

Transpiration and evaporation in a Californian oak-grass savanna: Field measurements and partitioning model results

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ABSTRACT

As the eddy-covariance technique enables intensive measurements of evapotranspiration (ET) at the ecosystem level, the interest in further partitioning ET into two main process-based components transpiration (T) and surface evaporation (E) is increasing. Although models for partitioning tower-measured ET have been developed, their reliability for different types of ecosystems still requires extensive validations. From 2001 to 2019, we measured CO_2 and H_2O vapor fluxes over an oak-grass savanna landscape from three eddy-covariance towers (i.e., one over an oak woodland; the other two over annual grasslands under tree canopy and in open area). Annual ET ($\pm$ standard deviation) from the oak woodland, understory grassland, and open grassland was 419 ± 85 mm, 167 ± 36 mm, 324 ± 43 mm, respectively. The differences between the above- and below-canopy ET indicated that oak canopy transpiration (T_{oak}) was 281 ± 48 mm year⁻¹, accounting for $67 \pm 8\%$ of the total ET of the woodland. The T_{oak}/ET ratio varied in seasons, similar to the pattern of oak's leaf area index but opposite to that of soil moisture. We then tested two ET -partitioning models: Scott's long-term-regression-interception (LTRI) model (Scott and Biederman, 2017) and Zhou's quantile-regression-maximum-slope (QRMS) model (Zhou et al., 2016). Even though we expected that the two models would give divergent results since they rely on different working principles, both models captured reasonable magnitudes and seasonal patterns of the T/ET ratio, as suggested by tower measurements. The study confirms that the LTRI and QRMS models are applicable for savanna ecosystems, but some modifications are necessary for tree dominated areas. In combination with field and modeling approaches, this study improves our understanding on the contributions of transpiration and evaporation to total ET from ecosystems with vertical vegetation layers.

1. Introduction

Transpiration (from vegetation) and evaporation (mainly from soil or other surfaces) are two main process-based components of evapotranspiration (ET), a critical parameter for understanding the carbon and water cycles on Earth (Schlesinger and Jasechko, 2014). With the eddy-covariance (EC) technique, we can now measure CO_2 fluxes, but also H_2O vapor fluxes (i.e., ET), intensively at the ecosystem level all over the world. Because of intrinsic interactions between the photosynthesis and transpiration processes, partitioning ET provides a fundamental data source for investigating water relations of carbon sequestration and their potential variability in changing climates (Nelson et al., 2018; Stoy et al., 2019). Specifically, we need the partitioned results to understand mechanisms of stomatal opening, leaf

growth, energy absorption, and water balance in controlling photosynthesis and transpiration processes. In return, these understandings will help us to better predict the temporal and spatial variability of CO_2 and H_2O vapor fluxes. Thus, partitioning ET is critical for better developing process-based models and upscaling plant-based measurements (e.g., sap flow data) (Saugier et al., 1997; Wilson et al., 2001). Also, partitioning ET is highly demanded by validations of remote-sensing and top-down models, which are essential for water management in the area with limited water resources, such as in semi-arid or arid areas, or even in mesic areas but threatened by increased drought events due to climate change (Fisher et al., 2017; Humphrey et al., 2018; Kool et al., 2014).

Savanna is a type of ecosystem where trees unevenly distribute in herbaceous communities, forming the mosaic of woodlands and open

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grasslands. Such a landscape is often found in semi-arid areas, covering approximately 20% of the total land area on Earth (Scholes and Archer, 1997). The coexistence of trees and herbaceous communities enhance competitions to water sources. In California, oak trees and annual grasses coexist on the foothill of the Sierra Nevada Mountains. Located in the typical Mediterranean Climate zone, the oak-grass savanna experience wet, mild winters and dry, hot summers. In general, oak trees and annual grasses grow fast in the spring. As the rainy season stops, soil surface and shallow layers become drier. Meanwhile, oak trees can still maintain their necessary metabolic activities by accessing soil moisture in deeper soil layers or tapping groundwater; annual grasses die out and spread seeds dormant until the following rainy season. Differences in phenological and water accessible niches suggest that oak trees and annual grasses all contribute to the total ET via transpiration, but their contribution fractions should vary over the growing season (Baldocchi et al., 2004, 1997). Because the vegetation structures in the savanna ecosystem are complex, horizontally and vertically, testing the hypothesis in savanna ecosystems is quite challenging (Baldocchi et al., 2004; Kool et al., 2014).

ET measured with the eddy-covariance technique is a rich data source for further quantifying T and E (Kool et al., 2014; Stoy et al., 2019). As ET is measured from a single EC tower, the ET signal is a combination of both T and E signals, which is a barrier to obtain accurate values of transpiration or evaporation directly. A field solution is to derive T from multiple EC towers, such as installing two towers above and below the tree canopy (Baldocchi and Vogel, 1996; Baldocchi et al., 1987; Paul-Limoges et al., 2020; Scott et al., 2003). The primary concern of this approach is the possibility of insufficient turbulent conditions around the understory tower. However, since tree canopy is relatively open in the savanna area, chances of sufficient turbulent conditions for valid field measurements are higher than closed-canopy forests (Baldocchi and Meyers, 1991; Baldocchi et al., 1997; Launiainen et al., 2005; Misson et al., 2007; Scott et al., 2003). Many studies have compared understory tower measurements with results of other direct approaches (e.g., sap flow, stable isotope) or biophysical models (Black et al., 1996; Paul-Limoges et al., 2020; Roupsard et al., 2006; Scott et al., 2003; Wilson et al., 2001). We, therefore, gain enough confidence in using the multi-tower approach in the savanna area.

In addition, it has been pointed out that the understory tower signals also include the contributions of the understory vegetation layer (e.g., herbaceous communities), although an understory tower is often considered as a measure of soil evaporation (Holwerda and Meesters, 2019). Thus, we are here interested in testing whether the understory ET could be further partitioned into the transpiration of annual grasses and evaporation from soil and other wet surfaces (e.g., trunks, branches, leaves, and litters). Certainly, partitioning the understory ET needs the help of ET -partitioning models.

ET -partitioning models have been developed based on tower measurements (Li et al., 2019; Scott and Biederman, 2017; Wei et al., 2017; Zhou et al., 2016). A key thought behind the algorithm is whether first to solve the T/ET or E/ET ratio. Since $T/ET + E/ET \approx 1$, either approach is possible to partition ET into T and E . For example, Zhou et al. (2016) proposed an algorithm based on leaf-level marginal water use efficiency, which is an application of the theory of stomatal controls on both photosynthesis and transpiration (more explanations in the Methods section). In contrast, Scott et al. (2017) solved the E/ET ratio with the assumption that transpiration should equal zero if gross primary productivity (GPP) equals zero. The assumption leads to the result that a mean value of E equals the interception of a valid linear relationship between ET and GPP . Since these two approaches are based on very different underlying principles, it will be interesting to compare them and see whether their partitioning results are comparable with what we learn from our field measurements.

Thus, our primary objectives for this study are: (1) to quantify the magnitude of transpiration of oak trees and annual grasslands with CO_2

and H_2O vapor flux measurements from three eddy-covariance towers; (2) to apply the two ET -partitioning models and compare their estimates of the T/ET ratio against our tower measurements; (3) to compare model results between each other. Based on differences in the phenology of oak trees and annual grasses, we hypothesize that maximum water loss via transpiration occurs in the spring when vegetation is in the most active photosynthesis, and consequently, transpiration contributes a large portion of the total ET . Moreover, the T/ET ratio would display seasonal variations, probably higher than the E/ET ratio during the growing season (Wei et al., 2018). For evaluating the model performance, we hypothesize that, at a minimum, they capture the correct seasonal patterns of T/ET as suggested by field measurements. In addition, we will discuss the model performance by comparing the magnitudes of partitioned results between different calculation approaches.

2. Methods

2.1. Study sites

Our two study sites are in an oak-grass savanna, representing an oak-dominated woody area (Tonzi Ranch, 38.438 N, 120.968 W) and open grassland area (Vaira Ranch, 38.418 N, 120.958 W). In the woodland area, oak trees are denser, and herbaceous communities coexist under the tree canopy and open space between trees (Fig. 1). The open grassland area is dominated by annual grasses with fewer oak trees scattered around the edge. The two sites are ~ 2 km apart, and the average elevation is 177 m above sea level (asl) at the woody area site and 129 m asl at the grassland site.

The study sites are within a typical Mediterranean Climate zone, which has mild, wet winters and hot, dry summers. Over the 90-year time frame from 1926 to 2016, average annual precipitation was 546 mm; mean annual temperature was 16.6 °C; the maximum temperature was 23.5 °C; the minimum temperature was 9.7 °C (according to climate data at the station of Camp Pardee, California, approximately 26 km from the study site; <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca1428>).

At the oak woodland site, deciduous blue oaks (*Quercus douglasii*) cover about 40% of the landscape with an average tree density ~ 144 stem ha^{-1} , an average height 10.6 ± 4.6 m, and a basal area ~ 0.1 m².

Annual grass species dominated under the tree canopy or in the open area are C_3 plants, such as *Brachypodium distachyon*, *Bromus hordeaceus*, *Erodium cicutarium*, *Hypochaeris glabra*, *Trifolium dubium* Sibth., *Trifolium hirtum* All., *Dichelostemma volubile* A., and *Erodium botrys* Cav. Their height varies over growing seasons. In normal years, grasses germinate in the autumn, stays at ~ 0.1 m high through the winter, and increased (almost linearly) up to ~ 0.7 m at the end of May, according to our field observations.

The soil is an Auburn type, very rocky silt loam (*Lithic haploxerepts*), about 0.75 m in depth (Tang et al., 2003; Xu and Baldocchi, 2003, 2004). Groundwater is ~ 8 m deep at the woody site and one-fold deeper (~ 16 m) at the open grassland site. Other than precipitation, groundwater is an important water resource for oak tree function during dry summers as tapping roots grow through the fractured rock layer (Ma et al., 2016; Miller et al., 2010).

2.2. Data collection and processing

Three EC towers, including two towers at the woody site and one at the open grassland site, were established between the autumn of 2000 and the spring of 2001. At the woodland site, one tower is above the tree canopy, ~ 23.5 m high, and the other two short towers (one below the canopy, and the other in the open grassland area) are ~ 2 m high.

On the top of each tower, a sonic anemometer (Model 1352, Gill Instruments Ltd., Lymington, United Kingdom) was installed for collecting three-dimensional wind velocities in 10 Hz (updated to 20 Hz

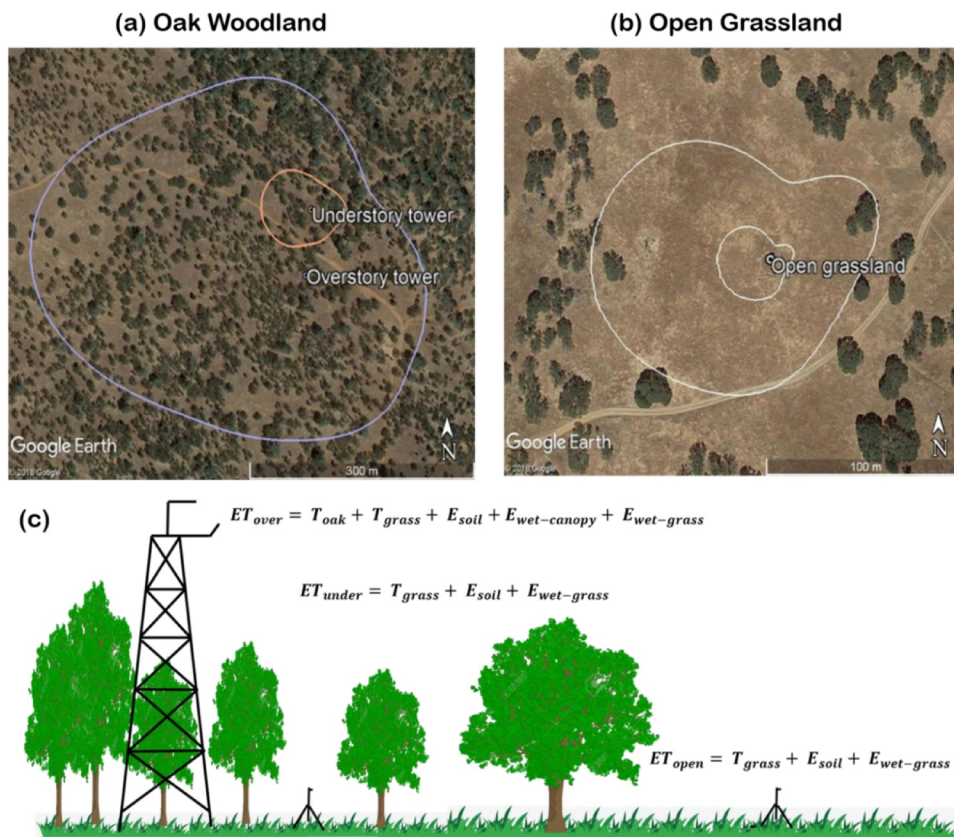


Fig. 1. (a) Cumulative footprints around the two eddy-covariance towers at the woody-area site and (b) around the tower at open grassland site for a period representative of the growing season, between Apr. 1 and Jun. 1, 2018. In (a), the contours represent the area where 80% of the daytime flux originated for that period, showing a much larger footprint for the overstory than for the understory tower. In (b), the inner and outer contours represent 50% and 80% footprint, respectively. (c) Savanna's vertical vegetation structure and water flux terms measured from each tower (see the text for explanations to the symbols and equations).

after 2017). An open-path infrared CO_2 and water vapor analyzer (IRGA, Li-7500, Li-cor, Lincoln, Nebraska, USA) measured CO_2 and water vapor concentration in 5 Hz (updated to 10 Hz after 2017). These high-frequency data were collected by either a laptop or a data logger (CR1000, Campbell Scientific, Inc., Logan, UT, USA), and then half-hour average CO_2 and H_2O fluxes were computed using the MATLAB (MathWorks Inc., R2015b, version 8.6.0) scripts written in house, including spike removal, coordinate rotation, application of standard gas laws, and corrections for density fluctuations (Webb, Pearman & Leuning 1980).

We also measured environmental variables within the same half-hour when CO_2 fluxes were averaged. Atmospheric pressure (P , hPa) was measured by using a barometer (PTB101B, Vaisala, Helsinki, Finland). Water vapor deficit pressure (VPD , kPa) was calculated based on air temperature and relative humidity measured by using a shielded and aspirated sensor (HMP-35 A, Vaisala, Helsinki, Finland). Precipitation (PPT , mm) with a rain gage (TE525, Texas Electronic, Dallas, Texas, USA). Also, incoming photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) with a quantum sensor (Kipp and Zonen PAR-Lite, Delft, Holland). Volumetric soil moisture ($\text{cm}^3 \text{cm}^{-3}$) was measured with a frequency-domain reflectometer probe (ML2x, Delta-T Devices, Burwell, Cambridge, UK). The meteorological and soil moisture sensors were scanned every 5 s, and the 30 min means or sums (for the rain gage) were calculated and stored with data-loggers (CR10X or CR23X, Campbell Scientific Inc., Logan, UT, USA).

For data quality control, we visited the study sites and maintained the instrument biweekly. The IRGA heads were calibrated every two or three months in lab conditions. The flux data collected under low turbulent mixing were screen out, determined by the half-hourly standard deviation of high-frequency vertical velocity (σ_w) to reduce uncertainties associated with the criterion of friction velocity (u_*) (Acevedo et al., 2009). We applied $\sigma_w < 0.08 \text{ m s}^{-1}$ for oak woodland, $\sigma_w < 0.03 \text{ m s}^{-1}$ for understory grassland, or $\sigma_w < 0.05 \text{ m s}^{-1}$ for open grassland. These criteria are equivalent to the threshold of friction

velocity u_* between 0.1 and 0.2 m s^{-1} at our study sites. Also, data collected under heavy rainfall (half-hour precipitation $> 10 \text{ mm}$) or other unpredictable situations (e.g., electronic reasons) were screened out and treated as missing data. Consequently, the fraction of missing data differed from year to year, approximately 32% on average. For the interest of integration, data gaps were filled by combining linear interpolations, mean diurnal variation, and spline smoothing methods; refer to Ma et al. (2017) for more details.

Gross primary productivity (GPP) was estimated by subtracting ecosystem respiration ($Reco$) from NEE on the half-hour scale (i.e., $GPP = Reco - NEE$), where $Reco$ was estimated by a series of linear regression models between nighttime NEE and soil temperature at 4 cm depth within the 15-day moving window. The canopy storage term of CO_2 was computed only for the woody site with the two-tower algorithm, which has been verified *in-situ* by a 4-layer CO_2 profile system along with the overstory tower (Ma et al., 2007, 2017; Xu and Baldocchi, 2004). All data are available on the AmeriFlux data website (Baldocchi and Ma, 2001; Baldocchi et al., 2000).

2.3. Cumulative flux footprints and water flux components from each tower

The heights and locations of the three towers were designed to obtain flux signals from distinguishable biophysical sources (Kim et al., 2006; Ma et al., 2007). To visualize this intention, we employed the footprint model of Hsieh et al. (2000) with a 2D expansion (Detto et al., 2006). Half-hourly daytime-only footprints were calculated for a period representative of the growing season (between Apr. 1 and Jun. 1, 2018). The aerodynamic canopy height of oak canopy was estimated using surface layer theory and turbulence measurements using the algorithm of Pennypacker and Baldocchi (2016), while the height of the vegetation for the understory and open grassland sites was estimated based on linear interpolations of biweekly measurements of the grass height. Roughness length was calculated as a constant through non-linear least square fit on the log wind equation for near-neutral

conditions (Maurer et al., 2015), while displacement height was variable and equal to 0.66 of the canopy height. Cumulative footprints for the period described above are shown on top of the site's satellite image obtained from Google Earth © with codes developed and tested in previous studies (Eichelmann et al., 2018; Knox et al., 2016).

Fig. 1a and b show the cumulative flux footprints at each tower. The overstory flux footprints covered a larger area (including oak trees, understory layer, and open spaces), while the understory flux footprints only covered smaller areas of grasses under the canopy and in the open spaces between trees (Fig. 1a). In comparison, the open-grassland tower mainly measured fluxes from the grasses (Fig. 1b). The bottom diagram of Fig. 1 illustrates the vertical structure of the savanna and the water flux components measured from each tower (Fig. 1c).

Theoretically, the fluxes from the overstory tower (ET_{over}), the understory tower (ET_{under}), and the open-grassland tower (ET_{open}) can be expressed in Eqs. (1) – (3), respectively, according to different biophysical sources (also shown in Fig. 1c):

$$ET_{over} = T_{oak} + T_{grass} + E_{soil} + E_{wet-canopy} + E_{wet-grass} \quad (1)$$

$$ET_{under} = T_{grass} + E_{soil} + E_{wet-grass} \quad (2)$$

$$ET_{open} = T_{grass} + E_{soil} + E_{wet-grass} \quad (3)$$

where T_{oak} is the transpiration from oak canopy; " T_{grass} " is the transpiration from annual grasses; " E_{soil} " refers to evaporation mainly from soil; " $E_{wet-canopy}$ " refers to evaporation from wet surfaces within the tree canopy layer, such as wet leaves and branches; " $E_{wet-grass}$ " refers to physical evaporation from wet surfaces below the tree canopy, such as grass leaves, tree trunks, grass litter, or coarse woody debris.

2.4. Deriving T_{oak} from the two-tower measurements

Our preliminary analysis showed that (1) $ET_{over} > ET_{under}$ in general; (2) the differences in the seasonal patterns of ET_{over} and ET_{under} . ET_{over} and ET_{under} both had a remarkable drop from wet season to dry season, but ET_{over} decreased slower than ET_{under} (Fig. 2a and b). This divergence reflected the fact that tree canopy continuously functioned during the dry summer, while annual grasses died out in the same summer months. With this observation, we subtract Eq. (2) from Eq. (1), canceling out E_{soil} and $E_{wet-grass}$:

$$ET_{over} - ET_{under} = T_{oak} + E_{wet-canopy} \quad (4)$$

Then, by arranging Eq. (4), we get Eq. (5):

$$T_{oak} = ET_{over} - ET_{under} - E_{wet-canopy} \quad (5)$$

$E_{wet-canopy}$ can be significant when surfaces are wet, following the occurrences of dew or rain interception. However, since the savanna experiences typical Mediterranean Climate, the wet season combines with cold temperature; grasses stay in green but grow very slowly; oak trees are dormant, having no leaves yet. Thus, during such a wet-cold period (e.g., from December to early March of the following year), $E_{wet-canopy} \simeq ET_{over} - ET_{under}$, as $T_{oak} \rightarrow$ zero. The cold temperature also limits the evaporation of the soil and other wet surfaces. Until temperature increases above 10°C in the late spring (e.g., from late March to late May), trees put on leaves, and $T_{oak} >> E_{wet-canopy}$. Thus, we considered $E_{wet-canopy}$ as a negligible term in most months. Approximately,

$$T_{oak} \simeq ET_{over} - ET_{under} \quad (6)$$

Thus, we used Eq. (6) for deriving T_{oak} from the two-tower measurements in general. We discussed the uncertainties associated with the approximation in the Discussion section.

2.5. T and E denoted by the partitioning models and related approximations

Because T_{grass} , E_{soil} , and evaporation from other wet surfaces were not measured directly and separately in the field, the ET partitioning

models were needed for further partitioning (see the next sub-section "2.6"). We noticed that the partitioning models give total results of transpiration or evaporation terms, which are not always the same as the source-specific terms expressed in Eqs. (1)–(3). For clarity, we defined T and E to refer to the "total transpiration" and "total evaporation", respectively, and referred them back to the source-specific terms (Table 1).

Because the savanna has a vetical vegetation structure, the total transpiration term from the overstory is the sum of water fluxes from oak canopy and understory grasses: $T = T_{oak} + T_{grass}$. For comparison purposes, we consider $T \simeq T_{oak}$. First, $T_{grass} \rightarrow$ zero after annual grasses die out at the beginning of the dry season (e.g., the end of May). Second, $T_{oak} >> T_{grass}$ once oak trees put on leaves in the late spring (e.g., the late March).

For the same reason for neglecting $E_{wet-canopy}$, the evaporation tems from other wet surfaces (i.e., $E_{wet-grass}$) was also negligible during the cold months and dry summer months. Thus, E_{soil} is the majority of E : $E \simeq E_{soil}$.

We discussed the uncertainties associated with these approximations in the Discussion section. In addition, no approximations were needed when ET_{under} or ET_{open} were partitioned with the models, as $T = T_{grass}$, where T_{grass} represents the grasses under the canopy or in open area. The open grassland tower provided an independent dataset representing the behaviors of annual grasslands, giving us an extra chance to refine our interpretations of the understory measurements (Fig. 2c).

2.6. ET -partitioning models

As explained earlier, we chose to focus on Scott's model (Scott and Biederman, 2017) and Zhou's model (Zhou et al., 2016). These models both start from the linear relationship between GPP and ET , but their working principles are different (Fig. 3). To be clear in comparisons, we renamed the two models to emphasize their statistical procedures, that is, Scott's model as the long-term-regression-intercept model (LTRI) and Zhou's model as the quantile-regression-maximized-slope model (QRMS).

The LTRI model is based on the ET - GPP linear regression analysis. On relatively larger temporal and spatial scales, transpiration should equal zero when GPP is zero, which means no primary productivity gains if there is no water investment. With this assumption, the intercept of the ET - GPP linear relationship can be interpreted as a mean value of E on a relatively large spatial scale. This approach requires multi-year flux measurements integrated over a relatively long period, such as annual or monthly integration (Scott and Biederman, 2017). Our preliminary results showed that the linear models could be significant on an annual basis but with higher uncertainties for individual towers. Thus, we pooled the three-tower data together for estimating a mean E value of the studied savanna landscape annually and monthly. For the convenience of discussion on longer timescales (e.g., monthly), we used the units of " $g\ C\ m^{-2}$ " for GPP and " mm " for ET and its components (equivalent to " $kg\ H_2O\ m^{-2}$ "), respectively. Also, using the unit of " mm " is consistent with the unit for precipitation commonly defined in meteorology or hydrology.

The QRMS model also relies on the linear relationship between tower-measured GPP and ET , but its working principle is built upon the theory of stomata's optimized behavior; that is, stomata intend to maximize carbon assimilation with a given water investment. Zhou et al. (2016) developed the algorithm for extending this theory on the ecosystem scale with the use of intensive tower data. First, a concept of "underlying water use efficiency" ($uWUE$) is defined: $uWUE = \frac{GPP \sqrt{VPD_f}}{ET}$, where VPD_f is a proxy of leaf-to-air water vapor mole fraction ($mol\ mol^{-1}$). In particular, VPD_f is converted from the fraction of water vapor pressure deficit (VPD) to air pressure (P): $VPD_f = VPD/P$, both in the unit of kPa. Second, the model defines two more related concepts: "apparent" $uWUE$ (i.e., $uWUE_a$) and "potential"

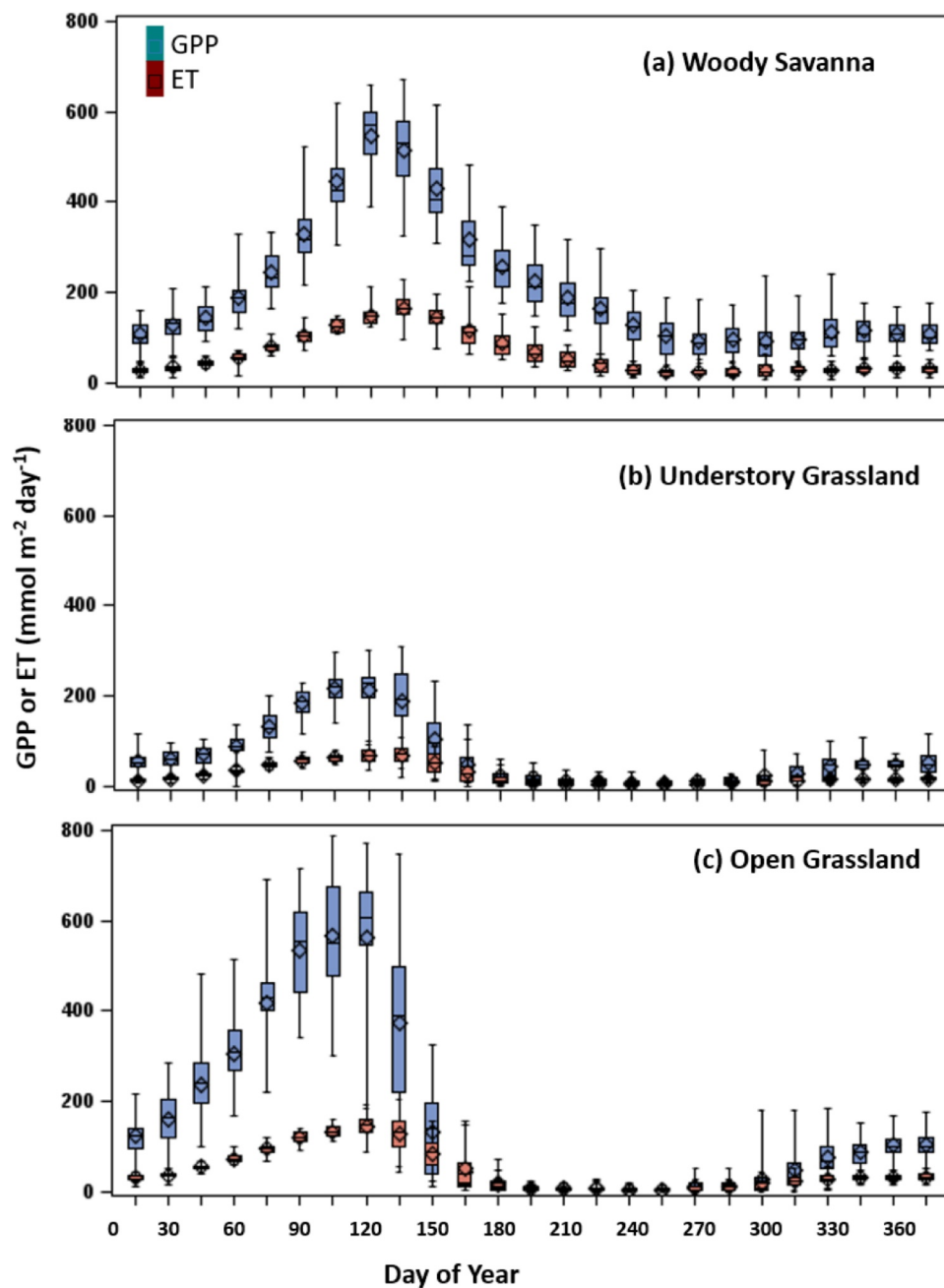


Fig. 2. Box-plots of daily sums of gross primary productivity (*GPP*) and evapotranspiration (*ET*) averaged over every 15-day period (Notes: the last period has five or six days.). The panels show the measurements above the tree canopy (a), below the tree canopy (b), and over the open grassland (c) over the study period from 2001 to 2019 (i.e., $n = 19$). Each box shows median, percentiles (1, 25, 75, and 99%), and mean (in circles).

Table 1

Theoretical and simplified equations of evapotranspiration (*ET*) in the expression with total transpiration (*T*) and total evaporation (*E*) and the source-specific terms (refer to the text and Fig. 1c for details).

Tower Location	Evapotranspiration (<i>ET</i>) in total terms	Source-specific terms of <i>T</i> or <i>E</i>	Simplified Equations
Overstory	$ET_{over} = T + E$	$T = T_{oak} + T_{grass}$ $E = E_{soil} + E_{wet-canopy} + E_{wet-grass}$	$ET_{over} \approx T_{oak} + E_{soil}$
Understory	$ET_{under} = T + E$	$T = T_{grass}$ $E = E_{soil} + E_{wet-grass}$	$ET_{under} \approx T_{grass} + E_{soil}$
Open area	$ET_{open} = T + E$	$T = T_{grass}$ $E = E_{soil} + E_{wet-grass}$	$ET_{open} \approx T_{grass} + E_{soil}$

uWUE (i.e., *uWUE_p*), depending on the time taken into account. The *uWUE_a* focuses on short periods (e.g., weekly or monthly), while the *uWUE_p* regards an entire growing season. In other words, the *uWUE_p* describes an ideal status determined by local climate and vegetation, while the *uWUE_a* reflects vegetation's biological responses to instant changes in environmental conditions. Furthermore, the *T/ET* ratio can be determined as $\frac{T}{ET} = \frac{uWUE_a}{uWUE_p}$ (refer to Zhou et al. (2016) for details).

Zhou et al. (2016) suggested applying the 95th percentile linear regression analysis for estimating the *uWUE_p* but using regular linear regression analysis for determining the *uWUE_a*. In this study, we first followed this suggestion, which resulted in a *T/ET* ratio lower than that of oak transpiration of the two-tower measurements. We realized that using the analysis of regular linear regression might underestimate *uWUE_a* because the regular linear regression analysis focuses on

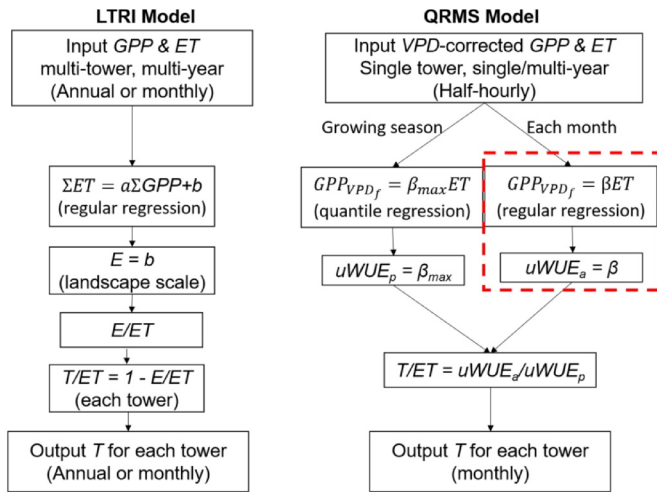


Fig. 3. Flowcharts of the frameworks of the two *ET*-partitioning models examined in this study: Scott's long-term-regression-intercept model (LTRI) and Zhou's quantile-regression-maximized-slope model (QRMS). Notice that *GPP* and *ET* are gross primary productivity and evapotranspiration derived from the CO_2 and H_2O fluxes, respectively; GPP_{VPDf} means gross primary productivity corrected by water vapor deficit in mole fraction, $GPP_{VPDf} = GPP\sqrt{VPD_f}$; *T* refers to transpiration; *E* refers to evaporation from soil or other surfaces). Also, the dash-line block indicates the part subject to a modification proposed in this study.

“average” conditions rather than “maximum” values, which might be inconsistent with the theory of optimized stomatal behavior. Thus, we tried the quantile regression analysis in estimating $uWUE_a$, instead. Also, because $uWUE_a$ must be determined for each short period, the number of flux data involved in calculation is smaller than that over the entire growing season. Therefore, the percentile threshold suggested for $uWUE_p$ (i.e., the 95th percentile) might be too high for $uWUE_a$ as outliers were involved. Thus, we tried the 70, 80, and 90th percentiles, respectively. Based on such comparisons, the 80th percentile gave the best agreement with the field measurements (see Results).

All statistical analyses were processed with the standard statistical software package SAS (Version 9.4, SAS Institute Inc., Cary, NC, USA). The significance level was set to the probability value (*p*-value) at 0.05.

3. Results

3.1. Tower-measured ET_{over} , ET_{under} , T_{oak} , and T/ET ratios

ET_{over} , ET_{under} , and T_{oak} all varied over the growing season with differences in the magnitude and the timing of their maxima (Fig. 4a). Their decreasing rates after the peaks were also different. T_{oak} peaked in the spring, and ET_{over} matched T_{oak} gradually as the understory annual-grass communities died out at the onset of dry summer, shown as a sharper decrease in ET_{under} with the decrease in soil moistures (Fig. 4c). It suggests that the total transpiration of the ecosystem (*T*) is dominated by T_{oak} , and the *T* is significantly larger than ET_{under} throughout the year except in the early spring when their magnitudes are comparable.

We calculated the T/ET ratios regarding each vegetation layer. First, the T_{oak}/ET_{over} ratio indicated the fraction of oak canopy transpiration versus the total *ET* of the woodland area. The ratio values clearly showed seasonal variations with a summer peak (Fig. 4b). T_{oak} accounted for a large percent of ET_{over} (> 90%) during the dry summer months, even though ET_{over} continued to decrease.

Second, we considered ET_{under}/ET_{over} as a proxy of grass transpiration over ET_{over} (i.e., T_{grass}/ET_{over}) since evaporation from the soil and other wet surfaces was considerably smaller than T_{grass} during the growing season (compare Fig. 5b with Fig. 4a). Compared with the seasonal pattern of the T_{oak}/ET_{over} ratio, the proxy of T_{grass}/ET_{over}

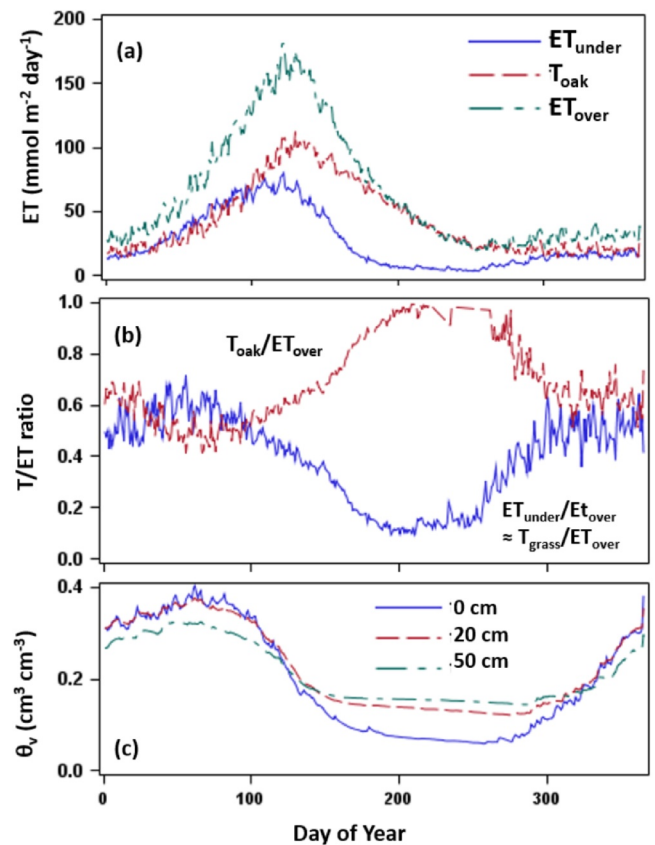


Fig. 4. Seasonal patterns averaged over the studied years: (a) daily integrations of evapotranspiration measured from the overstory (ET_{over}), understory tower (ET_{under}), and oak canopy transpiration (T_{oak}); (b) the ratio of oak canopy transpiration to the total evapotranspiration of the savanna (T_{oak}/ET_{over}) and an approximate ratio of grass transpiration to the total evapotranspiration of the oak woodland area (i.e., $T_{grass}/ET_{over} \approx ET_{under}/ET_{over}$); (c) volumetric soil moisture (θ_v) at the soil surface (0 cm) and the depths of 20 and 50 cm.

showed an opposite seasonal pattern, which agreed with the phenology of annual grasses. Due to the absence of annual grasses during the dry summer months, the contribution of plant transpiration (e.g., from perennial species) was limited, as low as 10%. Because annual grasses germinate in the autumn and grow fast in the spring, the transpiration of annual grasses contributed more to ET_{over} in the spring, up to 60%.

In those wet-season months, the values of the T_{oak}/ET_{over} ratio were close to those of the ET_{under}/ET_{over} ratio (Fig. 4b). As oak trees were dormant in winter months, the T_{oak}/ET_{over} ratio was determined mainly by the physical process of evaporation from wet surfaces within the oak canopy (i.e., $E_{wet-canopy}$), following dews or rain interceptions (more explanations in the Methods). During these cold months, transpiration from understory grasses was also low due to slow growth rate under low temperatures. That is why the magnitude of T_{oak}/ET_{over} ratio was similar to that of ET_{under}/ET_{over} (the proxy of T_{grass}/ET_{over}) (Fig. 4b).

3.2. The LTRI model: from *E* to T/ET

Since the LTRI model was designed for seeking the long-term, climate-determined pattern over a relatively large area, we pooled the data from the three towers altogether (Fig. 5a). The linear relationship between *ET* and *GPP* was significant on an annual basis ($R^2 = 0.93$, $p < 0.001$) with an intercept of $53 \pm 10\ mm\ year^{-1}$. Thus, a mean annual *E* over the savanna landscape was between 40 and 70 $mm\ year^{-1}$, which means 7%–12% of mean annual precipitation ($563 \pm 226\ mm$, see Table 2).

We then established the LTRI model for each month across three

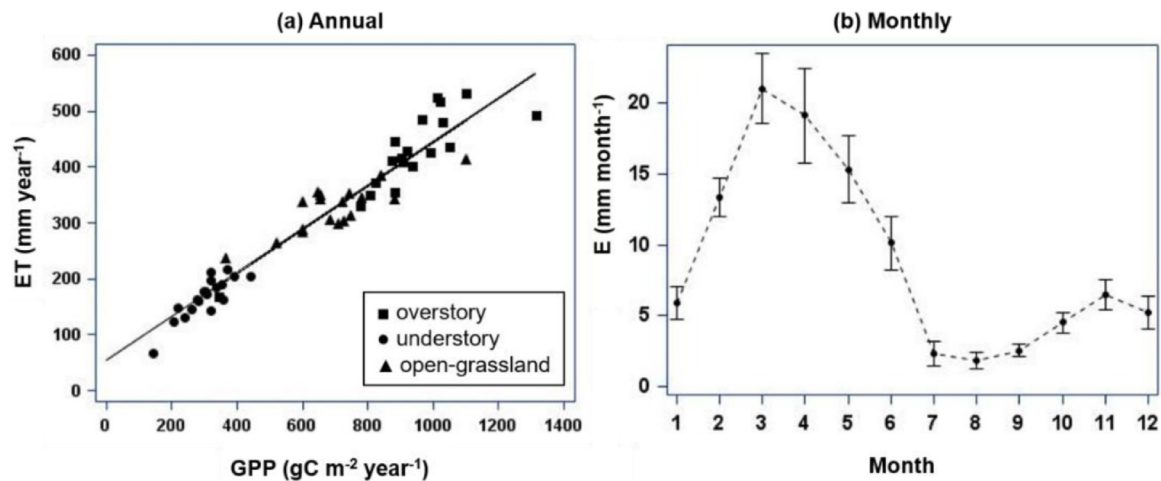


Fig. 5. Panel (a): The relationship between annual integrations of evapotranspiration (ET) and gross primary productivity (GPP) over the savanna landscape, including data measured from the overstory and understory towers at the woody savanna site and the open-grassland tower. Panel (b): Monthly surface evaporation (E) with standard error bars.

Table 2

Multi-year averages and standard deviation ($\pm$ std) of annual integrations of gross primary production (GPP), precipitation (PPT), and evapotranspiration (ET) measured at the woody savanna, understory grassland, and open grassland. For each location, transpiration (T) and evaporation (E) are partitioned by the LTRI model and the QRMS model with two algorithms for estimating $uWUE_a$: the regular regression analysis (QRMS-reg) or the 80% quantile regression analysis (QRMS-Q80). Refer to the Methods and Table 1 for variable notations. Notice that annual integration is based on the hydrological year, from Oct. 1 – Sep. 30 of the following calendar year.

Variable	Units	Method	Woody Savanna	Understory Grassland	Open Grassland
Field Measurements					
GPP	gC m ⁻² year ⁻¹	EC tower	924 $\pm$ 185	302 $\pm$ 70	708 $\pm$ 153
PPT	mm	Rain gage	563 $\pm$ 226	–	592 $\pm$ 199
ET	Mm	ECtower	419 $\pm$ 85	167 $\pm$ 36	324 $\pm$ 43
T_{oak}	Mm	Two-tower	281 $\pm$ 48	–	–
Model Results					
T	Mm	LTRI ^{fi}	309 $\pm$ 63	66 $\pm$ 15	214 $\pm$ 27
		QRMS-reg	162 $\pm$ 30	71 $\pm$ 16	153 $\pm$ 23
		QRMS-Q80	257 $\pm$ 47	107 $\pm$ 23	211 $\pm$ 30
E	Mm	LTRI	110 $\pm$ 22	101 $\pm$ 23	113 $\pm$ 17
		QRMS-reg	246 $\pm$ 58	92 $\pm$ 20	168 $\pm$ 27
		QRMS-Q80	151 $\pm$ 42	57 $\pm$ 14	109 $\pm$ 21

towers over the studied years. The partitioned mean monthly E values showed a strong seasonal pattern (Fig. 5b). In general, the evaporation value was high in the spring months (Feb. – Jun.), low in the summer months (Jul. – Sep.), and slightly increased again in autumn months (Oct. – Dec.) as raining season resumed. In other words, soil and surface evaporation was higher in the wet season than in the dry season, as expected.

With the estimates of monthly E , the E/ET ratio was calculated, and the T/ET was obtained according to $T/ET = 1 - E/ET$. In particular, for the overstory tower, $T/ET_{over} = 1 - E/ET_{over}$. Similarly, T/ET_{under} or T/ET_{open} could be explicitly calculated by using the data from either the understory or open grassland tower (Refer to Table 1 on labeling). To validate the LTRI modeled T/ET results, we compared their seasonal patterns with those suggested by tower measurements. Theoretically, regarding the overstory tower, the LTRI-modeled T/ET ratio could combine contributions from oak canopy and understory grass communities (i.e., $T = T_{oak} + T_{grass}$). However, since T is dominated by T_{oak} most of the time (Fig. 4a), the seasonal pattern of the LTRI-modeled T/ET

ET ratio resembles that of T_{oak}/ET_{over} derived from the two towers (i.e., $T/ET_{over} \approx T_{oak}/ET_{over}$, compare Fig. 6a with Fig. 4b). In the grass-dominated open area, the LTRI-modeled T/ET shows a pattern similar to that of the ET_{under}/ET_{over} ratio (i.e., $T_{grass}/ET_{open} \approx ET_{under}/ET_{over}$, compare Fig. 6b with Fig. 4b).

Also, Scott et al. (2017) suggested that the seasonal pattern of the T/ET ratio likely agreed with that of LAI. Thus, we compared their seasonal patterns regarding canopy and annual grass, separately (Fig. 6). The respective LTRI-modeled T/ET ratio highly covaried with oak's or grass' LAI over the growing season (Fig. 6b and e). Statistically, the seasonal variations in LAI of oak trees and annual grasses could explain 60% and 52% of seasonal variations of the T/ET ratios, respectively, with linear regression analysis ($p < 0.01$).

While the oak T/ET seasonal pattern was correlated to LAI, the seasonal pattern did not coincide with that of soil surface moisture (Fig. 6a and c). In contrast, the grasses T/ET seasonal pattern was corresponding to that of soil surface moisture (Fig. 6d and f). This dissimilarity reflects the difference in water availability between oak trees and annual grasses. While annual grasses much depend on soil moisture in shallow soil layers, oak trees could access soil water in deeper soil layers, even groundwater, allowing them to remain active during the dry summers.

3.3. The QRMS-model: from $uWUE$ to T/ET

We applied the QRMS model for estimating monthly $uWUE_p$ and $uWUE_a$ for each growing season (Fig. 7). Particularly, oak canopy had a multi-year mean $uWUE_p$ at 3.3 mol mol⁻¹ (CO₂ vs. H₂O vapor) with 0.37 mol mol⁻¹ standard deviation across years; the grasses' mean $uWUE_p$ was 1.6 $\pm$ 0.21 and 1.8 $\pm$ 0.25 mol mol⁻¹ for the understory or open grassland, respectively; the overstory tower (entire woody savanna) showed $uWUE_p = 2.2 \pm 0.20$ mol mol⁻¹.

The values of $uWUE_a$ estimated with the regular linear regression analysis tended to be lower than the values calculated with the quantile linear regression analysis (Fig. 7b and d). While the $uWUE_p$ was treated as a constant for each year, the $uWUE_a$ was determined by differences in biotic and abiotic conditions among months, reflecting how the T/ET ratio varied over the growing season. However, the magnitudes of value $uWUE_a$ highly depended on the regression methods (Fig. 8b and d).

For the oak woodland area (measured from the overstory tower), the QRMS-reg model showed a seasonal pattern of the T/ET ratio different from the two-tower result with the peak, about two months earlier than that of the two-tower result. In contrast, the 80% quantile regression analysis (QRMS-Q80) captured the seasonal pattern from the

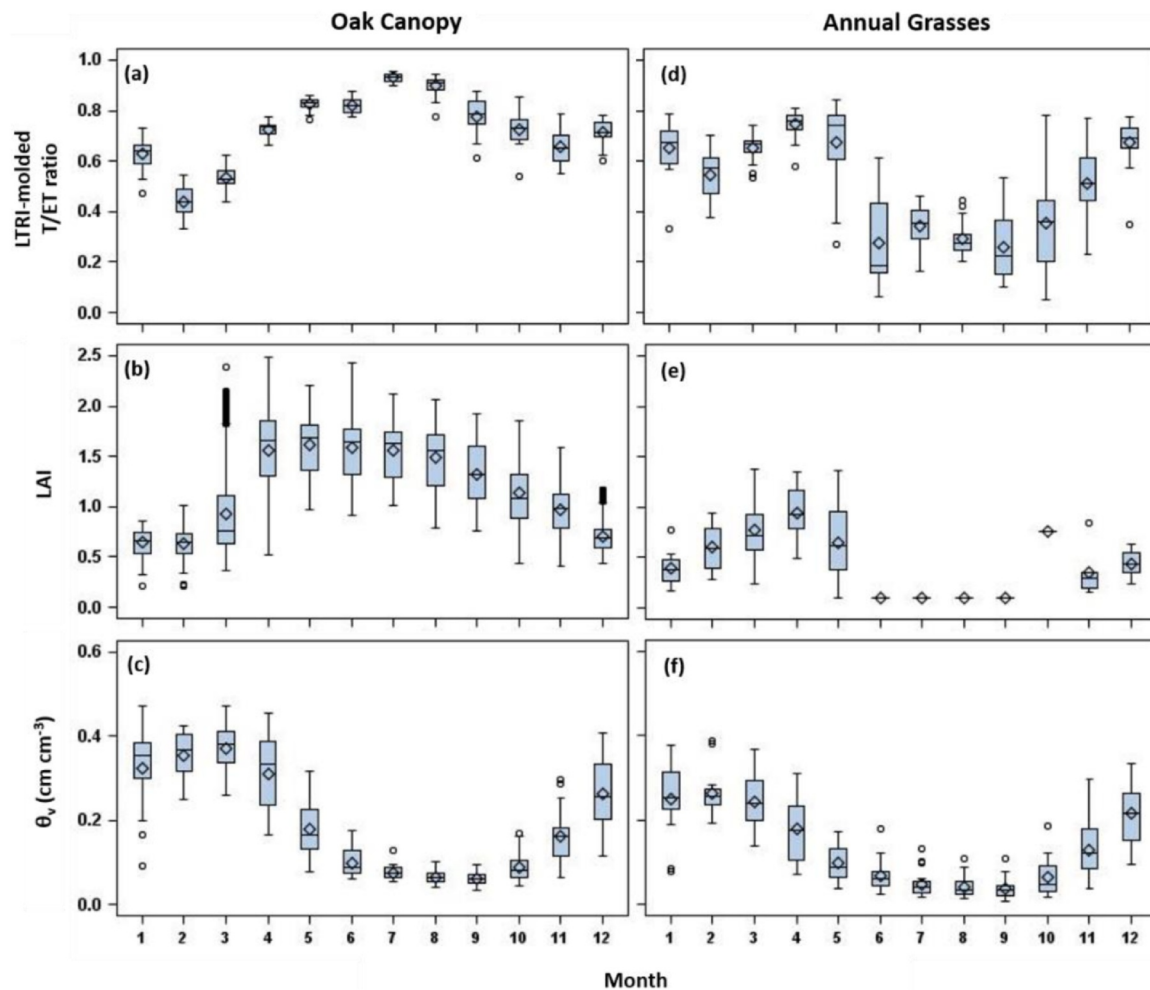


Fig. 6. Seasonal patterns of the LTRI modeled T/ET ratio, leaf area index (LAI), and soil surface moisture (θ_v) regarding oak canopy (a, b, and c) and annual grasses (d, e, and f), measured at the woody savanna site and open grassland site, respectively.

two towers. While the QRMS-reg algorithm produced the values of T/ET ratios lower than those values from the two-tower, the QRMS-Q80 algorithm reduced the divergence (Fig. 8a). Also, the LTRI results were comparable to the two-tower results (Fig. 8a). It confirms that the contribution of evaporation from within the oak canopy towards T_{oak} calculated with the two-tower method is likely negligible.

For the understory grassland, the QRMS-reg and QRMS-Q80 results showed the seasonal pattern of T/ET relatively comparable to the pattern suggested by ET_{under}/ET_{over} , but the QRMS-reg values during the wet, cold months were lower than the results of the QRMS-Q80 (Fig. 8b). Compared to the trend suggested by ET_{under}/ET_{over} , the LTRI model tended to underestimate the T/ET ratio in these spring months probably because the LTRI-estimated E is an ecosystem level average, ignoring the effects of the tree canopy on the evaporation of water from soil or other wet surfaces below the canopy. LTRI-estimated average ecosystem E is likely higher than the actual evaporation relevant for the understory tower. In addition, the ET_{under}/ET_{over} includes the contribution of soil evaporation in ET_{under} , causing T/ET overestimated. In other words, the QRMS-reg algorithm may be more suitable for grassland, as suggested by Zhou et al. (2016).

For the open grassland, the QRMS-reg, QRMS-Q80, and LTRS model results were comparable to one another, overall following the trend of the approximate pattern, overall (Fig. 8c). Again, during the wet, cold months, the QRMS-Q80 values were higher than the results of the QRMS-reg. And, the LTRI-estimated T/ET ratios were comparable to the results of QRMS-reg, agreeing with the suggestion of Zhou et al. (2016) that the QRMS-reg algorithm worked for grassland. Moreover, the LTRI-

estimated T/ET ratios in the summer months were considerably higher than the results of the QRMS-reg or QRMS-Q80. This result is also associated with the uncertainty in the estimation of E , combined with the fact that total ET is near-zero during those months at this site (Fig. 2c), so small changes in E have a disproportionately large effect on the T/ET ratio.

3.4. Model performances

The reasonable T/ET seasonal patterns gave us confidence in partitioned results of transpiration. However, the timescale for estimating reliable T/ET ratio can not be too fine (e.g., < one month) because these two ET partitioning models need data sample size large enough for operating statistical analysis. We tested model performances in two steps.

First, we applied the monthly T/ET ratio to estimate daily transpiration with the assumption that the monthly T/ET ratio should remain relatively stable within the same month. Overall, under the Mediterranean-type background climate, the magnitude and variation in daily transpiration were reasonable compared to tower measurements (as shown in Fig. 9).

To evaluate the performance of the models, we compared the results of the LTRI models, the QRMS-reg, and the QRMS-Q80 algorithms. For the oak woodland, since we have known that the QRMS-reg algorithm did not give a trustable seasonal pattern of T/ET ratio (as shown in Fig. 8a), we focused on the results of LTRI and QRMS-Q80 models. The LTRI model overestimated T_{oak} by about 30%, whereas the QRMS-Q80

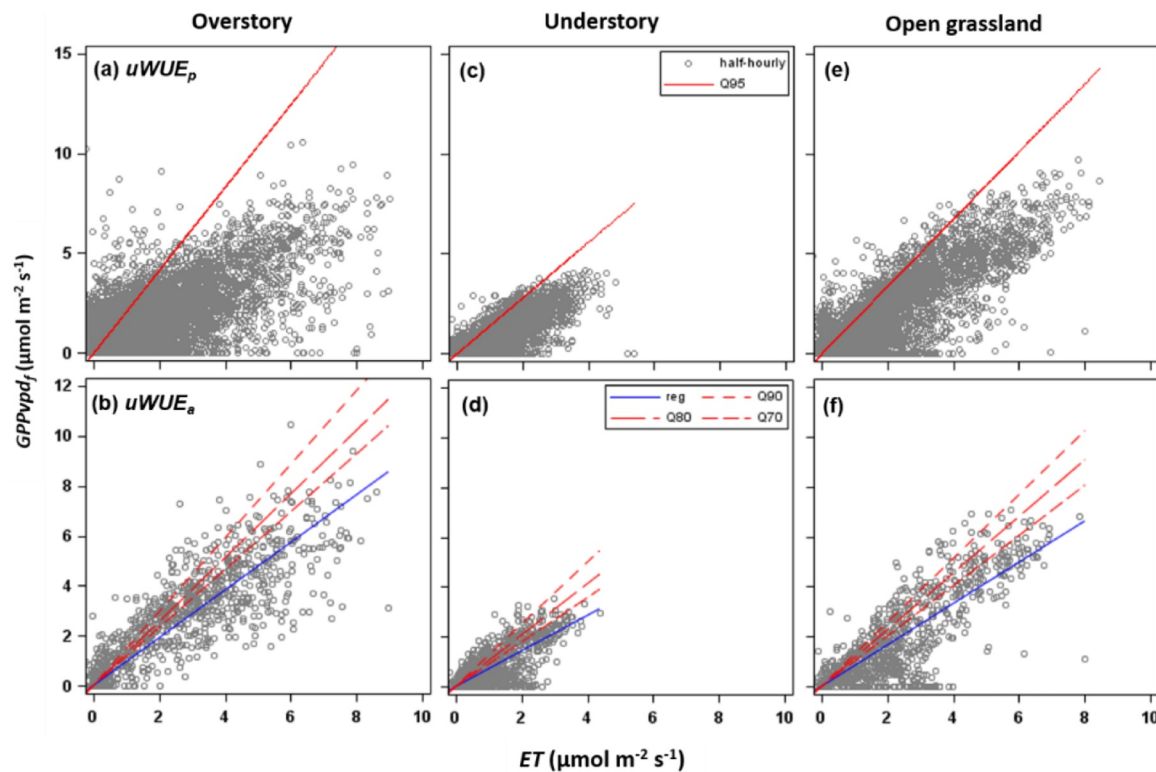


Fig. 7. Calculating potential ($uWUE_p$) and actual $uWUE_a$ with the linear relationship between half-hourly CO_2 and H_2O fluxes (gray circles). The panels include data from the overstory (a and b), understory (c and d), and open grassland (e and f) towers. The upper panels ($uWUE_p$) include data from the growing season of 2018, while the bottom panel ($uWUE_a$) show data from May 2018, as an example. Notice that, for consistency in labeling, the CO_2 and H_2O fluxes are labeled by gross primary productivity (GPP) and evapotranspiration (ET), respectively; GPP_{VPD} means gross primary productivity corrected by water vapor deficit in mole fraction. Lines are results of the 95% quantile regression (Q95) for $uWUE_p$, the regular linear regression analysis (reg) and 70% (Q70), 80% (Q80), and 90% (Q90) quantile regression for $uWUE_a$.

results showed only a 2% difference from the 1:1 line (Fig. 10a and b).

The three approaches left significant uncertainties for understory grasslands. The results of the LTRI model showed 25% and 47% underestimated understory grass transpiration, compared to the results of QRMS-reg and QRMS-Q80 models (Fig. 10c and d).

For the open grassland, the LTRI model results were about 6% different from the QRMS-reg results but about 18% lower than the QRMS-Q80 results (Fig. 10e and f). Still, the QRMS-reg algorithm performed better for the open grassland.

3.5. Contributions of annual transpiration and evaporation at the savanna

Based on the three-tower measurements, we observed that annual ET ($\pm$ standard deviation) was 419 ± 85 mm, 167 ± 36 mm, 324 ± 43 mm from the oak woodland, understory grassland, and open grassland, respectively (Table 2). The differences between the above- and below-canopy ET indicated that oak canopy transpiration (i.e., T_{oak}) was 281 ± 48 mm year⁻¹, accounting for 67% of the total ET in the woody savanna area (i.e., ET_{over}).

Further, the ET -partitioning models enabled us to quantify the amount of transpiration for each vegetation layer. In the oak woodland area, $\sim 67\%$ of the total ET (i.e., ET_{over}) was from oak canopy's transpiration, while the understory grass transpiration contributed $\sim 16\%$ of ET_{over} . The remaining $\sim 17\%$ were from physical evaporation from the soil or other plant surfaces. In the open grassland area, grass contributed $\sim 67\%$ of the total ET (i.e., ET_{open}), and soil evaporation contributed $\sim 33\%$ of the total ET (i.e., ET_{open}) (Table 2).

4. Discussion

This study provides a basic idea of the percentage of T and E over

the savanna landscape in California. In combination with field and statistical modeling approaches, our analysis shows that the percentage of oak canopy's transpiration contribution to the total ET in the oak woodland area is similar to the percentage that annual grasses' transpiration in the open area, $\sim 67\%$. This result is within the global range of 50% $\sim$ 76% (Schlesinger and Jasechko, 2014; Wei et al., 2017) and consistent with previous studies on ET partitioning with the eddy-covariance towers (Li et al., 2019; Scott and Biederman, 2017; Zhou et al., 2018). However, the contributed percentage increases up to 83% in the oak woodland area when the 16% contribution from understory grasses is taken into account as well. Thus, over the savanna landscape, the percentage of vegetation transpiration from the area with multiple vertical vegetation layers, such as the oak woodland area, is higher than that from the area with less vertical layers, such as the open grassland area. Meanwhile, the contributed percentage from understory grasses is much less than that of tree canopy, due to understory species features and overstory effects on grass growth. In addition, the uncertainties from neglecting evaporation from wet surfaces (e.g., $E_{wet-canopy}$ and $E_{wet-grass}$) are small, $\sim 2\text{--}4\%$.

We carefully compared the performances of two ET -partitioning models. Although we cannot compare all models in one single study, such a comparison study is helpful for better evaluating how well these models work for the savanna ecosystems in terms of predicted values and seasonal patterns. Intuitively, one may think that the seasonal pattern of T should be coincident with that of ET , which is what we see here, but the seasonal pattern of the T/ET ratio may not be similar to that of ET . Thus, we checked the seasonal pattern of the T/ET ratio first. As the results show, oak trees transpired at the peak in the late spring but contributed the most significant portion of ET in the summer, while annual grasses transpired and contributed the most altogether in the spring. The differences in the T/ET seasonal patterns indicate the role of

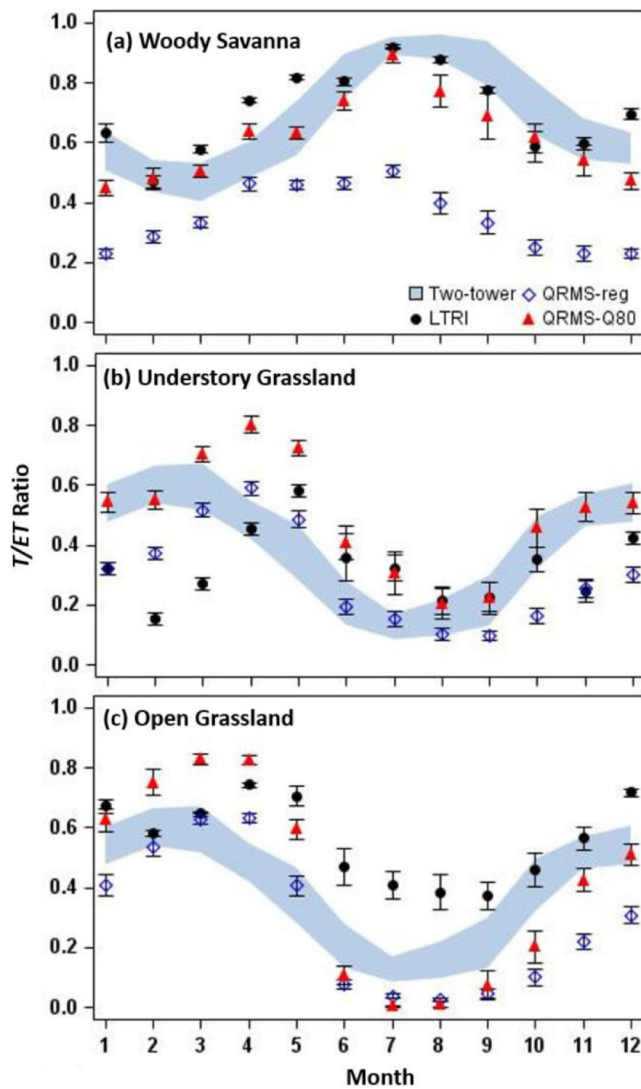


Fig. 8. Monthly T/ET ratios ($\pm$ standard error bars, $n = 18$) estimated by the long-term-regression-intercept model (LTRI) and the quantile-regression-maximum-slope model (QRMS) using the regular linear regression analysis (QRMS-reg) or quantile regression at the percentiles of 80% (QRMS-Q80) for estimating $uWUE_a$ at the oak woodland area, the understory grassland, and the open grassland. The band in (a) is the T/ET ratio of oak canopy based on the two-tower approach (i.e., T_{oak}/ET_{over}); the band in (b) and (c) is the ratio of understory to overstory ET (i.e., ET_{under}/ET_{over}) as an approximation of grass transpiration vs. total ET of the savanna (with no ET partitioning).

phenology in determining the T/ET ratio; the patterns are comparable to the seasonal variations in LAI of oak canopy and annual grasses. This finding agrees with the results of previous studies (Li et al., 2019; Saugier et al., 1997; Scott and Biederman, 2017; Wilson et al., 2001).

Nevertheless, the seasonality of soil moisture may drive that of transpiration in semi-arid ecosystems (Wang et al., 2018). Our analysis provides an opposite example. As oak trees maintain functioning throughout dry summers, but oak trees most likely utilize soil moisture in deeper soil layers and can obtain a small amount of groundwater with tapping roots growing through bedrocks (Miller et al., 2010). Thus, when soil moisture is measured only in shallow soil layers, those measurements cannot reflect the seasonal changes in oak canopy transpiration (as shown in Fig. 6).

In this study, T_{oak} derived from the overstory and understory eddy-covariance towers serves as an independent observation allowing further model validation. As mentioned earlier, although the two-tower setting is associated with uncertainties between tower footprints (as

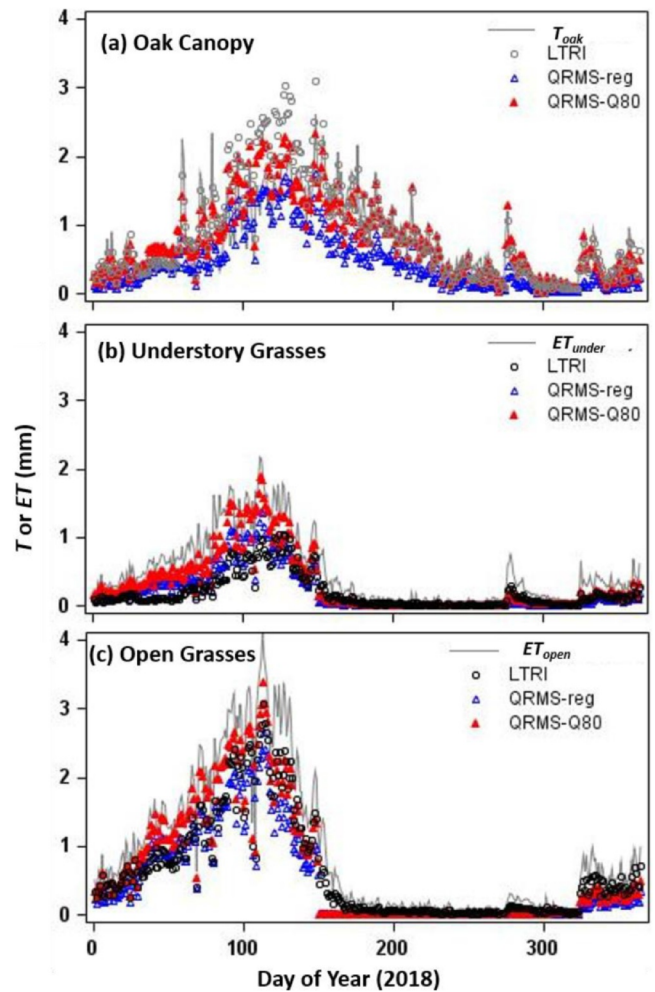


Fig. 9. Daily transpiration partitioned by the LTRI, QRMS-reg, and QRMS-Q80 methods, compared with tower measurements of (a) oak canopy (T_{oak}), (b) understory grassland (ET_{under}), and (c) open grassland (ET_{open}).

shown in Fig. 1), the flux data show seasonal patterns indicating biological performances of dominant vegetation within the footprints of individual towers. This two-tower partitioning approach is not perfect but provides independent field measurements for validating model results, especially for a site with relatively open canopy (Paul-Limoges et al., 2020; Scott et al., 2006).

The two ET -partitioning models that we tested here have different pros and cons. Besides those that we have summarized in the flowchart (Fig. 3), we notice a few other things in this study. First, the uncertainties of the LTRI model could be high if analyzed flux datasets have a limited number of years. Second, the multi-tower approach helps to reduce the model uncertainty, as shown by the improvement of R^2 value when moving from a single-tower to a multi-tower approach. Third, the LTRI model may underestimate the monthly T/ET ratio of the wet months. As we pooled the three-tower data together, we assumed that E values are the same at the three sites. As a result, the LTRI model estimates an E value averaged over the towers. This assumption is valid, given a relatively large timescale. However, the effects of tree canopy on understory soil evaporation could be significant when the timescale was reduced to one month while micro-environmental factors come into influence at individual locations. For example, oak canopy can affect understory energy balance significantly, causing an over-estimation of understory soil evaporation. Finally, we conducted a daily-value comparison of individual years by assuming that the seasonal pattern of T/ET is climatically stable (e.g., Mediterranean Climate). The QRMS model can be more reliable for estimating the year-

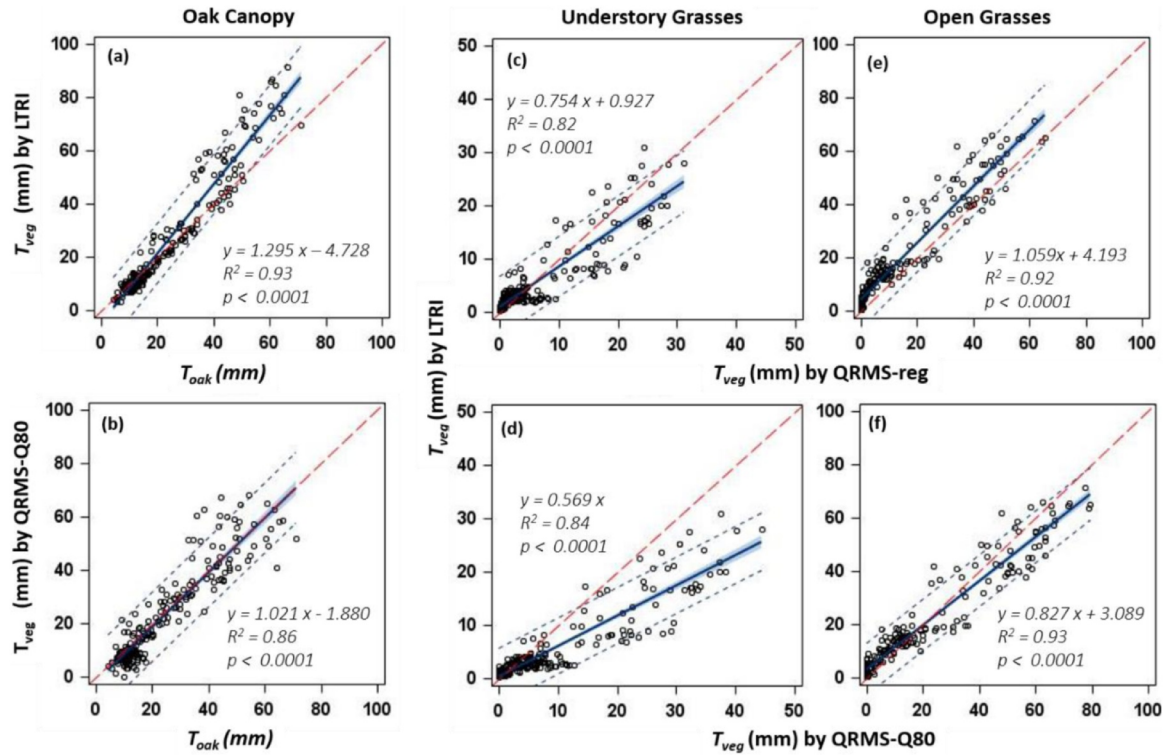


Fig. 10. Panel (a) and (b): comparing canopy transpiration (mm) partitioned by the LTRI model or by the modified QRMS model (QRMS-Q80) with two-tower-derived results during oak's growing season (between April – October). Panel (c) – (f): comparing grass transpiration (mm) partitioned by the LTRI model to the QRMS-reg or QRMS-Q80 modes for the understory grassland (c and d) and open grassland (e and f) during the growing season of annual grasses (between Nov. to following Jun). Notes: in each plot, the solid line indicates the predicted values of the linear regression model; short-dashed lines indicate the 95% upper and lower confidence limits for the expected values; the long-dashed line indicates the 1:1 line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

specific monthly transpiration because of the short period of half-hourly data used in the analysis (Zhou et al., 2018).

The QRMS model initially suggests the regular regression analysis (i.e., QRMS-reg) for estimating $uWUE_a$. This QRMS-reg approach works for the open grassland. However, in the case of oak woodland, the QRMS-reg approach underestimates $uWUE_a$ and later the T/ET . In this situation, the QRMS-Q80 modification improved the model performance. The reason for conducting the adjustment for each month is also according to the theory of stomatal behavior optimization. Probably, the stomatal behavior optimization of trees is more significant than that of grasses regarding a short period (e.g., a month). At the leaf level, stomata optimize its openness or closure for maximized carbon assimilation with a unit of water investment. In this sense, stomatal behaviors (i.e., openness or closure) intend to maximize the amount of CO_2 assimilation (A) for a given amount of water loss via transpiration (T), such that $\frac{\partial A}{\partial T} \rightarrow \text{maximum}$ (Lloyd, 1991). Thus, $uWUE_a \propto \frac{\partial A}{\partial T} \rightarrow \text{maximum}$. In other words, when $uWUE_a$ is estimated for each month, the quantile regression analysis is still valid for better representing the stomata-related behavior under the monthly circumstances, investigated at the ecosystem level (Lin et al., 2015; Medlyn et al., 2011). As the number of half-hourly tower flux data used for estimating $uWUE_a$ is much less than that for $uWUE_p$ over the entire growing seasons, the selection of the percentile depends on the actual size of data sets. For this 19-year data set, the 80% percentile gives the best agreement with the two-tower results. For a data set smaller than ours, the percentile threshold may initiate from somewhere between 70% and 80%.

A possible concern, regarding the quantile regression, is that the performance of the technique seems to depend on the setting of a threshold of the percentile. However, for large datasets, a quantile threshold should converge towards an underlying value according to probability theory. For smaller datasets, on the other hand, the quantile

threshold could be disproportionately influenced by individual outliers. For example, when the quantile regression is applied for a shorter period (a month), the sample size of the short period is smaller than that of a more extended period (an entire growing season). In this case, if the threshold of the percentile is set up too high (e.g., keeping the threshold at the 95th percentile), the outliers may overwhelm the rest of meaningful samples. We, therefore, took an empirical approach in determining the threshold of percentiles by testing the 70, 80, and 90th percentile thresholds. Based on this comparison, the 80th percentile provided the best agreement with the field measurements of oak canopy. The QRMS-Q80 modification is not a perfect solution but could be a starting point for partitioning ET from other woody savanna or forest ecosystems.

After all, the quantile regression approach adds a new vision of data analysis with a large sample size, which is meaningful for applications of the eddy-covariance tower data. The eddy-covariance tower settings are in the framework of “natural” experiments (non-manipulative, non-factorial experiments). The idea of seeking “maximum” (or “minimum”) slopes gives researchers a chance to look at the moment when photosynthesis and transpiration processes are fully coupled along with optimized stomatal behaviors. Such “ideal” situations probably occurred in daytime hours during the spring months because oak trees and annual grasses are active in photosynthesis and growth, and their transpiration rates peak at the same time. If we search for the “ideal” situations day by day, or period by period, we would miss them just because the working timescale is too rough. The QRMS model focuses on the half-hour scale. In other words, the “ideal” situations are sparse in thousands of discrete half hours. Our half-hourly flux data accumulated over 19 years empower this data-driven approach.

While we discuss uncertainties in estimating $uWUE_a$, it is also possible that the underestimated T/ET ratio results from the overestimation

of $uWUE_p$ because of water-stressed conditions in the growing season (Zhou et al., 2018). In this savanna landscape, oak trees' growing season covers the dry summers while annual grasses have already been senescent. Thus, the overstory tower has more chances to sample water-stressed situations than the open grassland tower does. We re-calculated oak canopy's $uWUE_p$ by excluding the summer months (e.g., from July to October), but the $uWUE_p$ values were not changed as much as expected. From the perspective of large-sample analysis, excluding "water-stressed" conditions is not a proper solution. It may be possible to run the quantile regression analysis without setting zero intercept to reduce the uncertainty caused by dry conditions. Also, we may borrow some machine learning methods to select a quantile value appropriate for running the quantile regression analysis (Nelson et al., 2018).

Also, it is worth pointing out that the QRMS model is based on the leaf-level model, but the leaf-to-air water vapor mole fraction difference, D , is difficult to be measured at the ecosystem level and replaced with VPD_f . This replacement involves an underlying assumption, that is, leaf and air temperature are approximately equilibrium. The presumption may hold in general on the daily or seasonal scale but not on finer timescales (e.g., hours). Since the timeframe of input data for establishing the $GPP-ET$ relationship is half-hourly, it may be necessary to test how much the assumption could influence the model results in the future. For the goal of this study, we kept VPD_f here. In this way, the units for $uWUE$ only depends on the units used for GPP and ET , such as mol mol^{-1} (CO_2 and H_2O fluxes), consistent with the unit used in typical leaf-level studies. By comparing the LTRI and QRMS models, we showed that the effects of VPD were not negligible on half-hourly flux data, but the effects diminished on longer timescales, such as monthly or annual. That is why the QRMS model needs VPD correction, but the LTRI model does not need it before establishing the $ET-GPP$ relationship.

Other than the two ET -partitioning models tested in this study, many different models have been reported. For example, Scanlon and Kustas (2010) applied the flux-variance-similarity theory and developed a model estimating the T/ET ratio from high-frequency measurements of CO_2 and water vapor concentrations and their variances and correlations (Skaggs et al., 2018). Li et al. (2019) presented a model that extracts the T/ET ratio from soil and canopy conductance by applying Penman-Monteith Equation. Nelson et al. (2018) introduced an alternative data-driven algorithm with a nonlinear machine learning method for identifying the transpiration-dominated period based on GPP and ET data from eddy-covariance towers. More comparison studies across these proposed models are needed in the regional or global flux data network (e.g., FLUXNET). Separating transpiration from evaporation enhances our process-based understanding, which will better constrain large-scale remote sensing and modeling efforts for furthering ecological and social adaptations in changing climates (Fisher et al., 2017).

5. Conclusions

In combinations with field measurements and ET -partitioning models, we learn that over this Californian savanna landscape, annual ET ($\pm$ standard deviation) from the oak woodland was 419 ± 85 mm. Among the total ecosystem-level evapotranspiration, oak canopy transpiration contributed $\sim 67\%$, understory grasses transpiration contributed $\sim 16\%$, and surface evaporation was $\sim 17\%$. In comparison, the open grassland has 324 ± 43 mm in total annual ET , including $\sim 67\%$ water lost via grass transpiration and $\sim 32\%$ via surface evaporation.

Long-term flux records are helpful for reducing uncertainties in the performances of these models. Overall, the LTRI and QRMS models performed reasonably for savanna ecosystems, even though the models take different working principles. However, the QRMS-Q80 works better for oak canopy, while the QRMS-reg works better for grasses. Also, the LTRI model is designed for large-scale estimation, expecting high uncertainties in the results of partitioning understory ET . For local

scales, the QRMS model may perform better than the LTRI model but need extra cautions in setting up a reasonable percentile threshold when the model is to be applied for woodlands or forests.

While long-term eddy-covariance measurements are continuously accumulated and becoming more accessible, the two models have the potential for partitioning evapotranspiration and comparing their results across the global flux data network. Such cross-site comparison studies would provide more reliable, process-based constraints for remote sensing and large-scale modeling efforts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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