Chapter 9
Partitioning of Net Fluxes

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9.1 Motivation

Eddy covariance measures the net exchange of matter and energy between ecosystems and the atmosphere. The net ecosystem exchange of CO_2 (NEE) results from two larger fluxes of opposite sign: CO_2 uptake by photosynthesis (gross ecosystem productivity – GEP) and CO_2 release from ecosystem respiration (R_{eco}) following the definition equation.

$$\text{NEE} = R_{\text{eco}} + \text{GEP} \tag{9.1}$$

with fluxes from atmosphere to biosphere considered negative per the meteorological convention. As per this definition, R_{eco} is always positive, and GEP is negative or zero at nighttime. NEE gives a valuable measure of ecosystem carbon sequestration, but by itself does not describe the processes responsible for carbon flux. Measurements or estimates of R_{eco} and GEP are necessary to

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obtain information about the processes that contribute to NEE for the purposes of ecosystem studies and modeling. Flux partitioning algorithms are necessary to estimate these fluxes over long time periods using eddy covariance data.

Inferring two dependent variables (R_{eco} and GEP) from one observation (NEE) is an ill-posed problem; the same net flux can result from an indefinite number of combinations of R_{eco} and GEP if both are simultaneously occurring or have occurred over the temporal averaging interval used to describe NEE. Hence, additional constraints or information about flux processes are needed. Most flux partitioning strategies are based on the notion that only R_{eco} occurs at night in ecosystems dominated by C_3 and/or C_4 photosynthesis, while GEP is virtually zero [but not with CAM photosynthesis, San-José et al. (2007)]. The challenge comes in extrapolating these nighttime R_{eco} measurements to daytime conditions to estimate GEP by difference using Eq. 9.1. These difficulties are compounded by the fact that nighttime flux measurements are often compromised by stable atmospheric conditions with insufficient turbulence to satisfy the assumptions of the eddy covariance measurement system. These observations must be filtered from the eddy covariance data record (Sect. 5.3), leaving incomplete information about R_{eco} and thereby GEP.

This chapter summarizes existing strategies for NEE flux partitioning and discusses their benefits and limitations, focusing on challenges of model formulation and parameterization. We describe briefly the standard flux partitioning approaches used in the FLUXNET database by Reichstein et al. (2005a) using nighttime data, and Lasslop et al. (2010) using primarily daytime data, noting that these algorithms are subject to improvement and additional algorithms may be added to FLUXNET in the future. We conclude with suggestions for future directions in flux partitioning research, including techniques for estimating assimilation, respiration, and respiratory sources directly using high-frequency eddy covariance measurements (Scanlon and Kustas 2010; Scanlon and Sahu 2008; Thomas et al. 2008) and stable isotope measurements (Zobitz et al. 2007, 2008), as well as challenges in partitioning eddy covariance-based evapotranspiration measurements into evaporation and transpiration for process-based studies in hydrology and for coupled carbon/water cycle science research. We emphasize the use of simple models for flux partitioning for a simple, data-driven understanding of the processes at hand, but also note the important contributions from other strategies including data assimilation, neural networks, and more complex process-based ecosystem models that provide a more complete picture of the processes that contribute to NEE (cf. Desai et al. 2008).

9.2 Definitions

R_{eco} is the combination of respiratory sources from autotrophic respiration, predominantly from organisms whose primary energy source is the sun (i.e., plants) and heterotrophic respiration, whose primary energy source comes from other organisms. In some ecosystems geologic CO_2 release or sequestration cannot be discounted (Emmerich 2003; Kowalski et al. 2008; Mielnick et al. 2005; Were et al. 2010), but we can consider these fluxes minor across most global ecosystems such that Eq. 9.1 represents biological processes.

Important flux quantities are defined here, to avoid ambiguities that might occur, because terms in the literature are sometimes used with different meanings. The following equations and definitions are valid throughout this chapter (see also Sect. 1.4.2),

$$\mathrm{NEE} = F_{\mathrm{C}}^{\mathrm{EC}} + F_{\mathrm{C}}^{\mathrm{STO}} = R_{\mathrm{eco}} + \mathrm{GEP} \tag{9.2}$$

where $F_{\mathrm{C}}^{\mathrm{EC}}$ is the net turbulent CO_2 flux through a horizontal plane above the canopy (conventionally positive when directed toward the atmosphere) (term IV in Eq. 1.24, where the considered component is CO_2), $F_{\mathrm{C}}^{\mathrm{STO}}$ is the change of carbon storage in the atmosphere below the horizontal plane (positive when increasing) (term I in Eq. 1.24), and NEE is the net ecosystem exchange of CO_2 (positive when emitted) (term V in Eq. 1.24). Net ecosystem CO_2 uptake (often called net ecosystem productivity – NEP) is equal to –NEE. With this definition of NEE, the ecosystem boundaries are leaf, stem, branch, (animal), and soil surfaces, which are in conformity with the models used for flux partitioning, described below. Gross ecosystem photosynthesis (GEP) is the CO_2 flux originating from primary production, and R_{eco} (ecosystem respiration) is the CO_2 flux originating from all respiring compartments of the ecosystem. Analogous to NEE and NEP having opposite signs, GEE can also be used as the negative of GEP. The eddy covariance method gives estimates of $F_{\mathrm{C}}^{\mathrm{EC}}$ (see, e.g., Sects. 1.4 and 3.3). Further, the storage term ($F_{\mathrm{C}}^{\mathrm{STO}}$) can be estimated by the integration of a vertical CO_2 concentration profile (see also Sects. 1.4.2 and 2.5), whereupon the middle term of Eq. 9.2 is determined.

Depending on research objectives, R_{eco} may be separated functionally into respiration of autotrophic and heterotrophic organisms, or spatially into above- and below-ground respiration (R_{above}, R_{soil}), where R_{soil} consists of root and microbial (i.e., edaphon) respiration. Neglected here is soil CO_2 efflux originating from inorganic processes (mainly weathering of carbonates in the soil) and from lateral transport into and out of the flux footprint, which is assumed to be minor.

Evapotranspiration (E_{tot}) is defined here as the flux of H_2O through a horizontal plane above the canopy (positive when directed toward the atmosphere, as with CO_2 flux). It consists of transpiration (E_{plant}), evaporation of intercepted water (E_{int}) and evaporation from the soil surface (E_{soil}).

$$F_{\mathrm{v}}^{\mathrm{EC}} = E_{\mathrm{tot}} = E_{\mathrm{plant}} + E_{\mathrm{int}} + E_{\mathrm{soil}} \tag{9.3}$$

Under turbulent conditions the eddy covariance method measures the total flux ($F_{\mathrm{v}}^{\mathrm{EC}} = E_{\mathrm{tot}}$) (term IV of Eq. 1.24, where the considered component is water vapor) (see also Sect. 3.3.3). Sapflow methods can be used to measure E_{plant}, which must be scaled to the volume of canopy measured by the eddy covariance flux footprint (see Sect. 11.3.4).

9.3 Standard Methods

9.3.1 Overview

Flux partitioning algorithms have been compared extensively across multiple measurement sites using multiple methods (Desai et al. 2008; Lasslop et al. 2010; Moffat et al. 2007; Reichstein et al. 2005a; Stoy et al. 2006b). Existing methods differ in: (1) the form of the model including driving variables, (2) parameterization including the cost function used to estimate parameters, (3) choices regarding temporal variability of parameters, and (4) the use of nighttime, daytime or all eddy covariance data used for model parameterization (Moffat et al. 2007).

For convenience, we classify flux partitioning approaches as those that use only filtered (Sect. 5.3) nighttime data to directly measure R_{eco} (Reichstein et al. 2005a), and those that exploit both day- and nighttime data or only daytime data, using light-response curves, to estimate R_{eco} either as the intercept parameter at zero light or a population of data points at zero light for further modeling (Table 9.1). (We note that data assimilation approaches rely on some a priori model structure rather than light- or temperature-response curves per se.) These two broad approaches have been compared by Falge et al. (2002), Stoy et al. (2006b), Lasslop et al. (2010), and others, resulting in generally good agreement, although some are prone to bias (Desai et al. 2008), and any output must be carefully interpreted and preferably compared against independent measurements or models should these exist.

9.3.2 Nighttime Data-Based Methods

Flux partitioning techniques that rely on nighttime data must first ensure that the quality of these data is reliable. The challenge is that turbulence is often suppressed at night and the assumptions of the eddy covariance system – that the transfer of mass between surface and atmosphere can be approximated as the vertical turbulent flux across a plane above the ecosystem, plus storage below this plane Eq. 9.2 – are often violated by nontrivial horizontal and vertical advective fluxes (Aubinet et al. 2010; Rebmann et al. 2010; Staebler and Fitzjarrald 2004). This issue is covered extensively in Chap. 5. Most techniques for ensuring flux data quality employ some friction velocity (u^*) filter (Aubinet et al. 2000; Barford et al. 2001; Falge et al. 2001; Papale et al. 2006; Reichstein et al. 2005a) (Sects. 5.3 and 5.4), but techniques that also account for atmospheric stability, thereby including both the buoyant and mechanical terms (Novick et al. 2004; van Gorsel et al. 2009), flux footprint dimensions (Rebmann et al. 2005; Stoy et al. 2006b), and those that approach the data filtering issue from comprehensive data quality rating systems (Foken et al. 2004) are also common. After filtering for data quality, the remaining population of

Table 9.1 Classification of currently available statistical flux-partitioning approaches to separate ecosystem respiration (R_{eco}) and gross ecosystem productivity (GEP) using eddy covariance-measured net ecosystem exchange of CO_2 (NEE)

Approach	Advantages	Disadvantages
A: Nighttime data	Flux data represents R_{eco}	Extrapolation to daytime periods is necessary, nighttime eddy covariance data quality concerns
1 R_{eco} is modeled as a time-invariant function of temperature Hollinger et al. (1994)	Simplicity, global applicability	Only applicable where no other factors than temperature influence R_{eco} significantly, not generic
2 R_{eco} is modeled as a time-invariant function of temperature and other environmental drivers (Rambal et al. 2003; Reichstein et al. 2002)	Simplicity, accounts for additional drivers of R_{eco}, allows for seasonally varying temperature sensitivity	Results in selection of site specific factors that determine R_{eco}, ancillary variables (e.g., SWC) may not be measured, or not measured uniformally, across ecosystems
3 R_{eco} is modeled using temporally varying base respiration (Rref) parameters and one single temperature sensitivity derived from annual data set (Falge et al. 2002; Law et al. 2002)	Accounts for temporally varying respiration rates at reference temperature resulting from varying substrate availability	Long-term temperature sensitivity from annual data may not reflect short-term responses to environmental variability, introduction of systematic error when extrapolating to daytime
4. R_{eco} is modeled using temporally varying functions of temperature (both Rref and temperature sensitivity varying) (this study)	Accounts for temporally varying respiration rates at reference temperature, caused by any factor, seasonally varying temperature sensitivity is accounted for (Davidson and Janssens 2006)	Often noisiness of eddy covariance data does not allow derivation of temperature sensitivity for large periods of the year, i.e., limited practical applicability

(continued)

Table 9.1 (continued)

Approach	Advantages	Disadvantages
B: R_{eco} derived from daytime NEE observations	Increases size of data set used to make inference; reduces reliance on night-time data.	Depends on specific light-response curve model; light-response curve can be confounded by other factors (e.g., vapor pressure deficit), sometimes yields unstable parameter estimates (high standard errors); R_{eco} estimate susceptible to storage flux problems, since those occur in the morning and evening during low-light conditions
1. R_{eco} as y-intercept from light-response curve of GEP (Falge et al. 2002)	Day-to-day variation of R_{eco} reflected	Only daily R_{eco} can be derived
2. R_{eco} (temperature driven) and GEP (radiation driven) are simultaneously modeled as parts of one fixed model equation (Gilmanov et al. 2003)	Uses all data (night- and daytime)	Resulting GEP is from a model and thus constrained by model assumptions (disallows comparison with other models), temperature sensitivity maybe confounded by response of GEP to environmental factors, that are hard to separate (e.g., is afternoon drop in NEE caused by R_{eco} as $f(T)$ or by high VPD, or even by plant-internal hydraulic constraints)
3. R_{eco} and GEP are simultaneously modeled as parts of one model equation with state dependent parameters (data-based mechanistic modeling approach)	Uses all data (night- and daytime); very flexible approach; parameters can evolve with time and state	Statistical assumptions (e.g., noncorrelated residuals) and robustness against violations may be problematic; maybe affected by confounding factors similar to B2.
4. R_{eco} (temperature driven) and GEP (radiation and VPD driven) are simultaneously modeled as parts of one model equation with state dependent parameters (Lasslop et al. 2010)	Uses nighttime data to derive the t-sensitivity and daytime data for GEP parameters and flux magnitude of R_{eco}	Equifinality and/or local minima in the cost function. Drought limitation of respiration. $-R_{eco}$ is strongly determined by morning and evening measurements where storage peaks can occur.
5. R_{eco} and GEP are derived via a posteriori analysis of an artificial neural network conditioned with all data. (cf. Papale and Valentini 2002) for gap-filling; flux-partitioning not explored	Uses all data (night- and daytime); very flexible approach; influence of different input data can be evaluated for best description of the data set	Extrapolation problem, since zero radiation has to be assumed estimating R_{eco} from neural network during the day; potentially confounded by other factors similar to B2.

nighttime data points, assumed to comprise R_{eco}, are modeled using approaches that make differing assumptions about model formulation and the temporal variability of model parameters (Reichstein et al. 2005a).

9.3.2.1 Model Formulation: Temperature – Measurements

Respiration is an enzyme-mediated biological reaction and thus depends on temperature and substrate availability. Therefore, the simplest possible mechanistic model of ecosystem respiration is a single equation that is a function of temperature and a so-called base respiration which is implicitly dependent on substrate availability.

The treatment of ecosystem respiration as a single temperature-dependent equation may be the simplest possible approach, but carries additional challenges. Which temperature should one choose given that ecosystems encompass some range of temperatures across which respiratory processes occur in the soil, roots, stems, leaves, and other organisms? How should temporal variability in respiration model parameters be treated given that a different mix of substrates with different temperature sensitivities are being respired across time and space (Fierer et al. 2005; Janssens and Pilegaard 2003)?

Despite these complexities, R_{eco} models that are a simple function of air temperature tend to explain more of the observed variance in R_{eco} models compared to models driven by soil temperature (Van Dijk and Dolman 2004), despite site-level differences (Richardson et al. 2006a), and despite the fact that few respiratory sources are at the measured temperature(s) of air at any one time. The better relationship, on average, between air temperature and R_{eco} is likely due to the fact that a larger percentage of soil respiration occurs near the surface; diurnal hysteresis effects are found for respiration when plotting R_{eco} against soil temperature at depth (Bahn et al. 2008; Vargas and Allen 2008). This indicates that soil temperatures are often measured at a level too deep for optimal correlation with ecosystem respiration. In theory, dual- or multiple source models (cf. Ciais et al. 2005; Reichstein et al. 2005b) where respiration is a multivariate function of different temperature should perform better, but empirical evidence to justify multiple source models is lacking. From the practical perspective, soil temperature measurements are lacking for some sites and site-years in the FLUXNET data record. Hence, air temperature is currently mostly used as the independent variable in R_{eco} models for flux partitioning in the FLUXNET database. Nevertheless, for studying individual sites it is recommended to analyze which temperatures correlate best with flux observations.

9.3.2.2 R_{eco} Model Formulation

A common approach to model R_{eco} using temperature as a dominant driver is the so-called Q_{10} equation:

$$R_{\mathrm{eco}} = R_{10} Q_{10}{}^{\frac{\theta-10}{10}} \tag{9.4}$$

Where R_{10} is ecosystem base respiration at 10°C and Q_{10} is the temperature sensitivity parameter, here describing the amount of change in R_{eco} for a 10°C change in temperature (i.e., a Q_{10} of 2 results in a doubling of R_{eco} for every 10°C change in temperature). Base temperatures other than 10°C can be used accordingly (Ryan 1991).

Respiration is also commonly empirically modeled using the Arrhenius equation or variants thereof; for example, Lloyd and Taylor (1994) used soil respiration data from multiple sources to arrive at a popular expression following Arrhenius kinetics:

$$\mathrm{R}_{\mathrm{eco}} = R_{10} \exp\left[E_0\left(\frac{1}{283.15 - \theta_0} - \frac{1}{\theta - \theta_{\mathrm{ref}}}\right)\right] \tag{9.5}$$

where E_0 is an activation energy parameter and is fitted to data, and the θ_{ref} parameter is often set to 227.13 K (–46.02°C) as recommended in the original study (see, e.g., Reichstein et al. 2005a). Numerous studies on ecosystem respiration using eddy covariance data have parameterized equations of this sort for the purposes of flux partitioning (Falge et al. 2001).

Other exponential temperature-based models derived on thermodynamic kinetics (e.g., Eyring model, Desai et al. 2005; Cook et al. 2004) or the modified Arrhenius equation (Gold et al. 1991) have also been proposed in the literature, but fundamentally they retain a functional form and sensitivity similar to the aforementioned equations.

9.3.2.3 Challenges: Additional Drivers of Respiration

R_{eco} responds to more than just temperature alone; sufficient water and nutrient levels are required for biological functioning to occur in the first place. Nutrient limitations may constrain the amount of biomass held by the ecosystem and do not tend to vary dramatically over short timescales in natural or minimally managed ecosystems. These dynamics may be best incorporated into the base respiration parameter rather than explicitly as an additional variable in R_{eco} models. The effects of soil moisture on R_{eco} are arguably more complicated to model for the purposes of flux partitioning because it is dynamic in time and space, constrains autotrophic and heterotrophic respiration differently, and quick changes related to precipitation may induce respiratory pulses, possibly in concert with changes in nutrient availability (e.g., Jarvis et al. 2007, and early references from H.F. Birch within).

Soil moisture strongly impacts R_{eco} and soil respiration by constraining biological activity under dry conditions and inhibiting oxygen availability under extremely wet conditions (Carbone et al. 2008; Irvine and Law 2002). Soil moisture effects enter models as different adjustment terms to the base respiration parameter, the temperature sensitivity parameter, or as multipliers to the entire temperature-based R_{eco} equation (Palmroth et al. 2005). To date, to our knowledge, no single model formulation that includes soil moisture has been demonstrated to perform better than others across multiple sites at the ecosystem level using eddy covariance data.

Unfortunately soil moisture is measured at a minority of FLUXNET sites to date, which limits the global applicability of soil moisture-inclusive models. Hence, in flux network-wide studies that include multiple sites, the effects of soil moisture variability and other limitations on biological functioning may be best approached by varying the parameters of the R_{eco} model in time, rather than changing model formulation given uncertainties regarding the best formulation and a lack of data availability. At the site level, it is critical to understand the effects of soil moisture on respiration from different carbon pools for a comprehensive understanding of ecosystem carbon metabolism, but from the flux network perspective, a simpler R_{eco} model formulation is preferred.

The role of photodegradation, the breakdown of organic matter by solar irradiance, on R_{eco} is beginning to be tested at eddy covariance research sites (Rutledge et al. 2010). The importance of photodegradation to R_{eco} and the best way to model this process across global ecosystems need to be explored further, but it is likely to be important across a wide range of ecosystems with exposed organic matter (Austin and Vivanco 2006; Rutledge et al. 2010).

9.3.2.4 Challenges: Photosynthesis – Respiration Coupling and Within-Ecosystem Transport

Recent research has demonstrated that much of the carbon respired as R_{eco} across many ecosystems was recently fixed as GEP (Barbour et al. 2005; Drake et al. 2008; Högberg et al. 2001; Horwath et al. 1994; Janssens et al. 2001; Knohl et al. 2005; Zhang et al. 2006). This provides an additional complication for R_{eco} modeling and partitioning: If R_{eco} is a function of GEP after some time lag (Mencuccini and Hölttä 2010), and R_{eco} is used to determine GEP by difference Eq. 9.1, a circularity ensues (Vickers et al. 2009). One may incorporate GEP estimates from previous days into an R_{eco} model following findings from isotopic studies (e.g., Table 1 in Stoy et al. 2007) but the time lags between GEP and root/soil respiration may be quite rapid if pressure/concentration waves in the phloem are considered (Mencuccini and Hölttä 2010; Thompson and Holbrook 2003).

Measuring ecosystem metabolism using the eddy covariance system is further complicated by lags due to gas transport from the location of the respiratory source to the eddy covariance instrumentation (Baldocchi et al. 2006; Stoy et al. 2007; Suwa et al. 2004). In other words, the eddy covariance system measures CO_2 efflux, which results from respiration that occurred sometime in the past, depending on the timescales of transport through the soil or plant and the atmosphere. These time lags between CO_2 production in the soil and transport to the above-canopy atmosphere often exceed the common 30-min averaging time for both flux and micrometeorological measurements. In other words, part of the CO_2 that the flux system "sees" as respiration was likely produced under different temperature conditions than measured at the time of its ejection from the ecosystem volume.

These lags decouple the measurement of temperature with the actual process of respiration. Comprehensive treatments of CO_2 production and transport in the soil

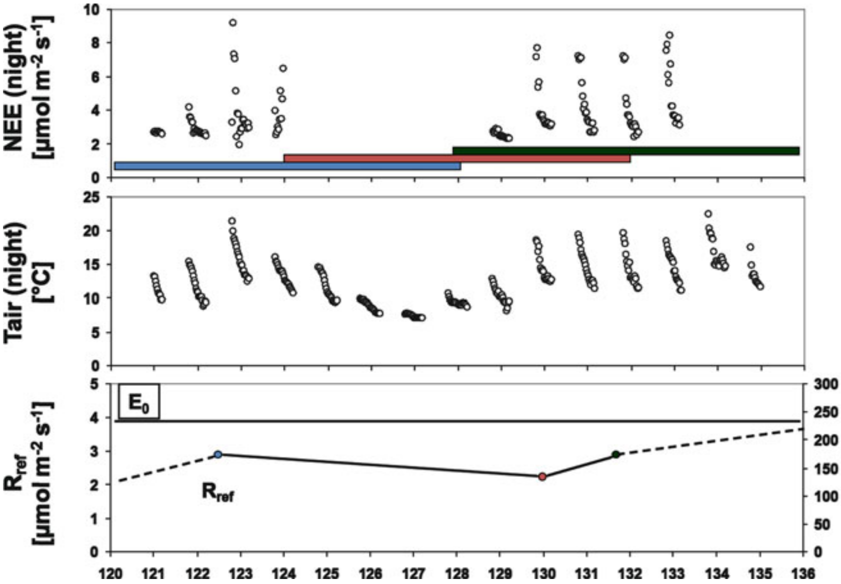

Fig. 9.1 Scheme for derivation of ecosystem respiration parameters from eddy covariance nighttime flux data. *Upper panel* shows the flux data (incl. gaps) with the bars being the 50% overlapping windows used for parameter estimation. *Lower panel* shows the estimates of the reference respiration (*Rref*) based on the data in the respective windows. The estimates of Rref are assigned to the data weighted center of the time window (*dots*) and then linearly interpolated. E_0 is kept constant here as an estimate for the whole year but that is not necessary

or whole ecosystem is commendable and advisable for elucidating the mechanisms responsible for CO_2 production and transport, but involve extensive additional measurements of CO_2 flux within the ecosystem domain (Baldocchi et al. 2006; Daly et al. 2009; Tang and Baldocchi 2005). Incorporating such knowledge into R_{eco} models for eddy covariance applications would involve making extensive assumptions about the location of respiratory sources and transport in the soil, which are not solvable using eddy covariance-based whole-ecosystem measurements alone. The aforementioned processes may be best incorporated into flux partitioning models by adding temporal variability to the R_{eco} model parameters rather than by incorporating additional processes into the model when little information about these processes exists in most cases. By estimating the reference respiration (R_{eco} at reference temperature), every few days with a moving window approach (Fig. 9.1), the reference respiration may vary implicitly as a function of any other factor not explicitly accounted for in the equation (e.g., phenology, soil moisture, substrate availability). The size of the moving window has to reflect a compromise between data availability to estimate statistical models and the necessity to have as small as possible window sizes. Desai et al. (2005) present an approach where the window size varies based on the amount of data, while Reichstein et al. (2005a) use a fixed window size. In any case, the assumption of this approach is that within the time-window used for parameter estimation, R_{ref} does not vary other than described by the linear interpolation. In particular if the reference respiration varies diurnally (e.g., because of links to GEP or short-term variation in soil moisture, or with CO_2 of geogenic origin), this is not reflected in the approach and will cause biases. Moreover, rapid response of the reference respiration, for example, to rain pulses cannot be described with this approach.

9.3.3 Daytime Data-Based Methods

A concern about using nighttime data for R_{eco} modeling is that the input data represent a subset of the total available data that are unlikely to be of the best quality. The alternate approach is to fit a model to daytime NEE observations that accounts for the effects of radiation and vapor pressure deficit (VPD) on GEP as well as the effects of temperature on R_{eco} (Falge et al. 2001; Gilmanov et al. 2003). This approach is to date less common than flux partitioning based on nighttime data, but has been used in earlier eddy covariance studies (Lee et al. 1999) and can complement nighttime data-based methods (Lasslop et al. 2010).

9.3.3.1 Model Formulation: The NEE Light Response

The rectangular hyperbola is a simple, common equation to model the effects of radiation (here the photosynthetically active photon flux density, PPFD) on NEE:

$$\mathrm{NEE} = \frac{\alpha_{\mathrm{RH}}\beta_{\mathrm{RH}}\mathrm{PPFD}}{\alpha_{\mathrm{RH}}\mathrm{PPFD} + \beta_{\mathrm{RH}}} + \gamma_{\mathrm{RH}} \tag{9.6}$$

R_g, the global radiation, can be used in place of PPFD in Eq. 9.6; the values and units for the fitted parameters α_{RH} (the initial slope of the light-response curve) and β_{RH} (GEP at light saturation) will change accordingly. γ_{RH}, the intercept parameter at zero light, represents R_{eco} and can be expanded using a temperature-driven equation (e.g., Gilmanov et al. 2010) (see Fig. 9.2). The rectangular hyperbola has a long history for gap-filling daytime flux data, often with slight modifications concerning the parameters (e.g., Wofsy et al. 1993).

The non-rectangular hyperbola adds a parameter that describes the degree of curvature (θ_{NRH}).

$$\mathrm{NEE} = -\frac{1}{2\theta_{\mathrm{NRH}}}\left(\alpha_{\mathrm{NRH}}\mathrm{PPFD} + \beta_{\mathrm{NRH}} - \sqrt{(\alpha_{\mathrm{NRH}}\mathrm{PPFD} + \beta_{\mathrm{NRH}})^2 - 4\alpha_{\mathrm{NRH}}\beta_{\mathrm{NRH}}\theta_{\mathrm{NRH}}\mathrm{PPFD}}\right) + \gamma_{\mathrm{NRH}} \tag{9.7}$$

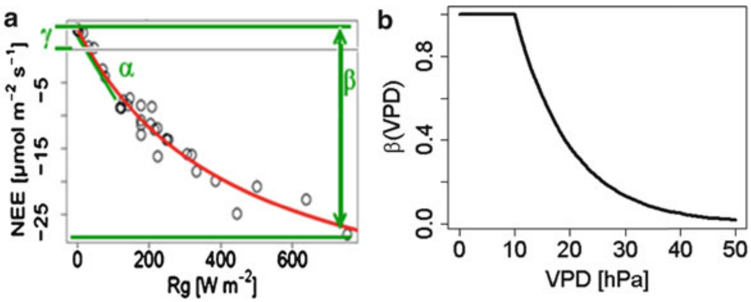

Fig. 9.2 (**a**) Observed net ecosystem exchange, as a function of global radiation, explaining the three parameters with respect to the function's shape: α the light utilization efficiency, is the initial slope, β, the maximum carbon uptake, is the range of NEE and γ, the respiration, is the offset. (**b**) The function decreasing the parameter beta as a function of VPD according to Eq. 9.9; note that the parameter k defining the steepness of the equation is estimated from the data

The non-rectangular light-response curve tends to fit measured data better than the rectangular hyperbola (Gilmanov et al. 2003; Marshall and Biscoe 1980) – as it should give the additional parameter – but the convergence of the parameter routine may be less frequent and logical parameter bounds and initial guesses are encouraged to ensure optimal parameter sets (Stoy et al. 2006b).

Lindroth et al. (2008) and Aubinet et al. (2001) used a slightly different form of a light-response function (Mitscherlich model):

$$\mathrm{NEE} = -\left(\beta_{\mathrm{M}} + \gamma_{\mathrm{M}}\right)\left(1 - \exp\left(\frac{-\alpha_{\mathrm{M}}\mathrm{PPFD}}{\beta_{\mathrm{M}} + \gamma_{\mathrm{M}}}\right)\right) + \gamma_{\mathrm{M}} \tag{9.8}$$

It is important to note that, whereas the various light-response models Eqs. 9.6–9.8 may fit the data equally well, the parameters of the equations need not take the same values (hence the different subscripts) and may not take realistic values of carbon exchange phenomena as demonstrated in Fig. 9.3 and Table 9.2. Here, 1 day of observed NEE from the Duke Hardwood forest ecosystem (US-Dk2) was modeled using Eqs. 9.6–9.8 and nonlinear least squares was chosen to find the optimum parameter values. For the rectangular hyperbola, the optimized value of β_{RH} is 0.66 mg $\mathrm{C\,m^{-2}\,s^{-1}}$, far greater than the largest observed flux that day (0.34 mg $\mathrm{C\,m^{-2}\,s^{-1}}$) which itself may be considered an outlier. This saturating value of β_{RH} exists at a light level that will never realistically be reached and is not the saturating value of NEE under field conditions, rather a parameter that describes the maximum value of the rectangular hyperbola fit to observations. Flux studies should take care to note this distinction, a more reasonable value of the maximum carbon uptake can be computed by using the model parameters and a radiation value that can be considered a maximum radiation. In Fig. 9.1, $\beta_{\mathrm{NRH}} = 0.29\mathrm{mgCm^{-2}s^{-1}}$, roughly the median of the points at high light. $\beta_{\mathrm{M}} = 0.39\mathrm{mgCm^{-2}s^{-1}}$, beyond the limits of what was observed but closer to a realistic value of NEE at saturation than

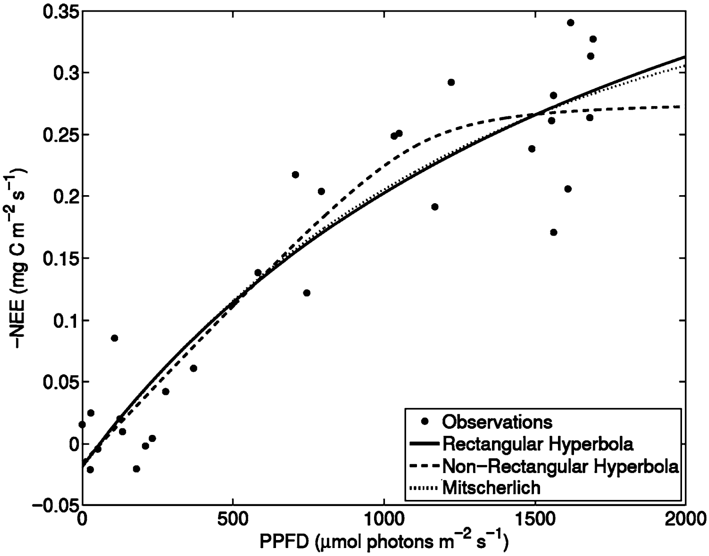

Fig. 9.3 Observed (negative) net ecosystem exchange (−NEE, i.e., net ecosystem productivity, NEP), as a function of photosynthetically active photon flux density (PPFD) for day of year 170, 2005 in the Duke Forest hardwood ecosystem fit using a rectangular hyperbola, a non-rectangular hyperbola, and the Mitscherlich model (Aubinet et al. 2001; Lindroth et al. 2008) Eqs. 9.6–9.8. Fitted parameters are listed in Table 9.2

β_{RH}. Whereas any of the above equations may result in defensible values of modeled NEE and partitioned GEP and R_{eco}, the parameter values themselves may not make physical sense.

9.3.3.2 Challenges: Additional Drivers and the FLUXNET Database Approach

Radiation is not the only driver of NEE; the photosynthetic term that dominates during the day may be constrained by stomatal closure, often modeled as a function of vapor pressure deficit (VPD) (Oren et al. 1999; Lasslop et al. (2010)). These effects are embodied in a hysteresis pattern in the light-response curve, with lower NEE values in the afternoon when temperature and vapor pressure deficit (VPD) are higher (Gilmanov et al. 2003). Stomatal behavior has been successfully explained by the so-called optimality hypothesis which assumes that stomata behave to maximize carbon gain while minimizing water loss (see, e.g., Cowan 1977; Mäkelä et al. 2002). The fundamental role of stomata in regulating both carbon and water fluxes suggests that transpiration estimates can be used to constrain GEP. From the eddy covariance perspective, such an approach would require additional modeling

Table 9.2 Parameter values, with units and logical bounds, for the light-response curves Eqs. 9.6–9.8 fit to 1 day of observed eddy covariance-measured NEE in the Duke Forest hardwood ecosystem on DOY 170, 2005 (Fig. 9.3)

Parameter	Units	Value (Fig. 9.3)	Logical bounds
Rectangular hyperbola			
α_{RH}	(mg C μmol photons^{-1})	0.00033 ± 0.00024	[a]
β_{RH}	(mg C m^{-2} s^{-1})	0.66 ± 0.52	$[\mathrm{NEE}_{\min}, R_{\mathrm{eco,max}}]$
γ_{RH}	(mg C m^{-2} s^{-1})	0.019 ± 0.042	$[0, R_{\mathrm{eco,max}}]$
Non-rectangular hyperbola			
α_{NRH}	(mg C μmol photons^{-1})	0.00026 ± 0.00013	[a]
β_{NRH}	(mg C m^{-2} s^{-1})	0.29 ± 0.10	$[\mathrm{NEE}_{\min}, R_{\mathrm{eco,max}}]$
θ_{NRH}	(unitless)	0.98 ± 0.13	[0, 1]
γ_{NRH}	(mg C m^{-2} s^{-1})	0.016 ± 0.036	$[0, R_{\mathrm{eco,max}}]$
Mitscherlich equation			
α_{M}	(mg C μmol photons^{-1})	0.00033 ± 0.00020	[a]
β_{M}	(mg C m^{-2} s^{-1})	0.39 ± 0.22	$[\mathrm{NEE}_{\min}, R_{\mathrm{eco,max}}]$
γ_{M}	(mg C m^{-2} s^{-1})	0.020 ± 0.040	$[0, R_{\mathrm{eco,max}}]$

$R_{\mathrm{eco,max}}$ is the maximum observed ecosystem respiration

[a] The positive and negative values of the slope where $\mathrm{NEE}_{\max}$ is reached at the lowest logical value of PPFD, that is, the greatest logical slope of the light-response curve

of transpiration from evapotranspiration while noting that eddy covariance-based evapotranspiration measurements are not independent from eddy covariance-based GEP estimates.

The degree to which R_{eco} is enhanced by higher temperatures and GEP is reduced by stomatal responses to VPD is uncertain. VPD is partly a function of temperature, and both R_{eco} and GEP occur simultaneously during the day when leaves are present. Despite these challenges, multiple approaches separating GEP and R_{eco} from daytime NEE observations have been tested.

Gilmanov et al. (2006, 2003) introduced an exponential function in the place of γ_{NRH} in Eq. 9.7 and added an exponential decrease of GEP with relative humidity to account for stomatal effects Lasslop et al. (2010) expanded on this approach by introducing the Lloyd and Taylor model Eq. 9.5 in place of γ_{RH} in Eq. 9.6 and added a VPD limitation on NEE that decreases β_{RH} exponentially from a maximum value β_0 for VPD higher than a limiting value (VPD_0), which was determined to be 1 kPa based on a synthesis of leaf-level findings (Körner 1995) (note also Oren et al. 1999) (see Fig. 9.3):

$$\beta_{\mathrm{RH}} = \begin{cases} \beta_0\, e^{-k\cdot(\mathrm{VPD}-\mathrm{VPD}_0)} & \text{for VPD} > \mathrm{VPD}_0 \\ \beta_0 & \text{for VPD} < \mathrm{VPD}_0 \end{cases} \tag{9.9}$$

Parameterizing a model that combines Eqs. 9.5, 9.6, and 9.9 is challenging and parameter equifinality is likely to occur: the decrease in GEP due to VPD has the same effect on NEE as an increase in R_{eco} due to temperature. Lasslop et al. (2010) estimated the parameters of the combined equation using a multistep process. The temperature sensitivity of R_{eco} was estimated first from nighttime data using 15-day windows after Reichstein et al. (2005a). In a second step, the temperature sensitivity was fixed and the remaining fitted parameters were estimated using 4-day windows of daytime data, noting that the base respiration parameter was fit alongside the other parameters using daytime data to ensure a degree of independence from the nighttime data. Including these five parameters in the optimization routine still results in an overparameterized model in certain situations. For instance if VPD is low, the parameter k is not well constrained, but it can influence the results if it is used for extrapolation to high VPD. Meaningless photosynthetic parameters are common for deciduous forests and polar ecosystems in winter. (Table A1 in Lasslop et al. 2010, explains how parameters were treated if they were not in a predefined range.)

The myriad choices available for modeling R_{eco} and GEP using daytime data from global ecosystems leaves open the possibility for multiple improvements to the FLUXNET flux partitioning algorithm in the future. Desai et al. (2008) demonstrated significant differences among light-response curve-based methods and showed that, whereas some methods may be more subject to biases than others, it is not possible to identify one superior method given flux observations and an unknown “true” flux. This suggests that future work on flux partitioning using multiple, complementary methods is an ideal way forward to ensure defensible partitioned estimates with conservative error bounds.

9.3.3.3 Unresolved Issues and Future Work

It has been reported that canopy assimilation is not only affected by the overall shortwave radiation flux density, but also by its direct or diffuse characteristics; higher assimilation rates have been observed at the same overall radiation flux density under conditions dominated by diffuse radiative flux (Baldocchi et al. 1997; Gu et al. 2003; Hollinger et al. 1994; Jenkins et al. 2007; Knohl and Baldocchi 2008; Niyogi et al. 2004). Diffuse radiation is measured at few FLUXNET sites to date, and incorporating the effects of diffuse radiation on NEE for global flux partitioning would require models to separate direct and diffuse radiation from net radiation measurements. This introduces the problem of using modeled data to drive a model. Diffuse radiation is also correlated with low VPD values, and the relative importance of each needs to be ascertained before modeling efforts proceed (Rodriguez and Sadras 2007; Wohlfahrt et al. 2008).

To summarize, we recommend simple, process-based R_{eco} models with varying parameters to incorporate rapid, seasonal, or interannual changes in canopy structure, soil moisture, ecosystem nutrient level, and carbon transport for the purpose of partitioning GEP and R_{eco} across the global eddy covariance tower network (Reichstein et al. 2005a). At the site level, we advocate integrating above-canopy eddy covariance instrumentation, below-canopy eddy covariance (Baldocchi et al. 1997), carefully designed respiration chambers (Bain et al. 2005; Subke et al. 2009; Xu et al. 2006), isotopic techniques (Ekblad et al. 2005; Ekblad and Hogberg 2001;

Högberg et al. 2001), laboratory analyses (Conant et al. 2008), and modeling studies (Adair et al. 2008; Thompson and Holbrook 2004) for developing a comprehensive ecosystem-level mechanistic understanding of R_{eco}.

9.4 Additional Considerations and New Approaches

9.4.1 Oscillatory Patterns

Circadian rhythms of stomatal conductance have not been formally considered for flux partitioning to date. They are either endogenous or caused by hydraulic limitations in the afternoon. These patterns in the diurnal cycle can persist for more than a week, independent of environmental influences (Hennessey and Field 1991). Although this effect has been widely observed (Gorton et al. 1993; Hennessey et al. 1993; Nardini et al. 2005), the degree to which they affect the carbon exchange under field conditions is less clear. Williams et al. (1998) suggested by using a modeling approach that these circadian rhythms do not significantly affect photosynthesis and stomatal conductance in field conditions. Recent laboratory-based findings have found the circadian rhythms of root functioning to be coupled to leaf function at the plant level (James et al. 2008), but ecosystem-level relationships have yet to be explored and for the moment oscillatory patterns may be best treated by model parameterization rather than changing model structure.

9.4.2 Model Parameterization

So far we have discussed model parameters but not methods for determining their value and associated uncertainty, which is critical for assimilating data into ecosystem models (Raupach et al. 2005; Williams et al. 2009). The form of the cost function, rather than the technique used to find the optimum parameter values, tends to be more important for accurate parameter estimation using flux data (Fox et al. 2009; Trudinger et al. 2007). It has been argued that the error in flux measurements follows a Laplace (double exponential) distribution such that least absolute deviations rather than least-squares techniques should be used for the cost function (Hollinger and Richardson 2005; Richardson et al. 2006b, see also Sect. 7.2.5), but other studies have suggested that error in eddy covariance flux measurements can be approximated as a normal distribution with nonstationary variances that are a function of flux magnitude (Lasslop et al. 2008). Rannik and Vesala (1999) presented relative systematic and random error distributions for sensible heat fluxes, which are qualitatively same for other scalars. Importantly, any method should not understate uncertainty in parameter values or resulting partitioned flux estimates.

A major theme of the discussion to this point is that half-hourly eddy covariance observations alone are not sufficient to understand the mechanisms responsible for R_{eco} and GEP fluxes. The simple models advocated to this point are but one approach for flux partitioning, albeit the most common. Additional techniques can and should be investigated to improve our understanding of ecosystem processes and the biosphere–atmosphere flux of CO_2.

9.4.3 Flux Partitioning Using High-Frequency Data

It has been argued that the high-frequency (e.g., 10 or 20 Hz) flux data contains more information about the sources of CO_2 (Thomas et al. 2008) and the assimilation/respiration dynamics (Scanlon and Kustas 2010; Scanlon and Sahu 2008) than is commonly acknowledged. To partition respiration sources into above- and below-canopy components Thomas et al. (2008) used a conditional sampling method to identify turbulent events that represented both a source of water vapor and CO_2 to the atmosphere, and attributed these events to transport from below the plant canopy. It was noted that the resultant respiratory fluxes agreed with chamber-based measurements and the intercept of eddy covariance light-response curves.

Scanlon and Kustas (2010) noted that stomatal processes (i.e., GEP and E_{transp}) and non-stomatal processes (R_{eco} and E_{soil}) each conform separately to flux-variance (Monin-Obukhov) similarity and provided an analytical expression based on the water use efficiency to partition both CO_2 and water vapor fluxes using high-frequency data (Scanlon and Sahu 2008). Seasonal patterns of these partitioned flux estimates followed closely canopy development in an agricultural ecosystem.

An obvious problem with these approaches for integration into the FLUXNET database is the lack of available or synthesized high-frequency flux data to perform these analyses globally, although for site-level studies and future research they may prove extremely valuable for not only quantifying ecosystem carbon and water dynamics, but also transport phenomena at the biosphere–atmosphere interface.

9.4.4 Flux Partitioning Using Stable Isotopes

As discussed, a fundamental problem with flux partitioning is that one measurement (NEE) is being used to infer two processes (R_{eco} and GEP). A natural solution would be to add measurements that provide additional information. Naturally abundant stable isotopes in the atmosphere provide a way forward. Stable isotope observations to better understand plant ecology and biochemistry have a long history (Dawson et al. 2002), but their use for partitioning eddy covariance-measured NEE is more recent (Bowling et al. 2001; Lloyd et al. 1996). The biochemistry of photosynthesis is such that plants prefer the lighter isotope of CO_2, thereby imprinting that signature on both organic matter (depleted in heavier isotopes) and in the atmosphere (enriched) (Yakir and da Silveira Lobo Sternberg 2000). Photosynthetic fractionation leads to atmospheric enrichment of ^{13}C in CO_2 and, through equilibration of transpired water and assimilation of CO_2, to enrichment of ^{18}O in CO_2. Additional fractionation of CO_2 isotopes during autotrophic and microbial respiration further separates the isotopic signature of respired products from assimilation (Knohl and Buchmann 2005).

An equation for isotopic fractionation by GEP and R_{eco} can be written following Ogée et al. (2004):

$$\delta_{\mathrm{N}}\mathrm{NEE} = \delta_{\mathrm{R}} R_{\mathrm{eco}} - \left(\delta_{\mathrm{a}} - \Delta_{\mathrm{canopy}}\right) \mathrm{GEP} \tag{9.10}$$

where the first term represents the product of NEE and its isotopic composition (δ_{N}), commonly called the isoflux, the second term the effect of respiration on atmospheric isotopic composition (δ_{R}), and the latter term the discrimination by photosynthesis ($\varDelta_{\mathrm{canopy}}$) for lighter isotopes of CO_2 in the atmosphere, which has its own isotopic composition (δ_{a}). Isotopic ratios are commonly expressed in units of per mil with respect to a benchmark standard. Combining Eq. 9.10 with Eq. 9.1, and observations of NEE, the isoflux, δ_{R}, δ_{a}, and a model of $\varDelta_{\mathrm{canopy}}$, allows one to infer R_{eco} and GEP.

Currently, eddy covariance observations of the isoflux are limited by the frequency responses of instrumentation, so it is instead generally inferred from flux-gradient or relaxed (or disjunct) eddy accumulation techniques. The isotopic composition of R_{eco} is typically measured from the intercept of a Keeling plot, which plots the inverse of nighttime CO_2 versus its isotopic composition (Pataki et al. 2003). Isotopic discrimination during assimilation ($\varDelta_{\mathrm{canopy}}$) is typically assumed from equations of stomatal conductance and leaf cellular CO_2 diffusion during the photosynthetic process.

There are a number of uncertainties in this approach that need to be propagated for defensible GEP and R_{eco} estimates. These include the mismatch between concentration profiles and flux footprints, the sensitivity of micrometeorological flux-gradient techniques to atmospheric stability and mixing, the assumptions made in Keeling plot analysis and the canopy discrimination model (which, for example, differs substantially for C3 and C4 photosynthesis), the sampling frequency of isotope observations, and assumptions made about isotopic equilibration with plant and soil water and equivalency in fractionation for autotrophic and heterotrophic respiration. For example, Ogée et al. (2004) demonstrated that uncertainty could exceed 4 μmol m^{-2} s^{-1} for half-hourly observations of GEP and R_{eco} using isotopic methods. Further, isotopic flux partitioning is strongly sensitive to the extent of isotopic disequilibrium between R_{eco} and GEP, which is relatively small for $^{13}CO_2$. Direct in situ high-frequency isotope observations (e.g., Zhang et al. 2006) and Bayesian parameterization of canopy photosynthetic and isotopic models (e.g., Zobitz et al. 2007) address some of the uncertainties associated with isotopic techniques. Isotopic partitioning of NEE is still primarily limited by the lack of stable isotope observations at most FLUXNET sites; however, these deficiencies will likely change in the future as sensor prices and stability improve.

9.4.5 Chamber-Based Approaches

Eddy covariance measurements of NEE can be partitioned to different component fluxes by upscaling chamber measurements (e.g., soil, leaf, bole, and coarse woody debris fluxes) of CO_2 uptake and release (Bolstad et al. 2004; Harmon et al. 2004; Lavigne et al. 1997; Law et al. 1999; Ohkubo et al. 2007; Wang et al. 2010). Upscaling involves extrapolation of measurements both in space (i.e., from individual chambers to the whole ecosystem) and in time (i.e., from periodic or intermittent measurements to a half-hourly time step commensurate with the tower-measured fluxes, or to an annual time step for ecosystem C budgets). Also required is information about the size of various C pools, for example, leaf area index and canopy density profiles, bole volume, and sapwood area of trees of different diameter classes, and the amount and state of decay of coarse woody debris. The overall approach to upscaling, and the way in which component fluxes interact with environmental drivers, varies among studies and is highly dependent on the data available and the assumptions that need to be made; the studies cited above provide a range of examples.

There are major uncertainties inherent in chamber-based approaches for measuring photosynthetic uptake or respiration from stems, leaves, and soil (Lavigne et al. 1997; Loescher et al. 2006). These include sampling uncertainties (representativity and spatial heterogeneity), scale mismatches between chambers and the tower footprint, as well as random and systematic measurement errors (e.g. Savage et al. 2008; Subke et al. 2009). For example, Lavigne et al. (1997) reported poor agreement between upscaled chamber measurements and nocturnal NEE measurements at six evergreen boreal field sites, largely because of the inherent noise in both estimates, but also because of a systematic bias on the order of 20–40%. These uncertainties will ideally be reduced as improved chamber designs are developed and improved spatiotemporal measurement strategies are adopted (Bain et al. 2005; Subke et al. 2009; Xu et al. 2006).

Estimating the uncertainties inherent in individual measurements, and then propagating these forward in the upscaling methodology is desirable, but is rarely done in a comprehensive manner. This is, however, a relatively straightforward task if the upscaling is conducted using a model-data fusion framework in conjunction with a process-based model of ecosystem C dynamics: posterior uncertainties in partitioned fluxes can be estimated conditional on both the model and the data used as constraints (e.g., Richardson et al. 2010). (For an alternative Monte Carlo approach conducted at the annual time step, see Harmon et al. 2004.)

9.4.6 Partitioning Water Vapor Fluxes

Eddy covariance flux partitioning need not be limited to carbon fluxes. Given the ubiquity of carbon flux investigations, and the relative paucity of water and energy flux studies to date, carbon flux partitioning has been the overwhelming focus. Process-based studies in hydrology can benefit tremendously from knowledge of the pathways by which water enters the atmosphere from the terrestrial surface.

In a similar manner to carbon fluxes, periods exist where terms of the evapotranspiration equation Eq. 9.3 are zero or negligible. For example, in deciduous forests, E_{transp} and E_{int} are near zero during leaf-off except immediately after rain events. Assuming that stem evaporation is minor, $E_{\text{tot}} \cong E_{\text{soil}}$. Stoy et al. (2006a) modeled E_{soil} as a function of radiation that penetrated the aboveground vegetation in temperate forest and grass ecosystems in southeastern USA. The model was parameterized using eddy covariance measured E_{tot} during dry periods when the respective canopies were known to be inactive. Partitioned E_{transp} estimates approximated well stand-level E_{transp} estimated by sapflux for the Duke Forest loblolly pine ecosystem (Schäfer et al. 2002). (Oishi et al. 2008) modeled E_{soil} as a function of VPD using a subset of dry, wintertime eddy covariance data from the Duke Forest hardwood ecosystem and found good agreement between annual eddy covariance-measured ET, and annual ET based on the sum of this evaporation model, stand-scaled sapflux measurements, and modeled canopy interception. Partitioning eddy covariance E_{tot} by directly using upsclaled sapflux measurements is another common technique (see Sect. 11.3.4).

Stable isotope-based approaches for partitioning evaporation and transpiration from evapotranspiration measurements have been explored (Wang and Yakir 2000) (Albertson et al. 2001) but not widely applied to date. We note that the US–based National Earth Observation Network (NEON) will use a stable isotope-based approach in conjunction with eddy covariance data to separate evaporation and transpiration and such approaches are likely to find wide applicability in the near future.

9.5 Recommendations

Extensive work on ecosystem carbon flux partitioning has been completed to date, but there is more to be done. We caution against using a single standard algorithm for partitioning R_{eco} and GEP given the potential for bias (Desai et al. 2008); multiple methods should be compared at each site to ensure that the outcome is robust. We recommend comparing both light-response curve and temperature response curve methods as quasi-independent checks (Lasslop et al. 2010; Reichstein et al. 2005a) and to develop additional flux partitioning routines to challenge and improve standard approaches.

An argument often arises: why not use more complex process-based models for the purpose of flux partitioning (Desai et al. 2008)? More complex models have the potential to deliver more accurate partitioned fluxes, but the uncertainty of the model formulation is difficult to quantify (Rastetter et al. 2010) and the partitioned estimates may be used to constrain model output or compare against model output, resulting in a circularity. By ensuring that flux estimates are data-driven to the extent that this is possible using the simplest physiologically reasonable models available, the values that are least contaminated by model assumptions can be found. Techniques that are entirely data-driven (e.g. artificial neural networks) are likewise of value but may have difficulties extrapolating observations.

We note that the techniques favored to date are not static or "final" and that ample opportunity for improvement exist. Checks of eddy covariance-derived net and partitioned fluxes against independent flux estimates continue to have the potential to improve algorithms. Given the centralized management of the FLUXNET database, new, different, and/or improved approaches can be integrated as additional derived products without extensive additional effort and will aid in the generation of conservative error bounds on NEE, GEP, and R_{eco}. We encourage continued investigations into partitioning carbon and water fluxes using the FLUXNET database.

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