuanced than the assumed relations based on leaf-scale theory. Efforts to model and predict the variability of $\delta^{13}\text{C}_{\text{R}}$ under changing environmental variables must characterize and parameterize the effects of unique combinations of weather conditions and variable precipitation regimes, in combination with the susceptibility of photosynthetic isotope discrimination to extreme air temperatures.

[30] 2. How consistent are these patterns across different hydrologic regimes (e.g., snowmelt, precipitation, drought) or in relation to previous studies reported for a single growing season at this site [e.g., Schaeffer *et al.*, 2008a]? Our study demonstrates that significant correlations between $\delta^{13}\text{C}_{\text{R}}$ and environmental variables (T_{AIR} , VPD) may be found only after removing periods highly influenced by recent precipitation events and the accompanying patterns of increasing atmospheric humidity that follow rainy periods. We were able to reproduce past reported negative correlations between $\delta^{13}\text{C}_{\text{R}}$ and decreased soil moisture or increased atmospheric VPD, but only during the driest periods of the 4 years of observations of this study. During other periods, however, we found that unique combinations of soil moisture, air temperature and atmospheric VPD may force the correlations into patterns that oppose those reported in past studies and those based on leaf-level gas-exchange theory.

[31] 3. Should process knowledge obtained at the leaf level be used to predict ecosystem level responses to environmental conditions? Based on our analysis, we conclude that process knowledge of leaf-level isotopic response to environmental conditions may be transferable to the entire ecosystem but only during the driest portions of the year. This conclusion should cause some caution to those scientists involved in the development of hierarchical process models. It is not likely that simple assumptions about the direct extrapolation of processes at the leaf scale to the ecosystem scale can be made; thus we bring to the forefront the need to broaden examination of these relations. Future studies should address the biophysical mechanisms underlying environmental influences on whole-ecosystem $\delta^{13}\text{C}_{\text{R}}$, the coupling of leaf- and ecosystem-scale processes, and the effects of superimposed snowmelt, precipitation, and increased atmospheric humidity on $\delta^{13}\text{C}_{\text{R}}$.

[32] **Acknowledgments.** We are thankful to Sean Schaeffer, Kurt Chowanski, Mark Losleben, Lucas Zukiewicz, Kelly Matheson, Dave Millar, John Knowles, and Kirk Ranno for field assistance and data collection. We thank the USDA Natural Resources Conservation Service, Colorado Snow Survey Program, for the SNOTEL network data. Logistical help and stream discharge data were provided by the NSF-funded Niwot Ridge LTER program. This research was supported by the Office of Science (BER), U.S. Department of Energy (grant DE-FG02-04ER63904) as part of the North American Carbon Program, and the U.S. National Science

Foundation (grant DEB-0743251). CO_2 isotope data from the Niwot Ridge AmeriFlux site are available for collaboration; please contact David Bowling (david.bowling@utah.edu). Two anonymous reviewers, the associate editor, and the editor Dennis Baldocchi provided valuable suggestions for the improvement of this manuscript.

References

- Alstad, K. P., C. T. Lai, L. B. Flanagan, and J. R. Ehleringer (2007), Environmental controls on the carbon isotope composition of ecosystem-respired CO_2 in contrasting forest ecosystems in Canada and the USA, *Tree Physiol.*, 27(10), 1361–1374.
- Amthor, J. S. (1994), Scaling CO_2 -photosynthesis relationships from the leaf to the canopy, *Photosynth. Res.*, 39(3), 321–350.
- Andrews, J. A., K. G. Harrison, R. Matamala, and W. H. Schlesinger (1999), Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE), *Soil Sci. Soc. Am. J.*, 63(5), 1429–1435.
- Atkin, O. K., L. J. Atkinson, R. A. Fisher, C. D. Campbell, J. Zaragoza-Castells, J. W. Pitchford, F. I. Woodward, and V. Hurry (2008), Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model, *Global Change Biol.*, 14(11), 2709–2726.
- Baldocchi, D., et al. (2001), FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bull. Am. Meteorol. Soc.*, 82(11), 2415–2434.
- Bowling, D. R., N. G. McDowell, B. J. Bond, B. E. Law, and J. R. Ehleringer (2002), ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit, *Oecologia*, 131(1), 113–124.
- Bowling, D. R., S. D. Sargent, B. D. Tanner, and J. R. Ehleringer (2003), Tunable diode laser absorption spectroscopy for stable isotope studies of ecosystem-atmosphere CO_2 exchange, *Agric. For. Meteorol.*, 118(1–2), 1–19.
- Bowling, D. R., S. P. Burns, T. J. Conway, R. K. Monson, and J. W. C. White (2005), Extensive observations of CO_2 carbon isotope content in and above a high-elevation subalpine forest, *Global Biogeochem. Cycles*, 19, GB3023, doi:10.1029/2004GB002394.
- Bowling, D. R., D. E. Pataki, and J. T. Randerson (2008), Carbon isotopes in terrestrial ecosystem pools and CO_2 fluxes, *New Phytol.*, 178(1), 24–40.
- Bowling, D. R., W. J. Massman, S. M. Schaeffer, S. P. Burns, R. K. Monson, and M. W. Williams (2009), Biological and physical influences on the carbon isotope content of CO_2 in a subalpine forest snowpack, Niwot Ridge, Colorado, *Biogeochemistry*, 95, 37–59, doi:10.1007/s10533-008-9233-4.
- Cerling, T. E., D. K. Solomon, J. Quade, and J. R. Bowman (1991), On the isotopic composition of carbon in soil carbon-dioxide, *Geochim. Cosmochim. Acta*, 55(11), 3403–3405.
- Chasmer, L., H. McCaughey, A. Barr, A. Black, A. Shashkov, P. Treitz, and T. Zha (2008), Investigating light-use efficiency across a jack pine chronosequence during dry and wet years, *Tree Physiol.*, 28(9), 1395–1406.
- Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu (2002), Stable isotopes in plant ecology, *Annu. Rev. Ecol. Syst.*, 33, 507–559.
- Eklblad, A., and P. Hogberg (2001), Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration, *Oecologia*, 127(3), 305–308.
- Eklblad, A., B. Bostrom, A. Holm, and D. Comstedt (2005), Forest soil respiration rate and $\delta^{13}\text{C}$ is regulated by recent above ground weather conditions, *Oecologia*, 143(1), 136–142.
- Farquhar, G. D., M. H. O'Leary, and J. A. Berry (1982), On the relationship between carbon isotope discrimination and the inter-cellular carbon-dioxide concentration in leaves, *Aust. J. Plant Physiol.*, 9(2), 121–137.
- Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick (1989), Carbon isotope discrimination and photosynthesis, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 40, 503–537.
- Fessenden, J. E., and J. R. Ehleringer (2003), Temporal variation in $\delta^{13}\text{C}$ of ecosystem respiration in the Pacific Northwest: Links to moisture stress, *Oecologia*, 136(1), 129–136.
- Gessler, A., H. Rennenberg, and C. Keitel (2004), Stable isotope composition of organic compounds transported in the phloem of European beech—Evaluation of different methods of phloem sap collection and assessment of gradients in carbon isotope composition during leaf-to-stem transport, *Plant Biol.*, 6(6), 721–729.
- Hu, J., D. J. P. Moore, S. P. Burns, and R. K. Monson (2010a), Longer growing seasons lead to less carbon sequestration in a subalpine forest, *Global Change Biol.*, 16, 771–783, doi:10.1111/j.1365-2486.2009.01967.x.
- Hu, J., D. J. P. Moore, and R. K. Monson (2010b), Weather and climate controls over the seasonal carbon isotope dynamics of sugars from subalpine forest trees, *Plant Cell Environ.*, 33, 35–47, doi:10.1111/j.1365-3040.2009.02049.x.
- Jarvis, P. G. (1995), Scaling processes and problems, *Plant Cell Environ.*, 18(10), 1079–1089.
- Kaufmann, M. R. (1982), Evaluation of season, temperature, and water-stress effects on stomata using a leaf conductance model, *Plant Physiol.*, 69(5), 1023–1026.
- Keeling, C. D. (1958), The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas, *Geochim. Cosmochim. Acta*, 13(4), 322–334.
- Knohl, A., R. A. Werner, W. A. Brand, and N. Buchmann (2005), Short-term variations in $\delta^{13}\text{C}$ of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest, *Oecologia*, 142(1), 70–82.
- Knohl, A., A. R. B. Soe, W. L. Kutsch, M. Gockede, and N. Buchmann (2008), Representative estimates of soil and ecosystem respiration in an old beech forest, *Plant Soil*, 302(1–2), 189–202.
- Kuzyakov, Y., and O. Gavrichkova (2010), Time lag between photosynthesis and carbon dioxide efflux from soil: A review of mechanisms and controls, *Global Change Biol.*, 16, 3386–3406, doi:10.1111/j.1365-2486.2010.02179.x.
- Lai, C. T., J. R. Ehleringer, A. J. Schauer, P. P. Tans, D. Y. Hollinger, K. T. Paw U, J. W. Munger, and S. C. Wofsy (2005), Canopy-scale $\delta^{13}\text{C}$ of photosynthetic and respiratory CO_2 fluxes: Observations in forest biomes across the United States, *Global Change Biol.*, 11(4), 633–643.
- McDowell, N. G., D. R. Bowling, A. Schauer, J. Irvine, B. J. Bond, B. E. Law, and J. R. Ehleringer (2004), Associations between carbon isotope ratios of ecosystem respiration, water availability and canopy conductance, *Global Change Biol.*, 10(10), 1767–1784.
- Misson, L., et al. (2007), Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: A synthesis based on FLUXNET data, *Agric. For. Meteorol.*, 144(1–2), 14–31.
- Monson, R. K., A. A. Turnipseed, J. P. Sparks, P. C. Harley, L. E. Scott-Denton, K. Sparks, and T. E. Huxman (2002), Carbon sequestration in a high-elevation, subalpine forest, *Global Change Biol.*, 8(5), 459–478.
- Monson, R. K., J. P. Sparks, T. N. Rosenstiel, L. E. Scott-Denton, T. E. Huxman, P. C. Harley, A. A. Turnipseed, S. P. Burns, B. Backlund, and J. Hu (2005), Climatic influences on net ecosystem CO_2 exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest, *Oecologia*, 146(1), 130–147.
- Mortazavi, B., J. P. Chanton, J. L. Prater, A. C. Oishi, R. Oren, and G. Katul (2005), Temporal variability in ^{13}C of respired CO_2 in a pine and a hardwood forest subject to similar climatic conditions, *Oecologia*, 142(1), 57–69.
- Pataki, D. E., J. R. Ehleringer, L. B. Flanagan, D. Yakir, D. R. Bowling, C. J. Still, N. Buchmann, J. O. Kaplan, and J. A. Berry (2003), The application and interpretation of Keeling plots in terrestrial carbon cycle research, *Global Biogeochem. Cycles*, 17(1), 1022, doi:10.1029/2001GB001850.
- Pereira, J. S., et al. (2007), Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems—The effect of drought, *Biogeosciences*, 4(5), 791–802.
- Riveros-Iregui, D. A., and B. L. McGlynn (2009), Landscape structure control on soil CO_2 efflux variability in complex terrain: Scaling from point observations to watershed scale fluxes, *J. Geophys. Res.*, 114, G02010, doi:10.1029/2008JG000885.
- Running, S. W., and S. T. Gower (1991), Forest-Bgc, a general-model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets, *Tree Physiol.*, 9(1–2), 147–160.
- Schaeffer, S. M., D. E. Anderson, S. P. Burns, R. K. Monson, J. Sun, and D. R. Bowling (2008a), Canopy structure and atmospheric flows in relation to the $\delta^{13}\text{C}$ of respired CO_2 in a subalpine coniferous forest, *Agric. For. Meteorol.*, 148(4), 592–605.
- Schaeffer, S. M., J. B. Miller, B. H. Vaughn, J. W. C. White, and D. R. Bowling (2008b), Long-term field performance of a tunable diode laser absorption spectrometer for analysis of carbon isotopes of CO_2 in forest air, *Atmos. Chem. Phys.*, 8(17), 5263–5277.
- Scott-Denton, L. E., K. L. Sparks, and R. K. Monson (2003), Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest, *Soil Biol. Biochem.*, 35(4), 525–534.
- Simon, E., F. X. Meixner, L. Ganzveld, and J. Kesselmeier (2005), Coupled carbon-water exchange of the Amazon rain forest. I. Model description, parameterization and sensitivity analysis, *Biogeosciences*, 2(3), 231–253.
- Smith, W. K., D. R. Young, G. A. Carter, J. L. Hadley, and G. M. McNaughton (1984), Autumn stomatal closure in 6 conifer species of the central Rocky Mountains, *Oecologia*, 63(2), 237–242.
- Turnipseed, A. A., P. D. Blanken, D. E. Anderson, and R. K. Monson (2002), Energy budget above a high-elevation subalpine forest in complex topography, *Agric. For. Meteorol.*, 110(3), 177–201.

- Wingate, L., J. Ogée, R. Burrell, A. Bosc, M. Devaux, J. Grace, D. Loustau, and A. Gessler (2010), Photosynthetic carbon isotope discrimination and its relationship to the carbon isotope signals of stem, soil, and ecosystem respiration, *New Phytol.*, *188*(2), 576–589, doi:10.1111/j.1469-8137.2010.03384.x.
- Wohlfahrt, G., A. Hammerle, A. Haslwanter, M. Bahn, U. Tappeiner, and A. Cernusca (2008), Seasonal and interannual variability of the net ecosystem CO_2 exchange of a temperate mountain grassland: Effects of weather and management, *J. Geophys. Res.*, *113*, D08110, doi:10.1029/2007JD009286.
- Xiao, J. F., et al. (2008), Estimation of net ecosystem carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data, *Agric. For. Meteorol.*, *148*(11), 1827–1847.
- Yakir, D., and L. D. L. Sternberg (2000), The use of stable isotopes to study ecosystem gas exchange, *Oecologia*, *123*(3), 297–311.
- Zobitz, J. M., J. P. Keener, H. Schnyder, and D. R. Bowling (2006), Sensitivity analysis and quantification of uncertainty for isotopic mixing relationships in carbon cycle research, *Agric. For. Meteorol.*, *136*(1–2), 56–75.

D. R. Bowling, Department of Biology, University of Utah, Salt Lake City, UT 84112, USA.

S. P. Burns and R. K. Monson, Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309, USA.

J. Hu, National Center for Atmospheric Research, Boulder, CO 80307, USA.

D. A. Riveros-Iregui, School of Natural Resources, University of Nebraska-Lincoln, 519 Hardin Hall, 3310 Holdrege St., Lincoln, NE 68583-0995, USA. (driveros2@unl.edu)