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## A simple method for estimating water loss by transpiration in wetlands

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**Abstract** Estimates of transpiration are often needed for hydrological management in wetlands. A new and simple method, using a portable steady-state porometer, is presented for estimating transpiration in three aquatic emergent macrophytes (reed, cut-sedge, and cattail). The method was established on the basis of the relationships between transpiration, solar radiation, relative humidity and air temperature. By assessing relationships between all variables in piecewise linear regressions with breakpoint, water loss by transpiration can be estimated. The regression equations are calculated from direct observations including daily averages of climatic variables. Other data used in the model are area-defined leaf density of macrophytes and yearly macrophyte cover. The results of this method in comparison with literature transpiration data confirm the importance of transpiration in the water balance in aquatic ecosystems. The advantage of this method relies on the possibility to determine the physiological variability of transpiration in relation to climatic variables determined in situ. This permits a closer approximation of processes taking place in nature. Given that the required information is easily obtainable and that good estimates of transpiration in emergent macrophytes are provided, the method serves as a valuable tool for wetland hydrology management.

**Key words** water loss; transpiration; emergent macrophytes; porometer; solar radiation; air temperature; relative humidity; piecewise linear regression; wetlands

#### Une méthode simple pour estimer les pertes d'eaux par transpiration dans les zones humides

Résumé Il est souvent nécessaire d'évaluer la transpiration pour le management hidrologique dans les zones humides. Dans cette étude nous proposons une nouvelle et simple méthode pour estimer la transpiration de trois macrophytes aquatiques émergents (roseau, couper-carex, et panicule de roseau) avec l'aide d'un poromètre stationnaire portatif. Cette méthode est basée sur le rapport entre la transpiration le rayonnement solaire, l'humidité relative et la température de l'air. La perte d'eau par transpiration peut s'estimer à partir de l'analyse par régression linéaire avec point de rupture des variables pairées. Ces équations sont calculées à partir d'observations directes qui incluient les variations journalières des variables climatiques. Les autres données utilisées sont la densité des feuilles des macrophytes et la couverture annuelle maximum. En comparant les résultats de la méthode avec données de transpiration de la littérature on peut réaffirmer l'importance de la transpiration pour l'équilibre de l'eau dans les écosystèmes aquatiques. L'avantage de la méthode utilisée est le suivant: Elle nous permet, à partir d'estimations directes, de déterminer la variabilité physiologique de la transpiration face aux conditions climatiques. Ainsi nous disposons d'une meilleure approximation aux mécanismes réels du phénomène étudié. Vu que l'information exigée est facilement disponible et qu'il existe de bonnes évaluations de la transpiration dans les macrophytes émergents, la méthode peut servir d'outil à la gestion hydrologique des zones humides.

Mots clefs perte de l'eau; transpiration; macrophytes émergents; poromètre; rayonnement solaire; température de l'air; humidité relative; zones humides; régression linéaire en pièces

#### INTRODUCTION

Wetland hydrology is widely recognized as the primary force controlling wetland ecology, development and persistence (Mitsch & Gosselink, 1993). The hydrological characteristics of wetlands reflect their interaction with atmospheric water, surface water and groundwater (Winter, 1992). Any change in one of these components will generally cause a change in one or both of the others. The effective management of a wetland depends on a thorough understanding of the way in which the components of the water budget interact to provide a stable, though seasonally varying, template against which wetland plant communities can develop (Gilman, 1994). In many wetlands, precipitation, runoff, or groundwater seepage contributes substantial amounts of water to the wetland. However, in all wetlands evapotranspiration causes a major loss of water (Winter, 1992). Despite evaporation and transpiration causing the largest water loss from wetlands, aspects of transpiration characteristics of wetland vegetation and their role in wetland hydrology are not well understood (Winter, 1992). Studies of transpiration are inconclusive, for it is not clear whether the presence of wetland vegetation increases or decreases water losses from a body of water. Obviously, the presence of vegetation retards evaporation from the water surface, but the question is whether the transpiration of water through the plants matches or exceeds the difference (Kadlec, 1989).

#### Evapotranspiration in wetlands

Evapotranspiration is related to climate, groundwater and surface-water characteristics, as well as to the physiology of plants. Evaporation and transpiration are enhanced by meteorological conditions, such as solar radiation or surface temperature, that increase the value of the vapour pressure at the water surface, or by factors such as the decreased humidity or increased wind speed that decrease the vapour pressure of the surrounding air (Mitsch & Gosselink, 1993). Despite adequate moisture, certain plants can also physiologically limit transpiration through the closing leaf stomata during a period of stress such as anoxia (Mitsch & Gosselink, 1993). Experiments under controlled conditions have revealed variables, which drive the mechanisms of transpiration (Collatz *et al.*, 1991; Decker & Wetzel, 1957). However, the unnatural character of these results does not permit for exact extrapolations to field conditions.

It is known that environmental variables can condition plant physiology markedly, thereby regulating transpiration (Snyder & Boyd, 1987; Van der Weert & Kamerling, 1974). Among the environmental factors at work, light intensity, humidity and temperature are the climatic variables which most influence the transpiration rates in macrophytes (Bernatowicz *et al.*, 1976; Collatz *et al.*, 1991; Decker & Wetzel, 1957; Snyder & Boyd, 1987). Other factors such as the soil water potential, which also significantly influences transpiration (Lhomme *et al.*, 1998), can be regarded as less important in environments with permanently waterlogged soils such as in certain wetland types. While evaporation rate is directly proportional to the wind speed, emergent hydrophytes reduce evaporation by sheltering the water surface from the wind (Eisenlohr, 1966). Moreover, the aerodynamic component affects plant physiology only in the border zones of the vegetation stands, therefore not conditioning significantly the global transpiration rates (Collatz *et al.*, 1991). Furthermore,

as pointed out by Lee (1967), transpiration seems to be controlled by stomata rather than by aerodynamic conditions. The present study shows that solar radiation, humidity and temperature control plant physiology (e.g. stomatal conductance) and hence transpiration rates.

So far, transpiration has been evaluated by direct and indirect methods, which unfortunately bear shortcomings. Direct estimations of transpiration have been attempted by using evaporation tanks with cultivated hydrophytes. These try to reflect the nature of processes taking place under different environmental conditions. Indirect methods such as energy budget (Burba *et al.*, 1999) and mass transfer (Anderson & Idso, 1987; Eisenlohr, 1966; Idso & Anderson, 1988), which estimate transpiration on the basis of the relationship between the vegetated areas and open water areas, require a costly monitoring of difficult-to-measure variables. Both methods have occasionally brought about contradictory results. This is due to methodological errors associated on the one hand with different heat advections between vegetated areas and tanks (Pribán & Ondok, 1985), and on the other to the exclusion of physiological aspects of the plants in function of the climatic conditions.

In this paper a method is presented that simplifies the estimation of water loss by transpiration considering the physiological response of macrophytes to climatic variability. This method quantifies water loss by transpiration in a wetland by means of direct measurements in emergent macrophyte stands and a simple monitoring of the main climatic variables which stimulate transpiration, thereby reducing to a minimum the introduction and processing of errors. On the basis of established regression equations with high correlation coefficient, the transpiration can be modelled for different years. Thus, the proposed method may be suitable for the hydrological management of wetlands.

#### STUDY SITE

The study was carried out in Las Tablas de Daimiel National Park (TDNP), a semiarid floodplain wetland situated in central Spain (Fig. 1). Since the 1970s the wetland has suffered a dramatic reduction of hydric resources, basically as a result of both aquifer overdrawing for escalating agricultural demands and a change of climate towards drier years. The maximum flooding area is 16.7 km², but in the period 1988–1998 the average was 6.8 km², with ample inter- and intra-annual fluctuations. The water balance in TDNP is highly variable between years (Fig. 2). The main water loss is due to evapotranspiration, except in humid years when the hydric excess is lost via runoff and infiltration (see ranges in Fig. 2). Reed (*Phragmites australis* (Cav.) Trin. Ex Steud.), cut-sedge (*Cladium mariscus* (L.) Pohl) and cattail (*Typha domingensis* Pers.) are the main emergent macrophytes. Vegetation changes induced by hydrological variations have occurred since the 1940s, which have generated a drastic increase in reed cover with a concurrent decline in cut-sedge extension (Alvarez-Cobelas *et al.*, 2001).

#### METHODS AND PROCEDURES

Measures of transpiration rates were conducted using a portable steady state porometer (LICOR model LI-1600). The measurements were carried out within the three

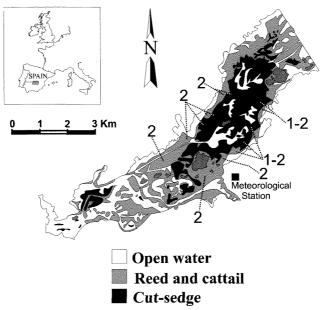
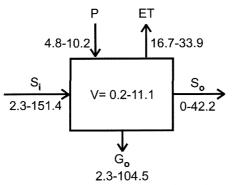


Fig. 1 Location of the study site showing vegetation cover in 1997. Cattail is included within reed because it formed small patches within reed and its total cover (2–5 Ha) was relatively insignificant (1: transpiration sampling stations; 2: sampling sites of leaf density.)



**Fig. 2** Annual water balance (in hm<sup>3</sup> year<sup>-1</sup>) in Las Tablas de Daimiel National Park from the period 1992–1998. (*P*: precipitation, *ET*: evapotranspiration,  $S_i$ : surface inflow,  $S_o$ : surface outflow,  $G_o$ : groundwater outflow.)

dominant emergent macrophytes in TDNP: reed, cut-sedge and cattail. Sampling zones in the wetland were selected in which the plants comprised monospecific stands with significant biomass. Sampling was carried out and measurements were taken in the sites as shown in Fig. 1. The porometer LI-1600 consists of a cuvette with a broadleaf aperture (2 cm²) which permits precise measurements of water loss by transpiration (in µg cm² s¹), as well as stomatal resistance and conductance (s cm²). Measurements were carried out by attaching the cuvette to the leaf surfaces. It simultaneously registers humidity conditions (%) and temperature (°C) in the cuvette during measurements.

Details about the theory of the operation of the apparatus can be found in LICOR Inc. (1982) and Idso *et al.* (1982). The porometer also measures the photosynthetic active radiation (PAR) with a quantum sensor LI-190S-1. Transpiration rates were converted to  $m^3 m^{-2} s^{-1}$  applying the density of evaporated water (1000 kg  $m^{-3}$ ).

Sampling was conducted on 5 and 17 August (summer aspects of transpiration) and 3 and 25 October (autumn aspects) at hourly intervals from sunrise to sunset in 1997 and 1998. Additional sampling was carried out at 30-day intervals from May to October of 1997 and 1998, the period of vegetation growth, at the time of maximum solar radiation (13:00–15:00 h). To avoid bias of the analysis by stomatic variability, five simultaneous measurements were taken from leaves of each macrophyte with different orientation and inclination within the plant stand. In August of 1997 and 1998, coinciding with the period of maximum vegetation development in the wetland, foliar surface area per square metre of each plant species was assessed in randomly chosen areas of the wetland (Fig. 1). Emergent macrophyte cover for the years 1992–1998 was estimated planimetrically from maps derived from aerial photographs (Cirujano, unpublished).

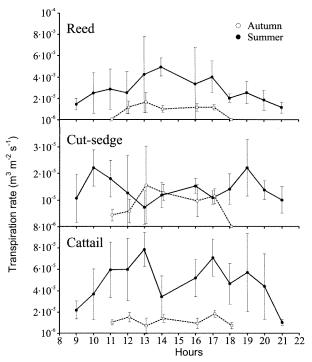
Climatic data were obtained from the automatic field station situated in the centre of TDNP (Fig. 1). Data of global radiation, temperature and humidity were obtained at 10-min intervals. Global solar radiation was transformed to PAR ( $PAR = 0.47 \times \text{global}$  radiation). Open water evaporation was estimated using a Class A pan situated in the automatic station.

A discontinuous multiple regression model was used to determine the relationship between climatic variables and transpiration rate. Because the dependent variable (transpiration rate) changed in response to the range of the independent variables (climatic variables), piecewise regressions with breakpoint were calculated to predict the range-dependent strength of the statistical relationship. The breakpoint reflected the value at which the behaviour of dependent variable changed as a function of the ranges of climatic variables, thereby establishing a regression with two equations. Statistical analyses were performed using STATISTICA 5.1 software (Statsoft Inc., 1995).

#### RESULTS AND DISCUSSION

#### Method calibration and validation

Daily cycles of transpiration rates for each emergent macrophyte species in summer (August) and autumn (October) in 1997 and 1998 are shown in Fig. 3. In summer, reed shows a curve with a maximum transpiration around midday. In contrast, cut-sedge demonstrated maximum values in the morning and evening hours with a midday depression. In the cattail stands the transpiration rates were lowest during hours of highest radiation and temperature. This phenomenon, which can be frequently observed in plants, is a physiological response associated with the regulation of stomatal conductance during periods of maximum thermal stress (Collatz *et al.*, 1991). In autumn, total daily transpiration was significantly reduced, owing basically to the reduction of the light period and lower solar incidence. Cut-sedge presented a transpiration curve which exhibited maxima during midday (Fig. 3) with values coinciding with those registered in summer. Reed and cattail showed lower transpiration rates in autumn and, furthermore, showed a curve with a central plateau, indicating that the

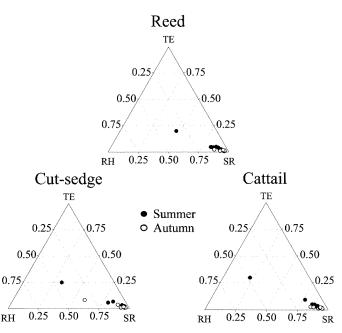


**Fig. 3** Daily course of transpiration rates for summer (hourly data of 5 and 17 August in 1997 and 1998) and autumn (hourly data of 3 and 25 October in 1997 and 1998). All data from transpiration sampling station 1 (see Fig. 1).

transpiration rates remained practically constant during the day (Fig. 3). Comparing the species, the transpiration rates were higher in cattail (average  $\pm$  standard deviation (SD) =  $4.7 \times 10^{-5} \pm 1.9 \times 10^{-5}$  (summer) and  $1.2 \times 10^{-5} \pm 0.4 \times 10^{-5}$  m<sup>3</sup> m<sup>-2</sup> s<sup>-1</sup> (autumn)), followed by reed ( $2.8 \times 10^{-5} \pm 1.2 \times 10^{-5}$  (summer) and  $0.8 \times 10^{-5} \pm 0.6 \times 10^{-5}$  m<sup>3</sup> m<sup>-2</sup> s<sup>-1</sup> (autumn)) and cut-sedge ( $1.4 \times 10^{-5} \pm 0.5 \times 10^{-5}$  (summer) and  $0.8 \times 10^{-5} \pm 0.5 \times 10^{-5}$  m<sup>3</sup> m<sup>-2</sup> s<sup>-1</sup> (autumn)).

In most cases, solar radiation explained more than 75% of the variance of transpiration, while relative humidity and temperature only explained residues (Fig. 4). These results concur with other studies from different environments (Brouwer, 1955; Decker & Wetzel, 1957; Lee, 1967; Lhomme *et al.*, 1998; Snyder & Boyd, 1987; Tuschl, 1970). In contrast to these authors, but in accordance with Price (1994) and Van der Weert & Kamerling (1974) among others, the authors believe that it is less convenient to construct models on the basis of a single variable considered most important in the transpiration process, given that the conjunction of more variables exerts a synergistic control over the process.

The relationship between the employed variables and transpiration did not demonstrate a simple linear relationship, but a more complex response, which complicated modelling of plant response. Besides the differences between summer and autumn transpiration rates (Fig. 3), the macrophytes demonstrated different responses as a function of the ranges of climatic variables. This indicates that transpiration modelling does not always follow the same standards. Accordingly, transpiration rises



**Fig. 4** Ternary graphs explaining variance on transpiration rate (full and empty circles) for each climatic variable (see Table 1 for abbreviations) for each macrophyte and season.

sharply from a specific limit marked by the independent variables (climatic data). To simplify the method and to localise the change of the plant behaviour, a series of equations was sought which model transpiration on the basis of all data obtained in the measurements of the daily cycles (hourly data).

Piecewise regressions with breakpoint, including the three climatic variables in the model, generated a series of equations with elevated statistical significance and high

**Table 1** Piecewise regression with breakpoint to predict transpiration,  $T (m^3 m^{-2} s^{-1})$ .

Macrophyte	Season	Equation	Breakpoint	$R^2$
Reed	Summer	$T = 2.4 \times 10^{-5} - 7.8 \times 10^{-5}RH + 1.2 \times 10^{-8}SR - 2.4 \times 10^{-7}TE$ $T = 1.5 \times 10^{-6} + 7.8 \times 10^{-6}RH + 1.5 \times 10^{-8}SR - 1.1 \times 10^{-6}TE$	2.8 10 <sup>-5</sup>	0.93
	Autumn	$T = 0.016 + 0.353RH - 0.012SR - 1.1 \times 10^{-6}TE$ $T = 5.9 \times 10^{-5} - 4.9 \times 10^{-7}RH + 1.2 \times 10^{-8}SR - 2.2 \times 10^{-6}TE$	8.8 10 <sup>-6</sup>	0.96
Cut-sedge	Summer	$T = -3.7 \times 10^{-5} + 3.4 \times 10^{-7} RH - 5.9 \times 10^{-9} SR + 1.2 \times 10^{-6} TE$ $T = 7.4 \times 10^{-5} - 4.7 \times 10^{-7} RH - 5.1 \times 10^{-9} SR - 8.9 \times 10^{-7} TE$	1.4 10 <sup>-5</sup>	0.92
	Autumn	$T = 0.101 - 0.057RH - 1.9 \times 10^{-5}SR + 0.217TE$ $T = 6.0 \times 10^{-5} - 5.2 \times 10^{-7}RH + 7.2 \times 10^{-9}SR - 1.8 \times 10^{-6}TE$	9.4 10 <sup>-6</sup>	0.99
Cattail	Summer	$T = -4.6 \times 10^{-5} + 7.3 \times 10^{-7} RH - 7.2 \times 10^{-9} SR - 1.5 \times 10^{-6} TE$ $T = 4.2 \times 10^{-5} - 1.1 \times 10^{-6} RH + 2.3 \times 10^{-8} SR + 2.1 \times 10^{-6} TE$	5.1 10 <sup>-5</sup>	0.77
	Autumn	$T = 2.7 \times 10^{-5} - 2.6 \times 10^{-7} RH - 7.1 \times 10^{-9} SR + 2.4 \times 10^{-7} TE$ T = 0.388 + 19.715 RH - 1.587 SR + 3.981 TE	2.0 10 <sup>-5</sup>	0.98

RH = relative humidity (%); SR = solar radiation (W m<sup>-2</sup>); TE = air temperature (°C). n = number of observations used in the analyses; summer: n = 96, autumn: n = 56. All statistically significant at p < 0.01.

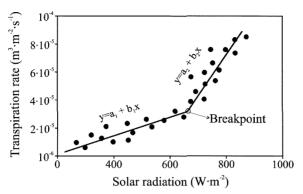


Fig. 5 Diagrammatic presentation of a piecewise linear regression with breakpoint.

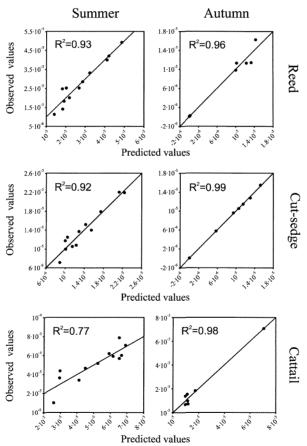


Fig. 6 Observed vs predicted values of transpiration rates (m<sup>3</sup> m<sup>-2</sup> s<sup>-1</sup>) from piecewise regression equations.

correlation coefficients  $R^2$  (Table 1, Fig. 5). Regression with two linear equations was obtained for each range of the independent variables, which are separated by a value of

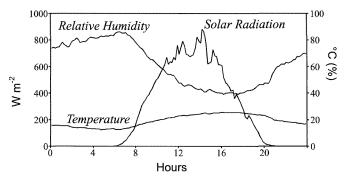


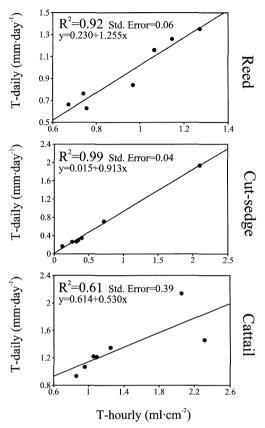
Fig. 7 Daily course of climatic data. Values are averages of the May-October data from 1997 and 1998.

the dependent variable, as indicated by the breakpoint (Fig. 5). Figure 5 represents a bivariate relationship, however, the method employs a multivariate relation, where the equations being defined by planes instead of lines. The overall model has eight parameters; however, a data transformation or a non-linear regression transformation was not considered, because a reduction of the number of parameters complicates computation and reduces the statistical significance. The highest significance was exhibited by cut-sedge in autumn, while cattail showed the lowest  $R^2$  in summer. Breakpoints of transpiration rates obtained in the equations were variable in each macrophyte. Thus, cut-sedge exhibited the lowest values, whereas cattail showed the highest (Table 1). Nevertheless, values of transpiration inferior to the breakpoint were almost always registered in modelling, indicating that transpiration behaved as in the first equations. The correlation between predicted and observed values of transpiration rate with different climatic data was strong in all macrophyte species (Fig. 6), verifying the validity of the equations.

The method presented a higher complexity when hourly data of the climatic variables were processed for obtaining daily global cycles of transpiration. Aiming at simplification through reduction of the number of data entering the model, the results obtained from hourly data were compared with average daily values. Figure 7 shows the daily variation of averages of the involved climatic variables for the period of vegetation growth (May–October). It can be observed that solar radiation and humidity exhibit a marked difference between day and night. The comparison between daily global transpiration calculated from daily averages and hourly values of climatic variables indicates a strong correlation, particularly in cut-sedge (Fig. 8). Hence it is possible to estimate transpiration using mean daily values of solar radiation, humidity and temperature, simplifying the method and reducing significantly the calculations.

#### Method application

Mean daily climatic variables registered in TDNP for the years 1992–1998 were applied in the equations (Table 2). The total rates of monthly transpiration were obtained for each hydrophyte for each year (Fig. 9(a)). However, the data only show the capacity of transpiration of each plant. To estimate water loss per unit of wetland surface by transpiration, there is need to include data of foliar density for each

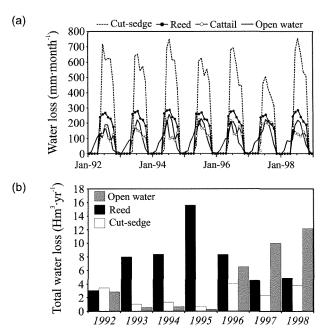


**Fig. 8** Relationships between transpiration rates (mm day<sup>-1</sup>) computed from hourly (T-hourly) and average daily (T-daily) climatic data.

**Table 2** Daily means  $\pm$  standard deviations of climatic values during the vegetation growth period (May–October) from 1992 to 1998. Rainfall and evaporation are total values.

	Wind speed (m s <sup>-1</sup> )	Air temperature (°C)	Relative humidity (%)	Global radiation (MJ m <sup>-2</sup> )	Rainfall (mm)	Evaporation (mm)
1992	$1.3 \pm 0.3$	$20.9 \pm 7.0$	48 ± 6	$21.8 \pm 5.3$	40.7	151.5
1993	$1.2 \pm 0.5$	$21.3 \pm 7.5$	$49 \pm 7$	$26.5 \pm 4.3$	26.5	159.2
1994	$1.5 \pm 0.3$	$22.7 \pm 7.3$	$41 \pm 9$	$27.7 \pm 4.2$	13.1	188.4
1995	$1.4 \pm 0.3$	$23.2 \pm 6.9$	$48 \pm 4$	$26.4 \pm 3.2$	10.5	185.5
1996	$2.1 \pm 1.0$	$19.7 \pm 6.6$	$55 \pm 14$	$25.2 \pm 4.2$	32.9	157.5
1997	$1.8 \pm 0.7$	$20.7 \pm 6.3$	$59 \pm 7$	$24.4 \pm 3.0$	27.2	175.7
1998	$1.8 \pm 0.4$	$21.7 \pm 7.5$	$56 \pm 14$	$24.1 \pm 5.1$	38.2	171.5

macrophyte species. The transpiration from stems was not considered in the model because it differs insignificantly from leaf transpiration. The results obtained in the 1997 and 1998 samplings are shown in Table 3. The highest average leaf surface was that of cattail, while the highest total leaf surface per square metre appeared in cut-sedge. Moreover, an increase in leaf number and total leaf surface per square metre was observed in 1998 compared to that of 1997, except in cattail (Table 3).



**Fig. 9** Time course of evapotranspiration in TDNP during 1992–1998: (a) monitoring of open water and plant specific water loss, and (b) annual total water loss by transpiration and evaporation. Data on transpiration from 1992–1996 are modelled while data from 1997–1998 are measured.

Transpiration rates in vegetation stands demonstrated an important variability between plant species (Table 4). Cut-sedge presented the highest mean rates, while cattail showed the lowest. The total transpiration rate registered in each stand depended on foliar density typical for each macrophyte (Table 4).

Finally, for establishing global water loss in the wetland, macrophyte cover data are required. Macrophyte cover data (Table 5) were obtained planimetrically from aerial photographs. In TDNP, reed was the dominant species throughout all years, even though the interannual fluctuations can be related to the prevailing hydrological conditions (Sánchez-Carrillo *et al.*, in press). In this sense an increase in total coverage in the period between 1992–1995 was observed, which correlated with a dry period and a posterior reduction owing to a wetter climate (Table 5; Sánchez-Carrillo & Alvarez-Cobelas, in press). Cattail cover could not be determined exactly on the maps because the plants formed isolated spots within the reed beds. Nevertheless, estimations based on field observations lead to suggest a total coverage of 0.02–0.05 km² of cattail in the wetland, indicating that the global water loss is insignificant compared with the other macrophyte species.

Temperature, leaf density in vegetation stands and macrophyte cover data, allow estimation of the global water loss by transpiration in a wetland. In the case described here, the loss by transpiration was estimated for the period 1992–1998 in TDNP (Fig. 9(b)). Because leaf density data were not available for the period 1992–1996, the average values for the period 1997–1998 were used to extrapolate for the previous years. It is assumed that the interannual variation of leaf density was not high enough to generate a significant error in the global transpiration rates. If an error were

Table 3 Macrophyte m	orphometric	features	and 1	leaf	surface	per	square	metre	in	vegetation	stands	at
TDNP.							-			_		

	Leaf number per area (no. m <sup>-2</sup> )		Leaf surface (cm <sup>2</sup> )		Total leaf surface per area (m² m-²)		
	1997	1998	1997	1998	1997	1998	
Reed	$3806 \pm 1776$	$6348 \pm 2122$	21.7 ± 9.8	14.4 ± 2.7	8.28 ± 5.06	9.13 ± 5.35	
Cut-sedge	$1009 \pm 80$	$1372 \pm 103$	$104.9 \pm 26.5$	$110.3 \pm 21.6$	$10.59 \pm 2.71$	$15.13 \pm 1.95$	
Cattail	$499 \pm 167$	$208 \pm 56$	$105.5 \pm 47.1$	$176.8 \pm 55.7$	$5.26 \pm 1.96$	$3.68 \pm 0.89$	

Data are average values ±SD.

Table 4 Average ±SD of transpiration rates (mm day<sup>-1</sup>) in vegetation stands in TDNP from May to October.

	Reed	Cut-sedge	Cattail	
1997	7.1 ± 1.1	11.7 ± 5.0	$6.4 \pm 0.2$	
1998	$7.8 \pm 1.2$	$17.8 \pm 7.1$	$4.3 \pm 0.7$	

Table 5 Yearly emergent macrophyte cover and open water area (km<sup>2</sup>) in TDNP.

	1992	1993	1994	1995	1996	1997	1998
Reed	2.20	5.55	5.74	11.10	5.88	3.50	3.40
Cut-sedge	1.10	0.35	0.44	0.25	1.40	1.10	1.15
Total plant	3.83	6.37	6.65	11.83	7.77	5.10	5.82
Open water	0.50	0.36	0.22	0.18	1.65	7.44	7.74

Cattail cover estimates were in the range 0.02–0.05 km² during the same period, based on field observations, but are omitted from the table because no exact planimetric calculations could be done (see text).

introduced by employing wet-year data for a dry period, it may be compensated for by the increase of transpiration rate as a result of the altered environmental variables associated with a drier climate (i.e. higher solar radiation and air temperature, lower relative humidity).

It can be observed that an important variation exists in the transpiration owing to annual macrophyte cover in TDNP. In absolute terms, reed generated the highest water loss  $(15.6 \times 10^6 \times \text{m}^3 \text{ year}^{-1} \text{ in 1995})$ , even though in relative terms (mm day<sup>-1</sup>) it was not the species with the highest transpiration rates (Table 4). The transpiration of cutsedge and cattail seems to depend most on the climatic conditions and also exhibits the highest inter- and intra-annual variability (Fig. 9(a)). In contrast, reed showed the most constant transpiration rates during the growth period and low interannual variability (Fig. 9(a)). For the period 1992–1998, the results indicate an overall water loss by transpiration of 6.5–16.3 hm<sup>3</sup> year<sup>-1</sup> (average = 9.9 hm<sup>3</sup> year<sup>-1</sup>; Fig. 9(b)). In contrast, global water loss by evaporation from the open water was significantly lower in the same period  $(0.3-12.1 \text{ hm}^3 \text{ year}^{-1}$ ; average = 4.7 hm<sup>3</sup> year<sup>-1</sup>; Fig. 9(b)). Obviously, the transpiration was lower than evaporation in humid periods (1997 and 1998), while in dry periods (1992–1996) were the opposite (Fig. 9(b)).

The results of this study referring to transpiration are similar to those obtained by Burba *et al.* (1999) and Tuschl (1970) (Table 6). The discrepancy between these results and those reported elsewhere may be attributed to the different climatic regions (e.g. temperate regions with lower light incidence) in which they have been carried out rather than to the methodology employed. The results of this study are similar to those

<b>Table 6</b> Comparison of different methods for estimating transpiration ( <i>T</i> ) in hydrophytes. Data of TDNF
averaged for 1997–1998.

Plants	T (mm year <sup>-1</sup> )	$E_0/E$	Method and site	Reference
Reed Cut-sedge Cattail	1369 2708 983	1.5 2.3 0.8	Porometer TDNP (Central Spain)	This study
Reed Cattail	365 220	0.9–1.3	Phytometer Poland	Bernatowicz et al. (1976)
Cattail and bulrush	234	0.4–1.2	Mass transfer North Dakota (USA)	Eisenlohr (1966)
Reed Bulrush	1606 1194	0.9 0.8	Energy budget Central Nebraska (USA)	Burba et al. (1999)
Bulrush	1497	1.2	Tanks California (USA)	Blaney & Ewing (1946)
Reed	940–1100		Gravimetric Austria	Tuschl (1970)
Cattail		0.9–1.4	Tanks Arizona (USA)	Idso & Anderson (1988)
Reed		1.3	Tanks-Energy budget Czech Republic	Šmíd (1975)
Cattail		1.0	Energy budget Ontario (Canada)	Price (1994)
Cattail		0.7–1.3	Tanks Mexico	Glenn et al. (1995)

 $E_0$ : transpiration, E: open water evaporation.

obtained from tanks and energy budget methods in comparable climatic regions. Nevertheless, since studies in arid regions are scanty at the present moment, the data so far available need to be regarded with certain caution until further studies enable further comparisons. Similarly, the transpiration data of cut-sedge in this study are unique, so they cannot be compared with data from other ecosystems (Table 6). It may seem sound to consider the differences of foliar density between ecosystems for the differences between the observed values (Idso & Anderson, 1988). However, published papers did not present this kind of information, other than as shown above, foliar density conditions the value of total global transpiration. In regard to the similarity of the data, the authors trust that the method described herein provides results with a lower error considering the *in situ* origin of the data. By not using tanks, one can reduce to a minimum the possibility of introducing an error by the "oasis effects" due to horizontal differences in wetness within a region and by heat advection, or by the "clothes-line effect" due to differences in stand geometry in the tank and in the adjacent areas (Pribán & Ondok, 1985). The results obtained in this study are similar to those calculated with the mass transfer and energy budget methods. This study provides the advantage that the data proceed from direct measures. Moreover, the number of variables to be monitored can be reduced to a minimum, thus making modelling easier. Furthermore, it provides the possibility to monitor the plant response to climatic conditions, which succeeds in reducing the complexity of the model.

The influence of transpiration in the water balance seems to be important (Table 7). For a further comparison with humid ecosystems, data from 1997 and 1998 (humid period) were used in Table 7. For these wet years, the open water area was

Table 7 Seasonal variation in the ratio transpi	iration /evaporation for the three different hydrophyte
species of Las Tablas de Daimiel National Park.	Data are averages of 1997 and 1998.

	Reed	Cut-sedge	Cattail	
January	≈0	≈0	≈0	
February	≈0	≈0	≈0	
March	≈0	≈0	≈0	
April	≈0	≈0	≈0	
May	2.1	0.9	1.5	
June	1.5	3.2	0.9	
July	1.2	2.8	0.7	
August	1.1	2.6	0.7	
September	1.4	3.2	1.2	
October	2.4	5.7	2.1	
November	≈0	≈0	≈0	
December	≈0	≈0	≈0	

notably higher than that of total plant area (Table 5). It can be seen (Fig. 9) that the ratio of  $E_0$  (transpiration) to E (evaporation) in TDNP during dry periods (1992–1996) was higher than during wet periods, showing the dominance of transpiration on the evaporation process. Most studies indicate ratios of  $E_0$  / E in cattail of 0.4–1.4 (Table 6). The TDNP ratio of 0.8 (Table 6) is within this range and is similar to those reported by Eisenlohr (1966) and Glenn et al. (1995). However, the reed data for TDNP indicate a major water loss from the vegetated zones containing this macrophyte compared to the open water (ratio: 1.5). The results are thus in agreement with the majority of the consulted papers (Table 6), being similar to those registered by Bernatowicz et al. (1976) and Śmíd (1975), though slightly higher (Table 6). As stated above, the ratio obtained for cut-sedge (2.3), which was the highest could not be compared with other references. The results of this study contradict Linacre's theory (Linacre, 1976), supported by Price (1994), which suggests a reduction of water loss by evapotranspiration when emergent macrophyte cover increases. Concurring with Idso & Anderson (1988), the water balance is believed to be strongly influenced by the vegetation cover which, in turn, shapes the variations of foliar density per unit area.

#### CONCLUSIONS

The method presented in this paper is thought to be the first to employ field data obtained from direct measurements within macrophyte stands. Besides being simple and cost-effective, it offers the possibility to extrapolate the obtained equations to periods for which daily climatic data are available. Foliar density and estimates about annual macrophyte cover are the only necessary additional data required. Nonetheless, it should be borne in mind that the method serves for estimates of overall transpiration of macrophyte species present in a wetland. The global character of the obtained results masks the introduced error by this methodology. Finally, the authors believe that this method can be very useful for the hydrological management of a wetland or other aquatic ecosystem in which emergent macrophytes comprise a significant proportion of the biological community. It may serve as a tool for the handling and control of emergent vegetation. This study shows the importance of emergent macro-

phytes in the hydrological dynamics of a wetland, generating occasional water losses greater than those of non-vegetated, open water sites.

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