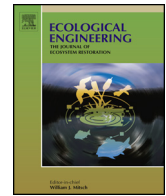




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Evidence of autumn phenology control on annual net ecosystem productivity in two temperate deciduous forests



Chaoyang Wu^{a,b,*}, Christopher M. Gough^c, Jing M. Chen^b, Alemu Gonsamo^b

^a The State Key Laboratory of Remote Sensing Science, Institute of Remote Sensing and Digital Earth, Chinese Academy of Sciences, Beijing, China

^b Department of Geography, University of Toronto, 100 St. George St., Room 5047, Toronto, ON, M5S 3G3 Canada

^c Department of Biology, Virginia Commonwealth University, Richmond, VA 23284-2012, USA

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ABSTRACT

Phenology exercises a critical control on annual carbon uptake by terrestrial ecosystems. Autumn phenology, while less studied relative to spring phenology, may also constrain annual net ecosystem productivity (NEP). Using 17-year (1992–2008) records of C flux phenology (CFP) derived from continuous eddy covariance (EC) measurements at the Harvard Forest (HF), here we show that the autumn phenology played a more significant role than the spring phenology in controlling annual NEP. We found that the onset of carbon uptake (CU) in spring only explained 39% of annual NEP, compared to 66% of end of CU in autumn. Though neither onset nor end of gross primary productivity (GPP) was correlated with annual NEP, the autumn lag, i.e., the time lag between ends of GPP and CU, was found to have a particularly high potential in explaining annual NEP ($R^2 = 0.82$, $p < 0.001$). We further showed that the autumn lag can be modeled as a function of entirely autumn (September–November) meteorological variables, including the water vapor pressure deficit, global shortwave radiation and the surface soil temperature, indicating the autumn lag and consequently the annual NEP can be modeled in areas lacking EC measurements. The usefulness of the modeled autumn lag was evidenced in its capability to explain 70% of annual NEP at HF site. A validation of the empirical function derived from HF site using 13-year (1999–2011) independent data at the University of Michigan Biological Station (UMB) forest was promising. Estimates of autumn lag using the exactly same meteorological variables proposed at HF site but different regression coefficients were highly correlated with the observed autumn lag ($R^2 = 0.87$, $p < 0.001$) at UMB site. The correlation decreased slightly ($R^2 = 0.83$, $p < 0.001$) if the regression coefficients found at HF site was also used, which subsequently explained 46% of annual NEP ($p = 0.011$) for UMB site. These results advocate for the inclusion of autumn phenology in terrestrial ecosystem models in order to predict the interannual variability of C sequestration more accurately, but also indicate challenges in deriving appropriate models even for the same plant functional types.

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1. Introduction

Phenology is one of the most important factors affecting the annual carbon (C) sequestration, i.e., the net ecosystem productivity (NEP), in terrestrial ecosystems (Richardson et al., 2012, 2013), and is thus important for ecosystem restoration of forests (Stokes et al., 2012; Wu et al., 2013a,b; Baldocchi et al., 2005). Interannual variability in NEP is primarily driven by year-to-year variability in climate (Desai, 2010; Tang et al., 2011), and, therefore, phenological indicators that detect the dates of first occurrence of biological events (e.g., leaf-out) have been shown to be effective predictors of changes in growing season duration and, consequently,

annual growth patterns and magnitude (Sun et al., 2003; White and Nemani, 2003; Richardson et al., 2010; Wu et al., 2012; Wu and Chen, 2013).

Traditional phenological indicators, including the start and end of the growing season in spring and in autumn, respectively, have been described by the dates when a strong change in leaf color is observed from remote sensing or ground measurements, or by the dates of bud-break in the spring and leaf senescence in the fall (White and Nemani, 2003; Zhang et al., 2004; Garrity et al., 2011; Gonsamo et al., 2012a). The main focus of these methods is detecting the dates when important changes were observed in vegetation color (particularly greenness) (Zhang et al., 2004). The limitation associated with such methods, however, is the empirically determined phenological indicators (e.g., spectral indices) and/or limited samples (e.g., bud-break and first flowering date) of trees that are not well representations of the whole ecosystem. With continuous

* Corresponding author. Tel.: +1 647 524 0310.

E-mail address: hefery@163.com (C. Wu).

measurements of C exchange using the eddy-covariance (EC) technique, an alternative method makes use of C flux phenology (CFP), which quantifies the starts and ends of growing season and C uptake by directly observed net ecosystem exchange (NEE) and modeled gross primary productivity (GPP) (Richardson et al., 2010; Garrity et al., 2011; Gonsamo et al., 2012b). For example, start of growing season could be determined when daily GPP exceeds certain thresholds, e.g., $1 \text{ g C/m}^2/\text{d}$ in Richardson et al. (2010), while C uptake phenology is modeled when the daily NEP curve crosses zero value (Wu et al., 2013a).

Spring phenology has been previously identified as an effective indicator of annual carbon uptake (e.g., Richardson et al., 2009), and considerable efforts have been made to quantify how spring canopy phenology relates to the timing of C cycling processes central to NEP. For example, warmer springs tended to increase annual NEP by causing earlier leaf-on in a boreal deciduous forest in Canada (Black et al., 2000). Later analysis by Barr et al. (2009) additionally demonstrated that spring temperature was a primary variable regulating annual NEP in boreal forests. However, a temperature-driven increase in NEP in the spring could be offset by higher ecosystem respiration (R_e) in autumn, indicating a possible net carbon loss in boreal ecosystems if warming occurs throughout the year (Piao et al., 2008). Such observations suggest a possible role for autumn phenology in controlling interannual variability of NEP. Recent stand and regional scale studies further indicate that a warmer climate may modify North America's terrestrial C sink by delaying the start to autumn (Dragoni et al., 2011; Zhu et al., 2012; Wu et al., 2012, 2013a). Therefore, more work should be focused on phenological events at the end of the growing season, considering that the initial growth of temperate forests may be less dependent on temperature than boreal ecosystems (Dragoni and Rahman, 2012; Richardson et al., 2013; Wu et al., 2013b).

To investigate the role of autumn phenology on interannual variability of NEP, long-term flux data and associated meteorological measurements at both Harvard Forest (HF) (1992–2008) and University of Michigan Biological Station (UMB) forest (1999–2011) were used in this study. The specific objectives were to (1) analyze how spring and autumn phenology control annual NEP, (2) develop appropriate algorithms for modeling seasonal phenology variation and thus annual NEP, and (3) test the broad applicability of an empirically derived phenological algorithm for annual C estimation using independent data acquired at a different site.

2. Materials and methods

2.1. Study sites

Two temperate deciduous broadleaf forest sites were used in this study: the Harvard Forest (HF) and the University of Michigan Biological Station (UMB) forest. Data from the HF site were mainly selected for algorithm development as a longer duration of observations was available (1992–2008) while data from the UMB site (1999–2011) were used for independent validation of a general phenology model.

The HF tower site ($42^\circ 32' 16'' \text{ N}$, $72^\circ 10' 17'' \text{ W}$, 340 m elevation) is located within the upland plateau between the Boston Basin to the east and the Connecticut Valley to the west. The vegetation is dominated by deciduous species, including red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*) and white pine (*Pinus strobus*) (Urbanski et al., 2007). Maximum canopy height is approximately 20–24 m and soils are composed of mainly sandy loam glacial till with alluvial and colluvial deposits. The climate is cool, moist temperate with July mean temperature 20° C and annual mean precipitation of about 1100 mm.

The UMB site is located on a level to gently sloping high outwash plain in northern lower Michigan ($45^\circ 33' 35'' \text{ N}$ $84^\circ 43' 01'' \text{ W}$, 234 m elevation). The forest is a secondary mixed northern hardwood ecosystem mainly composed of bigtooth aspen (*Populus grandidentata Michx.*) and trembling aspen (*Populus tremuloides Michx.*) with lesser representation by paper birch (*Betula papyrifera Marsh.*), red oak, red maple, and white pine. Canopy height is 22 m and soils are excessively drained, sandy, mixed frigid Entic Haplothsods consisting of 92% sand, 7% silt and 1% clay (Gough et al., 2009). Mean annual temperature is 55° C and mean annual precipitation is about 817 mm.

2.2. Flux and meteorological data

Level-4 products of C fluxes and meteorological variables for these two sites were downloaded from the AmeriFlux network (<http://publiccornlgov/ameriflux/dataproductshtml>), which contain gap-filled and friction velocity (u_*) filtered records at varying time intervals with flags regarding the quality of the original and gap-filled data. Annual GPP, NEP (i.e., $-NEE$), and R_e values for each year were extracted. The half-hourly measurements of NEE were gap-filled using the Artificial Neural Network (ANN) method (Papale and Valentini, 2003) and/or the Marginal Distribution Sampling (MDS) method (Reichstein et al., 2005). The ANN method is an empirical non-linear regression model consisting of nodes connected by weights which are effectively the regression parameters. Certain input variables, such as air temperature, daytime vapor pressure deficit (VPD), and global shortwave radiation, are needed in the training process to produce modeled NEP (Papale and Valentini, 2003). If the required variables for ANN method are not available, the MDS method is selected to gap-fill NEP and a short-term temperature sensitivity of ecosystem respiration is then used to partition NEP into GPP and R_e (Reichstein et al., 2005).

2.3. Phenological indicators

In this analysis, we used phenological metrics derived from both daily GPP and NEE, including the GPP onset (day of year), GPP end (day of year), CU onset (day of year), CU end (day of year) and the autumn lag (days).

A negative exponential model, using polynomial regression and weights computed from the Gaussian density function, was adopted to derive smoothed curves for daily NEE and GPP observations (Fig. 1). The respective start and end days with negative daily NEE can then be determined, hereafter referred to as the CU onset and CU end, respectively (White and Nemani, 2003). The GPP onset and GPP end were determined as the days when the smoothed daily GPP reached 10% of the seasonal maximum smoothed daily GPP (Wu et al., 2012). Unlike a fixed GPP threshold in previous analyses, the 10% of seasonal maximum GPP would allow the capture of spatial and temporal variations in growth rhythms. The autumn lag was calculated as the time lag between the ends of GPP and CU (Wu et al., 2012, 2013a).

3. Results

3.1. Interannual variations of phenological indicators at HF site

Interannual variations of CU onset for HF showed a significantly decreasing pattern ($R^2 = 0.39$, $p = 0.008$) from 1992 to 2008, implying that C uptake has advanced by 0.9 days/year during the study time period (Fig. 2a). The CU end, however, was delayed by 11 days/year ($R^2 = 0.56$, $p < 0.001$). GPP onset and GPP end also showed substantial interannual variations at HF site (Fig. 2b). While GPP onset did not show a significant pattern, we found that the GPP

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