

Radiation contributed more than temperature to increased decadal autumn and annual carbon uptake of two eastern North America mature forests



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ABSTRACT

The eastern North America mature deciduous forests are increasing their carbon (C) sink, which is believed to be due to a longer growing season. In this study, we investigated the impacts of land surface phenology (LSP) and carbon uptake phenology (CUP) on the net ecosystem productivity (NEP) of the two longest-running flux tower sites in the region. Our results show that there is no trend in the start (SOS), end (EOS), and length of growing season (LOS) at both sites; nor do they explain the interannual and long-term trend in NEP. We found no evidence for a changing growing season and cannot attribute the increasing C sink to growing season length. However, there is strong trend in end (ECU) and length of net positive carbon uptake (LCU) period. ECU is delaying and LCU is getting longer, and they both explain the interannual and long-term trends in NEP. There is increasing trend of photosynthetically active radiation (PAR) at both sites in line with increasing NEP. PAR is contributing the most both to NEP and ECU. CUP is affected more by the increased photosynthetic activity partially due to increased PAR, but not by timing of spring onset and autumn senescence of leaves. There is also significant ($p < 0.01$) reductions in emissions of sulfur oxides (SO_x), nitrogen oxides (NO_x), total nitrate ($\text{HNO}_3 + \text{NO}_3$) and ozone since 1992. The reductions in gaseous and particulate emissions imply the occurrence of direct aerosol mediated brightening and therefore increased PAR and enhanced C uptake by eastern North America mature forests.

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1. Introduction

Accurate assessments of carbon (C) sources and sinks, and their distribution among terrestrial biospheres are imperative to better understand the global C cycle, to support the development of climate policies and to project the impact of future global change. Pan et al. (2011) recently found a large and persistent sink in world's forests amounting to a total forest sink of $2.4 (\pm 0.4) \text{Pg C year}^{-1}$ globally for 1990 to 2007, using forest inventory data and long-term ecosystem carbon studies. However, due to several data gaps, the estimated terrestrial C sink, its size and location remain

uncertain. Pan et al. (2011) estimates the net global forest C sink of $1.1 (\pm 0.8) \text{Pg C year}^{-1}$ resides mainly in the temperate and boreal forests, consistent with previous estimates (Goodale and Aber, 2001; Sarmiento et al., 2010). One such area is the enhanced C sink of the New England forests, attributed to several explanations such as the enhanced C uptake due to: (1) the longer growing season, (2) the increased atmospheric CO_2 fertilization, (3) enhanced growth from increased nitrogen (N) deposition, and (4) forest regrowth.

It has been believed that the dominant sink mechanism of mature forests are the fertilizing effects of increased CO_2 concentrations in the atmosphere and the addition to soils of fixed nitrogen (N) from fossil-fuel burning and agricultural fertilizers. However, analysis of long-term free air CO_2 enrichment (FACE) observations of the change in biomass and growth rates suggests that such fertilization effects are much smaller than previously thought due to down-regulation of Rubisco activity and poor soil fertility (Hickler et al., 2008; Long et al., 2006). Nadelhoffer et al.

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(1999) show that N is not stimulating forest C uptake in temperate forests.

Traditionally, a longer growing season was attributed to an increase in C sequestration (Churkina et al., 2005; Desai, 2010; Dragoni et al., 2011; Keenan et al., 2014). But recent works indicate that the longer growing season due to climate warming has led to net loss of ecosystem C due to the prolonged period of autumn respiration and decline of snow water (e.g., Piao et al., 2008; Hu et al., 2010; Richardson et al., 2010; Wu et al., 2012a,b, 2013a,b). Due to challenges involved with estimating the slow senescence at the end of the growing season, most studies have previously focused solely on spring phenology. Recent findings have shown that not only autumn phenology, but also carbon uptake phenology can be estimated using remote sensing observations and CO₂ flux measurements (Gonsamo et al., 2013, 2012a,b; Gu et al., 2003, 2009; Wu et al., 2013a). Using these new land surface and carbon uptake phenology estimates, we study the phenological and environmental controls on C flux to answer as to why the eastern North America deciduous forests at the two longest-running flux tower sites in the region, Harvard Forest Environmental Monitoring and Borden Forest Research Station sites, despite being mature forests, their C sink strength is growing.

2. Materials and methods

2.1. Field sites

2.1.1. Harvard forest

The Harvard Forest Environmental Monitoring site (42°32'16"N and 72°10'17"W, 340 m elevation) is located in western Massachusetts, USA. The flux tower is located in a primarily deciduous temperate forest, about 110 km west of Boston, Massachusetts, USA. The vegetation is dominated by red oak (*Quercus rubra* L., 36% of basal area) and red maple (22% of basal area), with lesser quantities of other hardwoods (including black oak, *Quercus velutina* Lam., white oak, *Quercus alba* L., and yellow birch, *Betula alleghaniensis* Britton, totaling 15% of basal area) (Richardson et al., 2009). Conifers include eastern hemlock (13% of basal area), red pine (*Pinus resinosa* Aiton, 8% of basal area) and white pine (*Pinus strobus* L., 6% of basal area). The canopy height is approximately 20–24 m. Soils are mainly sandy loam glacial till with some alluvial and colluvial deposits. The climate is cool, moist temperate with daily mean air temperature of 8 °C. Annual mean precipitation is about 110 cm, and the precipitation is distributed approximately evenly throughout the year. Previous studies have shown the site to be strong sink for atmospheric C, with the annual C sequestration of 240 g C m⁻² year⁻¹ (mean ± 1 SD) (Urbanski et al., 2007) based on eddy covariance measurements. The forest contained ~100 Mg C ha⁻¹ in live aboveground woody biomass (AGWB) when the site was established. About 1/3 of the existing red oaks were established prior to 1895, another 1/3 prior to 1930, and the rest before 1940 (Urbanski et al., 2007); hence the stand is 82–117 years old. Although the stand was affected by a hurricane blowdown in 1938, many of the canopy trees now present would have already been established in the understory. Nearly continuous forest extends for several km northwest, west and southwest of the tower, the predominant wind direction.

2.1.2. Borden forest

The Borden Forest Research Station site (44°19'N, 79°56'W, 210 m elevation) is located in southern Ontario, Canada. The flux tower is located in a mixed hardwood and coniferous forest, about 80 km northwest of Toronto, Ontario, Canada. The vegetation is dominated by red maple (*Acer rubrum* L., 52.2% stem count), eastern white pine (*Pinus strobes* L., 13.5% stem count),

large-tooth aspen (*Populus grandidentata* Michx., 7.7% stem count), White ash (*Fraxinus americana* L., 7.1% stem count), american beech (*Fagus grandifolia*, 5.6% stem count), with lesser quantity of other overstorey species (including eastern hemlock (*Tsuga canadensis*), trembling aspen (*Populus tremuloides* Michx.), red ash (*Fraxinus pennsylvanica*), black cherry (*Prunus serotina* Ehrh.), red pine (*P. resinosa*), american elm (*Ulmus americana* L.), sugar maple (*Acer saccharum*), yellow birch (*B. alleghaniensis*), choke cherry (*Prunus virginiana*), 14% stem count) (Teklemariam et al., 2009). The canopy height is about 22 m tall on average. The forest soil is sand loamy. The climate is characterized by snow covered winter and humid continental climate with warm summer. Annual mean precipitation is about 79 cm, and the daily mean air temperature of 7 °C. The living tree stem density is 0.30 m⁻² (2996 trees ha⁻¹) while tree biomass is 25.1 Mg ha⁻¹ (Teklemariam et al., 2009). Living and dead trees together accounted for 0.41 m⁻² (4137 trees ha⁻¹) with the dead trees (standing or fallen but not fragmented) accounting for about 27% of this total. The forest is natural re-growth from abandoned farm land which is approximately 100 years old (Lee et al., 1999). The available forest fetch of the flux tower is about 4.3 km to the south, and 3 km to the southwest. Outside of this range was predominantly grass and cropland.

2.2. CO₂ flux and meteorology variables measurements

The eddy-covariance technique is used to measure fluxes of CO₂, momentum, and sensible and latent heat at 30 m and 33 m at Harvard and Borden forest sites, respectively. The Harvard site data were downloaded from Harvard Forest Data Archive/Exchange web portal (<ftp://ftp.as.harvard.edu/>). Daily measurements are calculated from the half-hourly readings of covariance of the fluctuations in vertical wind speed and CO₂ concentration. Half-hourly flux values are excluded from the analysis in the case of instrument malfunction or if half-hour sample periods are incomplete. Night-time flux values are excluding from analysis if the friction velocity (u^*) is below a threshold that varied among years. The net ecosystem exchange (NEE) measurements from 1992 to 2011 and 1996 to 2012 were used in this study for Harvard and Borden forest sites, respectively. Data for year 2004 for Borden forest site was excluded from analysis due to prolonged missing observations. We use the term net ecosystem productivity (i.e., NEP = -NEE) throughout the paper to indicate the net C balance of the site. Ecosystem respiration (R) is calculated from eddy covariance data during the night and outside the growing season, gap filled based on soil temperatures. Gross primary productivity (GPP) is estimated as difference between NEE and R . We used daily time integrated and gap filled GPP, R and NEP data for all dates of studied years. Daily data of gap filled air temperature and photosynthetically active radiation (PAR), the integrated incidence solar radiation from 400 to 700 nanometers, were also included in this study to study.

2.3. Land surface and carbon uptake phenology

Two distinct procedures were used each to retrieve the land surface phenology (LSP) and carbon uptake phenology (CUP) dates from GPP and NEP measurements, respectively (Fig. 1). LSP, defined as the study of the timing of recurring seasonal pattern of variation in vegetated land surfaces observed from synoptic sensors (Gonsamo et al., 2012b), was estimated from the daily GPP measurements based on double logistic curve fitting algorithm (Gonsamo et al., 2012a, 2013). The key LSP dates used in this study include the start of growing season (SOS), end of growing season (EOS), length of growing season (LOS). For the LSP determination

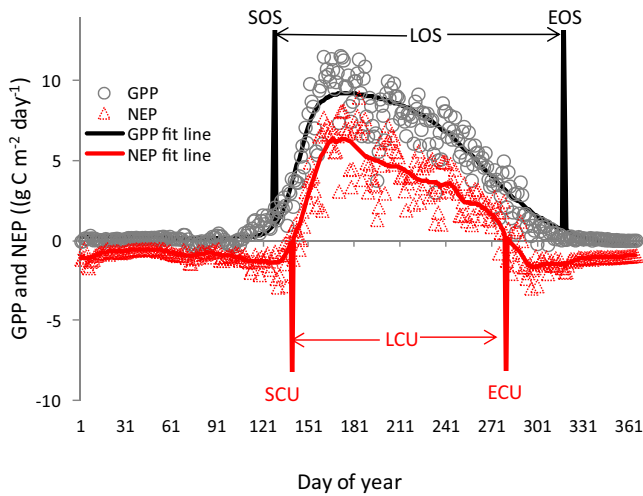


Fig. 1. A schematic of curve fitting mechanism for the gross primary productivity (GPP) and net ecosystem productivity (NEP) ($\text{g C m}^{-2} \text{ day}^{-1}$) time series for the Borden forest flux tower site for year 2007. The land surface phenology dates, i.e., start (SOS), end (EOS), and length of growing season (LOS) are shown as estimated from GPP indicated by vertical lines. Whereas, the carbon uptake phenology dates, i.e., start (SCU), end (ECU), and length of carbon uptake (LCU) period shown as estimated from NEP indicated by vertical lines.

from daily GPP, we used the seven parameter double logistic function:

$$y(t) = \alpha_1 + \frac{\alpha_2}{1 + e^{-\partial_1(t-\beta_1)}} - \frac{\alpha_3}{1 + e^{-\partial_2(t-\beta_2)}} \quad (1)$$

where $y(t)$ is the observed GPP at day of year (DOY) t , α_1 is the background GPP. $\alpha_2 - \alpha_1$ is the difference between the background and the amplitude of spring and early summer plateau, and $\alpha_3 - \alpha_1$ is the difference between the background and the amplitude of late summer plateau and autumn both in GPP units. ∂_1 and ∂_2 are the transition in slope coefficients, and β_1 and β_2 are the midpoints in DOY of these transitions for green-up and senescence/abscission, respectively. From the fitted parameters of Eq. (1), LSP from GPP is estimated (i.e., $\text{SOS} = \beta_1 - 4.562/(2\partial_1)$, $\text{EOS} = \beta_2 + 4.562/(2\partial_2)$, and $\text{LOS} = \text{EOS} - \text{SOS}$).

The key carbon uptake phenology (CUP) dates defined as the detrended zero-crossing timing of NEP from a source to a sink in spring and vice versa in autumn (Fig. 1), include the start of carbon uptake (SCU), end of carbon uptake (ECU), and length of carbon uptake (LCU) periods (Gonsamo et al., 2012b; Wu et al., 2012a,b, 2013a,b). A negative exponential model using polynomial regression and weights computed from the Gaussian density function was used to derive the smoothed curves for daily NEP observations. The three CUP dates were estimated from the zero-crossing of detrended NEP time series (Wu et al., 2013a,b, 2012a,b).

3. Results and discussion

3.1. Interannual variability of net ecosystem productivity

Net ecosystem productivity (NEP) is increasing at the rate of 109 g C/decade ($p=0.081$) and 156 g C/decade ($p=0.0032$) at Harvard and Borden forest sites, respectively (Fig. 2). The ratio of NEP to GPP also follows the same interannual dynamics as NEP but with slower long-term trend, indicating the growth enhancing factors responsible for recent increases in NEP are also responsible for increases in ecosystem respiration and GPP (Fig. 2 and Supplementary material Fig. 2).

The years 2010 and 2011 had abnormally low NEP at Harvard forest site (Fig. 2). The year 2010 at Harvard forest site was

meteorologically anomalous year. Leaf emergence for most of the plants started earlier (Keenan et al., 2014), the April to August months were the driest and hottest among the studied years (Supplementary material Fig. 1) and as a result both GPP and respiration were the largest among the studied years (Supplementary material Fig. 2). The June to October months' respiration consisted of 86% GPP for year 2010, the highest during the studied period. Hot autumns enhance ecosystem respiration more than photosynthesis while the latter is constrained by low PAR due to shorter day lengths. The low NEP in year 2011 could be explained by the lagged effect of the prolonged 2010 drought although meteorologically, year 2011 was not anomalous (Supplementary material Fig. 1). Years from 2005 to 2008 at Harvard forest site are characterized by highest NEP values (Fig. 2). These years have average seasonal meteorological conditions (Supplementary material Fig. 1), and lowest offseason (January–May and November–December) GPP and respiration values (not presented here for brevity). These suggest that meteorologically average years favour NEP, whereas extreme years particularly with low precipitation and high temperature favour both GPP and respirations decreasing the overall NEP at Harvard forest site.

At Borden forest site, year 1996 and 2000 had the lowest NEP (Fig. 2). Year 1996 had late start of carbon uptake (SCU) by more than 1 month from the average (Fig. 3a) and as a result had the shortest length of net positive NEP period (Fig. 3c). Both years were the wettest, and had the lowest temperature and PAR during June–August months (Supplementary material Fig. 1). This indicates the indirect effect of high precipitation on incidence PAR through changes in cloudiness at Borden forest site. This is further supported by the observed highest NEP in year 2007, although this year had the lowest GPP and respiration (Supplementary material Fig. 1). The year 2007 had the highest June–August PAR value among the studied years (Supplementary material Fig. 1) and as a result the highest NEP to GPP ratio during the summer period although both GPP and respiration were the lowest.

3.2. Phenology control on net ecosystem productivity

At Harvard forest, SOS in average is $124 (\pm 14)$ DOY, EOS is $309 (\pm 10)$, and the resulting length of growing season of $185 (\pm 17)$ days a year. SCU is in average $138 (\pm 10)$ DOY, ECU $283 (\pm 8)$, and the resulting length of net positive carbon uptake period of $145 (\pm 14)$ days a year. Our result for SOS is in good agreement with all-embraced 9-species spring bud break ($R^2 = 0.62$, $p=0.01$) for 1992–2002 (Gonsamo and D'Odorico, 2014), and also shows similar interannual variability but different long-term trend with Red oak bud break data for the entire study period (Keenan et al., 2014). NEP becomes positive two weeks after the start of growing season and negative about a month before the end of growing season. EOS is delaying by about 7.8 days/decade ($p=0.04$) (Fig. 3b). However, none of the LSP metrics explain the changes in NEP (Fig. 4). All of CUP show statistically significant trends, decrease of SCU by 7.5 days/decade ($p=0.04$), delay of ECU by 8.8 days/decade ($p=0.003$), and length of carbon uptake period is extending by about 16.3 days/decade ($p=0.001$) (Fig. 3). Both the delaying of end of carbon uptake period in autumn and the overall longer carbon uptake period explain the increasing NEP at Harvard forest site ($p < 0.01$) (Fig. 3b and c). A one-day increase in the number of net positive carbon uptake period days between SCU and ECU is associated with a $5.51 \text{ g C m}^{-2} \text{ day}^{-1}$ increase in annual NEP (significantly different from 0 at $p=0.04$).

There are no long-term trends in growing season phenology at Borden forest (Fig. 3). The average LSP dates at Borden forest are almost the same as Harvard forest site with SOS of $122 (\pm 8)$ DOY, EOS $307 (\pm 11)$, and the resulting length of growing season of $185 (\pm 12)$ days a year. SCU occurs on average on $138 (\pm 9)$ DOY, ECU

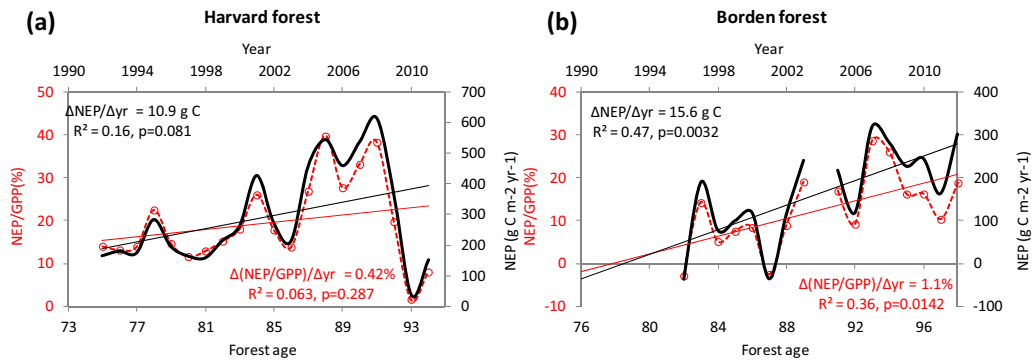


Fig. 2. Annual evolutions of measured net ecosystem productivity (NEP) ($\text{g C m}^{-2} \text{ day}^{-1}$), and NEP to gross primary productivity (GPP) ratio plotted against forest age and calendar year for (a) Harvard forest, and (b) Borden forest. Forest age is calculated as a median value of tree age ranges for each site.

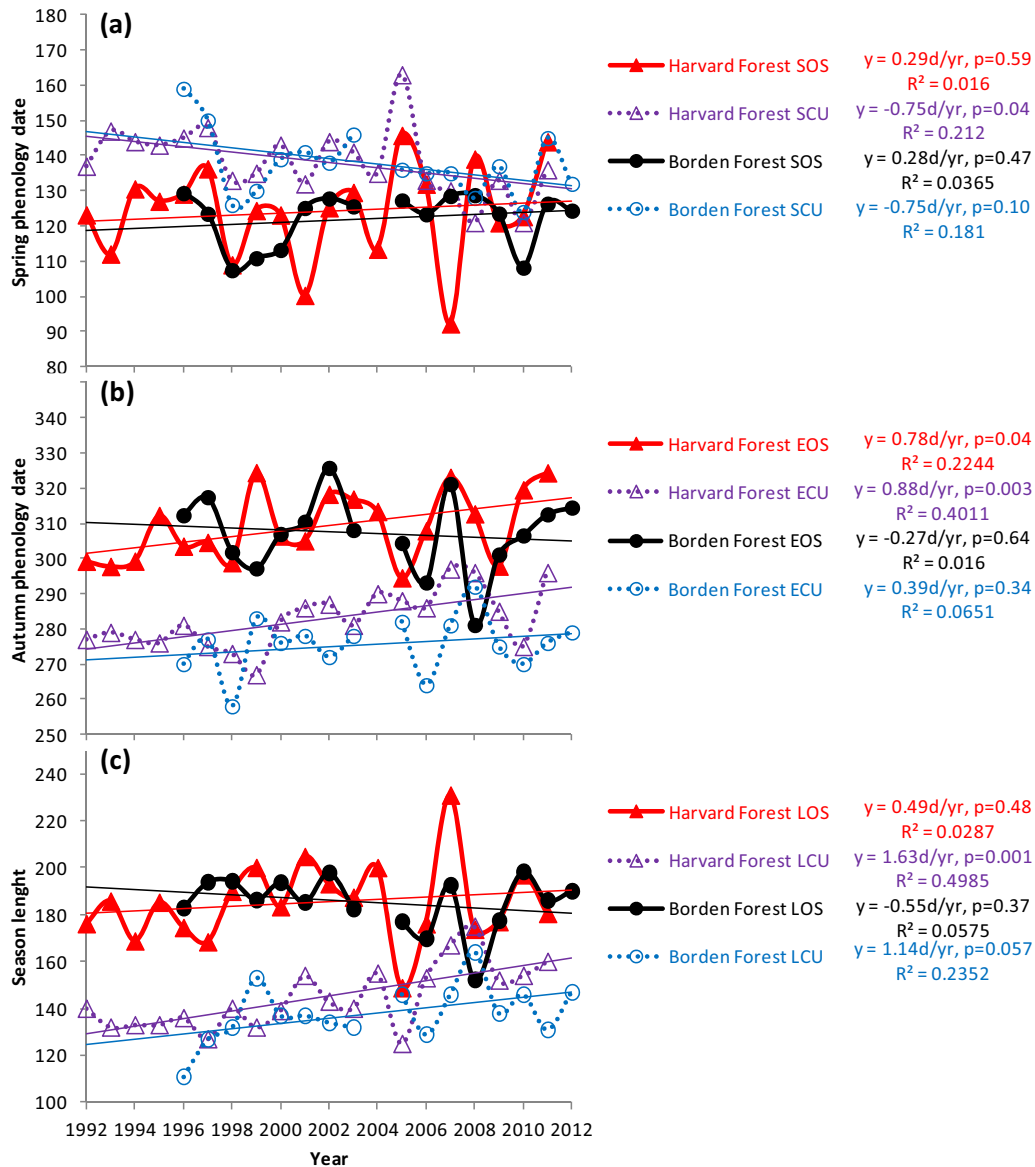


Fig. 3. The interannual evolution of (a) spring phenology dates: start of growing season (SOS) and start of carbon uptake (SCU), (b) autumn phenology dates: end of growing season (EOS) and end of carbon uptake (ECU), and (c) season length: length of season (LOS) and length of carbon uptake (LCU) at Harvard and Borden forest sites.

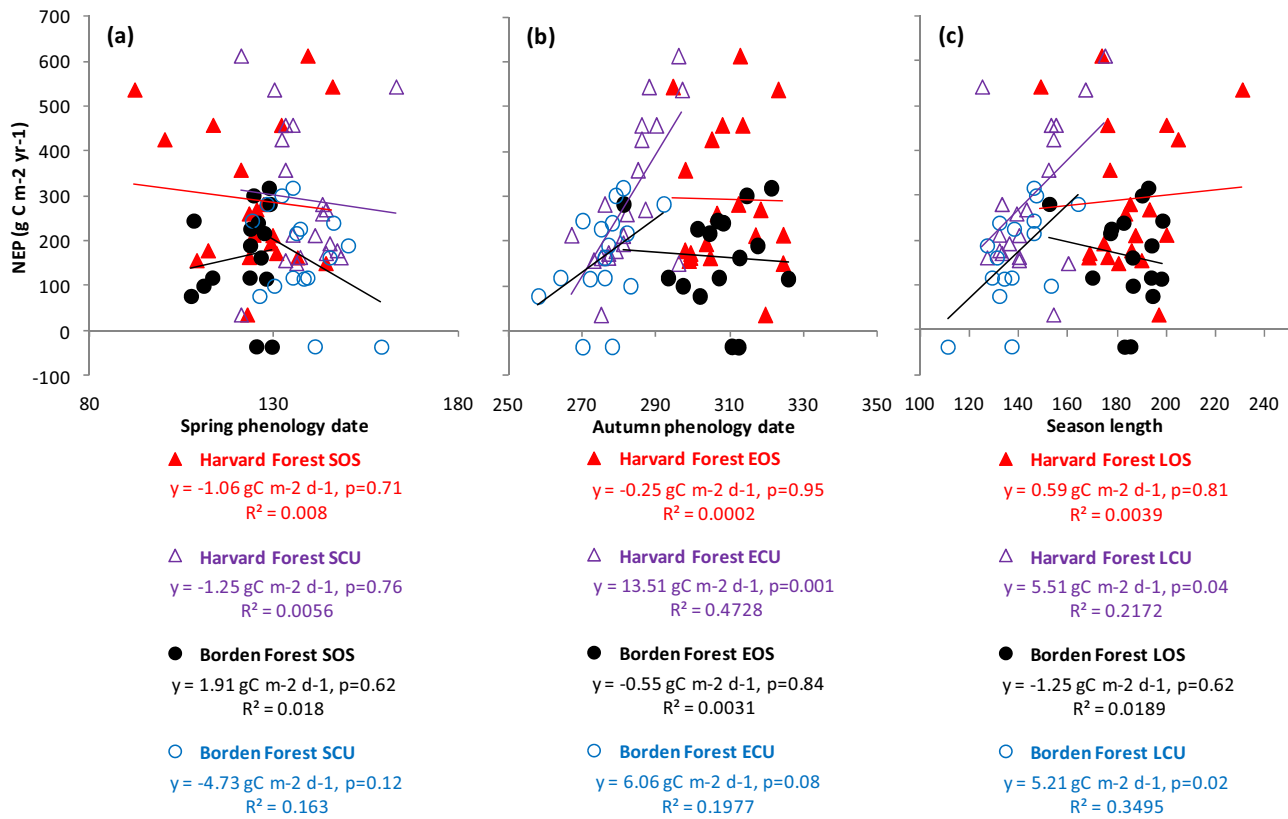


Fig. 4. Relationships of net ecosystem productivity (NEP) with (a) spring phenology dates: start of growing season (SOS) and start of carbon uptake (SCU), (b) autumn phenology dates: end of growing season (EOS) and end of carbon uptake (ECU), and (c) season length: length of season (LOS) and length of carbon uptake (LCU) at Harvard and Borden forest sites.

on 276 (± 8) DOY, and the resulting length of net positive carbon uptake period of 138 (± 12) days a year. SCU at Borden occurs on average the same time as Harvard but ECU and length of CUP is 1 week earlier and shorter, respectively. NEP becomes positive two weeks after the start of growing season and negative about a month before the end of growing season. Both LSP and CUP dates are more or less similar between the two sites although Borden forest is 2 degrees north of Harvard forest site. None of the LSP metrics explain the changes in NEP at Borden forest (Fig. 4). The length of carbon uptake period is extending by about 11.4 days/decade ($p = 0.057$) (Fig. 3c). The delaying of end of autumn carbon uptake period and the overall longer carbon uptake period explain the increasing NEP at Borden forest site ($p < 0.05$) (Fig. 4b and c). A one-day increase in the number of net positive carbon uptake days between SCU and ECU is associated with a $5.21 \text{ gC m}^{-2} \text{ day}^{-1}$ (significantly different from 0 at $p = 0.02$) increase in annual NEP (Fig. 4c).

(Churkina et al., 2005) found that the sensitivity of measured NEP to net positive carbon uptake period was $5.8 \pm 0.7 \text{ gC m}^{-2} \text{ day}^{-1}$ and in very close agreement with our measurement-years weighted average from Harvard and Borden forest sites of $5.38 \text{ gC m}^{-2} \text{ day}^{-1}$. There is also strong evidence that at Harvard and Borden forest sites, both gross and net ecosystem productivity phenology dates (i.e., LSP and CUP) are getting closer to each other through years (Fig. 3) indicating the diminishing spring and autumn LSP and CUP lags (Piao et al., 2008; Wu et al., 2013a,b, 2012a,b). Both at Borden and Harvard forest sites, CUP dates particularly in autumn explain the most changes in NEP compared to any LSP metrics (Fig. 4). Our results are in contrast with the vast majority of literature on phenology control of NEP in mid-latitude forests, which imply spring and LSP have strong influence on interannual and long-term trend of NEP (e.g., Jeong et al., 2012; Richardson et al., 2009). Our results however show

that, CUP particularly in autumn explains the most changes in NEP compared to all LSP metrics (Fig. 4), consistent with the recently increasing understanding of the importance of autumn and CUP (Piao et al., 2008; Wu et al., 2013a,b, 2012a,b).

3.3. Annual and seasonal climate control on net ecosystem productivity

We chose both the down-welling photosynthetically active radiation (PAR) and air temperature to analyse the interannual and seasonal changes in Harvard and Borden forest NEPs (Fig. 5). Both PAR and temperature were proven to be the major climatic controls on GPP and NEP at these sites much more than precipitation (Alton et al., 2007; Teklemariam et al., 2009; Wu et al., 2013b). There is a statistically significant trend in annual PAR (for reasons given below), increasing at both sites ($p < 0.01$). The increasing PAR significantly explains increases in NEP at Borden forest ($p = 0.002$), and also at Harvard forest although the later is not statistically significant ($p = 0.08$). Annual temperature has no significant correlation with NEP at both sites. The annual control of PAR and air temperature on GPP and R is given in Supplementary material Fig. 2.

Fig. 6 demonstrates the seasonal and annual air temperature and PAR relationships with seasonal and annual NEP. The trend of PAR is in better phase with that of NEP than temperature at both forest sites (Fig. 6). PAR alone statistically explains the entire seasonal and annual variations of NEP at Borden forest site (Fig. 6). The spring temperature explains the NEP of April–May, mostly coinciding with the fast leaf expansion period during the start of growing season (Fig. 6). Overall, both seasonally and annually, PAR controls the NEP of Harvard and Borden forests more than air temperature, although they are thought to be temperature controlled mid-latitude

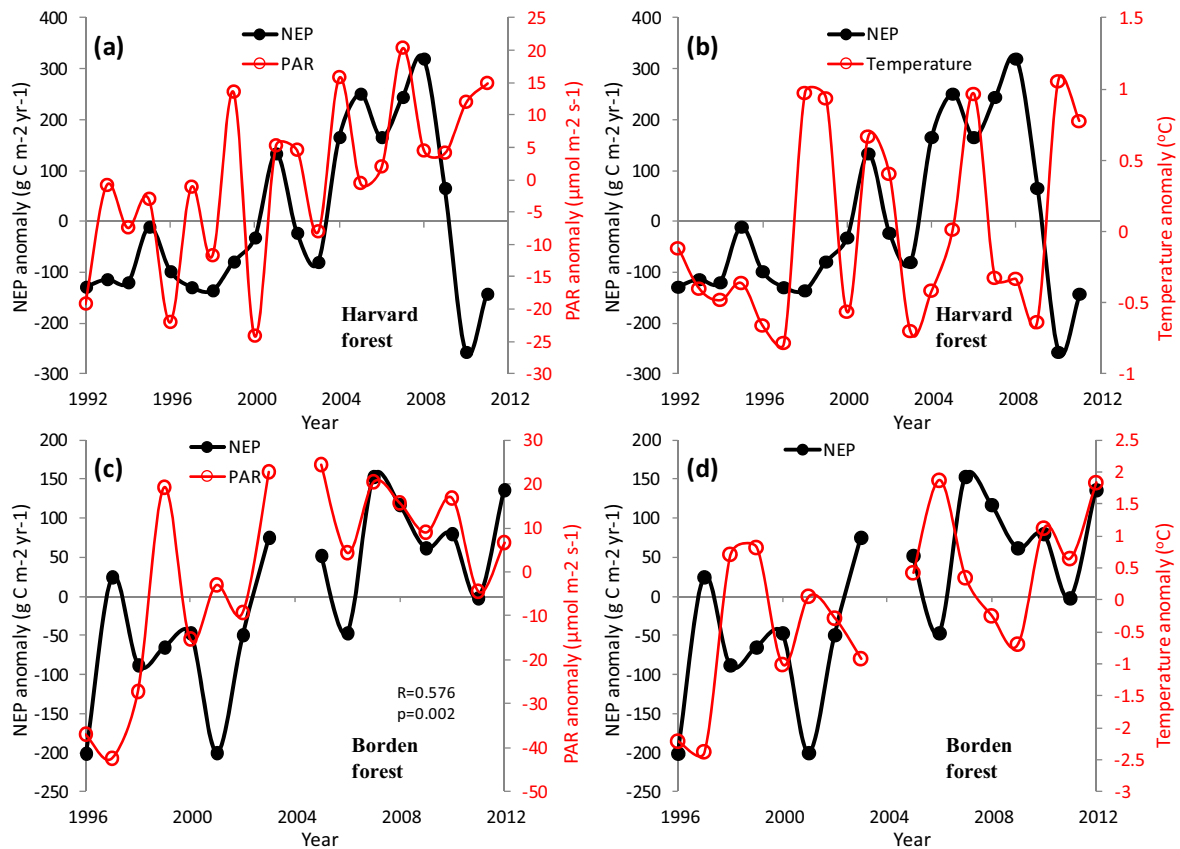


Fig. 5. The annual relationships of net ecosystem productivity (NEP) with photosynthetically active radiation (PAR) and air temperature. a and b are for Harvard forest. c and d are for Borden forest.

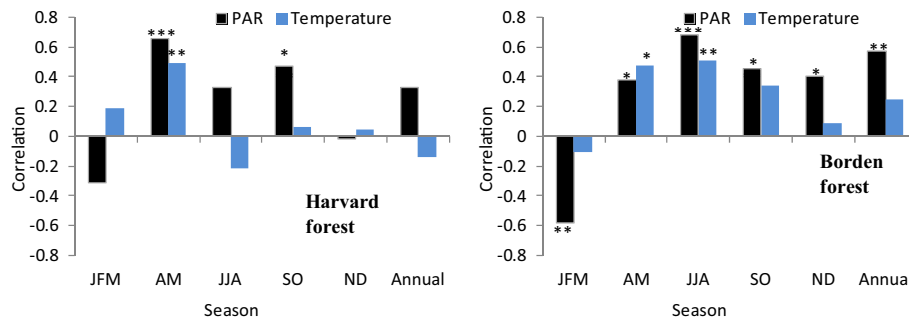


Fig. 6. The seasonal correlations (Pearson correlation coefficient) of net ecosystem productivity (NEP) with photosynthetically active radiation (PAR) and air temperature. Labels on x-axis denote months, e.g., AM denotes spring months of April and May. *p*-Value: *** < 0.001, ** < 0.01, and * < 0.05. Harvard forest (left) and Borden forest (right).

ecosystems. The seasonal control of PAR and air temperature on GPP and R is given in Supplementary material Fig. 3. The discrepancy of PAR controls on annual NEP between Harvard and Borden forests may be explained by Harvard site being more sensitive to higher temperature and lower precipitation (see Section 3.1) during summer months inducing lower NEP to GPP ratio. Year 2010 is typical of those years with the lowest annual NEP (Fig. 2).

We further analyse if the shift in termination of net positive carbon uptake in autumn is due to delayed senescence (EOS) or to overall increased canopy photosynthetic capacity. At both Harvard and Borden sites, there is no relationship between the ends of carbon uptake and end of growing season, meaning leaf phenology does not explain the ECU nor the annual variations in NEP (Fig. 4). Delayed ECU is also explained by increase in September–October GPP ($p < 0.05$). These results indicate that, (1) PAR is contributing the most to the interannual variability and long-term trends in NEP

and ECU, and (2) ECU is delaying due to increased photosynthetic activity but not delayed senescence (Fig. 3c). At both sites, the rate of increase in GPP is much higher than ecosystem respirations. Why ECU is delaying cannot fully be explained by meteorological variables only. These results warrant further analysis by combining soil moisture content, temperature, canopy light regime with global change factors such as CO₂ and N fertilizations, cloud, and aerosol trends in atmosphere to explain the delaying end and the longer net positive carbon uptake period, and the increasing NEP in this region.

Prior to 2002, however, only few years of NEP interannual variability were explained by the PAR, ECU and LCU. Beginning in 2002 and continuing through 2009 at Harvard and 2012 at Borden forest sites, PAR, ECU and LCU begin to explain the interannual NEP variability. These years, when PAR control on NEP become strong, coincides with the steepest decline in atmospheric SO₂, SO₄, NH₄,

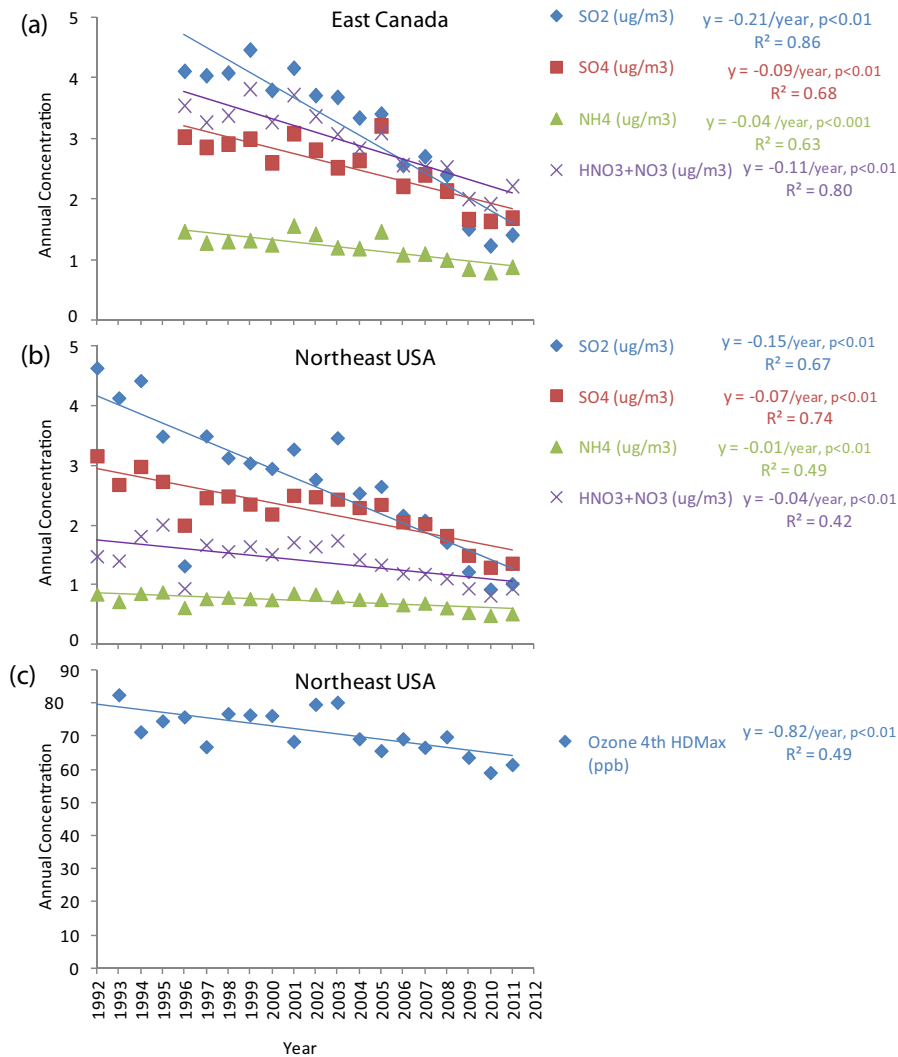


Fig. 7. Annual evolution of measured gaseous SO₂, particulate SO₄, particulate NH₄, total nitrate (HNO₃ + NO₃) and 4th highest daily maximum (HDMMax) ozone value for east Canada and northeast USA obtained from United States Environmental Protection Agency CASTNET database. The east Canada data is from Egbert, ON site. The northeast USA data are from: Abington, CT; Ashland, ME; Connecticut Hill, NY; Howland, ME; and Woodstock, NH sites.

HNO₃, NO₃, and ozone both in northeast USA and eastern Canada (Fig. 7).

4. Implications for global change

It is well established that plants can acclimate and adapt to global change to optimize their functioning. Over 30% of the global forest area is unmanaged primary forest containing the remaining mature forests (FAO, 2006). These mature forests are not only a C sink, but their sink is much bigger than previously thought and increasing at higher rate in recent years (Luyssaert et al., 2008; Pan et al., 2011).

Following the ecosystem development theory of (Odum, 1969), the widely held view in ecology has been that C flows in “old growth” forests should be in equilibrium. Young forests are usually net C source, the C sink peaks at intermediate age, and when the forests mature the C uptake slows and eventually reaches a steady state or declines over time at “old growth” stage. Although the eastern North America mature forests are not yet at the “old growth” stage as they are recovering from disturbances since the beginning of 20th century, the recent large decadal and interannual variability of C uptake and increase in C sink may more likely be influenced

by recent environmental changes. The view of “old growth” forests as having a steady C balance condition or equilibrium flow of C and therefore unimportant as sinks has also been challenged with reports describing continued C accumulation. Recent findings suggest “old growth” forests, which have not been accounted for when allocating the residual C sink of atmospheric CO₂ concentrations, provide up to 10% of the global net ecosystem productivity (Carey et al., 2001; Luyssaert et al., 2008).

Although neither Harvard nor Borden forest is “old growth”, their minimum tree age since the last major disturbance is 80 years, and the C sink of both forests are expected at least to stay in steady condition or decline. The obvious and favoured theories about the increasing C sinks of world’s mature forests such as increased productivity due to atmospheric CO₂ and N fertilizations, higher temperature and longer growing season do not explain the entire interannual and long-term trends in C budget. Incident solar radiation has changed in the last 50 years, as an initial dimming trend from 1960 to approximately 1990 was followed by an ongoing brightening period (Oliveira et al., 2011). PAR is increasing in eastern North America in recent decades (Gan et al., 2014; Hatzianastassiou et al., 2005; Pinker et al., 2005), due to substantial reductions in emissions of sulfur oxides (SO_x), nitrogen oxides

(NO_x), total column aerosol optical depth (AOD), surface total particulate matter less than 2.5 μm diameter (PM_{2.5}) and cloud cover (Gan et al., 2014).

Fig. 7 shows the significant ($p < 0.01$) declines of SO₂, SO₄, NH₄, total nitrate (HNO₃ + NO₃) and ozone while the gaseous SO₂ declining the fastest since 1992 across eastern North America. The significant decreases in gases, AOD and PM_{2.5} post-1990 imply the occurrence of direct aerosol mediated “brightening” and therefore increased PAR upon forest canopies. The changing atmospheric chemistry alters the stomatal responsiveness to elevated CO₂. Increased tropospheric ozone is known to damage plants, leads to stomatal closure and reduced overall plant primary productivity (Sitch et al., 2007). The decreasing ozone concentration in eastern North America reduces the damaging effect of ozone on plants and increases the stomatal opening while the parallel events such as increasing PAR and atmospheric CO₂ enhances the CO₂ uptake by plants, and therefore the net effect is the enhanced CO₂ fertilization of plants. High PAR means the photosynthetic capacity and CO₂ sequestration rate increases in mature forests. This partially explains the increased NEP, and delayed autumn end of net positive carbon uptake period in line with increased PAR obtained in our results. These results thus strengthen the claim that radiation effects on the increased productivity of eastern North America mature forests are not to be overlooked. Understanding the impacts of high PAR on forest C cycle will help to accurately project the vegetated biosphere responses to anticipated global change in the 21st century.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2014.11.007>.

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