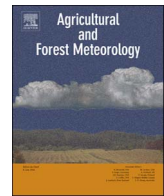




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Review

Inter-annual variability of net and gross ecosystem carbon fluxes: A review

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ABSTRACT

As the lifetime of regional flux networks approach twenty years, there is a growing number of papers that have published long term records (5 years or more) of net carbon fluxes between ecosystems and the atmosphere. Unanswered questions from this body of work are: 1) how variable are carbon fluxes on a year to year basis?; 2) what are the biophysical factors that may cause interannual variability and/or temporal trends in carbon fluxes?; and 3) how does the biophysical control on this carbon flux variability differ by climate and ecological spaces? To address these questions, we surveyed published data from 59 sites that reported on five or more years of continuous measurements, yielding 544 site-years of data.

We found that the standard deviation of the interannual variability in net ecosystem carbon exchange ($162 \text{ gC m}^{-2} \text{ y}^{-1}$) is large relative to its population mean ($-200 \text{ gC m}^{-2} \text{ y}^{-1}$). Broad-leaved evergreen forests and crops experienced the greatest absolute variability in interannual net carbon exchange (greater than $\pm 300 \text{ gC m}^{-2} \text{ y}^{-1}$) and boreal evergreen forests and maritime wetlands were among the least variable (less than $\pm 40 \text{ gC m}^{-2} \text{ y}^{-1}$).

A disproportionate fraction of the yearly variability in net ecosystem exchange was associated with biophysical factors that modulated ecosystem photosynthesis rather than ecosystem respiration. Yet, there was appreciable and statistically significant covariance between ecosystem photosynthesis and respiration. Consequently, biophysical conditions that conspired to increase ecosystem photosynthesis to from one year to the next were associated with an increase in ecosystem respiration, and vice versa; on average, the year to year change in respiration was 40% as large as the year to year change in photosynthesis. The analysis also identified sets of ecosystems that are on the verge of switching from being carbon sinks to carbon sources. These include sites in the Arctic tundra, the evergreen forests in the Pacific northwest and some grasslands, where year to year changes in respiration are outpacing those in photosynthesis.

While a select set of climatic and ecological factors (e.g. light, rainfall, temperature, phenology) played direct and indirect roles on this variability, their impact differed conditionally, as well as by climate and ecological spaces. For example, rainfall had both positive and negative effects. Deficient rainfall caused a physiological decline in photosynthesis in temperate and semi-arid regions. Too much rain, in the humid tropics, limited photosynthesis by limiting light. In peatlands and tundra, excess precipitation limited ecosystem respiration when it raised the water table to the surface. For deciduous forests, warmer temperatures lengthened the growing season, increasing photosynthesis, but this effect also increased soil respiration.

Finally, statistical analysis was performed to evaluate the detection limit of trends; we computed the confidence intervals of trends in multi-year carbon fluxes that need to be resolved to conclude whether the differences are to be attributed to randomness or biophysical forcings. Future studies and reports on interannual variations need to consider the role of the duration of the time series on random errors when quantifying potential trends and extreme events.

1. Introduction

Scientists have been making direct, quasi-continuous and long term eddy covariance measurements of net and gross carbon exchange between ecosystems and the atmosphere at solitary sites since the early

1990s (Black et al., 1996; Greco and Baldocchi, 1996; Saigusa et al., 2005a; Valentini et al., 1996; Wofsy et al., 1993). This set of early studies was influential because it gave the community confidence that eddy covariance measurements could be made on a quasi-continuous basis to produce annual budgets of carbon and water fluxes between

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ecosystems and the atmosphere. Starting in the late 1990s, a set of regional and global networks of eddy covariance flux measurements stations were formed, with the launching of the Euroflux, AmeriFlux, AsiaFlux and FLUXNET networks (Aubinet et al., 2000; Baldocchi et al., 2001; Yamamoto et al., 2005). Today, the sustained operation of many of these networks is providing us with many time series exceeding a decade in length, and some that are approaching twenty years in duration.

One of the overarching goals and aspirations of the flux networks was to collect time series long enough to assess the biophysical factors that may cause interannual variability and/or detect temporal trends in carbon fluxes. Until recently, too few of the time series from published eddy covariance study sites have been long enough to separate natural variability and emerging trends from sampling and measurement errors, as these sampling errors sum to the order of $20\text{--}50\text{ gC m}^{-2}\text{ y}^{-1}$ (Elbers et al., 2011; Hollinger et al., 2004; Richardson et al., 2007).

There are many possible climatic, physiological and ecological reasons why ecosystem-atmosphere carbon fluxes may experience different degrees of interannual variability. To find the best and most pertinent explanations for carbon flux variability, it is important to examine the modulation of the gross flux components that are combined to form the net carbon flux. From first principles, we know that net ecosystem carbon exchange of an ecosystem (N_E) consists of three constituent fluxes—gross photosynthesis (assimilation), autotrophic (plant) respiration (R_a) and heterotrophic (microbial) (R_h) respiration.

Gross photosynthesis (G) of an ecosystem is sensitive to a different set of anomalous weather and climate variability than ecosystem respiration (Frank et al., 2015). Weather and climatic based explanations for year to year changes in carbon assimilation start with variability in clouds and precipitation and their impact on such primary drivers of assimilation, such as light, temperature, humidity deficits and soil moisture (Law et al., 2002; van Dijk et al., 2005; Yi et al., 2010). The combination of clouds, rain/drought, sunlight, and humidity can interact to either promote or retard photosynthesis. Wetter years will be associated with less sunlight, which may reduce photosynthesis, compared to a baseline (Zeri et al., 2014). And, drier years will be associated with more sunlight, which may increase photosynthesis up to a point; greater deficits in humidity and soil moisture will cause stomatal closure and reduce photosynthesis (Reichstein et al., 2007; Wolf et al., 2016). Photosynthesis responds to changes in temperature in a non-linear, quadratic fashion that is highly plastic (Baldocchi et al., 2001; Way and Yamori, 2014); some warming increases photosynthesis, too much warming is deleterious and the optimal temperature are known to acclimate with mean growing season temperature. Temperature can also influence ecosystem photosynthesis through phenology (Baldocchi et al., 2005; Richardson et al., 2010); the timing of phenological events is generally associated with temperature sums (Kramer et al., 2000). Timing of leaf out affects the length of the growing season, which in turn, can modulate seasonally-integrated photosynthesis (Gu et al., 2003). Plant and soil respiration, on the other hand, tends to: 1) increase exponentially with temperature, given sufficient soil moisture (Atkin et al., 2005; Xu and Qi, 2001); 2) decline if soils are too dry or wet and 3) scale with carbon inputs into the rhizosphere from plant photosynthesis (Baldocchi, 2008).

In some regions, seasonal variations in climatic drivers, rather than variations in mean annual climate conditions, may be more important modulators in yearly summed carbon fluxes. For example, in cold regions the presence or absence of snow can have major impact on the amount of soil respiration during the winter (Monson et al., 2006a). In Mediterranean climate, the amount of rain during the spring growing season is more important than annual precipitation (Allard et al., 2008; Ma et al., 2007; Thomas et al., 2009); excess winter rain may run off and not contribute to the amount of water stored in the rhizosphere.

There can also be a disproportionate effect of ‘hot moments’ on the annual sums of net carbon fluxes. An analysis, using seven years of data from eight forested AmeriFlux sites, discovered that year to year

differences in annual carbon fluxes were best described by the number of hours that short term fluxes exceeded a specified percentile (Zscheischler et al., 2016).

Year to year changes in the structural and functional traits of an ecosystem can also explain a significant portion of interannual variability in net and gross carbon fluxes (Richardson et al., 2007; van Dijk et al., 2005). For example, variations in leaf area index affect light capture and the surface area of the sources and sinks. With regards to functional traits, changes in the nitrogen supply will alter photosynthetic capacity and seasonally integrated photosynthesis (Reichstein et al., 2014). Changes in basal rates in soil and root respiration can occur through differences in leaf litter fall (Granier et al., 2008) and photosynthetic activity (Tang et al., 2005).

In the case of agriculture, management practices and cropping choices can be important factors that modulate gross and net carbon fluxes (Baker and Griffis, 2009; Dold et al., 2017; Knox et al., 2016; Suyker and Verma, 2010); the alternating choice of a C_4 (maize) vs C_3 (soybean) crop or decisions to irrigate or whether or not to till the soils affects annually integrated carbon fluxes on a year to year basis. For natural ecosystems, disturbance by fire, logging, insects and disease are other exogenous factors that can introduce year to year variations in net and gross carbon fluxes (Amiro et al., 2010; Clark et al., 2010; Dore et al., 2012; Frank et al., 2014).

Long term carbon flux measurements are needed to capture the rare extreme events that may have a detrimental or beneficial impact on an ecosystem (Frank et al., 2015). To capture information on the occurrence of rare droughts or variability in rain associated with *El Nino* and *La Nina* one may need 7 years of data, or more (Chen et al., 2009b; Wharton and Falk, 2016). Time since disturbance can also cause long term fluxes to differ on a year by year basis, as the greening of the landscape will cause photosynthesis to outpace respiration after x number of years (Amiro et al., 2010; Odum, 1969). Legacy effects can modulate year to year carbon fluxes, especially in wetlands and grasslands. For example, years with excessive vegetation will produce plenty of dead standing mass which will compete with live vegetation the next year for photons (Ma et al., 2016; Rocha et al., 2008). There also may be legacy effects following the return to normal conditions after an excessive drought if there is much plant, stem, shoot or root mortality.

Superimposed on the decadal record are trends in carbon dioxide and temperature, as the Earth experiences global change (Keenan et al., 2013; Schimel et al., 2015). Before we can detect whether or not there are emerging trends in net ecosystem fluxes based on these chronic forcings we must understand the sources of natural variability and whether or not measurement uncertainty is greater or less than certain figures of merit. Finally, the duration of the time series must exceed a certain time threshold to be able to reduce measurement and sampling errors to an acceptable level and to be able to separate measurement and sampling errors from climatic and ecological sources of variation (Keenan et al., 2012).

Today, we are reaching a milestone where a large and diverse number of eddy covariance studies have been operating for more than a decade; more than 250 sites have been operating for 10 or more years (Chu et al., 2017; Pastorello et al., 2016). Subsequently, a growing and critical number of studies have been published in the peer review literature documenting the results from these long-term flux observations. Hence, we are at a juncture when this literature merits distillation and review. This review is intended to provide guidelines for future synthesis studies on interannual variability that are expected to be generated by the newest version of the FLUXNET database (Pastorello et al., 2016).

To perform this review, we harvested information from the suite of published carbon flux studies that report on long term measurements; they ranged between 5 and 18 years in duration. We divided the review into three sections. Part one is a panoramic view of interannual variability, which was conducted by examining the compiled dataset as an ensemble. Here we address the following questions: how variable is net

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