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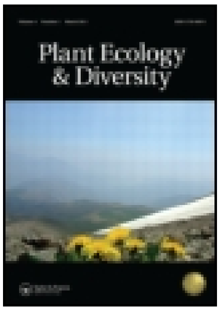

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Fluxes of energy, water, and carbon dioxide from mountain ecosystems at Niwot Ridge, Colorado

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Fluxes of energy, water, and carbon dioxide from mountain ecosystems at Niwot Ridge, Colorado

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Background: The eddy covariance (EC) technique provides a direct measure of water vapour and carbon dioxide fluxes between ecosystems and the atmosphere.

Aims: This review article highlights the findings of various studies that have integrated EC observations into basic meteorological, hydrological and ecological research questions in two ecosystems near Niwot Ridge, Colorado, and synthesises these studies into a catchment-scale model of water and carbon cycling, within the context of regional disturbance and environmental change.

Methods: EC was implemented continuously over subalpine forest and alpine tundra vegetation at Niwot Ridge, and resulting data were compared with discrete measurements and modelling studies.

Results: Sensible heat fluxes were generally in excess of latent heat fluxes, indicating that the forest and tundra ecosystems were moisture limited. Snow cover regulated the annual sum of primary productivity in the forest, and beneath-snow respiration represented a significant portion of ecosystem respiration at both locations.

Conclusions: Changes in the magnitude, timing, or spatial distribution of snow are likely to have the greatest impact on ecological processes in these semi-arid mountain catchments, but possibly in compensatory ways. Ultimately, the degree to which net carbon losses from alpine tundra offset forest carbon sequestration will determine the future magnitude of the Western United States carbon sink.

Keywords: alpine tundra; complex terrain; ecosystem respiration; eddy covariance; energy balance; evapotranspiration; gross primary productivity; net ecosystem exchange; subalpine forest; sublimation

Introduction

Mountains in many parts of the world are especially susceptible to the impacts of climate change, and so studies in these regions allow for the early detection of climate change effects on hydrological and ecological systems (Beniston 2003), with important ramifications for water yields, biological communities, and ecosystem dynamics (Williams et al. 2002; Pugh and Gordon 2012). Harsh climates and short growing seasons combine to reduce the ability of mountain ecosystems to withstand climate extremes and ecological disturbances (Baron et al. 2009), and the Rocky Mountains in many places are currently affected by drought, fire, and insect outbreak (Desai et al. 2011). The eddy covariance (EC) technique provides a direct measurement of ecosystem gas exchange, and is thus an important tool for understanding and monitoring forest growth, as well as rates of regional greenhouse gas emissions (Baldocchi et al. 2001; Foken et al. 2012). To investigate controls on the surface–atmosphere exchange of energy, water and carbon dioxide (CO_2) in the Rocky Mountains, EC measurements were established in the subalpine forest below Niwot Ridge, Colorado in 1998, and then expanded to the alpine tundra in 2007. Here, we review and synthesise past studies that have used these measurements, and organise the primary conclusions from these studies into a framework capable of local-to-regional assessment of how these mountain ecosystems respond to climate variation, and how they may respond to future climate change.

The airborne fraction of emitted CO_2 is rising, and models attribute this to a decrease in the uptake of CO_2 by terrestrial carbon sinks in response to climate change and variability (Le Quéré et al. 2009). In the Western United States (US), approximately 70% of the carbon sink occurs at elevations above 750 m above sea level (asl), where 50–85% of the land is dominated by hilly or mountainous topography (Schimel et al. 2002; Desai et al. 2011). It is therefore crucial to reduce the uncertainty associated with the nature of CO_2 uptake in the mountains, but our understanding of the physiological processes that affect CO_2 exchange is complicated by difficulties encountered when measuring and modelling ecosystem-scale processes in this complex terrain (Finnigan 2008). Recently, EC has been successfully used at several locations in mountainous/complex terrain without significant methodological violations (e.g. Hammerle et al. 2007), and this has greatly expanded the ability of scientists to investigate land–atmosphere exchange at the ecosystem level. For example, based on EC data from Niwot Ridge, simulations with the DAYCENT model indicated that forest carbon

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uptake in Western Colorado (approximately 160,000 km^2) was 12.6 Tg C per year, and that the majority of the carbon was sequestered by forests in mountainous terrain (Sun et al. 2010).

Many areas that receive relatively little precipitation during the summer months, such as the semi-arid Western US, are also heavily dependent on seasonal snowpacks to provide natural storage of water for agriculture, industry and drinking during the dry summer and fall seasons (Barnett et al. 2005). Spring snowmelt provides irrigation and municipal water supplies for over 60 million people in the Western US (Bales et al. 2006), and the annual snowpack in this region is also a significant factor in the structure and function of high-elevation forest and tundra ecosystems (Gustafson et al. 2010). Seasonally snow-covered regions are especially susceptible to climate change, however, because small changes in air temperature or precipitation may result in large changes in the amount and timing of snow cover (Mote et al. 2005; Brooks et al. 2011). Indeed, recent studies have documented that in most of this region, changes in patterns of snow accumulation and melt are causing substantial reductions in the natural storage of water (Clow 2010), and the current demand for water resources in many parts of the Western US will not be met under future climate conditions and the pressures of a larger population and economy (Barnett et al. 2004).

This review article aims to: (1) highlight the findings of various studies that have integrated EC into basic meteorological, hydrological and ecological research questions in two ecosystems near Niwot Ridge, Colorado; (2) synthesise these results into a regional picture of energy, water, and carbon cycling; and (3) place these results within the context of regional climate change and ecological disturbance to constrain the expected impacts on forest health, greenhouse gas emissions, and ecosystem services, such as provisioning of water.

Site descriptions

Subalpine forest

The AmeriFlux effort was initiated as an informal collaboration among investigators developing EC towers in North America in the mid-1990s, and researchers began data collection at the Niwot Ridge AmeriFlux tower (NWT) in November 1998. The tower is located in the subalpine forest ecosystem of the Rocky Mountains at 3050 m asl, 8 km east of the North American Continental Divide (40° 1′ 58.4″ N; 105° 32′ 47.0″ W). The mixed coniferous forest around the 26-m tower was established following clear-cut logging approximately 100 years ago, and the dominant tree species are currently lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). In 2002–2003, the mean canopy height was 11.5 m, mean tree density was 4000 stems ha^{-1}, maximum leaf area index (*LAI*) was 4.2 m^2 m^{-2}, and the canopy gap fraction was 17% (Turnipseed et al. 2002; 2003). A sparse understory of 10–15 cm blueberry plants (*Vaccinium myrtillus*) also covered approximately 25% of the ground. The tower is situated on a granitic glacial moraine that slopes west to east at approximately 5 degrees, covered by a shallow (5–10 cm) layer of organic soil. Mean annual air temperature (*MAT*) is 1.3 °C and the mean annual precipitation (*MAP*) is 692 mm at a Long-Term Ecological Research Program (LTER) monitoring site approximately 500 m northeast of the tower (C1; Greenland 1989). At the tower itself, the *MAT* was 1.3 °C and the *MAP* was 698 mm between 1999 and 2012 (Table 1). The seasonal snowpack typically exists from early November until early June and peak snowmelt generally occurs in May. See Turnipseed et al. (2002; 2003; 2004) and Burns et al. (2014) for a complete description of topographical, meteorological and energy balance measurements at this location.

Alpine tundra

Two identical 3-m tall EC towers were installed over alpine tundra on Niwot Ridge near the location locally referred to as ‘T-Van’ (40° 03′ 11″ N; 105° 35′ 11″ W; 3500 m asl) in June 2007. These towers, maintained by the Niwot Ridge LTER, and believed to be the highest-elevation EC towers in North America, are located 50 m apart along a 7.8% sloping west to east transect (following the prevailing wind direction). Each tower is fully equipped to quantify the turbulent fluxes of heat, water, and CO$_2$, as well as a suite of supporting meteorological and energy

Table 1. Mean annual air temperature (T_a; 2 m height) and total annual precipitation (P; 10.5 m height) at the Niwot AmeriFlux tower, maximum annual snow water equivalent (*SWE*) at the Niwot SNOTEL site (3021 m asl; less than 500 m north of the AmeriFlux tower), mean annual air temperature (3 m height) at T-Van, and total annual precipitation (2 m height) at the Saddle (3528 m asl; less than 500 m northwest of T-Van). Alpine *SWE* is not measured continuously on Niwot Ridge. The SD is the standard deviation.

	Forest			Tundra	
Year	T_a (°C)	P (mm)	Max *SWE* (mm)	T_a (°C)	P (mm)
1999	1.3	766	373		
2000	1.5	662	318		
2001	1.6	641	249		
2002	1.1	485	178		
2003	1.7	613	401		
2004	1.0	820	295		
2005	1.5	673	340		
2006	1.4	641	325		
2007	1.6	685	455		
2008	0.7	647	378	−1.9	1119
2009	0.9	585	406	−1.4	916
2010	1.4	652	318	−1.1	1046
2011	0.8	984	432	−1.4	1307
2012	2.3	914	279	0.2	846
Mean	1.3	698	339	−1.1	1047
SD	0.4	132	75	0.8	181

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balance measurements (Blanken et al. 2009). Leaf area index is 0.87 m^2 m^{-2}, and vegetation around the towers is predominantly a treeless, dry alpine fellfield, with dominant species including curly sedge (*Carex rupestris*), Bellardi bog sedge (*Kobresia myosuroides*), and Rocky Mountain nailwort (*Paronychia pulvinata*) (Walker et al. 2001). T-Van is situated in the lee of the Continental Divide and strong westerly (downslope) winds are common throughout the fall, winter, and spring, but to a lesser extent during summer. These winds scour snow from exposed areas, resulting in little to no snow accumulation throughout the winter (Erickson et al. 2005). The alpine tundra soils are spatially heterogeneous Inceptisols with Cryochrepts (less organic matter) and Cryumbrepts (more organic matter) intermixed throughout the landscape. At T-Van, the *MAT* and *MAP* were -1.1 °C and 1047 mm between 2008 and 2012, which was warmer and wetter than the long-term (31 years) average *MAT* (-2.2 °C) and *MAP* (884 mm) near this location (Table 1).

Eddy covariance measurements in complex terrain

The EC method is a micrometeorological technique that can be used to provide a direct measure of net CO_2 and water vapour fluxes between the surface and the atmosphere (Aubinet et al. 2000; Baldocchi et al. 2001). Since the upwind sample area, or "footprint", of these measurements typically ranges from 100 m to several kilometres, this allows for researchers to investigate hypotheses at the ecosystem scale (Baldocchi et al. 2000). In addition, EC provides an automated flux measurement that minimally interferes with the ground surface, so fieldwork is minimised, as is disturbance traditionally associated with destructive sampling. Historically, EC was developed over ecosystems with nearly flat topography and homogeneous vegetation (e.g. Desjardins 1985; Verma et al. 1989); however, EC can also be used to investigate surface–atmosphere trace gas exchange over complex, heterogeneous terrain, as long as both horizontal and vertical transport by mean circulations and turbulent fluxes are considered (Finnigan 2004; Sun et al. 2007).

The daytime turbulent flux footprint at the AmeriFlux tower was generally within acceptable limits for the calculation of flux statistics (Turnipseed et al. 2002, 2003), but stable atmospheric conditions were typical at night, which expanded the footprint beyond the scale of adequate fetch. To address this, and to quantify the influence of gravitationally induced cold-air drainage flows (horizontal advection) that are common in mountain ecosystems, a multiple tower observing system was deployed (Yi et al. 2005). Ensuing work showed that horizontally advected CO_2 dominated the total transport of CO_2 at night, and could even be significant during the day, when upslope and downslope flows were equally likely to occur (Sun et al. 2007; Yi et al. 2008; Burns et al. 2010). Consideration of vertical advection, resulting from the convergence of drainage flows and positive bias in the mean vertical wind velocity at the tower (see Turnipseed et al. 2004), introduced further uncertainty into the CO_2 flux estimates. Approximately 65% more CO_2 uptake was observed when the sum of the advection terms was used to correct cumulative annual net ecosystem CO_2 exchange (*NEE*) across the span of 6 years, compared with a traditional friction velocity (u_*) filtering approach (Yi et al. 2008). The error caused by using the traditional (u_*) filtering approach compared with multi-tower measurements of the actual advective fluxes was estimated to be approximately 10% at the monthly cumulative *NEE* time scale. Together, these studies conclusively showed that neglecting horizontally and vertically advected CO_2 could lead to errors that become large, especially when compounded over multiple years. Overall, the average uncertainty of flux measurements differenced over successive, meteorologically similar days between 1999 and 2007 was about 18% of *NEE* (Hu et al. 2010a).

The Carbon in the Mountains Experiment (CME04) expanded upon this work to further explore mechanisms of CO_2 transport (Sun et al. 2010), and described the flow of CO_2-laden air in terms of a "carbonshed", similar to the concept of a watershed. At night, respired CO_2 was transported downslope following the topography of the carbonshed, at times accumulating in the air up to 20 m above the surface at the carbonshed low point. During the day, CO_2-rich air was transported upslope by thermally driven flows under calm synoptic conditions, which contributed to the morning disappearance of the cold CO_2-rich air that pooled in the topographic low points at night (Sun et al. 2010). Ultimately, a consistent picture of CO_2 transport emerged as a result of the CME04: the distribution of CO_2 over this mountain terrain is complicated but not complex; that is, although hard to describe, it was describable. More recent work has shown that wind-sheltering and atmospheric decoupling (sub-canopy versus above-canopy) effects may contribute to CO_2 increases near the ground, which implies that dense canopy locations could be persistent 'hotspots' of anomalously high CO_2 concentrations (Burns et al. 2010).

In the alpine tundra, persistent windy conditions promoted turbulent conditions, near-neutral atmospheric stability and a short, consistent turbulent flux footprint even during the night. In fact, rejecting EC measurements at $u_* < 0.15$ m s^{-1} had no significant effect on *NEE* (Blanken et al. 2009). The windy environment also minimised cold-air drainage flows, and horizontal advection ranged from 1% of *NEE* during the winter to a maximum of 5–6% of *NEE* in summer (Blanken et al. 2009). Vertical advection was not measured, since the use of the double coordinate rotation (planar fit) method forced vertical advection to zero (Wilczak et al. 2001). A 6% reduction of *NEE*, similar to the maximum effect of horizontal advection, was also attributed to sensible heat exchange from the top, bottom, and spars of the open-path gas analyser following Burba et al. (2008). Over successive days, random error (e.g. Hollinger and Richardson 2005) averaged approximately 10% of summer midday fluxes (Knowles et al. 2012), which was comparable with random errors at

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grassland, forested, and agricultural AmeriFlux sites (Richardson et al. 2006). Random error was significantly greater when calculated from simultaneous measurements between the two towers, possibly due to the spatially heterogeneous nature of the study site.

Flux towers above and below the treeline at Niwot Ridge show that reliable EC data collection is possible in harsh, complex terrain, but that multiple towers are needed to accurately describe advection, and to constrain the land area, or carbonshed, from which turbulent fluxes originate. Careful site selection is paramount to successful EC data collection in complex terrain, given that every catchment poses unique challenges and topography. Notwithstanding, work at Niwot Ridge suggests that structurally simple sites such as ridgetops and glacial moraines may minimise advection terms. Taking all this into consideration, the introduction of micrometeorological flux techniques into increasingly heterogeneous and remote ecosystems is a field of active research.

The surface energy balance

The partitioning of energy within mountain ecosystems has a direct bearing on forest and tundra hydrology, including the formation of a snowpack, the timing of snowmelt, and the overall water status of vegetation and soils throughout the growing season (e.g. Turnipseed et al. 2002). In general, the surface energy balance describes how radiative energy absorbed by the earth's surface is partitioned between the turbulent energy fluxes of latent and sensible heat, and the soil heat flux. Sensible heat was the largest annual component of the energy balance over both forest and tundra ecosystems on Niwot Ridge (Table 2), indicating that evapotranspiration (*ET*) was generally limited by moisture, as is usually the case in the semi-arid and dry land ecosystems that characterise much of the Western US (Rodriguez-Iturbe 2000; Kurc and Small 2004). Overall, similar patterns of energy partitioning were observed throughout the year at both sites (Blanken et al. 2009). Although the Bowen ratio (β), the ratio of sensible to latent heat, was always higher over the forest (Table 2), the tundra and forest converged to similar β values in summer, but then diverged in winter, when the forest β was nearly 2.5 times greater. This reflects the strong orographic tendency of winter precipitation on Niwot Ridge (tundra precipitation much greater due to higher altitude), compared with the sporadic nature of convective summer precipitation (Greenland 1989). Neither sensible nor latent heat (nor β) increased or decreased significantly over the length of the EC record at either location. Intra-annually, forest β reached a maximum (4–6) in early spring (May or June) just prior to the beginning of net carbon uptake, before the onset of snowmelt and the percolation of liquid water into the soil. When water became available to tree roots, transpiration was initiated quickly, and β decreased to approximately unity (Turnipseed et al. 2002). During the summer, β was correlated with precipitation, and ranged from 3 or greater during periods of drought to slightly less than unity during periods of heavy 'monsoon' precipitation. Mean annual forest β in 2002 and 2003 indicated that sensible heat could be over twice the magnitude of latent heat during drought years (Table 2).

Surface energy balance closure, or the degree to which independently measured inputs of available energy (net radiation minus soil heat flux) balance the turbulent fluxes of latent and sensible heat, is a basic quality control used to evaluate EC measurements (Foken and Wichura 1996;

Table 2. Daytime-only (net radiation > 10 W m^{-2}) fluxes of sensible (H) and latent heat (LE), and the ratio of sensible to latent heat (ß), for the forest and tundra over the complete length of eddy covariance measurements at each location. The turbulent heat flux data are further separated into summer (JJA) and winter (DJF) seasons, including the mean and standard deviation (SD). Units for all fluxes and statistics are W m^{-2}; the ß is a ratio.

	Forest							Tundra						
	Summer		Winter		Annual			Summer		Winter		Annual		
Year	H	LE	H	LE	H	LE	ß	H	LE	H	LE	H	LE	ß
1999	141	135	64	43	162	91	1.77							
2000	173	138	48	49	169	93	1.82							
2001	145	148	72	31	159	92	1.73							
2002	176	125	77	27	181	79	2.28							
2003	144	123	59	38	162	81	2.01							
2004	134	127	53	31	144	82	1.75							
2005	157	131	55	41	160	82	1.95							
2006	135	131	70	41	159	84	1.90							
2007	128	133	64	38	146	85	1.71							
2008	148	135	47	45	156	90	1.73	120	113	10	13	93	69	1.35
2009	153	136	66	33	156	83	1.89	125	124	20	14	95	75	1.28
2010	149	138	55	35	160	87	1.84	135	135	−5	15	94	76	1.25
2011	153	150	65	34	164	89	1.84	122	131	6	17	99	86	1.15
2012	136	132	67	39	160	85	1.88	120	94	23	22	111	61	1.82
Mean	148	134	62	37	160	86	1.86	125	119	11	16	99	73	1.37
SD	14	8	9	6	9	4	0.15	6	16	11	3	8	9	0.26

Leuning et al. 2012; Stoy et al. 2013). On Niwot Ridge, good agreement was generally observed between non-turbulent and turbulent fluxes, especially given that lack of complete energy balance closure is typical for EC measurements, regardless of topography or terrain. Specifically, over the forest and the tundra, energy balance closure was 84% and 91% in summer, and 88% and 71% over the winter, respectively (Turnipseed et al. 2002; Blanken et al. 2009). Energy balance closure in the forest was tightly coupled to wind speed, which explains why the energy balance deficit was greater during the summer (Figures 1(a, b)), when upslope conditions associated with relatively low wind speeds and stable conditions were more common (Burns et al. 2010). Upslope winds rarely made it past treeline to the windier alpine site, however, and decreased wintertime closure at T-Van (Figures 1(c, d)) was likely due to the small turbulent fluxes (Blanken et al. 2009), together with extremely windy conditions that may have resulted in underestimation of the sensible heat flux (Burns et al. 2012). Across seasons and over the range of wind speeds, energy balance closure was generally better during the day at both locations.

Evapotranspiration and sublimation

Terrestrial *ET* is a key to climate change because it integrates the contribution of soils, snow, and vegetation to water vapour in the atmosphere. A study of cumulative *ET* over two summers and one winter at Niwot Ridge found that 408 and 688 mm water was evapotranspired from the alpine tundra and forest, respectively (Blanken et al. 2009), and that *ET* fluxes were greater over the forest during the growing season. Simultaneously modelled CO_2 and water fluxes suggest that this was the result of continued forest transpiration into the autumn, when air temperatures were high enough to maintain photosynthesis (Moore et al. 2008). The ecosystem water use efficiency (*WUE*) of the two sites, calculated as the ratio of the total carbon gain to the total water loss, was 0.25 g C kg H_2O^{-1} for the forest compared with 0.08 g C kg H_2O^{-1} for the tundra (Blanken et al. 2009). Within the forest, different tree species also differed in *WUE*, and ecosystem *WUE* was 19% lower for a forest community in which Engelmann spruce and subalpine fir were dominant, compared with lodgepole pine (Monson et al. 2010). These results have significant implications in the context of the current mountain pine beetle (*Dendroctonus ponderosae*) outbreak that has affected numerous Rocky Mountain catchments (Pugh and Gordon 2012), because ecosystem *WUE* could decline if lodgepole pines are systematically targeted by insect outbreaks in the future.

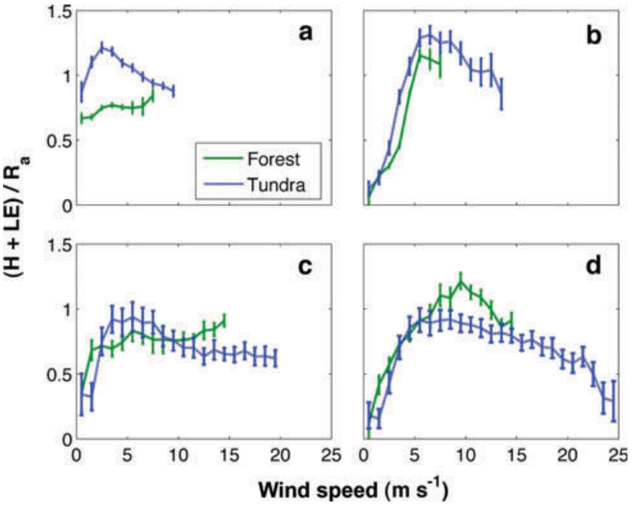

Figure 1. The surface energy balance closure fraction versus binned (increment = 1 m s^{-1}) horizontal wind speed where *H* is the sensible heat flux, *LE* is the latent heat flux, and R_a represents available energy (net radiation minus soil heat flux). Panels correspond to (a) summer (JJA) daytime (net radiation > 10 W m^{-2}), (b) summer nighttime (net radiation < -10 W m^{-2}), (c) winter (DJF) daytime, and (d) winter nighttime conditions. Bins containing less than 1% of data were omitted. Niwot Ridge AmeriFlux tower data span the period 1 January 2006 to 31 December 2007, and Niwot T-Van data are from 1 January 2008 to 31 December 2012. An empirical correction was applied to the sensible heat flux for the AmeriFlux tower data only following Burns et al. 2012 Equation 9. Error bars correspond to the standard error of the dependent variable.

Special attention has been devoted to sublimation studies at Niwot Ridge, because of the long winters and significant length of the snow-covered season. Since coniferous forests can intercept large quantities of snow, Molotch et al. (2007) investigated the partitioning of energy and sublimation above and below the forest canopy and found that sub-canopy snowpack sublimation increased in proportion to the percentage of net radiation that was converted to sensible heat flux above the canopy. Nevertheless, the overall sublimation rate was greater for intercepted (0.71 mm d^{-1}) versus snowpack (0.40 mm d^{-1}) snow (Molotch et al. 2007). Overall, the wintertime above-canopy sublimation to precipitation ratio was 0.68, and this promoted 29% greater snow accumulation in open areas versus under-canopy locations. A companion study that integrated total water vapour flux to the atmosphere over two winters with similar precipitation found that water vapour fluxes ranged from 274 to 351 mm during the snow-covered season, which represented 41–56% of total precipitation during that time (Molotch et al. 2009).

In alpine areas, water loss through *ET* and sublimation critically affects the timing and amount of surface runoff (Bales et al. 2006). From 2008 through 2012, the mean annual cumulative water vapour loss at T-Van was 376 mm, or 36% of precipitation. The redistribution of snow by wind complicates alpine snow accumulation, however, and snow on Niwot Ridge is predominantly governed by the interaction between westerly winds and topography, with most of the deposition occurring in leeward depressions and sheltered areas (Hood et al. 1999). Consequently, little snow accumulated around the EC towers at T-Van, as a result of the exposed, ridgetop location, and sublimation was moisture limited during the winter (Knowles et al. 2012). This contrasted water vapour fluxes from nearby dry meadow tundra, where the October through March sublimation

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was over twice that of T-Van due to the presence of a seasonal snowpack (Hood et al. 1999). This difference underscores that large moisture gradients can occur over very short horizontal distances in alpine areas.

Both forested and snow-free alpine systems on Niwot Ridge are moisture limited during the winter, late summer and fall. In the forest, EC data show that water vapour fluxes are predominantly tied to precipitation events and transpiration, whereas alpine *ET* is a function of the presence or absence of a snowpack that is controlled by the influence of blowing snow. Typically, β reached an annual minimum in the late spring and early summer at both sites during snowmelt and the annual precipitation maximum, therefore decreases in the magnitude and/or changes in the timing of snowmelt inputs to these systems may negatively impact productivity and transpiration. Changes in the moist, summer 'monsoon' weather pattern also have the potential to significantly alter moisture availability at both locations during a time when vegetation is photosynthetically active.

Carbon fluxes

Primary productivity

Gross primary productivity (*GPP*) represents the amount of carbon fixed by vegetation through photosynthesis and a key component of ecosystem carbon fluxes and the carbon balance (Mäkelä et al. 2008). Globally, the majority of this uptake occurs in forests (Jung et al. 2011), therefore accurate estimates of photosynthesis and forest *GPP* are required to improve our understanding of the carbon cycle under a changing climate (Gea-Izquierdo et al. 2010). In the United States, remote sensing suggests that the North Central and South Central regions have the highest *GPP*, followed by the Southeast, the Rocky Mountains and the Northeast (Xiao et al. 2010). Since coniferous forests represent the primary carbon sink in the Rocky Mountains, there is a continuing need to understand the magnitude and behaviour of *GPP* in relation to climate and disturbance in this region (Schimel et al. 2002).

At the ecosystem scale, *GPP* is often estimated by statistically modelling the photosynthetic and respiratory components of *NEE* measured by EC (e.g. Falge et al. 2002). We therefore modelled ecosystem respiration (R_{E}) using year-specific Arrhenius-type exponential regressions of binned nighttime soil (forest) and air (tundra) temperature on *NEE* (Lloyd and Taylor 1994), and then subtracted the resulting values from *NEE* measured by EC to calculate *GPP* as a residual for every year of EC data collection. Our results show that forest *GPP* averaged 766.8 g C m^{-2} yr^{-1} between 1998 and 2012, and that peak *GPP* (846 g C m^{-2} yr^{-1}) actually occurred during 2012 when snow water equivalent (*SWE*) was relatively low, but the summer monsoon was especially strong (Table 3). Alpine tundra *GPP* ranged between 105.0 and 137.2 g C m^{-2} yr^{-1}, and averaged 123.5 g C m^{-2} yr^{-1} (Table 3). For comparison, biometric data showed that alpine net primary productivity ranged from 280–600 g C m^{-2} across a dry to wet meadow gradient (Fisk et al. 1998), and extrapolation of alpine chamber measurements on Niwot Ridge (Welker et al. 1999) over a 90-day growing season would indicate that the tundra *GPP* ranges from 77.4–271.8 g C m^{-2}. In contrast, the mean annual (biometrically measured) above-ground net primary productivity for three Rocky Mountain forests including Niwot Ridge was only 240 g C m^{-2} (Bradford et al. 2010); however, the majority of forest productivity occurs belowground (Litton et al. 2007). Monson et al. (2005) used observations of intra-annual forest *GPP* to show that *GPP* peaked in the early summer immediately following snowmelt, and then decreased with the onset of relatively dry conditions as the season progressed. Interestingly, regional *GPP* has been shown to track the seasonal variation of the Niwot forest *GPP*, highlighting a potentially important ecological pattern across scales (Desai et al. 2011).

Table 3. Cumulative fluxes, means, and standard deviations (SD) of the annual forest and tundra ecosystem carbon balance in g C m^{-2} for all years of EC data collection. The R_{E} was modelled from regressions of binned (bin size = 1 °C) nighttime (23:00–4:00 Mountain Daylight Time) soil (forest) and air (tundra) temperature on *NEE*, fit with year-specific Arrhenius-type exponential functions. The *GPP* was then calculated by subtracting R_{E} from EC-measured *NEE*. Negative fluxes correspond to surface uptake.

	Forest			Tundra		
Year	*NEE*	R_{E}	*GPP*	*NEE*	R_{E}	*GPP*
1999	−215	528	743			
2000	−239	563	802			
2001	−262	541	804			
2002	−184	513	697			
2003	−202	575	777			
2004	−202	511	691			
2005	−187	540	727			
2006	−219	579	798			
2007	−220	583	803			
2008	−233	538	771	155	350	115
2009	−228	526	754	170	317	134
2010	−205	531	735	160	285	105
2011	−228	557	785	194	335	127
2012	−223	627	849	195	357	137
Mean	−217	551	767	175	329	124
SD	21	32	45	19	29	14

Model-data synthesis studies have also used SIPNET (Simple Photosynthesis EvapoTranspiration), a process-based model that uses measured climate variables, in combination with flux data to simulate ecosystem-scale carbon and water exchange, and to investigate the regulation of *GPP* by climate and substrate availability (Moore et al. 2008). In this way, forest *GPP* ranged from 565–708 g C m^{-2} yr^{-1} between 1999 and 2004, and averaged 652 g C m^{-2} yr^{-1} (Sacks et al. 2007). SIPNET has also been used to illustrate the downregulation of photosynthesis and foliar respiration when soils freeze in winter (Sacks et al. 2006), and model-data fusion analyses have identified that longer growing seasons may actually reduce forest *GPP*, in

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contrast to studies in other ecosystems (Goulden et al. 1996; Black et al. 2000). Isotopic partitioning (Bowling et al. 2005; Zobitz et al. 2008) can also be used to calculate net photosynthetic and respiration fluxes, and recent research has developed an approach to quantify *GPP* at the whole-tree scale based on the combination of sap flux measurements (for transpiration) and carbon isotope discrimination observed in the production of phloem sugars (for photosynthetic *WUE*). Using this technique, Hu et al. (2010b) found that forest *GPP* averaged 0.94 g C m^{-2} d^{-1} over the course of the growing season (would be 169.2 g C m^{-2} yr^{-1} over a 180-day growing season), and that values of *GPP* derived from this method were consistently lower than *GPP* modelled by SIPNET. Despite this difference, both models converged on similar *GPP* values during periods of high *GPP*, thus errors that are causing the gap between estimates may be lowest when fluxes are highest (Hu et al. 2010b). Possible explanations for this gap include the propagation of EC biases (possibly from nighttime advection) into SIPNET data, and also the few dates on which researchers were able to compare both types of modelling approaches (15 days total).

A primary conclusion to come out of all these studies is that *GPP* is tightly coupled to the regional snow regime (Monson et al. 2005; Desai et al. 2011). Currently, growing seasons are getting longer in the northern hemisphere (Keeling et al. 1996), and with reduced snow accumulation and mid-summer drought predicted for many areas, the strength of the forest carbon sink is therefore likely to decline over time (Wang et al. 2011). Scott-Denton et al. (2013) used coupled weather-generation and ecosystem models to test this hypothesis for the subalpine forest at Niwot Ridge. Their results predict a slight increase in air temperature during the late winter and early spring by the end of the 21st century, accompanied by higher precipitation, and that this would likely result in an earlier seasonal *GPP* maximum. Winter warming therefore has the potential to increase carbon sequestration by subalpine forests in the Western US, provided the presence of sufficient liquid soil water to meet photosynthetic demands.

Ecosystem respiration

The R_E is the respiration of all heterotrophic and autotrophic organisms summed per unit area and time (e.g. Chapin et al. 2006), and the magnitude of R_E determines *NEE* in many forested systems where R_E is more variable than *GPP* over time (Valentini et al. 2000). Soil respiration (R_S), in turn, or the total CO_2 production from intact soils by soil organisms and mycorrhizal fungi, represents the dominant component of R_E (Raich and Schlesinger 1992). Although the maximum R_E coincides with active plant growth in most locations, previous measurements in alpine tundra and subalpine forest ecosystems have shown that R_E can also be significant during the winter as a result of beneath-snow heterotrophic R_S (Sommerfeld et al. 1993; Mast et al. 1998). Given that liquid water is a prerequisite for biological activity, winter R_S is controlled primarily by interactions between the depth and timing of snow cover (Brooks et al. 2011), which is currently declining in the majority of mountain ecosystems throughout the Western US (e.g. Clow 2010). Since Liptzin et al. (this issue) reviews beneath-snow trace gas fluxes and R_S in detail, here we review R_E, and then provide only a brief synopsis of and chamber-based R_S work at Niwot Ridge.

During 5 years of simultaneous measurements (2008–2012), mean annual tundra R_E was 59% of that of the forest (Table 3). Given tundra and forest *LAI* of 0.87 and 4.2 m^2 m^{-2}, respectively, this speaks to the significance of the heterotrophic tundra R_S flux, and chamber measurements of growing season R_S averaged about 3 and 4 μmol m^{-2} s^{-1} for the tundra and forest, respectively (Bowman et al. 2004; Scott-Denton et al. 2003). Extrapolated over 90- and 150-day growing seasons, that works out to R_S values of 280 and 623 g C m^{-2} for the tundra and forest, or 85% and 113% of our modelled R_E at each location (Table 3). Soil temperature, moisture and nutrient availability represented the primary controls on both forest and tundra growing season R_S (Scott-Denton et al. 2003; Bowman et al. 2004). Trees also influenced heterotrophic R_S in the forest by priming the soil with sugar exudates during the late-spring snowmelt period (Scott-Denton et al. 2006; Weintraub et al. 2007). Over the winter, R_S remained significant from both snow-covered forest and tundra soils, and over-winter R_S accounted for 16–22% and 1–25% of growing season *GPP* at the forest and tundra sites, respectively (Monson et al. 2006b; Brooks et al. 1997). Integrating across Niwot Ridge, it has been proposed that the limiting factors on winter R_S shift from freeze–thaw cycles (alpine fellfield) to soil temperature (subalpine forest) to soil moisture (alpine meadow) to substrate availability (alpine snowbed) as the depth and duration of snow cover increases (Liptzin et al. 2009; Figure 2). This results in temporally distinct patterns of winter R_S across the ecosystem snow cover gradient, from discrete R_S pulses associated with freeze–thaw events near T-Van, to an R_S minimum during midwinter in the forest, to steadily increasing (with soil moisture; wet alpine meadow) or decreasing (with substrate availability; alpine snowbed) R_S. Although the curves in Figure 2 are not drawn to scale, total winter R_S is expected to be greatest from moist alpine meadows on Niwot Ridge, as a result of high above-ground primary productivity and a long snow-covered season with soil temperatures near 0 °C (Liptzin et al. 2009). Likewise, the lowest winter R_S generally corresponds to dry alpine fellfields such as T-Van, although EC data from T-Van likely represent an amalgamation of many small pockets of adjacent and co-occurring alpine fellfield and dry-to-moist meadow vegetation. Following this model, total winter R_S from the forest should fall somewhere between these two end member values.

In the forest, winter R_S was indeed especially sensitive to snow cover and resultant soil temperature, and this was attributed to a unique soil microbial community that exhibited exponential growth at low temperatures (Monson et al. 2006a). In the tundra, microbial biomass (primarily fungi) peaked during the winter, and there was nearly complete seasonal turnover by the microbial

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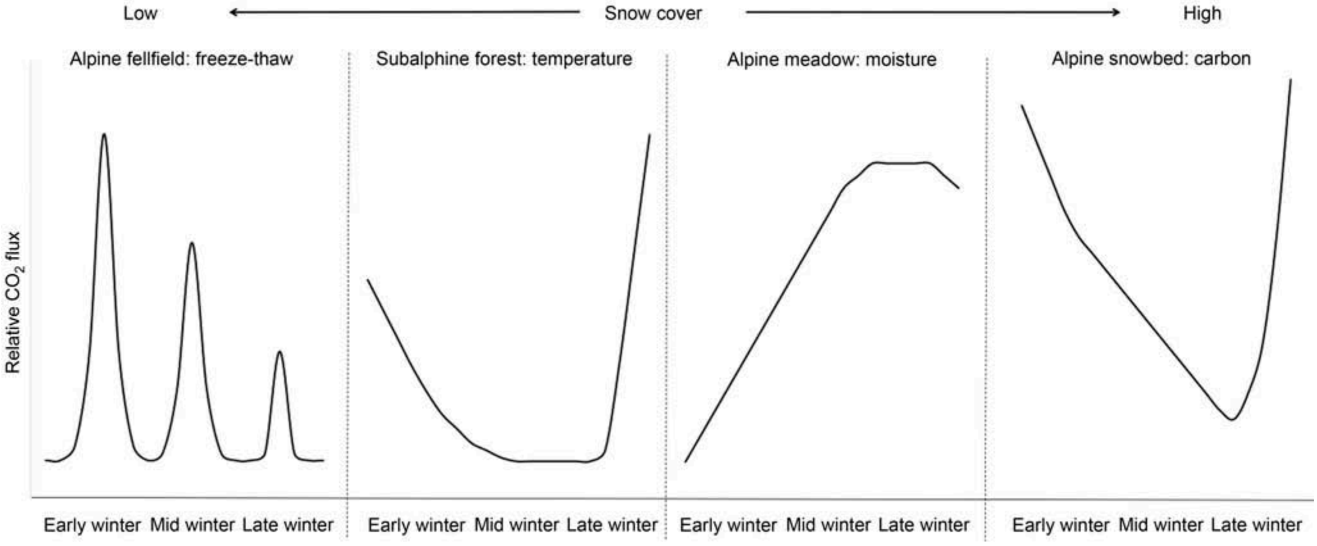

Figure 2. Conceptual model shows the seasonal evolution of the wintertime CO_2 flux across four different ecosystem types on Niwot Ridge. Factors limiting CO_2 production shift from freeze–thaw cycles to soil temperature to soil moisture to carbon substrate availability as snow depth increases along a continuum from alpine fellfield through snowbed ecosystems. The total CO_2 flux varies between zones and is not drawn to scale (after Liptzin et al. 2009, figure 7).

community at both sites (Schadt et al. 2003; Monson et al. 2006a). Together, these studies suggest that deceases in the depth and/or duration of the snowpack in mountain ecosystems could decrease R_S, and thereby increase carbon sequestration, but accompanied changes in litterfall and/or soil frosts potentially complicate this scenario (e.g. Brooks et al. 2005). Attempts to model the variability of R_S, and therefore R_E, under changing climatic conditions must also take into account the effects of unique meteorological and hydrological interactions to accurately describe the significant variability between seasons and years. For example, in the forest, analysis of the $^{13}CO_2$ of R_E showed that patterns of $^{13}CO_2$ generally agreed with leaf-level gas exchange theory during the driest portion of average-wetness years, but that conventional relationships deteriorated during snowmelt and also during periods of very hot summertime conditions (Riveros-Iregui et al. 2011).

Net ecosystem exchange (NEE)

The *NEE* is the difference between opposing CO_2 fluxes of *GPP* and R_E that can be measured directly with EC. Transitioning from winter to summer, the *NEE* changed from positive (surface was a carbon source) to negative (surface was a carbon sink) over both the forest and tundra ecosystems. In the forest, many starts and stops in the recovery of net daily CO_2 uptake were initially observed over the course of the transition, in response to the passage of synoptic weather systems, and full recovery did not occur until after the snowpack became isothermal at 0 °C (Monson et al. 2005). This allowed for consistent percolation of melted snow water through the snowpack, resulting in peak *GPP*, the most negative *NEE*, and the greatest fraction of annual carbon sequestration. Interestingly, the eventual reduction of *NEE* (less negative) through the summer was alternately due

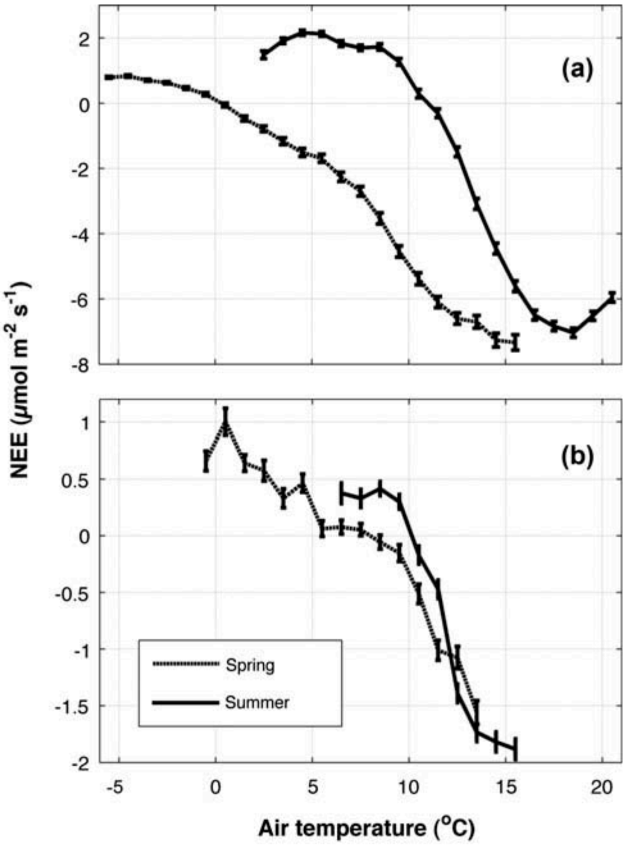

Figure 3. Net ecosystem exchange (*NEE*) as a function of binned air temperature (bin size = 1 °C) for the (a) forest and (b) tundra. Bins containing less than 1% of data were omitted. The spring period is 1 May to 31 May for the forest and 1 June to 30 June for the tundra, corresponding to the period of peak snowmelt. Summer is 1 August to 30 August for both sites. Error bars are the standard error of *NEE*. Note the panels have different *y*-axes.

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to higher R_E in wet years and lower *GPP* in dry years, which means that both wet and dry summers are capable of suppressing *NEE* at this location. Air temperature also affected *NEE* at both sites, but the sign of the effect could be positive or negative depending on the season (Figure 3). Air temperature and *NEE* were always positively correlated during the spring as daytime air temperatures increased from near freezing, but rising air temperatures began to have a negative impact on summertime *NEE* in the forest, likely because of inhibition of net photosynthesis at temperatures greater than the photosynthetic temperature optimum (Huxman et al. 2003). This underscores that the seasonality of future warming may ultimately determine patterns of forest *GPP*. A corresponding effect was not observed in the alpine tundra, presumably as a result of the much lower air temperatures.

In all, we found that the cumulative annual forest *NEE* ranged from -183.6 to -262.4 g C m^{-2} (mean *NEE* = -217.5 g C m^{-2}) between 1999 and 2012 (Table 3), and that the least negative *NEE* occurred in 2002 when both *P* and *SWE* were the lowest of all 14 years (Table 1). These values are comparable with a recent assessment (Scott-Denton et al. 2013), but represent significantly greater carbon uptake than previous estimates (e.g. Hu et al. 2010a), because the AmeriFlux data were recalculated in 2011 after it was found that water vapour was being doubly accounted for (both a dilution and WPL correction applied) during post processing. The interannual variability of *NEE* was more than twice the random measurement error at both sites. Interannual variability in the forest *NEE* was mostly a function of *NEE* during the snowmelt period, not *NEE* during the snow-free part of the growing season, and earlier snowmelt was consequently linked to less negative annual *NEE* (Monson et al. 2005; Hu et al. 2010a). These findings contrast the prevailing notion that a longer growing season should result in more carbon sequestration, as is the case in a broad range of ecosystems, including deciduous forests (Churkina et al. 2005). One possible reason for this difference is the ability of the coniferous growth form to rapidly upregulate photosynthetic CO_2 uptake during the spring warm-up, which allows the trees to capitalise quickly on favourable weather conditions (Monson et al. 2005). Another factor is precipitation; the timing of snowmelt is closely linked to snow accumulation in the Western US, which means that earlier springs are indicative of years with less snow accumulation. Hu et al. (2010a) studied the isotopic composition of xylem water to reinforce the idea that trees rely heavily on snowmelt water even late in the growing season, and also that longer growing seasons correlate with reduced *SWE*. Together, these results support the prevailing idea that earlier snowmelt is often a precursor to moisture stress and/or drought, and that precipitation primarily controls *NEE* in mountainous, forested ecosystems of the Western US (Schimel et al. 2000). With regard to the current beetle outbreak, recent work has shown that patterns of *GPP* and R_E are expected to decline in commensurate fashion after infestation, resulting in no significant change in *NEE* (Moore et al. 2013).

The alpine tundra cumulatively lost 874 g C m^{-2} to the atmosphere over the course of 5 years between 2008 and 2012, and mean annual *NEE* averaged 174.8 g C m^{-2} (Table 3). Although seasonal patterns of *NEE* were similar between the forest and tundra, forest CO_2 uptake continued much longer into the fall, and the switch to CO_2 uptake occurred much earlier in the spring, resulting in a longer carbon uptake period (Blanken et al. 2009; Figure 4). The CO_2 that was sequestered during the short alpine growing season was ultimately offset by significant R_E during the rest of the year (2.7 times greater than mean annual *GPP* on average), resulting in net carbon loss to the atmosphere. At both sites, the shift from positive to negative *NEE* corresponded to the date when air temperatures reached 10 °C, and the switch back to positive *NEE* coincided with air temperatures decreasing below -10 °C (Blanken et al. 2009), thus air temperature may be an important photosynthetic cue (e.g. Monson et al. 2002).

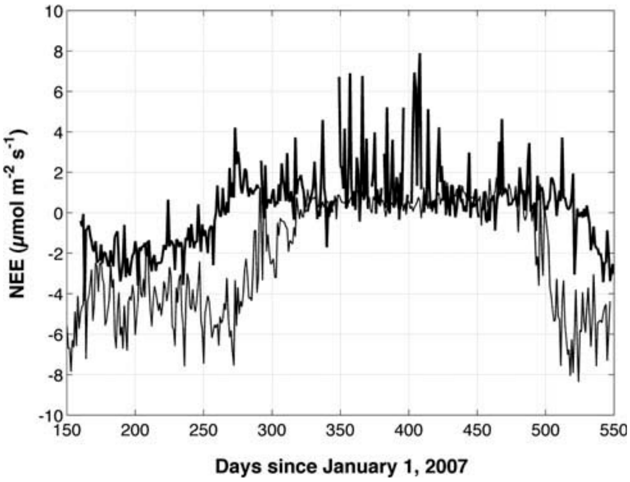

Figure 4. Mean daytime (net radiation > 0 W m^{-2}) *NEE* for the forest (thin line) and tundra (thick line) over 13 months between 9 June 2007 and 3 July 2008. Negative values correspond to CO_2 uptake by the surface (after Blanken et al. 2009, figure 12).

Although the reasons for net annual carbon loss from alpine fellfield tundra remain unclear, work from the International Tundra Experiment (ITEX) demonstrated that climate warming of 2–3 °C had the potential to turn dry alpine tundra from a carbon sink to a source (Welker et al. 1999), and both air temperature and positive degree-days have increased at higher elevations (D1; 3740 m elevation) on Niwot Ridge since 1980 (Caine 2010). Similarly, Oechel et al. (2000) documented that long-term carbon sequestration in Alaskan arctic tundra was reversed by climate warming and drying in the early 1980s. One possible mechanism for this switch, and for net annual carbon loss from alpine tundra at T-Van, is permafrost thaw and the microbial decomposition of previously frozen organic carbon, which is considered one of the most likely positive climate feedbacks in response to increasing air temperatures (e.g. Zimov et al. 2006), and there is evidence of disappearing permafrost on Niwot Ridge over the past 40 years (Janke 2005). Alternatively, high-elevation watersheds in the Colorado Rocky Mountains are exposed to high rates of nitrogen deposition due to their close proximity to metropolitan and

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agricultural areas to the east (Williams et al. 2011), and studies have shown that long-term nitrogen fertilisation stimulates carbon loss from both alpine (Neff et al. 2002) and arctic (Mack et al. 2004) tundra. Future analysis considering the age of respired carbon would likely help to constrain the physical process(es) responsible for net carbon loss at T-Van. Alpine wet meadow and shrubland systems in Tibet (Zhao et al. 2010) and Spain (Reverter et al. 2010) show similar patterns of net annual carbon loss to the atmosphere, and so this may be a sign that recent changes have already begun to have widespread effects.

Synthesis and conclusions

Linear regression analysis between mean annual air temperature, total annual precipitation, and maximum *SWE* (forest only), and mean annual fluxes of latent and sensible heat, *GPP*, and *NEE* from the forest and tundra, yielded only one significant ($P < 0.10$) relationship: higher air temperatures resulted in decreased alpine tundra latent heat fluxes. We thus synthesised the results of previous work to conceptually model the behaviour of turbulent fluxes over alpine and subalpine forest ecosystems, given a warmer and wetter climate scenario in the future (Figure 5). Although the model does not account for potential feedbacks, it provides baseline information about the constituent fluxes of energy, water, and carbon on Niwot Ridge. Figure 3 suggests that forest *GPP* may be inhibited by increasing air temperatures, and so we predict reduced forest *GPP* in the future, although we recognise that earlier-season warming could produce the opposite effect. Conversely, we expect warmer and wetter conditions to stimulate R_E due to both reaction kinetics, and also to increased soil temperature and moisture as a result of increased winter snow cover (Figure 2). The net result of these changes would be increased (less negative) *NEE*, therefore less forest carbon sequestration over time. Neither previous work nor this review provides the basis to predict significantly changed latent or sensible heat fluxes over the forest in the future. Since the alpine tundra showed no evidence of photosynthetic inhibition, we expect increased air temperature to stimulate *GPP*, but together with increased R_E (same mechanisms as the forest), we do not expect the alpine *NEE* to change significantly. However, regression analysis showed that alpine latent heat fluxes declined significantly with air temperature, which could produce a non-linear β increase. In sum, the relative lack of significant correlation between meteorology and turbulent fluxes on Niwot Ridge denotes either 1) a relatively stable system, or 2) the inability of this simplistic model to account for seasonal variability and/or feedbacks between and among meteorology and fluxes. Future work that considered these dynamics at the ecosystem scale would be helpful to reduce the uncertainty of our model.

The placement of EC into unique ecosystems allows for increasingly refined estimates of regional- to global-

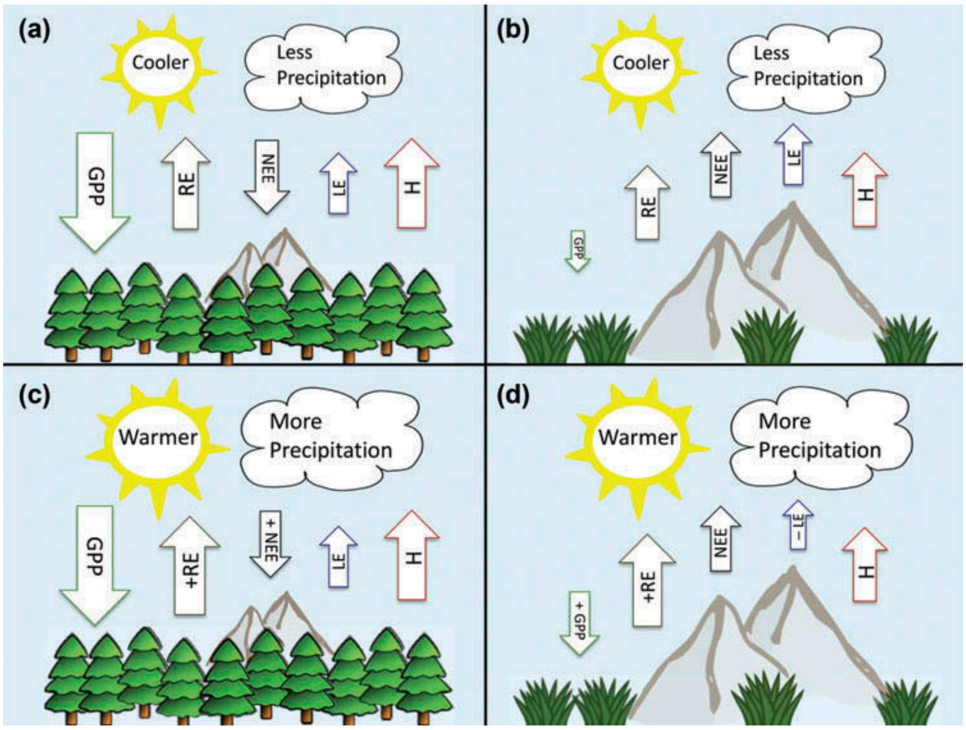

Figure 5. Conceptual diagram summarises how current (a) forest and (b) tundra ecosystem fluxes of energy and carbon are expected to change given (c and d) projected increases in precipitation and air temperature. Feedbacks between precipitation and air temperature are not considered in this model. Upward and downward arrows correspond to net ecosystem losses and gains, respectively. Arrows are not drawn to scale, but the magnitude of each flux is approximately denoted by the size of each arrow, and also by a plus or minus sign preceding the flux. Any flux without a plus or minus sign is not expected to change significantly in this scenario.

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scale water and carbon budgets, to the direct benefit of land and water managers and the research community. Given that semi-permanent EC installations are particularly suited to long-term ecological monitoring, they often serve as scientific research hubs, and the EC towers on Niwot Ridge have been the focus of prolific scientific inquiry since they were originally deployed. It is clear that both subalpine forest and alpine tundra ecosystems on Niwot Ridge are moisture limited to some degree. As a result, changes in the magnitude and/or timing of precipitation, or to the wind and air temperature patterns that govern snow accumulation and ablation, sublimation, precipitation type, and subsurface thaw at high elevations, can be expected to induce the strongest environmental responses from these ecosystems, and future work should focus on these interactions. In the forest, the connection between *SWE* and *GPP* implies that *NEE* is regulated by the timing of precipitation, as opposed to the cumulative magnitude over the course of a year, and so future changes in winter and spring precipitation may have a disproportionately large effect. Notwithstanding, our results suggest that intensification of the summer monsoon may be sufficient to alter this pattern. In the tundra, net annual carbon loss suggests that environmental changes may have already begun to impact this alpine ecosystem. On top of these factors, disturbances such as insect outbreak, drought, and fire have the potential to drastically alter current hydrologic and ecologic regimes in a very short time. For example, the major forest *ET* pathways – canopy interception of snow during the winter, and transpiration of subsurface water during the growing season – would be greatly curtailed by substantial tree mortality, thereby increasing the surface water runoff ratio. Above treeline, *ET* was less variable, and perhaps less susceptible to the aforementioned disturbances. Altogether, forest carbon gains exceeded alpine tundra carbon losses, and so the subalpine/alpine ratio of a given catchment, together with the trajectory and variability of *NEE* from each respective ecosystem, will ultimately determine the carbon sink or source status of the Western US as a whole. The EC-based experiments summarised here highlight specific ecological and hydrological relationships within and between adjacent ecosystems that we hope will serve to inform future studies, ecosystem modellers and policy makers alike. These results identify the utility of long-term ecological monitoring studies, and also the growing capability to collect reliable EC data in mountainous and/or complex ecosystems that are responsible for majority of the carbon and water exchange in many areas across the globe.

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