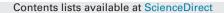
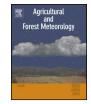
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Land-atmosphere carbon and water flux relationships to vapor pressure deficit, soil moisture, and stream flow



Stephen R. Mitchell^{a,*}, Ryan E. Emanuel^b, Brian L. McGlynn^c

^a Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

^b Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

^c Division of Earth and Ocean Sciences, Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

ARTICLE INFO

Article history: Received 21 July 2014 Received in revised form 31 March 2015 Accepted 8 April 2015

Keywords: Carbon dioxide flux Net ecosystem production Net ecosystem exchange Evapotranspiration Climate change Subalpine forests Stream flow Water-use efficiency

ABSTRACT

Climatic change is exerting considerable influence on the hydrologic and biogeochemical cycles of snowdominated 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

* Corresponding author. Tel.: +1 919 491 0398.

http://dx.doi.org/10.1016/j.agrformet.2015.04.003 0168-1923/© 2015 Elsevier B.V. All rights reserved. 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.

E-mail address: srm12@duke.edu (S.R. Mitchell).

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_{NFP/FT}), 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_{NFP/FT} 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 engelmanii) 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. engelmanii 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 H_2O and CO_2 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 continuous 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). Towerbased micrometeorological measurements were complemented by

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