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The application of $\delta^{18}O$ and δD for understanding water pools and fluxes in a *Typha* marsh

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ABSTRACT

The $\delta^{18}O$ and δD composition of water pools (leaf, root, standing water and soil water) and fluxes [transpiration (*T*), evaporation (*E*)] were used to understand ecohydrological processes in a managed *Typha latifolia* L. freshwater marsh. We observed isotopic steady-state *T* and deep rooting in *Typha*. The isotopic mass balance of marsh standing water showed that *E* accounted for 3% of the total water loss, *T* accounted for 17% and subsurface drainage (*D*) accounted for the majority (80%). There was a vertical gradient in water vapour content and isotopic composition within and above the canopy sufficient for constructing an isotopic mass balance of water vapour during some sampling periods. During these periods, the proportion of *T* in evapotranspiration (*T*/*ET*) was between 56 ± 17% and 96 ± 67%, and the estimated error was relatively high (>37%) because of non-local, background sources in vapour. Independent estimates of *T*/*ET* using eddy covariance measurements yielded similar mean values during the *Typha* growing season. The various *T*/*ET* estimates agreed that *T* was the dominant source of marsh vapour loss in the growing season. The isotopic mass balance of water vapour yielded reasonable results, but the mass balance of standing water provided more definitive estimates of water losses.

Key-words: *Typha latifolia*; Craig–Gordon enrichment; evaporation; evapotranspiration partitioning; isotopic steady state; stable isotopes; transpiration.

INTRODUCTION

Water balance plays an integral role in the functioning of wetlands, influencing ecology, water supply and quality, and carbon storage (Lafleur 2008; Rocha & Goulden 2010), and its understanding is important for effective wetland management. There is a long-standing debate concerning many aspects of wetland water balance components, such as the relative importance of transpiration (*T*) to evaporation (*E*). Many studies have shown that most wetlands have lower evapotranspiration (*ET*) than would be expected from open water under similar conditions (Linacre *et al*. 1970; Idso & Anderson 1988; Lafleur 1990; Burba, Verma & Kim 1999). However, other reports show that the presence of wetland reed vegetation increases *ET* (Price 1994; Herbst & Kappen 1999; Pauliukonis & Schneider 2001; Acreman *et al*. 2003; Goulden, Litvak & Miller 2007). In addition, it is believed that *ET* usually represents the dominant water loss from ecosystems (Drexler *et al*. 2004), but few studies have examined the complete water budget of wetlands, including groundwater flows (e.g. Owen 1995; Hunt, Krabbenhoft & Anderson 1996).

The stable isotopic composition ($\delta^{18}O$ and δD) of ecosystem water pools such as leaf, root and surface water and atmospheric water vapour may help resolve some of the uncertainties associated with wetland ecohydrologic processes. Fractionating processes lead to distinct isotopic signatures of water pools (Lai *et al*. 2006; Welp *et al*. 2008). Variations in the isotopic composition of water can provide information about water sources and transport within ecosystems, but there are few data sets on temporal variability in water pools other than precipitation (e.g., IAEA/WMO 1981; Rozanski, Araguas-Araguas & Gonfiantini 1993; Johnson & Ingram 2004), in part because it is usually necessary to extract water from plant or soil material (West, Patrickson & Ehleringer 2006) or condense atmospheric vapour (Helliker *et al*. 2002) for conventional measurements.

Differences in the isotopic composition of pools and fluxes can be used to construct the isotopic mass balance of the standing water in a wetland and thereby understand hydrologic dynamics (Hunt *et al*. 1996, 1998; Clay *et al*. 2004; Sikdar & Sahu 2009; Nyarko *et al*. 2010). Isotopic mass balance has the ability to quantify both *T* and *E*, which both transport large amounts of water to the atmosphere, but are experimentally difficult to distinguish. Water subject to *E* becomes enriched, while drainage and *T* are believed to be non-fractionating (Gonfiantini 1986; Dawson & Ehleringer 1991; Dawson *et al*. 2002). Thus, in a system where *E* is the only fractionating outflow, it is possible to estimate evaporative losses when combined with direct measurements of *ET*.

Several studies have highlighted the potential of stable isotopes to detect *T* in canopy water vapour in a variety of ecosystems (Brunel *et al*. 1992, 1997; Yakir & Wang 1996;

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Wang & Yakir 2000). By understanding the $\delta^{18}O$ and δD isotopic composition of water vapour that is transpired or evaporated, as well as the remaining or 'background' vapour, it can be possible to obtain quantitative estimates of the contribution of each component, provided that they are isotopically distinct (Zhang *et al*. 2010). The isotopic composition of water evaporated from soil or water bodies may be isotopically lighter than transpired water vapour, which is similar to plant source water, assuming steady state. Studies of the isotopic composition of canopy water vapour have previously shown that T can be the dominant component of ET in forests (Moreira *et al*. 1997; Harwood *et al*. 1999), savannah woodlands (Yepez *et al*. 2003) and orchards (Williams *et al*. 2004). However, evaporative fluxes may play a large or even dominant role in wetlands with standing water.

The isotopic composition of leaf water can be predicted using a simple model based on evaporative enrichment (Craig & Gordon 1965), and is useful for physiological and paleoclimatic analyses (Epstein & Yapp 1977; Edwards *et al*. 1985; Edwards & Fritz 1988; Roden & Ehleringer 1999), as well as understanding the oxygen isotope composition of CO_2, which equilibrates with leaf water (Farquhar & Lloyd 1993). This model has been modified to describe progressive enrichment along the length of the elongated leaves such as grasses using the string-of-lakes model (Gat & Bowser 1991; Helliker & Ehleringer 2000). However, two effects may cause discrepancies between measured and modelled leaf water. The 'Péclet effect' is a result of advection and back diffusion between less enriched water in veins and enriched water at evaporative sites (Barbour *et al*. 2004). Gan *et al*. (2002) emphasized the need to include Péclet effects when applying the string-of-lakes model to leaves. Secondly, leaves may not be transpiring in isotopic steady state if leaf water pools change in size (Flanagan, Comstock & Ehleringer 1991; Farquhar & Cernusak 2005; Lai *et al*. 2006; Seibt *et al*. 2006; Lee, Kim & Smith 2007). It is possible to take both of these effects into account when modelling leaf water. We measured the isotopic composition of leaf water, root water, soil water, standing water and water vapour over the course of a growing season in a managed *Typha latifolia* L. freshwater marsh in Orange County, CA, USA where eddy covariance measurements of ET were also available. Previous analyses of direct flux measurements at this site have shown that despite a large area of standing water, E rates were low and T dominated ET (Goulden *et al*. 2007). The previous study also suggested that plants were deeply rooted, even though high soil moisture availability was expected to promote surficial roots.

We followed up on these findings with a focus on the following questions: (1) Are ecosystem water pools and fluxes isotopically distinct?; (2) Is there support for a Péclet effect and/or isotopic non-steady state T in *Typha*?; (3) Is there evidence of shallow rooting in *Typha* using isotopic methods?; (4) What is the water balance of the system studied?; and (5) What is the proportion of T in ET (T/ET), and how do estimates based on the isotopic mass balance of standing water (T/ET_{SW}) and the isotopic mass balance of water vapour (T/ET_{WV}) compare with an eddy covariance-based approach (T/ET_{EC})?

We hypothesized that plant T would be primarily in isotopic steady state, as has been shown for short canopies (Yakir & Wang 1996; Welp *et al*. 2008). We expected that T would dominate ET and that plants would be deeply rooted. Consequently, we expected that a small percentage of total marsh water loss would be caused by E, and that the largest water losses would be T and subsurface drainage (D). In general, we sought to assess the extent to which isotope mass balance studies can inform wetland ecology and ecohydrology.

MATERIALS AND METHODS

Study site

This research was conducted at the San Joaquin Freshwater Marsh (SJFM) Reserve in Orange County, CA, USA, which is 3 m above sea level and 8 km from the Pacific Ocean (Fig. 1, 33° 39′ 43.008″ N, 117° 51′ 7.519″ W). SJFM is located on the campus of University of California, Irvine, CA, USA,

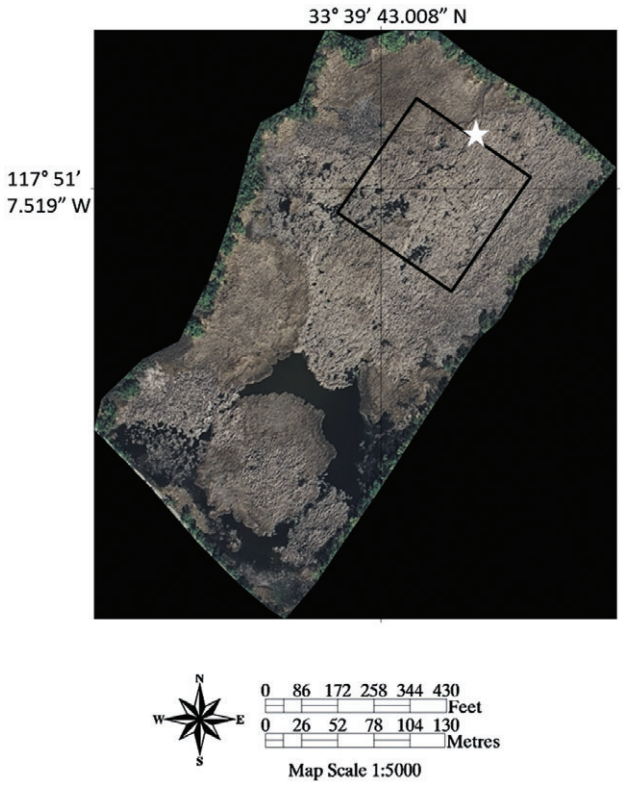

Figure 1. United States Department of Agriculture geospatial data gateway image of the pond in San Joaquin Marsh which was the subject of this study, accessed on 28 March 2010. The photo was taken after the marsh was flooded in winter and before plant growth started in spring. The white star indicates the position of the eddy covariance tower. The open water is black, the primarily senesced canopy is tan and live trees around the periphery are green. The 100 × 100 m area upwind of the tower is 3.2% water, and is indicated by a box.

where it is protected and managed as part of the University of California's Natural Reserve System. The climate at SJFM is Mediterranean, and rainfall generally occurs during December to April. The average annual temperature (1960–2008) is 16.4 ± 0.8 °C and average annual precipitation is 270 ± 145 mm (http://www.wrcc.dri.edu, Newport Beach Harbor station #046175). The SJFM soil is primarily composed of silty clay, alternating with layers of black silty peat and a couple layers of micaceous sands (Davis 1992). The hydrology of the SJFM is managed. In winter, SJFM is flooded to a depth of ~1 m with water pumped from the nearby San Diego Creek, which is composed almost entirely of urban runoff. Following the initial flooding event(s), no additional water is added except a relatively small amount via precipitation (105 mm during our 2007 study year); consequently, SJFM loses standing water in the following months by *ET* and *D*. There is no standing water left by midsummer. We recorded marsh water height with a staff gauge at one location at weekly or shorter intervals, which was assumed to be representative as basemaps showed variations in depth <0.3 m. The site was instrumented with an eddy covariance tower for water vapour, CO_2 and energy exchange measurements, as previously reported (Goulden *et al*. 2007; Rocha & Goulden 2008, 2009; Rocha, Potts & Goulden 2008; Rocha & Goulden 2010). Instrumentation and flux calculations for these towers have been discussed in detail previously. Briefly, the net ecosystem exchange (NEE) and *ET* were calculated from the average half hour covariance between vertical wind fluctuations measured by a 3D sonic anemometer (CSAT3; Campbell Scientific, Logan, UT, USA) and the mole fractions of CO_2 for NEE and H_2O for *ET* measured by a closed path infrared gas analyser (IRGA; model 7000 or 6262; Li-Cor Inc., Lincoln, NE, USA). Fluxes were rotated to the mean wind streamlines, and corrected for underestimation of high frequency flux caused by attenuation in the sampling tube and the density effect caused by sensible and latent heat transfer. Turbulent fluxes of sensible and latent heat captured 78–80% of the available energy at each of the sites, which is consistent with energy budget closure observed for other eddy covariance studies (Wilson *et al*. 2002). The underestimation of latent heat was corrected by forcing the energy budget closure, assuming an accurate Bowen ratio measurement (Goulden *et al*. 2007).

SJFM is dominated by a dense stand of cattail (*T. latifolia* L.), with a few patches of bullrush (*Scirpus californicus* C.A. Mey. Steud.) and willows (*Salix* spp.) at the periphery, and it contains a large amount of standing litter that acts as a mulch layer. *Typha* begins growing in the spring and is mostly senesced by late summer. The fractional area of open water and standing litter was determined for a 100 × 100 m area upwind of the eddy covariance tower, using a 28 March 2010 high resolution aerial photograph (Fig. 1) obtained from the United States Department of Agriculture Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/). The photo was taken after the marsh was flooded in winter and before plant growth started in spring. The image was imported into the Environment for Visualizing Images (ENVI) software, and classified into exposed water versus litter using a red band threshold, which was determined by histogram analysis.

Sample collection

We conducted intensive day-long field campaigns to sample water pools approximately fortnightly from May through October 2007, which corresponded with the *Typha* growing season. In 2008, sampling days were weekly or fortnightly from January to March, a period when standing water was present, but live vegetation was sparse or absent.

On sampling days, water vapour was collected near the eddy covariance tower at two levels above the standing water or soil: within canopy (0.1 m) and above canopy (4 m). The water vapour was collected using a method based on Helliker *et al*. (2002). Air was drawn through a low absorption plastic tube (Bev-a-Line; Thermoplastic Inc., Stirling, NJ, USA) at a rate of 450 cc min^{-1} for 90 min and condensed in a 15-cm-long glass cold finger condenser (Chemglass, model CG-1222–01, Vineland, NJ, USA) which was submerged in a –80 °C ethanol/dry ice bath. The cold finger was sealed with parafilm after vapour collection. When the frozen vapour melted, the water was poured into a sample vial, sealed with Parafilm (Pechiney Plastic Packaging, Inc., Chicago, IL, USA) and frozen until analysis. Using this method, we obtained ~0.5–1 mL of water vapour during each sampling event. Over the course of each sampling day, we collected water vapour three times at each height (six total vapour collections). Air temperature and humidity were recorded at 5 s intervals within ~3 cm of the point for water vapour collection (HOBO Pro V2 Temperature/Relative Humidity datalogger, Bourne, MA, USA). From September 2007 to March 2008, vapour was collected simultaneously at a nearby beach for comparison to marsh vapour.

On each sampling day, leaves, roots, standing water or soil were collected for measurement of the $\delta^{18}O$ and δD composition of water. All samples were collected within about 10 m of the vapour collection. To account for progressive isotopic enrichment along the leaf axis, 5-cm-long segments were collected from the base, middle and top of leaves three times over the course of a day ($n = 5$ for each section of leaf). Leaf samples were collected once in the middle of each vapour sampling event (about 45 min into the vapour sampling). We collected root samples from five plants at midday on each sampling day during the 2007 growing season. Standing water from the top centimetre was collected at five locations on a weekly basis and on sampling days. Surface soil samples (0–5 cm depth) were collected at five locations during the period without standing water. Leaf, water, soil and root samples were immediately placed in screw cap vials after collection, sealed with parafilm and stored frozen. Prior to isotopic analysis, water was extracted from leaves, soils and roots using cryogenic vacuum distillation (West *et al*. 2006).

Leaf water content (LWC), stomatal conductance and specific leaf area (SLA) were also measured. Leaves were collected for LWC measurements ($n = 50$) on each sampling

day. Leaves were measured on-site for wet weight after clipping. Leaf biomass was oven-dried at 70 °C for at least 48 h and measured for dry weight in the lab. LWC was determined as the difference between fresh and dry weight. Stomatal conductance was measured on each sampling day with a porometer (SC-1; Decagon Devices, Pullman, WA, USA). Measurements were taken during midday on five leaves in five equally spaced sections of the leaf from base to top. SLA was measured twice during the study period, on 23 May and 28 June 2007. SLA was estimated by determining leaf area on a subset of harvested fresh leaves (ImageJ software, US National Institute of Health, http://rsb.info.nih.gov/ij/) and dividing leaf area by dry weight.

Isotope analysis

All water samples were analysed at the University of California, Irvine for oxygen and hydrogen isotope ratios (δ^{18}O and δD) using a thermal conversion elemental analyser (TCEA) (Thermo Finnigan, San Jose, CA, USA) coupled to an isotope ratio mass spectrometer (Delta Plus XP; Thermo Finnigan) as per Gehre *et al*. (2004). Oxygen and hydrogen isotope measurements were expressed in common δ notation. δ^{18}O and δD was referenced to V-SMOW with a precision of 0.15 and 1.0‰ (SD), respectively.

Statistical analyses

All statistical analyses were performed on SAS 9.1.3 software (SAS Institute Inc, Cary, NC, USA). Repeated measures analyses of variance (ANOVAS) were performed for time series of plant, surface water and water vapour properties using the general linear model for ANOVA. Post-hoc tests were conducted using the Tukey standardized range test. Least square linear regressions were used to assess changes in stomatal conductance, leaf isotopic composition and water content over time. $P < 0.05$ was considered significant for all analyses, and $P < 0.1$ was considered marginally significant.

Calculation of marsh water balance and T/ET_{SW}

Surface water bodies subject to E become isotopically enriched. The level of enrichment is related to evaporative loss, thus the fractional loss of water by E can be quantified if other water loss processes do not isotopically fractionate (Gonfiantini 1986). As drainage and T are not expected to fractionate (Gonfiantini 1986; Dawson & Ehleringer 1991; Dawson *et al*. 2002), it was possible to estimate evaporative losses as a fraction of total water loss from the marsh. To do this, we used an isotopic mass balance equation based on Gonfiantini (1986). When combined with measurements of total water loss and ET, it was possible to estimate E and the proportion of ET that is E or T. We began our analysis following the transfer of some marsh standing water to another pond on 23 March 2007. This caused a drop in standing water height by almost 0.15 m. Marsh water after this date was not manipulated and water losses were dominated by E, T and D. We modelled the proportion of evaporative water loss since the last sampling day according to Gibson (2002), or $E/(E + T + D)$. According to Gibson (2002), for a lake in which inflow (I) equals zero, and E and non-fractionating outflows (Q) such as T and D are not negligible, the mass balance of the pond is represented as

$$dV/dt = -Q - E, \quad (1)$$

where V is pond volume, and the isotope balance is represented as

$$\delta_L = \delta^* - (\delta^* - \delta_0) f^{mE/(E+Q)}, \quad (2)$$

where δ_L is the isotopic composition of the lake, δ^* is the limiting isotopic composition under local meteorological conditions as defined by Gat & Levy (1978) and Gat (1981), m is a measure of the rate of approach to isotopic steady state as defined by Welhan & Fritz (1977) and Allison & Leaney (1982), and f is the remaining fraction of lake water. Moreover, f was estimated by the pond depth on a particular day divided by original pond depth (0.7 m). For each time step, we solved for $E/(E + Q)$, which equals $E/(E + T + D)$ by rearranging Eqn 2:

$$E/(E+T+D) = \ln[(\delta^* - \delta_L)/(\delta^* - \delta_0)]/[m + \ln(f)], \quad (3)$$

The depth of water loss on a particular day $(E + T + D)$ was calculated as the difference between initial depth on 23 March (0.7 m), and depth on that day (H_t):

$$0.7 - H_t = E + T + D, \quad (4)$$

This was multiplied by $E/(E + T + D)$ from Eqn 3 to obtain depth of water lost via E:

$$E + T + D * E/(E+T+D) = E, \quad (5)$$

For the marsh water balance, E was subtracted from depth of ET loss obtained via the eddy covariance method to obtain T. Depth of ET loss was subtracted from depth of water loss $(E + T + D)$ to obtain D.

E was divided by depth of ET loss to obtain E/ET. Finally, T/ET for the time step was calculated as

$$T/ET = 1 - E/ET \quad (6).$$

Calculation of T/ET_{WV}

The isotopic mass balance of water vapour in the marsh canopy was used to determine the contribution of E and T fluxes. We assumed there were three primary sources of vapour within the marsh canopy: E from standing or soil water, T from *Typha* and background vapour originating from outside the marsh. We also assumed that the relative contribution of the three sources did not significantly change during the measurement period, and there was no condensation or other losses of water vapour other than by turbulent mixing with air. Typically, linear mixing models or

'Keeling plots' relating the isotopic composition of water vapour to the inverse of water vapour concentrations are used to distinguish the isotopic composition of *ET* from that of the background vapour (Keeling 1961; Moreira *et al*. 1997; Yepez *et al*. 2003, 2005; Williams *et al*. 2004). Instead of the Keeling plot approach, we separately measured/modelled the isotopic composition of the 'endmembers' or components of total canopy vapour: *E*, *T* and background vapour. We used a mass balance approach based on Lai *et al*. (2006) to estimate the relative contributions of the sources to canopy vapour. The fractional contribution of each source to marsh canopy vapour is

$$F_c = F_b + F_e + F_t, \tag{7}$$

where *F* is the fractionation contribution and the subscripts c, b, e and t stand for canopy vapour, background air, *E* and plant transpiration, respectively. Using conservation of mass,

$$\delta^{18}O_C F_C = \delta^{18}O_B F_B + \delta^{18}O_E F_E + \delta^{18}O_T F_T \tag{8}$$

$$\text{and } \delta D_C F_C = \delta D_B F_B + \delta D_E F_E + \delta D_T F_T, \tag{9}$$

The isotopic composition of background vapour ($\delta^{18}O_B$, δD_B) was assumed to be similar to vapour collected above-canopy (4 m above the marsh water/soil surface).

We solved for the fractional contributions of each source, and *T* efficiency (*T*/*ET*) was calculated as a percent, $F_T/(F_E + F_T)$ * 100. We used the approach of Phillips & Gregg (2001) to calculate the errors associated with this three-endmember source partitioning model, and took into account analytical error and correlation between $\delta^{18}O$ and δD.

We used the model by Craig & Gordon (1965) to estimate the isotopic composition of evaporated vapour ($\delta^{18}O_E$ and δD_E) from the marsh surface, as described by Moreira *et al*. (1997):

$$R_E = (1/\alpha_K)[(R_S/\alpha^*) - R_A h]/(1-h), \tag{10}$$

where R_E is the molar ratio of heavy to light isotopes of ^{18}O or D of the evaporated water from the surface, R_S is the molar ratio of the liquid water at the surface and R_A is the molar ratio of the atmospheric vapour above the surface. α^* is the temperature-dependent equilibrium fractionation factor (Majoube 1971), and α_K is the kinetic fractionation factor for molecular diffusion in air. We used the kinetic fractionation factors of 1.021 (21‰) for oxygen and 1.011 (11‰) for hydrogen, which include the effects of a turbulent boundary layer (Cappa *et al*. 2003), which were appropriate for the well-mixed conditions usually at the site during daytime (friction velocity or $u^* > 0.2$). Finally, *h* is the relative humidity of the air.

We tested whether *T* was in isotopic steady state in order to better understand its isotopic composition. To do this, we estimated leaf water isotopic composition using a model of steady-state behaviour. If modelled *Typha* leaf water isotopic composition matched observations, we would assume that plants were in steady state during our daytime measurement period and that the isotopic composition of water transpired by the plants ($\delta^{18}O_T$, δD_T) was equivalent to the isotopic composition of plant root water, which reflects source water. If leaf water departed from steady-state predictions, we planned to model the isotopic composition of plant *T* after Farquhar & Cernusak (2005).

For the steady-state test, we modelled the isotopic composition of five equally spaced sections of each leaf with the string-of-lakes model by Gat & Bowser (1991), which describes progressive enrichment along parallel veins of grasses in steady state as shown by Helliker & Ehleringer (2000). The modelled leaf segments were averaged to obtain a value for bulk leaf water. We then corrected bulk leaf water for the Péclet effect using an expression of bulk leaf water as a mixture of enriched water in the leaf lamina and less enriched water in stems (Flanagan 1993):

$$\delta^{18}O_{leaf} = \delta^{18}O_{model} * p + \delta^{18}O_{stem} * (1-p), \tag{11}$$

where *p* is the proportion of the bulk leaf water subjected to mixing with stem water; the subscripts leaf and stem refer to bulk leaf water and stem water, respectively; and model refers to leaf water at the site of evaporative enrichment as calculated by the Gat & Bowser (1991) model.

Calculation of T/ET_{EC}

E was modelled during the growing season using an empirical model that was parameterized using periods when the plant canopy was senesced during winter and fall. Daily incoming shortwave explained 40% of the daily variability in *E*, and this relationship with shortwave radiation did not differ between flooded and non-flooded conditions [analysis of covariance (ANCOVA); $F_{1,109}$: 0.71; $P = 0.40$]. A bootstrap analysis (Zoubir 1993) of the parameters of the empirical model was used to determine the effect of *E* estimate variability on *T*/*ET* ($T/ET = 1 - E/ET$). The bootstrap method provides a measure of the uncertainty in calculated *E* by randomly removing a portion of the data, recalculating the empirical model parameters and then recalculating predicted *E*. One thousand estimates of *E* were used to determine the 95% confidence intervals of predicted *E*. *T*/*ET* estimates and their uncertainty were smoothed with a 14 d moving average.

RESULTS

There were linear relationships between $\delta^{18}O$ and δD for all samples in this study (Fig. 2a–c), thus we focus our results on $\delta^{18}O$ to avoid redundancy.

The isotopic composition of standing water, soil water and root water

The isotopic composition of root water, standing water and soil water were all evaporatively enriched relative to the

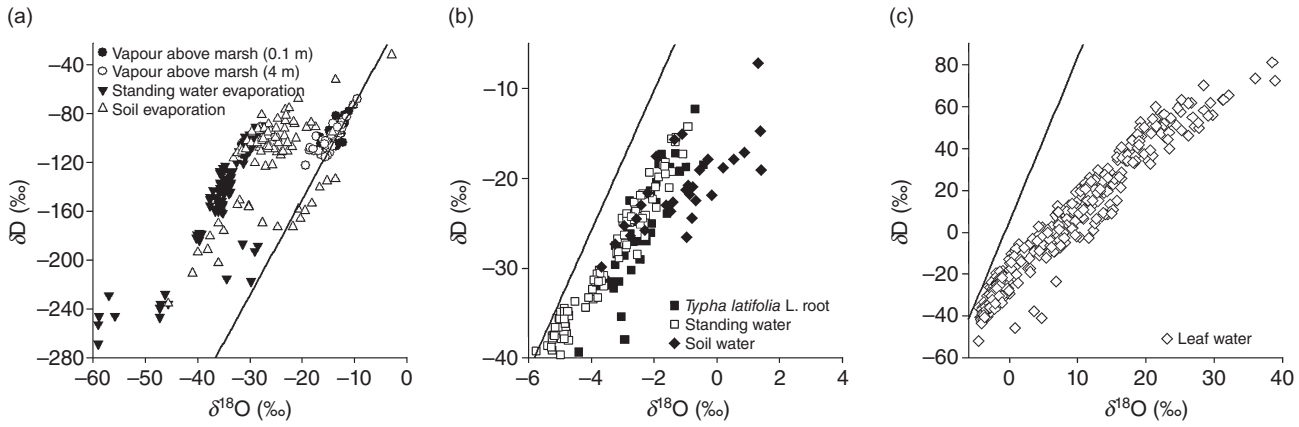

Figure 2. The $\delta^{18}O$–δD relationships of (a) within-canopy vapour collected 0.1 above marsh standing water and above-canopy vapor collected 4 m above marsh standing water and modelled evaporation (E) from marsh standing water and soil water (b) *Typha latifolia* L. root water and marsh standing water (c) leaf waters. In all plots, the solid line indicates the California meteoric water line as determined by Kendall & Coplen (2001). Note that figure axes vary in scale.

local meteoric water line (LMWL) for California by Kendall & Coplen (2001), as they fell to the right (Fig. 2b). The marsh water level and sequence of water transfers are shown in Fig. 3a. Marsh standing water in January and February following initial flooding was isotopically similar in 2007 and 2008 (Fig. 3b; $P > 0.1$). The isotopic composition of surface standing water became progressively enriched following initial flooding on 5 January 2007 until the second flooding event on 22 February 2007 ($P < 0.01$), when it became depleted (Fig. 3b). After this flooding event, there was an overall enrichment in the isotopic composition of standing water ($P < 0.0001$). Standing water disappeared on 18 June 2007 (Fig. 3a). The isotopic composition of soil water was constant following 13 July 2007 (Fig. 3b, $P > 0.1$).

The isotopic composition of root water and standing water were similar, except on 23 May 2007, when standing water was enriched relative to root water (Fig. 3b, $P < 0.05$). Surface soil water (0–5 cm) was always isotopically enriched relative to root water, except on 28 June 2007 when root water was marginally enriched (Fig. 3b, $P < 0.01$).

Leaf properties and isotopic composition

Over the *Typha* growing season in 2007, there was a decline in average daily LWC (Fig. 4a, $P = 0.0005$) and stomatal conductance (Fig. 4b, $P = 0.0137$). The average SLA was 53.2 ± 7.1 (SD) $cm^2\ g^{-1}$.

The isotopic composition of leaf water was evaporatively enriched relative to the California LMWL (Fig. 2c). Leaf water showed progressive isotopic enrichment from the base of the leaf to the tip of 18.6 ± 9.0‰ for $\delta^{18}O$ (not shown; $P < 0.05$). The middle portion of the leaf was 10.9 ± 3.6‰ $\delta^{18}O$ more enriched than the base, and the top of the leaf was 7.7 ± 6.9‰ $\delta^{18}O$ more enriched than the middle. Thus, the $\delta^{18}O$ isotopic difference between the base and middle of the leaf was slightly greater and less variable than the difference between the middle and top of the leaf. The $\delta^{18}O$ isotopic difference between the top and bottom portions of the leaves decreased with increasing humidity (not shown; $P < 0.0001$), as would be expected based on the string-of-lakes model (Helliker & Ehleringer 2000), and we did not find an apparent relationship with the $\delta^{18}O$ of vapour within the canopy ($P > 0.05$). The average isotopic composition of whole leaves varied between 1.0 and 13.2‰ for $\delta^{18}O$, and became enriched over time on sampling days (Fig. 5a; $P < 0.0001$). Modelling leaf water without taking into account the Péclet effect (Flanagan 1993) resulted in values that were isotopically enriched relative to observed leaf water by 3.5 ± 2.0‰ $\delta^{18}O$ (Fig. 5b). Accounting for the Péclet effect using 0.72 for p in Eqn 11 reduced the difference between measured and modelled leaf water isotopic composition to 1.3 ± 0.8‰ $\delta^{18}O$ (Fig. 5b). There was no trend in model residuals with time of day or over the growing season ($P > 0.1$).

The isotopic composition of water vapour

The isotopic composition of vapour samples collected within canopy (0.1 m above the marsh water/soil surface) was within 1.0 ± 0.8‰ for $\delta^{18}O$ and 8.1 ± 6.5‰ for δD of the California LMWL (Fig. 2a). Vapour samples collected above canopy (4 m above the marsh standing water/soil) were within 0.7 ± 0.8‰ for $\delta^{18}O$ and 5.2 ± 6.5‰ for δD (Fig. 2a). A repeated measures ANOVA showed no overall difference between vapour above and within canopy (Fig. 6; $P > 0.1$). However, there were differences between above- and within-canopy vapour during individual sampling events up to 5.3‰ for $\delta^{18}O$ (13 July 2007; Fig. 7). The average modelled isotopic composition of vapour derived from evaporated surface water was –31.2 ± 7.8‰ for $\delta^{18}O$, and was the most isotopically depleted source of local water vapour we considered (Fig. 6). E was isotopically depleted relative to other days on 16 January 2008, as humidity was high (73%) and temperature was low (15 °C).

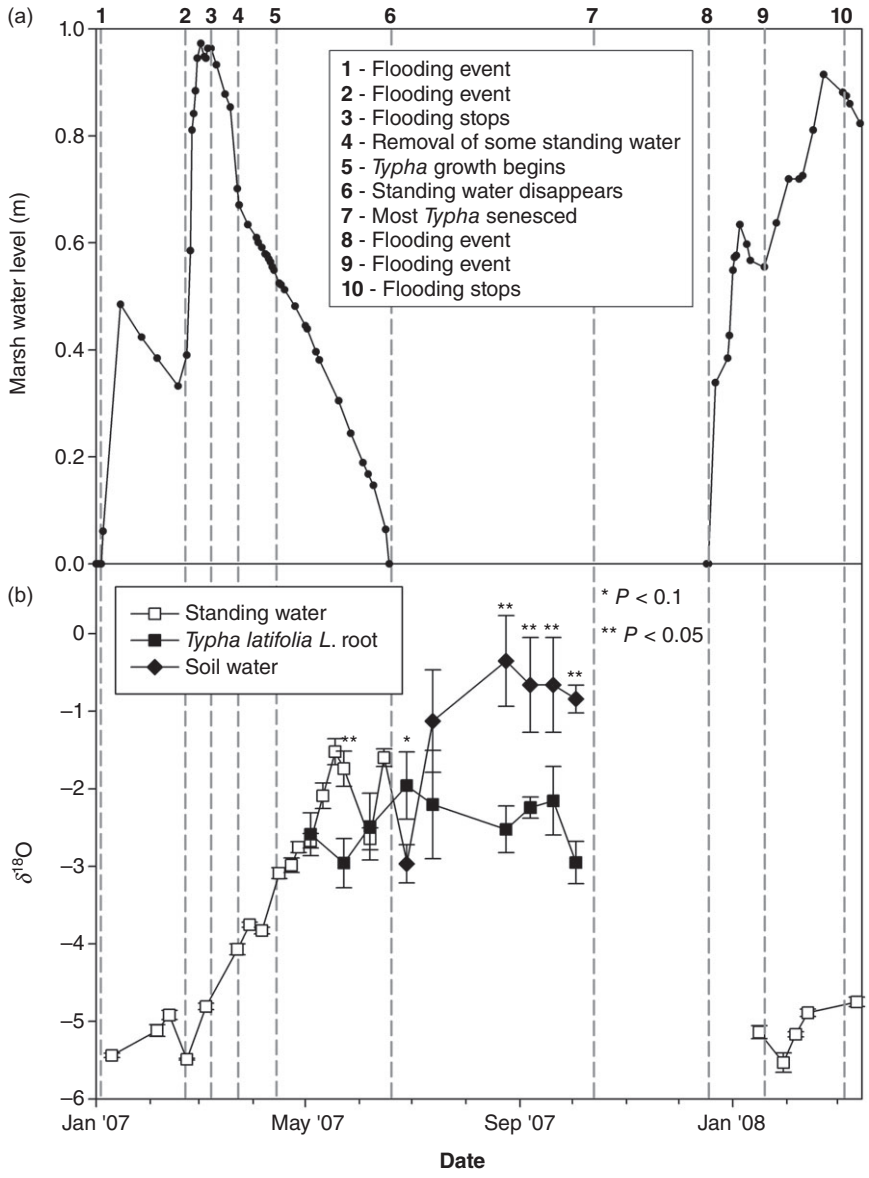

Figure 3. (a) Marsh water level during 2007–2008. (b) The isotopic composition of standing water, soil water and *Typha latifolia* L. root water during 2007–2008. The asterisk (*) shows a marginal difference ($P = 0.5$–0.1) between root water and standing water/soil water, and double asterisks (**) show a significant difference ($P < 0.05$).

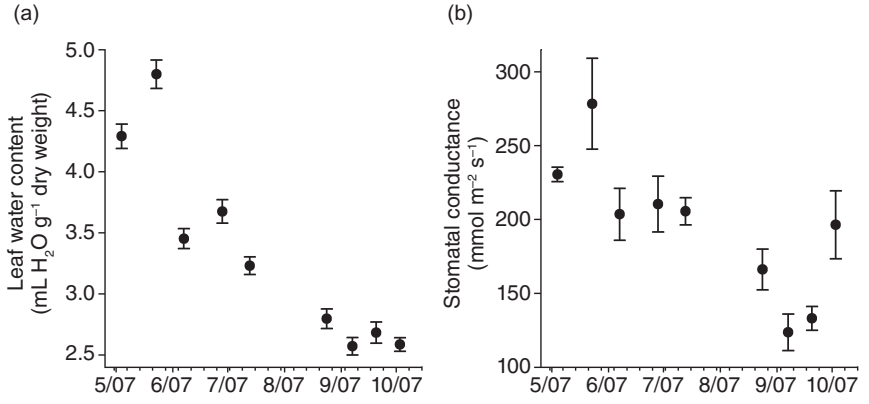

Figure 4. (a) Leaf water content (LWC) over time for *Typha latifolia* L. (b) Stomatal conductance over time for *T. latifolia* L.

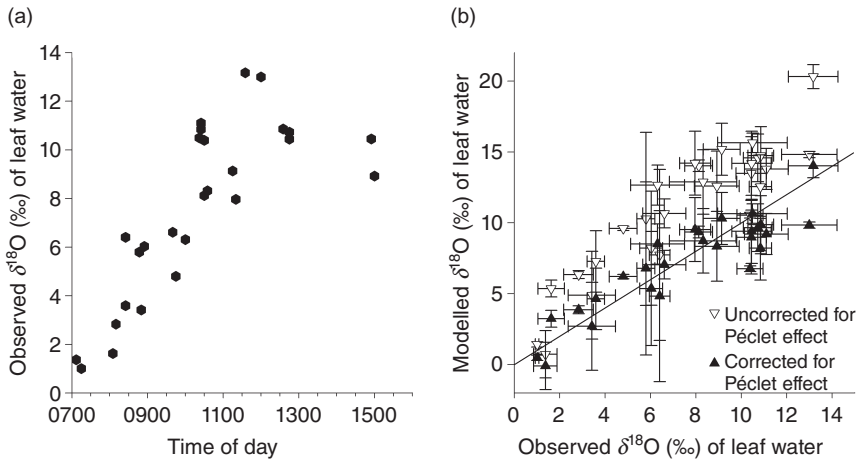

Figure 5. (a) Diurnal variation in isotopic composition of leaf water for all sampling days. (b) The isotopic composition of observed versus modelled leaf waters, with and without the Péclet correction. The solid line is the 1:1 line.

Estimates of *T*/*ET*

The ENVI classification of the 100 × 100 area upwind of the tower into exposed water versus litter showed that the percentage of exposed water was 3.2%. Total ET averaged 2 mm d^{-1} during the spring and summer growing season, and <1 mm d^{-1} during winter when plants were senesced (Fig. 8a). T/ET_{SW} estimates increased over time (Fig. 8b, $P = 0.0007$) and indicated that T generally occurred at a higher rate than E (Fig. 8b, $P = 0.0007$). The low error of T/ET_{SW} measurements was representative of the low variability of the isotopic compositions of water samples from each sampling event (Fig. 3b). On 15 June 2007, three days prior to complete absence of standing water, there was only

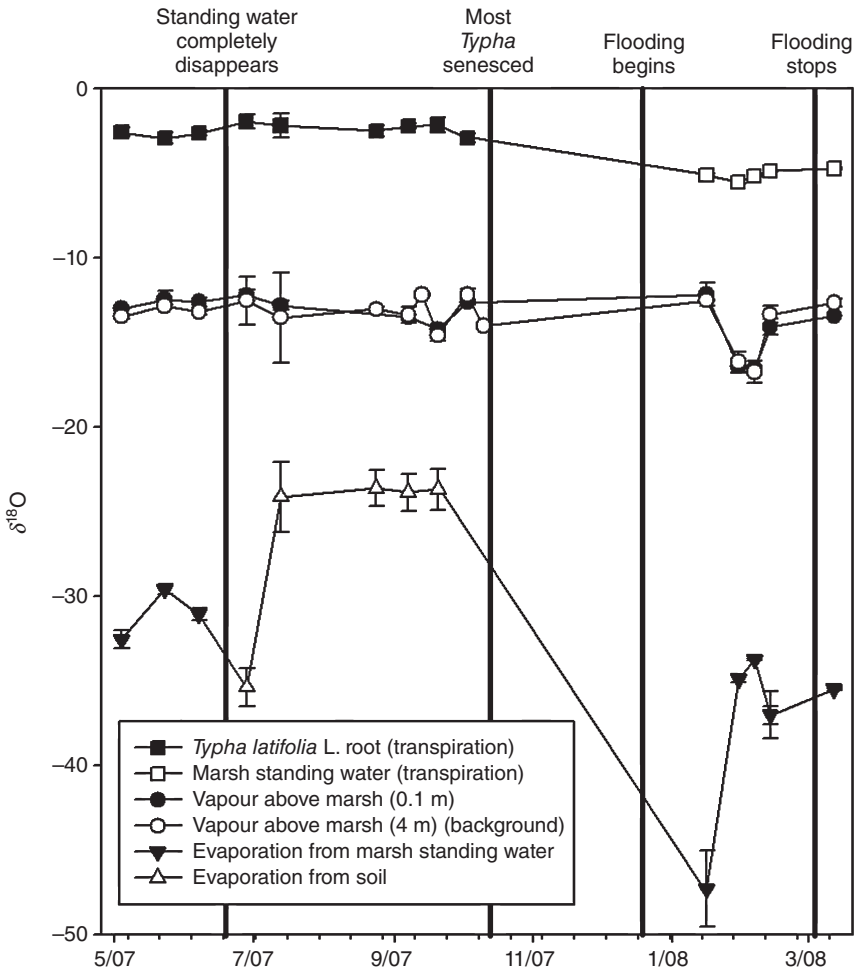

Figure 6. The isotopic composition of endmembers used for distinguishing between evaporation (E) and transpiration (T) in canopy vapour (collected at 0.1 m height above marsh water/soil surface). The endmembers were background vapour collected 4 m above the marsh water/soil surface, E from standing water and soil, and T (assumed to be similar to *Typha latifolia* L. root water in 2007, and marsh standing water in 2008).

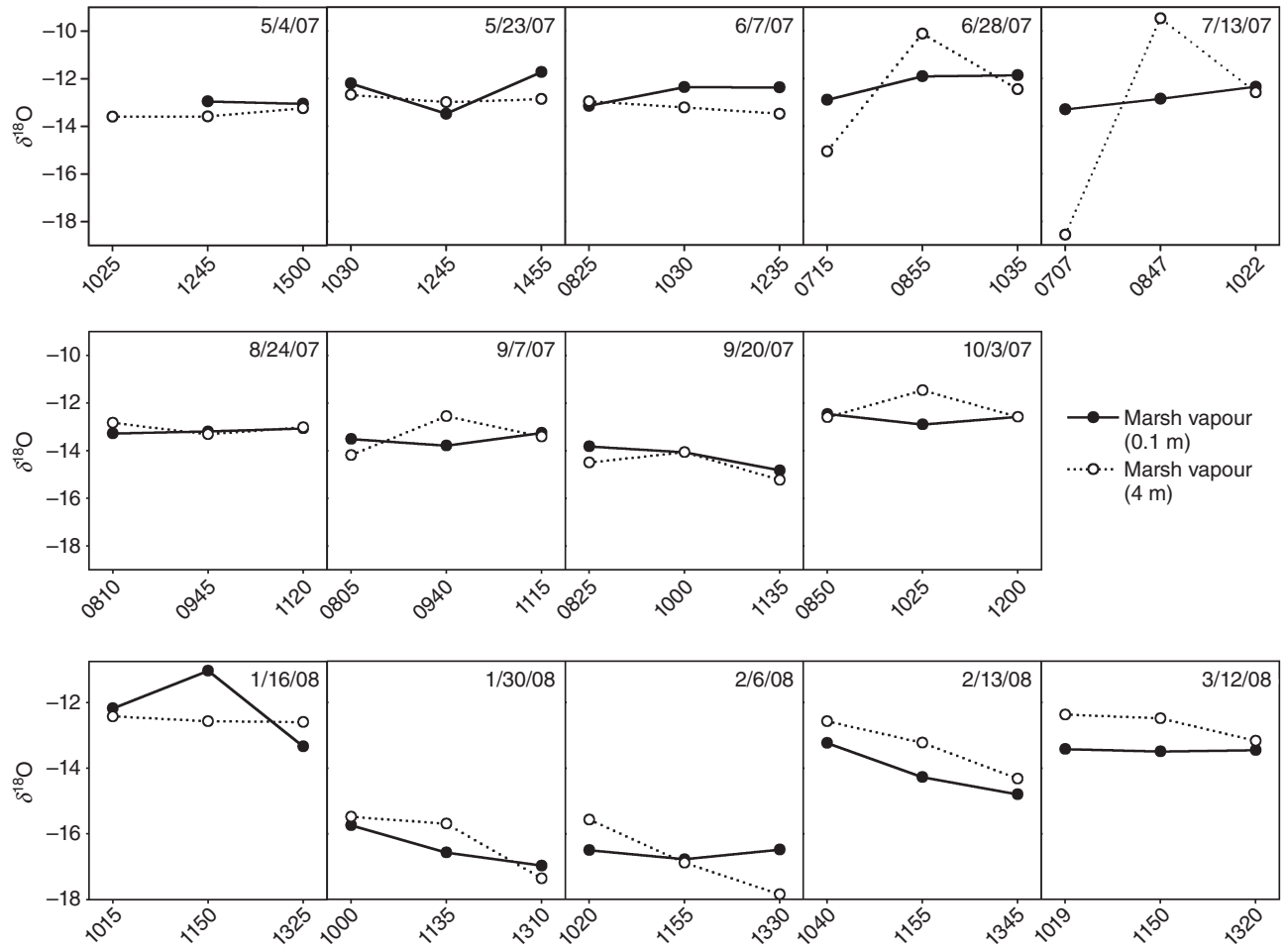

Figure 7. Diurnal variations in the isotopic composition ($\delta^{18}O$ and δD) of within-canopy vapour collected 0.1 and 4 m above marsh water or the soil surface on sampling days during the 2007 *Typha latifolia* L. growing season and in 2008 when standing water was present, but plants had greatly senesced. Note that figure axes vary in scale.

6 cm of standing water left, and 83 ± 2% of marsh *ET* loss since 23 March 2007 was caused by *T* (Fig. 8b). *E* accounted for 3.4% of total water loss at the marsh, while drainage accounted for 79.5%.

T/ET_{WV} ranged from 56 ± 17% to 96 ± 67% in the growing season of 2007 (Fig. 8c). In 2008, when most (but not all) plants had senesced and standing water was present, T/ET_{WV} ranged from 38 ± 67% to 91 ± 30%. Background vapour comprised 83 ± 10% of canopy vapour for these measurements, and the average percent errors of T/ET_{WV} estimates ($SD/T/ET_{WV}$) were 48% in 2007 and 82% in 2008. The highest percent errors were 177.5 and 168.9% on 13 February 2009 and 12 March 2009, when the proportion of *T* was low (*T*/*ET* is ≤40%) and the contribution of background vapour to the total water vapour concentration was high (>90%) (Fig. 9a,b). Excluding these two data points, there was a linear relationship between the contribution of background vapour to the total vapour, and the percent error of the *T*/*ET* estimate (Fig. 9b, $P = 0.0017$). Mean T/ET_{EC} estimated using eddy covariance measurements followed a seasonal cycle, being near zero when plants emerged, and increasing to ~70% during the peak growth period from June to August, and declining thereafter (Fig. 8c.)

DISCUSSION

We first discuss the isotopic variability within and among the liquid water pools to provide context for interpreting the isotopic values of sources and fluxes used for constructing mass balances. Leaf water was highly variable (7.5 ± 3.6‰ $\delta^{18}O$) (Fig. 5a), while soil water and root water showed little variability (–1.1 ± 1.4‰ $\delta^{18}O$ and –2.5 ± 0.9‰ $\delta^{18}O$, respectively) (Fig. 3), comparable to Lai *et al.* (2006) and Welp *et al.* (2008). Standing water was initially 5.4‰ $\delta^{18}O$, and became progressively enriched by 3.8‰.

Canopy water vapour at 4 m was within 1.1 ± 1.0‰ $\delta^{18}O$ of the isotopic composition of vapour collected simultaneously at the nearby coast (–13.8 ± 1.0‰ $\delta^{18}O$) ($P > 0.1$), suggesting a large influence of marine *E*. The isotopic composition of vapour varied slightly (–13.6 ± 1.5‰ $\delta^{18}O$

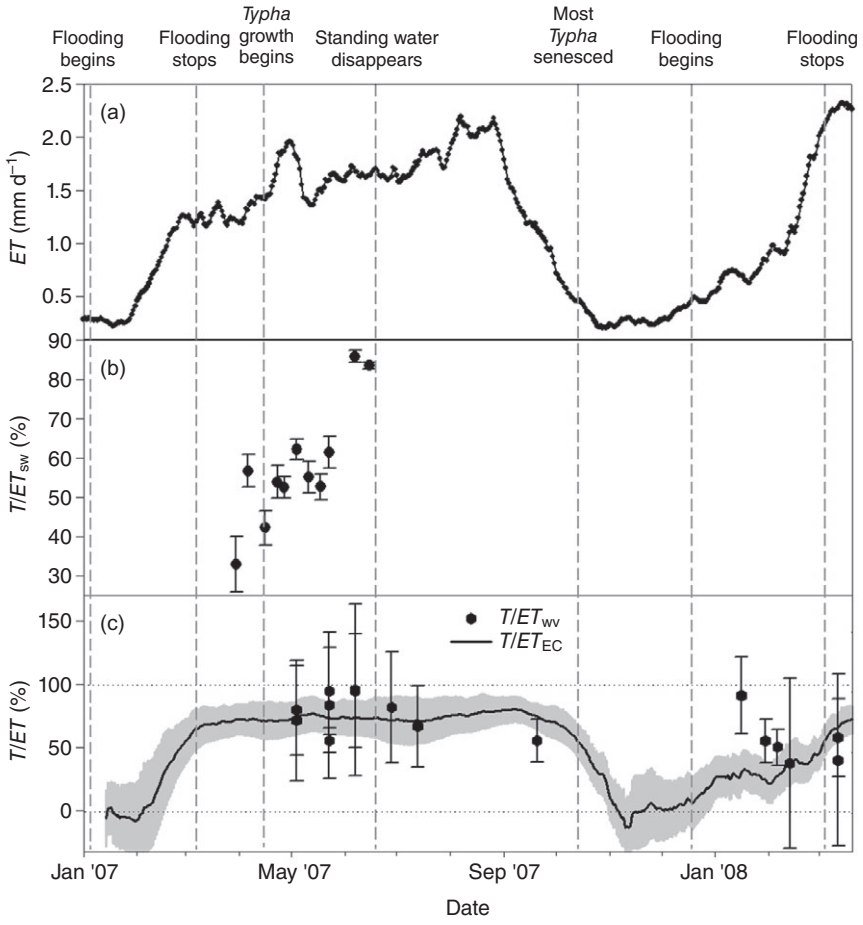

Figure 8. (a) Marsh *ET*, (b) T/ET_{SW}, (c) T/ET_{EC} and T/ET_{WV} during the study period.

for within-canopy vapour and −14.0 ± 2.1‰ $\delta^{18}O$ for above-canopy vapour). We observed diurnal variations as high as 2.3‰ $\delta^{18}O$ within canopy (16 January 2008) and 9.1‰ $\delta^{18}O$ above canopy (13 July 2007) in Fig. 7. Barnard *et al*. (2007) also showed high diurnal variations up to 8‰ $\delta^{18}O$ within canopy in a *Pinus sylvestris* forest. For comparison, Lai *et al*. (2006) observed diurnal variations as high as 4‰ above and within an old-growth coniferous forest, and Welp *et al*. (2008) found the mean isotopic composition of vapour to vary over the season by nearly 15‰.

Péclet effect and steady-state *T*

The isotopic composition of leaf water was calculated using a steady-state model and compared to observed leaf water. The results of these calculations, which predict the isotopic composition of water at the sites of *E*, were enriched relative to observed leaf water by 3.5 ± 2.0‰ for $\delta^{18}O$ (Fig. 5b). Several studies have shown that Péclet corrections can improve the agreement between modelled and measured leaf water (Cernusak, Pate & Farquhar 2002; Farquhar &

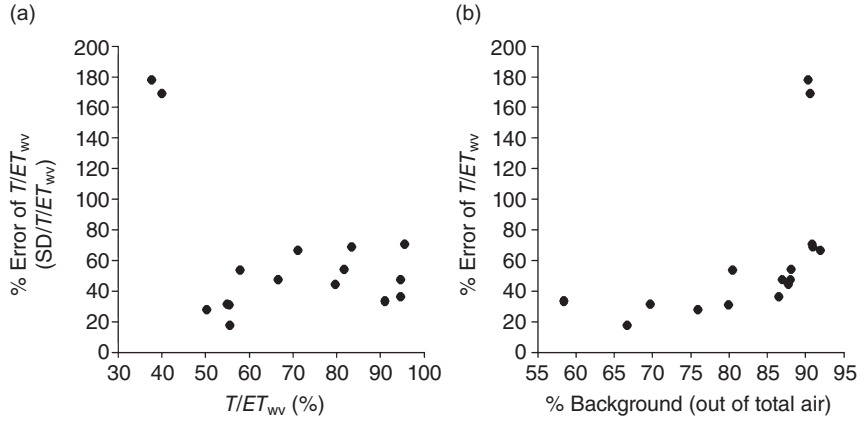

Figure 9. The relationship between percent error (SD/*T*/*ET*) of T/ET_{WV} estimates and (a) T/ET_{WV} (%) and (b) % background water vapour in total canopy vapour.

Gan 2003; Ripullone *et al*. 2008). To correct for the Péclet effect, we used 0.72 for p in Eqn 11. This estimate fell within the range of other studies, which have reported that the pool of unfractionated water $(1 - p)$ varies between 0.10 and 0.30 of the total water volume (Allison, Gat & Leaney 1985; Leaney *et al*. 1985; Walker *et al*. 1989; Flanagan *et al*. 1991; Roden & Ehleringer 1999). As plant ET increases, $1 - p$ is expected to increase in a fractional curvilinear fashion (Barbour *et al*. 2004). We did not find any trend in the model residuals with time of day or over the growing season (not shown; $P > 0.1$), implying that p remained constant. Consideration of the Péclet effect improved similarity between observed and modelled values (Fig. 5b). Because Péclet-corrected steady-state modelled values for $\delta^{18}O$ of leaf water were similar to observed values (within 1.3 ± 0.8‰), we assumed the plants operated primarily in isotopic steady state, concurrent with our hypothesis, and that the isotopic composition of transpired vapour was similar to the water found in plant roots. In winter 2008, when most plants had senesced and standing water was present, we assumed the small amount of remaining green vegetation continued to operate in isotopic steady state during daytime and that the isotopic composition of T was similar to that of marsh standing water. T was thus the most enriched source of canopy vapour (Fig. 6). During the daytime, short crop canopies similar to our 1-m-tall canopy have been shown to be at or near to steady state (Yakir & Wang 1996; Welp *et al*. 2008).

Evaporative influence on standing water

The isotopic composition of surface standing water was enriched following initial flooding at the marsh on 5 January 2007 ($P < 0.01$), consistent with E, until another pulse of water was added on 21 February 2007 (Fig. 3). This resulted in isotopic depletion (Fig. 3b). After flooding stopped on 7 March 2007, there was a steady evaporative enrichment of the standing water until standing water disappeared on 18 June 2007 ($P < 0.01$). E was expected to cause isotopic enrichment of soil (mud) water following E of standing surface water (i.e. Allison 1982; Allison & Hughes 1983), but following 13 July 2007, the isotopic composition of soil water did not change ($P > 0.1$), implying low E rates from marsh soil. This is consistent with high resistance to water vapour loss from below the canopy. On 7 and 28 June 2007, the isotopic compositions of standing water and soil water, respectively, were anomalously low relative to the general trend of enrichment. On 18 December 2007, water was again diverted into the marsh for the next growing season (Fig. 3a), and became evaporatively enriched following an additional pulse of water on 19 January 2008 (Fig. 3b). Marsh standing water in January–February 2008 was depleted to values similar to the previous January–February period of 2007 because of re-flooding of unevaporated water. These values were within 0.39 ± 0.2‰ $\delta^{18}O$ of the California LMWL and are consistent with an origin of primarily native recharge and local precipitation, rather than imported Colorado River water (Williams 1997).

Plant water use

Surface standing water was sometimes isotopically enriched relative to root water, indicating that evaporative enrichment primarily affected the surface of the standing water pool, and that roots were accessing deeper, more depleted water (Fig. 3b). Root water was initially similar in isotopic composition to marsh surface water when plants were very young on 4 May 2007 ($P > 0.1$), but as plants grew, the isotopic composition of root water became depleted relative to surface water ($P < 0.05$ on 23 May 2007), suggesting use of deeper water. Roots were isotopically depleted relative to surface soil water in August and October, following the disappearance of standing water, which suggests T of deeper soil water (Fig. 3b). Deep rooting was suggested by Goulden *et al*. (2007), who found that high rates of ET continued following the disappearance of standing water. In this study, declines in LWC and stomatal conductance indicated that plants experienced increased water stress over the course of the season (Fig. 4, $P < 0.05$), but sustained high rates of T/ET (Fig. 8b,c), probably because of deep roots. Deep rooting has been previously observed in *T. latifolia* grown in containers (Weaver & Himmel 1930). In fully saturated soils, root depths were 30 cm, and in moist, well-aerated soils, roots penetrated 40–53 cm.

Plant vegetation density

The ENVI classification of the 100×100 area upwind of the tower into exposed water versus litter showed that the percentage of exposed water was 3.2%, and thus the plant vegetation density is very high, 96.8%. The approach used may have inadvertently classified some shadows as standing water because both are dark, which would have led to an overestimation of standing water. The approach may also have missed smaller areas of standing water that were below the image resolution (30.5 cm), which would have led to an underestimation of standing water. Despite these uncertainties, the measure of open water is probably within a factor of two of the true value, and the conclusion that open water covers only a small fraction of the marsh is robust.

Marsh water balance and comparison of T/ET_{SW}, T/ET_{WV} and T/ET_{EC}

T/ET_{SW} showed a progressively larger proportion of total marsh water lost via T over the course of the season (Fig. 8b). This indicates a higher proportion of T to E, as hypothesized by Goulden *et al*. (2007), who found low rates of subcanopy water flux (E) in the SJFM and attributed this to cool water temperatures, because of shading by *Typha* mulch. The high rate of T/ET is plausible because the proportion of marsh surface that is free water as viewed by the sun is very low, 3.2%, while the remaining percentage, 96.8%, is covered by vegetation or mulch (Fig. 1). The high density of plant material explains the low rate of marsh E relative to T. The total ET of SJFM shows a great deal of

year-to-year variability, and *ET* in 2007 was generally lower than in previous years (Goulden *et al.* 2007 and unpublished data), likely because of variability in *T*. Our findings agree with other studies that have suggested wetland *T* exceeds open water *E* (Price 1994; Herbst & Kappen 1999; Pauliukonis & Schneider 2001; Acreman *et al.* 2003). T/ET_{SW} represents the cumulative *T* efficiency, while T/ET_{EC} represents the instantaneous *T* efficiency, which is why T/ET_{SW} shows a stronger tendency to increase over time than T/ET_{EC}. Although T/ET_{SW} is not directly comparable to T/ET_{EC}, both methods agreed that *T* exceeded *E* for most of the growing season (Fig. 8b,c). On 15 June 2007, when only 6 cm of standing water remained, 82 ± 2% of total, cumulative *ET* loss since 23 March 2007 could be attributed to *T* (Fig. 8b). Only a small amount of total marsh water loss was caused by *E* (3.4%), while *T* accounted for 17.1%, and the largest loss was from *D* (79.5%). In contrast to the dominant water loss by drainage found in this study, others have suggested that *ET* represents the greatest water loss from wetlands, and that the inflow of groundwater is more important than outflow (Owen 1995; Hunt *et al.* 1996; Drexler *et al.* 2004).

Although the drainage rate at the marsh was higher than *T* or *E*, it was nevertheless relatively low as would be characteristic of poorly drained wetland soils, at an average rate of only 6.4 mm d^{-1} from 23 March until water disappearance on 18 June. This rate (6.4 mm d^{-1}) corresponds to an average saturated hydraulic conductivity within the expected range for the soil type present at the marsh, which was primarily silty clay and black silty peat (Davis 1992). Saturated hydraulic conductivity (K_s) can be solved using Darcy's law (Hillel 1998),

$$K_s = Q/(\Delta H/L), \quad (12)$$

where *Q* is drainage rate, ΔH is the difference in hydraulic head between the inflow and outflow boundary, and *L* is the depth to the water table, which was unknown in our system. When standing water depth is negligible, $\Delta H/L$ is unity, and the saturated hydraulic conductivity is equal to the drainage rate,

$$K_s = Q, \quad (13)$$

If there were no standing water at the marsh, the average drainage rate, 6.4 mm d^{-1}, would equal the saturated hydraulic conductivity ($10^{-7.13}$ m s^{-1}). As standing water was initially present at the marsh, $\Delta H/L$ was greater than unity and the saturated hydraulic conductivity in our system was $\leq 10^{-7.13}$ m s^{-1}. This is within the expected range of saturated hydraulic conductivity for silt, which is 10^{-8} to 10^{-6} m s^{-1} (Boeker & van Grondelle 1995 as cited in Hillel 1998), thus our estimate of drainage is reasonable for the marsh soil type.

The local influence of *ET* has been shown to be detectable in atmospheric vapour in several studies (e.g. Brunel *et al.* 1992, 1997; Moreira *et al.* 1997; Yepez *et al.* 2003). In our study, the isotopic mass balance of canopy vapour showed that there was an influence of *ET* in canopy vapour during some sampling events, which are shown in Fig. 8c. *ET* was not detectable when the isotopic composition of above-canopy background vapour at 4 m and canopy vapour at 0.1 m were similar, which suggests strong turbulent mixing. On these days, the isotopic composition of atmospheric water vapour was sometimes outside of the range of possible sources (*E*, *T* and background vapour), indicating that strong mixing may have transported water vapour sources from outside of the marsh area. The isotopic composition of canopy vapour was within the range of sources when vapour above and within canopy was isotopically distinct, and when the water vapour content in the canopy exceeded the content above canopy, indicating the presence of a local *ET* signal in the canopy because of stable atmospheric conditions. Specifically, this occurred when the difference between above- and within-canopy vapour exceeded 0.19‰ $\delta^{18}O$ and 4.0‰ δD in 2007, and 0.9‰ $\delta^{18}O$ and 0.8‰ δD in 2008, and when the canopy atmospheric water vapour content exceeded above-canopy content by 0.9 g H_2O m^{-3} in 2007, and 0.25 g H_2O m^{-3} in 2008. These conditions occurred only on 38% of sampling days. The amount of *ET* in canopy vapour varied considerably, from 8 ± 5% on 4 May 2008 to 42 ± 12% on 18 January 2008. Overall, the local contribution of *ET* was small, as the average was 17 ± 10% of canopy vapour.

T/ET_{WV} ranged from 56 ± 17% to 96 ± 67% with an average of 78 ± 20% in the growing season of 2007 (Fig. 8c). This is within the range reported by Herbst & Kappen 1999, who found *T*/*ET* up to 83%. Mean values of T/ET_{EC} were similar to T/ET_{WV} during the growing period, and following *E* of standing water (Fig. 8c). At least 38% or more of *ET* in the canopy can be attributed to *T* according to T/ET_{WV}, but the large error limits the usefulness of these calculations and their ability to detect temporal patterns. We expected temporal patterns as seen in T/ET_{EC}, which increased at the beginning of the growing season and waned as *Typha* senesced.

In winter 2008, when most plants had senesced and standing water was present, T/ET_{WV} ranged from 38 ± 67% to 91 ± 30%, or 55 ± 19% on average (Fig. 8c). Although the errors of T/ET_{WV} estimates were high, they often did not overlap with zero (Fig. 8c), indicating an influence of *T*. It was somewhat surprising that *T* was detected during this period because of relatively low green leaf area. However, because the *E* rate was also likely low because of cooler water and higher relative humidity in this winter period (Goulden *et al.* 2007), a detectable fraction of *T*/*ET* is plausible. Alternatively, water vapour from *T* of other vegetation, such as riparian trees approximately 40 m away, may have been present in these samples, and during other periods in the study. Uncertainties in the measurement footprint complicate the interpretation of studies that rely on concentration rather than direct flux measurements.

The large errors in the T/ET_{WV} estimates are likely caused by a relatively small contribution of *ET* to total atmospheric water vapour. The two estimates with the highest percent error (SD/T/ET_{WV}), 177.5 and 168.9%, are

during the presence of standing water and senescence of *Typha* in February and March 2008. These occurred when the proportion of T was low (T/ET_{WV} is ≤40%), and the contribution of background water vapour was very high (>90%) (Fig. 9a,b). Excluding these two extreme data points, the percent error of the T/ET_{WV} estimate increased with proportion of background vapour in the total canopy water vapour (Fig. 9b; $P = 0.0017$). This relationship can provide a guideline for conditions that are favourable to distinguishing between E and T (i.e. when the contribution of non-local, background water vapour to the total is less than about 80%).

CONCLUSIONS

The $\delta^{18}O$ and δD isotopic composition of water pools (leaf, root, standing water and soil water) and fluxes (T, E) showed that: (1) plants were generally transpiring in isotopic steady state without large short-term changes in LWC. However, there were longer-term, seasonal declines in LWC concurrent with declines in stomatal conductance. (2) The isotope mass balance of standing marsh water was more useful in distinguishing among pathways of water loss than the isotope mass balance of water vapour. (3) There were differences in isotopic composition and water vapour content above versus within canopy, indicating stable atmospheric conditions during which the influence of local T and E was detectable. Other periods indicated strong atmospheric mixing, which obscured the influence of local sources on atmospheric water vapour. T/ET estimates based on the isotopic mass balance of standing water (T/ET_{SW}), the isotopic mass balance of water vapour (T/ET_{WV}) and eddy covariance (T/ET_{EC}) agreed on a dominant influence of T on total ET, despite the presence of standing water. In general, measurements of the isotopic composition of liquid water pools in standing water, soil water and plants provided very useful information about local ecohydrology and water balance, while distinguishing between E and T with the isotopic composition of water vapour was possible only under specific atmospheric conditions, such as when there was a large vertical gradient in water vapour concentrations and isotopes.

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