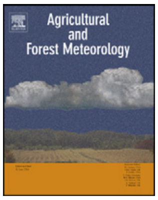
Agricultural and Forest Meteorology 164 (2012) 29–38

Contents lists available at SciVerse ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



Interannual variability of net carbon exchange is related to the lag between the end-dates of net carbon uptake and photosynthesis: Evidence from long records at two contrasting forest stands

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ARTICLE INFO

Article history:
Received 5 December 2011
Received in revised form 2 May 2012
Accepted 4 May 2012

Keywords:
Phenology
Forest
Carbon uptake
Climate change

ABSTRACT

The availability of long-term (15 years) continuous CO_2 eddy-covariance data at both deciduous and evergreen forest sites has allowed decadal analysis of the relationship between annual net ecosystem production (NEP) and the time intervals between gross primary production (GPP) and net carbon uptake (CU) transitions (e.g., start and end dates of GPP and net carbon uptake). No relationships were observed between annual NEP and the interval between the start-dates of GPP (GPP_{start}) and CU (CU_{start}) in spring (hence $CU_{start} - GPP_{start}$ is termed the "spring interval"). Conversely, we found that interannual variability of annual NEP was strongly related to the interval between the end-dates of GPP (GPP_{end}) and CU (CU_{end}) in autumn (hence $GPP_{end} - CU_{end}$ is termed the "autumn interval"). Extended ecosystem respiration occurring in years with late autumns could not alone explain the correlation between NEP and the autumn interval at the deciduous site, but normalization with annual GPP facilitated understanding of decreased NEP during years with longer autumn intervals at both sites. Interpretation of the autumn interval based on site-level meteorological variables showed that autumn temperature (either air temperature or soil temperature) alone cannot be used to interpret autumn interval variations for either site. Autumn global shortwave radiation caused contrasting impacts on the autumn intervals at these two sites. High autumn radiation shortened the autumn interval at the deciduous site (i.e., it increased NEP) but lengthened it at the evergreen site (i.e., it decreased NEP). To our knowledge, this is the first analysis to assess the impacts of the lag between the dates when measurable gross photosynthesis and net carbon uptake occur, and to relate these to annual NEP. Our results suggest that in contrast to previously reported emphasis on spring phenology, autumn phenology may also have a major role in regulating annual NEP, even in northern boreal forest ecosystems where temperature is considered a major limiting factor. Further, it appears that other variables, notably radiation and soil moisture, are critical for determining interannual variability in net carbon exchange.

1. Introduction

Forest ecosystems play a significant role in the global carbon (C) cycle (Pan et al., 2011). Therefore, a better understanding of forest ecosystem responses to climate will aid in the development of ecosystem models used to assess potential impacts of future climate change on forests, including increased drought occurrence (e.g., Zhao and Running, 2010), rising CO_2 concentration (e.g., Norby et al., 2010) and changes in precipitation regimes (e.g., Knapp et al., 2002). One important issue in climate change research is variations in plant phenology, which might be used to interpret the temporal and spatial variability of ecosystem–atmosphere fluxes (Richardson et al., 2010; Wang et al., 2011).

Recent changes in climate have been shown to affect plant phenology, which in turn have affected ecosystem processes (e.g., Richardson et al., 2010; Pan et al., 2011). Effects of recent observed changes in climate on plant phenology have been reported both at local (Dragoni et al., 2011), and continental scales (Wang et al., 2011), indicating an urgent need to evaluate phenological responses to climate variability to improve our understanding of terrestrial ecosystem sensitivity to future climate change (Morisette et al., 2009). In boreal regions, warmer spring

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http://dx.doi.org/10.1016/j.agrformet.2012.05.002

temperatures tend to advance leaf out in spring, and thus contribute to increased annual carbon sequestration (Black et al., 2000; Chen et al., 2006a). However, a lack of consideration of climate change impacts on autumn temperatures may cause misinterpretation of effects on the annual carbon cycle because increased net ecosystem production (NEP) due to warmer springs can be offset by higher respiration in autumn (Piao et al., 2008). While most existing phenological analyses focus on either the growing season length (GSL) or net carbon uptake period (CUP) alone, the impacts of the lags between growing season (GS) and carbon uptake (CU) transitions (i.e., the first and last days of the GS and CU in both spring and autumn) on annual NEP are not well understood. Investigating these lags in the transitions could provide important insights into understanding the causes of interannual variability of NEP (Richardson et al., 2010).

Phenological controls of interannual variability in ecosystem productivity are an active research area among global change scientists, due largely to availability of eddy-covariance (EC) measurements of ecosystem CO_2 fluxes (Richardson et al., 2010; Pan et al., 2011; Wang et al., 2011). However, a key previous restriction to understand interannual variability in NEP has been the limited availability of long-term flux data. In general, time series longer than 10 years are desirable, because carbon cycle analysis over shorter periods is likely to have insufficient representation of interannual variability (Dragoni et al., 2011). With continuous observations occurring at some sites in North America since circa 1993, decadal-scale time-series data are now available for several sites. Here we use 15 years of continuous observations at deciduous broadleaf and evergreen needleleaf stands in the Canadian boreal region where temperatures have increased in recent decades (Black et al., 2000; Stone et al., 2002; Chen et al., 2006a). Furthermore, these data sets also provide an opportunity to evaluate the phenological controls on interannual variability in NEP in contrasting plant functional types (PFT). We present analyses of then phenological intervals (namely the time intervals in days between photosynthesis (i.e., GPP) and net carbon uptake transitions in both spring and autumn) affecting annual NEP at these two sites.

Further analyses were conducted using the autumn temperature, global shortwave radiation, and the ecosystem respiration (R_e), in comparison with the autumn interval between the end-dates of CU and GPP. These analyses tested the potential of relating the autumn interval to climate variables, and may enhance understanding of possible impacts of future climate change on forest carbon sequestration at regional to global scales. Our suggestion is that variations in the time interval between sink-source transition and the cessation of photosynthesis in autumn are a potentially important contributor to interannual variability of NEP in both deciduous and evergreen forest stands.

2. Methods

2.1. Study sites

Two mature forest sites where continuous eddy covariance measurements of CO_2 fluxes had been made for 15 years were selected for this study (Table 1). The Saskatchewan Old Aspen site (SK-OA, 53.63°N, 106.20°W) is a predominantly deciduous broadleaf stand located in Prince Albert National Park, approximately 50 km northwest of Prince Albert, Saskatchewan, Canada (Barr et al., 2007). Meteorological and EC instrumentation were installed in October 1993 for NASA's Boreal Ecosystem–Atmosphere Study (BOREAS) (1993–1996) (e.g., Black et al., 1996) and after BOREAS, measurements continued as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (Black et al., 2000). The stand is composed mainly of trembling aspen (*Populus tremuloides* Michx.). The continuous understory reaches a mean height of 1.5–2.0 m and is composed of beaked hazelnut (*Corylus cornuta* Marsh), wild rose (*Rosa woodsii*), willows (*Salix* spp.), alder (*Alnus crispa*) and a variety of grasses and herbs.

Table 1
Description of the two study sites in this study.

Description	Site	
	SK-OA	MB-OBS
Vegetation type	Deciduous boreal forest	Evergreen boreal forest
Dominant species	Mature aspen with a few balsam poplar, thick hazel understory	Black spruce with occasional larch in poorly drained areas and diverse understory
Stand age (2010)[a]	89	172
Stand density (trees ha^{-1})	980	5450
Canopy height (m)	20.1	9.1
Leaf area index (LAI, m^2 m^{-2})[b]	2.1	4.2
Elevation (m)	601	259
Soil texture	Clay-loam	Clay-silt
Mean annual air temperature (°C)	0.4	−3.2
Mean annual precipitation	467	517

[a] Stand age for these two sites were from Barr et al. (2004) and Dunn et al. (2007).
[b] Data from Chen et al. (2006b).

The second site is an evergreen conifer stand, known as the Manitoba Northern Old Black Spruce site (MB-OBS, 55.88°N, 98.48°W) located in west of Thompson, Manitoba, Canada. Meteorological and EC instrumentation were also installed in 1993 as part of BOREAS (Dunn et al., 2007). The vegetation is composed predominantly of black spruce trees (*Picea Mariana* (Mill.). The groundcover is primarily moss, with feather moss (*Pleurozium schreberi* and *Hylocomium splendens*) occupying the upland areas, and hummocky peat moss (*Sphagnum* spp.) in the bog areas.

2.2. Flux and meteorological measurements

Flux and meteorological data were obtained from Fluxnet-Canada archives (http://www.fluxnet-canada.ca). Data durations for SK-OA and MB-OBS were 1996–2010 and 1994–2008, respectively. Wind velocity components, air temperature, water vapor pressure, and CO_2 concentration were sampled at 20 and 4 Hz for SK-OA and MB-OBS, respectively. CO_2 fluxes were calculated as the half-hourly covariances of the vertical wind velocity component and the CO_2 mole fraction, corrected for air density effects. Net ecosystem exchange (NEE) was obtained by adding the associated rate of change of CO_2 storage in the air column beneath the EC sensors to each half-hourly CO_2 flux. Half-hourly mean values of meteorological variables were also obtained from measurements using sensors mounted on the tower and archived for later analysis (Dunn et al., 2007; Barr et al., 2007).

A standard procedure was used to obtain annual NEP from the half hourly NEE observations (i.e., NEP = −NEE). First, NEE values were removed when values of the friction velocity (u_*) were less than a threshold value (u_{*th}) (u_{*th} was 0.35 m s^{-1} for SK-OA and 0.20 m s^{-1} for MB-OBS). Then NEE was adjusted to account for the lack of energy balance closure (i.e., latent plus sensible heat fluxes being less than net radiation minus the energy storage fluxes) assuming that lack of closure results from EC measurements underestimating the magnitudes of the turbulent fluxes. Next, measured R_e was estimated as R_e = NEE during periods when GPP was known to be zero. Finally, GPP was estimated as −NEE + R_e (daytime) or as zero (nighttime and during periods when both air temperature (T_a) and soil temperature (T_s) were less than 0 °C). Empirical regressions