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Comparing methods for partitioning a decade of carbon dioxide and water vapor fluxes in a temperate forest

Benjamin N. Sulman[a,b,c,*], D. Tyler Roman[a,d], Todd M. Scanlon[e], Lixin Wang[f], Kimberly A. Novick[a]

[a] School of Public and Environmental Affairs, Indiana University, 702 N Walnut Grove Ave., Bloomington, IN 47405, USA
[b] Department of Biology, Indiana University, 1001 E 3rd St., Bloomington, IN, 47405, USA
[c] Program in Atmospheric and Oceanic Sciences, Department of Geosciences, Princeton University, 300 Forrestal Rd, Princeton, NJ 08544, USA
[d] U.S. Department of Agriculture, Forest Service, Northern Research Station, 1831 Hwy. 169 E., Grand Rapids, MN, 55744, USA
[e] Department of Environmental Sciences, University of Virginia, 291 McCormick Rd, Charlottesville, VA, 22904, USA
[f] Department of Earth Sciences, Indiana University-Purdue University Indianapolis (IUPUI), 723 W. Michigan St, Indianapolis, IN 46202, USA

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ABSTRACT

The eddy covariance (EC) method is routinely used to measure net ecosystem fluxes of carbon dioxide (CO_2) and evapotranspiration (ET) in terrestrial ecosystems. It is often desirable to partition CO_2 flux into gross primary production (GPP) and ecosystem respiration (RE), and to partition ET into evaporation and transpiration. We applied multiple partitioning methods, including the recently-developed flux variance similarity (FVS) partitioning method, to a ten-year record of ET and CO_2 fluxes measured using EC at Morgan Monroe State Forest, a temperate, deciduous forest located in south-central Indiana, USA. While the FVS method has previously been demonstrated in croplands and grasslands, this is the first evaluation of the method in a forest. CO_2 fluxes were partitioned using nonlinear regressions, FVS, and sub-canopy EC measurements. ET was partitioned using FVS and sub-canopy EC measurements, and sub-canopy potential evapotranspiration was calculated as an additional constraint on forest floor evaporation. Leaf gas exchange measurements were used to parameterize a model of water use efficiency (WUE) necessary for the FVS method. Scaled leaf gas exchange measurements also provided additional independent estimates of GPP and transpiration. There was good agreement among partitioning methods for transpiration and GPP, which also agreed well with scaled leaf gas exchange measurements. There was higher variability among methods for RE and evaporation. The sub-canopy flux method yielded lower estimates of evaporation and RE than FVS and lower estimates of RE than the nonlinear regression method, likely due to the exclusion of flux sources within the canopy but above the top of the sub-canopy tower for the sub-canopy flux method. Based on a sensitivity test, FVS flux partitioning was moderately sensitive to errors in WUE values, and underestimates of WUE significantly reduced the rate at which the algorithm was able to produce a physically valid solution. FVS partitioning has unique potential for retroactive ET partitioning at EC sites, because it relies on the same continuous measurements as EC and does not require additional specialized equipment. FVS also has advantages for partitioning CO_2 fluxes, since it does not rely on the mechanistic assumptions necessary for the commonly used nonlinear regression technique.

1. Introduction

Eddy covariance (EC) instrumentation (Baldocchi et al., 1988) measures ecosystem-scale net turbulent fluxes of carbon dioxide and water vapor between the land surface and the atmosphere. It is often desirable to decompose these net fluxes into ecologically relevant components. Net ecosystem exchange (NEE) of carbon dioxide (CO_2) measured by EC instrumentation can be decomposed into gross primary production (GPP) and ecosystem respiration (RE). In this paper, we define NEE = RE − GPP, so that NEE is negative when photosynthesis exceeds respiration, while GPP and RE are always considered to be positive quantities. The most common method for CO_2 flux partitioning uses nonlinear regressions based on quasi-empirical models describing the relationship between these fluxes and meteorological drivers (Lasslop et al., 2009; Reichstein et al., 2005; Stoy et al., 2006). Because photosynthesis does not occur in

* Corresponding author at: Program in Atmospheric and Oceanic Sciences, Department of Geosciences, Princeton University, 300 Forrestal Rd, Princeton, NJ 08544, USA.
E-mail addresses: bsulman@princeton.edu, bsulman@gmail.com (B.N. Sulman).

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darkness, nighttime NEE is often used to parameterize a simple model of RE that depends on soil temperature. The observed NEE is then subtracted from the modeled daytime RE in order to determine GPP (Reichstein et al., 2005). An alternative method fits NEE to a light response curve, determining RE using the intercept of the curve as incoming shortwave radiation approaches zero (Lasslop et al., 2009). A more recently developed alternative to the nonlinear regression methods uses measurements of carbonyl sulfide (COS), which is taken up by leaves through a similar pathway to CO_2 but is not emitted by respiration-like processes in significant amounts in terrestrial ecosystems (Blonquist et al., 2011). The COS technique is a promising approach for estimating GPP that does not depend on assumed relationships between NEE and its meteorological drivers. However, it is sensitive to assumptions about the rate of COS uptake by soil and the ratio of CO_2 to COS assimilation at the leaf scale (Asaf et al., 2013).

In the case of water vapor, EC measures evapotranspiration (ET), the combination of evaporation and transpiration. These two components are controlled by different processes and are likely to have different responses to environmental drivers such as temperature, humidity, and soil water content (Kool et al., 2014; Wang et al., 2014). Transpiration results from the movement of water through leaf stomata and is controlled by transport of water through plant tissues and by plant physiological control of leaf stomata. Because it is physiologically controlled and tightly coupled with plant tissue properties, transpiration contains important information about plant physiology and responses to environmental drivers such as drought (Chaves et al., 2003; Matheny et al., 2014; Sperry and Love, 2015). Evaporation, in contrast, is not directly limited by biological processes but rather results from the diffusion of water through the soil matrix and evaporation at the soil surface, as well as evaporation from intercepted precipitation in the canopy (Baldocchi and Meyers, 1991; Wilson et al., 2000). Because evaporation is typically smaller than transpiration as a component of the total flux in closed canopy, forested ecosystems, total ET is often used as a proxy for transpiration in studies of forest water use efficiency and ecosystem-scale transpiration (e.g. Keenan et al., 2013; Law et al., 2002; Novick et al., 2015). However, controls on forest floor evaporation rates are poorly characterized and could contribute error to similar analyses if the ratio of evaporation to transpiration varied over time or in response to drivers such as vapor pressure deficit (VPD). This makes ET partitioning a valuable complement to ecosystem-scale studies of forest water use, water use efficiency, and responses to drought.

Partitioning ET into its components requires a different approach from partitioning NEE, because the components of ET are both positive fluxes to the atmosphere that are large during the day, small at night, and sensitive to the same meteorological drivers. Several ET partitioning methods have been developed (Kool et al., 2014; Schlesinger and Jasechko, 2014; Williams et al., 2004). These include the use of oxygen and hydrogen isotope signatures (Wang et al., 2010; Wang and Yakir, 2000), modeling of canopy and sub-canopy fluxes driven by energy balance measurements from different heights (Shuttleworth and Wallace, 1985), eddy covariance measurements of above-canopy and below-canopy fluxes (e.g. Baldocchi and Ryu, 2011), up-scaling of sap-flow and leaf gas exchange measurements (Oren et al., 1998), and flux-variance similarity (FVS) partitioning (Scanlon and Kustas, 2010).

Recently, a new technique – the FVS method – has emerged that is capable of simultaneously partitioning both ET and NEE into their primary components. The technique uses continuous, high-frequency measurements of boundary layer water vapor and carbon dioxide concentrations along with an estimate of mean leaf-scale water use efficiency (WUE) to simultaneously partition ET and NEE into their respective components. Because these gas concentrations are already measured at high frequencies as part of the EC measurement technique, the FVS method can be easily applied to existing EC data records. FVS is uniquely suited for retroactive partitioning of ET at EC flux sites, because it does not require additional measurement equipment. Furthermore, it provides alternative estimates of GPP and RE that are not dependent on the model assumptions inherent to commonly used nonlinear regression partitioning methods, and does not require additional specialized measurement equipment such as that necessary for the carbonyl sulfide and isotope methods. The method has been applied and evaluated in agricultural systems (Scanlon and Kustas, 2010) and grass fields (Good et al., 2014). To our knowledge, this study represents the first effort to evaluate the FVS approach in a forest ecosystem or over decadal time scales. We applied the FVS method to a ten year record of carbon dioxide and water vapor fluxes from the Morgan Monroe State Forest (MMSF; south-central Indiana, USA) flux tower site, leveraging an extensive set of canopy leaf gas exchange measurements collected over three recent growing seasons (2011–2013, Roman et al., 2015) at the site to produce the WUE estimates required for the method. We used the FVS partitioning method along with leaf gas exchange measurements, sub-canopy flux measurements, and nonlinear-regression-based CO_2 flux partitioning in order to accomplish the following objectives:

1 Parameterize a site-specific model of WUE using leaf-level measurements for use with the FVS method
2 Evaluate the sensitivity of the FVS partitioning algorithm to errors in estimated WUE
3 Characterize agreement or disagreement between FVS flux partitioning and alternative partitioning methods

Ecosystem flux partitioning has important applications in the areas of biogeochemistry, plant physiology, and ecohydrology, and the development of partitioning techniques is an important component of advancing these fields. This evaluation of the recently developed FVS flux partitioning method in forests provides a foundation for future applications of the technique in applied studies relating to flux components and WUE.

2. Methods

2.1. Site description

Measurements were conducted at the MMSF Ameriflux site located in south-central Indiana, USA. The site is located in a deciduous broadleaf forest with a mean canopy height of approximately 27 m and a stand age of 80–90 years. The dominant tree species in the forest are sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), white oak (*Quercus alba*), black oak (*Quercus velutina*), and red oak (*Quercus rubra*). The forest species composition is typical of other hardwood forests in the region. The site topography is characterized by a ridge-ravine pattern. For additional details about the site, see Schmid et al. (2000).

2.2. Data collection and processing

Ecosystem-atmosphere fluxes of heat, water vapor, and CO_2 have been measured using the EC method at the MMSF site since 1998 at heights of 46 m, 34 m, and 2 m. The 2 m sub-canopy flux measurement station is located approximately 14 m from the main tower. Each of the three flux measurement stations includes a sonic anemometer (CSAT3; Campbell Scientific, Logan, UT, USA) and a connection to a closed-path infrared gas analyzer (IRGA; LI-7000, Li-Cor, Lincoln, NE, USA) at the base of the tower. The IRGAs are calibrated weekly. Measurements of wind speed, CO_2 concentration,

and water vapor concentration are collected at a rate of 10 Hz and processed into fluxes using standard eddy covariance techniques at a one-hour timescale (see Schmid et al., 2000 for details of flux processing). We excluded time periods with above-canopy friction velocity (u^*) less than 0.3 m s^{-1} from the analysis, based on the value that has been historically used at this site (Dragoni et al., 2011). Changes in CO_2 and water vapor storage in the canopy air space were not included in the fluxes presented in this paper. While storage change can be significant at certain times of day and under low u^* conditions (Schmid et al., 2004; Oliphant et al., 2004), it generally represents a small fraction of total flux when periods of low u^* are excluded and fluxes are averaged to daily time scales and therefore has not historically been included in publications using data from this site (e.g. Dragoni et al., 2011; Brzostek et al., 2014). We calculated storage change during one year (2014) in order to establish an upper limit on error due to omitting this term. Storage change was calculated by integrating CO_2 and H_2O concentration over the vertical concentration gradient system at the tower, calculating the difference in total storage between hours, and correcting for measured changes in concentration above the canopy (which were assumed to be due to advection). When averaged over the same time scales as the fluxes analyzed in this study, the storage term was on the order of 0.1 μmol m^{-2} s^{-1} for CO_2 and 1 W m^{-2} for H_2O, an order of magnitude less than RE and evaporation (respectively) as estimated using any of the partitioning methods. We therefore assumed that storage fluxes were negligible for the purposes of this study.

Because spectral losses can be an important issue with closed path gas analyzer systems like those used at this site (Massman, 2000; Novick et al., 2013), we applied a spectral loss correction to CO_2 and water vapor fluxes. After removing spurious spikes and correcting for lags between the sonic anemometer and the IRGA, covariance spectra with vertical wind were calculated for CO_2, water vapor, and temperature for each hour of data using a Fourier transform. The spectra were averaged into 56 logarithmically spaced frequency bins. Average spectral corrections were calculated on a monthly basis separately for different categories of atmospheric stability and relative humidity (RH). Atmospheric stability (ζ) was calculated based on tower measurements:

$$\zeta = \frac{z-d}{L}, \quad (1)$$

where z is measurement height (46 m), d is displacement height (75% of canopy height, or 19.5 m), and L is Obukhov length:

$$L = \frac{-(u^*)^3 T}{0.4gH}, \quad (2)$$

where T is air temperature, g is gravitational acceleration (9.8 m s^{-2}), and H is sensible heat flux. Stability was divided into unstable ($\zeta < -0.1$), stable ($\zeta > 0.1$), and approximately neutral ($-0.1 < \zeta < 0.1$) conditions, and RH was divided into five equally spaced bins between 0 and 100%. An ensemble average spectrum was calculated for each monthly RH-stability category by averaging together spectra from that month matching those categories. Each ensemble average spectrum was normalized by the mean power over the spectral range in which power was approximately constant, at frequencies high enough to avoid highly variable contributions from large eddies but before the beginning of the inertial subrange. Based on inspection of spectra, this range was approximately 0.007–0.1 Hz. A frequency-dependent spectral correction was then calculated by dividing the normalized water vapor or CO_2 cospectrum by the normalized temperature cospectrum at each point in the inertial subrange. The total spectral correction was calculated by dividing the integrated corrected cospectrum by the integrated uncorrected cospectrum. This correction was then applied to the previously calculated CO_2 and water vapor fluxes from hours in that month matching the appropriate combination of RH and stability. Because the FVS partitioning method recalculated fluxes from high-frequency measurements, spectral corrections had to be applied separately to the resulting flux components. The same spectral correction was applied to stomatal and non-stomatal flux components calculated using the FVS technique, based on the assumption that the same spectral losses applied to both components of each flux. Corrections to ET were on the order of 10–35%, and corrections to CO_2 flux were on the order of 1–10% (Fig. 1).

Relevant associated meteorological measurements at the site included air temperature, soil temperature, RH, photosynthetically active radiation (PAR), incoming and outgoing shortwave and longwave radiation, and precipitation. Vapor pressure deficit (VPD) was calculated using observed air temperature and RH. Soil water content (SWC) in the upper 30 cm of soil was monitored at four locations in the tower footprint using time domain reflectometer (TDR) probes (CS615 and CS616; Campbell Scientific, Logan, UT) and adjusted using gravimetric samples collected weekly at the TDR monitoring locations. Measurements were averaged among the four locations to calculate representative soil moisture for the site. Precipitation measurements were used to remove data that were within two days following rainfall from the analysis. The analysis presented here used measurements from the ten-year period 2004–2013.

Leaf-level CO_2 and water vapor fluxes, necessary to determine WUE, were measured in field campaigns during the growing seasons of 2011, 2012, and 2013 (Roman et al., 2015). Leaf gas fluxes were measured using a hand-held gas analyzer (LI-6400; Li-Cor, Logan, UT), using an elevated work platform with a maximum height of 24 m to access canopy leaves. Measurements were taken on 12 individual trees, whose species together represented 75% of total basal area and 58% of total canopy leaf area at the site. The species and leaf area fractions were sugar maple (38%), tulip poplar (11%), sassafras (4%), white oak (3%) and red oak (2%). These leaf area fractions were calculated based on leaf litter collected in 2013. Five sunlit and five shaded leaves from each tree were measured on an approximately weekly basis (subject to weather). Leaf-scale WUE was calculated as the ratio of measured leaf photosynthesis and transpiration. Canopy-scale average WUE was calculated by weighting species-specific WUE by the relative leaf area of each measured tree species, ignoring the non-measured tree species. Sun and shade leaves were both included in the calculation, but did not lead to significantly different estimates of WUE. Canopy-scale transpiration and photosynthesis based on leaf gas exchange measurements were calculated by scaling the leaf-level measurements from each tree species by the fraction of leaf area represented by that species relative to the total leaf area of all measured species (adding up to 100%). An additional scaling factor was applied to the summed fluxes based on the ratio of mean daytime growing season photosynthesis between EC measurements and scaled leaf measurements, in order to make leaf gas exchange photosynthesis and transpiration directly comparable to EC values (this factor was approximately 2.1). This factor was necessary in order to relate fluxes scaled per unit leaf area to fluxes scaled per unit ground area. Fluxes calculated per unit ground area are larger than fluxes per unit leaf area because leaf area index (LAI) is greater than 1. The factor was less than LAI because shaded leaves have lower photosynthesis and transpiration rates than sunlit leaves. The same factor was applied to scaling of photosynthesis and transpiration, and did not affect the WUE estimates used for parameterization of the WUE model.

LAI has been measured at the site since 1999 using a LAI-2000 system (Li-COR, Logan UT). Measurements were made along three radial transects within the tower footprint. Ten points per transect were measured, each 15 m apart. These measurements were

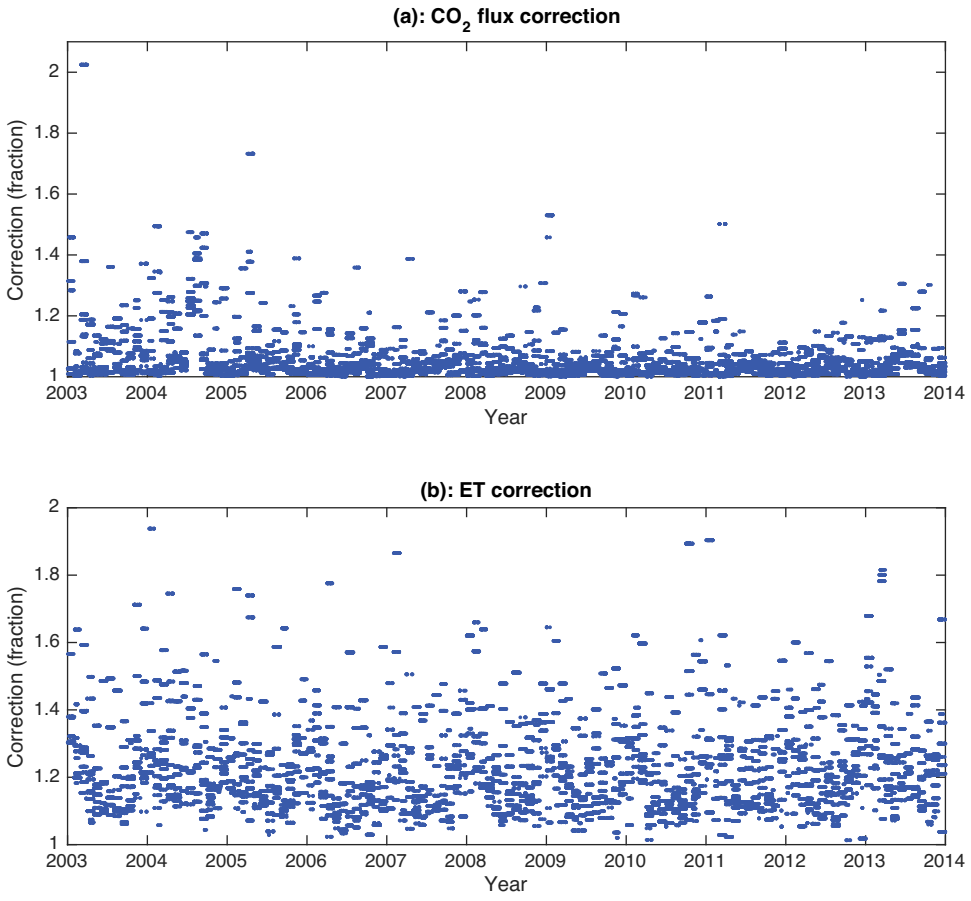

Fig. 1. Spectral corrections applied to CO_2 flux (a) and evapotranspiration (ET) (b).

repeated weekly during spring and fall, and biweekly during the peak growing season. The biweekly sampling period varied by year, but was typically between Julian day 150 and 250, when LAI was approximately stationary. The mean summer LAI at the site was approximately 4.5 over the study period, with spring leaf growth typically occurring between Julian day 110 and 140 and fall senescence occurring between day 285 and 310 (Fig. 2).

2.3. Water use efficiency model

While leaf-level gas exchange measurements were collected multiple times during the growing season, variations in WUE could not be measured at the temporal resolution necessary for the FVS method. Thus, a time series of modeled WUE was calculated using the equation:

$$WUE = \frac{1}{1.6} \times \frac{C_a - C_i}{m - m_s}, \quad (3)$$

where C_a is atmospheric CO_2 concentration, C_i is intra-cellular CO_2 concentration, m is atmospheric water vapor concentration, and m_s is saturation water vapor concentration. Note that $m-m_s$ is equivalent to VPD in concentration units. While C_a and m were measured by the gas analyzers used for EC measurements and m_s could be calculated from air temperature, continuous estimates of C_i required a model. We chose a model based on the model of Leuning (1995) as simplified by Katul et al. (2000), because it gave the most accurate results for our site after comparing multiple models summarized by Katul et al. (2000):

$$\frac{C_i}{C_a} \approx 1 - \frac{1 - \Gamma/C_a}{m_L}\left(1 + \frac{VPD}{VPD_0}\right), \quad (4)$$

where Γ is the leaf CO_2 compensation point, and m_L and VPD_0 are empirical parameters. While Γ can be measured on a leaf-specific basis, we left it as a free parameter that was estimated along with m_L and VPD_0 using nonlinear regression between measured and modeled leaf-scale WUE (Fig. 3d). All WUE measurements (including sunlit and shaded leaves) were used to fit the model. Fitting separately for sunlit and shaded leaves did not result in significantly different parameters. We calculated a time series of canopy average WUE for the ten-year study period by applying the model to observed time series of VPD and atmospheric CO_2 concentration. These values were estimated for a 22 m height representing the middle of the canopy by calculating the gradient of CO_2 and H_2O concentration between the 46 m and 34 m flux levels and assuming a constant rate of change to the 22 m level. We calculated alternative estimates of WUE using temperature and RH measurements from the 46 m, 34 m, and 2 m flux stations in order to estimate the dependence of WUE on height within the canopy (Fig. 3e). While the MMSF site has a vertical gradient system that measures CO_2 and water vapor concentrations at multiple heights within the canopy, we relied on the flux station measurements because they have been subject to more rigorous quality control and are considered more reliable at this time. Because it is based on leaf-level transpiration and photosynthesis, this estimate of WUE represents an average of the leaf-level relationship, rather than ecosystem WUE defined in some studies as GPP/ET (e.g. Keenan et al., 2013). As a result, leaf WUE does not explicitly change in response to changes in LAI, because fluxes from the existing leaf area should still obey the relationships used to derive this estimate, even as the total leaf area changes.

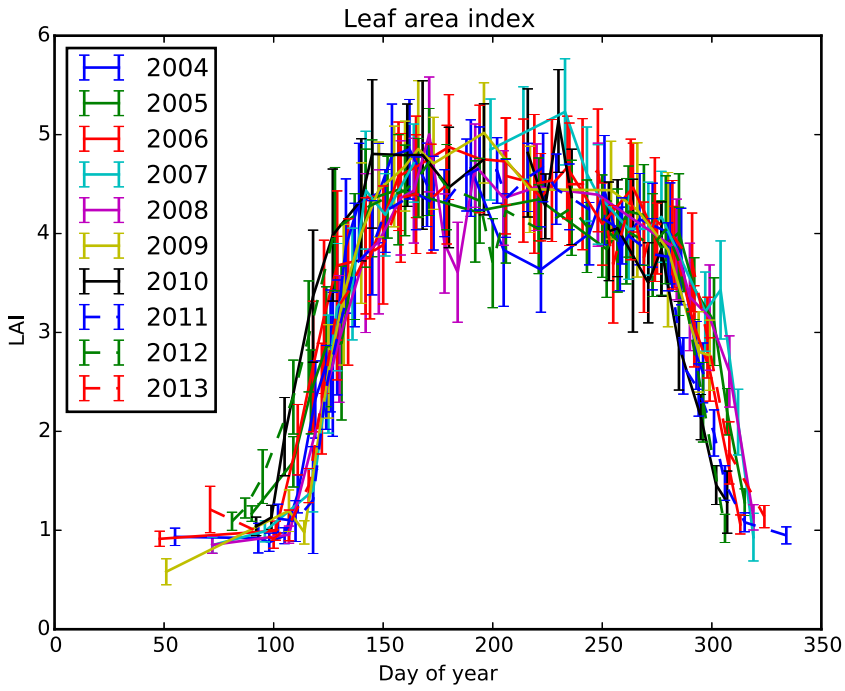

Fig. 2. Annual patterns of leaf area index (LAI) at the Morgan Monroe State Forest study site from 2004 to 2013. Error bars show standard deviation among measurements taken on each date.

2.4. Partitioning methods

Fluxes were partitioned using three different methods. The FVS and sub-canopy flux methods were applied to both CO_2 and ET partitioning, while the nonlinear regression method was applicable only to CO_2 fluxes. In addition, sub-canopy potential evapotranspiration (PET) was calculated for comparison with estimates of evaporation.

The FVS method (Scanlon and Kustas, 2010) relies on the assumption that stomatal fluxes of CO_2 and water vapor (photosynthesis and transpiration) and non-stomatal fluxes (respiration and evaporation) separately obey flux-variance similarity in the boundary layer. Based on this assumption, high-frequency variations in CO_2 concentrations derived from photosynthesis and water vapor concentrations derived from transpiration (together comprising stomatal fluxes) should be perfectly anticorrelated with each other and related by leaf WUE. Similarly, high-frequency variations in these concentrations derived from respiration and evaporation (comprising non-stomatal fluxes) should have a perfect correlation. Variations in CO_2 and water vapor concentrations measured by a gas analyzer above the canopy represent a superposition of their component signals. Given an estimate of leaf-scale WUE, the known relationship between photosynthesis and transpiration can be used to decompose the total flux back into its stomatal and non-stomatal components. The method depends on the following assumptions:

1 Stomatal fluxes (photosynthesis and transpiration) have identical source/sink distributions (i.e. they are perfectly coupled at the leaf scale);
2 Photosynthesis is equal to transpiration multiplied by a known leaf-scale WUE;
3 Non-stomatal fluxes (respiration and evaporation) have identical source distributions, with sources consisting of the forest floor (soil respiration and bare soil evaporation) and canopy (aboveground respiration and direct evaporation of intercepted water);
4 Flux-variance similarity is obeyed by both stomatal and non-stomatal fluxes, so that the identical source/sink distributions translate into perfect correlations or anticorrelations at the measurement point (which are superimposed to produce the actual measured fluctuations in CO_2 and water vapor concentrations).

The derivation of the FVS method and the details of the numerical calculations are described in the Appendix. A comprehensive description of the method can be found in Scanlon and Kustas (2010). Our analysis assumes that these assumptions are met most of the time; in the Discussion, we discuss conditions under which they may be violated and resulting implications for derived component fluxes. We applied the method to 10 Hz measurements from the 46 m EC instrumentation, using the time series of WUE described above. Partitions were produced at an hourly time scale. The algorithm used for FVS partitioning sometimes fails to converge to a valid set of values, either producing unphysical results (e.g. evaporation less than zero) or failing to converge on a solution at all (see Appendix). Evaporation and transpiration for hours that were not successfully partitioned were gap-filled by applying the ratio of evaporation to transpiration from the closest successfully partitioned hour in the same day to total measured ET. This gap-filling method was used for all daily averages of partitioned water vapor fluxes. Days with fewer than three successfully partitioned hours were excluded. Partitioned CO_2 fluxes were gap-filled using a similar method, but using the ratio of RE or GPP to NEE. The method was applied to hours with significant sunlight, defined as PAR greater than 250 $\mu mol\ m^{-2}\ s^{-1}$, for Julian day 80–320. This time period included the transition seasons of spring leaf growth and fall senescence, but excluded the majority of the winter season when photosynthesis and transpiration were assumed to be zero. We applied the method to ten years of flux measurements from the MMSF site (2004–2013).

The necessity of continuous estimates of WUE for the FVS method is a potential source of error given that most sites lack repeated leaf-level observations of WUE like those that informed the analysis for MMSF. Furthermore, vertical variations in temperature and RH through the forest canopy likely result in a range of actual WUE values at different canopy levels (Fig. 3e), making it

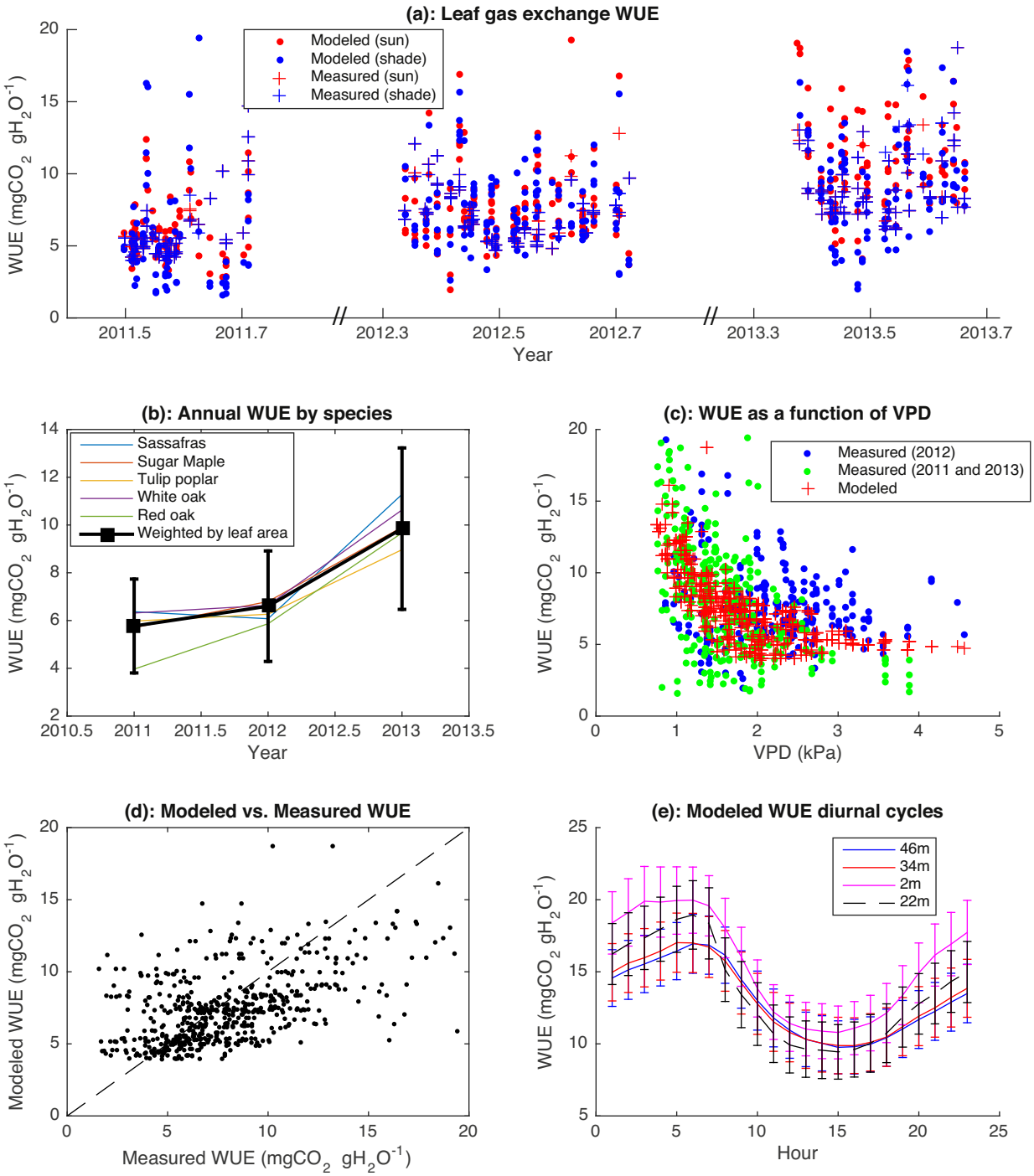

Fig. 3. Results of the water use efficiency (WUE) model. (a): Measured and modeled WUE over three years of leaf gas exchange measurements. Only modeled time points that corresponded to measurements are shown. Sun leaves are shown in red, and shade leaves in blue. (b): Annual average leaf WUE by species. Black lines show the leaf-area-weighted average. (c): Measured and modeled WUE as a function of VPD. Only modeled time points that corresponded to measurements are shown. Measurements from 2012 are shown separately to highlight the difference observed in that year. (d): Modeled and measured WUE. Dashed line shows 1:1 relationship. (e): Diurnal patterns of modeled WUE for four canopy heights. The 22 m estimate used temperature from the 22 m height and RH from the 34 m height. Error bars show standard deviation across the entire study period.

difficult to evaluate the accuracy of a single canopy-average value of WUE. In order to evaluate the impact of errors in WUE on partitioned fluxes, we recalculated the FVS partitioned fluxes using WUE adjusted to 50%, 75%, 90%, 110%, 125%, and 150% of the modeled values used in the main analysis. We conducted this sensitivity analysis using a subset of 1000 time points chosen at random from the time series of successfully partitioned fluxes. We analyzed the effect of WUE on both the values of partitioned fluxes and the fraction of points that were successfully partitioned.

The sub-canopy partitioning method used a comparison of EC fluxes from the 46-m-height above-canopy flux station and the 2-m-height below-canopy flux station to partition ET and estimate forest floor respiration. Fluxes from hours when sub-canopy u* was below 0.04 m s^{-1} were excluded from the analysis, based on an inspection of the variability in measured sub-canopy fluxes as a

function of u*. Sub-canopy fluxes were tested for non-stationarity by calculating ET and NEE separately for three 20-min periods of each hour and comparing the results to the fluxes calculated over the full hour. Hours when the mean of the fluxes from the three shorter periods differed by more than 30% from the hourly flux were discarded, following Wohlfahrt et al. (2005). Sub-canopy fluxes were not gap-filled, because they did not have a strong diurnal cycle and no well-tested gap-filling method was available at this time. We assumed that ET from the sub-canopy tower represented soil evaporation, and calculated transpiration by subtracting sub-canopy ET from 46 m ET. Similarly, we assumed that CO_2 fluxes measured by the sub-canopy tower represented soil respiration and did not include photosynthesis, and estimated canopy photosynthesis by subtracting above-canopy NEE from sub-canopy NEE. Note that this method likely underestimates GPP because it ignores stem and leaf respiration. The sub-canopy method assumes that transpiration and photosynthesis from leaf area below a height of 2 m are negligible, and that evaporation from the surfaces of leaves and wood above 2 m is also negligible. Canopy leaf area at the site is much greater than sub-canopy leaf area, supporting the first assumption. Based on LAI measurements taken in 2013 at 2 m height and ground level, sub-canopy LAI represents at most 15% of total leaf area. Furthermore, sub-canopy leaf area is generally shaded, limiting its contribution to photosynthesis and transpiration. While sub-canopy vegetation may have higher light use efficiency than canopy trees, we believe that total photosynthesis below 2 m is likely to be severely limited by the low biomass and light availability. To limit the impact of evaporation from leaf and wood surfaces, we excluded data from within two days following rainfall from the analysis.

As an additional basis for estimating forest floor evaporation, we calculated potential evapotranspiration (PET) by applying measurements of air temperature, RH, wind speed, and net radiation from the 2 m sub-canopy flux station to the Penman-Monteith equation:

$$\mathrm{PET} = \frac{S(R_{net} - G) + C_p \rho_a g_a VPD}{\lambda \rho_w \left(S + \gamma \left(1 + \frac{g_a}{g_c}\right)\right)}, \quad (5)$$

where S is the slope of the water vapor saturation function, R_{net} is net radiation, C_p is specific heat capacity of dry air, g_a is aerodynamic conductance (proportional to wind speed), λ is the latent heat of vaporization of water, ρ_w is the density of water, ρ_a is the density of air, γ is the psychometric constant, and g_c is the surface conductance. We assumed that surface conductance was not limiting and used a relatively high g_c value of 0.15 m s^{-1} in order to estimate an upper limit on forest floor evaporation. Additional increases in g_c above this level did not significantly affect PET. Adequate meteorological measurements from the sub-canopy flux station were available for this calculation starting in 2006.

The nonlinear regression method partitioned NEE using a standard approach that has been applied in previous investigations of fluxes from this site (Dragoni et al., 2011; Schmid et al., 2000): Nighttime NEE was assumed to be equal to RE. Daytime RE was calculated by fitting an exponential function of temperature to nighttime NEE (from the entire year). RE was then subtracted from daytime NEE in order to calculate GPP. Gaps in GPP were filled using a function of PAR fitted to GPP from available daytime measurements.

3. Results

3.1. Results of flux partitioning

The FVS partitioning method successfully converged to a physically valid solution on 49% of the time points to which it was applied. This was lower than previous studies in cropland and grassland ecosystems, which produced successful partitions for 77–78% of time points (Scanlon and Kustas, 2012, 2010). In comparison, approximately 75% of daytime ET and 70% of daytime NEE measurements from the 46 m flux station were used, and approximately 31% of daytime sub-canopy NEE and 25% of daytime sub-canopy LE measurements were used.

Partitioning of carbon dioxide and water vapor fluxes using the FVS method produced results that were qualitatively consistent with estimates from the other partitioning approaches (Figs. 4 and 5). GPP followed the same annual and inter-annual patterns derived from the nonlinear regression and sub-canopy partitioning approaches (Fig. 4a), and daily average values were well correlated among the methods ($r = 0.76$ between FVS and nonlinear regression; $r = 0.78$ between FVS and sub-canopy; Fig. 5a). RE resulting from the FVS partitioning method (mean growing season value of 4.1 μmol m^{-2} s^{-1}) was generally higher in magnitude compared to sub-canopy CO_2 flux measurements (mean growing season value of 1.2 μmol m^{-2} s^{-1}) and similar to nonlinear-regression-based RE (mean growing season value of 3.1 μmol m^{-2} s^{-1}; Fig. 4b). Nonlinear-regression-based RE had a higher summer peak and lower short-term variability than the other methods. This was not unexpected, because the nonlinear regression for RE used a single set of parameters calculated for the year. Correlation was low between FVS and the alternative methods (FVS with nonlinear regression: $r = 0.07$; FVS with sub-canopy: $r = 0.02$; nonlinear regression with sub-canopy: $r = 0.21$), and sub-canopy-based RE was consistently lower than the other methods (Fig. 5b). Transpiration from the FVS partitioning method was well matched with estimates based on above-canopy and below-canopy EC measurements ($r = 0.94$), although FVS transpiration was slightly lower than the sub-canopy-based estimate (Figs. 4c and 5c). FVS evaporation was typically higher than sub-canopy ET during the growing season, although the two methods predicted similar magnitudes of fluxes in early spring and late fall (Fig. 4d). PET calculated using the sub-canopy flux station was well correlated with sub-canopy ET ($r = 0.45$), while FVS evaporation was not correlated with PET ($r = -0.11$) and was substantially higher than sub-canopy PET during some growing season periods. The methods agreed more closely during the growing season of 2012, when the site experienced a severe drought with exceptionally low soil moisture and exceptionally high VPD (Brzostek et al., 2014; Roman et al., 2015). Sub-canopy ET and PET were unusually high during the 2012 growing season (mean flux 25.2 and 30.3 W m^{-2} for ET and PET, respectively) compared to other years in the record (mean flux 11.0 and 17.7 W m^{-2} for ET and PET, respectively). As with RE, correlation was low ($r = 0.1$) between FVS and sub-canopy-based evaporation (Fig. 5d).

Evaporation as a fraction of total ET had a consistent annual pattern, accounting for a high fraction during spring and fall and declining to a much lower fraction during the growing season (Fig. 6b). This pattern was evident in sub-canopy-based partitioning, sub-canopy PET as a fraction of ET, and FVS partitioning, although sub-canopy ET suggested a lower median summer evaporation fraction (6%) than FVS partitioning (18%). Daily-average FVS and sub-canopy-based evaporation fraction were fairly well correlated ($r = 0.48$; Fig. 6d). Evaporation fraction based on sub-canopy PET was closely matched with the fraction based on sub-canopy flux measurements ($r = 0.78$) and less well correlated with the FVS-based fraction ($r = 0.37$). The partitioning methods agreed more closely on evaporation fractions in the summer of 2012, when the site experienced a severe drought. During that time period, median evaporation fraction was 16% based on FVS and 11% based on sub-canopy ET.

The annual pattern of RE as a fraction of GPP was similar to that of evaporation fraction, with higher values during spring and fall and

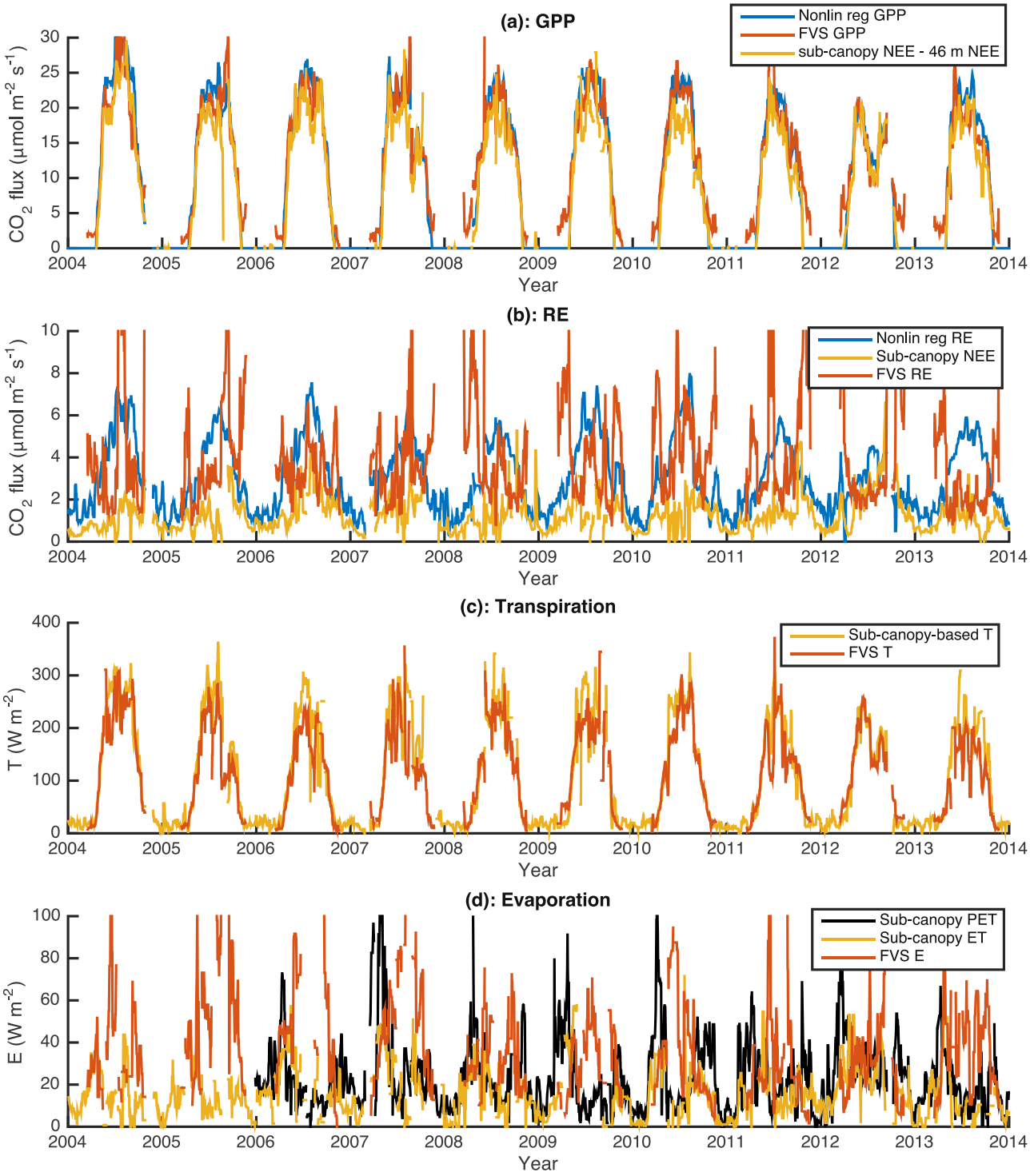

Fig. 4. Time series of partitioned fluxes, with a 10 day moving average applied. "Nonlin reg" refers to the nonlinear regression CO_2 flux partitioning method. (a): GPP, (b): RE, (c): transpiration (T), and (d): Evaporation (E).

lower, slowly increasing values during the growing season (Fig. 6a). Sub-canopy NEE suggested a lower daytime RE as a fraction of GPP (median of 7%) than either FVS partitioning (median of 15%) or nonlinear regression partitioning (median of 22%) (Fig. 6a,c). Daily FVS RE fraction was more closely correlated with nonlinear regression RE fraction ($r = 0.58$) than with sub-canopy-based RE ($r = 0.38$). Sub-canopy-based and nonlinear-regression-based RE fractions were somewhat well correlated with each other ($r = 0.48$).

As a further independent comparison with partitioned fluxes, we compared daily average transpiration and photosynthesis from partitioned EC fluxes with scaled leaf gas exchange measurements from 2012 and 2013, when full growing seasons were available from the field campaign (Fig. 7). The scaled leaf gas exchange measurements generally agreed with the trends observed in the partitioned EC fluxes for both photosynthesis and transpiration. Declines in photosynthesis and transpiration during the 2012 drought were observed using all three methods, as were the inter-

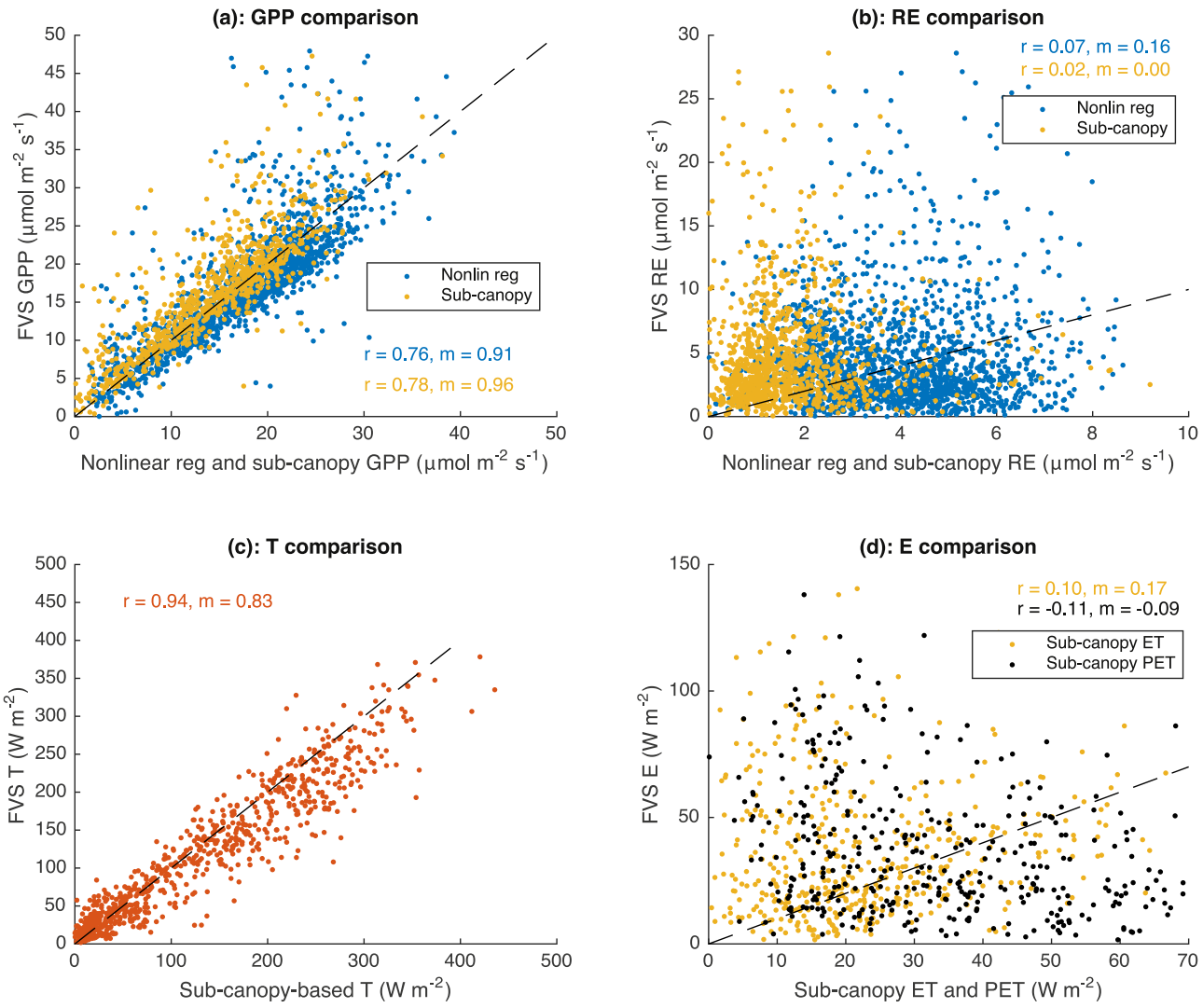

Fig. 5. Comparisons of multiple partitioning methods, showing daily average values across the entire study period. Dashed lines show the 1:1 lines. Correlation coefficient (r) and slope parameter (m) are color-matched with the corresponding data points. (a): GPP for non-linear regression and sub-canopy-based partitioning compared to FVS. (b): RE from FVS compared to nonlinear regression and sub-canopy methods. (c): Transpiration for FVS compared to sub-canopy method. (d): Evaporation from FVS compared to sub-canopy ET and PET.

annual patterns, with photosynthesis generally higher in 2013 compared to 2012, and transpiration maintaining a similar magnitude between the two years.

3.2. WUE model results

The WUE model produced reasonable results when compared to leaf-level observations (Fig. 3a). The model successfully reproduced the higher WUE observed in 2013 compared to the other years (due to wetter conditions in 2013 compared to 2011 and 2012), as well as the seasonal patterns observed in 2011 and 2012. In 2011, mid-summer WUE was low compared to later in the season. Similarly, mid-summer WUE in 2012 was low compared to early and late in the season. The model successfully reproduced these patterns. The mean modeled WUE for time points corresponding to leaf gas exchange measurements was 8.05 mg CO_2 gH_2O^{-1}, while the mean of measured values was 8.2 mg CO_2 gH_2O^{-1}. These values were within the range of previously published estimates of WUE based on leaf gas exchange measurements from other sites (e.g. Cienciala and Lindroth, 1995; Harley and Baldocchi, 1995). Observed WUE varied by tree species, but inter-species differences were generally smaller than temporal variability (Fig. 3b). The model also successfully reproduced the observed relationship between WUE and VPD (Fig. 3c). Note that the observed relationship was slightly different in 2012 compared to other years, possibly due to the severe drought that occurred in 2012. Modeled WUE was moderately well correlated with measured WUE (r = 0.4; Fig. 3d). WUE estimated using measurements from different heights varied over the diurnal cycle, with the largest differences occurring at night (Fig. 3e). WUE estimates using 46 m and 34 m measurements were almost identical, while daytime WUE estimates using 2 m measurements were higher by approximately 1 mg CO_2 gH_2O^{-1}, or approximately 10%. Interpolating to a mid-canopy height of 22 m introduced daytime variations of approximately 10% as well. Mean modeled WUE for FVS partitioned points over the entire time series was 18.3 mg CO_2 gH_2O^{-1}.

3.3. Sensitivity of FVS to estimates of WUE

Sensitivity tests of the response of FVS partitioning to changes in WUE showed that WUE did directly influence the values of partitioned fluxes (Fig. 8a–d). Partitioned transpiration decreased with increasing WUE, while partitioned evaporation increased (Fig. 8a,c). GPP and respiration both increased with increasing WUE

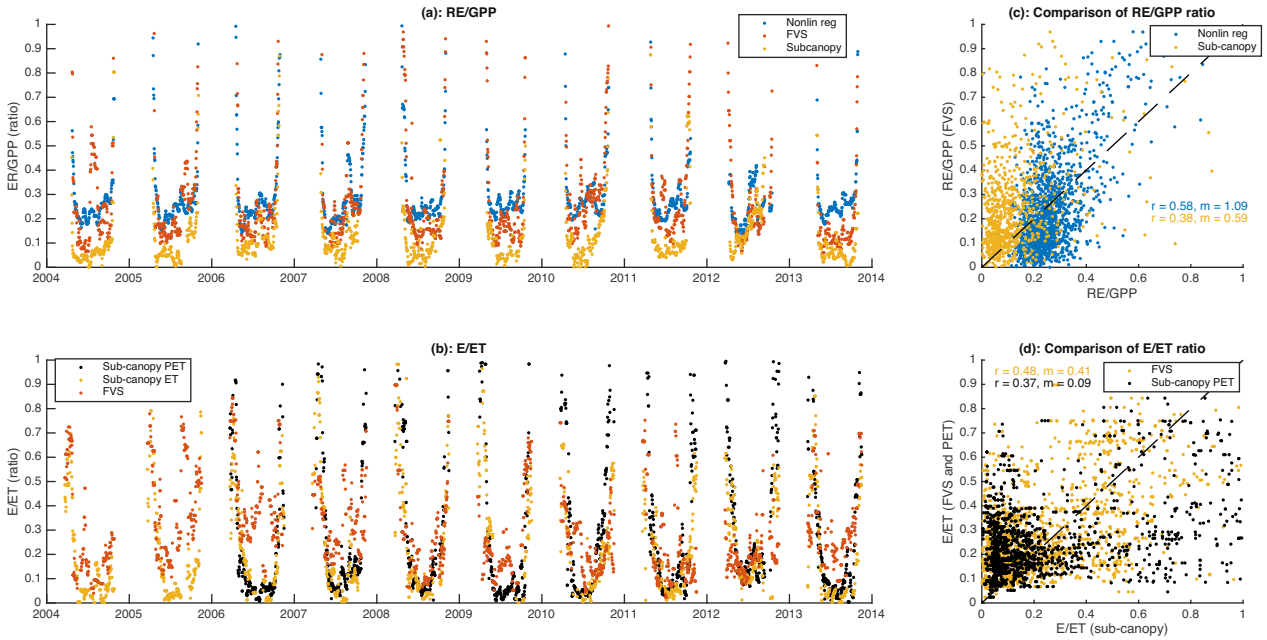

Fig. 6. Flux ratios, with a 10-day smoothing filter applied. (a): Ratio of RE to GPP based on nonlinear regression partitioning, FVS partitioning, and sub-canopy EC partitioning. (b): Ratio of evaporation to ET based on sub-canopy ET partitioning and FVS partitioning. Ratio between sub-canopy PET and ET is also shown. (c): Comparison of RE/GPP ratios from FVS compared to nonlinear regression and sub-canopy methods. Correlation coefficient (r) and slope parameter (m) are color-matched with the corresponding data points. (d): Comparison of evaporation/ET ratios from FVS and sub-canopy methods and sub-canopy PET.

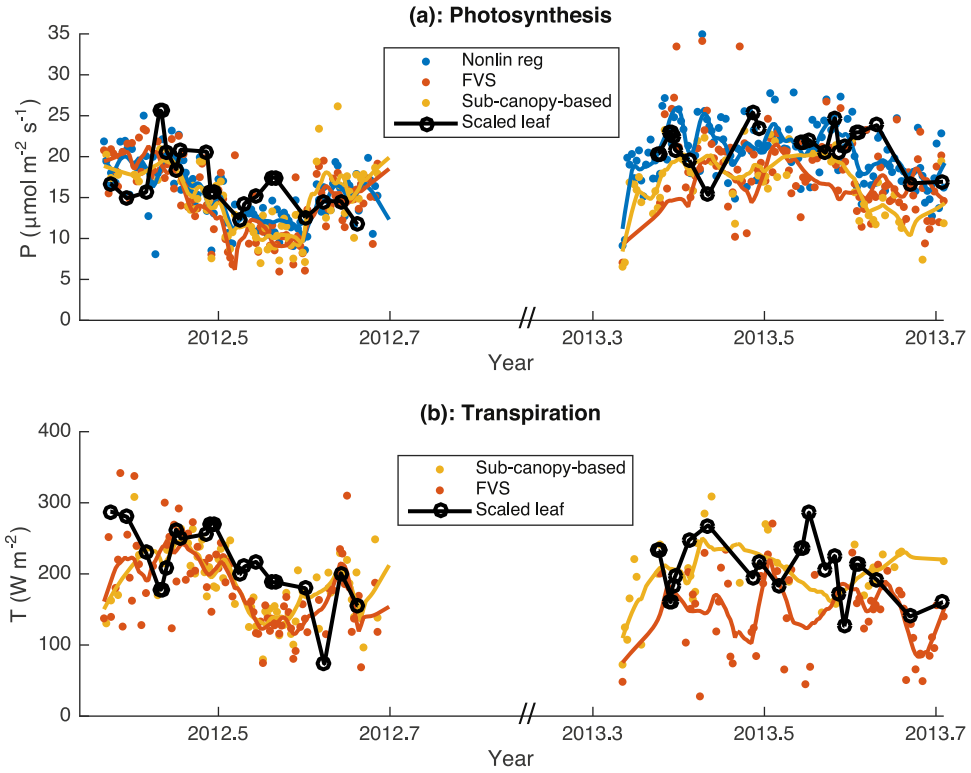

Fig. 7. Comparison of photosynthesis (a) and transpiration (b) from partitioned tower fluxes to scaled leaf gas exchange measurements for the growing seasons of years 2012 and 2013. Colored lines show 10-day moving averages of partitioned fluxes.

(Fig. 8b,d). GPP and transpiration change in opposite directions in response to WUE because a higher WUE implies less water loss to transpiration per unit photosynthesis. The fractional changes in transpiration and GPP were generally less than the fractional changes in WUE. Underestimates of WUE caused minor fractional changes in all fluxes, while overestimates of WUE caused fractional changes in evaporation and respiration that were greater than the fractional change in WUE. Because the stomatal and non-stomatal components of fluxes were required to sum to the total observed flux, the magnitude of change in each component was compensated by a change in the opposite component (e.g. an increase in transpiration was matched by an equal decrease in evaporation

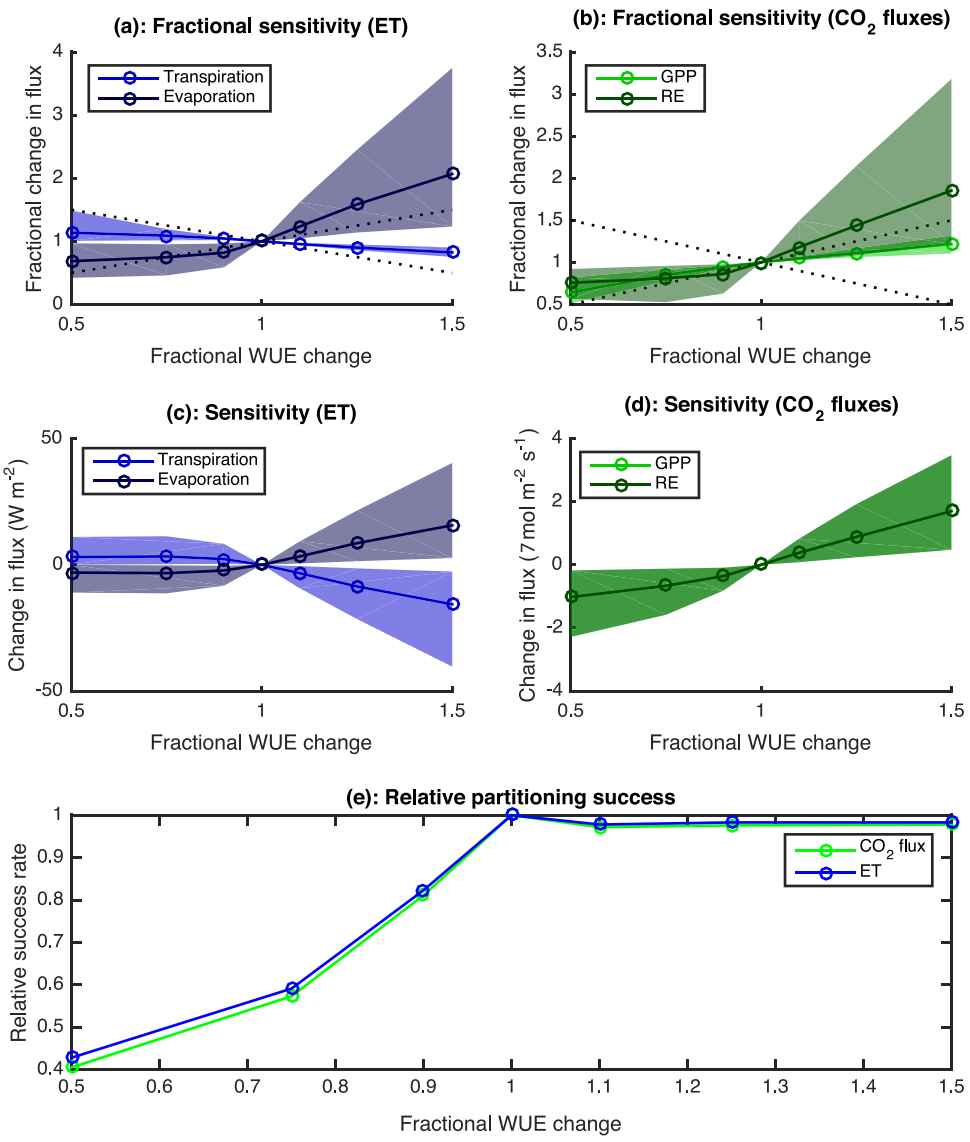

Fig. 8. Estimated sensitivity of partitioned fluxes to error in WUE estimates, from a 50% underestimate to a 50% overestimate. (a) and (b): Change in partitioned fluxes normalized by the magnitude of the partitioned flux components. (c) and (d): Total change in flux components (note that changes in GPP and RE are identical). Circles show median values, and shaded regions show the 25th-75th percentile ranges. Dashed lines in fractional change plots show the level at which the fractional change in a flux is the same as the fractional change in WUE (e.g. where a 25% underestimate of WUE causes a 25% underestimate of the flux component). (e): Relative number of valid partitions produced for each WUE error level.

for a particular partitioned time point). Because of this, absolute changes in GPP and RE were identical (Fig. 8d). This led to higher fractional error in evaporation and RE than in transpiration and GPP, because the magnitudes of non-stomatal fluxes were generally smaller than those of stomatal fluxes. The success rate of the FVS partitioning method was highly sensitive to underestimates of WUE, decreasing by up to 60% at a 50% underestimate of WUE (Fig. 8e). The partitioning success rate was not sensitive to overestimates of WUE.

4. Discussion

Our comparison of flux partitioning methods found good agreement among methods for GPP and transpiration and lower correlations for RE and evaporation. Sub-canopy EC measurements of evaporation were lower than FVS evaporation but agreed well with sub-canopy PET, while sub-canopy EC measurements of CO_2 flux were lower than both FVS and nonlinear-regression-based RE. Our WUE model successfully replicated seasonal and interannual variations in WUE. A sensitivity analysis of the FVS method showed a moderate sensitivity of partitioned values to changes in WUE and a strong decline in the rate of successful partitioning with declining WUE estimates.

4.1. WUE model

The model of WUE that we chose (based on Leuning, 1995) successfully reproduced both seasonal and interannual variations in WUE when compared to leaf gas exchange measurements. The model of Leuning (1995) ultimately produced the most accurate results for our site, but alternative models such as those summarized by Katul et al. (2000) may be useful at other sites. The model we chose was driven by atmospheric CO_2 concentration and VPD. Since these quantities are routinely measured by the same equipment used for EC measurements of NEE and ET, the model is well suited for use at EC sites. However, parameterization of the model may be difficult in the absence of leaf gas exchange measurements. In our study, leaf gas exchange measurements were primarily col-

lected during midday of sunny days during the growing season, and therefore may not have adequately sampled the variation in WUE over more diverse meteorological conditions, reducing confidence in FVS partitioning results during meteorological conditions that were not well represented in the leaf gas exchange measurements. Furthermore, our model estimated a single representative WUE based on VPD and CO_2 concentration at one point within the canopy. Actual WUE can vary with tree species and canopy position, with sunlit leaves experiencing different light and VPD conditions than shaded leaves. Measurements showed that sunlit and shaded leaves did not have systematically different WUE (Fig. 3a) and that WUE variation due to changes in VPD and CO_2 concentration with canopy height was on the order of 10% during the day. Observed differences in leaf-scale WUE among tree species were also on the order of 10% (Fig. 3b). While the FVS calculation requires a single estimate of WUE, the actual relationship between photosynthesis and transpiration that is observable at the measurement height is driven by a distribution of leaf-level WUE and flux rates. Further study using techniques such as large eddy simulation (LES) may be warranted in order to determine the effects of vertical variations in WUE on the accuracy of the FVS method. The sensitivity analysis of the FVS method suggests that systematic underestimation of WUE would result in overestimates of transpiration relative to evaporation combined with underestimates of GPP and RE. WUE could have been underestimated if lower VPD at lower canopy levels had a higher role than expected in driving total leaf fluxes, or if the focus of leaf gas exchange measurements on sunny, midday conditions led to underestimates of WUE during other times of day and other meteorological conditions.

WUE most likely responds to other drivers in addition to VPD and atmospheric CO_2 concentration. Well-established plant physiological responses to soil moisture limitation likely cause changes in the parameters of WUE models such as the one we applied (Chaves et al., 2003; Manzoni et al., 2011). This may lead to errors in WUE estimation and flux partitioning during dry periods. Furthermore, plant species have different responses to variations in leaf water potential. Species can be divided into isohydric and anisohydric classifications based on different responses of stomatal conductance to declining leaf water potential (Tardieu and Simonneau, 1998), and the contrasts between isohydric and anisohydric species in an ecosystem may influence canopy-scale WUE and its response to variations in VPD and soil moisture (Roman et al., 2015). Photosynthesis rates and stomatal conductance of isohydric trees decline under dry conditions, while photosynthesis rates and stomatal conductance of anisohydric trees are less responsive. This could cause canopy average WUE to shift toward higher values typical of anisohydric trees during dry conditions, potentially leading to underestimates of WUE by models. Our WUE model did not explicitly account for changes related to phenology, based on the assumption that the physiological factors driving WUE were constant at the leaf scale, even if total leaf area changed. In reality, leaf-scale WUE can change in response to leaf age (Wullschleger and Oosterhuis, 1989). Furthermore, the distribution of leaf area by plant species could change significantly during spring and fall periods due to differences in phenological timing among species. This potentially reduced the accuracy of the FVS partitioning method during leaf-out and senescence periods. At our study site, these seasons accounted for approximately 12% of total GPP.

4.2. Accuracy of FVS assumptions in a forest canopy

While the FVS method has previously been applied in short-stature agricultural and grassland systems, it has not previously been evaluated in a forest. Compared to a crop or grassland vegetation canopy with a height of 1 m or less, a 27 m forest canopy introduces significant complexity in turbulent airflow within and through the canopy. Furthermore, the distinctive vertical profile of a forest, with most of the leaf area at height and a relatively open region near the ground, could lead to distinct airflow patterns compared to shorter canopies. These complexities introduce potential for violations of the key assumptions of the FVS method. The heterogeneous composition of leaf area with respect to height and plant species could lead to heterogeneous distributions of stomatal fluxes, violating Assumption 1. Likewise, the significant above-ground biomass of trees could lead to spatial heterogeneity in non-stomatal fluxes (violating Assumption 3), since evaporation from the forest floor may not be coupled with respiration fluxes that include sources from both the forest floor and plant tissues. Variations in WUE within the canopy could violate the assumption of a known coupling between transpiration and photosynthesis (Assumption 2), since these fluxes would no longer be related by a single known WUE. Flux-variance similarity (Assumption 4) may also be violated due to complex airflow and mixing below and within the canopy. These effects may be responsible for the lower rate at which the partitioning algorithm was able to converge on a physically valid solution compared to previous applications in shorter canopies (Scanlon and Kustas, 2010; Scanlon and Sahu, 2008). The role of turbulence in scalar transport through the canopy was investigated by Huang et al. (2013) using a LES approach. Their analysis found that scalar correlations observed above the canopy did respond to photosynthesis and transpiration rates in the manner expected by the FVS method, but that the properties of observed turbulent fluctuations were dependent on the role of coherent structures in turbulent transport through the canopy. Additional LES studies focusing specifically on the FVS method could facilitate more precise estimation of potential errors related to airflow through and within the canopy.

4.3. Comparison of partitioning results among methods

The FVS partitioning method produced qualitatively similar results compared to the alternative methods, in terms of seasonal and interannual variations. GPP and transpiration were very closely matched among the methods, while RE and evaporation were less well correlated. The high level of agreement for GPP and transpiration was mostly due to the fact that GPP and transpiration represented the vast majority of total daytime fluxes during the growing season, meaning that stomatal fluxes resembled the observed patterns of total flux and would agree among methods unless the non-stomatal fluxes were greatly overestimated. The largest differences occurred for non-stomatal fluxes during the growing season, when FVS estimates of both RE and evaporation were generally higher than estimates based on sub-canopy flux measurements. Recent soil CO_2 flux measurements in the vicinity of the tower were on the order of 3–4 $\mu mol\ m^{-2}\ s^{-1}$ (Brzostek et al., 2015), which suggests that sub-canopy NEE (with a mean growing season value of 1.2 $\mu mol\ m^{-2}\ s^{-1}$) underestimated soil respiration. Nonlinear regression and FVS produced higher mean RE estimates of 3.1 and 4.1 $\mu mol\ m^{-2}\ s^{-1}$, respectively. The FVS and nonlinear regression methods produced estimates of RE of 15% and 22% of daytime GPP, respectively. These fractions are consistent with the diurnal cycles observed in a comparison of NEE partitioning methods across sites (Desai et al., 2008). The lower fraction of 7% given by sub-canopy EC was low, even in the context of soil respiration measurements. Differences between the flux footprints of the 46 m EC station and the 2 m sub-canopy EC station could have contributed to the discrepancies between the FVS and sub-canopy methods. Horizontal advection due to sub-canopy airflow at the site (Froelich and Schmid, 2006) could also have contributed to the discrepancy. Photosynthesis by plants on the forest floor could also have lowered the measured sub-canopy CO_2 flux. In addition, sub-canopy NEE omits respiration sources above the forest floor, such as stem

and leaf respiration. The important roles of stem and leaf respiration are supported by a study in a northern Michigan forest that estimated that leaf and wood respiration accounted for 16–20% and 10–12% of total respiration, respectively (Curtis et al., 2005). Other recent studies found that sub-canopy CO_2 flux measurements accounted for only an average of 55–65% of total ecosystem respiration (Misson et al., 2007; Novick et al., 2014). These missing fluxes would also have affected the estimates of GPP calculated by subtracting 46 m NEE from sub-canopy NEE, leading to underestimates of GPP. As discussed above, significant aboveground sources of respiration could also pose problems for the FVS method if there are no associated aboveground sources of evaporation.

During spring and fall seasons, the FVS method estimated that non-stomatal fluxes dominated the total flux. Leaf area was low during these seasons due to the site phenology, and stomatal fluxes were expected to be low as a result. WUE estimates were likely less accurate during these time periods as discussed above, making the accuracy of the FVS method questionable, but the general pattern supports observed patterns of the flux response to phenological transitions.

The sub-canopy and FVS methods diverged concerning the typical fraction of summer ET that is represented by evaporation. FVS partitioning suggested that evaporation makes up approximately 18% of growing season ET at the MMSF site, excluding days with recent rainfall, while sub-canopy measurements indicated a substantially smaller fraction (6%). The sub-canopy estimates were consistent with a similar sub-canopy flux analysis in a Tennessee forest, which estimated that sub-canopy evapotranspiration was less than 10% of total ET (Wilson et al., 2000). Sub-canopy estimates were also supported by their high correlation and quantitative agreement with sub-canopy PET. However, the fact that sub-canopy CO_2 fluxes were less than typical soil respiration measurements at the site suggests that the technique could have underestimated soil evaporation as well. The FVS estimate was more consistent with estimated soil evaporation at a forest in North Carolina, USA, where soil evaporation was estimated to make up 15% of growing season ET (Oishi et al., 2010), and with a multisite synthesis of annual E/ET ratios based primarily on sap-flow and isotope approaches, which estimated a mean fraction of 33% for temperate deciduous forests (Schlesinger and Jasechko, 2014). That estimate included evaporation from water intercepted by the canopy, which can account for up to 30% of annual totals (Oishi et al., 2010), and which was excluded from our study by removing data measured within two days after significant rainfall. The fact that FVS evaporation exceeded sub-canopy PET during the growing season in most years suggests that a significant fraction of the evaporation flux diagnosed using this method originated from higher in the canopy profile. This is also consistent with the studies that produced similar estimates of evaporation as a fraction of ET (Oishi et al., 2010; Schlesigner and Jasechko, 2014), since these studies used approaches such as sap flow measurements and the relationship between wintertime ET and meteorological drivers rather than sub-canopy flux measurements. As a result, they were more likely to include evaporation sources from higher in the canopy, if those sources were significant fractions of the total.

Sub-canopy ET was higher than usual during the summer of 2012, when the site was subject to a severe drought, leading to closer agreement among the methods that year. Sub-canopy PET was also higher than usual during that time period. These effects were most likely due to the exceptionally high VPD observed during the 2012 drought (Brzostek et al., 2014). Analyses of transpiration and WUE using EC data often assume that evaporation is negligible during dry periods (e.g. Keenan et al., 2013; Novick et al., 2015), and our results suggest that this may not be an accurate assumption, especially during high VPD conditions.

While there were differences among the partitioning methods, the magnitudes of disagreements were not unreasonable when placed in the context of known uncertainty in EC measurements. Novick et al. (2015) compared two partitioning methods for CO_2 fluxes (both based on deriving temperature response functions for RE) and found that the RE and GPP components differed by up to 11% between the two methods. In another comparison, Stoy et al. (2006) found differences of 20–35% in mean annual RE and GPP resulting from two different nonlinear-regression-based CO_2 flux-partitioning methods. van Gorsel et al. (2009) compared four approaches for estimating nocturnal respiration in 25 forests, and found that the estimated monthly mean respiration could differ by up to 25% among methods. Furthermore, EC measurements contain significant random error due to the role of atmospheric turbulence in the method. These random errors can account for variations on the order of 25% at the hourly scale in both CO_2 flux and ET in forests (Richardson et al., 2006).

4.4. FVS sensitivity to WUE

Our sensitivity analysis suggested that errors in WUE could lead to biases in partitioned fluxes, especially for evaporation and respiration. In fractional terms, bias due to the direct impact of WUE on transpiration and GPP resulting from the partitioning method was generally smaller than the fractional error in WUE itself and behaved in predictable ways that could likely be quantified in future applications of the FVS partitioning method. The small magnitudes of evaporation and respiration, however, meant that even relatively small errors in fluxes could represent significant fractional errors. The convergence of the algorithm on a physically valid solution was very sensitive to underestimates of WUE. This asymmetry was likely due to the difference in magnitude between evaporation and transpiration. Because evaporation decreased with decreasing WUE, low values of WUE were more likely to produce a physically unrealistic negative estimate of evaporation. The asymmetry of this response means that randomly distributed errors in WUE would not result in the same distribution of error in resulting partitioned fluxes, because underestimates would be more likely to result in a failure of the partitioning algorithm while overestimates would be more likely to affect the values of flux components. This could lead to a positive bias in ER, GPP, and transpiration and a negative bias in evaporation. This result suggests that further work is needed in estimating bias due to non-convergence of the algorithm, developing methods for estimating WUE within the FVS partitioning framework, and developing strategies for gap-filling of time points in which the algorithm fails to converge.

4.5. Comparison of partitioning methods

The primary disadvantage of the sub-canopy flux partitioning method is that it depends on the assumption that all fluxes above the sub-canopy measurement point are stomatal and all fluxes from below the sub-canopy measurement point are non-stomatal. As discussed above, this assumption ignores some potentially important flux sources, including photosynthesis and transpiration from forest floor vegetation, evaporation from leaf and woody surfaces following rainfall or condensation, and respiration from leaves and woody tissue. Excluding time periods following rain can reduce the influence of evaporation of intercepted water, but the other ignored flux sources could still lead to significant error. In addition, the sub-canopy flux tower has a very small footprint compared to the 46 m above-canopy measurement station, and the sub-canopy flux measurements may not be representative of the same area as the ecosystem-scale fluxes observed by the taller tower, especially given the topographical variability of the site. Sub-canopy EC measurements are also sensitive to periods of low turbulence, which

may lead to underestimation of fluxes due to low rates of vertical mixing. We did apply a u* filter and a non-stationarity test to sub-canopy fluxes in an attempt to exclude periods of low turbulence, but the systematic differences in wind speed and turbulence between the above- and below-canopy stations could still pose problems for direct comparisons.

The primary disadvantage of the FVS partitioning method is the need for continuous estimates of WUE. We were able to parameterize a model of WUE using repeated leaf gas exchange measurements, but the vast majority of EC flux sites do not have access to similar datasets. Even our extensive set of leaf gas exchange measurements did not include a wide enough range of weather conditions to fully characterize the actual variability in meteorology. The role of VPD in commonly used WUE formulas, including the model we used, could be problematic for studies where observed relationships between VPD and partitioned fluxes are important, because relationships between VPD and partitioned ET based on this method may be partially determined by assumptions about the effect of VPD on WUE. For example, one important application of partitioned transpiration is the estimation of ecosystem-scale WUE without the assumption of negligible evaporation. If a model of WUE is used in the partitioning method, then model assumptions about WUE responses to VPD and other drivers will influence the partitioned values and propagate through the analysis. The assumed WUE directly affects the ratio between photosynthesis and transpiration that results from the FVS method, and therefore will affect any later assessment of WUE based on those partitioned fluxes.

Despite issues with WUE estimation, the FVS partitioning method has many significant advantages (Table 1). It does not require additional specialized equipment such as isotope analyzers, and as a result can be applied retroactively to existing EC flux measurements. Furthermore, it produces estimates of GPP and RE that do not depend on the assumptions inherent to the nonlinear regression methods that are most commonly used for CO_2 flux partitioning. These methods can be sensitive to errors in flux observations driven by non-negligible advection fluxes (van Gorsel et al., 2009) and typically require the application of models parameterized at weekly to monthly time steps (Lasslop et al., 2009). Besides being required for the FVS method (Fig. 8), WUE is also a driver of the ratio of COS:CO_2 assimilation necessary for the COS technique (Asaf et al., 2013). Thus, efforts to characterize the spatial and temporal variability of WUE will improve the applicability of both the FVS and COS partitioning approaches. The stable isotope method for partitioning ET does not depend on WUE, though it does require estimates of the isotopic signatures of evaporation, transpiration, and evapotranspiration (Wang et al., 2010). Overall, the FVS method shows great promise as a method for estimating evaporation and transpiration as well as for producing alternative estimates of GPP and RE at flux tower sites.

5. Conclusions

Our comparison of the FVS partitioning method with independent methods based on sub-canopy flux measurements and non-linear regressions suggests that the FVS method can accurately partition CO_2 and water vapor fluxes in forests, but that it is sensitive to errors (particularly overestimates) in WUE. Transpiration and photosynthesis agreed well among alternative methods. Evaporation and respiration differed among methods, with the FVS

Table 1
Comparison of flux partitioning methods.

Method	Fluxes partitioned	Theoretical basis	Equipment required	Notes	References
Nonlinear regression	GPP and RE	Known relationships between shortwave radiation and photosynthesis, and between temperature and respiration	Uses existing EC measurements. Requires basic meteorological measurements (temperature and PAR).	Imposes model equations on partitioned fluxes. Forms that depend on nighttime respiration can be vulnerable to low-turbulence conditions and diurnal variations in respiration. Only applicable to CO_2 fluxes.	Lasslop et al. (2009) and Reichstein et al. (2005)
Stable isotopes	GPP, RE, E, and T	Flux components have different isotope fractionation signatures.	Water vapor isotope analyzer for E and T, or C isotope analyzer for GPP and RE	E and T require repeated measurements of evaporation and transpiration isotope signatures using chambers. GPP and RE require estimates of isotope-specific flux from gradient or flask measurements, and assume no ^{13}C fractionation in respiration.	Bowling et al. (2001), Knohl and Buchmann (2005), Wang et al. (2010) and Wang and Yakir (2000)
Carbonyl sulfide (COS)	GPP and RE	COS is assimilated in leaves by a similar pathway to photosynthesis, but is not emitted by respiration.	COS gas analyzer	Requires estimates of leaf-scale ratio of COS to CO_2 assimilation rates, as well as soil uptake of COS.	Asaf et al. (2013) and Blonquist et al. (2011)
Flux-variance similarity (FVS)	GPP, RE, E, and T	CO_2 and H_2O fluxes from stomatal or non-stomatal sources are tightly coupled as they propagate through the atmospheric boundary layer.	Uses same high-frequency measurements as EC. May require leaf chamber measurements for site-specific estimates of WUE.	Requires continuous estimate of leaf WUE.	Scanlon and Kustas (2010); this study
Sub-canopy EC measurements	GPP, RE, E, and T	Fluxes measured by a sub-canopy EC station represent RE and E, while measurements from an above-canopy tower represent total ecosystem fluxes.	EC flux towers above and below the canopy	Towers have different footprints. Sub-canopy measurements may miss important sources of evaporation and respiration.	Baldocchi and Ryu (2011), Misson et al. (2007) and Novick et al. (2014)
Up-scaling of biometric measurements	All fluxes	Small-scale measurements of fluxes such as soil respiration, sap flow, and leaf gas exchange are scaled to the ecosystem level.	Specialized equipment and measurements for each flux component (soil and stem respiration chambers, sap flow probes, and leaf gas exchange chambers)	Temporal and spatial scaling requires additional assumptions about the spatial and temporal distribution of fluxes, and may require empirical or process-based models.	

method generally predicting higher fluxes than other methods, but the variations were consistent with the magnitude of variations among partitioning methods observed in previous studies. Our results support the utility of the FVS method for partitioning fluxes in forest ecosystems but suggest that more work may be needed in the areas of gap filling and WUE estimation. Despite the remaining challenges, the FVS method retains significant advantages over the use of sub-canopy EC measurements for ET partitioning, including a larger flux footprint than sub-canopy measurements and freedom from assumptions such as negligible evaporation and respiration from stems and branches. FVS partitioning has unique potential for retroactive flux partitioning at EC sites, because it relies on the same continuous measurements as EC and does not require additional specialized equipment.

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Appendix A.

Derivation and numerical methods used in FVS partitioning

This summary description of the FVS method is adapted from Scanlon and Kustas (2010). See Scanlon and Kustas (2010) and Scanlon and Sahu (2008) for a comprehensive description and derivation.

Monin-Obukhov similarity theory predicts that scalar time series measured at the same location should exhibit perfect correlation, provided that their source/sink distributions are identical. In an ecological context, this implies that fluctuations in atmospheric CO_2 and water vapor concentrations driven by common source or sink distributions should be perfectly correlated with each other. Ecological CO_2 and water vapor fluxes can be divided into two main groups. "Stomatal" fluxes include transpiration and photosynthetic uptake of CO_2. Since these fluxes pass through the same leaf stomata, they have identical source/sink distributions and the resulting fluctuations in concentration at the measurement point should be perfectly anticorrelated:

$$\rho_{c_p,q_t} = -1.0, \tag{A.1}$$

where ρ_{c_p,q_t} is the correlation coefficient of CO_2 concentration fluctuations driven by photosynthesis and water vapor concentration fluctuations driven by transpiration. Likewise, non-stomatal fluxes can be assumed to originate from the forest floor and should also have identical source distributions and perfect correlations:

$$\rho_{c_r,q_e} = 1.0, \tag{A.2}$$

where ρ_{c_r,q_e} is the correlation coefficient of CO_2 concentration fluctuations driven by respiration and water vapor concentration fluctuations driven by forest floor evaporation. Because the stomatal and non-stomatal source distributions are not identical to each other (and because stomatal and non-stomatal exchange are assumed to have perfectly negative and perfectly positive correlations, respectively), perfect correlation does not hold for the actual observed CO_2 and water vapor concentrations, which result from a superposition of the two components. However, the coupling of c_p with q_t and of c_r with q_e does guarantee an equal correlation between the fluctuations of CO_2 components and water vapor components:

$$\rho_{c_r,c_p} = -\rho_{q_e,q_t} \tag{A.3}$$

Because stomatal fluxes originate higher in the vegetation canopy than non-stomatal fluxes, the transfer efficiencies of stomatal scalar fluctuations can be assumed to be much greater than the transfer efficiencies of non-stomatal scalar fluctuations. As a result, the following approximations of ρ_{c_r,c_p} and ρ_{q_e,q_t} can be used:

$$\rho_{c_r,c_p} \approx \frac{\rho_{w,c_r}}{\rho_{w,c_p}} = \frac{\overline{w'c_r'}}{\overline{w'c_p'}}\frac{\sigma_{c_p}}{\sigma_{c_r}} \tag{A.4}$$

$$\rho_{q_e,q_t} \approx \frac{\rho_{w,q_e}}{\rho_{w,q_t}} = \frac{\overline{w'q_e'}}{\overline{w'q_t'}}\frac{\sigma_{q_t}}{\sigma_{q_e}}, \tag{A.5}$$

where w is vertical wind speed, σ is standard deviation, prime ($'$) indicates variations from the mean, and a bar indicates averaging. Finally, because the components of the q' and c' time series are not independent, their variances are related:

$$\sigma_q^2 = \sigma_{q_t}^2 + \sigma_{q_e}^2 + 2\rho_{q_t,q_e}\sigma_{q_t}\sigma_{q_e} \tag{A.6}$$

$$\sigma_c^2 = \sigma_{c_p}^2 + \sigma_{c_r}^2 + 2\rho_{c_p,c_r}\sigma_{c_p}\sigma_{c_r} \tag{A.7}$$

These equations can be combined to derive an expression relating WUE to the two unknown parameters σ_{c_p} and ρ_{c_p,c_r}:

$$\mathrm{WUE} = \frac{\overline{w'c'}}{\overline{w'q'}}\frac{\left(-2\sigma_{c_p}^2 WUE^{-2} \pm \sqrt{4\sigma_{c_p}^4 WUE^{-4} - 4\sigma_{c_p}^2 WUE^{-2}\rho_{c_p,c_r}^{-2}\left(\sigma_{c_p}^2 WUE^{-2} - \sigma_q^2\right)}\right)/2\sigma_{c_p}^2 WUE^{-2}\rho_{c_p,c_r}^{-2} + 1}{\frac{-2\sigma_{c_p}^2 \pm \sqrt{4\sigma_{c_p}^4 - 4\sigma_{c_p}^2\rho_{c_p,c_r}^{-2}(\sigma_{c_p}^2 - \sigma_c^2)}}{2\sigma_{c_p}^2\rho_{c_p,c_r}^{-2}} + 1} \tag{A.8}$$

At each time point, this equation was numerically evaluated and combined with Eqs. (A.4)–(A.7) to derive $\overline{w'c_r'}/\overline{w'c_p'}$ and $\overline{w'q_e'}/\overline{w'q_t'}$ as functions of ρ_{c_p,c_r}. These values were constrained to satisfy the realistic flux conditions of photosynthesis being negative and the other three fluxes being positive. If no physically realistic values resulted from the analysis at this point, the partitioning for that hour was discarded. This could occur for a number of reasons including mismatch of WUE with observed fluxes or random variations in high-frequency data. At this point in the analysis ρ_{c_p,c_r} is still unknown. Further manipulation of the equations (see Scalon and Sahu, 2008) yields the relationship:

$$\rho_{q,c} = \frac{\frac{\sigma_{c_p}^2}{WUE} + \rho_{c_p,c_r}\sigma_{c_p}\sigma_{c_r}\left(WUE^{-1} + \frac{\overline{w'q_e'}}{\overline{w'c_r'}}\right) + \sigma_{c_r}^2\overline{w'q_e'}/\overline{w'c_r'}}{\sigma_c\sigma_q} \tag{A.9}$$

Since $\rho_{q,c}$ is a measured quantity and relationships have already been determined relating ρ_{c_p,c_r} to σ_{c_p} (Eq. (A.7)), this relation can be numerically solved for ρ_{c_p,c_r}, allowing $\overline{w'c_r'}/\overline{w'c_p'}$ and $\overline{w'q_e'}/\overline{w'q_t'}$ to be determined. In some

instances, no solution existed, and the partitioning for that hour of data was discarded.

Prior to carrying out the process described above, the high-frequency time series was filtered using a wavelet transform in order to remove the influence of large eddies, which can degrade the quality of the FVS partitioning results (Scanlon and Sahu, 2008; Scanlon and Kustas, 2010). The first two (lowest frequency) wavelet levels (out of a total of 15 levels) were removed prior to partitioning each hour of high-frequency data. If the partitioning procedure did not yield a valid result, then an additional wavelet level was discarded and this process was repeated until either the partitioning process produced a valid result or the minimum wavelet level was reached, at which point the partition was marked as a failure for that hour. Of partitions that produced valid results, 60% incorporated 13 of the 15 wavelet levels, and less than 10% incorporated fewer than 8 wavelet levels.

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