

Land–atmosphere carbon and water flux relationships to vapor pressure deficit, soil moisture, and stream flow



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ABSTRACT

Climatic change is exerting considerable influence on the hydrologic and biogeochemical cycles of snow-dominated montane forest ecosystems. Growing season drought stress is a common occurrence after snowmelt-derived soil water content (WC) and stream flow (Q) have declined, leading to an increase in atmospheric water demand (*i.e.*, vapor pressure deficit, VPD). Here, we analyzed a 6-year record (2006–2011) of H₂O and CO₂ fluxes from the Tenderfoot Creek Experimental Forest, a montane forest in the northern Rocky Mountains to examine (1) how growing season evapotranspiration (ET), net ecosystem production (NEP), and water-use efficiency (WUE, NEP/ET) respond to changing WC and VPD, (2) how stream flow (Q), an integrated measure of catchment-level water availability, relates to NEP, and (3) how annual NEP is related to annual precipitation and the temperature-defined growing season length (GSL). Growing season NEP exhibited a linear relationship with WC and a log-linear relationship with Q, indicative of persistent water limitations when streamflow and soil moisture reach their annual minima late in the growing season. Nevertheless, years with long GSLs had relatively higher NEP, with a small net carbon sink maintained even at low levels of WC and Q, suggesting that trees are able to obtain water from deeper portions of the soil profile (>30 cm) during droughts. However, the warmer, drier climate projected for this region could bring this system closer to a critical threshold of GSL, WC, and VPD, introducing vegetation water stress that could alter the current relationship between GSL and annual NEP.

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1. Introduction

Subalpine forests are among the ecosystems with the greatest sensitivity to continued climatic change (Körner, 2003), and the high-elevation evergreen forests of the Intermountain West are already exhibiting effects of a warming climate, largely as a consequence of reduced water availability (Allen et al., 2010; Breshears et al., 2005; van Mantgem et al., 2009; Westerling et al., 2006). Water inputs into these systems are largely supplied by the melting of winter snowfall, providing vegetation with a slow, transitory pulse of water that accounts for the majority of ecosystem water use (Hunter et al., 2006; Monson et al., 2002). Widespread warming has led to a decrease in winter snowpack in the Intermountain West (Hamlet et al., 2005), and continued increases in surface temperatures in future years could result in earlier snow melt, thereby

altering the timing and magnitude of water available for terrestrial ecosystems (Barnett et al., 2005; Mote, 2006).

Evapotranspiration (ET) is typically the largest flux of water out of these ecosystems. ET is constrained by solar radiation, air and soil temperature, atmospheric vapor pressure deficit, and soil water content (Monteith, 1973). Thus the water balance of subalpine ecosystems is regulated by seasonal changes in these variables. Like other ecosystem processes, ET can be limited by a single variable or co-limited by a combination of variables, resulting in a ‘switching’ *sensu* Baldocchi et al. (2006) among the variables that regulate ecosystem processes. For subalpine forest ecosystems that are dependent upon snowmelt, growing season ET is thought to respond to VPD until later in the growing season, when soil water content becomes more limiting to ET potentially inducing vegetation water stress (Emanuel et al., 2010).

Understanding the ecohydrology of water-limited subalpine forests during extended periods of low soil water content (WC) and high atmospheric water demand (VPD) could be crucial to projecting future patterns of CO₂ uptake and storage under future climatic conditions (Hu et al., 2010a,b; Monson et al., 2010, 2002; Sacks et al., 2007; Schimel et al., 2002). The components of net ecosystem pro-

Abbreviations: NEP, net ecosystem production; WUE, water use efficiency; VPD, vapor pressure deficit; GSL, growing season length.

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duction of CO₂ (NEP), namely photosynthesis (GPP) and ecosystem respiration (RE), are differentially influenced by soil water, humidity, temperature, and resulting VPD (Chapin and Matson, 2011), meaning that NEP may respond differently than ET to atmospheric water demands, especially given that NEP integrates vegetation and soil microbial fluxes of carbon acting in opposition to one another. The ratio of NEP to ET, also known as water use efficiency (WUE_{NEP/ET}), can be a useful metric for examining ecosystem stability, particularly during periods of water stress (Emmerich, 2007). Most of the differences in WUE_{NEP/ET} between sites are due to differences in ET rather than NEP (Ponton et al., 2006). Thus, higher levels of atmospheric water demand can increase water losses from the system via ET, leading to a decrease in WUE_{NEP/ET} as demonstrated by Monson et al. (2010) who found that growing season WUE_{NEP/ET} at the Niwot Ridge LTER decreased under conditions of low WC, a time during which daytime VPD is often highest.

Given the role of snowmelt in determining patterns of growing season water availability in many mountainous forested ecosystems (Trujillo et al., 2012), there is reason to believe that a warming climate may lead to changing patterns of NEP. However, the response of NEP to a changing climate is not straightforward; NEP is an aggregate of biophysical processes, gross ecosystem productivity (GPP) and ecosystem respiration (RE), which have unique (but not always independent) responses to climate and which transport CO₂ in opposite directions. For example, higher temperatures can increase both RE (Ryan and Law, 2005) and GPP (Law et al., 2002). Similarly, increases in growing season soil water can increase GPP (Welp et al., 2007) and RE (Pacific et al., 2009; Riveros-Iregui et al., 2012) in water limited portions of the landscape, although characteristically wetter landscape positions could experience reductions in RE with increased growing season soil water (Pacific et al., 2009; Riveros-Iregui et al., 2012). However, even though photosynthetic and respiratory CO₂ fluxes can respond similarly (but with different signs) to changing temperatures and soil water regimes, the magnitudes and sensitivities of these responses differ, resulting in complex NEP responses (Bond-Lamberty and Thomson, 2010; Flexas et al., 2006; Sage and Kubien, 2007; Xu et al., 2004). Furthermore, without a compensatory increase in summer precipitation to recoup the loss of snowpack-supplied soil water content (WC) by ET, a warmer climate would likely lead to a decrease in growing season WC that could reduce growing season NEP in systems where the reduction in WC induces drought stress. In extreme cases, decreased WC could lead to forest mortality; indeed, climate change and associated drought stress have already been implicated in the dieback of some western North American forest ecosystems (Allen et al., 2010; Breshears et al., 2005; van Mantgem et al., 2009). Responses may also depend on species composition. Common tree species of the Intermountain West such as lodgepole pine (*Pinus contorta*) could respond to warmer temperatures and earlier snowmelt with increased productivity, as long as they are not water-limited (Kueppers and Harte, 2005). By contrast, other common tree species of the region such as Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) do not share this response to increasing temperatures (Kueppers and Harte, 2005). Early season droughts could even induce a lagged mortality in *P. engelmannii* and *A. lasiocarpa* over the course of 5 and 11 years, respectively (Bigler et al., 2007). With longer, drier growing seasons potentially leading to different productivity responses among forest species and different respiration responses between wet and dry landscape positions, it follows that long-term NEP responses are uncertain across the complex landscapes that characterize much of the Intermountain West.

To better understand influences of meteorological and hydrological factors on H₂O and CO₂ fluxes during the longer, drier growing seasons expected to occur as a result of continued climatic change, we analyzed a 6-year record (2006–2011) of continu-

ous biosphere–atmosphere ecosystem fluxes from the Tenderfoot Creek Experimental Forest (TCEF), a mostly forested, subalpine watershed in central Montana. We examined (1) how growing season ET, NEP, and WUE_{NEP/ET} respond to changing soil water content and atmospheric water demand, (2) how stream flow (an integrated measure of catchment-level water availability) relates to NEP, and (3) how annual NEP is related to annual precipitation and the temperature-defined growing season length (GSL).

2. Methods

2.1. Study site

This study was conducted in the Tenderfoot Creek Experimental Forest (TCEF), in the Little Belt Mountains of central Montana (46°55' N; 110°54' W). This location is characteristic of the lodgepole-dominated forests of the northern Rocky Mountains, believed to contribute significantly to the North American carbon sink (Schimel et al., 2002). Mean annual precipitation is 880 mm with 70% falling as snow (Farnes et al., 1995) and peak snowpack accumulations between late March and mid-April (Woods et al., 2006). Mean annual temperature is 0 °C, with the majority of annual CO₂ uptake occurring between early June and late August. Woody vegetation is primarily *P. contorta* (lodgepole pine) and to a lesser extent *A. lasiocarpa* (subalpine fir) and *P. engelmannii* (Engelmann spruce), with an understory comprised primarily of *Vaccinium scoparium* (Whortleberry). Upland soils comprise approximately 97% of the study watershed (Jencso et al., 2010) and have been classified as loamy Typic Cryochrepts (Holdorf, 1981).

TCEF includes seven gauged catchments occupying a total area of 3591 ha. An eddy covariance micrometeorological flux tower is located within the 393 ha Upper Stringer Creek catchment (Fig. 1). Elevation in the Upper Stringer Creek catchment ranges from 2090 m to 2426 m AMSL, exhibiting a relatively high degree of topographic heterogeneity (Jencso and McGlynn, 2011). Measurements of NEP within the footprint of the flux tower should be interpreted as the spatial integration of this heterogeneity (Riveros-Iregui and McGlynn, 2009; Emanuel et al., 2010).

2.2. Flux tower measurements

Tower-based measurements of ecosystem fluxes and micrometeorology were initiated in September 2005. Instruments were located 30 m above the upland forest floor in the Upper Stringer Creek catchment. The lodgepole pine dominated canopy surrounding the tower had an average height of 20 m, and the base of the tower is 2243 m AMSL. Half-hourly net ecosystem exchange of CO₂ (NEE) and half-hourly latent heat flux (LE) were measured by eddy covariance using a triaxial sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and an open-path infrared gas analyzer (LI7500, Licor Biosciences, Lincoln, NE). A sign change and time integration converted half-hourly NEE to NEP (where positive NEP represents sequestration of carbon by the biosphere) and a unit change converted LE to ET ($ET = LE \lambda^{-1} \rho^{-1}$, where λ is the latent heat of vaporization and ρ is water density). Half-hourly sensible heat flux was measured using the sonic anemometer. Half-hourly air temperature and relative humidity (HMP45C, Campbell Scientific), photosynthetically active radiation (LI190, Licor Biosciences), net radiation (CNR1, Kipp and Zonen, Delft, Netherlands), and rainfall (tipping bucket model TE525, Texas Electronics, Dallas, TX) were also measured on the tower at 30 m above the forest floor. Standard tilt correction, spike filtering, sonic anemometer virtual temperature correction, and Webb correction were performed on half-hourly eddy covariance fluxes (Kaimal and Finnegan, 1994; Paw U et al., 2000; Schotanus et al., 1983; Webb et al., 1980). Tower-based micrometeorological measurements were complemented by

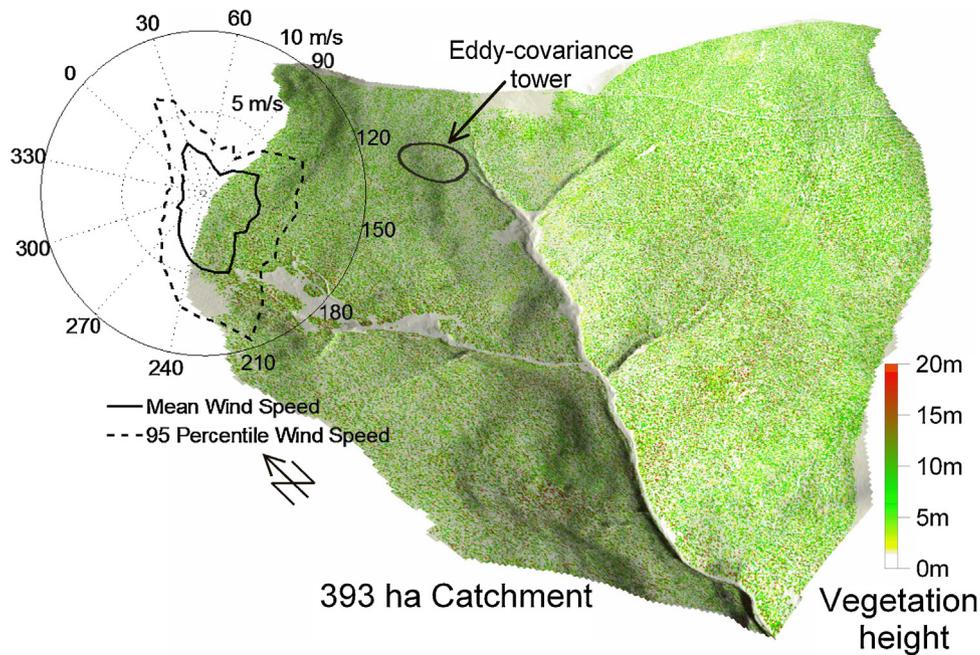


Fig. 1. Stringer Creek watershed within the Tenderfoot Creek Experimental Forest. Inset shows mean horizontal wind speed and 95 percentile of horizontal wind speed measured at the flux tower.

three nests of buried instruments that measured soil temperature at 2.5 and 7.5 cm (Thermocouple, Omega Engineering, Stamford, Conn.), soil heat flux at 5 cm (HFT3, Radiation and Energy Balance Systems, Inc., Seattle, WA), and soil water content integrated over 0–30 cm using time domain reflectometry (CS616, Campbell Scientific). Buried instrument nests were located approximately 10–20 m away from the base of the tower and were separated by approximately 120° arcs around the central data logger. The instrumentation was powered continuously by a 0.5 kW photovoltaic array and 12 VDC battery bank.

2.3. Flux tower data processing

Data from fast-response instruments were collected at a 10-Hz frequency and used to compute half-hourly fluxes using eddy covariance. Prior to 16 September 2010, 10-Hz data were not stored by the datalogger (CR23X, Campbell Scientific) for post-processing of fluxes. Instead, eddy covariance calculations were performed online by the datalogger every 30 min, and 10 Hz data were purged thereafter due to data storage limitations. After 16 September 2010, 10-Hz data were stored on a CompactFlash card attached to a datalogger (CR3000, Campbell Scientific) for offline computation of fluxes using EddyPro™ 4.0 (www.licor.com/eddypro).

Covariances computed online prior to 16 September 2010 were subjected to an unintentional 0.1 s lag between turbulence measurements and gas concentration measurements. We performed an analysis to determine whether such an offset significantly influenced half-hourly covariances and resultant fluxes. Using 65 days of 10-Hz data (27 April–1 July 2011), we compared half-hourly fluxes computed using no time lag to half-hourly fluxes computed using a 0.1 s time lag. Over this time period, we determined that the 0.1 s lag had no systematic effect on the measured fluxes, with a nearly 1:1 correspondence between the two half-hourly estimates (slope = 1.0054x, $R^2 > 0.999$). The no-lag half-hourly CO₂ flux estimates were, on average, 0.54% greater than the erroneously lagged estimates. Thus, we deemed the 0.1s time lag that was present throughout the pre-16 September 2010 data to be immaterial.

Prior to gap-filling the time series of NEE and LE, we conditioned the data by filtering out instances where incoming global

short-wave radiation (R_g) measured by the CNR1 was $< 1 \text{ W m}^{-2}$ and where NEE was positive, conditions that would suggest unrealistic nighttime CO₂ uptake. We also filtered out any estimates of CO₂ uptake when temperatures were below -7°C , a previously cited minimum growing temperature for *P. contorta* forests and other pine-dominated ecosystems (Coops and Waring, 2011). Additionally, we removed half-hourly NEE measurements $< -40 \mu\text{mol/m}^2/\text{s}^{-1}$ and $> 10 \mu\text{mol/m}^2/\text{s}^{-1}$ as conservative estimates for the limits of half-hourly photosynthetic gains and respiration losses for terrestrial ecosystems.

Once these data were filtered from the time series, we gap-filled NEE and LE using the Max Planck Institute of Biogeochemistry's online eddy-covariance gap-filling and flux-partitioning tool (see <http://www.bgc-jena.mpg.de/MDIwork/eddyproc/>), which utilizes the methods of Reichstein et al. (2005), a method developed from the earlier work of Falge et al. (2001). The gap-filling routine uses half-hourly measurements of NEE, LE, air temperature (T_{air}), wind speed (u^*), sensible heat flux (H), global short-wave radiation (R_g), percent relative humidity (RH), and VPD. Gap-filled data were categorized according to the level of data quality. The highest quality category of gap-filling uses direct meteorological observations of T_{air} , R_g , and VPD during the gap to estimate missing fluxes of NEE, LE, and H . When either T_{air} or VPD are unavailable, it uses R_g only. The gap-filling tool assigns gap-filled data with 3 levels of data quality, and provides samples of data gaps filled for each respective level of data quality. We examined the performance of each level of data quality and compared it to data gaps filled by mean diurnal variation. We found that the first 2 levels of data quality produced more accurate estimates of measured NEE and LE data than those provided by mean diurnal variation (MDV). Thus, we filled gaps using the first two levels of data quality, and filled any remaining gaps with estimates based on MDV.

2.4. Precipitation and stream flow measurements

Long-term measurements (> 10 years) at this site include stream flow (Q), snow depth, and snow water equivalent (SWE) (McCaughy, 1996; Woods et al., 2006; Nippgen et al., 2011). Stream flow was measured every 30 min at the outlet of Upper

Stringer Creek using an H-Flume instrumented with a capacitance rod to measure stage at ± 1 mm resolution (TruTrack Inc., Christchurch, New Zealand). Snowmelt-derived hydrological inputs into the Upper Stringer Creek watershed, where the tower is located, were estimated using data available from two nearby NRCS-SNOTEL sites, Stringer Creek (SNOTEL site number 1009) located approximately 3 km from the flux tower at an elevation of 1996.5 m AMSL, and Onion Park (SNOTEL site number 1008) located approximately 5 km from the flux tower at an elevation of 2261 m. Snow was not considered as an input until it melted; thus, the precipitation inputs into the ecosystem were calculated as the sum of rainfall and snowmelt measured at the SNOTEL stations. Winter snow sublimation was therefore excluded from annual totals of precipitation inputs, although it was included in ET measured by the flux tower.

A linear interpolation of precipitation inputs to the ground based on data from the two SNOTEL sites was applied to the elevation distribution of the 393-ha Upper Stringer Creek catchment, resulting in an elevation-weighted estimate of annual precipitation inputs (Nippgen et al., 2011). Precipitation was recorded at a three-hour resolution, and subsequently interpolated to half-hourly resolution, with units of $\text{mm } 0.5 \text{ h}^{-1}$ for compatibility with the temporal resolution of flux tower data.

2.5. Growing season length and annual discretization

We employed a simple method to define the length of the growing season using air temperature. Several studies have used a mean daily air temperature threshold of 5°C in ecosystems with short summer growing seasons (Carter, 1998; Wagner-Cremer et al.,

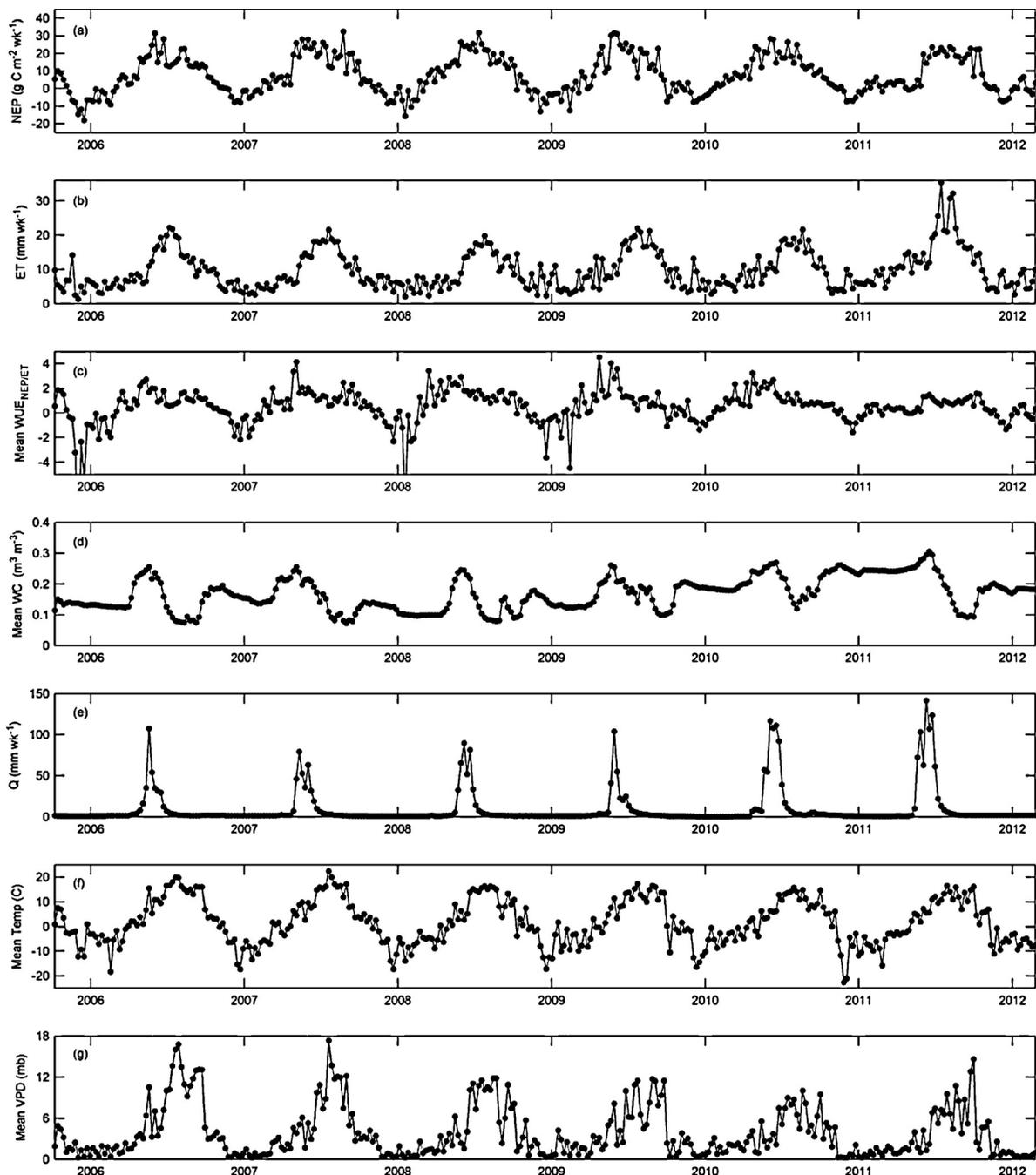


Fig. 2. Weekly net ecosystem production (NEP, a), evapotranspiration (ET, b), water-use efficiency ($WUE_{NEP/ET}$, c), mean soil volumetric water content (WC, d), weekly stream flow (Q, e), mean temperature (T, f), and mean vapor pressure deficit (VPD, g).

2010). We also used a 5 °C threshold to define growing season length (GSL) for 2006–2011 at TCEF using air temperature measured on the flux tower by the radiation-shielded HMP45C. We defined the beginning of the growing season as the 5th day of a 10-day moving window in which the mean air temperature was ≥ 5 °C. Similarly, we defined the end of the growing season as the 5th day of a 10-day moving window in which mean air temperature was ≤ 5 °C. The duration of the growing season at TCEF averaged less than half (~42%) of the year.

We discretized each year for annual estimates based on the post growing season date that a 10-day moving average of air temperatures was below 0 °C following the approach employed by Thomas et al. (2009). Over our entire 6 year study period at TCEF, the average date was 29 October. Thus, our annual estimates of carbon and water fluxes began on 29 October. We compared our annual estimates based on this discretization approach to both calendar year and water year (October 1) discretizations and found no discernable difference in the results.

2.6. Data analysis

We focused on weekly statistics of micrometeorological variables and ecosystem H₂O and CO₂ fluxes to analyze the patterns of ecosystem responses to soil water availability and atmospheric water demand during the growing season. Specifically, we considered weekly estimates of mean VPD, mean WC, total Q, total ET, total NEP, and mean WUE_{NEP/ET} occurring during the thermally-defined growing season. To limit the effects of gap-filling on our analyses and interpretations, we constrained statistical analyses to weeks containing fewer than 25% gap-filled fluxes during any time of the week, not just during the daytime hours.

We applied a modified version Lohammar's function (Lohammar et al., 1980; Oren et al., 1999) relating stomatal conductance to VPD to represent the relationship between weekly VPD and weekly ET:

$$ET = a \times \log VPD + b \quad (1)$$

where a and b are empirical coefficients for specific species when relating VPD to stomatal conductance. In our formulation a and b are fit to the relationship between mean weekly VPD and weekly ET to assess any changes in the sensitivity of ET to VPD over the course of the growing season.

Regressions between weekly VPD and NEP, weekly WC and NEP, and weekly WC and ET were fit to a series of linear, polynomial, and Lohammar functions, whereby strongest fits achieved (without over fitting) were retained. The linear function provided the best fit for NEP–VPD and NEP–WC, while a 2nd order polynomial curve provided the best fit to ET–WC (see Section 4). Weekly estimates of WUE_{NEP/ET} were best fit to weekly averages of VPD and WC using the form:

$$WUE = aX^b + c \quad (2)$$

where X is the independent variable (mean weekly VPD or mean weekly WC) and empirical coefficients are represented by a and b . We also compared weekly estimates of NEP to total weekly stream flow (Q) for each year using a separate log-linear function to represent each year:

$$NEP = a + b \times \log(Q) \quad (3)$$

where a and b are empirical coefficients that are fit separately for each year. This comparison allowed us to assess the associated NEP response to varying levels of growing season Q , and how these responses varied from one year to another. This analysis is based on the premise that stream flow serves as an integrated response to the hydrologic conditions across the contributing watershed.

Finally, we compared annual estimates of ecosystem fluxes (NEP, ET) and WUE to growing season lengths and precipitation inputs for calendar years 2006–2011. Annual NEP and annual ET were computed using the full, gap-filled dataset for each calendar year. Data analyses were performed using MATLAB software (Mathworks Inc., Natick, MA).

3. Results

Water fluxes at TCEF were characterized by a high degree of seasonality (Fig. 2). Patterns of weekly ET (Fig. 2b) closely tracked mean weekly temperature and vapor pressure deficits (VPD) and usually peaked at around 20 mm week⁻¹. Stream flow (Q), while usually less than 5 mm week⁻¹, could be as high as 100 mm week⁻¹ during the early portion of the growing season as a result of water supplied by snowmelt (Fig. 2e). Soil water content (WC) measured at the base of the flux tower peaked at approximately 0.25 m³ m⁻³, usually during the same week in which Q was highest, before following a pattern of general decline with interspersed increases in WC resulting from rainfall (Fig. 2d). Water use efficiency (WUE_{NEP/ET}) was also highly seasonal, with negative values during the winter due to negative NEP (Fig. 2c). During the summer growing season, WUE_{NEP/ET} was positive and closely tracked patterns of WC and, to a lesser degree, Q .

Patterns of NEP (Fig. 2a) appear to track mean weekly temperature and VPD, but during the growing season this relationship was not as strong as it may appear. Weekly ET and NEP during the growing season exhibited contrasting responses to VPD and WC (Fig. 3a,b,d,e). High levels of weekly ET were observed for a range of VPD and WC values, with the highest values occurring at intermediate values of WC and VPD (Fig. 3c,f). By contrast, weekly estimates of NEP were highest under conditions of high mean WC (WC >0.20) and low mean VPD (mean VPD <4 mb, Fig. 3), indicating a divergence in the responses of H₂O and CO₂ fluxes to changing patterns of WC and atmospheric water demand (VPD). An additional divergence in the responses of ET and NEP to hydrological conditions is evident in plots of weekly ET and NEP versus WC, whereby ET peaked at intermediate WC, while NEP exhibited a positive response to increasing WC, albeit a response that can only be partially explained by differences in WC alone ($R^2 = 0.15$, $p < 0.001$). WUE_{NEP/ET} showed significant responses to both WC and VPD. WUE_{NEP/ET} decreased as a power function of VPD ($R^2 = 0.23$, $p < 0.001$), declining more sharply at low VPD than at high VPD. WUE_{NEP/ET} exhibited an even stronger correlation with WC, increasing as a power function of WC ($R^2 = 0.41$, $p < 0.001$, Fig. 3) with higher sensitivity of NEP to WC at higher values of WC.

Weekly NEP exhibited a log-linear relationship to weekly Q , with low sensitivity of NEP to Q during high flow conditions ($Q > 50$ mm week⁻¹, Fig. 4). The relationship between weekly NEP and weekly Q was strongest during 2009 ($R^2 = 0.55$) and lowest during 2006 ($R^2 = 0.18$), the year with the lowest NEP (Fig. 4). However, with the exception of data collected from 2006, the rest of the years exhibited a relatively predictable response to changes in catchment-wide water availability represented by Q , with weekly Q explaining 40–55% of the variation in weekly NEP.

Annual NEP showed a moderate range of inter-annual variability, varying from 392 g C m⁻² year⁻¹ in 2009 to 480 g C m⁻² year⁻¹ in 2010. Growing season length ranged from 138 days in 2009 to 170 days in 2007 (Table 1). Annual precipitation inputs, which include snowmelt and rainfall, were highly variable, ranging from 681 mm in 2007 to 1024 mm in 2010. NEP was positively correlated with GSL ($R^2 = 0.90$, $p < 0.05$, Fig. 5), although the relationship between annual NEP and GSL was affected by annual precipitation as well. NEP could be relatively high during years with a long grow-

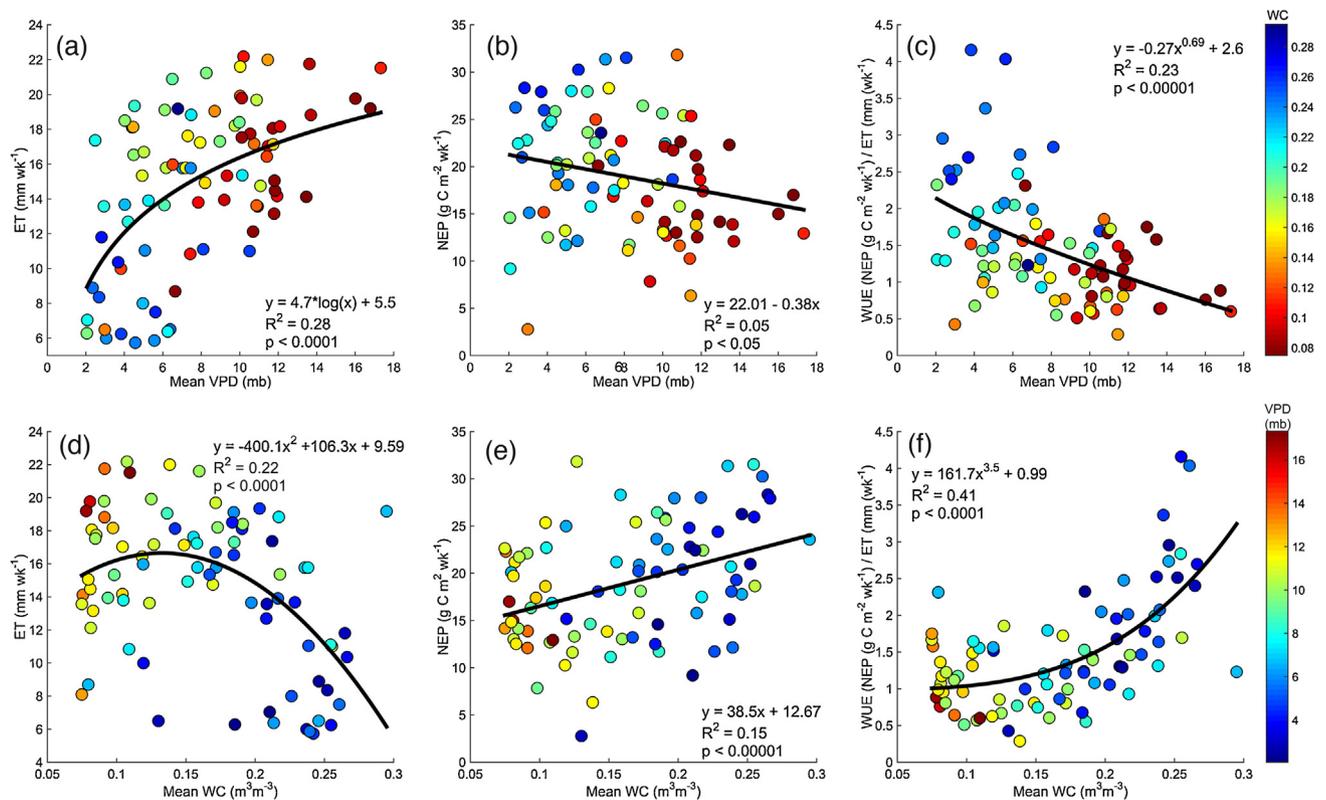


Fig. 3. Scatterplots of high quality (<25% gap-filled) weekly NEP, ET, and water use efficiency (NEP/ET) data from the growing season, plotted against weekly mean VPD (on top) and mean WC (bottom), color-coded by mean weekly WC (on top) and VPD (bottom). Weekly ET and NEP exhibit contrasting responses to VPD, with high ET occurring under high VPD, while weekly NEP is highest when VPD is low and WC is high. WUE is highest when WC is high and VPD is low, suggesting that NEP is highest when WUE is highest. WUE is positively correlated with soil moisture and shows a much more consistent response to it than NEP.

Table 1

Annual ET, NEP, precipitation, WUE, and growing season length.

Hydroecological year	ET (mm H ₂ O year ⁻¹)	NEP (g C m ⁻² year ⁻¹)	Precipitation (mm H ₂ O year ⁻¹)	WUE (NEP / ET)	Growing season length (Days)
2006	504	349	879	0.69	155 ^a
2007	481	486	833	1.01	170
2008	466	448	922	0.96	146
2009	524	397	843	0.76	138
2010	508	482	1087	0.95	160
2011	654	411	998	0.63	145

^a Missing temperature data during the latter part of the growing season and was reliant upon gap-filling.

ing season (2007), but not as high as during years with a slightly shorter growing season but more precipitation (2010).

Evapotranspiration at the Tenderfoot Creek Experimental Forest includes contributions from the sublimation of snow as well as soil evaporation, interception, and transpiration. Like NEP, ET showed a moderate range of inter-annual variability, with estimates of annual ET ranging from 465 mm year⁻¹ in 2008 to 655 mm year⁻¹ in 2011. However, unlike NEP, annual ET was not related growing season length. We also found no relationship between ET and annual precipitation or NEP.

We compared 2006–2011 results from TCEF to data from 13 flux tower sites summarized by Arain and Restrepo-Coupe (2005) using annual NEP, mean growing season temperature, and annual precipitation for individual site-years (Fig. 6). These sites represent a wide range of conifer species, ages, management strategies and other factors (Arain and Restrepo-Coupe, 2005). Although annual NEP at TCEF was relatively high compared to other evergreen, needle-leaf forests, the values fell within the envelope of NEP variability with respect to temperature and precipitation among all sites, with NEP at TCEF most similar to Tharandt (Germany) and Vielsam (Belgium)

study sites. Mean annual NEP at TCEF was highest among all sites in the Intermountain West summarized here (TCEF, Niwot Ridge, Metolius and Wind River).

4. Discussion

4.1. Responses of CO₂ and H₂O fluxes to VPD and WC within the growing season

We observed a divergence in the growing-season responses of ET and NEP to VPD at the weekly time scale. Compared to NEP, ET was much more responsive to changes in VPD and exhibited a monotonic, positive response to mean weekly VPD (Fig. 3a). Low values of VPD coincided with the lowest values for ET, suggesting that low atmospheric water demand was responsible for reduced ET during periods of high soil moisture. The non-monotonic response of ET to WC (Fig. 3d) reflects the influences of both soil water supply and atmospheric water demand on ET. When soils were relatively dry (WC less than approximately 0.15 m³ m⁻³) and when atmospheric demand for water was relatively high (VPD

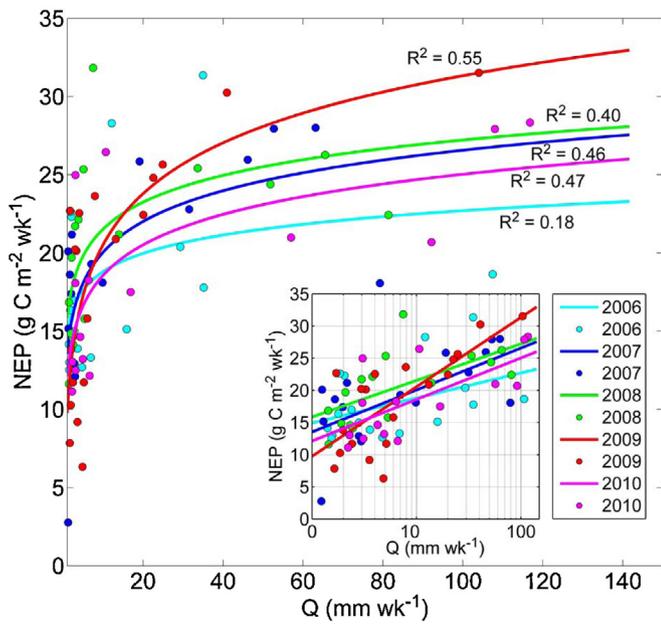


Fig. 4. Scatterplot of high quality (<25% gap-filled) weekly NEP plotted against weekly stream flow (Q) by year. Relationships between weekly NEP and weekly Q were strongest during 2009 ($R^2 = 0.55$) and lowest during 2006 ($R^2 = 0.18$), the year with the lowest NEP (Fig. 4). Most years exhibited a relatively predictable response to changes in catchment-wide water availability represented by Q, with weekly Q explaining 40–55% of the variation in weekly NEP.

greater than approximately 10 mb), ET increased with increasing WC. When soils were wetter than approximately $0.15 \text{ m}^3 \text{ m}^{-3}$, conditions that also corresponded to lower atmospheric demand for water (VPD less than approximately 10 mb), ET declined with increasing WC (Fig. 3d). This non-monotonic behavior of ET in response to soil moisture results in peak ET occurring at intermediate levels of soil moisture, which is consistent with observations of ET and soil moisture from a range of North American flux tower sites (Emanuel et al., 2007).

Weekly NEP increased linearly with mean weekly WC and in contrast to ET, NEP declined with increasing VPD (Fig. 3b). The negative correlation between weekly NEP and VPD could reflect stomatal down-regulation in response to elevated VPD (Oren et al., 1999), but could also reflect the negative correlation between VPD and WC ($R^2 = 0.49$) caused by the seasonality and timing of spring snowmelt relative to warm and dry summer weather that charac-

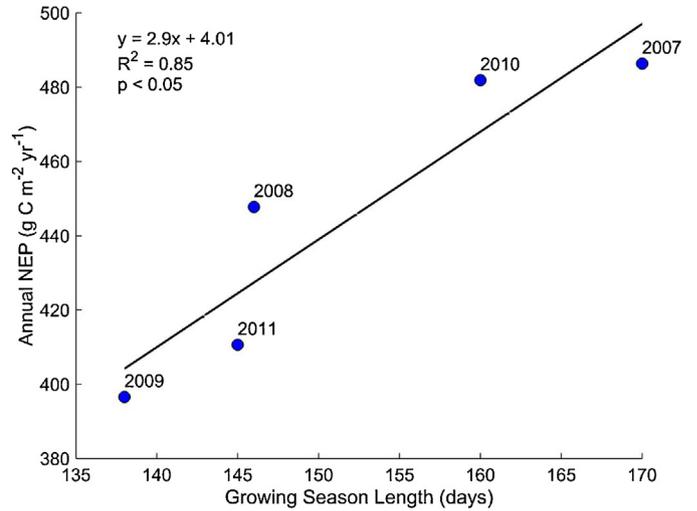


Fig. 5. Annual NEP plotted against temperature-defined growing season lengths. 2006 was excluded due to a lack of temperature data toward the end of the growing season.

terizes the continental climate of TCEF. The behavior of both NEP and ET during the growing season suggests that both of these fluxes were influenced not only by VPD and WC individually, but also by the timing of soil water availability relative to atmospheric water demand. Indeed, ecohydrological modeling from the 2006 growing season at TCEF suggested that vegetation across most of the Upper Stringer Creek catchment experienced water stress due to the interaction between rising VPD and declining WC that characterizes the TCEF growing season (Emanuel et al., 2010). One effect of the increasing intensity of vegetation water stress during the TCEF growing season would be a declining correlation between ET and VPD coincident with an increasing correlation between ET and WC as water stress initiated, spread, and intensified across the catchment (Emanuel et al., 2010). The present results (Fig. 3) suggest that the general mechanism of water stress-mediated ET responses to VPD and WC holds across multiple years. The relatively low variance of ET and NEP explained by WC may result from the inability of a single, point measurement of soil moisture to fully represent the spatial heterogeneity of soil water availability and associated land-atmosphere exchange across this topographically complex landscape. Prior work at TCEF has shown that the lateral redistribution of soil water can lead to complex biogeochemical responses at the landscape scale (Riveros-Iregui and McGlynn, 2009; Emanuel

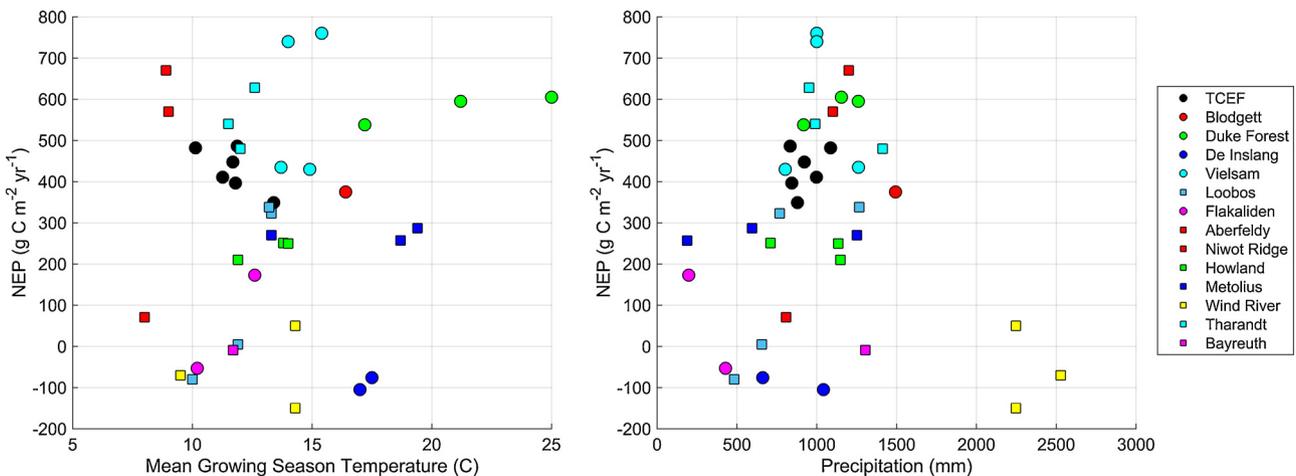


Fig. 6. Scatterplot of mean annual growing season temperature, annual precipitation, and annual NEP at the Tenderfoot Creek Experimental Forest (shown in black), compared to other flux sites for context. Data from comparison sites are taken from Arain and Restrepo-Coupe (2005).

et al., 2010). Therefore, spatially averaged tower measurements may not capture the full complexity of these responses, which may explain why the correlations between weekly WC and NEP, while linear and statistically significant, were comparatively weak. However, measurements of stream flow (Q) explained much more of the variation in NEP (Fig. 4, discussed in more detail below) and may be a better indicator of catchment-level water availability.

4.2. Water-use efficiency and its relationship to VPD and WC within the growing season

We focused on $WUE_{NEP/ET}$ rather than $WUE_{GPP/ET}$ (e.g., Law et al., 2001; Ponton et al., 2006) because NEP was based on directly observed carbon flux rather than modeled or derived GPP, and NEP is the ecosystem flux whose magnitude most directly influences the atmospheric carbon balance. Since our analysis focused on the growing season, we anticipated that photosynthesis would exceed the respiratory component of NEP; thus, we expected $WUE_{NEP/ET}$ to be similar in pattern if not in magnitude to $WUE_{GPP/ET}$. During the growing season at TCEF, mean weekly $WUE_{NEP/ET}$ was negatively correlated with mean weekly VPD and positively correlated with mean weekly WC (Fig. 3c). The negative correlation between $WUE_{NEP/ET}$ and VPD is consistent with patterns observed in many different ecosystems (e.g., Law et al., 2001) and suggests that during the early part of the growing season at TCEF, low VPD and relatively high WC combined to yield high productivity with relatively low ET due to reduced atmospheric demand for water during this time of year. During the later period of the growing season however, high VPD and relatively low WC combined to limit carbon uptake while facilitating continued ET due to the relatively large atmospheric demand for water. These conditions led to reduced $WUE_{NEP/ET}$ later in the growing season. Overall, the strong negative correlation ($R^2 = 0.49$) between VPD and WC during the growing season at TCEF influenced the monotonic decline of $WUE_{NEP/ET}$ as VPD increased and WC decreased through time.

On a weekly time scale, growing season $WUE_{NEP/ET}$ was more strongly correlated with WC ($R^2 = 0.41$) than with VPD ($R^2 = 0.23$) (Fig. 3c,f). Thus, even though there is little doubt that atmospheric water demand strongly influences ET and thus $WUE_{NEP/ET}$, our results suggest that $WUE_{NEP/ET}$ could be influenced more by WC than by VPD in this system. We also note that the positive curvature of the power-law response of $WUE_{NEP/ET}$ to increasing WC was steeper than the negative curvature of the response of $WUE_{NEP/ET}$ to increasing VPD. The steep $WUE_{NEP/ET}$ -WC curve appears to result from lower rates of ET under conditions of low VPD (VPD < 3 mb), which were also associated with higher WC: these conditions facilitated higher rates of NEP (Fig. 3b,e). Together, the conditions that facilitated low ET and a high NEP combine and yielded a relatively high $WUE_{NEP/ET}$ during the early growing season (Fig. 3c,f).

4.3. Stream flow and net ecosystem production within the growing season

Stream flow (Q) is influenced by catchment-wide water storage (Spence, 2007), and can arguably provide a better indicator of spatially-integrated soil water availability than point measurements of soil moisture located near a tower. This is especially likely at sites such as TCEF where one large snowmelt-derived input drains from uplands to streams over the course of the year (Jencso et al., 2010; Nippgen et al., 2011). As a result, both Q and WC at TCEF experience monotonic declines during the growing season. In fact, we found a strong correlation between WC (0–30 cm below the surface) at one landscape position measured near the tower (Fig. 2d) and $\log(Q)$ at the outlet of the 393 ha catchment containing the flux tower (Fig. 1; Fig. 2e) at both half-hourly and daily time steps

($R^2 = 0.51$ and $R^2 = 0.61$, respectively) and similar relationships with riparian groundwater levels (Pacific et al., 2011).

Given the co-occurrence of decreasing catchment-wide water availability and increasing VPD during the growing season at TCEF, we anticipated a pattern of decreasing NEP with decreasing Q , as NEP responded to both reduced soil water availability and increased atmospheric demand for water (Fig. 3). Indeed, weekly NEP declined with weekly Q , exhibiting a log-linear response with high NEP occurring across a range of moderate and high flow conditions characteristic of the early growing season, with NEP declining sharply with respect to Q across a range of lower flow conditions characteristic of the later growing season (Fig. 4). The log-linear relationship between NEP and Q provides evidence that early growing season conditions are characterized by sufficient soil water to facilitate both vigorous carbon uptake and runoff supported by soil water drainage and associated hydrologic connectivity (viz. Jencso et al., 2009), whereas mid and late growing seasons may be better characterized by a competition for soil water between gravity-driven drainage and plant water uptake as suggested by prior TCEF work by Emanuel et al. (2014).

While the relationship between NEP and Q changed over the course of the growing season, the strength of the correlation between NEP and Q remained relatively high, except during 2006, when annual NEP was low. In 2007, 2008 and 2009, the three driest years of our analysis (annual precipitation inputs = 681, 795 and 719 mm, respectively), we found relatively strong correlations between NEP and Q ($R^2 = 0.46$, $R^2 = 0.40$, and $R^2 = 0.55$, respectively). The wettest year, 2010, had 1023 mm of precipitation, and likewise had a high correlation between Q and NEP ($R^2 = 0.47$). Weekly, growing season data from 2011 did not meet our data quality criterion (<25% gap-filled data) and were thereby excluded from this part of our analysis. To our knowledge, this is the first such comparison of tower fluxes and stream flow from an area that is approximately equal to the time-integrated tower footprint. Our findings suggest that future research on the relationships between landscape water availability, NEP, and other ecosystem processes could use catchment-scale Q as an indicator of landscape wetness state.

4.4. Growing season length, annual precipitation inputs, and annual net ecosystem production

Growing season length (GSL) significantly influenced the magnitude of annual NEP. We found a strong positive correlation between annual NEP and GSL at TCEF (Fig. 5), which is similar to patterns observed at other tower flux sites (e.g., Churkina et al. (2005)). Model results from Niwot Ridge (Colorado, USA) another subalpine forest in the Intermountain West, also predict increased productivity with longer growing seasons in response to climate change during the late 21st century (Scott-Denton et al., 2013). However, those model results contradicted recent observations of reduced annual NEP in years with longer growing seasons at Niwot Ridge (Hu et al., 2010a; Scott-Denton et al., 2013). The Metolius flux tower sites in central Oregon, a semi-arid system dominated by ponderosa pine, also had lower annual NEP than TCEF (Fig. 6). Differences in annual NEP between TCEF and Metolius appear to be largely due to differences in precipitation. While annual precipitation at Metolius is highly variable, it averages around 550 mm year⁻¹, 97% of which falls between October and June, mostly as snow (Law et al., 2001). While TCEF also receives most of its precipitation as snowfall, annual precipitation is much higher than that of Metolius, with an average of 927 mm year⁻¹ during our study period. Additionally, TCEF receives a greater portion of its precipitation during the growing season; during July–September, TCEF averaged 148 mm of precipitation between July–September compared to an average of 17 mm at Metolius during the same period. Consequently, growing

season NEP at Metolius appears even more water-limited than that observed at TCEF.

Our results indicate that at the annual time scale, precipitation inputs are largely sufficient to meet vegetation water demands, even during relatively dry years (Fig. 5). High annual NEP during the relatively dry year of 2007 further emphasizes this finding. In other cases where annual NEP has been observed to decrease with growing season length (Angert et al., 2005; Piao et al., 2008), water or other resources are thought to limit carbon uptake late in the growing season while ecosystem respiration persists, offsetting earlier carbon gains. Although modeling results suggested that vegetation water stress can exist during the growing season at TCEF (Emanuel et al., 2010), the degree and duration of water stress do not appear to limit carbon uptake strongly relative to ecosystem respiration, given the strong positive correlation between annual NEP and GSL across a range of wet and dry years at TCEF (Fig. 5). These results suggest that this system has not yet reached a point where water availability limits annual carbon uptake relative to ecosystem respiration (i.e., NEP) in years with longer growing seasons.

Most model projections of future climate change predict a warmer, drier climate throughout the Intermountain West (IPCC, 2013). Consequently, the GSL–NEP relationship that we observed at TCEF could shift from a positive correlation to a negative one if annual precipitation inputs do not continue to sustain present rates of carbon uptake during longer growing seasons associated with a warmer climate. This hypothesized shift from increasing annual NEP to decreasing annual NEP with changes in growing season length could also result from altered timing of precipitation inputs and soil water availability relative to atmospheric water demand during the growing season, or from differential sensitivities of productivity and respiration to changes in growing season length (e.g., Kueppers and Harte, 2005). How annual NEP of TCEF and similar ecosystems will respond to longer growing seasons and less precipitation will likely depend on the sufficiency and timing of water supplies as well as the individual responses of productivity and respiration.

5. Conclusions

Based on six years of eddy flux data from a subalpine forest, we determined that evapotranspiration and net ecosystem production responded differently to atmospheric water demands during the growing season. High levels of atmospheric water demand resulted in high levels of evapotranspiration and low levels of net ecosystem production. Strong seasonality in atmospheric water demands and soil moisture availability were related to the observed changes in growing season dynamics of CO₂ and H₂O flux in this system. The negative relationship observed between weekly NEP and mean weekly vapor pressure deficit appears to be a consequence of soil moisture availability, which was inversely correlated with atmospheric water demands. Thus, weekly NEP was highest under conditions of high soil moisture, and there was a positive relationship between NEP and growing season length across six years of analysis. Together, this suggests that the TCEF ecosystem did not reach a point where prohibitively low levels of soil moisture availability were limiting photosynthesis, and, by extension, NEP. However, modeled predictions of future climate for the region project an increase in temperature and a decrease in precipitation, conditions that will increase atmospheric water demand and decrease soil moisture availability (IPCC, 2013). Consequently, the TCEF ecosystem could reach a threshold at which longer growing seasons could result in lower annual NEP. Understanding the conditions leading to such a reversal of the current positive relationship between GSL and NEP would require more detailed knowledge about the balance between water availability and water demand. Our current understanding of this relationship is limited under-

standing of how complex terrain mediates the persistence and redistribution of snowmelt-derived soil moisture during the growing season, thereby influencing NEP. Research efforts addressing the role of topographic heterogeneity in the lateral redistribution of water across mountainous landscapes could therefore prove essential to our ability to predict future patterns of carbon flux and storage in a changing climate.

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