

## Factors that control *Typha* marsh evapotranspiration

Michael L. Goulden<sup>\*</sup>, Marcy Litvak<sup>1</sup>, Scott D. Miller<sup>2</sup>

Department of Earth System Science, University of California, Irvine, CA 92697-3100, USA

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### Abstract

There is continuing debate about the controls on wetland evapotranspiration ( $E_t$ ) and whether marshes are profligate water users. We used eddy covariance to measure the  $\text{CO}_2$  exchange and  $E_t$  by a California Tule marsh in 2003. The marsh was dominated by *Typha* and *Scirpus*, and there was a large amount of standing litter that acted as a mulch. Canopy development was broadly related to air temperature, with rapid growth in May and senescence in October.  $E_t$  was a few tenths of a  $\text{mm d}^{-1}$  in winter, and 3–4  $\text{mm d}^{-1}$  in summer. The midsummer Bowen ratio was  $\sim 1$ , and the annual  $E_t$  was 49 cm. The peak rate of  $E_t$  was lower than has been reported for marshes based on lysimeter studies, somewhat lower than has been reported for marshes based on micrometeorological studies, and equivalent to, or somewhat lower than, has been reported for upland grassland. The midsummer water use efficiency was  $0.0025 \text{ mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ , and the  $\delta^{13}\text{C}$  of foliage was  $-27.1\text{‰}$ , which are both typical for productive  $\text{C}_3$  ecosystems. Transpiration accounted for 80% of total  $E_t$ . Evaporation from water standing beneath the canopy and mulch layer was only a minor component of the marsh's hydrological budget. The low rate of evaporation from standing water was a result of cool water temperatures, which remained within a few degrees of the nocturnal minimum on most days. We believe the mulch layer acted in a way analogous to an electrical diode that allowed the upward loss of heat from the water to the atmosphere at night, and shut off the flux of heat from the atmosphere to the water during daytime, resulting in cool subcanopy water and low rates of evaporation. Our observations are inconsistent with the hypothesis that Tule marshes are inefficient water users, or that their rates of transpiration and  $\text{CO}_2$  uptake are unusual compared to upland ecosystems.

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**Keywords:** Tule marsh; *Typha latifolia*; *Scirpus californicus*; Cattail; Evaporation; Canopy conductance; Water balance; Eddy covariance; Mulch

### 1. Introduction

The controls on wetland evapotranspiration ( $E_t$ ) remain poorly understood despite nearly a century of investigation (Otis, 1914; Linacre, 1976; Crundwell, 1986; Allen et al., 1997; Królikowska et al., 1998; Drexler et al., 2004). A number of reports indicate freshwater marsh  $E_t$  is large and often exceeds open water evaporation ( $E_{\text{open}}$ ) (Snyder and Boyd, 1987; Price, 1994; Herbst and Kappen, 1999; Pauliukonis and Schneider, 2001; Acreman et al., 2003). Other reports indicate wetland  $E_t$  is less than  $E_{\text{open}}$  (Rijks, 1969; Linacre et al., 1970; Lafleur, 1990; Burba et al., 1999) and broadly comparable to what would be expected for productive upland grassland. Efforts to understand wetland evapotranspiration have been confounded

by the likelihood that different wetlands differ markedly in  $E_t$  and also by the reality that different methodologies produce widely divergent measures of  $E_t$ .

Water evaporates from marshes by several parallel pathways, including transpiration from emergent vegetation ( $E_{\text{canopy}}$ ), evaporation from standing water beneath vegetation ( $E_{\text{subcanopy}}$ ), and evaporation from open water (see Table 1 for summary of variables). Each of these fluxes is controlled by a different mechanism, and the relative importance of each pathway varies both spatially and temporally.  $E_{\text{canopy}}$  is controlled by the density of foliage, the stomatal conductance, and the meteorological conditions that determine the leaf-to-air vapor pressure deficit (Campbell and Norman, 1998). Wetland-to-wetland differences in leaf area or stomatal conductance may cause large differences in  $E_{\text{canopy}}$ .  $E_{\text{subcanopy}}$  is a function of the meteorological and biophysical conditions that impact aerodynamic exchange and the water-to-air vapor pressure deficit. Wetland-to-wetland differences in litter or leaf area may cause differences in  $E_{\text{subcanopy}}$ . Wetlands differ in the extent of open water and the duration of subcanopy flooding, and hence the relative importance of  $E_{\text{open}}$ ,  $E_{\text{canopy}}$ , and  $E_{\text{subcanopy}}$ . The

<sup>\*</sup> Corresponding author. Tel.: +1 949 824 1983; fax: +1 949 824 3256.

E-mail address: [mgoulden@uci.edu](mailto:mgoulden@uci.edu) (M.L. Goulden).

<sup>1</sup> Present address: School of Biological Sciences, University of Texas, Austin, TX, USA.

<sup>2</sup> Present address: Atmospheric Sciences Research Center, State University of New York, Albany, NY, USA.

Table 1  
Summary of measured and derived variables

Variable	Definition	Method
Surface flooding	Presence or absence of standing water at the meteorological tower	Recorded during periodic site visits
$K$	Incoming solar radiation	Measured at SJFM
$H$	Sensible heat flux	Measured by eddy covariance at SJFM
$F_{\text{CO}_2}$	Net CO <sub>2</sub> exchange	Measured by eddy covariance at SJFM
$T_{\text{air}}$	Air temperature	Measured at Santa Ana Airport or at SJFM
$T_{\text{canopy}}$	Effective canopy temperature	Calculated from inverted Penman–Monteith equation
$T_{\text{water}}$	Temperature of water beneath the canopy	Measured by submerged thermocouples
$q$	Specific humidity of ambient air	Measured at Santa Ana Airport
$E_{\text{t}}$	Total evapotranspiration	Measured by eddy covariance at SJFM
$E_{\text{canopy}}$	Transpiration from plant canopy	Measured by eddy covariance during periods when marsh surface was dry
$E_{\text{subcanopy}}$	Evaporation from water beneath the canopy	Measured by eddy covariance during periods when marsh surface was wet and no appreciable canopy
$D_{\text{canopy}}$	Difference in vapor pressure between ambient air and inside of leaves	Calculated as the difference between specific humidity and the saturated vapor pressure at canopy temperature
$D_{\text{subcanopy}}$	Difference in vapor pressure between ambient air and water beneath canopy	Calculated as the difference between specific humidity and the saturated vapor pressure at the water temperature
$G_{\text{canopy}}$	Conductance for water vapor transport from inside leaves to outside of leaves	Calculated from inverted Penman–Monteith equation
$G_{\text{subcanopy}}$	Conductance for water vapor transport from beneath canopy to atmosphere	Calculated by dividing $E_{\text{subcanopy}}$ by $D_{\text{subcanopy}}$

existence of multiple evaporation pathways undoubtedly contributes to large wetland-to-wetland differences in  $E_{\text{t}}$ , and argues that the debate should shift from generalizations about the relative rates of evaporation by vegetated and open water surfaces, and toward the development of a mechanistic understanding of what controls wetland  $E_{\text{t}}$ .

Many of the reports of high rates of wetland  $E_{\text{t}}$  were based on lysimeter studies, which may be biased by horizontal energy advection (Allen et al., 1997) and the absorption of light on the sides of plants at low solar elevation (Idso and Anderson, 1988). Allen et al. (1997) and Drexler et al. (2004) discussed the methodologies available for quantifying wetland evapotranspiration and concluded that eddy covariance is a particularly promising tool. Eddy covariance is a micro-meteorological technique that can provide half-hour observations of the net exchanges of water vapor and CO<sub>2</sub> between a few hectares of wetland and the atmosphere (Baldocchi et al., 1988). Recent advances in the reliability of eddy covariance instrumentation have allowed the collection of long-term eddy covariance data sets above a range of vegetation types (c.f., Wofsy et al., 1993; Hollinger et al., 1994; Goulden et al., 1997), including wetlands (Souch et al., 1996; Acreman et al., 2003). Analysis of eddy covariance observations provides information for identifying which physiological and physical processes play dominant roles in controlling water vapor and CO<sub>2</sub> exchange.

We used the eddy covariance technique from 1999 to 2004 to continuously measure the CO<sub>2</sub> exchange ( $F_{\text{CO}_2}$ ) and evapotranspiration by a Typha- and Scirpus-dominated Tule marsh in Southern California (the San Joaquin Freshwater Marsh, or SJFM). Tule marshes were once common in California, covering 750,000 ha of the Central Valley

(Küchler, 1964; Barbour and Major, 1988; Schoenherr, 1992). Nearly all of these marshes were drained for agriculture and few Tule marshes remain. In this paper we focus on the seasonal and diel controls on  $E_{\text{t}}$ . We emphasize two questions: (1) What are the relative rates of  $E_{\text{t}}$ ,  $E_{\text{canopy}}$ , and  $E_{\text{subcanopy}}$  and how do they vary diurnally and seasonally? (2) What controls and limits  $E_{\text{t}}$ ,  $E_{\text{canopy}}$ , and  $E_{\text{subcanopy}}$ ? We restricted our analysis to data from 2003 because the data set was comparatively continuous during this period, with fewer gaps than in other years, and because the diel patterns, seasonal patterns, and relative rates of  $E_{\text{t}}$ ,  $E_{\text{canopy}}$ , and  $E_{\text{subcanopy}}$  during 2003 were similar to those observed during the other years. The absolute rates of  $E_{\text{t}}$  observed during 2003 were similar to those observed in 2001 and higher than those observed in 1999, 2001 and 2002. The interannual variability in  $E_{\text{t}}$  and  $F_{\text{CO}_2}$  will be the subject of a second paper (Rocha and Goulden, 2007).

## 2. Methods

### 2.1. Site

We investigated the controls on  $E_{\text{t}}$  in the San Joaquin Freshwater Marsh (SJFM, Schoenherr, 1992), an 82 ha Tule marsh (Mason, 1957; Küchler, 1964) in the Bulrush-Cattail Series (Sawyer and Keeler-Wolf, 1995) that is located on the University of California's Irvine campus. The SJFM is in coastal Orange County at 3 m above sea level (a.s.l.) and 8 km northeast of the Pacific Ocean (33°39'44.4"N, 117°51'6.1"W). The SJFM is protected and managed for research and education as a component of the University of California's Natural Reserve System.

The SJFM formed along the San Diego Creek, which historically flowed from the foothills of the Santa Ana Mountain to the Pacific Ocean. The SJFM is a remnant of La Cienega de las Ranas (The swamp of the Frogs), a wetland that once covered 2100 ha along the San Diego Creek. Most of La Cienega de las Ranas was drained for agriculture in the early 20th century, though aerial photographs from the late 1920s to the early 1950s show that our site remained a wetland throughout this period. Aerial photographs indicate most of the vegetation at our site was cleared in the late 1950s and the area of open water increased to improve duck hunting. Aerial photographs show a steady encroachment of emergent vegetation into the areas of open water since the late 1950s, with 73% of the area within 330 m upwind of our meteorological tower covered with cattail, 20% of the area with bulrush, and 7% of the area with open water or mudflat in 2003. The site did not experience a major natural or human disturbance such as fire or scouring flood since the 1950s. The site was a mature Tule marsh in 2003 with dense stands of *Typha latifolia* and *Scirpus californicus* and a large amount of standing litter that acted as a mulch layer.

The main flow of the San Diego Creek was diverted to an adjacent channel in the 1960s, and the SJFM's hydrological regime was subsequently managed to approximate the natural hydrological cycle. The SJFM is flooded to a depth of  $\sim 1$  m in December or January of most years by pumping water from the San Diego Creek Channel. No additional water is added after March, except for natural precipitation. The marsh dries by evapotranspiration and subsurface drainage through the spring and summer, with standing water disappearing by midsummer.

## 2.2. Meteorological observations

Eddy covariance provides a measure of the turbulent exchange of gases and energy between the atmosphere and a patch of vegetation that is upwind of a meteorological tower. The SJFM experiences a steady sea breeze from the southwest during more than 90% of the daylight periods, which allowed us to maximize the extent of wetland upwind of our sensors (the fetch) by locating the meteorological tower near the northeast edge of the SJFM. Tule marsh extended for 500–900 m upwind of our meteorological instruments, with areas of open water at 200–225 and 370–420 m, and a dike with sparse trees at 330 m from the tower. The upwind patch of marsh sampled during daytime, which is referred to as the “footprint”, often extends a distance of 10–20 times the effective measurement height (Schmid, 2002). The footprint becomes larger at night with atmospheric stability, but this expansion has a minor impact on a water balance study since the rates of nocturnal  $E_t$  are very small compared to those during daytime. Our instruments were mounted at 5.5 m above ground level, which was 2–3 m above the height of the vegetation, indicating the daytime footprint was concentrated in a  $\sim 100$  m  $\times$  100 m patch of the marsh to the southwest of the tower. This area was vegetated almost entirely by *Typha* in 2003, with only a few small patches of *Scirpus*, no areas of open water, and little vertical relief.

The flux measurements were made from a 6 m tall, 46 cm cross-section tower (Rohn 55G, Peoria, IL) on a 4 m  $\times$  4 m

floating dock that was accessed by a floating boardwalk from a dike 40 m to the northeast. The floating dock was held in place by the vegetation, and, aside from gradual changes in elevation caused by changing water level, it remained stationary, even during particularly windy periods. The infrastructure and flux instruments were installed in June 1998, and reliable measurements began in January 1999. The flux system was controlled by a data logger (Campbell Scientific CR10x, Logan, UT) that was connected to a laptop computer. The data logger prepared two types of data files: slow files with 30 min statistics and fast files with raw 4 or 0.5 Hz observations. The laptop computer collected both slow and fast data from the data logger every 4 min (Campbell Scientific PC208), appending the most recent observations to separate slow and fast files.

The turbulent fluxes of sensible heat, latent heat,  $\text{CO}_2$ , and momentum were determined by the eddy covariance technique (Baldocchi et al., 1988; Wofsy et al., 1993). Wind and temperature were measured at 4 Hz with a three-axis sonic anemometer pointed to the southwest (Campbell Scientific CSAT-3, Logan, UT). The molar densities of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  were measured by ducting 6–10 standard liter  $\text{min}^{-1}$  of air through a closed-path InfraRed Gas Analyzer (IRGA) that was located in an instrument enclosure at the base of the tower (a LI6262 from December 1998 to February 2001 and October 2001 to May 2003; a LI7000 from February 2001 to October 2001 and May 2003 to December 2005, both instruments from LI-COR, Lincoln, NE). Air was drawn through a 0.45  $\mu\text{m}$  pore 47 mm diameter Teflon filter located just behind the sonic anemometer, down a 4 mm inner-diameter 7 m long Teflon PFA tube, through a flow meter and a second Teflon filter, through the IRGA, through a ballast to dampen pressure fluctuations, and through a diaphragm pump. The sample tube was heated to 40  $^\circ\text{C}$  to prevent condensation and reduce water vapor exchange with the wall. The pressure in the IRGA cell was actively controlled at 83 kPa (MKS Instruments, Andover, MA). The IRGA was calibrated automatically for  $\text{CO}_2$  by sequentially sampling  $\text{CO}_2$  standard in air (Scott Marin, Riverside, CA) and  $\text{CO}_2$  free air. The IRGA was calibrated periodically for water vapor by flowing air through a thermoelectrically cooled condensing column (LI-COR LI610, Lincoln, NE). The LI6262 raw mV outputs, or the LI7000 absorptances, were recorded and the gains, instrument non-linearity, temperature, pressure and effects of water vapor accounted for in subsequent processing.

The  $\text{CO}_2$  and water vapor fluxes were calculated as the 30 min covariances of the vertical wind velocity and the  $\text{CO}_2$  or  $\text{H}_2\text{O}$  mixing ratios after subtracting the 30 min means. The time lag for the closed path IRGA ( $\sim 1.5$  s) was determined separately for  $\text{CO}_2$  or  $\text{H}_2\text{O}$  by maximizing the correlation between the fluctuations in air temperature measured by the sonic anemometer and the fluctuations in either  $\text{CO}_2$  or  $\text{H}_2\text{O}$  mixing ratio. The fluxes were rotated to the plane with no mean vertical wind, and the underestimation of high frequency flux due to tube attenuation and instrument response were corrected separately for  $\text{CO}_2$  or  $\text{H}_2\text{O}$  assuming similarity in transport between sensible heat and gas flux (Goulden et al., 1997).

Observations of the physical environment were recorded at 0.5 Hz. Incoming and reflected photosynthetically active photon

flux density at 5.5 m were measured with silicon quantum sensors (LI-COR LI190, Lincoln, NE). Net radiation was measured with a thermopile net radiometer (REBS Q\*7.1, Seattle, WA). Incoming and reflected solar radiation were measured with thermopile pyranometers (Kipp & Zonen CM3, Delft, The Netherlands). Water temperatures at three heights above the soil surface were measured with copper–constantan thermocouples (Omega Engineering, CT). Hourly air temperature, specific humidity, and precipitation were recorded at the Santa Ana airport (KSNA), which was 2 km to the north of the SJFM. The temperature, humidity and precipitation data collected at KSNA were more continuous, and had better long-term precision, than the comparable measurements we made at the SJFM. Comparisons of the specific humidity at KSNA with other weather stations within 10 km of the SJFM showed that specific humidity was uniform throughout the area. The hourly air temperature measured at KSNA was used to calibrate the speed-of-sound air temperature observed at the SJFM with the sonic anemometer using a quadratic polynomial. The calibrated speed-of-sound temperatures were then used for the calculation of canopy conductance.

We visited the site every 3–10 days for maintenance and to collect the most recent data. The water table depth adjacent to the meteorological tower was measured manually during these visits using a fixed ruler that was installed in a sampling well. Subjective observations of plant phenology, including leaf development, senescence and flowering, were recorded during visits. We measured the late growing season live plant biomass each year by sampling thirty  $0.25 \text{ m}^{-2}$  quadrates along a 100 m transect that extended from the tower to the southwest. Live plants were pulled from the marsh, cleaned to remove roots and lateral rhizomes, dried at  $65^\circ\text{C}$ , and weighed. The  $\delta^{13}\text{C}$  of subsamples of leaf tissue were determined for each year by continuous-flow mass spectrometry.

### 2.3. Energy budget closure and treatment of calm periods

A preliminary analysis of the energy budget indicated the sum of latent ( $\lambda E$ ) and sensible heat ( $H$ ) was only 75% of the measured net radiation ( $R_n$ ). The storage of energy in chemical bonds during photosynthesis and the thermal storage of energy in biomass are generally considered minor. The storage of energy in standing water can be significant in wetlands, though measurements indicated the water warmed by only  $0.5^\circ\text{C}$  over most days, corresponding to an average flux of  $30 \text{ W m}^{-2}$  for a water depth of 50 cm and a 10 h day, or less than 10% of  $R_n$ . We did not measure the storage of heat in the soil, but assume it was less than the storage of heat in the water. The remaining imbalance of 15–20% is similar to that observed in many other eddy covariance studies, and is presumably caused by transport in low-frequency circulations that are underestimated by a 30 min averaging interval (Mahrt, 1998; Twine et al., 2000).

Our main goal was to determine how  $E_t$  varies seasonally and whether the absolute rates are comparable to the rates of  $E_t$  that have been reported for other wetlands. We therefore forced our energy budget to close by multiplying  $\lambda E$  and  $H$  by correction coefficients so that the long-term sum of the

turbulent fluxes equaled  $R_n$  (Twine et al., 2000). A single coefficient was determined for  $H$  by multiple linear regression for the entire study, since the sonic anemometer was never changed. Separate coefficients were determined for  $\lambda E$  for the five intervals when different IRGAs were operated. The  $\lambda E$  coefficients accounted for both the underestimation of turbulent flux and possible IRGA-to-IRGA biases.

The eddy covariance technique is thought to underestimate the true surface exchange on calm nights, possibly as a result of the transport of  $\text{CO}_2$ , energy, and water vapor by cold air drainage (Goulden et al., in press). Flux underestimation on calm nights presents a severe problem for carbon balance studies since a modest systematic underestimation of nighttime  $\text{CO}_2$  efflux relative to daytime uptake will cause a large overestimation of annual uptake (Goulden et al., 1996). In contrast,  $E_t$  underestimation on calm nights presents only a modest problem for water balance studies since nocturnal  $E_t$  is generally much smaller than daytime  $E_t$  and a systematic underestimation of nighttime  $E_t$  relative to daytime  $E_t$  will have a minor effect on calculated annual  $E_t$ . We analyzed the half-hour  $E_t$  measurements to determine whether they were underestimated on calm nights. We found that the rate of  $E_t$  on calm nights averaged  $0.09 \text{ mmol m}^{-2} \text{ s}^{-1}$  less than that measured on windy nights (friction velocity ( $u_*$ )  $> 0.2 \text{ m s}^{-1}$ ). This difference is a combined result of the underestimation of  $E_t$  on calm nights by eddy covariance (e.g., Goulden et al., 1996) and a decrease in the true surface  $E_t$  caused by calm conditions. Seventy-two percent of the nocturnal periods at the SJFM had a friction velocity ( $u_*$ )  $< 0.2 \text{ m s}^{-1}$ , which indicates that the underestimation of  $E_t$  on calm nights was a minor effect, leading to an underestimation of annual  $E_t$  of no greater than 1.8 cm in 2003, or  $\sim 4\%$  of the total observed.

## 3. Results

### 3.1. Seasonal patterns of meteorology and plant growth

The climate at the SJFM is maritime Mediterranean, with mild temperatures year-round, a wet season from November to March, and a predictable drought from May to September. The cumulative precipitation at the Santa Ana airport was 21.6 cm in 2003. Rainfall accounts for only a portion of the hydrological input to the SJFM, with most of the water coming from the nearby San Diego Creek channel. Water was diverted into the SJFM beginning in December 2002, and continued to flow through the marsh throughout most of the 2003 winter. The marsh was flooded to a depth of approximately 50 cm at the meteorological tower until early April, when the inflow ceased. The water level subsequently declined by  $0.5\text{--}1 \text{ cm d}^{-1}$ , with the water table dropping below the soil surface at the meteorological tower on 16 July (Fig. 1a).

The mean air temperature at the nearby Santa Ana airport was  $17.3^\circ\text{C}$  in 2003, the minimum observed temperature was  $2.2^\circ\text{C}$  and the maximum observed temperature was  $33.9^\circ\text{C}$  (Fig. 1b). Canopy development was broadly correlated with air temperature, and was not related to the occurrence of rainfall or flooding. Sparse cattail shoots began to appear in January and



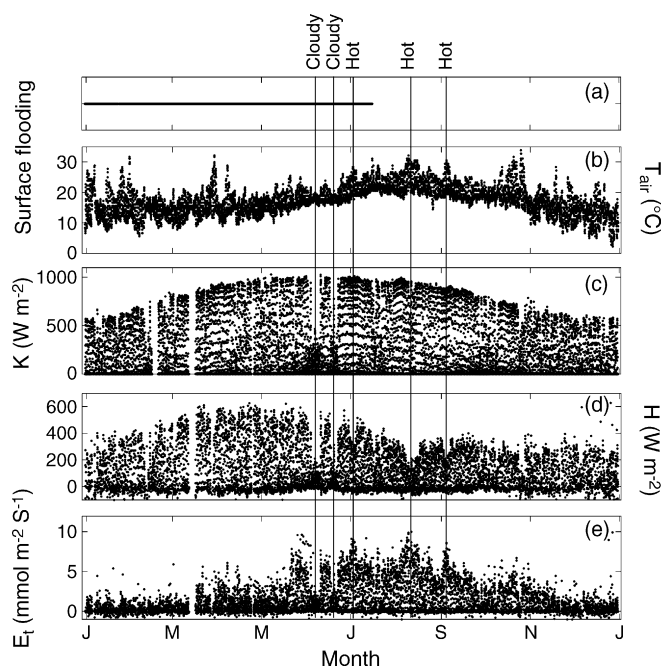


Fig. 1. (a) Presence of standing water at the meteorological tower in the San Joaquin Freshwater Marsh (SJFM) from 1 January 2003 to 31 December 2003; (b) 60 min mean air temperature at the Santa Ana Airport, which is 2 km north of the SJFM ( $T_{\text{air}}$  in  $^{\circ}\text{C}$ ); (c) 30 min mean solar radiation at the SJFM ( $K$  in  $\text{W m}^{-2}$ ); (d) 30 min mean sensible heat flux at the SJFM determined by eddy covariance during periods with wind from the southwest ( $H$  in  $\text{W m}^{-2}$ ); (e) 30 min mean evapotranspiration at the SJFM determined by eddy covariance during periods with wind from the southwest ( $E_t$  in  $\text{mmol m}^{-2} \text{s}^{-1}$ ). Vertical lines indicate extended periods of cloudiness or above-average temperature.

February, and the canopy developed slowly until early April, when growth accelerated. The marsh developed a dense canopy by early June, and the cattails began to flower in mid-June. The plants showed visible signs of senescence in October. Senescence accelerated in November, and only a few green leaves remained by early December. The seasonal patterns of meteorology, flooding, and plant phenology were consistent from year-to-year from 1999 to 2003. The summer growing season at the SJFM is similar to that described for other *Typha* marshes in North America (Grace and Harrison, 1986), and out of phase with the winter- and spring-growing season that is typical for Mediterranean-climate plant communities (Schoenherr, 1992). The slow rate of plant growth from January to March at the SJFM is somewhat surprising given the availability of water and moderate air temperature (Fig. 1a and b).

The surface of the marsh was covered year-round by a 1–2 m thick layer of standing and partially fallen leaf litter that had accumulated from previous years, and that functioned as a mulch layer. The mulch covered the standing water completely. Many, but not all, of the green leaves in the midsummer canopy extended above the mulch. The seasonal cycle in the marsh was divisible into four phases. (1) Flooded winter from January to March, with daytime high temperatures of 16–25  $^{\circ}\text{C}$ , standing water at the meteorological tower that was covered by mulch, and no appreciable green canopy. (2) Flooded summer from May to June, with daytime high temperatures of 18–25  $^{\circ}\text{C}$ ,

standing water that was covered by mulch, and a well-developed canopy of green leaves that stood above the litter. (3) Dry summer from July to August, with daytime high temperatures of 20–28  $^{\circ}\text{C}$ , no standing water at the meteorological tower, a thick mulch layer and a well-developed canopy of green leaves that stood above the mulch. (4) Dry late autumn, with daytime high temperatures of 16–20  $^{\circ}\text{C}$ , no standing water at the meteorological tower, a thick mulch layer and no appreciable green canopy.

### 3.2. Seasonal patterns of energy and $\text{CO}_2$ exchange

The dissipation of incoming radiation ( $K$ ; Fig. 1c) as sensible heat ( $H$ ; Fig. 1d) and evaporation (Fig. 1e) varied seasonally. The seasonal pattern of  $E_t$  was closely related to the development and senescence of the plant canopy, and poorly related to the presence or absence of standing water (Fig. 1a). The seasonal pattern of  $H$  was related to the difference between incoming net radiation and the latent heat flux ( $\lambda E$ , the product of  $E_t$  and the latent heat of vaporization).  $E_t$  was low before canopy development in January through March, and most of the incoming radiation was dissipated as  $H$  during this period.  $E_t$  increased rapidly in May, which caused  $H$  to gradually decline during this period even though  $K$  was still increasing.  $E_t$  remained high from May through September during the peak growing season, with rates of up to 8  $\text{mmol m}^{-2} \text{s}^{-1}$ . The peak midsummer  $E_t$  is equivalent to a  $\lambda E$  of 350  $\text{W m}^{-2}$  and indicates a minimum Bowen ratio (the ratio of  $H$  to  $\lambda E$ ) of  $\sim 1$ . Extended cloudy periods in June caused both  $E_t$  and  $H$  to decrease. Extended hot periods in early July, August, and September (Fig. 1b) increased  $E_t$ , with an offsetting reduction in  $H$ .  $E_t$  began to decrease in September, before canopy senescence was visible, which caused  $H$  to remain steady during this period despite declining  $K$ .  $E_t$  continued to decline in October, reaching a low rate with complete canopy senescence in late November and December.

The midsummer rate of daily  $E_t$  was 3–4  $\text{mm d}^{-1}$  (Fig. 2), which is comparable to, or somewhat lower than, what would be expected for a well-watered, upland grassland (Kelliher et al., 1993). The daily  $E_t$  during the growing season was largely insensitive to the presence of standing water near the meteorological tower (Fig. 1a), and high rates of  $E_t$  were observed in August and early September after most of the

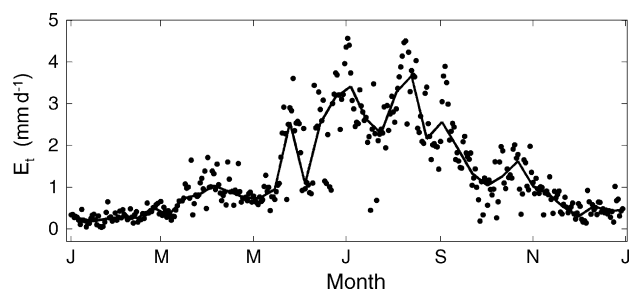


Fig. 2. Daily evapotranspiration at the SJFM from 1 January 2003 to 31 December 2003 during periods with wind from the southwest ( $E_t$  in  $\text{mm d}^{-1}$ ). 2). Daily totals were calculated after filling missing observations as a function of solar radiation. Points show individual days; solid line connects 10-d averages.

marsh surface had dried. The winter rates of  $E_t$  were only a few tenths of a  $\text{mm d}^{-1}$ . The rates of dormant-season  $E_t$  were similar before and after the growing season, even though there was a large difference between periods in the presence of standing water. The low rates of winter  $E_t$ , and the observation that dormant season  $E_t$  was largely insensitive to the presence of standing water beneath the mulch layer, imply that evaporation through the litter ( $E_{\text{subcanopy}}$ ) is slow.

The annual  $E_t$  was 49 cm in 2003, with 21 cm occurring while the marsh was fully flooded (Fig. 2). The annual  $E_{\text{subcanopy}}$  was estimated by summing observed  $E_t$  during

periods without a green canopy, and extrapolating these fluxes to periods with standing water and a green canopy. The resulting annual  $E_{\text{subcanopy}}$  was 9.5 cm, which indicates that transpiration accounted for 80% of total  $E_t$ . The cumulative  $E_t$  before 16 July was less than half the initial flooding depth at the meteorological tower of  $\sim 50$  cm, implying that a significant amount of water was lost from the marsh by subsurface drainage. The large cumulative  $E_t$  after the disappearance of surface water at the meteorological tower implies that the plants transpired a large amount of soil moisture, and that Typha has some deep roots.

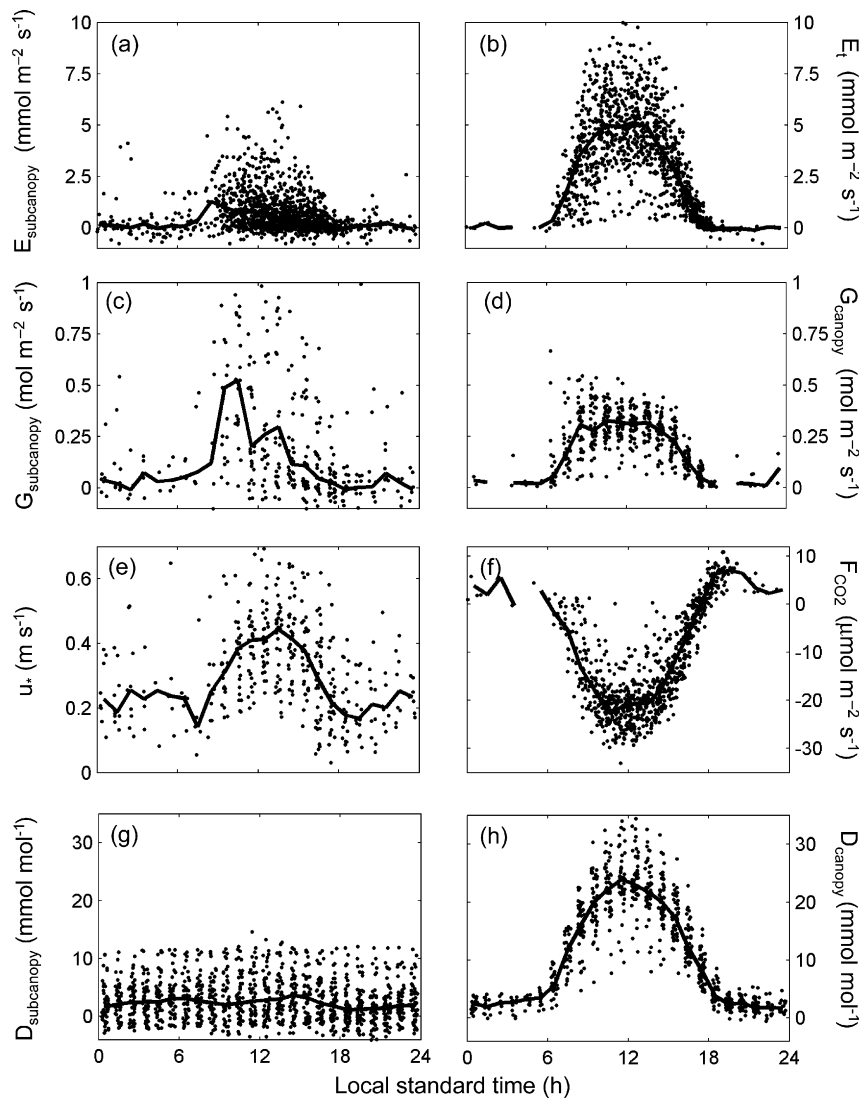


Fig. 3. (a) Diel changes in evaporation ( $E_{\text{subcanopy}}$  in  $\text{mmol m}^{-2} \text{s}^{-1}$ ) during periods with standing water at the tower and without a significant green canopy (before 10 April). (b) Evapotranspiration ( $E_t$  in  $\text{mmol m}^{-2} \text{s}^{-1}$ ) during periods with a well-developed canopy and no standing water at the tower (16 July–7 September). (c) Conductance for water vapor transport from standing water beneath the canopy to the atmosphere ( $G_{\text{subcanopy}}$  in  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) before 10 April. (d) Conductance for water vapor transport from the inside to the outside of leaves ( $G_{\text{canopy}}$  in  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) from 16 July to 7 September. (e) Friction velocity ( $u_*$  in  $\text{m s}^{-1}$ , a measure of windiness) before 10 April. (f) Net  $\text{CO}_2$  exchange ( $F_{\text{CO}_2}$  in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) from 16 July to 7 September. Negative fluxes indicate  $\text{CO}_2$  uptake by the marsh (photosynthesis); positive fluxes indicate  $\text{CO}_2$  loss from the marsh (respiration). (g) The difference in vapor pressure between ambient air and the water beneath the canopy ( $D_{\text{subcanopy}}$  in  $\text{mmol H}_2\text{O mol}^{-1}$ ) before 10 April. (h) The difference in vapor pressure between ambient air and the vapor pressure inside the leaves ( $D_{\text{canopy}}$  in  $\text{mmol H}_2\text{O mol}^{-1}$ ) from 16 July to 7 September. The time of each observation was randomly changed by as much as 15 min to separate the points. The lines show hourly medians. Conductance data were screened to eliminate periods with rain within 96 h or a  $\lambda E$  of less than  $1 \text{ W m}^{-2}$ .  $G_{\text{subcanopy}}$  data were screened to eliminate periods with  $D_{\text{subcanopy}} < 0.2 \text{ mmol mol}^{-1}$ .  $E_{\text{subcanopy}}$ ,  $E_t$ , and  $F_{\text{CO}_2}$ , were screened to eliminate calm periods ( $u_* < 0.2 \text{ m s}^{-1}$ ). All data were screened to eliminate periods with wind from the northeast.

### 3.3. Controls on $E_t$

$E_{\text{subcanopy}}$  showed a weak diel cycle, with very low rates of evaporation at night, moderate rates of evaporation in the early morning, and a decrease in evaporation after ~09:00 Local Time (LT) in the morning (Fig. 3a).  $E_t$  during periods with a full canopy and no standing surface water showed a much stronger diel cycle, with very low rates of evaporation at night, and high rates of  $E_t$  in the middle of the day (Fig. 3b). The diel cycle of  $E_t$  during periods with a canopy was symmetrical about noon, whereas the cycle of  $E_{\text{subcanopy}}$  was asymmetrical, with a peak at 08:30 LT.

$E_{\text{subcanopy}}$  is the product of the turbulent and diffusive conductance for the transfer of water vapor from beneath the canopy to the atmosphere ( $G_{\text{subcanopy}}$ ) and the difference in vapor pressure between the local atmosphere and the standing water beneath the canopy ( $D_{\text{subcanopy}}$ ). Similarly,  $E_t$  during periods without standing water is the product of the conductance for the transfer of water vapor out of the leaves ( $G_{\text{canopy}}$ ) and the difference in vapor pressure between the local atmosphere and the leaf intercellular spaces ( $D_{\text{canopy}}$ ). We further analyzed the flux and meteorological observations to determine the extent to which  $E_{\text{canopy}}$  and  $E_{\text{subcanopy}}$  are controlled by the conductances and vapor pressure gradients.  $D_{\text{subcanopy}}$  was calculated as the difference between the observed ambient vapor pressure and the vapor pressure at the water temperature for periods when there was standing water and the plants were dormant.  $G_{\text{subcanopy}}$  was calculated by dividing  $E_t$  by  $D_{\text{subcanopy}}$  during periods when the plants were dormant.  $G_{\text{canopy}}$  and  $D_{\text{canopy}}$  were calculated using the Penman–Monteith equation for periods when the plants were active and the marsh surface was dry at the meteorological tower (Kelliher et al., 1993).

Peak midday  $G_{\text{subcanopy}}$  and  $G_{\text{canopy}}$  were around  $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$ , which is comparable to, or somewhat lower than, the  $G_{\text{canopy}}$  that has been reported for productive, well-watered upland grassland (Kelliher et al., 1993). For comparison, the  $G_{\text{canopy}}$  of a low productivity upland ecosystem is often below  $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$ , and the midday conductance for open water may be  $2\text{--}5 \text{ mol m}^{-2} \text{ s}^{-1}$ . The observation that  $G_{\text{subcanopy}}$  is markedly lower than the conductance expected for open water implies that the mulch imposes a restriction on subcanopy evaporation. The observation that  $G_{\text{subcanopy}}$  is comparable to  $G_{\text{canopy}}$  implies that this restriction is not severe, and that it cannot account for the low rates of evaporation observed in January through March (Figs. 1e and 2).

In principle,  $G_{\text{subcanopy}}$  is controlled by the diffusion and forced ventilation of the mulch layer (Novak et al., 2000), which, in turn, is controlled by the atmospheric stability and momentum transport to the surface.  $G_{\text{subcanopy}}$  decreased at night (Fig. 3c) with darkness and decreasing windiness and turbulent transfer.  $G_{\text{subcanopy}}$  increased during the morning, reaching a peak before noon, and then declining throughout the afternoon. The morning increase in  $G_{\text{subcanopy}}$  coincided with the morning increase in windiness and atmospheric turbulence (Fig. 3e), confirming that  $G_{\text{subcanopy}}$  is partially

controlled by the forced ventilation of the mulch layer. However, the afternoon decline in  $G_{\text{subcanopy}}$  occurred despite a further increase in atmospheric turbulence, indicating that  $G_{\text{subcanopy}}$  is not controlled solely by above-canopy wind.

In principle,  $G_{\text{canopy}}$  is controlled by the amount of leaf area and the plants' stomatal conductance (Campbell and Norman, 1998). Both the seasonal (Fig. 4) and diel (Fig. 3d) patterns of  $G_{\text{canopy}}$  were closely related to the rates of whole marsh photosynthesis (Figs. 4 and 3f).  $G_{\text{canopy}}$  increased markedly in May, coincident with the development of the canopy and the increase in  $\text{CO}_2$  uptake.  $G_{\text{canopy}}$  decreased in September, coincident with a gradual decline in canopy photosynthesis and canopy senescence. Similarly, the diel cycle of  $G_{\text{canopy}}$  (Fig. 3d) paralleled the  $\text{CO}_2$  uptake (Fig. 3f) and irradiance, with no indication of afternoon drought stress and stomatal closure, a pattern that is similar to that observed for many well-watered upland ecosystems. The seasonal correspondence between  $F_{\text{CO}_2}$  and  $G_{\text{canopy}}$  is presumably driven by the development and senescence of leaf area. The diel correspondence is presumably driven by the adjustment of stomatal aperture to match the photosynthetic demand for  $\text{CO}_2$  (Wong et al., 1979).

There was a marked difference in both the diel pattern and absolute magnitude of  $D_{\text{canopy}}$  compared to  $D_{\text{subcanopy}}$  (Fig. 3g and h). The ambient specific humidity ( $q$ ) was nearly constant over the day, and the diel patterns of  $D$  were driven by diel changes in the temperature of either the canopy or the standing water.  $D_{\text{canopy}}$  increased markedly during daytime with the warming of the canopy by sunlight. In contrast, the temperature

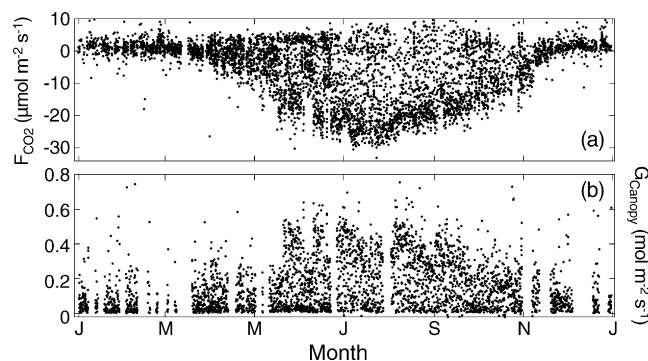


Fig. 4. (a) Net  $\text{CO}_2$  exchange at the SJFM from 1 January 2003 to 31 December 2003 determined by eddy covariance ( $F_{\text{CO}_2}$  in  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Individual points show the half-hour average net flux. Negative fluxes indicate  $\text{CO}_2$  uptake by the marsh (photosynthesis); positive fluxes indicate  $\text{CO}_2$  loss from the marsh (respiration). Observations include both day and night measurements. The upper envelope of points shows the seasonal pattern of nocturnal respiration; the lower envelope shows the seasonal pattern of net daytime  $\text{CO}_2$  uptake; the difference between envelopes approximates the seasonal pattern of whole-marsh photosynthesis. (b) Conductance for water vapor transport from the inside to the outside of the leaves ( $G_{\text{canopy}}$  in  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ). Individual points show half-hour conductance. The upper envelope of points shows the seasonal pattern of daytime  $G_{\text{canopy}}$ ; the lower envelope shows the seasonal pattern of nocturnal  $G_{\text{canopy}}$ .  $F_{\text{CO}_2}$  data were screened to eliminate observations during calm periods or wind from the northeast. Conductance data were screened to eliminate periods with rain within 96 h or a  $\lambda E$  of less than  $1 \text{ W m}^{-2}$  or wind from the northeast.

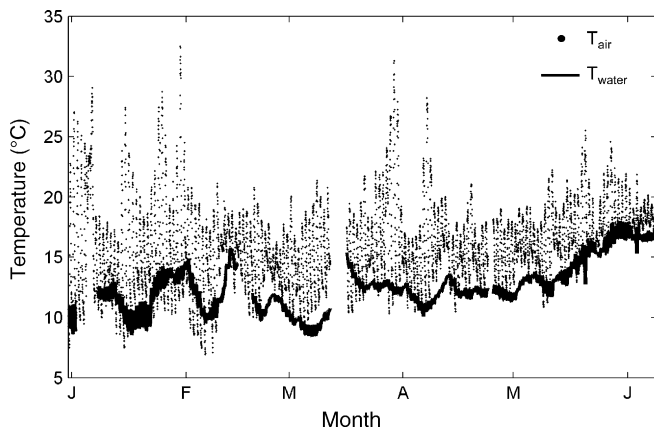


Fig. 5. Air temperature ( $T_{\text{air}}$  in  $^{\circ}\text{C}$ ; filled circles show 30 min means) and water temperature beneath the litter layer ( $T_{\text{water}}$  in  $^{\circ}\text{C}$ ; solid lines connect 30 min means) at the San Joaquin Freshwater Marsh from 1 January 2003 to 9 June 2003.  $T_{\text{air}}$  was measured with the sonic anemometer, which was calibrated to the physical air temperature using the observations at the Santa Ana Airport.

of water beneath the mulch remained cool and nearly constant over the day (Fig. 5), which resulted in a consistently low  $D_{\text{subcanopy}}$ . The low  $D_{\text{subcanopy}}$  (Fig. 3g) accounted for the low rate of  $E_t$  observed in January through March (Figs. 1e and 2) despite the presence of standing water (Fig. 1a) and the moderately high  $G_{\text{subcanopy}}$  (Fig. 3e). In contrast,  $D_{\text{canopy}}$  increased markedly during daytime (Fig. 3h), providing a driving gradient for high rates of  $E_t$  when leaves were present and the stomata open. The temporal patterns of  $E_t$  were driven most strongly by  $G_{\text{canopy}}$ , with leaf growth and senescence determining the seasonal pattern (Fig. 4) and leaf physiology determining the diel cycle (Figs. 3d and f and 5). In turn,  $E_t$  (Fig. 1e), along with solar radiation (Fig. 1c), helped to control the sensible heat flux (Fig. 1d).

#### 4. Discussion

The rate of  $E_t$  was markedly lower than has been reported for marshes based on lysimeter studies (Bernatowicz et al., 1976; Snyder and Boyd, 1987; Pauliukonis and Schneider, 2001), somewhat lower than has been reported for marshes based on micrometeorological studies (Rijks, 1969; Linacre et al., 1970; Lafleur, 1990; Price, 1994; Burba et al., 1999; Acreman et al., 2003), and equivalent to, or somewhat lower than, has been reported for productive upland grasslands (Kelliher et al., 1993). The low rate of  $E_t$  we observed is not a result of persistent drought since the marsh was fully flooded for 7.5 months of the year (Fig. 1a). Moreover, the low rate of  $E_t$  we observed is not a result of low primary production, since the live plant biomass at the end of the 2003 growing season excluding roots and rhizomes was  $2360 \text{ g m}^{-2}$ , which is comparable to, or greater than, that reported for other *Typha* marshes (Bradbury and Grace, 1983). Finally, the low rate of  $E_t$  we observed cannot be attributed to interannual variability, and the suggestion that  $E_t$  was anomalously low in 2003 since the annual  $E_t$  observed in 2003 was similar to that observed in 2001 and higher than that observed in 1999, 2001 and 2002 (Rocha and Goulden, 2007).

#### 4.1. Why is evaporation less than expected?

$E_{\text{subcanopy}}$  was a minor component of the marsh's hydrological budget, accounting for  $\sim 20\%$  of annual  $E_t$ . The low rate of  $E_{\text{subcanopy}}$  was a result of the very low  $D_{\text{subcanopy}}$ , which largely suppressed evaporation. The temperature of water beneath the mulch remained within  $\sim 1^{\circ}\text{C}$  of the daily minimum air temperature over most days (Fig. 5), which resulted in the consistently low  $D_{\text{subcanopy}}$ . The relative humidity increased to 100% on most nights, and the ambient dew point changed little from day to night. The ambient dew point during most days was therefore similar to the minimum air temperature at night, and the vapor pressure of subcanopy water remained close to the ambient specific humidity throughout most days, resulting in a consistently low  $D_{\text{subcanopy}}$  (Fig. 3g). The cool water temperature beneath the litter layer is unexpected since the temperature of soil is often close to the mean daily air temperature (Campbell and Norman, 1998). The low water temperatures we observed cannot be accounted for by evaporative cooling, since  $E_{\text{subcanopy}}$  was low. We believe the low water temperatures are a result of the heat transfer properties of the mulch layer.

The mulch layer shaded the water and prevented direct solar warming. The upper surface of the litter was heated during daytime, which we suspect caused atmospheric stability within the mulch layer, with a warm upper boundary at the surface and a cool lower boundary at the water surface. The occurrence of cool, heavy air near the bottom of the mulch layer would be expected to suppress vertical air movement in the mulch, and curtail the downward transport of energy to warm the water during daytime. A midday reduction in transfer through the mulch layer is consistent with the diel patterns of  $G_{\text{subcanopy}}$  (Fig. 3c) and  $u_*$  (Fig. 3e). The afternoon decrease in  $G_{\text{subcanopy}}$  occurred despite an increase in  $u_*$ , a pattern that is consistent with a reduction in transfer through the mulch layer with surface heating. By contrast, the surface of the mulch was cooled by the loss of thermal radiation at night. The cooling of the upper surface would be expected to create an unstable temperature profile through the mulch at night, resulting in natural convection in the mulch layer, and promoting the upward transfer of heat out of the water (Novak et al., 2000). We believe the mulch acted in a way analogous to an electrical diode that allowed the upward loss of heat from the water to the atmosphere at night, and shut off the flux of heat from the atmosphere to the water during daytime. Stability-driven patterns of exchange are well known in aquatic systems (Wetzel, 2001), and have been described for tall plant canopies such as tropical forest (Goulden et al., in press), but have only recently begun to receive attention for litter and mulch layers (Novak et al., 2000).

#### 4.2. Why is transpiration less than expected?

The midsummer rates of transpiration and the canopy conductances and Bowen ratios were broadly comparable to those observed in upland grasslands. The water use efficiency in midsummer was typically  $0.0025 \text{ mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  (Figs. 1e



and 4a), which is more efficient than has been reported for upland grasslands (Law et al., 2002). Similarly, the  $\delta^{13}\text{C}$  of foliage in 2003 was  $-27.1\text{‰}$ , which is typical for  $\text{C}_3$  vegetation and indicates the Typha at the SJFM uses its water efficiently (Jones, 1992). The midsummer rates of  $\text{CO}_2$  uptake we observed (Fig. 4a) are typical or somewhat greater than upland grasslands (Xu and Baldocchi, 2004), even though the  $E_t$  and  $G_{\text{canopy}}$  are no greater than have been reported previously (Kelliher et al., 1993). Our observations are inconsistent with the hypothesis that Tule marshes are profligate water users, or that their rates of transpiration and  $\text{CO}_2$  uptake are unusual when compared to upland ecosystems. Rather, our observations indicate the Typha canopy at the SJFM exhibits physiology that is typical for a productive  $\text{C}_3$  ecosystem.

#### 4.3. Why is Tule marsh $E_t$ less than the $E_t$ reported for other wetlands?

Comparisons of wetland  $E_t$  are confounded by the possibility of technique-to-technique differences and also site-to-site differences in vegetation and meteorology. A number of papers have pointed out that the  $E_t$  averaged over an extensive area such as the SJFM cannot be much larger than the incoming net radiation (Jarvis and McNaughton, 1986). Experimental artifacts probably account for the extraordinarily high rates of  $E_t$  reported in some lysimeter studies (Allen et al., 1997), and the  $E_t$  above extensive wetlands is unlikely to exceed  $10 \text{ mm d}^{-1}$ . On the other hand, several previous investigations using micrometeorological techniques have also reported rates of wetland  $E_t$  that are considerably higher than we observed. We believe the differences between these reports and our observations reflect real wetland-to-wetland differences in energy partitioning. The SJFM differs from most marshes studied previously in two important respects: (1) the local semi-arid Mediterranean climate and (2) the buildup of a thick litter layer that acted as a mulch.

Tule marshes in general, and the SJFM in particular, occur in semi-arid climates (Küchler, 1964). Typha shows considerable ecotypic differentiation (McNaughton, 1966), and it is likely that the plants at the SJFM are adapted to occasional drought. The occurrence of Tule marshes in the western US is limited to areas where there is standing water for part of the year. From the perspective of plant competition, it makes sense that the Typha in a Tule marsh would be adapted to avoid wasting water, provided there is no cost to the plants.

The SJFM has not been subject to a major disturbance for  $\sim 50$  years. Combined with the high rates of production, and the possibility that the lack of summer rain decreases decomposition, this has led to the accumulation of a mulch layer. Similar thick litter layers occur in many wetlands, especially ones that are not flooded year-round (Haslam, 1971). The relatively efficient use of water during gas exchange by the Typha at the SJFM, combined with the thick layer that suppressed  $E_{\text{subcanopy}}$ , accounted for the low rates of  $E_t$ . It appears likely that the rates of transpiration are at least partly a result of adaptations by the plants at the SJFM to minimize water loss. Moreover, it is

tempting to hypothesize that the creation of the thick litter layer is also related to a plant strategy to minimize water use. In this sense, the Typha at the SJFM may act as an autogenic ecosystem engineer (Jones et al., 1994) that modifies the local physical environment by causing the buildup of a thick mulch layer.

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#### References

- Acreman, M.C., Harding, R.J., Lloyd, C.R., et al., 2003. Evaporation characteristics of wetlands: experience from a wet grassland and a reedbed using eddy correlation measurements. *Hydrol. Earth Syst. Sci.* 7, 11–21.
- Allen, L.H., Sinclair, T.R., Bennett, J.M., 1997. Evapotranspiration of vegetation of Florida: perpetuated misconceptions versus mechanistic processes. *Soil Crop Sci. Soc. Florida Proc.* 56, 1–10.
- Baldocchi, D.D., Hicks, B.B., Meyers, T.P., 1988. Measuring biosphere–atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* 69, 1331–1340.
- Barbour, M.G., Major, J. (Eds.), 1988. *Terrestrial Vegetation of California*. California Native Plant Society, Davis, CA.
- Bernatowicz, S., Leszczynski, S., Tyczynska, S., 1976. The influence of transpiration by emergent plants on the water balance in lakes. *Aquat. Bot.* 2, 275–288.
- Bradbury, I.K., Grace, J., 1983. Primary production in wetlands. In: Gore, A.J.P. (Ed.), *Ecosystems of the World. Mires: Swamp, Bog, Fen, and Moor*, vol. 4A. Elsevier Science Publishers, New York, NY, pp. 285–310.
- Burba, G.G., Verma, S.B., Kim, J., 1999. Surface energy fluxes of *Phragmites australis* in a prairie wetland. *Agric. For. Meteorol.* 94, 31–51.
- Campbell, G.S., Norman, J.M., 1998. *Introduction to Environmental Biophysics*, 2nd ed. Springer, New York.
- Crundwell, M.W., 1986. A review of hydrophyte evapotranspiration. *Rev. Hydrobiol. Trop.* 19, 215–232.
- Drexler, J.Z., Snyder, R.L., Spano, D., et al., 2004. A review of models and micrometeorological methods used to estimate wetland evapotranspiration. *Hydrol. Process.* 18, 2071–2101.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Glob. Change Biol.* 2, 169–182.
- Goulden, M.L., Miller, S.D., da Rocha, H.R., in press. Nocturnal cold air drainage and pooling in a tropical forest. *J. Geophys. Res.: Atmos.* 111, Art. No. D08S04.
- Goulden, M.L., Daube, B.C., Fan, S.M., et al., 1997. Physiological responses of a black spruce forest to weather. *J. Geophys. Res.: Atmos.* 102, 28987–28996.
- Grace, J.B., Harrison, J.S., 1986. The biology of Canadian weeds. 73. *Typha-Latifolia L., Typha-Angustifolia L. and Typha-Xglauca Godr.* *Can. J. Plant Sci.* 66, 361–379.
- Haslam, S.M., 1971. Community regulation in *Phragmites-Communis Trin.* 2. *Mixed stands.* *J. Ecol.* 59, 75.
- Herbst, M., Kappen, L., 1999. The ratio of transpiration versus evaporation in a reed belt as influenced by weather conditions. *Aquat. Bot.* 63, 113–125.

- Hollinger, D.Y., Kelliher, F.M., Byers, J.N., et al., 1994. Carbon-dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75, 134–150.
- Idso, S.B., Anderson, M.G., 1988. A comparison of 2 recent studies of transpirational water-loss from emergent aquatic macrophytes. *Aquat. Bot.* 31, 191–195.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, H.G., 1992. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge.
- Kelliher, F.M., Leuning, R., Schulze, E.D., 1993. Evaporation and canopy characteristics of coniferous forests and grasslands. *Oecologia* 95, 153–163.
- Królikowska, J., Smid, P., Pribán, K., 1998. Microclimate conditions and water economy of wetland vegetation. In: Westlake, D.F., Kvet, J., Szczepanski, A. (Eds.), *The Production Ecology of Wetlands: The IBP Synthesis*.
- Küchler, A.W., 1964. *Potential Natural Vegetation of the Conterminous United States*. American Geographical Society, New York.
- Lafleur, P.M., 1990. Evapotranspiration from sedge-dominated wetland surfaces. *Aquat. Bot.* 37, 341–353.
- Law, B.E., Falge, E., Gu, L., et al., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric. For. Meteorol.* 113, 97–120.
- Linacre, E.T., Hicks, B.B., Sainty, G.R., Grauze, G., 1970. Evaporation from a swamp. *Agric. Meteorol.* 7, 375.
- Linacre, E.T., 1976. Swamps. In: Monteith, J.L. (Ed.), *Vegetation and the Atmosphere, Case Studies*, vol. 2. Academic Press, London, pp. 329–347.
- Mahrt, L., 1998. Flux sampling errors for aircraft and towers. *J. Atmos. Oceanic Technol.* 15, 416–429.
- Mason, H.L., 1957. *A Flora of the Marshes of California*. University of California Press, Berkeley.
- McNaughton, S.J., 1966. Ecotype function in typha community-type. *Ecol. Monogr.* 36, 297.
- Novak, M.D., Chen, W.J., Orchansky, A.L., et al., 2000. Turbulent exchange processes within and above a straw mulch. Part II. Thermal and moisture regimes. *Agric. For. Meteorol.* 102, 155–171.
- Otis, C.H., 1914. The transpiration of emerged water plants: its measurement and its relationships. *Bot. Gazette* 58, 457–494.
- Pauliukonis, N., Schneider, R., 2001. Temporal patterns in evapotranspiration from lysimeters with three common wetland plant species in the eastern United States. *Aquat. Bot.* 71, 35–46.
- Price, J.S., 1994. Evapotranspiration from a lakeshore Typha marsh on Lake-Ontario. *Aquat. Bot.* 48, 261–272.
- Rijks, D.A., 1969. Evaporation from a papyrus swamp. *Quart. J. Roy. Meteorol. Soc.* 95, 643.
- Rocha, A.V., Goulden, M.L., 2007. Interannual variability in the exchanges of CO<sub>2</sub> and energy between a freshwater marsh and the atmosphere. *J. Geophys. Res.: Biogeo.*
- Sawyer, J.O., Keeler-Wolf, T., 1995. *A Manual of California Vegetation*. California Native Plant Society, Sacramento, CA.
- Schmid, H.P., 2002. Footprint modeling for vegetation atmosphere exchange studies: a review and perspective. *Agric. For. Meteorol.* 113, 159–183.
- Schoenherr, A.A., 1992. *A Natural History of California*. University of California Press, Berkeley.
- Snyder, R.L., Boyd, C.E., 1987. Evapotranspiration by *Eichhornia-Crassipes* (Mart) Solms and *Typha-Latifolia* L. *Aquat. Bot.* 27, 217–227.
- Souch, C., Wolfe, C.P., Grimmond, C.S.B., 1996. Wetland evaporation and energy partitioning: Indiana dunes national lakeshore. *J. Hydrol.* 184, 189–208.
- Twine, T.E., Kustas, W.P., Norman, J.M., et al., 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agric. For. Meteorol.* 103, 279–300.
- Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*. Academic Press, San Diego.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., et al., 1993. Net exchange of CO<sub>2</sub> in a midlatitude forest. *Science* 260, 1314–1317.
- Wong, S.C., Cowan, I.R., Farquhar, G.D., 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282, 424–426.
- Xu, L.K., Baldocchi, D.D., 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agric. For. Meteorol.* 123, 79–96.