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Warmer temperatures reduce net carbon uptake, but do not affect water use, in a mature southern Appalachian forest

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ABSTRACT

Increasing air temperature is expected to extend growing season length in temperate, broadleaf forests, leading to potential increases in evapotranspiration and net carbon uptake. However, other key processes affecting water and carbon cycles are also highly temperature-dependent. Warmer temperatures may result in higher ecosystem carbon loss through respiration and higher potential evapotranspiration through increased atmospheric demand for water. Thus, the net effects of a warming planet are uncertain and highly dependent on local climate and vegetation. We analyzed five years of data from the Coweeta eddy covariance tower in the southern Appalachian Mountains of western North Carolina, USA, a highly productive region that has historically been under-represented in flux observation networks. We examined how leaf phenology and climate affect water and carbon cycling in a mature forest in one of the wettest biomes in North America. Warm temperatures in early 2012 caused leaf-out to occur two weeks earlier than in cooler years and led to higher seasonal carbon uptake. However, these warmer temperatures also drove higher winter ecosystem respiration, offsetting much of the springtime carbon gain. Interannual variability in net carbon uptake was high (147 to 364 $g\,C\,m^{-2}\,y^{-1}$), but unrelated to growing season length. Instead, years with warmer growing seasons had 10% higher respiration and sequestered ~40% less carbon than cooler years. In contrast, annual evapotranspiration was relatively consistent among years (coefficient of variation = 4%) despite large differences in precipitation (17%, range = 800 mm). Transpiration by the evergreen understory likely helped to compensate for phenologically-driven differences in canopy transpiration. The increasing frequency of high summer temperatures is expected to have a greater effect on respiration than growing season length, reducing forest carbon storage.

1. Introduction

Increasing air temperature (T_{air}) is a highly ubiquitous and influential climate driver affecting terrestrial ecosystems, with the potential to alter key ecosystem services such as carbon sequestration and water yield. Warmer temperatures can advance the date of leaf-out and delay the date of leaf senescence in a variety of ecosystems, particularly temperate, boreal, and subalpine forests, increasing the number of days for plants to assimilate carbon (C) and transpire water (Richardson et al., 2013). However, warmer temperatures will also affect ecosystem processes throughout the year, with potentially positive or negative impacts on C and water dynamics. Higher T_{air} leads to an increase in potential evapotranspiration linked to rising atmospheric demand for water (vapor pressure deficit; *D*), which could result in reduced water yield (Creed et al., 2014). However, actual evapotranspiration (ET) and photosynthesis may be constrained by reduced stomatal conductance at high *D* (Novick et al., 2016a) and non-stomatal temperature limitations to photosynthesis (Zhou et al. 2014). Although photosynthesis represents the gross input of C to the ecosystem, the net ecosystem C balance depends on the difference between photosynthesis and respiration, both of which may be enhanced with warmer temperatures (Baldocchi et al., 2017; Davidson and Janssens, 2006)). During comparatively warmer seasons, the magnitude of increased ecosystem photosynthesis tends to exceed the increase in respiration during the

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Table 1
Species list, basal area, and maximum leaf area index, based on allometric equations from four 25 × 25 m plots near the base of the eddy covariance tower, sorted by leaf area index (see Methods).

Scientific name	Common name	Basal area		Leaf area index	
		($m^2\,ha^{-1}$)		($m^2\,m^{-2}$)	
Betula lenta L.	Black (sweet) birch	3.19	10.9%	1.05	22.6%
Liriodedron tulipifera L.	Tulip (yellow) poplar	6.94	23.8%	0.81	17.5%
Quercus alba L.	White oak	5.09	17.5%	0.65	14.0%
Rhododendron maximum L.	Great (rosebay) rhododendron	4.39	15.1%	0.60	12.9%
Acer rubrum L.	Red maple	2.18	7.5%	0.44	9.5%
Nyssa sylvatica Marsh.	Blackgum	2.06	7.1%	0.33	7.1%
Oxydendrum arboreum L. (DC.)	Sourwood	1.89	6.5%	0.27	5.8%
Carya spp.	Hickory species	0.80	2.7%	0.13	2.8%
Fagus grandifolia Ehrh.	American beech	0.62	2.1%	0.10	2.2%
Quercus velutina Lam.	Black oak	0.46	1.6%	0.08	1.7%
Cornus florida L.	Flowering dogwood	0.32	1.1%	0.05	1.1%
Kalmia latifolia L.	Mountain laurel	0.25	0.9%	0.04	0.9%
Carpinus caroliniana Walter	American hornbeam	0.19	0.7%	0.03	0.6%
Quercus rubra L.	Red oak	0.17	0.6%	0.02	0.4%
Fraxinus americana L.	White ash	0.14	0.5%	0.02	0.4%
Tsuga canadensis L.	Eastern hemlock	0.31	1.1%	0.01	0.2%
Pinus strobus L.	Eastern white pine	0.08	0.3%	0.01	0.2%
Magnolia fraseri Walter	Mountain (Fraser) magnolia	0.05	0.2%	< 0.01	< 0.2%
Ilex opaca Aiton	American holly	0.02	0.1%	< 0.01	< 0.2%
TOTAL		29.14		4.64	

spring (Richardson et al., 2010), but increases in respiration may exceed the increase in photosynthesis in the fall (Piao et al., 2008). Thus, through respiration, global trends in temperature can have a large influence on ecosystem C balance (Ballantyne et al., 2017).

Maintaining high primary productivity and water use throughout the growing season requires favorable climatic conditions beyond just temperature. Without an adequate water supply, an earlier start to the growing season has the potential to lead to a more rapid depletion of soil water, limiting both photosynthesis and transpiration later in the growing season (Williams et al., 2013), offsetting any gains from earlier leaf-out (Wolf et al., 2016). However, soil respiration may be suppressed during dry periods (Davidson et al., 1998) resulting in lower annual soil and ecosystem respiration during warm, drought years compared to more mild years (Novick et al., 2015; Palmroth et al., 2005). At the other end of the spectrum, periods of high precipitation (*P*) are often characterized by cloudy days, where radiation may limit photosynthesis and high humidity may limit ET. Therefore, the magnitude and timing of precipitation, particularly during the growing season, also affects C and water dynamics.

The dynamics governing precipitation and temperature impacts on primary productivity and water use are particularly important in areas of complex terrain, where orographic rainfall patterns can lead to exceptionally high water inputs, and where topographic complexity can result in large spatial variability in microclimate (Daly et al., 2017; Burt et al., 2017). Coves and valleys can benefit from a downslope subsidy of soil water (i.e. water drainage from upslope area), reducing the impacts of lower precipitation on transpiration, conductance (Hawthorne and Miniat 2017) and productivity (Elliott et al., 2015a, Elliott et al., 2015a, b). Furthermore, nocturnal cold air drainage into low-lying valleys can suppress respiration, enhancing the C sink (Novick et al., 2016b) and isolating down-slope positions from macro-scale climate variability. Therefore, topographic complexity may help to buffer the local microclimate from regional climate change (McLaughlin et al., 2017). These montane ecosystems can therefore play an important role in sequestering C and regulating water yield, but due largely to methodological challenges (Novick et al. 2014), have been historically underrepresented in flux observation networks and thus may not be accurately characterized by global models.

Our goal was to examine the long- and short-term climate drivers of carbon gain and water loss in a southern Appalachian deciduous forest located in a low-elevation, cove position. These forests have high diversity of overstory tree species, exhibiting isohydric and anisohydric hydraulic strategies, and dense understory vegetation with a significant evergreen shrub component. The southern Appalachian region of the southeastern United States is an extensively forested area, characterized by complex topography and large amounts of annual rainfall, often exceeding 2 m of rain per year. This region's mesic, temperate climate has high potential for carbon gain and provides a critical source of drinking water to major cities in the southern US (Caldwell et al., 2016). T_{air} in this region has been increasing since the early 1980s at approximately 0.5 °C per decade (Ford et al., 2011). This trend is affecting both dormant and growing season temperatures. Warmer temperatures in these forests are expected to lead to an earlier start and later end to growing seasons and subsequently greater ET (Hwang et al., 2014). Mean precipitation has not shown a temporal trend at the annual scale, in part due to decreases in July compensated by increases in late fall, but variability in mean annual precipitation is increasing (Ford et al., 2011).

We analyzed five years of eddy covariance data (2011–2015) from Coweeta Hydrologic Laboratory in western North Carolina, United States. Leaf phenology was used to estimate growing season length. To address methodological challenges associated with using eddy covariance techniques in complex terrain (Novick et al., 2013), we incorporated forest water yield data from gauged watersheds and shorter-duration measurements of subcanopy eddy covariance and soil CO_2 efflux, to examine seasonal and interannual ecosystem exchange of carbon and water. Using these multiple data sets, we explored the relative importance of growing season length versus intra-annual variability in climate as drivers of annual ET and net C uptake. Finally, we leveraged eight decades of local climate records to assess the impact of long-term trends in climate on forest water yield and C storage in a relatively understudied biome.

2. Materials and methods

2.1. Site description

The forest surrounding the Coweeta flux tower (35.059N, 83.427W, 690 m asl) was selectively harvested in the 1930s and has naturally regenerated since then. Tree surveys were conducted in four, 25 by 25 m plots near the base of the tower. All trees with diameter at breast height (DBH, cm) greater than 10 cm were tagged and re-measured