

Lecture 6, ESPM 228

**'Breathing' of the Terrestrial Biosphere:
Lessons Learned from a Global Network of Carbon Dioxide Flux Measurement
Systems**

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Abstract

Published eddy covariance measurements of carbon dioxide (CO_2) exchange between vegetation and the atmosphere from a global network are distilled, synthesized and reviewed according to time scale, climate and plant functional types, disturbance and land use. Other topics discussed include history of the network, errors and issues associated with the eddy covariance method, and a synopsis how these data are being used by ecosystem and climate modelers and the remote sensing community.

Spatial and temporal differences in net annual exchange, F_N , result from imbalances in canopy photosynthesis (F_A) and ecosystem respiration (F_R), which scale closely with one another on annual time scales. Key findings reported include: (1) ecosystems with the greatest net carbon uptake have the longest growing season, not the greatest F_A ; (2) ecosystems losing carbon were recently disturbed; (3) many old-growth forests act as carbon sinks; and (4) year-to-year decreases in F_N are attributed to a suite of stresses that decrease F_A and F_R in tandem. Short-term flux measurements revealed emergent-scale processes including: (1) the enhancement of light use efficiency by diffuse light; (2) dynamic pulses in F_R following rain; and (3) the acclimation F_A and F_R to temperature. They also quantify how F_A and F_R respond to droughts and heat spells.

Introduction

Networks of sensors spread across a region, a continent or the globe have been instrumental in producing many scientific advances in the past century. For example, cosmologists have used an array of radio telescopes to peer deep into the universe and observe the remnants of the primordial explosion. Astrophysicists are employing the Laser Interferometer Gravitational Wave Observatory (LIGO) to study the behavior of gravity waves and they are utilizing data from a global network of detectors buried under mountains or deep in mines to observe neutrinos emitted by the Sun and to warn of exploding supernovae.

Networks of sensors also play a unique and valuable role in environmental sciences. Geophysicists use networks of seismographs and electric potential sensors to map the occurrence and location of earthquakes (Turcotte 1991). And atmospheric scientists study spatio-temporal variations in weather, climate, air chemistry and solar radiation with networks of meteorological instruments (Tsonis *et al.* 2006). The detection of acid rain (Driscoll *et al.* 2001), global dimming of solar radiation (Stanhill and Cohen 2001), evidence for global warming (Easterling *et al.* 2000), the transport of dust and pollution plumes across and from Asia (Ramanathan *et al.* 2001) and trends in carbon dioxide and greenhouse gases (Tans *et al.* 1996) are among the more noteworthy results detected with networks of meteorological instruments.

Over the past decade, scientists studying ecosystem-atmosphere interactions have implemented networks of instrument systems to measure eddy fluxes of carbon dioxide, water and energy (Baldocchi *et al.* 2001a; Running *et al.* 1999; Valentini *et al.* 2000). With this network, information on ecosystem metabolism has been obtained across a

spectrum of biomes and climate zones. And groups of flux towers spread across a landscape, in meso-networks, have evaluated the effects of disturbance, complex terrain, biodiversity, stand age, land use, land management (e.g. irrigation, fertilization, thinning, grazing, cultivation, prescribed burning) and low probability events (e.g. summer droughts/heatspells in temperate and boreal zones, wind-throw, insect/pathogen infestation) on carbon and water fluxes. At the biome, continental and global scales, the network of flux measurement towers, in conjunction with remote sensing information, have enabled investigators to examine spatial scales of coherence that are associated with the coupling of carbon fluxes to persistent weather events (e.g. droughts, rain-spells, snow) or episodes (storms, freeze events).

At individual nodes of the network, the eddy covariance method is used to measure mass and energy exchange across a horizontal plane between vegetation and the free atmosphere. Fluxes of carbon dioxide, water vapor and heat are determined by measuring the covariance between fluctuations in vertical velocity (w) and the mixing ratio of trace gases of interest (c) (Aubinet *et al.* 2000; Baldocchi 2003; Massman and Lee 2002); negative covariance values of net ecosystem CO₂ exchange (F_N) represent a loss of CO₂ from the atmosphere and a gain by the surface. The temporal information being produced at each network node ranges across the scales of seconds, hours, days, weeks, seasons and years. The spatial scales of observations at each tower extends through the flux footprint around the tower (ranging between 100 and 1000 m) (Gockede *et al.* 2004). However, the information produced at each node reaches far beyond its proximate geographical region due to its wider-scale and ecological representativeness (Granier *et al.* 2002; Hargrove and Hoffman 2005).

In this Turner Review article, I distill and synthesize the rapidly growing literature on long-term measurements of net ecosystem CO₂ exchange between vegetation and the atmosphere. To give the reader perspective of this literature's growth, a search of Web of Science produced over 1300 papers associated with the key word 'ecosystem CO₂ exchange'. The earliest citations started around 1990 and over 500 papers have been published since 2005. In order to filter through this large body of literature, I concentrated on papers that evaluated collections of data from a number of sites and I extracted information from a database of published results that I have collated over the past decade (available upon request). In terms of content, the report focuses on gross and net fluxes of carbon at annual time scales, but I report information on seasonal and daily time scales when relevant.

This review is divided into several inter-connected sections. First, I discuss the history and background of the long-term flux networks. Second, I discuss the methodological issues associated with measuring integrated carbon fluxes on daily, annual and inter-annual time scales. Third, I report on how carbon flux measurements vary by time, on seasonal-to-annual and inter-annual time scales and by space according to plant functional type and climate. Fourth, I examine how net ecosystem CO₂ exchange is modulated by its component fluxes, canopy photosynthesis and ecosystem respiration, as they respond to light, temperature, soil moisture, plant functional type and length of growing season. Fifth, I survey results from local networks of towers (mesonets) that measure carbon fluxes along chronosequences or environmental gradient to address issues associated with disturbance (fire, logging, flooding, drainage, wind-throw), land use and management (native forests and plantations, crops, grasslands, cropping

methods), and nitrogen deposition. Finally, I discuss, briefly, how net carbon flux data are being utilized by the remote sensing and modeling communities to validate their estimates of land surface fluxes or are being inverted to derive model parameters.

History

Our current capacity to quantify the ‘breathing of the biosphere’ via measurements of carbon dioxide, water vapor and energy fluxes reflects an evolving process that spans a quarter of a century. The first successful eddy flux measurements of carbon dioxide were performed in the 1980’s over natural and agricultural vegetation for relatively short (weeks to months) campaigns during the growing season (Anderson and Verma 1986; Desjardins *et al.* 1984; Kim and Verma 1990; Leuning *et al.* 1982; Ohtaki 1980; Verma *et al.* 1986). Rapid growth in the use of the eddy covariance method to measure ecosystem carbon dioxide exchange soon followed, based on technical advances in microcomputers and micrometeorological theory (McMillen 1988; Moore 1986; Webb *et al.* 1980) and the development of CO₂ sensors that relied on fast-responding, solid-state infrared detectors (Auble and Meyers 1992).

The earliest, long-term eddy covariance measurements of CO₂ exchange were made on an *ad hoc* basis at a handful of research sites across the globe, starting in the early 1990’s (Black *et al.* 1996; Greco and Baldocchi 1996; Valentini *et al.* 1996; Wofsy *et al.* 1993; Yamamoto *et al.* 1999). In 1995, a group of scientists met at La Thuile, Italy and developed a plan for executing a global and regional sets of networks that would make long-term measurement of carbon dioxide and water vapor (Baldocchi *et al.* 1996). Regional networks in Europe (EuroFlux) (Aubinet *et al.* 2000; Valentini *et al.* 2000) and North America (Ameriflux) were soon operating, though in limited size and scope. And

a global network of collaborating regional networks, FLUXNET, began in 1997 (Baldocchi *et al.* 2001a).

Today, carbon dioxide and water vapor fluxes, and many ancillary meteorological, soil and plant variables, are being measured at over four hundred research sites, spread world-wide. Individual research sites, in this dispersed network, are associated with the AmeriFlux and Fluxnet-Canada (Coursolle *et al.* 2006; Margolis *et al.* 2006) networks in North America, the Large Biosphere Amazon (LBA) project in South America (Keller *et al.* 2004), the EuroFlux and CarboEurope networks in Europe (Ciais *et al.* 2005; Valentini *et al.* 2000), OzFlux in Australasia, China Flux (Yu *et al.* 2006) and AsiaFlux in Asia and AfriFlux in Africa (Fig. 1). There also exists an urban flux network and a regional network across India is in the planning stages (Sundareshwar *et al.* 2007).

The research mission and priorities of the regional and global flux networks have evolved as the network has grown and matured. During the initial stages, the priority of research was to develop value-added products, such as gap-filled data sets of net ecosystem carbon exchange, evaporation, energy exchange and meteorology (Falge *et al.* 2001). The rationales for this undertaking were: (1) to compute daily, monthly and annual sums of net carbon, water and energy exchange; and (2) to produce continuous, gap-filled datasets for the execution and testing of a variety of biogeochemical/biophysical models and satellite-based remote sensing algorithms (Papale and Valentini 2003; Running *et al.* 1999; Thornton *et al.* 2002). The production of gap-filled datasets was also needed to conduct cross-site comparison and synthesis studies (Falge *et al.* 2002a; Law *et al.* 2002).

The research priority during the second stage of flux network operation involved the partitioning of net ecosystem carbon exchange (F_N) into its component fluxes, gross canopy assimilation (F_A) and ecosystem respiration (F_R). The partitioning of F_N into its components was needed to derive mechanistic understanding attributed to temporal and spatial variations in F_N (Falge *et al.* 2002a; Law *et al.* 2002). In addition, this step was required to make the networks a tool for validating estimates of terrestrial carbon exchange derived from the MODIS sensor on the TERRA and AQUA satellites (Heinsch *et al.* 2006; Running *et al.* 1999; Sims *et al.* 2005). This is because algorithms driven by satellite-based remote sensing instruments are unable to assess F_N directly, and instead compute F_A (Running *et al.* 2004). Furthermore, measurements of F_A are needed derive canopy scale-parameters for carbon cycle models (Braswell *et al.* 2005; Owen *et al.* 2007; Reichstein *et al.* 2003; Wang *et al.* 2007).

In the early stage of the flux networks, synthesis papers were biased towards relatively small subsets of coniferous and deciduous forests growing near their maximum productivity stage (Law *et al.* 2002; Valentini *et al.* 2000). This limited scope attracted some criticism by ecologists (Korner 2003; Piovesan and Adams 2000), and counter-arguments by the flux researchers (Jarvis *et al.* 2001). Today, many of the early limitations have been remedied as the global network has expanded exponentially over the most recent 5 years. The global carbon flux network now includes a broader representation of vegetation types, climates and disturbance stages. For example, the current version of the network includes numerous tower sites over tropical and alpine forests, savanna, chaparral, grasslands, wetlands and an assortment of crops. The roles of natural and human induced disturbance have grown in importance, too, since the

network was originally planned. Chronosequence studies, which substitute space for time, have been conducted in a number of regions to examine the effects of disturbance by fire, logging and wind-throw on ecosystem carbon, water and energy exchange (Amiro *et al.* 2006; Amiro *et al.* 2003; Beringer *et al.* 2007; Goulden *et al.* 2006; Knohl *et al.* 2002; Law *et al.* 2003; Litvak *et al.* 2003; Schulze *et al.* 1999; Wirth *et al.* 2002). These new data are allowing the flux measurement community to test the disturbance-recovery theory of Odum (1969).

In the early phases of the global flux network, the data records were too short to study inter-annual variability, but now many long datasets exist. At present, the dataset acquired at Harvard Forest site is over 15 years long (Urbanski *et al.* 2007), the Walker Branch, Tennessee and Takayama, Japan datasets and many Euroflux sites have been operating for a decade and more. With these extended datasets, scientists are starting to ask how climate fluctuations (temperature, precipitation, solar radiation), antecedent conditions (drought, freezes, extreme weather events) and length of growing season affect net carbon exchange and its component fluxes (gross canopy photosynthesis and ecosystem respiration).

Methods: Eddy Flux Measurements

In principle, the eddy covariance method produces a direct measurement of the flux density between vegetation and the atmosphere. But, this ability holds only when the terrain is flat, there is an extended and uniform fetch of vegetation upwind, the atmospheric conditions are steady and the sensors and the data-logging system are able to sense and record the fastest and smallest eddies (Baldocchi 2003; Finnigan *et al.* 2003; Foken and Wichura 1996). Unfortunately, very few natural stands of vegetation meet

these strict standards. Many of the more interesting science questions are associated with ecosystems that are on non-ideal terrain, situated in and among complex landscapes and when they are experiencing varying atmospheric conditions. It is under these non-ideal conditions when the eddy covariance method is vulnerable to large and systematic bias errors (Finnigan *et al.* 2003; Goulden *et al.* 1996a; Moncrieff *et al.* 1996). Over the past few years many efforts have been conducted to evaluate sources of error and their magnitude when fluxes are made under non-ideal conditions. These efforts are discussed further in the following.

Typically, scalar concentration fluctuations are measured with open- or closed-path infrared gas analyzers and three-dimensional sonic anemometers are used to measure wind velocities. Systematic bias errors in hourly-integrated eddy fluxes occur when high frequency fluctuations are filtered or dampened by the sensor's mechanical or electrical design, its placement above the ground or the data acquisition system (Massman 2000; Moore 1986; Suyker and Verma 1993). Standardized data processing routines are generally used to compute flux covariances, so bias errors associated with different sensors configurations and processing of turbulence data are generally minimized and kept small (5 to 10%) (Aubinet *et al.* 2000; Loescher *et al.* 2006; Massman and Lee 2002). Random errors, associated with natural variation in atmospheric turbulence and the underlying vegetation, are generally small (~5%) as the datasets reach a year in duration (Loescher *et al.* 2006; Moncrieff *et al.* 1996; Oren *et al.* 2006; Richardson *et al.* 2006).

Varying atmospheric conditions can produce turbulent fluxes that are not biological. For example, large emission rates in CO₂ are often detected near sunrise

when turbulent mixing re-initiates and respiratory CO₂ stored in the canopy air space is vented to the atmosphere (Aubinet *et al.* 2000; Baldocchi *et al.* 2000; Moncrieff *et al.* 1996). Changes in storage are typically accommodated by measuring temporal changes in the CO₂ concentration profile (Yang *et al.* 1999). Whether or not the storage term is measured or measured well has small influence on measuring daily and annually integrated carbon budgets because they average to zero on daily and annual time scales (Greco and Baldocchi 1996; Yang *et al.* 1999).

In patchy landscapes, the flux measurement system views different types of vegetation from different wind sectors. In this situation, seasonal and annual fluxes need to be interpreted in terms of flux footprint models (Gockede *et al.* 2004; Rebmann *et al.* 2005; Schmid 2002; Soegaard *et al.* 2003).

Advection, due to complex topography or patchy vegetation causes the flux divergence to be non-zero (Finnigan *et al.* 2003; Lee 1998). General corrections for bias errors introduced by advection in complex topography or patchy landscape are not available at present. First order corrections can be made in moderately undulating terrain by rotating the three-dimensional velocity vectors. This procedure makes the mean vertical velocity zero and ensures that fluxes are measured across the mean streamlines (Baldocchi *et al.* 1988; McMillen 1988). An improvement to this approach uses the planar-fit method; it defines the rotation angles on the basis of an ensemble of wind vectors (Finnigan 2004; Lee 1998; Paw U *et al.* 2000). Efforts to measure advection fluxes directly involve implementation of large and complex systems of instrumentation that can only be applied practically in the campaign mode with multiple sets of towers measuring flux divergence or horizontal gradients in fluxes and scalars (Aubinet *et al.*

2003; Feigenwinter *et al.* 2004; Marcolla *et al.* 2005; Sun *et al.* 2007). In practice, corrections based on direct measurement of advection are difficult to implement due the need to resolve small horizontal gradients in CO₂ along the ever-changing wind vector (Feigenwinter *et al.* 2004).

Flux measuring scientists routinely subject their data to a variety of quality control and assurance criteria (Foken and Wichura 1996; Rebmann *et al.* 2005). Doing so, however, introduces many gaps in the data record; gap typically reach 30 to 40% on an annual basis (Falge *et al.* 2001; Moffat *et al.* 2007). Subsequently, gap filling algorithms must be applied to produce continuous data sets, so one can compute daily and yearly flux integrals. The simplest method replaces missing data with information, for the corresponding hour, from the mean diurnal average (Falge *et al.* 2001). Other options include interpolating between missing data points, replacing missing data with estimates derived from non-linear regression models or look-up tables that depend upon climatic drivers like light, temperature and humidity as independent variables (Falge *et al.* 2001; Iwata *et al.* 2005; Ruppert *et al.* 2006; Stauch and Jarvis 2006). Newer and more sophisticated statistical approaches to gap-filling have been implemented in recent years. These new methods include the multiple imputation method (Hui *et al.* 2004), neural networks (Papale and Valentini 2003), genetic algorithms (Ooba *et al.* 2006) and process-based models that are parameterized with existing data (Gove and Hollinger 2006). Inter-comparisons of gap filling methods indicate that the neural network method is among the best, but in general, biases associated with different gap filling methods tend to be small and academic (Falge *et al.* 2001; Moffat *et al.* 2007; Papale *et al.* 2006).

The most severe and controversial gap-filling correction being made is the so-called ‘ u^* correction’ to night-time respiration measurements. This correction is introduced because the atmosphere’s thermal stratification becomes stable at night and the flow near and below the vegetation can become decoupled with that above. In this situation, CO_2 may drain out of the control volume under investigation and not be measured by the eddy covariance system (Aubinet *et al.* 2005; Sun *et al.* 2007). Numerous teams have shown that the bias error increases as turbulent mixing, measured by friction velocity (u^*), decreases below a threshold (Aubinet *et al.* 2000; Barford *et al.* 2001; Carrara *et al.* 2003; Goulden *et al.* 1996a; Gu *et al.* 2005; Saleska *et al.* 2003; Wohlfahrt *et al.* 2005). The threshold, above which nocturnal CO_2 fluxes are insensitive to mixing, ranges between 0.1 and 0.5 m s^{-1} , depending on topography and canopy height (Aubinet *et al.* 2000; Loescher *et al.* 2006). Subsequently, correction factors are developed that re-scale nighttime respiration fluxes to the windy, well-mixed condition and are normalized by temperature, soil moisture and growth stage.

One alternative to the u^* correction involves extrapolating of the daytime CO_2 flux-light response curve to zero (Falge *et al.* 2002a; Gilmanov *et al.* 2003; Hollinger *et al.* 1998; Lee *et al.* 1999; Suyker and Verma 2001; Xu and Baldocchi 2004). At the daily time scale, there is a strong correlation between the two methods, but respiration rates, based on the extrapolation of light response curve, tend to underestimate (by 78 to 94%) respiration values corrected for u^* . A second alternative assumes that the rate of nocturnal respiration equals the maximum sum of the turbulent and storage fluxes observed over the night (Van Gorsel *et al.* 2007). This maximum respiratory efflux is noted to occur early in the evening before advection is established, so potential biases can

be avoided. It is noteworthy, that this latest approach produces respiration rates that match independent estimates based on upscaling soil and leaf respiration measurements well.

Energy balance closure is another metric used to assess the data quality of eddy covariance measurements and to diagnose problems (Oncley *et al.* 2007; Twine *et al.* 2000; Wilson *et al.* 2002). There is some controversy about how well one can close the surface energy balance using latent and sensible heat flux densities measured with the eddy covariance method. Several assessments of energy balance, across many sites, find that that energy balance closure is underestimated by 10 to 30% when the eddy covariance method is used (Li *et al.* 2005; Oncley *et al.* 2007; Twine *et al.* 2000; Wilson *et al.* 2002). On the other hand, a cohort of investigators, at individual sites, attain and report reasonable levels of energy balance closure (within 10%) when net radiation, soil heat flux, bole/canopy heat storage and photosynthetic energy conversion are measured properly and appropriate spectral corrections are applied to the eddy flux measurements (Gu *et al.* 2007; Heusinkveld *et al.* 2004; Meyers and Hollinger 2004). Furthermore, it is important to note that lack of energy balance closure may not necessarily indicate poor CO₂ flux measurements. There are many unresolved issues relating to: (1) differential attenuation of water vapor over time when sampling air through a tube; (2) differences in footprints sensed by the energy sensors and the eddy flux instruments and (3) spatial and statistical sampling of net radiation, soil heat flux and storage. Consequently, this author acknowledges the value of testing for energy balance closure, as a standard diagnostic tool, but he does not recommend correcting eddy flux measurements of CO₂ for the

fractional imbalance of the energy balance closure, as has been done in some instances (Barr *et al.* 2006).

A key question associated with data evaluated in this review is: how accurate are the annual sums? Annual errors in F_N typically range between 30 and 100 gC m⁻² y⁻¹, with larger and smaller values having been reported (Anthoni *et al.* 2004a; Goulden *et al.* 1996a; Hagen *et al.* 2006; Hollinger and Richardson 2005; Loescher *et al.* 2006; Moncrieff *et al.* 1996; Oren *et al.* 2006; Rannik *et al.* 2006). Correcting F_N for insufficient nighttime mixing typically adds an additional respiratory flux on the order of 30 to 50 gC m⁻² y⁻¹, and thereby reduces F_N . The magnitude of this correction depends on the choice of the cut-off value for u^* , how tall the vegetation is and local topography (Anthoni *et al.* 2004a; Aubinet *et al.* 2000; Barr *et al.* 2002; Loescher *et al.* 2006; Papale *et al.* 2006; Saleska *et al.* 2003; Xu and Baldocchi 2004).

For visual perspective of these annual carbon budget errors, consider a piece of computer printer paper, expanded in size to one meter, square. It weighs 76 g. So in essence, the annual error in eddy flux measurements of carbon exchange is often less than the mass associated with a single piece of paper laid on the ground.

Observations

Seasonal Patterns

Seasonal patterns in F_N can be used to distill the relative and time-sensitive controls of leaf area index, plant functional type, solar radiation, temperature, phenology, extreme weather events, photosynthetic capacity, soil carbon pools and soil water deficits on F_N and its components, F_A and F_R (Falge *et al.* 2002b). General patterns of seasonal variations in F_N for a cross-section of plant functional types are illustrated Fig. 2 and are

discussed next. Specific features associated with seasonality in ecosystem carbon fluxes are tabulated in Table 1 (with relevant citations) for a wider group of plant functional types.

In temperate ecosystems, seasonal trend in CO₂ exchange (F_N) follows the seasonal cycle of the sun, with qualifications. In temperate coniferous forests, seasonal patterns of F_A and F_R are in phase, causing F_N to peak (most negative values, indicating uptake) when F_A and F_R do. In cold regions, temperate conifer forests lose carbon in the winter and gain it during the frost-free, growing season. And in milder regions, like the Pacific Northwest, southwest France and the southeastern part of the United States, temperate conifer forests can be net carbon sinks year-round. In contrast, F_R is delayed compared to F_A in temperate deciduous and boreal coniferous forests. This lag is attributed to cold spring-time soils, which restrict F_R and enable F_N to be most negative then. Arid and semi-arid systems, like Mediterranean and tropical savannas and annual grasslands, are water-limited. Consequently, the most negative rates of net carbon exchange occur during the wet winter and spring in Mediterranean-type climates and during the summer wet period for tropical savannas. Tropical forests (not shown) experience little seasonality in F_N , but greatest rates of carbon uptake occur during the wettest season because they experience lower rates of net carbon uptake during the dry season. Boreal forests and Arctic tundra ecosystems are temperature and light-limited, so their seasonal cycles is moderated by the length of the snow-free season. These ecosystems can flip from being a carbon sink to a source during the growing season when a reduction in photosynthesis occurs due to clouds, a rise in the water table or drought. Boreal and Arctic ecosystems continually lose carbon, at low rates, during the cold frozen

winter, which on a cumulative basis is significant fraction of annual carbon exchange. Perennial grasslands, growing in temperate climates, experience summer rainfall, so their annual cycle of carbon exchange is moderated by the freeze-free period of the year, changes in leaf area index and vapor pressure deficits. Greatest rates of carbon uptake occur for C_4 grasslands, C_3 and mixed C_3/C_4 grasslands, during the summer growing season. Agricultural crops achieve the highest short-term rates of carbon uptake. But, ironically, their net annual uptake is not the greatest. Spring-sown crops, like soybeans and corn, experience a short season of effective net carbon uptake because they must grow from seed and they experience a long period when the canopy is bare or sparse and losing carbon. Fall sown crops, like winter wheat, are small carbon sources or remain close to carbon neutral during the cold winter with low light levels.

Inspection of power spectra of F_N , produced by Fourier transforms of year-long time series, enables one to examine and quantify the critical time scales that are associated with carbon flux variance (Baldocchi *et al.* 2001b; Katul *et al.* 2001; Richardson *et al.* 2007; Stoy *et al.* 2005). Fig. 3 shows a conceptual power spectrum for CO_2 exchange with data from a deciduous forest. The most spectral power is associated with diurnal and seasonal time scales. Some spectral power is associated with the passage of weather fronts, on 3 to 7 days, and there is a well-defined spectral gap at the monthly time scale.

Annual Sums

The compiled database of published carbon dioxide flux measurements, used for this analysis, contains 504 site-years of data from 125 study sites. The probability distribution of these published F_N data has a mean of $-181 \pm 269 \text{ gC m}^{-2} \text{ y}^{-1}$ and it

ranges between -1000 and 1300 gC m⁻² y⁻¹ (Fig. 4). Superimposed on the histogram is a Gaussian probability distribution. Comparing the two probability distributions informs us that the median (-170 gC m⁻² y⁻¹) is smaller than the mean and the distribution is skewed positively (Skewness = 0.545). Ecosystems losing the most carbon (positive sign) have been disturbed recently. Ecosystems gaining the most carbon (negative sign) tend to be evergreen and mid-age forests, having year-round growing seasons and small pools of decomposing detritus on the soil.

For perspective, the mean net ecosystem carbon flux tends to be much greater than regional estimates of land-atmosphere CO₂ exchange derived from some atmospheric inversion models; for example, net atmosphere-biosphere carbon exchange, derived from inversion model studies, for the European continent, range between -19 and -53 gC m⁻² y⁻¹ (Bousquet *et al.* 2000; Gurney *et al.* 2002; Janssens *et al.* 2003).

From first principles carbon fluxes measured with bottom-up methods, like the eddy covariance technique, are not expected to equal those derived from top-down methods, like the atmospheric inversion modeling, which measure net biome exchange (Canadell *et al.* 2000; Schulze *et al.* 2000). For example, tower-based eddy flux measurements over intact stands do not account for carbon lost from regional fires, harvesting and disturbance (Chapin *et al.* 2006; Janssens *et al.* 2003; Schulze *et al.* 2000). In contrast, atmospheric inversion models derive and infer carbon fluxes for large basis regions using a sparse network of atmospheric concentration measurements. And inversion calculations are sensitive to how well wind fields are computed (Gurney *et al.* 2003). Nevertheless, the ‘bottom-up’ and ‘top down’ methods are expected to be in the same ‘ball-park’ and not differ by a factor of ten.

As I write this paper, new data have been published suggesting a convergence between the two different approaches of measuring and assessing land-atmosphere carbon dioxide exchange. Deng et al (2007) performed a global inversion of the carbon dioxide concentration measurement network and examined North American (US and Canada) in higher resolution by dividing it into 30 regions. With their higher resolution model, they report that net carbon fluxes over mid-age productive forest in Ontario/Quebec are on the order of $-117 \pm 77 \text{ gC m}^{-2} \text{ y}^{-1}$. They also reported that net carbon fluxes over much of the eastern United States and Europe ranges between -78 and $-180 \text{ gC m}^{-2} \text{ y}^{-1}$.

The ranking of F_N , at annual time scales, is not explained well by variations in climate variables, plant functional type or photosynthetic potential (Arain and Restrepo-Coupe 2005; Law *et al.* 2002; Reichstein *et al.* 2007b; van Dijk *et al.* 2005). A step-wise, multiple regression analysis revealed that only 45% of the variance in annual F_N , for forests across central and northern Europe, is explained by a combination of sunlight, leaf area index and air temperature (van Dijk *et al.* 2005). More productive ecosystems (those with greater values of F_A), which occur under wetter and warmer climates, do not necessarily produce large values of F_N because F_R scales linearly with available light, moisture and temperature, too (Arain and Restrepo-Coupe 2005; Reichstein *et al.* 2007b; van Dijk *et al.* 2005). This point is illustrated with data in Fig. 5, which shows that variations in F_A explain only 42% of the variation in F_N . Consequently, it is better to partition F_N into its components, F_A and F_R and relate the components to abiotic and biotic drivers, as will be shown below.

There is some controversy about the causes of spatial variability in annual sums of F_N . One ‘school-of-thought’, inferred from a network of forest sites across Europe, reports that spatial variations in F_N are determined by latitudinal variations in F_R because F_A is rather constant (Valentini *et al.* 2000). Other and more recent cross-site analyses show that F_A and F_R are highly correlated with one another (Janssens *et al.* 2001; Law *et al.* 2002) and that the latitudinal dependence on F_N fails when one considers North American sites (Jarvis *et al.* 2001). The analysis of Valentini *et al.* was based on a regional network of temperate European forests, while the later three references were based on a larger and more global assessment that included grasslands and crops and semi-arid forests and woodlands.

F_N is the relatively small difference between two rather large fluxes, F_A and F_R , so it is better to explore the relationship between these latter two variables to gain an understanding of the factors that modulate F_N . Using the large and global database, Fig. 6 shows that F_A and F_R are tightly correlated ($r^2 = 0.89$) with one another, on annual time scales. In general, $77 \text{ gC m}^{-2} \text{ y}^{-1}$ of carbon is lost by ecosystem respiration for every $100 \text{ gC m}^{-2} \text{ y}^{-1}$ gained by gross photosynthesis when an ecosystem has not experienced recent and significant disturbance. The slope between F_A and F_R is very similar to the regression based on data from the European network, for a smaller population of sites and plant functional types (Janssens *et al.* 2001).

Data that deviate from the regression line occur when external factors cause F_A to outpace F_R , or vice versa. For example, ecosystems that have experienced recent disturbance via logging, stand-replacing fire, drainage or wind throw have elevated

ecosystem respiration and large positive values in F_N (Fig. 6) (Amiro *et al.* 2006; Goulden *et al.* 2006; Hirano *et al.* 2007; Humphreys *et al.* 2006; Valentini *et al.* 2000). The ‘disturbance offset’ is attributed to an incremental increase in CO₂ emissions from the soil carbon pool and litter detritus. This respiratory ‘cost’ scales linearly with F_A and ranges between 330 and 1000 gC m⁻² y⁻¹. This magnitude depends, in part, upon whether the bulk carbon remains on site (e.g. windthrow, drainage) or is removed (e.g. logging and fire). After considering the carbon flux offset by disturbance, F_R continues to scale with gross canopy photosynthesis but with a slightly steeper slope (0.94) as one moves across a global gradient of sites ranging from the boreal to temperate and tropical forests. This steeper slope between F_A and F_R for distributed ecosystems reflects the greater photosynthetic efficiency of younger plant stands. It is noteworthy that data from ecosystems with frequent fires, like tropical savanna (Beringer *et al.* 2003; Beringer *et al.* 2007) do not fall on the line with other types of disturbance. In this case, fires are a form of rapid respiration and the fire frequency is too short to build up large carbon pools.

Several systematic analyzes have evaluated which climate drivers best explain variations in annual F_A . One study found that the ratio between actual and potential evaporation, a measure of water deficits, explained 50% of the variance in F_A across sites in southern Europe and temperature explained 83% of the variance in F_A across northern Europe (Reichstein *et al.* 2007b). Another analysis of data from the European network found that leaf area index explained 66% of the variance in F_A and the r^2 valued increased to 0.75 and 0.86 as one added information on available sunlight and temperature, respectively (van Dijk *et al.* 2005).

Temperature is the main driver of annual respiration, F_R , in moist regions with light and leaf area index providing additional explanatory power (Reichstein *et al.* 2007b; van Dijk *et al.* 2005). In semi-arid and tropical regions, soil moisture is a better explanatory variable, but its dependence still relies on temperature (Hutyra *et al.* 2007; Ma *et al.* 2007; Rambal *et al.* 2003; Reichstein *et al.* 2007b; Saleska *et al.* 2003).

One of the stronger determinants of annual net ecosystem exchange, across an ecological gradient, is length of the carbon uptake period. This effect has been demonstrated for a network of temperate deciduous forests, evergreen needle leaf forests and herbaceous vegetation (crops and grasslands) (Baldocchi *et al.* 2001a; Barr *et al.* 2007; Barr *et al.* 2004; Churkina *et al.* 2005; Suni *et al.* 2003). In general, net carbon exchange of deciduous broadleaved forests increases by about 5.57 gC m^{-2} for each additional day of the photosynthetic growing season (Fig. 7). But the result is conditional. A separate regression line (with a slope of $3.7 \text{ gC m}^{-2} \text{ d}^{-1}$) explains F_N for evergreen broadleaved forest (Leuning *et al.* 2005) and deciduous Mediterranean oak-grass savanna (Ma *et al.* 2007); these are semi-arid ecosystems whose growing season length is determined by the period of available soil moisture rather than the length of the frost free period. Corresponding values for the sensitivity of evergreen needle-leaved forests and herbaceous vegetation to length of the photosynthetic period are 3.4 and $7.9 \text{ gC m}^{-2} \text{ d}^{-1}$, respectively (Churkina *et al.* 2005). In addition, it is noteworthy that F_N is weakly related to the canopy duration period, as detected by remote sensing, because it includes periods when leaves are not physiologically functional or senescent (White and Nemani 2003).

Interannual Variation

Long-term flux records enable investigators to quantify how climate fluctuations (temperature, precipitation, solar radiation), antecedent conditions (drought, freezes, extreme weather events, previous site management), length of growing season and time since disturbance affect net carbon exchange and its component fluxes, F_A and F_R . To date, only a few flux studies exceeding five years in duration have been published. The paucity of long-term data stems partly from the fact that the first cohort of FLUXNET field studies did not start until the early to mid-1990s (Baldocchi *et al.* 2001a; Valentini *et al.* 2000). Examples of long term (greater than or equal to 5 years) CO₂ flux studies include reports from deciduous and evergreen boreal forests (Barr *et al.* 2007; Dunn *et al.* 2007; Hollinger *et al.* 2004; Richardson *et al.* 2007; Suni *et al.* 2003), temperate deciduous forests (Barford *et al.* 2001; Carrara *et al.* 2003; Curtis *et al.* 2005; Goulden *et al.* 1996b; Ito *et al.* 2006; Saigusa *et al.* 2005; Stoy *et al.* 2006; Urbanski *et al.* 2007; Wilson and Baldocchi 2001), temperate conifer forests (Grunwald and Bernhoffer 2007), sub-tropical savanna (Beringer *et al.* 2007), Mediterranean woodland (Pereira *et al.* 2007) and herbaceous or shrubland vegetation (Gilmanov *et al.* 2006; Haszpra *et al.* 2005; Ma *et al.* 2007).

Inter-annual variability in net ecosystem CO₂ exchange at a temperate deciduous forest site is attributed to a combination of factors including occurrence of a summer drought, extent of summer cloudiness and absence or presence of winter snow (Goulden *et al.* 1996b; Urbanski *et al.* 2007; Wilson and Baldocchi 2001). A different set of factors explains interannual variability of net ecosystem CO₂ exchange in different biomes and climate spaces. Inter-annual variability of CO₂ exchange for a boreal conifer forest corresponds to variations in water table, air temperature, and summertime solar

radiation (Dunn *et al.* 2007). Meanwhile, inter-annual variability of CO₂ exchange for a boreal and deciduous aspen site is linked to inter-annual differences in leaf area index and summer drought (Barr *et al.* 2007; Kljun *et al.* 2006). Interannual variability of semi-arid ecosystems and those with Mediterranean-type climates depend upon the duration of the wet season (Luo *et al.* 2007; Ma *et al.* 2007; Paw U *et al.* 2004; Pereira *et al.* 2007).

Most recently Richardson *et al.* (2007) used a combination of statistical and ecosystem modeling to evaluate the sources of variation on a 9 year carbon flux record for a conifer forest growing at the boreal/temperate interface. They reported that 40% of the variance (in interannual fluxes) is attributed to environmental variables (light, rainfall and temperature) and the 55% of the variance is attributed to variations in model parameters for biotic processes like photosynthesis and respiration.

Because a body of flux studies is showing a tight correlation between photosynthesis and respiration (Fig. 6), it can be argued that year-to-year changes in F_N are associated with simultaneous increases or decreases in F_A and F_R , too (Reichstein *et al.* 2007a; Richardson *et al.* 2007). This emerging idea is supported with data in Fig. 8, which shows that year-to-year differences in F_A account for about 60% of the year-to-year variability in F_R . In general, a year-to-year change in F_A of 100 gC m⁻² will produce a 70 gC m⁻² change in F_R , with the residual (30 gC m⁻²) being attributed to F_N . Furthermore, the positive correlation between F_A and F_R was robust whether or not the data were divided into broad functional groups, like broad-leaved and conifer forests, herbaceous vegetation and disturbed ecosystems.

On the other hand, these results do not dismiss the possibility that there can be specific cases when year-to-year changes in F_A and F_R are anti-correlated or are independent of one another. For example, a reduction in F_R and an increase in F_A occurs in tropical forests when they experience seasonal drought (Saleska *et al.* 2003). Nor, can we dismiss multi-year carry over effects that may be instigated by inter-annual changes in litter inputs and nutrient availability by its delayed mineralization. However, we do not detect any multi-year carry over effects with this dataset by phase shifting the dependent (dF_R/dt) and independent (dF_A/dt) variables one year ahead or behind each other.

With data records exceeding a decade, one can start to investigate temporal trends in CO₂ exchange, too. Fig. 9 shows the annual time series of F_N , F_A and F_R for the longest extant data record, Harvard Forest (Urbanski *et al.* 2007). Over the 13 year record, annual F_N has increased in magnitude systematically from about -150 gC m⁻² y⁻¹ during the 1990s to -400 gC m⁻² y⁻¹ in recent years. This trend is in-synch with a temporal increase in leaf area index and occurs because trends in F_A have outpaced trends in F_R , despite the advanced age of the forest (75 to 100 years).

Emergent Processes

The continuous operation of flux stations has enabled scientists to produce new information on a variety of scale-emergent processes. They have also enabled scientists to observe responses in ecosystem metabolism to environmental perturbations that tend to be missed with short-term field campaigns or studies based on soil chambers and stand inventory. Examples of emergent-scale processes detected by the flux networks include:

(1) how F_N and F_A respond to diffuse light, (2) how F_N , F_A and F_R acclimate to temperature and (3) how F_N is partitioned between its vegetative and soil components.

Diffuse Light

For over a decade, investigators having been observing that canopy light use efficiency (the slope of the F_N vs sunlight (R_g) response curve) was sensitive to whether the sky was clear or cloudy (Baldocchi 1997; Hollinger *et al.* 1994; Price and Black 1990). With the advent of the flux networks, investigators were able to study this phenomenon at the continental-scales. The general consensus is that light use efficiency (LUE) nearly doubles when incident sunlight is diffuse as compared to when it is mostly direct (Gu *et al.* 2002; Niyogi *et al.* 2004)—LUE increases from 0.025 to 0.05 $\mu\text{mol m}^{-2} \text{s}^{-1}/(\text{W m}^{-2})$ as the ratio between diffuse and total solar radiation increased from about 0.1 to 0.9. Under cloudy skies, incoming sunlight is more isotropic, so light transmits deeper into the canopy. This process allows more light to reach and illuminate shaded leaves. On sunny days, the photosynthetic rate of upper sunlit leaves tend to be light-saturated. They also experience a higher heat load, which enhances respiration, so it lowers their photosynthesis rates. But the enhancement of F_N and F_A by diffuse light effect is not universal. It was not observed over a peatland, for example (Letts *et al.* 2005).

Ecosystem photosynthesis also responds positively to dust injected into the atmosphere by volcanoes (Gu *et al.* 2003a) and by aerosols generated by the emission of biogenic hydrocarbons (Kulmala *et al.* 2004; Misson *et al.* 2005). Mid-day canopy photosynthesis at Harvard Forest was 23% greater the year after the Mt. Pinatubo volcano

injected fine aerosols into the stratosphere (Gu *et al.* 2003a) and late in the afternoon F_N is increased by 8% when diffuse light is produced by aerosols associated with VOC emissions (Misson *et al.* 2005).

Temperature Acclimation

Plants and microbes acclimate to their thermal environment by adjusting their photosynthetic and respiration rates with temperature (Atkin *et al.* 2005), and so does net ecosystem carbon exchange (Hollinger *et al.* 1994). At the ecosystem scale, the optimal temperature for canopy photosynthesis scales with mean summer temperature (Baldocchi *et al.* 2001a). Specifically optimal temperatures for many sites across Europe were in the 15 to 20 °C range and optimal temperatures for many sites across North America were in the 20 to 30 °C range. One consequence of this regional proclivity is that canopy photosynthesis of North American forests is better able to withstand the deleterious effects of summer heat spells. In contrast, canopy photosynthesis of European forests is more inclined to suffer more during summer heat spells. This phenomenon occurred across Europe in 2003 when mean temperatures exceeded the long term mean by more than 6 °C (Ciais *et al.* 2005; Reichstein *et al.* 2007a).

Ecosystem respiration acclimates and responds to temperature in a subtle but critical way (Jarvis *et al.* 2001). It is widely held that ecosystem respiration increases with temperature, when soil moisture is adequate (Reichstein *et al.* 2005; Reichstein *et al.* 2003). However, data derived from the flux network show that respiration rates of ecosystems in northern latitudes, adapted to cool temperatures (5-10 °C), are similar to respiration rates of ecosystems in more southerly latitudes, that have adapted to warmer temperatures (20 to 30 °C) (Enquist *et al.* 2003).

There remains some debate in the literature regarding the temperature sensitivity of ecosystem respiration and its acclimation with temperature; this sensitivity is defined by Q_{10} , the ratio by which respiration changes with a 10 °C increase in temperature. There is one body of literature that evaluates Q_{10} using flux and temperature measurements from monthly to seasonal durations. In many situations, large values of Q_{10} are produced (exceeding 3 and approaching 10) (Curtis *et al.* 2005; Desai *et al.* 2005; Van Dijk and Dolman 2004). Conversely, another set of studies shows that Q_{10} is conservative and close to the typical value for enzyme kinetics (2 +/- 10%) when Q_{10} is computed for shorter time windows (Flanagan and Johnson 2005; Reichstein *et al.* 2005; Reichstein *et al.* 2002a; Xu and Baldocchi 2004). Instead, it is the reference respiration rate, R_o , that varies seasonally with biological activity (Reichstein *et al.* 2005; Van Dijk and Dolman 2004). Exceedingly large values for Q_{10} are often artifacts introduced by convolving growth and maintenance respiration when it is evaluated on monthly and seasonal time scales (Janssens and Pilegaard 2003). Hence, one should be cautious using such results to interpret how ecosystem respiration may respond to global warming. On the other hand, it is clear that Q_{10} decreases below values of 2.0 with soil water deficits (Reichstein *et al.* 2007b).

Soil/Vegetation Partitioning

In order to examine the differential controls of foliage and soil on net carbon fluxes, a subset of investigators have implemented paired sets of eddy flux instrumentation over the canopy and in the stem space of forests (Baldocchi *et al.* 1997; Constantin *et al.* 1999; Falk *et al.* 2005; Launiainen *et al.* 2005; Law *et al.* 1999; Ma *et al.* 2007). A synthesis study based on measurements from 10 canopies found that

understorey carbon effluxes scaled with canopy F_A and that understorey respiration accounted for 55% of F_R (Misson *et al.* 2007). Other investigators have used over-story eddy covariance and soil chamber measurements in tandem to partition ecosystem respiration into its autotrophic component and to separate gross and net photosynthesis from one another (Griffis *et al.* 2004). For a study over a boreal aspen forest, autotrophic respiration was found to be 61% of ecosystem respiration and net primary productivity was 54% of gross primary productivity (Griffis *et al.* 2004).

Episodic and Transient Events

Episodic and transient events of interest include how F_N and F_R respond to rain pulses and drought and the phenological switch in F_N that is prompted in spring when leaves emerge and photosynthesis commences.

Rain pulses

In arid and semi-arid regions, precipitation often falls as infrequent pulse events (Huxman *et al.* 2004). Wetting rapidly activates microbial activity, based on studies that add water to dry soil in small field plots or in the laboratory (Birch 1958; Orchard and Cook 1983). In accordance with this mechanism, there is a growing number of studies reporting that ecosystem respiration of arid and semi-arid ecosystems increases immediately after rain events, especially when rain occurs during the dry season (Huxman *et al.* 2004; Ivans *et al.* 2006; Jarvis *et al.* 2007; Xu *et al.* 2004). There is also a smaller body of papers showing that pulses in soil respiration occur in wetter temperate climates, too (Jassal *et al.* 2005; Lee *et al.* 2004). In general, the size of the pulse depends on the amount of labile carbon available. For example, the first seasonal rain event tends to produce the greatest respiratory pulse, whether the rain event is large or

small (Huxman *et al.* 2004; Jarvis *et al.* 2007; Xu *et al.* 2004). The extent and duration of the respiration pulses, on the other hand, depends on the amount of rain—large rain events keep the soil and microbes wetter, longer. Often, F_A does not respond favorably to rain pulses in semi-arid regions, despite the fact it is a water-limited ecosystems. Meager rain events do not re-wet the root zone and are unable to benefit photosynthesis of wilted or dead plants. Only large rain events (> than 5 mm) provide enough moisture trigger metabolic activity in desert vegetation (Huxman *et al.* 2004).

Drought

It is well known that soil moisture deficits and extreme temperatures—environmental features that accompany droughts—are deleterious to physiological processes like photosynthesis at the leaf and plant level (Flexas and Medrano 2002; Lawlor and Cornic 2002) and respiration from the soil (Qi and Xu 2001; Reichstein *et al.* 2002a). The behavior of whole ecosystems to drought is less well documented because droughts in humid and temperate climate zones are relatively unpredictable in timing, duration and intensity. To solve this knowledge gap, we either turn to study semi-arid ecosystems that experience seasonal droughts (Pereira *et al.* 2007; Rambal *et al.* 2003; Reichstein *et al.* 2002a; Reichstein *et al.* 2002b; Williams and Albertson 2005; Xu and Baldocchi 2004) or exploit large-scale droughts, like the one that occurred across Europe in 2003 (Ciais *et al.* 2005; Granier *et al.* 2007; Reichstein *et al.* 2007a), North America in 1995 (Baldocchi 1997) or across the boreal zone of western Canada between 2001 and 2003 (Kljun *et al.* 2006).

Among the set of carbon flux studies reporting drought, several general patterns have emerged. First, the magnitude of F_N is negatively affected during drought, but its

reduction is less than that associated with F_A because there tends to be a compensatory reduction in F_R , too (Reichstein *et al.* 2007a). Second, photosynthesis and respiration rates drop abruptly when soil moisture or a water stress index drops below a critical threshold (Granier *et al.* 2007). Third, reductions in evaporation co-occur with reductions in F_N (Beer *et al.* 2007; Granier *et al.* 2007). Fourth, conifers seem to withstand the deleterious effects of drought better than broadleaved forests in Canada and Europe (Granier *et al.* 2007; Kljun *et al.* 2006). And fifth, mature forest stands are better able to withstand the effect of drought on carbon exchange than young stands (Law *et al.* 2001).

On the other hand, there are situations when the generalities cited above break. For the case of the multi-year drought across the boreal zone of Canada, the response of F_N to drought was different during the first and later years. During first year of drought, F_R was reduced while the warm spring and adequate soil moisture at depth lead to an increase in F_A and F_N . During the subsequent years, both F_R and F_A decreased and produced a conservative reduction in F_N . In tropical and humid temperate forests, moderate drought leads to additional carbon uptake by increasing photosynthesis and retarding respiration (Saleska *et al.* 2003). This unexpected result occurs because less rain is associated with fewer clouds, which make more light available and increase photosynthesis. Consequently, the term ‘drought’ can be viewed as qualitative in the tropics because in the cited instance drought-stressed tropical forests received 100 mm of rain per month, instead of superabundant levels (400 mm per month) during the wet period.

Phenology

In deciduous forests, it is common knowledge that the sign of the net carbon flux changes across the transition between the leafless dormant stage and the foliar growing season. Questions that are less well-understood include: (1) which weather variables are responsible for triggering the transition? And (2) how do traditional phenological measures like bud-burst, first flower, full leaf expansion relate to canopy photosynthesis and respiration? Analysis of data from 11 deciduous forest sites in North America, Europe and Asia indicates that the commencement of canopy photosynthesis corresponds well with the date when soil temperature crosses mean annual air temperature (Fig. 10) (Baldocchi *et al.* 2005). This simple metric does not need calibrating, like phenology models that depend upon growing degree days (Badeck *et al.* 2004). Plus, eddy flux measurements provide a measure of physiological function that is integrated across a rather large flux footprint and can be used to develop new phenology metrics, like photosynthetic development and recession velocities and photosynthetic growing season length (Gu *et al.* 2003b).

Disturbance, Using Space for Time

In recent years one of the most significant advances among the carbon flux community has been the development and implementation of meso-scale networks of flux towers to study logging and fire disturbance by substituting time for space (chronosequences) (Amiro *et al.* 2006; Coursolle *et al.* 2006; Gholz and Clark 2002; Goulden *et al.* 2006; Kolari *et al.* 2004; Kowalski *et al.* 2004; Law *et al.* 2001; Litvak *et al.* 2003; Meroni *et al.* 2002; Schulze *et al.* 1999; Schwalm *et al.* 2007; Wirth *et al.* 2002). Mesonets have also enabled investigators to examine CO₂ exchange for cases, like nitrogen deposition (Magnani *et al.* 2007), wind-throw (Knohl *et al.* 2002), old-field

succession (Emanuel *et al.* 2006), woody encroachment (Potts *et al.* 2006; Scott *et al.* 2006), different land use types (Ma *et al.* 2007; McFadden *et al.* 2003; Sakai *et al.* 2004; Sellers *et al.* 1997), prescribed burning (Owensby *et al.* 2006), grazing (Owensby *et al.* 2006; Soussana *et al.* 2007) and multiple cropping and tillage systems (Baker and Griffis 2005; Hollinger *et al.* 2005; Verma *et al.* 2005).

Chronosequence studies are not without limitations and critics. For example, they may introduce artifacts due to regional differences in soils, water table and local climate (Dunn *et al.* 2007). However, Goulden *et al.* (2006) tested the validity of a chronosequence network in Canada using remote sensing time series. They found that long-term trends in vegetation indices at single sites matched temporal trends in F_N being produced by the meso-scale network of towers in Canada.

Disturbance by Logging and Fire

A number of chronosequence studies are testing the succession hypothesis of Odum (1969) by quantifying: (1) how much carbon is lost after disturbance?; (2) how long does it take for the ecosystem to recover and become a carbon sink?; and (3) when does an ecosystem become carbon neutral as it ages, and if so at what age? Fig. 11 shows an example of the relationship between net carbon fluxes and time since disturbance; this case is for a set of conifer forests across the boreal region of Canada and the Pacific Northwest. In general, there is a large respiratory pulse from the ecosystem within a few years after disturbance. Many sites become carbon neutral within a decade, plus/minus a few years through natural and managed stand re-establishment—former plant colonies sprout from roots, pioneer species invade and establish seedlings/saplings, or managers plant new seedlings. Maximum amounts of net carbon uptake occur when the forests

stands are between 50 and 100 years old, then their rates of carbon uptake gradually decrease with additional age. In other regions, maximum carbon uptake occurs in forests between 50 and 200 years old (Arain and Restrepo-Coupe 2005; Law *et al.* 2004).

It is noteworthy that many investigators report that old-growth forest stands continue to act as net carbon sinks (Amiro *et al.* 2006; Arain and Restrepo-Coupe 2005; Desai *et al.* 2005; Guan *et al.* 2006; Knohl *et al.* 2003; Paw U *et al.* 2004; Wirth *et al.* 2002). On the other hand, only a few investigators report that old-growth forests are net carbon sources (Hutyra *et al.* 2007; Saleska *et al.* 2003). Some old-growth forests are carbon neutral because they experience natural and episodic disturbance, at the patch scale (Hutyra *et al.* 2007; Law *et al.* 2003; Saleska *et al.* 2003). An alternative explanation suggests that canopy photosynthesis of conifer forests plateaus with stand age and ecosystem respiration continues to increase in naturally regenerated forests, forcing F_N towards zero with age (Arain and Restrepo-Coupe 2005). In contrast, F_A and F_N decrease with age in plantations, but plantations possess much greater rates in F_A and F_R than natural forests stands of similar age (Arain and Restrepo-Coupe 2005).

There are some differences in the carbon flux trajectory between sites that have been burnt and logged (Amiro *et al.* 2006). Burnt sites tend to produce a smaller, post-disturbance respiratory pulse compared to logged sites. This is because burnt sites have many aerial snags that take several years to rot at the base, fall and come in contact with the wetter soil to begin respiration (Amiro *et al.* 2006). They may also experience a rapid recovery in photosynthesis, as do boreal forests when aspen stems shoot out from below ground roots. Logged sites, in contrast, have much residue on the surface and organic matter in the soil that readily decomposes (Amiro *et al.* 2006; Clark *et al.* 2004;

Law *et al.* 2003). For example, F_N was as high as $1269 \text{ gC m}^{-2} \text{ y}^{-1}$ one year after a pine plantation in Florida was cut (Clark *et al.* 2004).

Nitrogen Deposition

It is nearly impossible to attribute changes in net carbon uptake to nitrogen deposition without detangling age effects of forests. To achieve this objective, Magnani *et al.* (2007) evaluated carbon flux data from several European chronosequence studies. They clearly showed that F_N increases in magnitude with wet deposition of nitrogen, once age effects are removed. Furthermore, they reported that no signs of nitrogen saturation were detected.

Land Use and Carbon Exchange

The landscape mosaic captured by remote sensing pixels, model grids pixels or flux footprints consist of multiple carbon sinks and sources, operating simultaneously and responding differentially to the environment (Papale and Valentini 2003; Soegaard *et al.* 2003). Several large-scale, multi-investigator campaigns have been conducted to evaluate spatial variations in carbon exchange using networks of towers, flux instrumentation mounted on airplanes and remote sensing from satellites (Desjardins *et al.* 1997; Dolman *et al.* 2006; Miglietta *et al.* 2007; Sellers *et al.* 1997). But these campaigns are unable to be sustained for annual time increments to assess annual carbon budgets for the region.

On the other hand, single groups of investigators have been successful in measuring carbon fluxes at multiple sites across a landscape on seasonal or annual time scales to address questions related to the role of land management or vegetation type on carbon fluxes. A study of the temporal transition from an actively cultivated field to an

unmanaged field found that ecosystem respiration exceeded photosynthesis causing the atmosphere to gain between 600 and 900 gC m⁻² y⁻¹ (Emanuel *et al.* 2006). Another study examined carbon fluxes across multiple land uses in Germany (Anthoni *et al.* 2004b). Carbon uptake by managed and unmanaged beech forests was substantial, but relatively conservative (-500 gC m⁻² y⁻¹) and carbon exchange by a spruce forest was nearly neutral. In contrast, managed crops experience a relatively short carbon uptake period and took up much less carbon (-34 to -193 gC m⁻² y⁻¹). Furthermore, crops were substantial carbon sources when one considered carbon removed via harvest.

Spatial variations in CO₂ exchange across a transect of Arctic ecosystems during the summer growing season was related to differences in photosynthesis, which in turn scaled with leaf area index (McFadden *et al.* 2003). Greatest rates of uptake, during the summer growing season, were found over shrubs, followed by moist and coastal tundra, wet and dry tundra, barrens, forests and lakes.

In the Amazon, land use is changing via logging and conversion to pasture (da Rocha *et al.* 2004). Under midday light levels, the greatest rates of net carbon uptake were achieved by primary and cut forests, followed by rice and wet pastures and dry pastures. Bare fields, in the landscape, were carbon sources.

With efforts to rectify the secular trend in increasing atmospheric CO₂ there is much interest in how cropping and tillage systems may help agricultural systems serve as a carbon sink. Typical practices include corn/soybean rotations, till and no till and irrigate versus rainfed. One study found that F_N of a field cultivated with conventional methods was -27 gC m⁻² y⁻¹ more negative than one experiencing reduced tillage, over two years (Baker and Griffis 2005). More carbon stock was removed from the

conventional field, so the overall tillage effects were smaller ($10 \text{ gC m}^{-2} \text{ y}^{-1}$). A second study found that over six years found that no-till corn was a carbon sink ($-184 \text{ gC m}^{-2} \text{ y}^{-1}$) and a no-till soybean crop was a carbon source ($93.8 \text{ gC m}^{-2} \text{ y}^{-1}$) on the bases of eddy covariance measurements of F_N and consideration of grain removal (Bernacchi *et al.* 2005). In comparison, conventional-tillage corn and soybeans were carbon neutral.

In the Central Great Plains of North American, farmers grow either irrigated or rainfed rotations of soybeans and corn or grow irrigated corn continuously. A set of studies, conducted over three years, found that rainfed corn and soybean rotations were carbon neutral (-2 to $36 \text{ gC m}^{-2} \text{ y}^{-1}$), irrigated and continuous corn cultivation was a slight carbon source (25 to $46 \text{ gC m}^{-2} \text{ y}^{-1}$) and irrigated corn-soybean rotation is a moderate source of carbon (85 to $102 \text{ gC m}^{-2} \text{ y}^{-1}$) (Suyker *et al.* 2005; Suyker *et al.* 2004; Verma *et al.* 2005).

Validating and Parameterizing Ecosystem Models and Remote Sensing Algorithms

The network of eddy flux measurements is discrete and sparse in space. Consequently, it is ill advised to simply sum or average fluxes to estimate terrestrial carbon fluxes at the continental or global scales. On the other hand, the flux networks can play an important role in determining large scale carbon fluxes when used in conjunction with ecosystem models or remote sensing (Canadell *et al.* 2000; Janssens *et al.* 2003; Papale and Valentini 2003). In this section, we discuss how information from the flux network is being used to improve climate and ecosystem models and algorithms being used with remote sensing data to estimate carbon assimilation.

Models and Eddy Fluxes

With the carbon flux network database spanning a global range of plant functional types, disturbance features, and climates, ecosystem and climate modelers have seized the opportunity to either use such data to validate their land-surface subroutines or test parameter sensitivity and model uncertainty (Alton *et al.* 2007; Friend *et al.* 2007; Grant *et al.* 2006; Kucharik *et al.* 2006; Medlyn *et al.* 2005; Rambal *et al.* 2003; Thornton *et al.* 2002; Verbeeck *et al.* 2006; Woodward and Lomas 2004). But there are ‘perils and pitfalls’ in using eddy covariance data to test ecosystem models (Medlyn *et al.* 2005). First, one does not validate a model. One can only attempt to falsify a model with flux data. And falsifying a model is challenging because uncertainty is abundant; it exists in model parameters, model structure and in the eddy flux data itself. Furthermore, models are subject to the condition of ‘equifinality’ where different sets of parameters can yield the same results as the flux data (Hollinger and Richardson 2005; Medlyn *et al.* 2005). Use of maximum likelihood approaches to parameter estimation, as opposed to least squares minimization, is preferred because the eddy flux data are not homogeneous (Gove and Hollinger 2006; Medlyn *et al.* 2005).

Despite the ‘perils’ and ‘pitfalls’, there remain many benefits in using eddy flux data to test models. Friend and colleagues (Friend *et al.* 2007; Friend and Kiang 2005) report significant improvements in the simulation of climate and the diurnal pattern of climate variables being produced by the NASA GISS global climate model after flux data from four vegetation types were used to calibrate the land surface transfer scheme. They conclude that the greatest value of flux data for global carbon cycle modeling is evaluating process representation rather than providing an unbiased estimate of carbon fluxes.

Other groups of investigators are inverting flux data to derive stand-scale model parameters (Aalto *et al.* 2004; Braswell *et al.* 2005; Gove and Hollinger 2006; Jarvis *et al.* 2004; Knorr and Kattge 2005; Raupach *et al.* 2005; Reichstein *et al.* 2003; Richardson and Hollinger 2005; Schulz and Jarvis 2004; Wang *et al.* 2004; Wang *et al.* 2001; Williams *et al.* 2005). One goal of inverting flux data is to produce models that can be used in a data assimilation mode to improve spatial and temporal integration. A variety of mathematical and statistical techniques have been developed based on Maximum Likelihood (least-squares fit, Levenberg-Marquardt Optimization, Dynamic Linear Regression, Boundary-Line Analysis) and Bayesian (Markov Chain Monte Carlo method, the Metropolis-Hasting algorithm, Kalman Filtering) statistical theories and Genetic Algorithms. An advantage of retrieving parameter values simultaneously is that they are self-consistent. In addition, model parameters determined independently ignore important covariances that may occur between two model parameters (Braswell *et al.* 2005). And Knorr and Kattge (2005) found that their model could produce the probability distribution of measured carbon fluxes for two years simply by assimilating 7 days of flux data to parameterize their model.

Together, these data inversion studies are producing a new generation of information on the seasonal variation of such pertinent parameters as light use efficiency, photosynthetic capacity and evaporative fraction from eddy covariance and remote sensing measurements. Among key features being revealed is the need for incorporating the effects of seasonal dynamics into such central model parameters like photosynthetic capacity (Braswell *et al.* 2005; Wang *et al.* 2007).

To assess canopy-scale carbon fluxes for use by ecosystem and biogeochemical cycling models numerous investigators have related short-term carbon fluxes to such environmental drivers as sunlight, temperature and plant functional type (Buchmann and Schulze 1999; Gilmanov *et al.* 2007; Owen *et al.* 2007; Ruimy *et al.* 1995; van Dijk *et al.* 2005; Yi *et al.* 2004). The common approach is to fit carbon flux and light (Q) measurements to the Michaelis-Menten or rectangular hyperbola function (Eq 1) and evaluate key parameters like the quantum efficiency (α), the saturation rate of carbon uptake (β) and dark respiration (γ)

$$NEE = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma \quad (1)$$

In a survey of 20 European grassland sites (Gilmanov *et al.* 2007), light use efficiency (α) was 49.3 +/- 16.8 $\mu\text{mol mol}^{-1}$, the maximum carbon uptake rate at light saturation (Q) was 35.22 +/- 11.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and dark respiration (γ) was 6.8 +/- 2.27. In another study, Owen *et al.* (2007) quantified the coefficients in Equation 1 for 18 European and 17 North American and Asian forests, wetlands, tundra, grassland and crop sites under well-watered conditions. They found that the sum of the maximum carbon uptake and ecosystem respiration terms ($\beta + \gamma$) scaled with daily integrated ecosystem assimilation (FA) in a linear manner. The ranking was rather tight, but the highest values were associated with crops and the lowest values were with wetlands. For additional information, the reader is referred to the original publications for listings of model parameters for ecosystems of interest.

Remote Sensing and Eddy Fluxes

Reflected sunlight detected by satellites in a discrete set of wavebands is converted to estimates of net or gross primary productivity through a series of steps (Running *et al.* 2004; Yuan *et al.* 2007). First, reflectance data are converted into vegetation indices, like the normalized difference vegetation index, *NDVI*, the photochemical reflective index (*PRI*) or the enhanced vegetation index, *EVI* (Gamon *et al.* 2004; Rahman *et al.* 2004; Ustin *et al.* 2004). Next, vegetation indices are correlated with the fraction of absorbed visible sunlight, *fpar*, to estimate leaf area index or they are incorporated into algorithms to produce estimates of light use efficiency, gross and net primary productivity (Ruimy *et al.* 1996; Running *et al.* 2004; Yuan *et al.* 2007).

The data record compiled by the carbon flux measurement network is overlapping measurements produced by the Moderate Resolution Imaging Spectroradiometer (MODIS) on the *TERRA* and *AQUA* satellites (Running *et al.* 2004). So opportunities have arisen to ask: how well can remote sensing indices be converted into physiological, functional and structural variables or model parameters? Some indices, like *NDVI*, ‘saturate’ when the leaf area index exceeds three (Myneni *et al.* 2002; Sellers 1987). Derived products, such as satellite-based estimates of F_A , are subject to significant absolute errors in carbon fluxes and infidelity in producing the seasonal time course, when tested against direct carbon flux measurements. Errors are generally attributed to how well for stresses associated with soil moisture, humidity deficits and temperature are quantified (Heinsch *et al.* 2006; Leuning *et al.* 2005; Turner *et al.* 2005; Xiao *et al.* 2004; Yuan *et al.* 2007; Zhao *et al.* 2005). Others have shown that inferred estimates of F_A are improved when direct carbon fluxes are compared with the product of *NDVI* and *PRI* (Nichol *et al.* 2000; Rahman *et al.* 2004; Rahman *et al.* 2001).

One issue relating to the translation of satellite measurements into carbon fluxes is representativeness. Satellites view a single scene nearly instantly and then derive daily mean fluxes that are further extrapolated in time between subsequent acquisitions. Sims et al (2005) recently compared daily integrated carbon fluxes measured by an array of FLUXNET sites and compared them with measurements made at a given time with satellites. They found a strong correlation between the two metrics, proving that it is reasonable to upscale indirect satellite based measurements to determine carbon fluxes.

Closing Remarks

At present long-term and continuous measurements are being made at over 400 sites spanning the globe, and many sites have been in operation for over a decade. These measurements are providing environmental scientists and policy makers with direct, rather than inferred, measurements of net and gross carbon exchange at the stand-scale. Hence, these data are contributing to a new and integrated understanding of the ‘breathing of the terrestrial biosphere’. Moreover, these data are laying the foundation for improvements in predictive models that will be used to assess how ecosystem metabolism will respond to climate trends and perturbations and remote sensing products that will integrate fluxes regionally and globally.

Despite the litany of potential problems due to instrumentation, topography, and gap-filling, it was shown here that the carbon flux community is producing many coherent findings. Most importantly, we are learning that information on disturbance needs to be incorporated into model schemes that rely on climate drivers and plant functional type to upscale of tower fluxes to landscapes and regions—adding another level of complexity. We are also learning about interannual variability in net carbon

fluxes and how it results from a tight coupling between photosynthesis and respiration. Emergent-scale processes have been detected too, like the roles diffuse light, temperature acclimation and rain pulses play on long and short term carbon fluxes.

As the network has grown, it has also been able to overcome many early criticisms and weaknesses in using the eddy covariance method. One of the criticisms of the early configuration of the flux network was that it was biased too much towards managed temperate forests at mid-age near their most productive years (Piovesan and Adams 2000; Woodward and Lomas 2004) or it missed the effects of disturbance and aging forests (Adams and Piovesan 2002; Korner 2003; Schulze *et al.* 2000). As shown in Fig. 4, the probability distribution of annual carbon fluxes now contains many instances where there is carbon lost by disturbance and there has been a gradual shift in the grand mean towards zero as the network has grown. Hence, the latest configuration of the global network is better suited to serve as a database for evaluating process representation in an assortment of models that compute fluxes of mass and energy between vegetation and the atmosphere.

The carbon flux network is still unable to measure fluxes over complex terrain, well. And this limitation is expected to remain unless theoretical corrections can be developed and applied based using advection models (Katul *et al.* 2006).

Finally, global flux networks provide many opportunities for expansion into new venues, including the measurement of additional trace gases like ozone, VOCs, methane and nitrous oxide and NO_x (Pattey *et al.* 2006) and full greenhouse gas accounting (Soussana *et al.* 2007). And finally, continued operation of the global network into the

future is encouraged and necessary because it will provide new and direct observations of biosphere metabolism in a changing world.

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Table 1 Seasonal Attributes of net ecosystem carbon exchange by plant functional group

Biome	winter	spring	Summer	Autumn	Reference
Subalpine, conifer forest	Snow cover. F_R occurs from the soil at or slightly below freezing; F_A is zero	Frost events limits F_A for several days afterward; spring snow-melt produces burst in F_R	Peak F_N occurs; carbon loss occur on cloudy days; F_A is light limited; F_R increases as soils warm.	Frost and freezing inhibits F_A ; Soils are warm and promote F_R .	(Monson <i>et al.</i> 2002)
Temperate conifer forest	F_R at low level due to cool temperatures; F_A occurs on fair weather days.	F_A and F_R increase gradually with warming weather, longer days and more sunlight	F_A acclimates to warm summer temperature; F_A is reduced if summer drought occurs,	F_A and F_R decrease gradually with cooling weather, shorter days and less sunlight.	(Anthoni <i>et al.</i> 1999; Berbigier <i>et al.</i> 2001; Clark <i>et al.</i> 2004; Dolman <i>et al.</i> 2002; Morgenstern <i>et al.</i> 2004; Paw U <i>et al.</i> 2004; Stoy <i>et al.</i> 2005)
Temperate, deciduous, broadleaved forest	Trees are leaf-less; F_A is zero; F_R is modulated by presence or absence of snow; F_N is positive;	Rapid expansion of leaf area; F_A peaks at full leaf, F_R is relatively low due to cool soils; Peak (most negative) F_N occurs.	F_A is sensitive to direct and diffuse light, vapor pressure deficits and the absence of clouds; occasional drought limits F_A ; F_R increases with warmer temperature; F_N declines in magnitude below spring peak	Leaf senescence; F_A stops; Pulse in soil respiration due to introduction of new and fresh litter; soil is warm. F_R is relatively large.	(Greco and Baldocchi 1996; Knohl <i>et al.</i> 2003; Pilegaard <i>et al.</i> 2001; Saigusa <i>et al.</i> 2005; Schmid <i>et al.</i> 2003; Urbanski <i>et al.</i> 2007; Valentini <i>et al.</i> 1996; Wilson and Baldocchi 2001) (Granier <i>et al.</i> 2000)
Tropical Savanna, open woodlands	Winter dry season and cool period Lowest rates of F_A , F_R and F_N	F_A , F_R and F_N gradually increase with periodic rains and warming temperature	Summer wet and hot season; Peak values of F_A , F_R and F_N	F_A diminishes as soil moisture is depleted. Fire season Fraction of landscape burns every few years	(Beringer <i>et al.</i> 2003; Hutley <i>et al.</i> 2005; Leuning <i>et al.</i> 2005; Vourlitis <i>et al.</i> 2001)
Mediterranean woodlands and chaparral	High daily sums of F_A for evergreen trees and shrubs; adequate soil moisture, mild temperature; deciduous trees are leafless; F_A is zero and F_N is positive.	Photosynthesis and respiration peaks, producing greatest F_N	Drought, high temperatures limit F_A and F_R ; F_N is negative but declining in magnitude	Autumn rains commence and grass germinates; new carbon uptake season begins; F_N is negative, but relatively low due to low	(Luo <i>et al.</i> 2007; Ma <i>et al.</i> 2007; Pereira <i>et al.</i> 2007; Rambal <i>et al.</i> 2004; Reichstein <i>et al.</i> 2002b; Scott <i>et al.</i> 2004; Tirone <i>et al.</i> 2003)

				leaf area index	
Northern wetlands/ tundra	F_R depends on whether snow was present, if the soil was frozen or water logged, length of growing season, frost events, nutrient availability and the size of underlying carbon stores.	Snow melt, Emergent growth	Peak rates of F_N , though relatively small because there is a close balance between F_A and F_R from large carbon pools; the most negative values occur on cool days; Water table is lowest when temperature is warmest, causing F_N to be anti-correlated with temperature;	Senescence when temperature drops below freezing; photosynthesis is suspended.	(Lafleur <i>et al.</i> 2003; Laurila <i>et al.</i> 2001)
Annual and Perennial Grasslands	Annual grasslands are net sinks of carbon, but at low daily rates; temperate grasslands are dormant with frozen soils or snow covered surface.	F_A accelerates after last frost; Peak rates of F_N occur in annual grasslands; F_A initiates in perennial grasslands; Jump in F_R during reproductive phase	$F_N=f(LAI)$; Drought and chronic soil water deficits retard photosynthesis; plant respiration jumps at reproductive stage; C_4 grasslands achieve higher photosynthetic rates than C_3 grasslands; Annual grasslands are senescent.	Temperate grasslands have senesced; Annual grasslands germinate with resumption of autumn rains	(Flanagan <i>et al.</i> 2002; Kim <i>et al.</i> 1992; Owensby <i>et al.</i> 2006; Suyker and Verma 2001; Xu and Baldocchi 2004)
Crops	Bare fallow fields, except autumn sown crops; may or may not be snow covered; small source of carbon	Seeding, sparse canopy develops as plants grows; carbon uptake eventually outpaces soil respiration	Short peak period of photosynthesis; respiration is high after reproductive organs are set	Senescence, harvesting; photosynthesis ceases, residue is incorporated into soil; soil is warm and respiration is significant	(Anthoni <i>et al.</i> 2004a; Baker and Griffis 2005; Desjardins 1985; Hollinger <i>et al.</i> 2005; Moureaux <i>et al.</i> 2006; Suyker <i>et al.</i> 2004; Verma <i>et al.</i> 2005)
Tropical Forests	Wet season Less radiation due clouds reduces daily F_A and warm temperatures keep F_R appreciable F_N is generally most negative	Little seasonality in F_N	Summer dry season Reduces F_N , though rates are still relatively high compared to drier biomes; Old-growth forests are carbon sinks during dry season	Dry Season Clearer skies and more available radiation for photosynthesis F_N is negative over old-growth stands	(Araujo <i>et al.</i> 2002; Carswell <i>et al.</i> 2002; Goulden <i>et al.</i> 2004; Malhi <i>et al.</i> 1998; Saleska <i>et al.</i> 2003)
Boreal Conifer forests	Snow cover, frozen, basal soil respiration	F_A commences after last frost; F_N sensitive to warm days and can change sign	Close balance between canopy P_s and ecosystem respiration, F_N +/- 0 (growing season xxx days)	Frost and freezing events disrupt F_A F_R decreases with cooling soils and first snow	(Barr <i>et al.</i> 2007; Black <i>et al.</i> 1996; Griffis <i>et al.</i> 2003; Suni <i>et al.</i> 2003)

Desert	Winter precipitation enables peak daily sums of F_A and most negative values of F_N	Ecosystems switches from being a sink to a carbon source; F_N is positive	Carbon lost in respiration pulses stimulated by monsoon rains	F_A increases gradually with rain and cooler temperatures	(Hastings <i>et al.</i> 2005)
Peatlands/temperate wetlands	Cold and dark, but vegetation is green; low daily sums of F_A and F_R ; F_N can be positive or negative	Daily values of F_A and F_R increase after start of growing season; F_N	Peak daily sums of F_A and F_R ; most negative values of F_N ; peak daily sums of F_A , F_R and F_N occur in early summer, but can occur in late summer if water table is low	Daily values of F_A and F_R diminish; F_N can be positive or negative	(Heinsch <i>et al.</i> 2004; Hendriks <i>et al.</i> 2007; Lloyd 2006)

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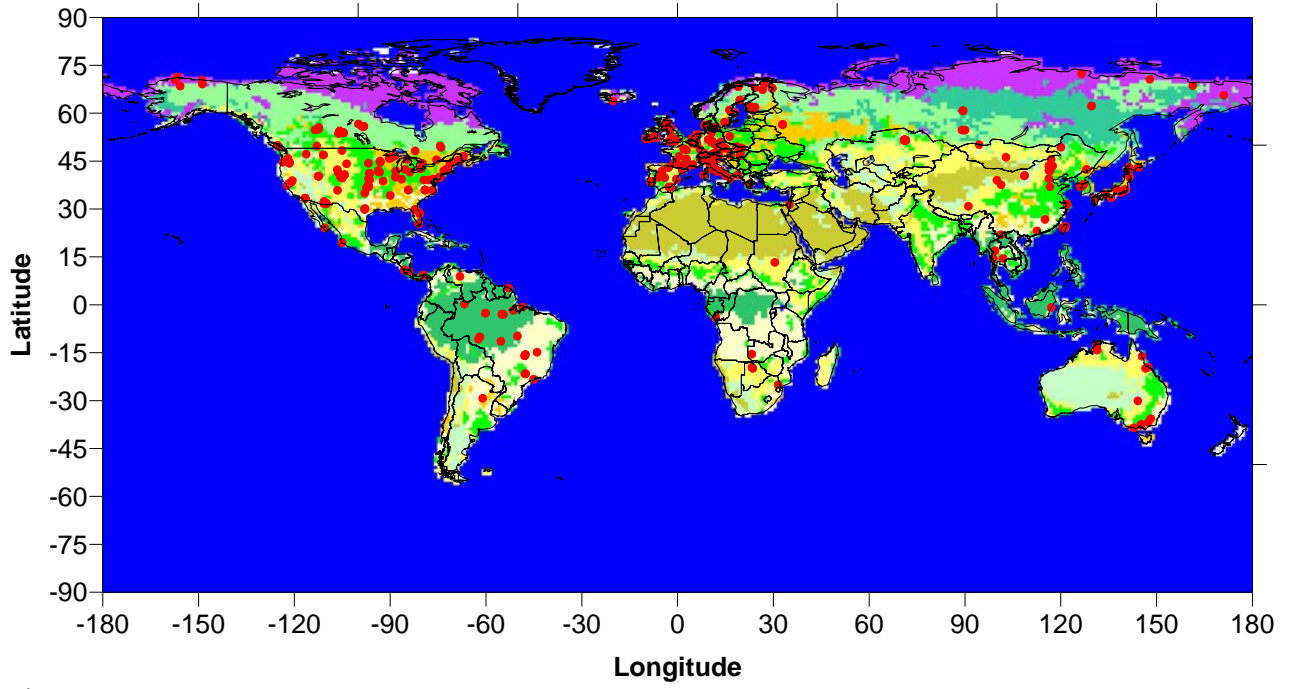


Fig. 1

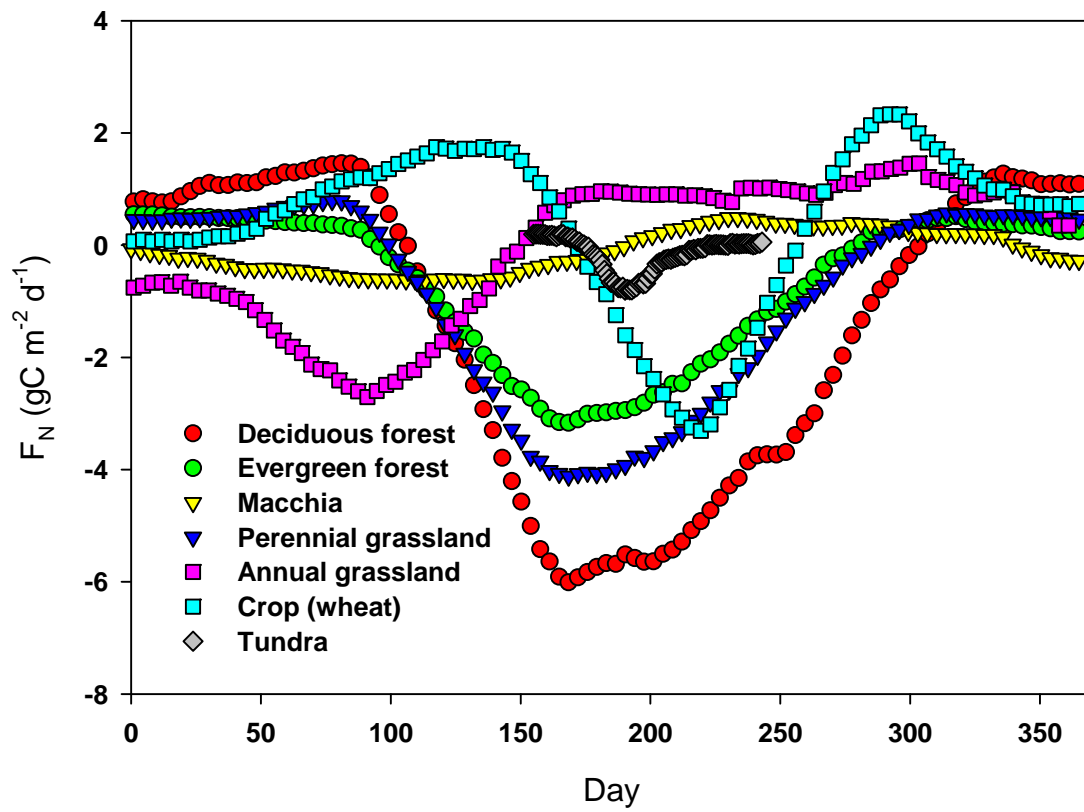


Fig. 2

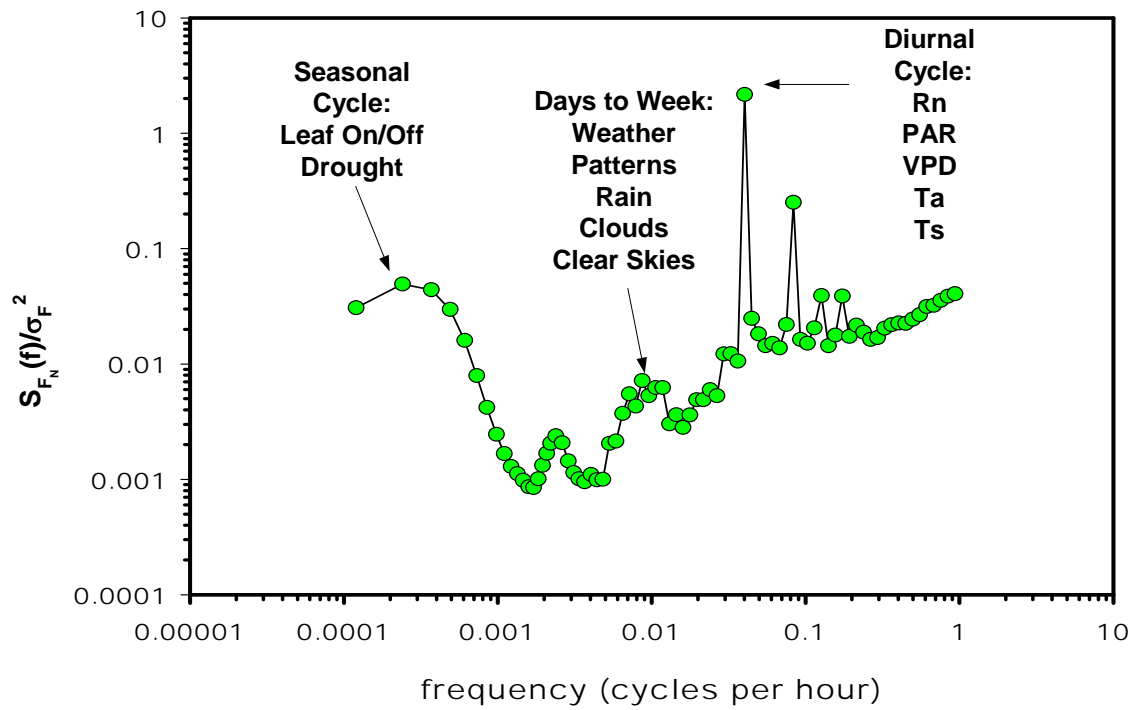


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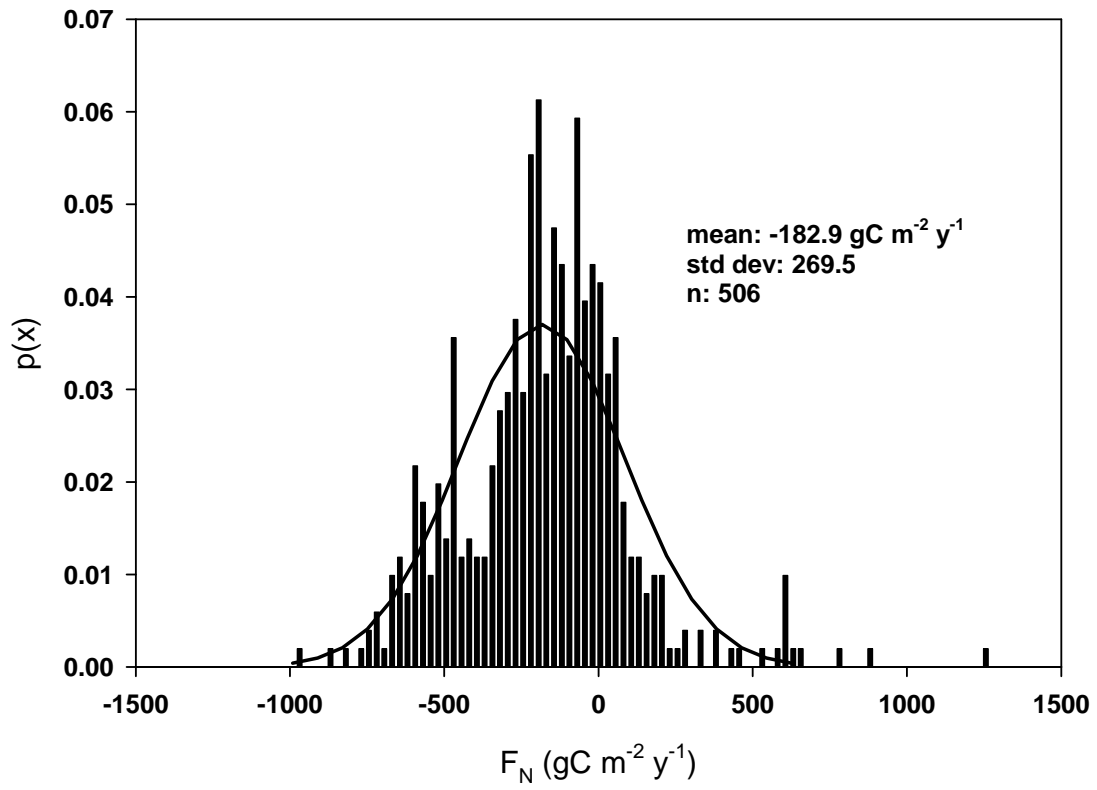


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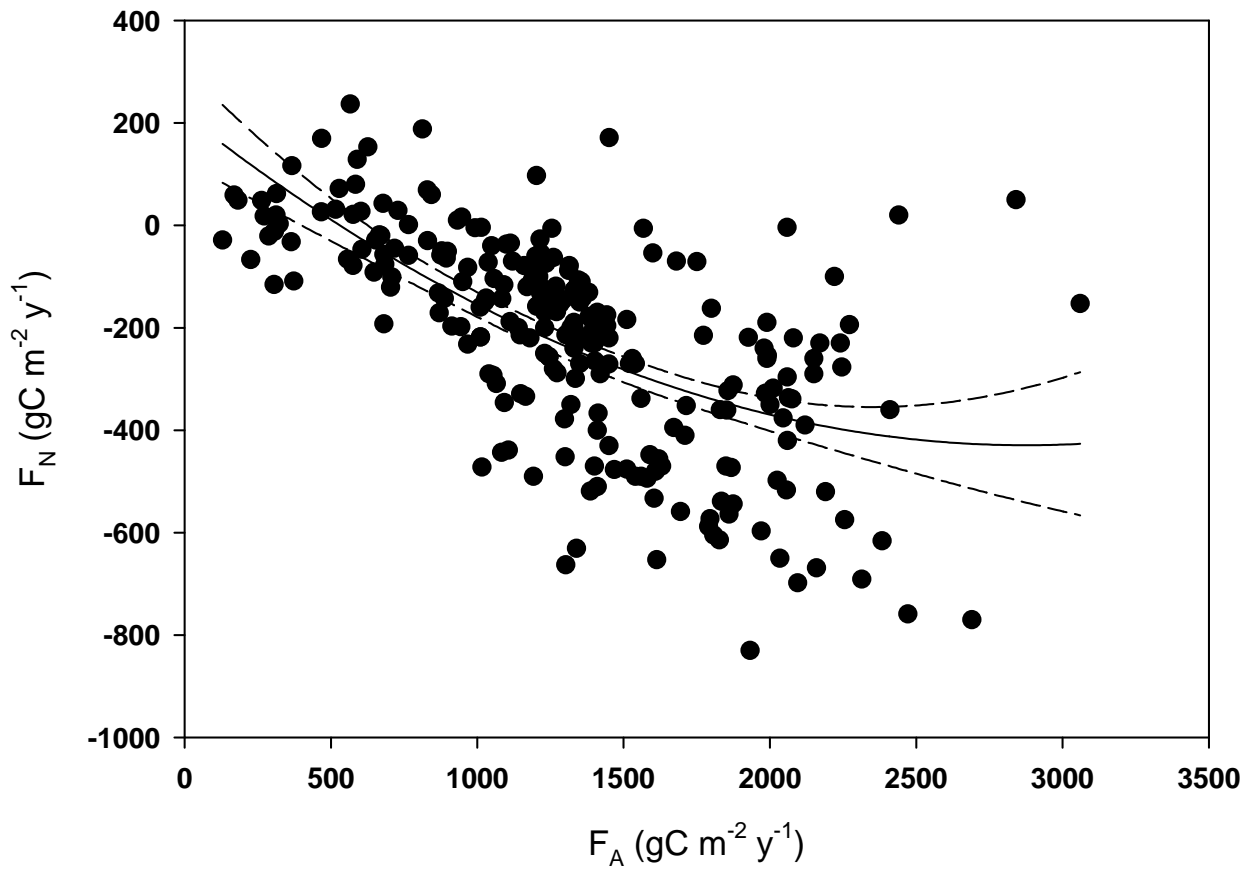


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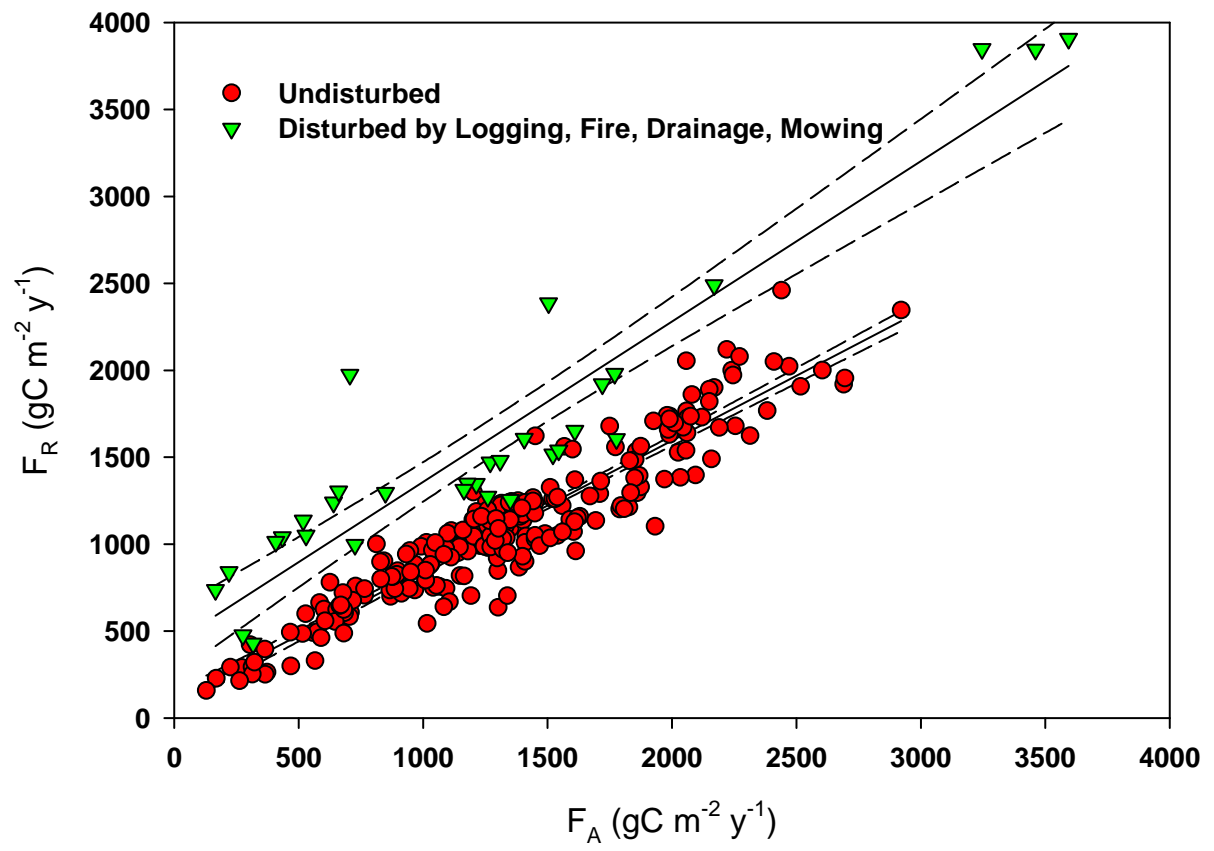


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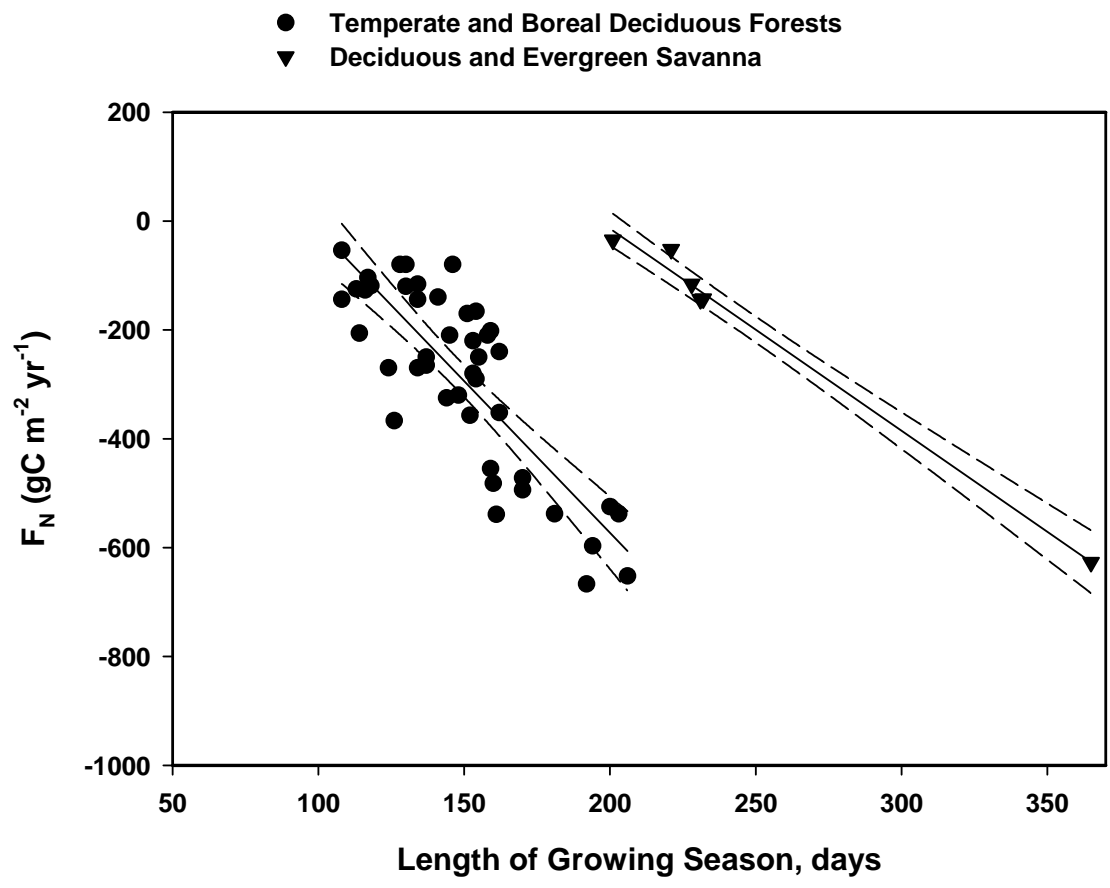


Fig. 7.

Interannual Variability in F_N

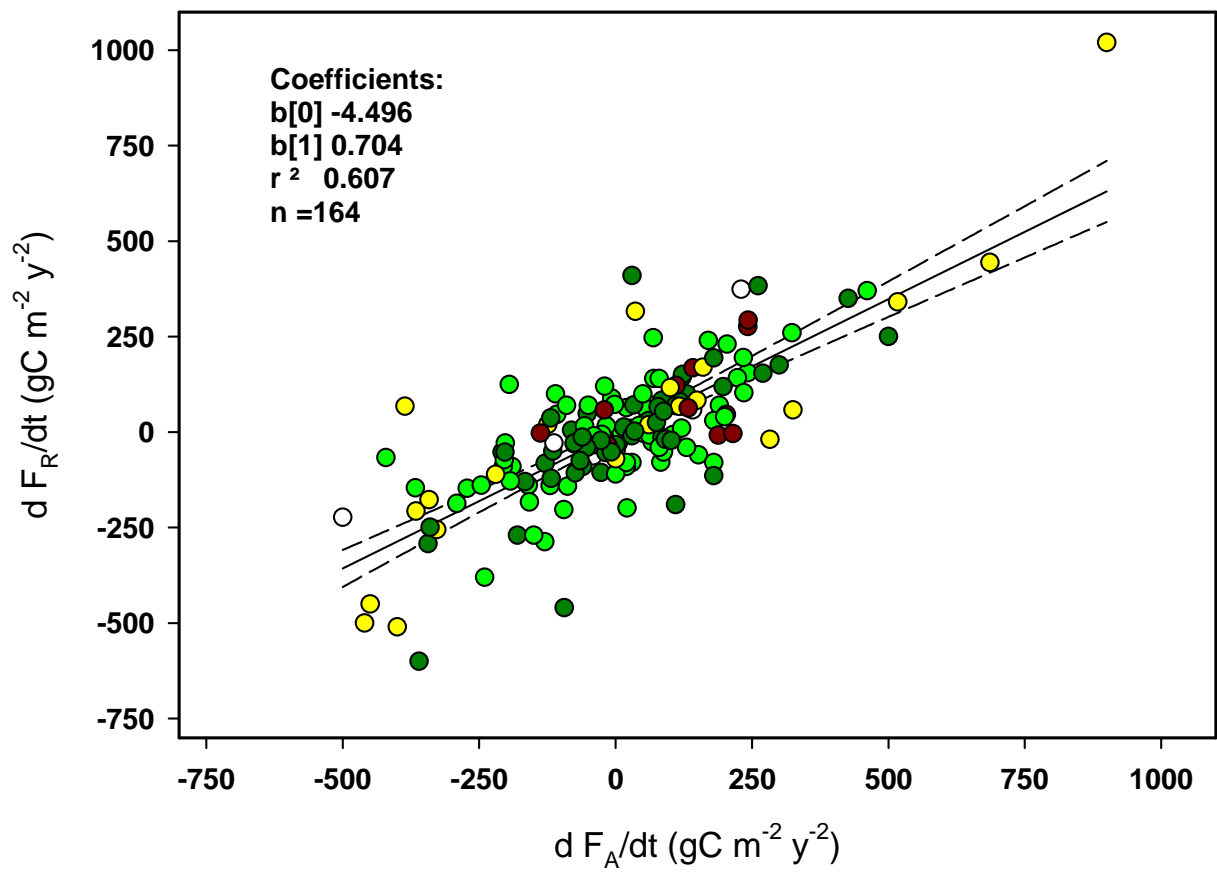


Fig. 8

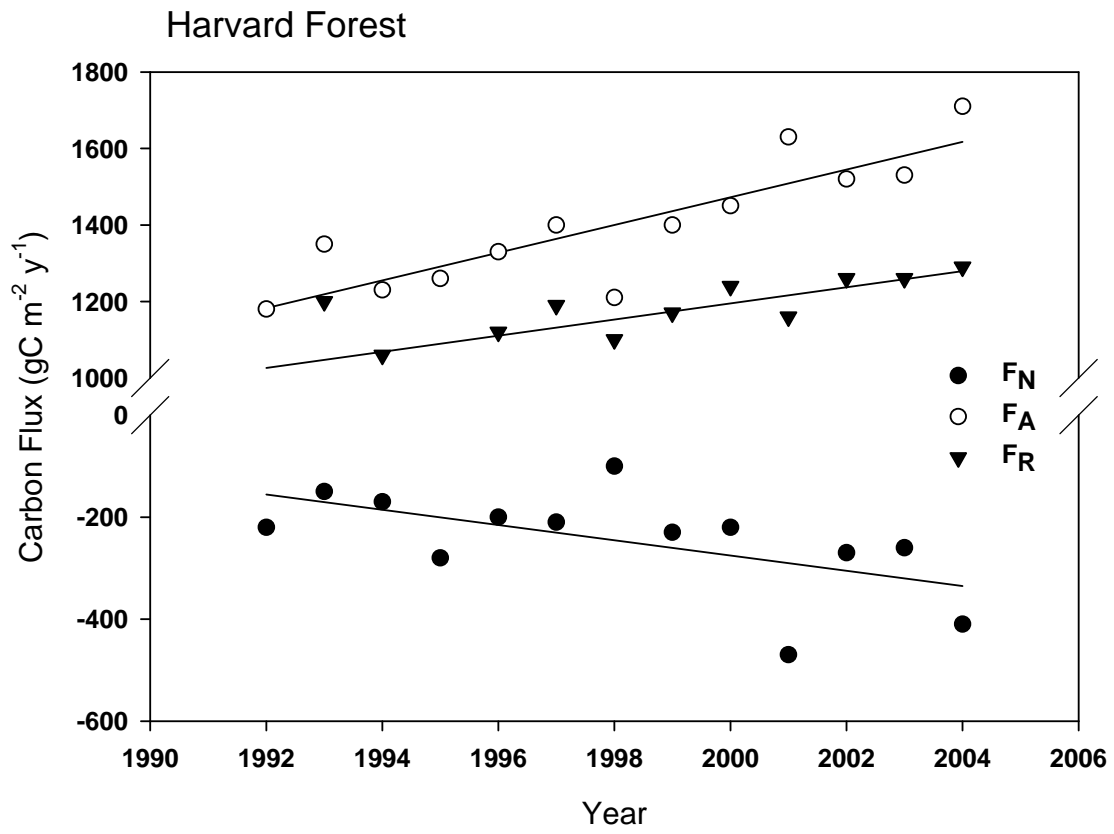


Fig. 9.

Temperate Deciduous Forests

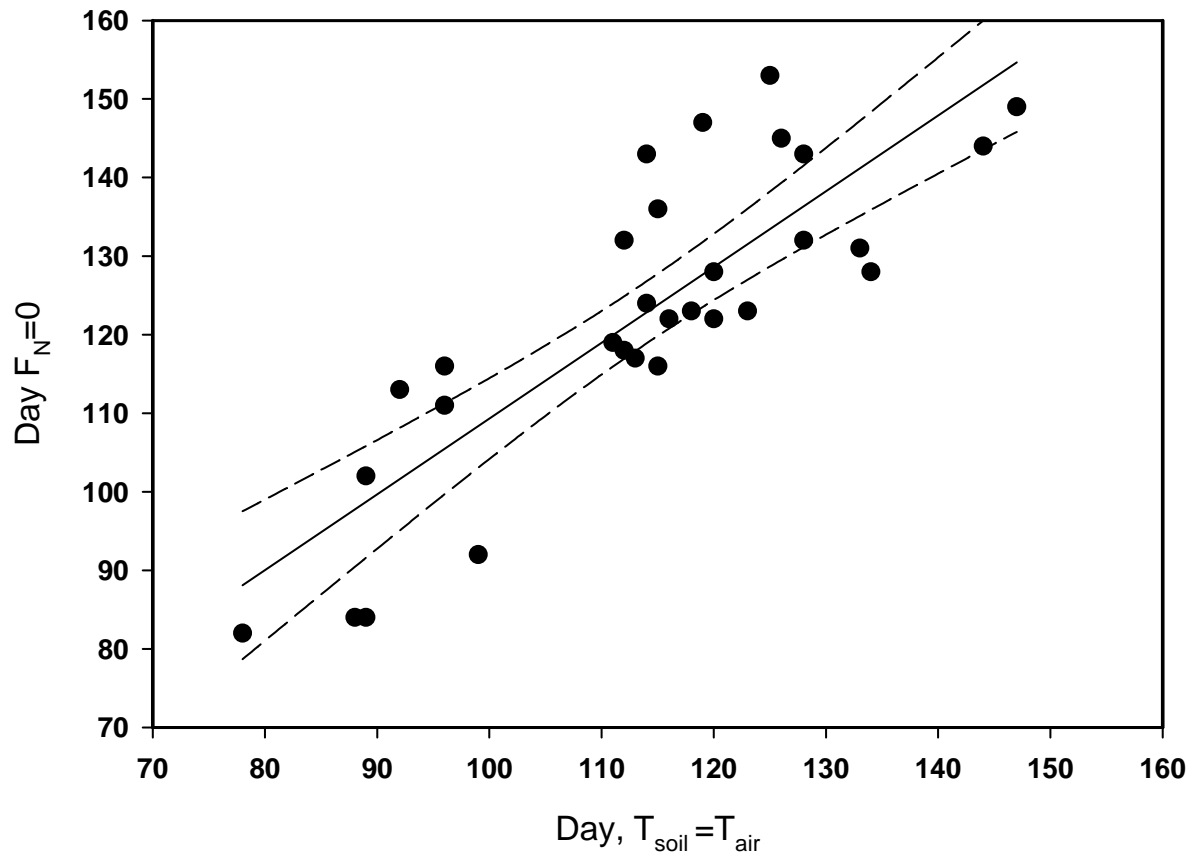


Fig. 10.

Conifer Forests, Canada and Pacific Northwest

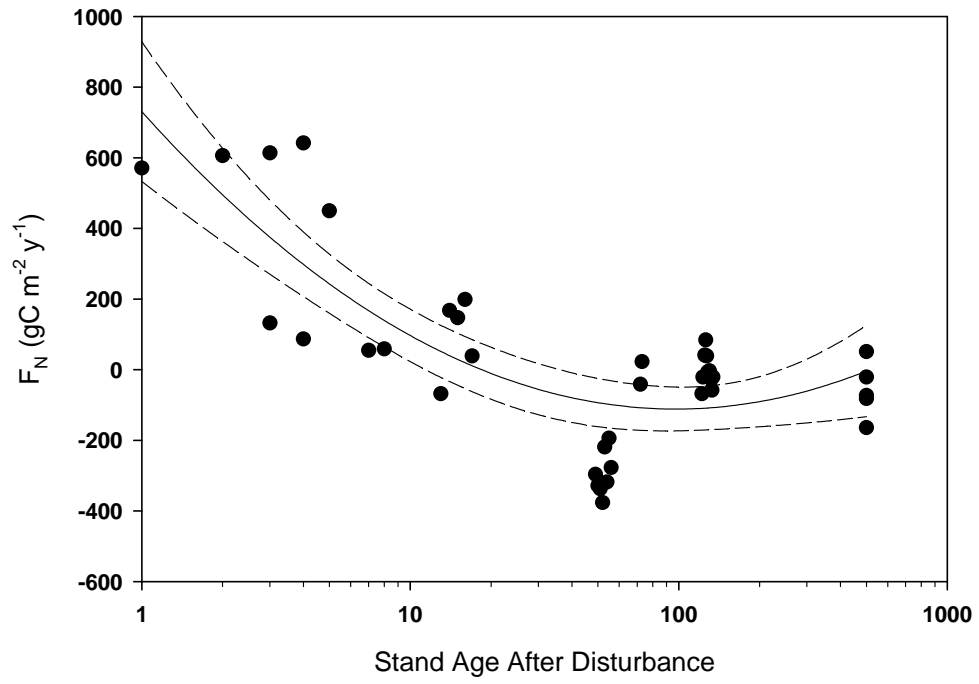


Fig. 11