

## TURNER REVIEW No. 15

**‘Breathing’ of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems***Dennis Baldocchi*

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**Abstract.** Published eddy covariance measurements of carbon dioxide ( $\text{CO}_2$ ) exchange between vegetation and the atmosphere from a global network are distilled, synthesised 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 of how these data are being used by ecosystem and climate modellers 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 the following: (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 behaviour of gravity waves and they are utilising 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  $\text{CO}_2$  and greenhouse gases (Tans *et al.* 1996) are among the more noteworthy results detected with networks of meteorological instruments.

During the past decade, scientists studying ecosystem–atmosphere interactions have implemented networks of instrument systems to measure eddy fluxes of  $\text{CO}_2$ , water and energy (Running *et al.* 1999; Valentini *et al.* 2000; Baldocchi *et al.* 2001a). 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, fertilisation, 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  $\text{CO}_2$ , water vapour 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; Massman and Lee 2002; Baldocchi

2003); negative covariance values of net ecosystem CO<sub>2</sub> exchange ( $F_N$ ) represent a loss of CO<sub>2</sub> 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 extend 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 because of its wider scale and ecological representativeness (Granier *et al.* 2002; Hargrove and Hoffman 2004).

In this Turner Review article, I distil and synthesise the rapidly growing literature on long-term measurements of net ecosystem CO<sub>2</sub> exchange between vegetation and the atmosphere. To give the reader a perspective of the growth of this literature, a search of Web of Science produced over 1300 papers associated with the key word 'ecosystem CO<sub>2</sub> exchange'. The earliest citations started *c.* 1990 and more than 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 several sites and I extracted information from a database of published results that I have collated during the past decade (available on request). In terms of content, the report focuses on gross and net fluxes of carbon at annual time scales, but also information on seasonal and daily time scales is reported when relevant.

The present 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 CO<sub>2</sub> 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 utilised by the remote-sensing and modelling communities to validate their estimates of land-surface fluxes or how they are being inverted to derive model parameters.

## History

Our current capacity to quantify the 'breathing of the biosphere' via measurements of CO<sub>2</sub>, water vapour and energy fluxes reflects an evolving process that spans a quarter of a century. The first successful eddy flux measurements of CO<sub>2</sub> were performed in the 1980s above natural and agricultural vegetation or relatively short (weeks to months) campaigns during the growing season (Ohtaki 1980; Leuning *et al.* 1982; Desjardins *et al.* 1984; Anderson and Verma 1986; Verma *et al.* 1986; Kim and Verma 1990). Rapid growth in the use of the eddy covariance method to measure ecosystem CO<sub>2</sub> exchange soon

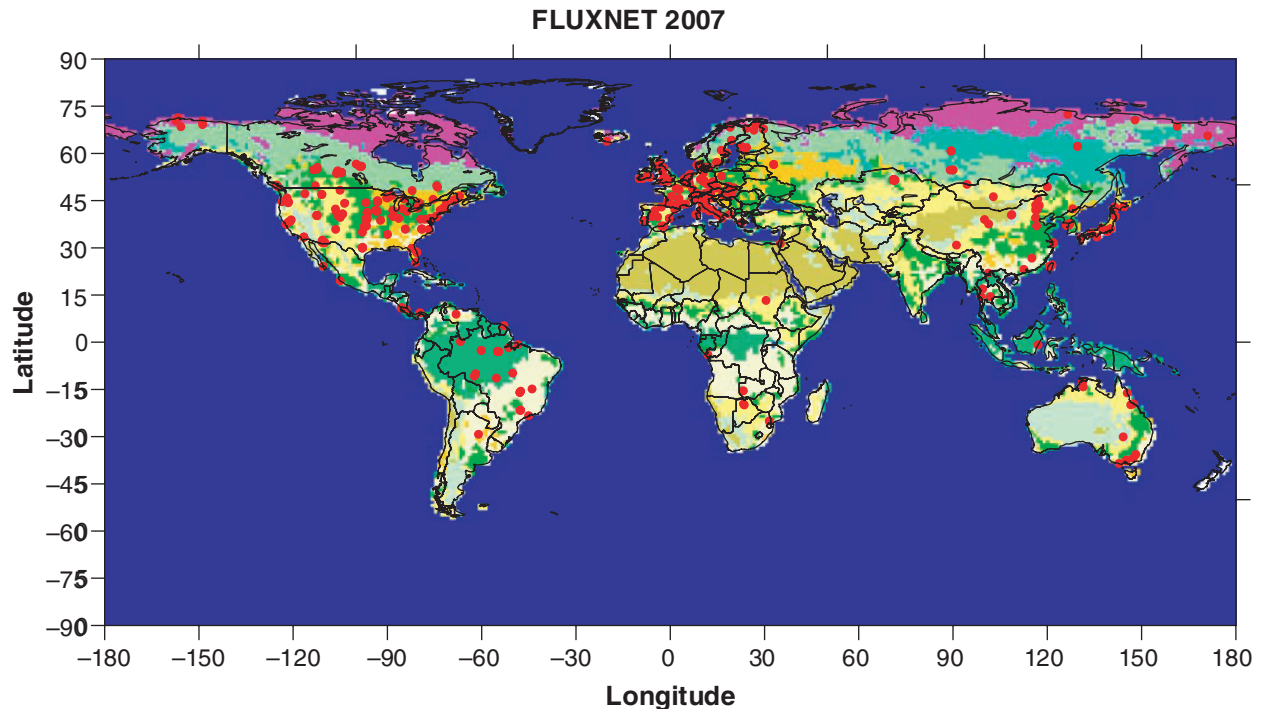
followed, based on technical advances in microcomputers and micrometeorological theory (Webb *et al.* 1980; Moore 1986; McMillen 1988) and the development of CO<sub>2</sub> sensors that relied on fast-responding, solid-state infrared detectors (Auble and Meyers 1992).

The earliest, long-term eddy covariance measurements of CO<sub>2</sub> exchange were made on an *ad hoc* basis at a handful of research sites across the globe, starting in the early 1990s (Wofsy *et al.* 1993; Black *et al.* 1996; Greco and Baldocchi 1996; Valentini *et al.* 1996; Yamamoto *et al.* 1999). In 1995, a group of scientists met at La Thuile, Italy, and developed a plan for executing global and regional sets of networks that would make long-term measurement of CO<sub>2</sub> and water vapour (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, CO<sub>2</sub> and water vapour fluxes, and many ancillary meteorological, soil and plant variables, are being measured at >400 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 (Valentini *et al.* 2000; Ciais *et al.* 2005), 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 datasets 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 (Running *et al.* 1999; Thornton *et al.* 2002; Papale and Valentini 2003). 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 (Running *et al.* 1999; Sims *et al.* 2005; Heinsch *et al.* 2006). 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



**Fig. 1.** Global distribution of long-term CO<sub>2</sub>, water-vapour and energy-flux measurement sites, associated with the FLUXNET program and its regional partners. The sites overlay the University of Maryland land-use map.

of  $F_A$  are needed to derive canopy-scale parameters for carbon-cycle models (Reichstein *et al.* 2003; Braswell *et al.* 2005; Owen *et al.* 2007; 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 (Valentini *et al.* 2000; Law *et al.* 2002). This limited scope attracted some criticism by ecologists (Piovesan and Adams 2000; Korner 2003) 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 during 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 in 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 several regions to examine the effects of disturbance by fire, logging and wind-throw on ecosystem carbon, water and energy exchange (Schulze *et al.* 1999; Knohl *et al.* 2002; Wirth *et al.* 2002; Amiro *et al.* 2003, 2006; Law *et al.* 2003; Litvak *et al.* 2003; Goulden *et al.* 2006; Beringer *et al.* 2007). 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 >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 the 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 (Foken and Wichura 1996; Baldocchi 2003; Finnigan *et al.* 2003). 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 (Goulden *et al.* 1996a; Moncrieff *et al.* 1996; Finnigan *et al.* 2003). During the past few years, many efforts have been made 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 analysers 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 (Moore 1986; Suyker and Verma 1993; Massman 2000). Standardised data-processing routines are generally used to compute flux covariances, so bias errors associated with different sensor configurations and processing of turbulence data are generally minimised and kept small (5–10%) (Aubinet *et al.* 2000; Massman and Lee 2002; Loescher *et al.* 2006). 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 (Moncrieff *et al.* 1996; Loescher *et al.* 2006; 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 CO<sub>2</sub> are often detected near sunrise when turbulent mixing re-initiates and respiratory CO<sub>2</sub> stored in the canopy air space is vented to the atmosphere (Moncrieff *et al.* 1996; Aubinet *et al.* 2000; Baldocchi *et al.* 2000). Changes in storage are typically accommodated by measuring temporal changes in the CO<sub>2</sub> 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 (Schmid 2002; Soegaard *et al.* 2003; Gockede *et al.* 2004; Rebmann *et al.* 2005).

Advection, due to complex topography or patchy vegetation, causes the flux divergence to be non-zero (Lee 1998; Finnigan *et al.* 2003). 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, which defines the rotation angles on the basis of an ensemble of wind vectors (Lee 1998; Paw U *et al.* 2000; Finnigan 2004). Efforts to measure advection fluxes directly involve implementation of large and complex systems of instrumentation that can be applied practically only 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 because of the need to resolve small horizontal gradients in CO<sub>2</sub> 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; gaps typically reach 30–40% on an annual basis (Falge *et al.* 2001; Moffat *et al.* 2007). Subsequently, gap-filling algorithms must be applied to

produce continuous datasets, 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 on climatic drivers such as 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 parameterised with existing data (Gove and Hollinger 2006). Inter-comparisons of gap-filling methods indicate that the neural-network method is among the best, although in general, biases associated with different gap-filling methods tend to be small and academic (Falge *et al.* 2001; Papale *et al.* 2006; Moffat *et al.* 2007).

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<sub>2</sub> 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 (Goulden *et al.* 1996a; Aubinet *et al.* 2000; Barford *et al.* 2001; Carrara *et al.* 2003; Saleska *et al.* 2003; Gu *et al.* 2005; Wohlfahrt *et al.* 2005). The threshold, above which nocturnal CO<sub>2</sub> fluxes are insensitive to mixing, ranges between 0.1 and 0.5 m s<sup>-1</sup>, depending on topography and canopy height (Aubinet *et al.* 2000; Loescher *et al.* 2006). Subsequently, correction factors are developed that rescale night-time respiration fluxes to the windy, well mixed condition and are normalised by temperature, soil moisture and growth stage.

One alternative to the u\* correction involves extrapolating the daytime CO<sub>2</sub> flux–light-response curve as light goes to zero (Hollinger *et al.* 1998; Lee *et al.* 1999; Suyker and Verma 2001; Falge *et al.* 2002a; Gilmanov *et al.* 2003; Xu and Baldocchi 2004). At the daily time scale, there is a strong correlation between the two methods, although respiration rates, based on the extrapolation of light-response curve, tend to underestimate (by 78–94%) 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 (Twine *et al.* 2000; Wilson *et al.* 2002; Oncley *et al.*

2007). There is some controversy about how well one can close the surface energy balance using latent and sensible heat-flux densities measured by the eddy covariance method. Several assessments of energy balance, across many sites, find that that energy balance closure is underestimated by 10–30% when the eddy covariance method is used (Twine *et al.* 2000; Wilson *et al.* 2002; Li *et al.* 2005; Oncley *et al.* 2007). 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 (Heusinkveld *et al.* 2004; Meyers and Hollinger 2004; Gu *et al.* 2007). Furthermore, it is important to note that lack of energy balance closure may not necessarily indicate poor CO<sub>2</sub>-flux measurements. There are many unresolved issues relating to (1) differential attenuation of water vapour during the time of 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, the present author acknowledges the value of testing for energy balance closure, as a standard diagnostic tool; however, he does not recommend correcting eddy flux measurements of CO<sub>2</sub> 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<sup>-2</sup> year<sup>-1</sup>, with larger and smaller values having been reported (Goulden *et al.* 1996a; Moncrieff *et al.* 1996; Anthoni *et al.* 2004a; Hollinger and Richardson 2005; Hagen *et al.* 2006; Loescher *et al.* 2006; Oren *et al.* 2006; Rannik *et al.* 2006). Correcting  $F_N$  for insufficient night-time mixing typically adds an additional respiratory flux of the order of 30–50 gC m<sup>-2</sup> year<sup>-1</sup>, 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 (Aubinet *et al.* 2000; Barr *et al.* 2002; Saleska *et al.* 2003; Anthoni *et al.* 2004a; Xu and Baldocchi 2004; Loescher *et al.* 2006; Papale *et al.* 2006).

For visual perspective of these annual carbon-budget errors, consider a piece of computer printer paper, expanded in size to 1 m<sup>2</sup>; 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 distil 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 in 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.

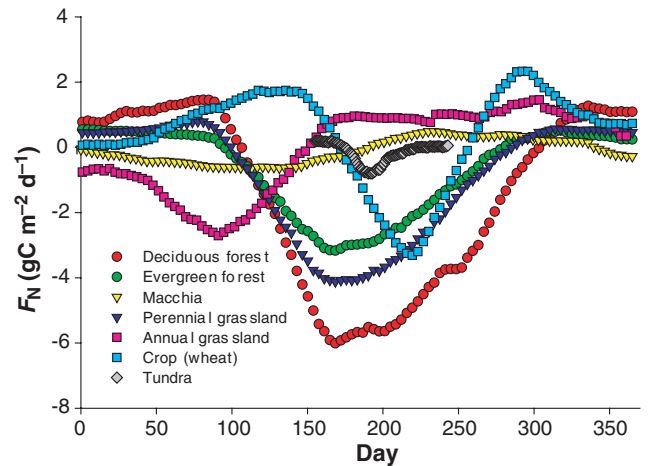


Fig. 2. Seasonal patterns in net ecosystem CO<sub>2</sub> exchange. Adapted from Baldocchi and Valentini (2004).

In temperate ecosystems, seasonal trend in CO<sub>2</sub> 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, such as the Pacific North-west, south-western France and the south-eastern part of the United States, temperate conifer forests can be net carbon sinks year-round. In contrast,  $F_R$  is delayed compared with  $F_A$  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, such as 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  $F_N$ , and the greatest rates of carbon uptake occur during the wettest season because these forests 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 cycle is moderated by the length of the snow-free season. These ecosystems can flip from being a carbon sink to being a carbon source during the growing season when a reduction in photosynthesis occurs owing 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 constitutes a 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 vapour-pressure deficits. The greatest rates of carbon uptake occur for C<sub>4</sub>, C<sub>3</sub> and mixed C<sub>3</sub>–C<sub>4</sub> 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, such as soybeans and corn, experience a short season of effective net carbon uptake because they must grow from seed

**Table 1. Seasonal attributes of net ecosystem carbon exchange by plant functional group**

Biome	Winter	Spring	Summer	Autumn	References
Subalpine, conifer forest	Snow cover; $F_R$ occurs from the soil at or slightly below freezing; $F_A$ is zero	Frost events limit $F_A$ for several days afterwards; spring snow-melt produces burst in $F_R$	Peak $F_N$ occurs; carbon loss occurs on cloudy days; $F_A$ is light-limited; $F_R$ increases as soils become warmer	Frost and freezing inhibit $F_A$ ; soils are warm and promote $F_R$	(Monson <i>et al.</i> 2002)
Temperate conifer forest	$F_R$ is 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 leafless; $F_A$ 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, vapour 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 $F_N$ occur	$F_A$ , $F_R$ and $F_N$ gradually increase with periodic rains and warming temperature	Summer wet and hot season; peak values of $F_A$ , $F_R$ and $F_N$ occur	$F_A$ 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)
editerranean 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 the 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 leaf area index	(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)
Northern wetlands/tundra	$F_R$ depends on whether snow was present, if the soil was frozen or waterlogged, length of growing season, frost events, nutrient availability and the size of underlying carbon stores	Snow melts, emergent growth is evident	Peak rates of $F_N$ occur, although 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 occurs when temperature drops below freezing; photosynthesis suspended	(Lafleur <i>et al.</i> 2003; Laurila <i>et al.</i> 2001)

Table 1. (continued)

Biome	Winter	Spring	Summer	Autumn	References
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 the last frost; peak rates of $F_N$ occur in annual grasslands; $F_A$ initiates in perennial grasslands; jump in $F_R$ during reproductive phase	$F_N = f(\text{LAI})$ ; 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 grow; 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 $F_N$ , although rates are still relatively high compared with 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 the last frost; $F_N$ sensitive to warm days and can change sign	Close balance between canopy $P_s$ and ecosystem respiration, $F_N \pm 0$	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 the most negative values of $F_N$	Ecosystem switches from being a sink to being 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 the start of growing season; $F_N$	Peak daily sums of $F_A$ and $F_R$ occur; most negative values of $F_N$ occur; 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)

and they experience a long period when the canopy is bare or sparse and losing carbon. Fall-sown crops, such as winter wheat, are small carbon sources or remain close to carbon neutral during the cold winter with low light levels.

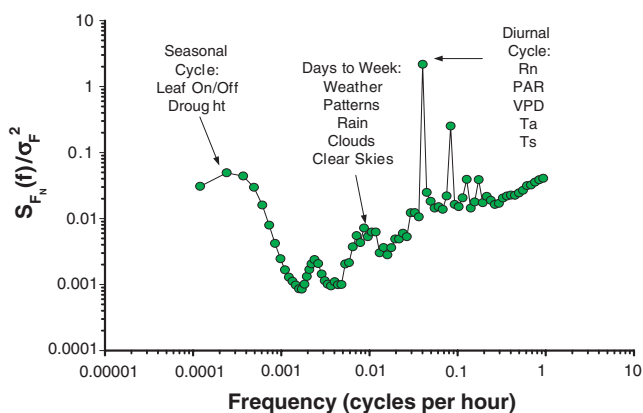
Inspection of power spectra of  $F_N$ , produced by Fourier transforms of year-long time series, enables one to examine and quantify the critical time scales that are associated with carbon-

flux variance (Baldocchi *et al.* 2001b; Katul *et al.* 2001; Stoy *et al.* 2005; Richardson *et al.* 2007). Figure 3 shows a conceptual power spectrum for  $\text{CO}_2$  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 3–7 days, and there is a well defined spectral gap at the monthly time scale.

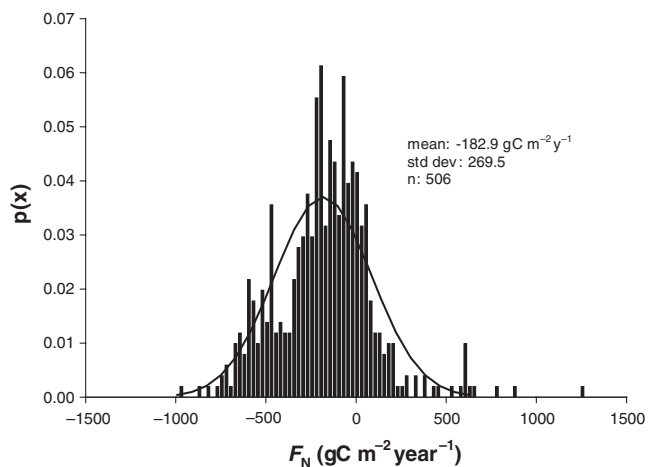
### Annual sums

The compiled database of published CO<sub>2</sub> 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  $-181 \pm 269 \text{ gC m}^{-2} \text{ year}^{-1}$  and it ranges between  $-1000$  and  $1300 \text{ gC m}^{-2} \text{ year}^{-1}$  (Fig. 4). Superimposed on the histogram is a Gaussian probability distribution. When the two probability distributions are compared, the median ( $-170 \text{ gC m}^{-2} \text{ year}^{-1}$ ) 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 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 CO<sub>2</sub> exchange derived from some atmospheric inversion models;



**Fig. 3.** Power spectrum of net CO<sub>2</sub> exchange of temperate ecosystems.  $R_n$  is net radiation, PAR is photosynthetically active radiation, VPD is vapour pressure deficit,  $T_a$  is air temperature and  $T_s$  is soil temperature. Sources: Baldocchi *et al.* (2001b), Katul *et al.* (2001) and Stoy *et al.* (2005).



**Fig. 4.** Probabilistic histogram of published measurements of annual net ecosystem CO<sub>2</sub> exchange. Superimposed is a Gaussian probability distribution. The mean is  $-183$ , the median is  $-169$  and the standard deviation is  $270 \text{ gC m}^{-2} \text{ year}^{-1}$  from 506 site-years of data.

e.g. net atmosphere–biosphere carbon exchange, derived from inversion model studies, for the European continent, range between  $-19$  and  $-53 \text{ gC m}^{-2} \text{ year}^{-1}$  (Bousquet *et al.* 2000; Gurney *et al.* 2002; Janssens *et al.* 2003).

From the first principles, carbon fluxes measured by bottom-up methods, such as the eddy covariance technique, are not expected to equal those derived from top-down methods, such as the atmospheric inversion modelling, which measure net biome exchange (Canadell *et al.* 2000; Schulze *et al.* 2000). For example, tower-based eddy flux measurements above intact stands do not account for carbon lost from regional fires, harvesting and disturbance (Schulze *et al.* 2000; Janssens *et al.* 2003; Chapin *et al.* 2006). In contrast, atmospheric inversion models derive and infer carbon fluxes for large basis regions by 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 10.

As I write the present paper, new data have been published, suggesting a convergence between the two different approaches of measuring and assessing land-atmosphere CO<sub>2</sub> exchange. Deng *et al.* (2007) performed a global inversion of the CO<sub>2</sub> concentration measurement network and examined North America (USA and Canada) in higher resolution by dividing it into 30 regions. With their higher-resolution model, these authors reported that net carbon fluxes above mid-age productive forests in Ontario/Quebec are of the order of  $-117 \pm 77 \text{ gC m}^{-2} \text{ year}^{-1}$ . They also reported that net carbon fluxes across much of the eastern United States and Europe range between  $-78$  and  $-180 \text{ gC m}^{-2} \text{ year}^{-1}$ .

The ranking of  $F_N$ , at annual time scales, is not explained well by variations in climate variables, plant functional type or photosynthetic potential (Law *et al.* 2002; Arain and Restrepo-Coupe 2005; van Dijk *et al.* 2005; Reichstein *et al.* 2007b). 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 (Arain and Restrepo-Coupe 2005; van Dijk *et al.* 2005; Reichstein *et al.* 2007b). 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 is 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.* (2000) was based on a regional



network of temperate European forests, whereas the later three references were based on a larger and more global assessment that included grasslands and crops and semi-arid forests and woodlands.

Net ecosystem carbon exchange is the relatively small difference between two rather large fluxes,  $F_A$  and  $F_R$ ; thus, it is better to explore the relationship between these latter two variables to gain an understanding of the factors that modulate  $F_N$ . By 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 an annual time scales. In general, 77  $\text{gC m}^{-2} \text{year}^{-1}$  of carbon is lost by ecosystem respiration for every 100  $\text{gC m}^{-2} \text{year}^{-1}$  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, on the basis of 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

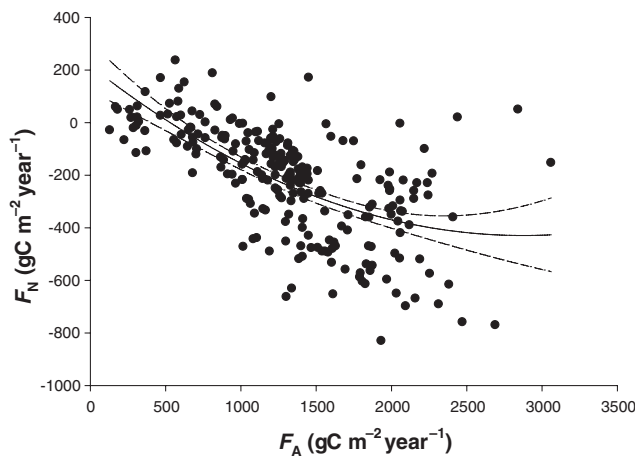


Fig. 5. Relationship between net ecosystem carbon exchange and canopy photosynthesis at annual time scales.  $r^2 = 0.42$ .

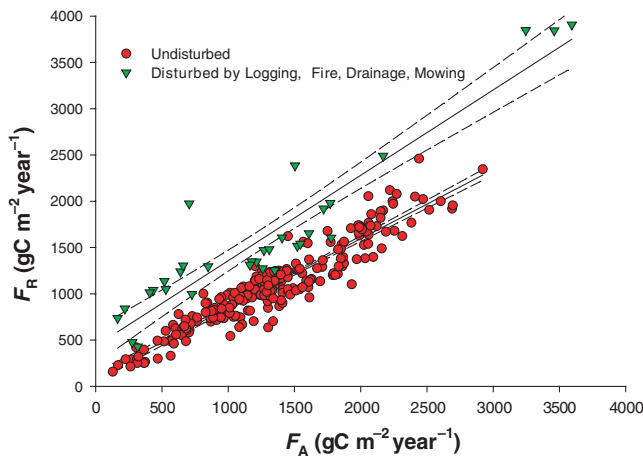


Fig. 6. Relationship between published values of gross canopy photosynthesis ( $F_A$ ) and ecosystem respiration ( $F_R$ ).

elevated ecosystem respiration and large positive values in  $F_N$  (Fig. 6) (Valentini *et al.* 2000; Amiro *et al.* 2006; Goulden *et al.* 2006; Humphreys *et al.* 2006; Hirano *et al.* 2007). The ‘disturbance offset’ is attributed to an incremental increase in  $\text{CO}_2$  emissions from the soil carbon pool and litter detritus. This respiratory ‘cost’ scales linearly with  $F_A$  and ranges between 330 and 1000  $\text{gC m}^{-2} \text{year}^{-1}$ . This magnitude depends, in part, on whether the bulk carbon remains on site (e.g. wind-throw, 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 stands with younger plants. It is noteworthy that data from ecosystems with frequent fires, such as tropical savanna (Beringer *et al.* 2003, 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 analyses 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  $r^2$  value increased up 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 (van Dijk *et al.* 2005; Reichstein *et al.* 2007b). In semi-arid and tropical regions, soil moisture is a better explanatory variable, but its dependence still relies on temperature (Rambal *et al.* 2003; Saleska *et al.* 2003; Hutrya *et al.* 2007; Ma *et al.* 2007; Reichstein *et al.* 2007b).

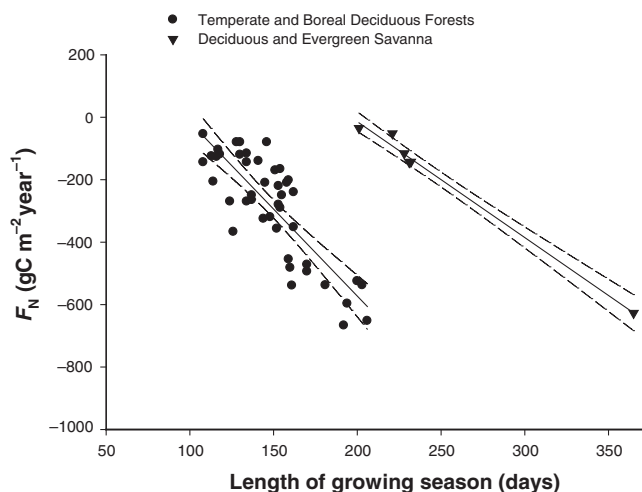
One of the stronger determinants of annual net ecosystem exchange, across an ecological gradient, is the length of the carbon-uptake period. This effect has been demonstrated for a network of temperate deciduous forests, evergreen needle-leaved forests and herbaceous vegetation (crops and grasslands) (Baldocchi *et al.* 2001a; Suni *et al.* 2003; Barr *et al.* 2004; Churkina *et al.* 2005; Barr *et al.* 2007). In general, net carbon exchange of deciduous broadleaved forests increases by  $\sim 5.57 \text{ gC m}^{-2}$  for each additional day of the photosynthetic growing season (Fig. 7). However, the result is conditional. A separate regression line (with a slope of  $3.7 \text{ gC m}^{-2} \text{day}^{-1}$ ) 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 the length of the photosynthetic period are 3.4 and  $7.9 \text{ gC m}^{-2} \text{day}^{-1}$ , 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).

### Inter-annual 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  $F_R$ . Only a few flux studies exceeding 5 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 (Valentini *et al.* 2000; Baldocchi *et al.* 2001a). Examples of long-term (greater than or equal to 5 years)  $\text{CO}_2$ -flux studies include reports from deciduous and evergreen boreal forests (Sun *et al.* 2003; Hollinger *et al.* 2004; Barr *et al.* 2007; Dunn *et al.* 2007; Richardson *et al.* 2007), temperate deciduous forests (Goulden *et al.* 1996b; Barford *et al.* 2001; Wilson and Baldocchi 2001; Carrara *et al.* 2003; Curtis *et al.* 2005; Saigusa *et al.* 2005; Ito *et al.* 2006; Stoy *et al.* 2006; Urbanski *et al.* 2007), temperate conifer forests (Grunwald and Bernhofer 2007), subtropical savanna (Beringer *et al.* 2007), Mediterranean woodland (Pereira *et al.* 2007) and herbaceous or shrubland vegetation (Haszpra *et al.* 2005; Gilmanov *et al.* 2006; Ma *et al.* 2007).

Inter-annual variability in net ecosystem  $\text{CO}_2$  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

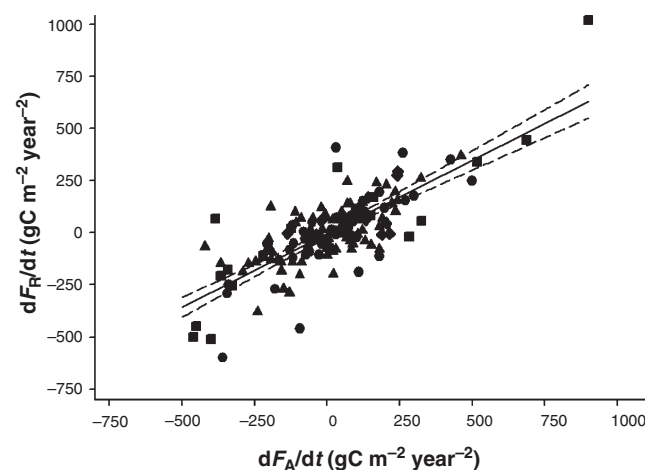


**Fig. 7.** Impact of the length of carbon-uptake period, a measure of growing-season length, on net ecosystem carbon exchange,  $F_N$ , of temperate broadleaved and savanna forests. This plot updates the figure published by Baldocchi *et al.* (2001a) by adding more recent data from Schmid *et al.* (2003), Barr *et al.* (2004), Knohl *et al.* (2003), Leuning *et al.* (2005), Owen *et al.* (2007) and Ma *et al.* (2007). The coefficient of determination is 0.686 and the regression slope is  $-5.57 \text{ gC m}^{-2}$  per day for temperate deciduous forests. The coefficient of determination is 0.99 and the regression slope is  $-3.709 \text{ gC m}^{-2}$  per day for savannas.

(Goulden *et al.* 1996b; Wilson and Baldocchi 2001; Urbanski *et al.* 2007). A different set of factors explains inter-annual variability of net ecosystem  $\text{CO}_2$  exchange in different biomes and climate spaces. Inter-annual variability of  $\text{CO}_2$  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  $\text{CO}_2$  exchange for a boreal and deciduous aspen site is linked to inter-annual differences in leaf area index and summer drought (Kljun *et al.* 2006; Barr *et al.* 2007). Inter-annual variability of semi-arid ecosystems and those with Mediterranean-type climates depend on the duration of the wet season (Paw U *et al.* 2004; Luo *et al.* 2007; Ma *et al.* 2007; Pereira *et al.* 2007).

Most recently, Richardson *et al.* (2007) used a combination of statistical and ecosystem modelling 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 inter-annual fluxes) is attributed to environmental variables (light, rainfall and temperature) and 55% of the variance is attributed to variations in model parameters for biotic processes such as 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 also in  $F_A$  and  $F_R$  (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  $\sim 60\%$  of the year-to-year variability in  $F_R$ . In general, a year-to-year change in  $F_A$  of  $100 \text{ gC m}^{-2}$  will produce a  $70 \text{ gC m}^{-2}$  change in  $F_R$ , with the residual ( $30 \text{ gC m}^{-2}$ ) 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, such as broad-leaved and conifer forests, herbaceous vegetation and disturbed ecosystems.



**Fig. 8.** Year-to-year changes in net ecosystem carbon exchange,  $F_N$ , are interpreted by a correlation between year-to-year changes in ecosystem respiration ( $F_R$ ) and gross canopy assimilation ( $F_A$ ). The regression slope is 0.704 on 163 degrees of freedom and the coefficient of determination ( $r^2$ ) is 0.607. Triangles are deciduous forests, circles are conifer forests, squares are crops and grasslands and diamonds are disturbed sites.

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  $F_A$  occur 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 mineralisation. However, no multi-year carry-over effects are detectable with this dataset by phase-shifting the dependent ( $dF_R/dt$ ) and independent ( $dF_A/dt$ ) variables one year ahead or behind each other.

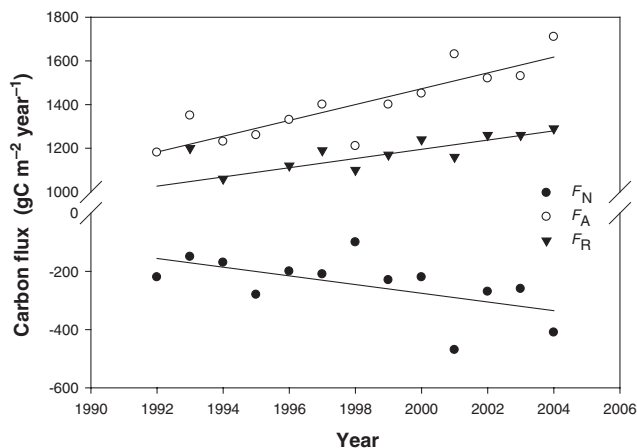
With data records exceeding a decade, one can start to investigate temporal trends also in  $\text{CO}_2$  exchange. Figure 9 shows the annual time series of  $F_N$ ,  $F_A$  and  $F_R$  for the longest extant data record, Harvard Forest (Urbanski *et al.* 2007). During the 13-year record, annual  $F_N$  has increased in magnitude systematically from about  $-150 \text{ gC m}^{-2} \text{ year}^{-1}$  during the 1990s to  $-400 \text{ gC m}^{-2} \text{ year}^{-1}$  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 (75–100 years).

### Emergent processes

The continuous operation of flux stations has enabled scientists to produce new information on a variety of scale-emergent processes. It has also enabled scientists to observe responses in ecosystem metabolism to environmental perturbations that tend to be missed with short-term field campaigns or studies that use 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 more than a decade, investigators have observed that canopy light use efficiency (the slope of the  $F_N$  v. sunlight ( $R_g$ ) response curve) was sensitive to whether the sky was clear or cloudy (Price and Black 1990; Hollinger *et al.* 1994; Baldocchi 1997).



**Fig. 9.** Long-term record of net  $\text{CO}_2$  exchange, gross photosynthesis and ecosystem respiration, on annual time scales at Harvard Forest, MA (Urbanski *et al.* 2007).

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, compared with 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 increases from  $\sim 0.1$  to  $0.9$ . Under cloudy skies, incoming sunlight is more isotropic, so that 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, and thus lowers their photosynthesis rates. However, the enhancement of  $F_N$  and  $F_A$  by diffuse light is not universal. It was not observed above 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) or 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 Mount Pinatubo volcano injected fine aerosols into the stratosphere (Gu *et al.* 2003a), than before the eruption, whereas 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  $15\text{--}20^\circ\text{C}$  range and optimal temperatures for many sites across North America were in the  $20\text{--}30^\circ\text{C}$  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  $6^\circ\text{C}$  (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.* 2003, 2005). However, data derived from the flux network show that respiration rates of ecosystems in northern latitudes, adapted to cool temperatures ( $5\text{--}10^\circ\text{C}$ ), are similar to respiration rates of ecosystems in more southerly latitudes that have adapted to warmer temperatures ( $20\text{--}30^\circ\text{C}$ ) (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  $10^\circ\text{C}$  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) (Van Dijk and Dolman 2004; Curtis *et al.* 2005; Desai *et al.* 2005). Conversely, another set of studies shows that  $Q_{10}$  is conservative and close to the typical value for enzyme kinetics ( $2 \pm 10\%$ ) when  $Q_{10}$  is computed for shorter time windows (Reichstein *et al.* 2002a, 2005; Xu and Baldocchi 2004; Flanagan and Johnson 2005). Instead, it is the reference respiration rate,  $R_o$ , that varies seasonally with biological activity (Van Dijk and Dolman 2004; Reichstein *et al.* 2005). Exceedingly large values for  $Q_{10}$  are often artefacts 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 in 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 above the canopy and in the stem space of forests (Baldocchi *et al.* 1997; Constantin *et al.* 1999; Law *et al.* 1999; Falk *et al.* 2005; Launiainen *et al.* 2005; Ma *et al.* 2007). A synthesis study of 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-storey 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). In a study of a boreal aspen forest, autotrophic respiration was found to be 61% of the ecosystem respiration and net primary productivity was 54% of the 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, according to the 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; Xu *et al.* 2004; Ivens *et al.* 2006; Jarvis *et al.* 2007). There is also a smaller body of papers showing that pulses in soil respiration occur also in wetter temperate climates (Lee *et al.* 2004; Jassal *et al.* 2005). 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; Xu *et al.* 2004; Jarvis *et al.* 2007). The extent and duration of the respiration pulses, on the other hand, depend on the amount of rain—large rain events keep the soil and microbes wetter longer. Often,  $F_A$  does not respond favourably to rain pulses in semi-arid regions, despite the fact these are 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 (>5 mm) provide enough moisture to 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 such as 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 behaviour of whole ecosystems in response 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 (Reichstein *et al.* 2002a, 2002b; Rambal *et al.* 2003; Xu and Baldocchi 2004; Williams and Albertson 2005; Pereira *et al.* 2007) or exploit large-scale droughts, similar to 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 also tends to be a compensatory reduction in  $F_R$  (Reichstein *et al.* 2007a). Second, photosynthesis and respiration rates drop abruptly when soil moisture or a water stress index drop 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 do (Kljun *et al.* 2006; Granier *et al.* 2007). And fifth, mature forest stands are better able to withstand the effect of drought on carbon exchange than young stands (Law *et al.* 2001).

However, there are situations when the generalities cited above break. In 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 the first year of drought,  $F_R$  was reduced whereas the warm spring and adequate soil moisture at depth lead to increases 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 the following: (1) which weather variables are responsible for triggering the transition; and (2) how do traditional phenological measures such as bud-burst, first flower and full leaf expansion relate to canopy photosynthesis and respiration? Analysis of data from 11 deciduous-forest sites in North America, Europe and Asia indicated 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 on growing degree days (Badeck *et al.* 2004). In addition, 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, such as photosynthetic development and recession velocities and photosynthetic growing-season length (Gu *et al.* 2003*b*).

### Disturbance, by substituting space for time

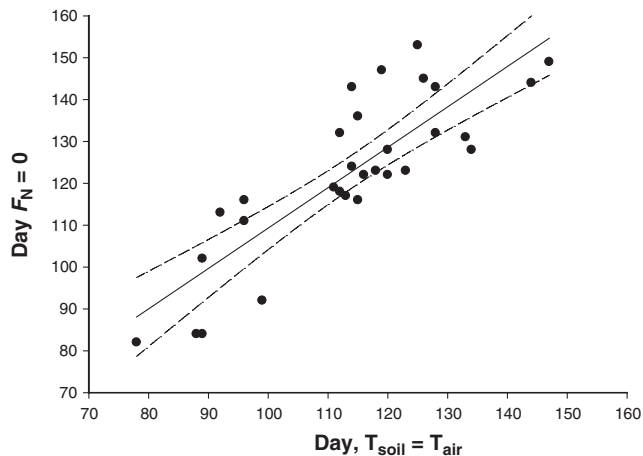
In recent years one of the most significant advances among the carbon-flux community has been the development and implementation of meso-scale networks of flux towers to study logging and fire disturbance by substituting space for time (chronosequences) (Schulze *et al.* 1999; Law *et al.* 2001; Gholz and Clark 2002; Meroni *et al.* 2002; Wirth *et al.* 2002; Litvak *et al.* 2003; Kolari *et al.* 2004; Kowalski *et al.* 2004; Amiro *et al.* 2006; Coursolle *et al.* 2006; Goulden *et al.* 2006; Schwalm *et al.* 2007). Meso-nets have also enabled investigators to

examine CO<sub>2</sub> exchange for cases, such as 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 (Sellers *et al.* 1997; McFadden *et al.* 2003; Sakai *et al.* 2004; Ma *et al.* 2007), 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).

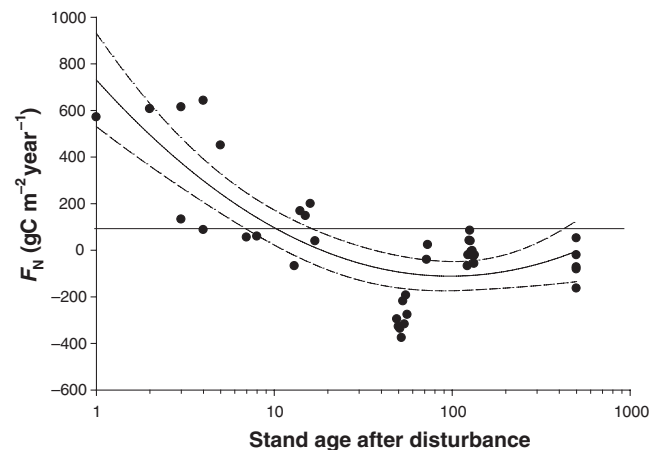
Chronosequence studies are not without limitations and critics. For example, they may introduce artefacts because of regional differences in soils, water table and local climate (Dunn *et al.* 2007). However, Goulden *et al.* (2006) tested the validity of a chronosequence network in Canada by using remote-sensing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

### Disturbance by logging and fire

Several chronosequence studies are currently 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) at what age does an ecosystem recover and become carbon neutral? Figure 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 North-west. 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 forest 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



**Fig. 10.** The relationship between the day when net ecosystem carbon exchange,  $F_N$ , equals zero and the day when soil temperature equals mean annual air temperature in temperate deciduous forests. Adapted from Baldocchi *et al.* (2005).



**Fig. 11.** The relationship between net carbon exchange and age since disturbance. The data are drawn from several chronosequence studies done in central and western Canada and the Pacific North-west over conifers. Sources: (Paw U *et al.* 2004; Amiro *et al.* 2006; Dunn *et al.* 2007; Schwalm *et al.* 2007).

in forests between 50 and 200 years old (Law *et al.* 2004; Arain and Restrepo-Coupe 2005).

It is noteworthy that many investigators have reported that old-growth forest stands continue to act as net carbon sinks (Wirth *et al.* 2002; Knohl *et al.* 2003; Paw U *et al.* 2004; Arain and Restrepo-Coupe 2005; Desai *et al.* 2005; Amiro *et al.* 2006; Guan *et al.* 2006). On the other hand, only a few investigators have reported that old-growth forests are net carbon sources (Saleska *et al.* 2003; Hutrya *et al.* 2007). Some old-growth forests are carbon neutral because they experience natural and episodic disturbance, at the patch scale (Law *et al.* 2003; Saleska *et al.* 2003; Hutrya *et al.* 2007). An alternative explanation suggests that canopy photosynthesis of conifer forests reaches a plateau 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 also possess much greater rates in  $F_A$  and  $F_R$  than natural forest stands of similar age (Arain and Restrepo-Coupe 2005).

There are some differences in the carbon-flux trajectory among sites that have been burnt and logged (Amiro *et al.* 2006). Burnt sites tend to produce a smaller, post-disturbance respiratory pulse than do 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 (Law *et al.* 2003; Clark *et al.* 2004; Amiro *et al.* 2006). For example,  $F_N$  was as high as  $1269 \text{ gC m}^{-2} \text{ year}^{-1}$  1 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-grid 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 with networks of towers, flux instrumentation mounted on airplanes and by remote sensing from satellites (Desjardins *et al.* 1997; Sellers *et al.* 1997; Dolman *et al.* 2006; Miglietta *et al.* 2007). However, 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  $900 \text{ gC m}^{-2} \text{ year}^{-1}$  (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 ( $-500 \text{ gC m}^{-2} \text{ year}^{-1}$ ) and carbon exchange by a spruce forest was nearly neutral. In contrast, managed crops experienced a relatively short carbon-uptake period and took up much less carbon ( $-34$  to  $-193 \text{ gC m}^{-2} \text{ year}^{-1}$ ). Furthermore, crops were substantial carbon sources when one considered carbon removed via harvest.

Spatial variations in  $\text{CO}_2$  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 above 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  $\text{CO}_2$ , 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 irrigated v. rainfed. One study found that  $F_N$  of a field cultivated with conventional methods was  $-27 \text{ gC m}^{-2} \text{ year}^{-1}$  more negative than one experiencing reduced tillage, across 2 years (Baker and Griffis 2005). More carbon stock was removed from the conventional field, so the overall tillage effects were smaller ( $10 \text{ gC m}^{-2} \text{ year}^{-1}$ ). A second study across 6 years found that no-till corn was a carbon sink ( $-184 \text{ gC m}^{-2} \text{ year}^{-1}$ ) and a no-till soybean crop was a carbon source ( $93.8 \text{ gC m}^{-2} \text{ year}^{-1}$ ) on the basis 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 America, farmers grow either irrigated or rainfed rotations of soybeans and corn or grow irrigated corn continuously. A set of studies, conducted across 3 years, found that rainfed corn and soybean rotations were carbon neutral ( $-2$  to  $36 \text{ gC m}^{-2} \text{ year}^{-1}$ ), irrigated and continuous corn cultivation was a slight carbon source ( $25$ – $46 \text{ gC m}^{-2} \text{ year}^{-1}$ ) and irrigated corn-soybean rotation was a moderate source of carbon ( $85$ – $102 \text{ gC m}^{-2} \text{ year}^{-1}$ ) (Suyker *et al.* 2004, 2005; Verma *et al.* 2005).

#### **Validating and parameterising 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 modellers have seized the opportunity to either use such data to validate their land-surface subroutines or test parameter sensitivity and model uncertainty (Thornton *et al.* 2002; Rambal *et al.* 2003; Woodward and Lomas 2004; Medlyn *et al.* 2005; Grant *et al.* 2006; Kucharik *et al.* 2006; Verbeeck *et al.* 2006; Alton *et al.* 2007; Friend *et al.* 2007). 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 minimisation, is preferred because the eddy flux data are not homogeneous (Medlyn *et al.* 2005; Gove and Hollinger 2006).

Despite the ‘perils’ and ‘pitfalls’, there remain many benefits in using eddy flux data to test models. Friend and colleagues (Friend and Kiang 2005; Friend *et al.* 2007) reported 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 concluded that the greatest value of flux data for global carbon-cycle modelling 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 (Wang *et al.* 2001; Reichstein *et al.* 2003; Aalto *et al.* 2004; Jarvis *et al.* 2004; Schulz and Jarvis 2004; Wang *et al.* 2004; Braswell *et al.* 2005; Knorr and Kattge 2005; Raupach *et al.* 2005; Richardson and Hollinger 2005; Williams *et al.* 2005; Gove and Hollinger 2006). 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 has been developed on the basis of maximum likelihood (least-squares fit, Levenberg–Marquardt optimisation, 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). Knorr and Kattge (2005) found that their model could produce the probability distribution of measured carbon fluxes for 2 years simply by assimilating 7 days of flux data to parameterise 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 as 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 (Ruimy *et al.* 1995; Buchmann and Schulze 1999; Yi *et al.* 2004; van Dijk *et al.* 2005; Gilmanov *et al.* 2007; Owen *et al.* 2007). The common approach is to fit carbon flux and light ( $Q$ ) measurements to the Michaelis–Menten or rectangular hyperbola function (Eqn 1) and evaluate key parameters such as the quantum efficiency ( $\alpha$ ), the saturation rate of carbon uptake ( $\beta$ ) and dark respiration ( $\gamma$ ) as follows:

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

In a survey of 20 European grassland sites (Gilmanov *et al.* 2007), light use efficiency ( $\alpha$ ) was  $49.3 \pm 16.8 \mu\text{mol mol}^{-1}$ , the maximum carbon-uptake rate at light saturation ( $Q$ ) was  $35.22 \pm 11.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  and dark respiration ( $\gamma$ ) was  $6.8 \pm 2.27$ . In another study, Owen *et al.* (2007) quantified the coefficients in Eqn 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 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, such as the normalised 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,  $f_{par}$ , to estimate leaf area index or they are incorporated into algorithms to produce estimates of light use efficiency, and 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, such as *NDVI*, 'saturate' when the leaf area index exceeds three (Sellers 1987; Myneni *et al.* 2002). 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 stresses associated with soil moisture, humidity deficits and temperature are quantified (Xiao *et al.* 2004; Leuning *et al.* 2005; Turner *et al.* 2005; Zhao *et al.* 2005; Heinsch *et al.* 2006; Yuan *et al.* 2007). 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.* 2001, 2004).

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 >400 sites spanning the globe, and many sites have been in operation for more than 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 resulting from 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 tower fluxes to landscapes and regions, adding another level of complexity. We are also learning about inter-annual variability in net carbon fluxes and how it results from a tight coupling between photosynthesis and respiration. Emergent-scale processes have been detected too, such as 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 too biased towards managed temperate forests at mid-age, near their most productive years (Piovesan and Adams 2000; Woodward and Lomas 2004), or that it missed the effects of disturbance and aging forests (Schulze *et al.* 2000; Adams and Piovesan 2002; Korner 2003). 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 above complex terrain, well. And this limitation is expected to remain unless theoretical corrections can be developed and applied by 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 such as ozone, VOCs, methane, nitrous oxide and  $\text{NO}_x$  (Pattey *et al.* 2006) and full greenhouse gas accounting (Soussana *et al.* 2007). 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.

### Acknowledgements

The FLUXNET project has received support from NASA, NSF and ILEAPS. The author is currently supported by NSF grant DEB 0639235, by the Office of Science (BER), US DOE grant DE-FG02-06ER64308 and the Berkeley Water Center/Microsoft e Science project. Much appreciation is expressed to the many collaborators and colleagues who have helped collect the data and have discussed results and findings. In particular, I thank Riccardo Valentini, Steve Running, Bev Law and Bob Cook for helping me shepherd the FLUXNET project during the past decade and to all the collaborating scientists in the regional networks. I also thank Markus Reichstein and Dario Papale, and my former FLUXNET post-docs, Eva Falge, Lianhong Gu and Matthias Falk, for bringing new ideas and energy to the project. Finally, appreciation is extended to Alexander Knohl, Siyan Ma, Markus Reichstein, Youngryel Ryu and Rodrigo Vargas for their internal reviews of this manuscript.

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Manuscript received 10 August 2007, accepted 24 December 2007