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Article

Quantification of the Evaporation Rates from Six Types of Wetland Cover in Palo Verde National Park, Costa Rica

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Abstract: The hydrology of tropical seasonal wetlands is affected by changes in the land cover. Changes from open water towards a vegetated cover imply an increase in the total evaporation flux, which includes the evaporation from open water bodies and the transpiration from vegetated surfaces. This study quantified the total evaporation flux of six covers of the Palo Verde wetland during dry season. The selected wetland covers were dominated by *Neptunia natans* (L.f.) Druce, *Thalia geniculata* L., *Typha dominguensis* Pers., *Eichhornia crassipes* (Mart.) Solms, a mixture of these species, and open water conditions. The plants were collected from the wetland and placed in lysimeters (59.1 L) built from plastic containers. The lysimeters were located in an open area near the meteorological station of the Organization for Tropical Studies (OTS). The evaporated water volume and meteorological data were collected between December 2012–January 2013. A completely randomized design was applied to determine the total evaporation (E), reference evaporation (E_{ref} , Penman-Monteith method) and crop coefficient (K_c) for all the covers. *T. geniculata* (E : 17.0 mm d⁻¹, K_c : 3.43) and open water (E : 8.2 mm d⁻¹, K_c : 1.65) showed the highest and lowest values respectively, for daily evaporation and crop coefficient. Results from the ANOVA indicate that *E. crassipes* and *N. natans* were statistically different ($p=0.05$) from *T. dominguensis* and the species mixture, while the water and *T. geniculata* showed significant differences with regard to other plant covers. These results indicate that the presence of emergent macrophytes as *T. geniculata* and *T. dominguensis* will increase the evaporation flux during dry season more than the floating macrophytes or open water surfaces.

Keywords: lysimeters; macrophytes; transpiration; marshland; Guanacaste; Tempisque river; Costa Rica

1. Introduction

Seasonal wetlands as swamps, marshes or floodplains are characterized by their dynamism in terms of water availability [1,2]. These ecosystems shelter huge populations of birds, mammals, reptiles, amphibious, fishes, and invertebrates [3]. The seasonal wetlands in Central America are important shelters for migratory bird species [4] and also provide important environmental services as water quality regulators [5]. The Ramsar convention was signed in the city of Ramsar, Iran in 1971. It is an international treaty aiming for the conservation and sustainable use of wetlands of international importance [2]. Caño Negro National Park and Palo Verde National Park, both located in Costa Rica

are among the most important Ramsar sites in Central America [6]. Palo Verde National Park has an extension of 18 418 ha covering an area of marshes and dry forest. This national park has a long dry season, conditioning the aquatic vegetation and bird presence [7–11]. Aquatic plants are also known as macrophytes, they grow fully or partially submerge in water [12]. Its traditional classification is based on the life form as emergent plants, floating-leaved plants, submerged plants, and free-floating plants [13]. Palo Verde National Park have 100 species of macrophytes distributed in all the classes, representing the 31% of the total macrophytes species reported for Costa Rican wetlands [14,15]. Macrophytes species do not only provide shelter for animal species, but also can remove pollutants from soil and water. Additionally, submerged plants as *Najas guadalupensis* (Spreng.) Magnus and *Najas arguta* Kunth work as oxygenators or participate in carbon storage. Moreover, the macrophytes are the primary producers of the wetlands together with the macro-algae and phytoplankton [16].

Historically, the wetland from Palo Verde National Park was used for livestock grazing. This activity maintained under control the wetland cover dominated by Cattail plants (*Typha domingensis* Pers.), leaving an extensive open water surface on the wetland. The abandonment of this activity with the creation of the national park in 1970s along with the infrastructure and extensive agriculture development in the surroundings, triggered the deterioration of the ecosystem quality [11,17–20]. Moreover, this affected the presence of open water surfaces used by the migratory bird species, as well as the hydrological and nutrient cycles of the wetland. Consequently, the institutions involved with the management of this national park in Costa Rica developed a wetland restoration program. This program includes activities as the restoration of water fluxes and Cattail wetland cover control through livestock grazing and mechanical management locally known as “Fanguero” [21,22]. These activities have been carried out with the aim to remove and destroy the emergent vegetation, and to restore the open water surfaces on the wetland [23]. The partial elimination of Cattail cover led to an increase in macrophytes species in the open water surfaces. Thus allowing the reappearance of plant species such as *Thalia geniculata* L., *Neptunia natans* (L.f.) Druce, *Nymphaea pulchella* DC., *Eichhornia crassipes* (Mart.) Solms, and *Salvinia minima* Baker [24]. Therefore, it is necessary to understand the effects of the new wetland cover conditions on the water fluxes.

The seasonality in wetland ecosystems drives the variation in aquatic diversity depending on water availability [25]. Palo Verde wetland seasonality is driven by the orographic influence of Guanacaste and Tilarán mountain ranges, which affect the air humidity conditions during the pass of the intertropical convergence zone (ITCZ) [26]. This climatic variation allows the presence of a rainy and a dry season. The rainy season provides the main water input to the wetland via precipitation and occasional flooding from the Tempisque river. On the contrary, the dry season consists mainly of evaporation from the wetland covers and open water bodies [10,24]. The timing of open water surfaces in seasonal wetlands depend on the water inputs during the rainy season while evaporation plays an important role during the rainy-dry transition and dry season. The evaporation flux during these two periods will be influenced by the wetland cover change, since precipitation ceased and the dryer conditions prevail increasing the transpiration on the wetland [27].

Evaporation (E) from any ecosystem includes transpiration (E_t), open water evaporation (E_w), evaporation from intercepted water on plant surfaces (E_i), and evaporation from soil (E_s) [28,29]. In an aquatic ecosystem, the proportion of each evaporation component depends on the wetland cover characteristics. Important evaporation differences among open water and aquatic plant covers have been reported worldwide [30–33]. The evaporation from aquatic plant covers plays an important role on the wetland hydrology [34]. However, information on evaporation rates are limited for tropical plant species. From the 100 macrophytes reported in Palo Verde National Park [14,15], only *T. dominguensis* and *E. crassipes* [28,34–37] have published values of evaporation in other regions (e.g., Suriname, South Africa, United States). The effect of invasive plants as *T. dominguensis* and *E. crassipes* in wetlands is linked to the increment of evaporation and the subsequent reduction of the water surfaces [38–40].

Macrophytes information is available worldwide by their use in waste water treatment plants [41–43]. However, most of the tropical macrophytes lack the information about its evaporation rates.

The active management of Palo Verde National Park has generated changes on wetland surface cover. Hence, it is important to quantify the evaporation flux from the different macrophyte species to understand the effect of cover changes on the wetland hydrology. The estimation of evaporation rates in wetlands has been performed with eddy covariance systems and lysimeters [28,33,44]. The eddy covariance system allows to estimate the evaporation at ecosystem scale but its reliability depends on the homogeneity of the footprint [45]. Additionally, it is important to investigate the difference between individual wetland covers where the eddy covariance system is not suitable. Therefore, the lysimeter technique allows the estimation of evaporation rates of individual covers at a smaller scale [46]. This work determines the evaporation rates of six wetland covers from Palo Verde National Park during dry season by calculating the evaporation, the reference evaporation and the crop coefficient for each wetland cover.

2. Materials and Methods

2.1. Study Site

Palo Verde National Park (N: 10°20'35"–W: 85°20'26") is situated in the Guanacaste Province, in the North–West of Costa Rica [10]. It is located 20 km North from the Tempisque river mouth into the Gulf of Nicoya (Figure 1). Palo Verde National Park covers a seasonal marshland between the Tempisque river and limestone hills in the North of the wetland, as well as one of the last relicts of tropical dry forests in Costa Rica [47,48]. Climatic data recorded between 2000–2017 report a mean annual precipitation of 1380.5 mm year^{−1} (Figure 2). A precipitation surplus can be observed between May and November (wet season), with a short dry period in July. While the dry season of the national park is between December and April. The mean annual temperature is 27.5 °C and varies between 26.3 °C and 29.3 °C on a yearly basis. The potential evaporation is 1834.3 mm year^{−1}. Winds are present all over the year, but they get stronger (>3 m s^{−1}) during the dry season coming from the North–East.

The wetland soil is classified as Vertisol (USDA Soil Taxonomy) [49]. They have a high content of expansive clay with a strong acidity [50] as a consequence of the seasonal flooded conditions [19]. The soil is completely saturated at the beginning of the dry season (December and January), developing cracks at the end of the dry season while the lagoon gets dry [7]. Two geomorphological units describe the area: the plain region with slopes between 0–5% and an inclination towards the Tempisque river; and the hills formed from limestone and the Nicoya complex with maximum elevations of 170 m.a.s.l. Both geomorphological formations lack of a developed drainage system [11]. The meandered drainage pattern of Tempisque river allows the alluvial plain formation, as well as the lagoons and marshlands that surround it [51]. This drainage pattern enhances the side bank erosion in the river margins, altering the water course creating sediment sequences in different sections of the fluvial system [52, 53]. The wetland vegetation is dominated by emergent plants such as *T. geniculata*, *Canna glauca* L. and *T. dominguensis*. With the presence of floating plants such as *Ceratopteris pteridoides* Brongniart, *Salvinia auriculata* Aubl.; and submerged species such as *N. guadalupensis*. Some herb species are also important such as *Paspalum repens* P.J. Bergius in the driest areas and *N. natans* in small ponds [15,24]. The presence of these species decrease gradually with the lagoon water level reduction, excepting for *T. dominguensis*.

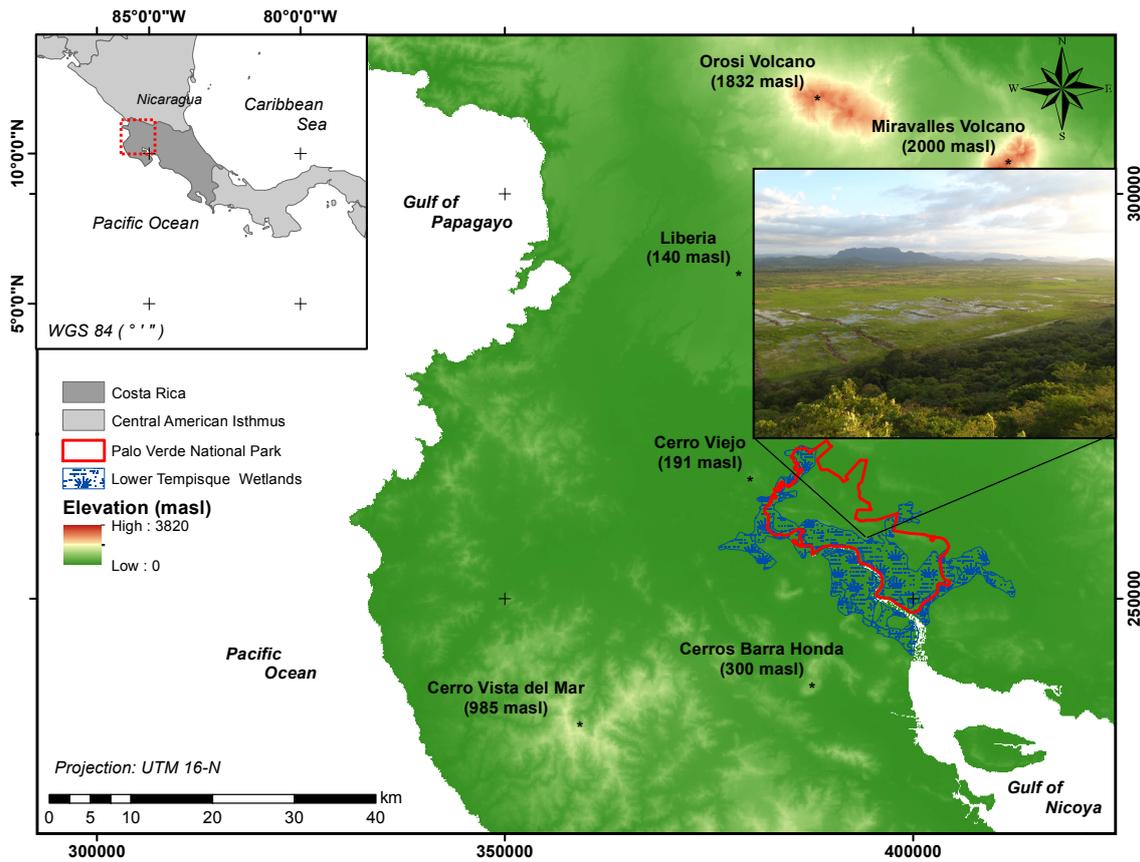


Figure 1. Geographical location of Palo Verde National Park in the Pacific North–West of Costa Rica. The photograph in the map shows the result of mechanical management activities within the lagoon with the consequently vegetation growth on the open water surfaces (GIS data source: Ortiz-Malavassi [49]).

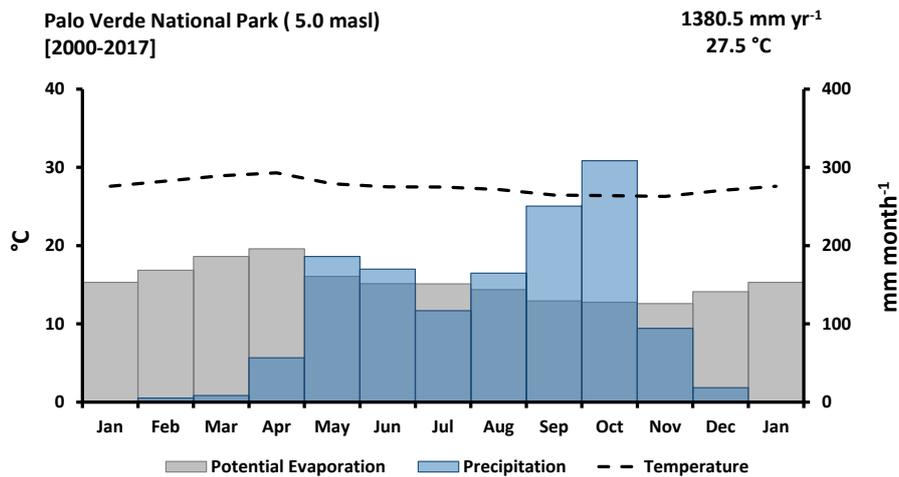


Figure 2. Climate diagram of Palo Verde National Park based on 18 years of measurements (2000–2017) of the meteorological station from the Organization for Tropical Studies in Palo Verde Research Station.

2.2. Experimental Design

Four plant species forming patches in the open water bodies of Palo Verde wetland were selected to evaluate the evaporation rates during the beginning of the dry season. *N. natans* is a floating plant of the Fabaceae family used as ornamental [54]. This plant is characterized by the presence of floating

stems covered by a spongy tissue allowing it to float [15] and by the presence of N_2 -fixing nodules in the roots [55,56]. This species does not have information about evaporation rates and/or its influence on the evaporation process of a wetland. *E. crassipes* is a rooted Pontederiaceae plant characterized by its floating life form [15]. This species is used for waste water treatment [57,58] or as biofuel [59]. Information about its evaporation rates is available, but it is scattered in different climate conditions around the world [34,37,60–62]. *T. geniculata* is an erectus plant from the Marantaceae family. It grows in dense populations along the marsh edges attached to the ground [63]. There is no data published on the evaporation rates of this plant. The last plant selected in this study was *T. dominguensis*. It is an emergent plant [15] from the Typhaceae family. During the first growing stages in solitary, the roots allow the anchorage to the ground during flooding periods. Later on during its adulthood this species has a well-developed root system. This species has been widely studied worldwide and information about its evaporation is available [28,31,36,64–68].

The plant species selection was done based on a preliminary sampling, where *N. natans* was the most abundant species. Specimens of all species were collected from the wetland, placed in lysimeters filled with water and the required substratum. Six experimental units were established in the trial and each experimental unit included five replicates. Four experimental units represented the selected species, one with all the species together (Mixed) (one plant of *N. natans*, two plants of *T. geniculata*, one plant of *E. crassipes* and one plant of *T. dominguensis*), and the last one the open water body (Water) (Figure 3). Mature plants of *N. natans* (three plants per lysimeter), *T. geniculata* (five plants per lysimeter) and *E. crassipes* (three plants per lysimeter) were collected to use them in the lysimeters. However, young plants of *T. dominguensis* (four plants per lysimeter) were chosen accordingly with the growing stage of the specimens of this species available in the open water bodies from the managed sections of the wetland. These sections are characterized by a water level of 1 m depth at the beginning of the dry season. Lysimeter plant densities were determined through 35 samplings performed in different locations within the wetland. The plant sampling was based on a PVC frame representing the same area of the lysimeters (0.19 m^2).



Figure 3. Pictures of the selected wetland covers. (A): *Neptunia natans*; (B): *Thalia geniculata*; (C): *Eichhornia crassipes*; (D): species mix (Mixed); (E): *Typha dominguensis*; (F): Open Water.

Evaporation rates were quantified using the lysimeters due to their capability to be adapted to different plant species and substratum. Additionally, they allow the estimation of evaporation rates from complete plants [33,44,69]. Each lysimeter had a capacity of 59.1 L and were made with Sterilite® containers. The lysimeters were filled with a layer of non-disturbed soil from the lagoon floor (5 cm depth) and a layer of 25 cm depth filled with wetland water (Figure 4). The water level was kept at 1.4 cm below the container edge through a pipe placed in one side of the lysimeter. The water excess was drained towards an overflow reservoir next to the lysimeter. The lysimeters were randomly distributed in a 50 m² area next to the meteorological station of the Organization for Tropical Studies (OTS) within the Palo Verde National Park.

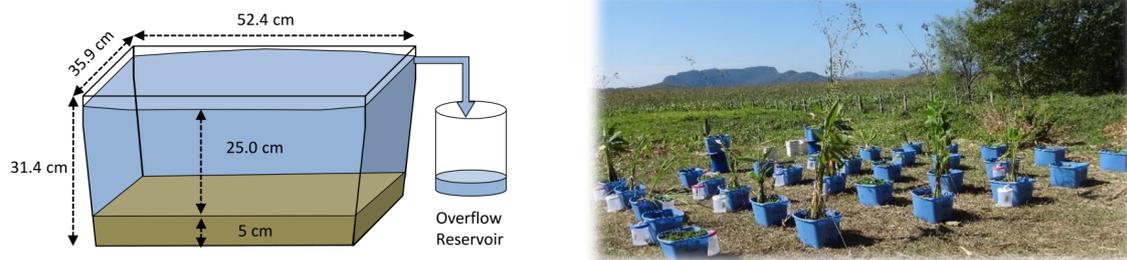


Figure 4. Lysimeter design used during the experiment (left image) and the distribution of lysimeters (right image) at the experimental site in Palo Verde National Park.

2.3. Measurement and Estimation of Evaporation Rates

The measurements were carried out during the beginning of the dry season, considering the importance of the evaporation flux as the main driver of the wetland hydrology during this season. The water availability and growing stage of the macrophytes during this period allowed to determine the crop coefficient of each of the wetland covers. Daily measurements were performed along 45 consecutive days between December 2012 and January 2013. Each lysimeter measurement was done on a daily basis before 07:00 a.m. The meteorological data was collected every second and summarized in 30 min time intervals by the meteorological station from the OTS (Detailed data showed in Figure A1). This data was used to calculate the reference evaporation (E_{ref}) with Penman-Monteith equation (Equation (1)) according to Allen et al. [70] (Equation (3) of their manuscript). In this equation, E_{ref} is the reference evaporation ($m s^{-1}$), R_n is the surface net radiation ($MJ m^{-2} d^{-1}$) and G is the soil heat flux ($MJ m^{-2} d^{-1}$). The term $(e_s - e_a)$ is the air vapor pressure deficit (VPD) in kPa, defined as the difference between the saturation vapor pressure (e_s) and the actual vapor pressure (e_a). ρ_a is the air density ($1.225 kg m^{-3}$), ρ_w is the water density ($1.0 kg m^{-3}$) and c_p is the specific heat of the air ($1.013 \times 10^{-3} MJ kg^{-1} \text{ } ^\circ C^{-1}$). Δ is the slope of the vapour-pressure relationship ($kPa \text{ } ^\circ C^{-1}$), λ is the latent heat of vaporization ($2.45 MJ kg^{-1}$) and γ is the psychrometric constant ($0.054 kPa \text{ } ^\circ C^{-1}$). r_s and r_a are the bulk surface resistance ($s m^{-1}$) and aerodynamic resistance ($s m^{-1}$), respectively. The r_s and r_a values were determined for a hypothetical reference crop with 0.12 m of height and $70 s m^{-1}$ of surface resistance.

$$E_{ref} = \frac{1}{\lambda \rho_w} \frac{\Delta(R_n - G) + \rho_a c_p \frac{(e_s - e_a)}{r_a}}{\Delta + \gamma(1 + \frac{r_s}{r_a})} \quad (1)$$

Daily evaporation rates (E) in $mm d^{-1}$ were calculated with the water balance equation (Equation (2)). In this equation, P is the daily precipitation ($mm d^{-1}$) recorded by the meteorological station and Q is the water excess ($mm d^{-1}$) measured as the overflow (mL) from the lysimeter. The term $\frac{dS}{dt}$ is the change in the lysimeter water storage ($mm d^{-1}$), which corresponds to the water added manually every morning (mL) to replenish the evaporated water. Water was added in case the precipitation was not enough to fill the lysimeter or if the water level was lower than the overflow

drainage outlet in the lysimeter. All the volumetric measurements were performed with a measuring cylinder of 1.0 L with a scale of 1 mL. The collected values in mL d^{-1} were translated into mm d^{-1} according with the lysimeters area and water density (ρ_w). Crop coefficient (K_c) was calculated from the relationship between E and E_{ref} as it was proposed by Allen et al. [70] in the Equation (3):

$$E = P - Q - \left(\frac{dS}{dt} \right) \quad (2)$$

$$K_c = \frac{E}{E_{\text{ref}}} \quad (3)$$

The accumulated evaporation (E_{ac}) for each lysimeter was estimated using Equation (4). In this equation, E_i is the evaporation rate of each lysimeter, i represents each day of measurement and n corresponds to the total number of consecutive measurements performed.

$$E_{\text{ac}} = \sum_{i=1}^n E_i \quad (4)$$

2.4. Data Analysis

The first five days of measurements were not used during the analysis because they were considered as the minimum time required for the plants to adapt to the lysimeters. The analysis of variance (ANOVA) was performed to determine the differences among the evaporation rates of the wetland covers. This was done based on a completely randomized experimental design by evaluating independently the reference evaporation (E_{ref}), evaporation (E) and crop coefficient (K_c). When significant differences were identified ($p = 0.05$) a Fisher Least Significant Difference (LSD) test was applied to identify the homogeneous groups. The assumptions of normality and homocedasticity of the residuals were tested with the Shapiro-Wilk normality test and Levene's test, respectively. The data satisfied the assumptions of normality and homocedasticity during the analyses. A Pearson correlation analysis was also applied among the evaporation rates of each cover and the main meteorological variables measured by the OTS station. This analysis was performed with three different significance levels: $p = 0.05$, $p = 0.01$ and $p = 0.001$. Wind speed data were plotted using the open source software WRPLOT [71]. All the analyses were performed with the software R [72].

3. Results

The daily meteorological conditions were similar for all the 40 days of the study period. The mean daily temperature was 27.6°C . Values above 25°C were registered around noon. Few nights registered temperatures between 20°C and 25°C (Figure 5). Relative humidity kept a mean daily value of 56.7%, oscillating between 40% to 70% on a daily basis. This condition led to a maximum vapor pressure deficit of 3.62 kPa around noon and 1.0 kPa at night. The wind blew from NNE with an average speed of 2.96 m s^{-1} . Specifically, 3% of the time the wind speed was recorded to be less than 0.5 m s^{-1} , 26.6% between 0.5 m s^{-1} and 3.0 m s^{-1} , and 70.4% of the time higher than 3 m s^{-1} (Figure 6). Only one precipitation event was registered during the 40 days of measurements, with a total precipitation of 1.27 mm d^{-1} on 27 December 2012.

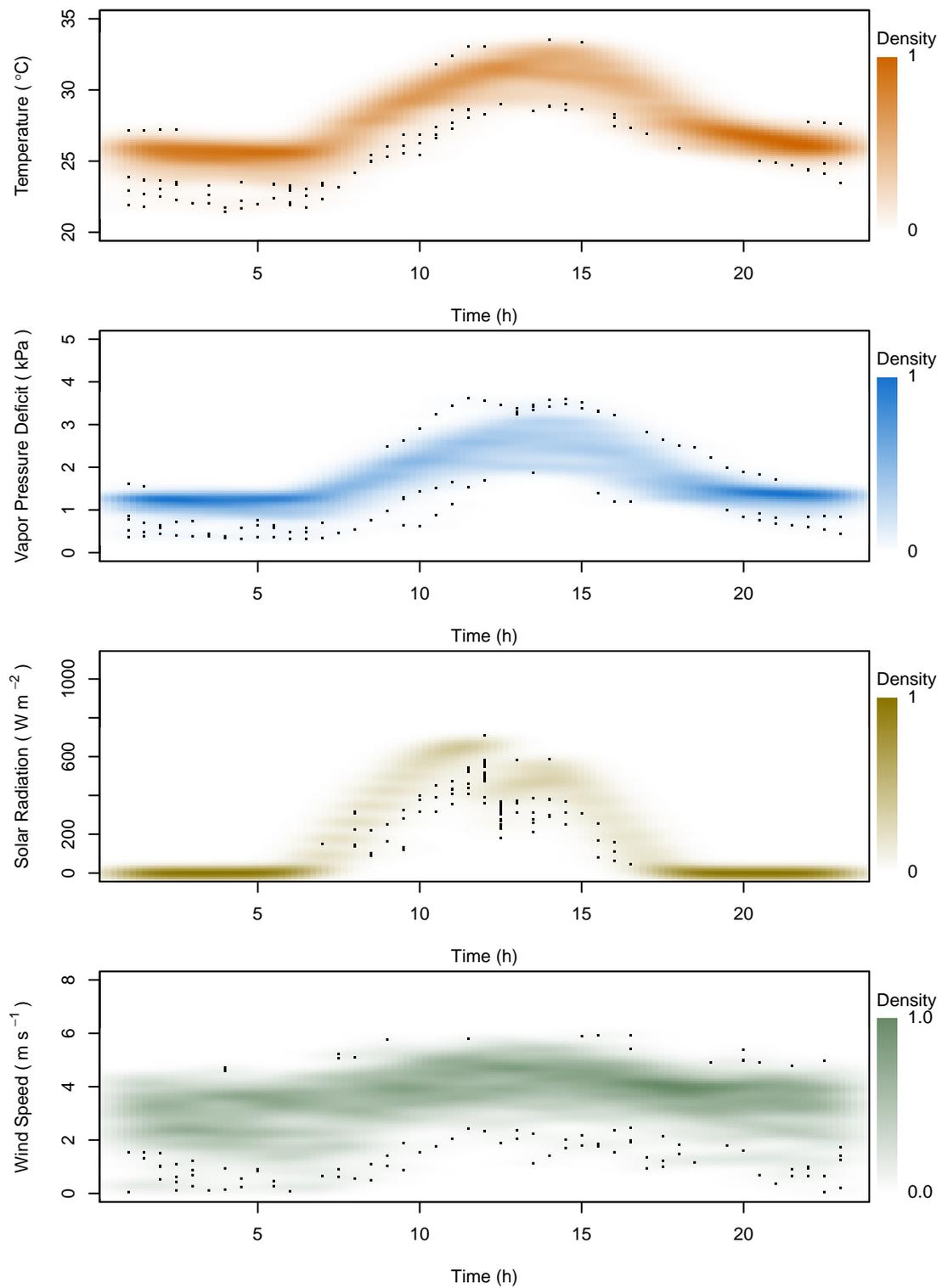


Figure 5. Density plots from the meteorological measurements during the study period at Palo Verde National Park, Costa Rica. Data recorded by the meteorological station of Palo Verde research station. The dots represent the first 50 points with lower densities among all measurements. Detailed data showed in Figure A1.

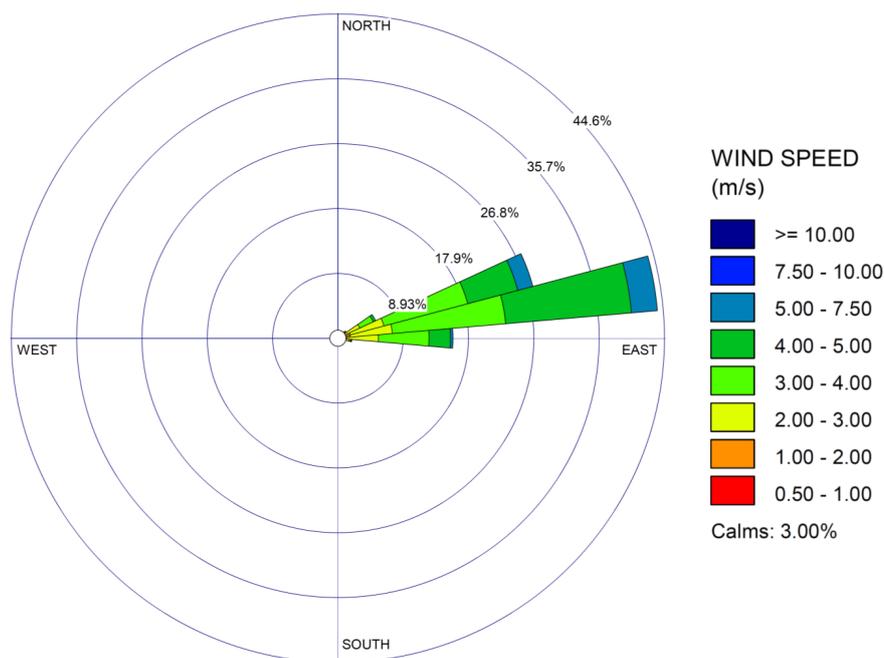


Figure 6. Wind speed distribution per azimuth and scalar category of Palo Verde National Park during the study period. Plot generated with WRPLOT [71].

The average E_{ref} was 5.0 mm d^{-1} with small variability during the study period considering the standard deviation of 0.41 mm d^{-1} . An accumulated evaporation of 200.0 mm was lower than all the evaporation measured from the wetland covers for both accumulated and daily values. The wetland covers *T. geniculata*, *T. dominguensis* and Mixed, showed the highest evaporation rates with values above 10 mm d^{-1} (Table 1). *T. geniculata* evaporates $17.0 \pm 2.42 \text{ mm d}^{-1}$ on average, with a slightly decreasing trend towards the end of the period. Contrary to *T. geniculata*, *T. dominguensis* intensified the evaporation in January but the average evaporation remained lower than *T. geniculata* with $14.3 \pm 3.39 \text{ mm d}^{-1}$. Evaporation from the Mixed cover was $13.5 \pm 2.44 \text{ mm d}^{-1}$ with standard deviation similar to *T. geniculata* (Figure 7).

Water cover had the lowest daily evaporation from all the covers with a value of $8.23 \pm 1.56 \text{ mm d}^{-1}$, while the evaporation rates from *N. natans* and *E. crasipes* were $9.3 \pm 1.61 \text{ mm d}^{-1}$ and $9.5 \pm 1.48 \text{ mm d}^{-1}$, respectively. These two species did not show tendency to increase nor decrease the evaporation rates as *T. dominguensis* and Mixed covers do (Figure 7). During the only precipitation event registered (December 27th), the average evaporation rates from *T. geniculata*, *T. dominguensis*, *E. crasipes* and *N. natans* experienced a reduction of almost 50% with respect to their own average. Meanwhile, the reduction on the mixed cover was about 40% of the daily average.

The estimated K_c values of the different covers were bigger than 1.5. The open water cover had the lowest K_c (1.65). K_c values of *N. natans* and *E. crasipes* were close to each other (1.85 and 1.90, respectively), meanwhile *T. geniculata* had the highest K_c value (3.43). The Mixed cover and *T. dominguensis* had similar K_c values, with evaporation rates of about 2.68 and 2.83 times more than E_{ref} , respectively (Table 1).

The statistical differences ($p < 0.05$) among daily evaporation rates of the wetland covers showed Open Water and *T. geniculata* as the ones with the lowest and highest daily evaporation rates, respectively (Table 1). Additionally, *N. natans* and *E. crasipes* were grouped with the second lowest evaporation rates. Mixed and *T. dominguensis* resulted as the second highest evaporation rates. Despite these differences, the accumulated evaporation among Open Water, *N. natans* and *E. crasipes* did not differ. The estimated crop coefficients showed values higher than one, depicting high evaporation with respect to the reference evaporation. Open Water resulted with lowest crop coefficient (1.65), while *T. geniculata* evaporated 3.43 times more than the reference evaporation (Table 1). The statistical

differences ($p < 0.05$) showed by the six wetland covers, grouped the crop coefficients into four homogeneous groups. All of them followed the same pattern as the daily evaporation.

Table 1. Average values of crop coefficient, daily and accumulated evaporation rates for the selected wetland covers at Palo Verde National Park, Costa Rica. Each average is based in 40 days of measurements and five replicates. Average values on the same column with similar lower case letters (^{a,b,c,d}) do not show statistical differences ($p = 0.05$) according to the Fisher LSD test.

Wetland Cover	Foliar	Evaporation		Crop
	Area (cm ²)	Daily Averages (mm d ⁻¹)	Accumulated (mm)	Coefficient (-)
Reference Evaporation	N.A.	5.0	200.0	1.0
Open Water	0	8.2 ^a	329.2 ^a	1.65 ^a
<i>N. natans</i>	11.8	9.3 ^b	369.8 ^a	1.85 ^b
<i>E. crasipes</i>	61.1	9.5 ^b	379.6 ^a	1.90 ^b
Mixed	70.4	13.5 ^c	537.8 ^b	2.68 ^c
<i>T. dominguensis</i>	55.6	14.3 ^c	570.6 ^b	2.83 ^c
<i>T. geniculata</i>	152.9	17.0 ^d	681.0 ^c	3.43 ^d

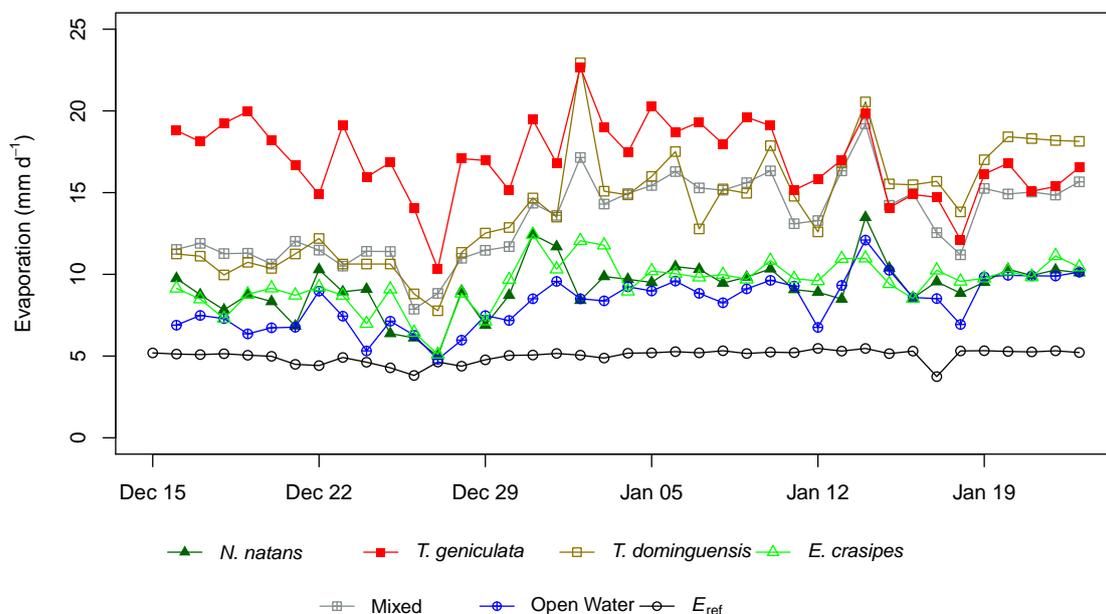


Figure 7. Mean daily evaporation from six wetland covers of Palo Verde National Park, Costa Rica. Sampling period: 40 days.

Correlation analysis among daily evaporation values and meteorological variables showed to be significant ($p < 0.001$) ranging from 0.53 to 0.73 (Table 2) for air temperature, solar radiation and wind speed. Relative humidity was inversely proportional to daily evaporation rates with correlation values between -0.83 to -0.63 , except for *T. geniculata* (Detailed information if Figure A2). Daily evaporation rates of *N. natans* ($r = 0.38$, $p < 0.05$) and *T. geniculata* ($r = 0.32$, $p < 0.05$) were poorly correlated to air temperature. All the other wetland covers were equally influenced by the meteorological parameters ($p < 0.001$). Excepting for *T. geniculata*, the atmospheric pressure exerted a similar effect during the evaporation process for all the covers with a correlation coefficient close to 0.5 ($p < 0.05$).

Table 2. Person correlation analysis among the evaporation from wetland covers and meteorological variables during the study at Palo Verde National Park, Costa Rica. Significant correlations among evaporation and meteorological variables were tested with the following significance levels: $p = 0.05$ (*), $p = 0.01$ (**) and $p = 0.001$ (***)

Wetland Cover	Air Temperature	Solar Radiation	Relative Humidity	Wind Speed	Atmospheric Pressure	Vapor Pressure Deficit
Open Water	0.53 ***	0.61 ***	−0.75 ***	0.58 ***	0.44 *	0.77 ***
<i>N. natans</i>	0.38 *	0.60 ***	−0.63 ***	0.54 ***	0.45 *	0.60 ***
<i>E. crasipes</i>	0.50 ***	0.62 ***	−0.70 ***	0.59 ***	0.55 **	0.68 ***
Mixed	0.70 ***	0.73 ***	−0.83 ***	0.63 ***	0.40 *	0.85 ***
<i>T. dominguensis</i>	0.56 ***	0.62 ***	−0.77 ***	0.65 ***	0.50 **	0.75 ***
<i>T. geniculata</i>	0.32 *	0.41 **	−0.21	0.02	−0.06	0.27

4. Discussion

Water temperature in tropical wetlands is affected by water depth, plant cover thickness, air temperature and solar radiation [73]. Evaporation differences among wetland plants are influenced by microclimatic conditions, which regulate the stomata opening and closure processes [34,65,67,74]. This leads to a total contribution of 38% from the total evaporation in marshland ecosystems [75] similar to Palo Verde National Park. Reported values of evaporation for *E. crasipes* range from 1.02 mm d^{−1} to 9.8 mm d^{−1} depending on the ecosystem, season and climatological conditions [35]. Floating plants as *N. natans* and *E. crasipes* are influenced mainly by radiation and vapor pressure deficit. Temperature has a strong influence ($p < 0.001$) on the evaporation of the *E. crasipes*, Open Water, Mixed and *T. dominguensis* covers. Meanwhile, the evaporation rates of *N. natans* and *T. geniculata* are driven by solar radiation, and the vapor pressure deficit also influences *N. natans*. The emergent macrophyte *T. dominguensis* and the Mixed cover are strongly influenced ($p < 0.001$) by wind speed. Despite the differences of foliar area among wetland covers, the accumulated evaporation in Open Water, *N. natans* and *E. crasipes* do not differ. The estimation of the VPD based on the relative humidity measurements provides an indication of the maximum water vapor that can be allocated to the atmosphere. The VPD and relative humidity are the main drivers of the evaporation process during this period for all the covers excepting *T. geniculata*. This reflects the lack of correlation between evaporation and VPD or relative humidity is not unusual and it has been documented with other macrophytes as *Typha latifolia* L., *Hacer rubrum* L. and *Salix babylonica* L. with correlations between −0.14 and −0.46 in the United States [33].

Differences and similarities among evaporation rates and crop coefficients of wetland covers are driven by the physiological characteristics of the plants [34]. Stomatal conductance of any plant determines the maximum water vapor transfer during transpiration, and it is an important factor in worldwide wetlands [76]. *N. natans* and *E. crasipes* are floating macrophytes with leaves located close to the water surface (the plants are not taller than 20 cm). This keeps the plants within a more saturated atmosphere reducing the total evaporation. Previously, it was thought that floating macrophytes such as *E. crasipes* reduce evaporation from open water surfaces because of its shadow effect [34]. However, this assumption does not include the transpiration process, which increases the evaporation rates from *E. crasipes* plants compared to open water surfaces [37,60,61]. Consequently, both covers *N. natans* and *E. crasipes* behave similar.

The presence of macrophytes increases considerably the evaporation from open water bodies [30,40]. Any increment in the number of plants per unit of area in an open water surface represents an augment in the physiological water demand for those plants [38]. For this reason the intermediate daily evaporation rate of the Mixed cover is similar to the evaporation rate of the *T. dominguensis* cover. *T. dominguensis* has leaves up to 50 cm above the water surface, exposing the plants to a less saturated atmosphere but more windy, leading to high evaporation. *T. dominguensis* is adapted to hypoxia thanks to the presence of aerenchyma tissues [77]. Additionally, it is a drought tolerant species highly efficient during its

photosynthesis process [78]. This enables the species to adapt to dehydration, increasing the water supply through the root system and reducing the water consumption when it is not available [32]. Evaporation rates in *Typha* sp. show high values per unit of foliar area as a consequence of the stomata distribution on both sides of the leaf [33]. Additionally, the leaf age affects considerably the evaporation rates, making younger leaves to be more efficient due to the high productivity fixing new tissues. Thus leading towards a higher evaporation rate than older plants [76]. Previous studies showed the dependency of evaporation rates from macrophytes to the plant size as a proxy of the fixed plant biomass [34]. In this case, the evaporation rates of *E. crasipes* and *Typha latifolia* depend on plant diameter, height and solar radiation. Unpublished data from Palo Verde National Park showed that evaporation rates of *T. dominguensis* depend on total biomass during lysimeter experiments. These evaporation rates differ between dry and wet season evaporating between 3.7 mm d^{-1} to 4.7 mm d^{-1} , respectively [79]. This implies that even the younger plants of *T. dominguensis* export more water to the atmosphere than mature plants of *N. natans* or *E. crasipes*. Meanwhile, younger plants of *T. dominguensis* export the 84% of the evaporation registered by *T. geniculata*.

T. geniculata is the plant with the biggest leaf area (152.9 cm^2) allowing the plant to pump more water to the atmosphere than the other wetland vegetated covers and open water. *T. geniculata* develops its foliar architecture according to the resources availability [32], reason why this species is able to produce bigger leaves in Palo Verde wetland. *T. dominguensis* is a highly adaptable species, with high evaporation rates when fully adult [67]. The high numbers of *T. geniculata* can affect the wetland hydrology by increasing the evaporation during shorter periods of time than *T. dominguensis* due to its senescence at the end of the dry season. Despite *E. crasipes* is an abundant species in the wetland, it would affect less the wetland than *T. geniculata* and *T. dominguensis*. Under subtropical climate conditions, *E. crasipes* exhibits a crop coefficient value between 1.31 and 2.52, whilst *T. latifolia* show 1.05 to 2.50 [34,62]. There is no data reported for *N. natans* nor *T. geniculata* in its adult stage.

Some authors have referred to the ratio between macrophytes evaporation (E) and open water evaporation (E_w) as an alternative to the crop coefficient in wetland ecosystems. As an example, *E. crasipes* in the Nile Delta is characterized by a value of $\frac{E}{E_w}$ of 2.12 [38], meanwhile in this experiment this value is 1.15 (value estimated from the results of Table 1). The crop coefficient has been widely used in agriculture for irrigation management [80,81] and it can be applied in hydrological modelling of agricultural wetlands [82]. The same principle can be also applied to wetlands with seasonal vegetation where the plant growing patterns follow a similar trend like short term crops. The estimation of the crop coefficients for macrophytes in the Palo Verde wetland describes the evaporation rates of full growth plants except for *T. dominguensis*. Because the growing stage of the selected plants of *T. dominguensis* matches the earlier growing stage shared with the other covers in the recently cleared zones in Palo Verde wetland. Considering the lack of an eddy covariance system to measure the evaporation from the wetland, the crop coefficients can be used in combination with the monitoring of the wetland cover and the meteorological data. This to determine the evaporation rate from the managed ecosystem. Unlike eddy covariance systems, meteorological data is more accessible in tropical wetlands.

5. Conclusions

This study quantified the evaporation rates of six wetland covers of Palo Verde National Park during the dry season. The observed evaporation rates were comparably higher than the open water cover. The reported differences among evaporation values can be explained due to the added effect of the transpiration of macrophytes. This as a consequence of different foliar areas and biomass as a result of plant size and age. Additionally, the evaporation rates were strongly correlated to the vapour pressure deficit for all the covers excepting for *T. geniculata* which was dependent on solar radiation. These results demonstrate that the increment of vegetated areas within the Palo Verde wetland of floating-leaved and emergent macrophytes, increase the water vapor flux to the atmosphere. Hence, controlling the extent and growth of these plants, is a necessary management practice for the restoration of the natural habitats. Among the aquatic plants investigated, *T. dominguensis* and *T. geniculata* have the highest evaporation

rates and the biggest impact on the evaporation flux. Hence, further research should focus on studying how to improve the methods to control the population grow of these two species.

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Appendix A

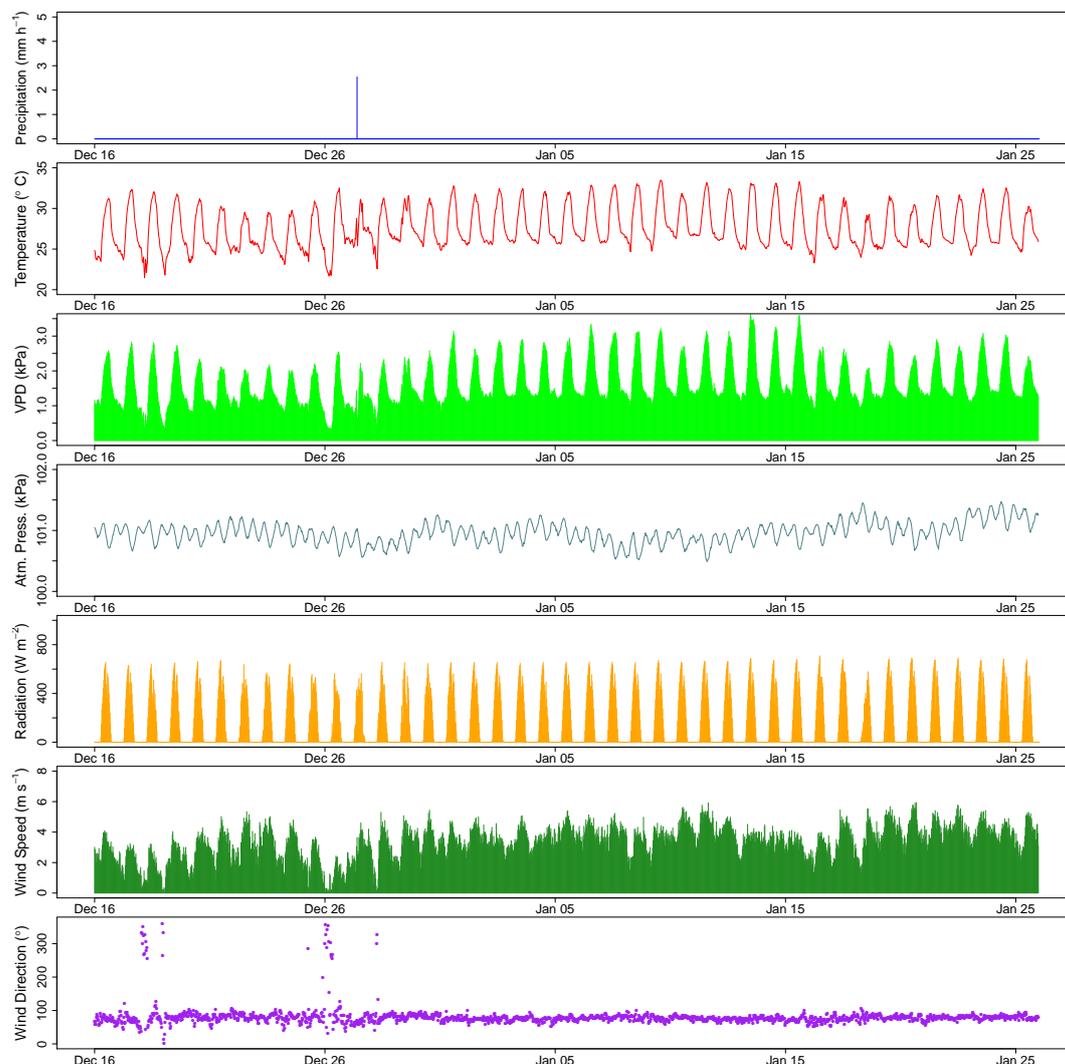


Figure A1. Meteorological parameters measured in 30 min intervals at the meteorological station of Palo Verde Research Station, Costa Rica.

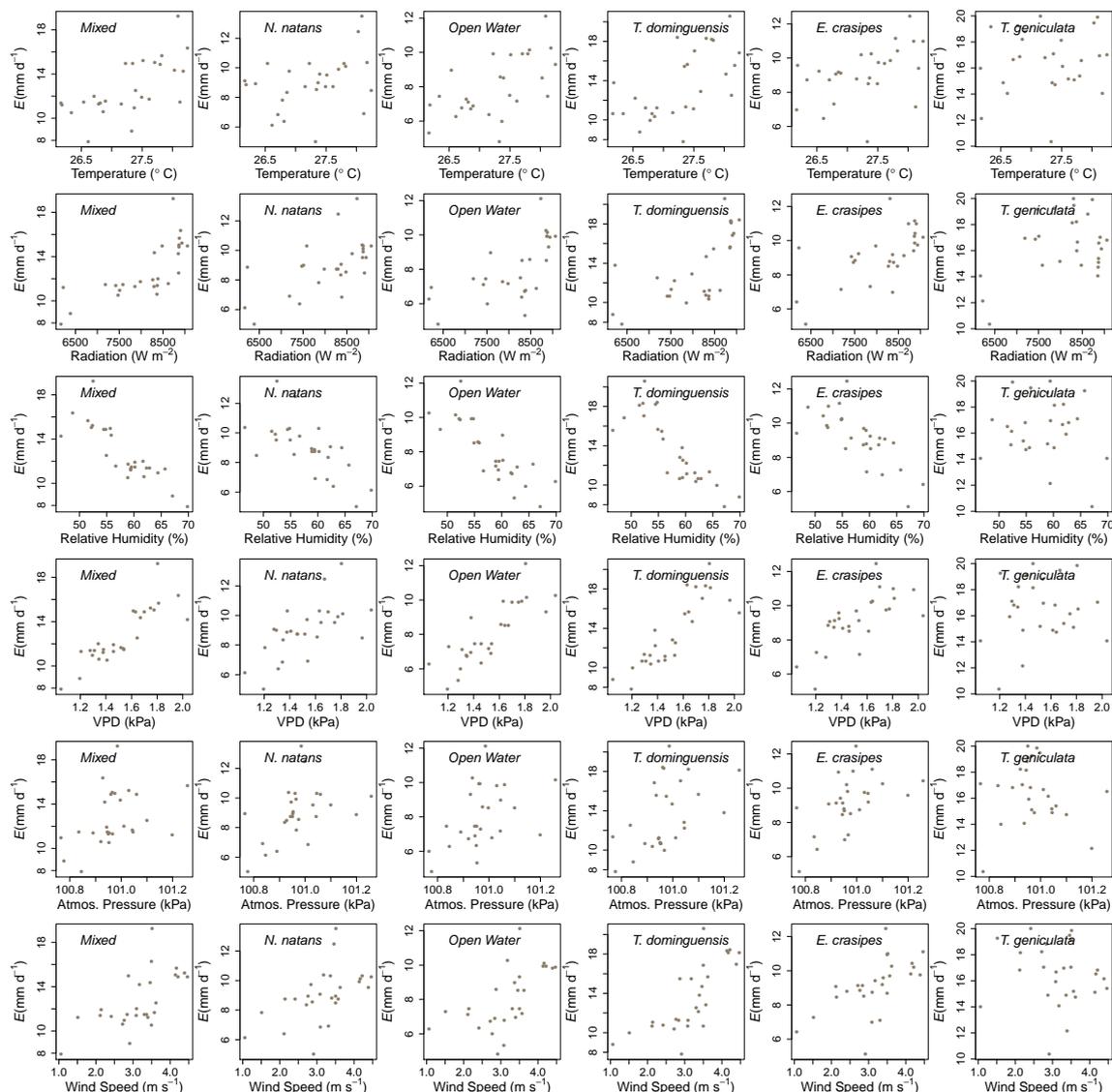


Figure A2. Pearson correlation matrix among the evaporation rates of the selected wetland covers and daily averages of the measured meteorological parameters.

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