



Approximations of stand water use versus evapotranspiration from three mangrove forests in southwest Florida, USA



Ken W. Krauss^{a,*}, Jordan G. Barr^b, Vic Engel^c, Jose D. Fuentes^d, Hongqing Wang^a

^a U.S. Geological Survey, National Wetlands Research Center, Lafayette, LA 70506, USA

^b National Park Service, South Florida Natural Resource Center, Everglades National Park, Homestead, FL 33030, USA

^c U.S. Geological Survey, Southeast Ecological Research Center, Gainesville, FL 32653, USA

^d The Pennsylvania State University, Department of Meteorology, University Park, PA 16802, USA

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ABSTRACT

Leaves from mangrove forests are often considered efficient in the use of water during photosynthesis, but less is known about whole-tree and stand-level water use strategies. Are mangrove forests as conservative in water use as experimental studies on seedlings imply? Here, we apply a simple model to estimate stand water use (S), determine the contribution of S to evapotranspiration (ET), and approximate the distribution of S versus ET over annual cycles for three mangrove forests in southwest Florida, USA. The value of S ranged from 350 to 511 mm year⁻¹ for two mangrove forests in Rookery Bay to 872 mm year⁻¹ for a mangrove forest along the Shark River in Everglades National Park. This represents 34–49% of ET for Rookery Bay mangroves, a rather conservative rate of S , and 63–66% of ET for the Shark River mangroves, a less conservative rate of S . However, variability in estimates of S in mangroves is high enough to require additional study on the spatial changes related to forest structural shifts, different tidal regimes, and variable site-specific salinity concentrations in multiple mangrove forests before a true account of water use conservation strategies can be understood at the landscape scale. Evidence does suggest that large, well-developed mangrove forests have the potential to contribute considerably to the ET balance; however, regionally most mangrove forests are much smaller in stature in Florida and likely contribute less to regional water losses through stand-level transpiration.

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1. Introduction

Water use efficiency (WUE) in plants relates to the amount of carbon (CO₂) taken up by leaves relative to the amount of water used by the plant. As such, variation in WUE and composition among different tree species growing in a stand can influence how much water is lost through transpiration (Wullschleger et al., 2001). Yet, despite adequate supply of seawater in many marine environments, water deficiency in plants manifests through osmotic or other physiological barriers that further limit uptake of fresh water to growing plant tissues (Scholander, 1968; Milburn, 1996), forcing the need for efficiency among physiological processes. Water use characteristics of mangrove trees are of particular interest because while trees are often affected by salinity, as facultative halophytes they are still able to complete all aspects of their life cycle in marine environments, including survival as rather large trees in settings with strong soil-imposed osmotic gradients and, in some cases,

limited freshwater inputs (Ball, 1988; Lugo and Snedaker, 1974; Medina, 1999). Thus, we understand the physiological impacts of osmotic stress on mangroves, but whether mangrove forests are pressed to conserve water at the landscape scale through reduced transpiration has not been well documented.

Much of what is known about water conservation strategies in mangroves stems from WUE studies conducted on seedlings in controlled settings (Krauss et al., 2008), which collectively suggest that mangroves are efficient at using water during photosynthesis. However, assessments are often not from the field and WUE can be sensitive to extreme environmental conditions; e.g., WUE has been documented to increase during drought (Sobrado, 1999) or under elevated salinity (Reef et al., 2012). Furthermore, water is supplied to leaves through symplastic water transport involving a series of xylem-associated aquaporins, which are themselves directly sensitive to environmental changes (Maurel and Chrispeels, 2001). From this account, we would expect water use by mangrove ecosystems to be low, especially in hypersaline, low rainfall, or frequently flooded environments.

The best direct evidence of water conservation comes from a few sap flux studies, which indicate that mangrove trees

* Corresponding author. Tel.: +1 337 266 8882; fax: +1 337 266 8586.
E-mail address: kkrauss@usgs.gov (K.W. Krauss).

Table 1
Summary of sap velocity and sap flux density studies conducted in natural mangrove wetlands.

Species	Location	Technique ^a	Size class Height (m)	n	Duration	Sap velocity/flux ^b cm H ₂ O h ⁻¹	Source
<i>Rhizophora mangle</i>	Oahu Is., Hawaii, USA	SHB	1–2	2	16	18–48	Zimmermann et al. (1994)
<i>Rhizophora apiculata</i> , <i>Avicennia alba</i>	Brunei Darussalam, Borneo	HPV	–	4	1–3	32.4–57.6	Becker et al. (1997)
<i>Rhizophora mangle</i>	Biscayne Bay, Florida, USA	HPV	<1	9	165	3.5–6.9 (approx.)	Hao et al. (2009)
<i>Rhizophora mangle</i>		HPV	5–10	8	165	5.0–12.5 (approx.)	
<i>Avicennia marina</i>	Moreton Bay, Australia	HPV	5	3	6	5.2–18.9	Vandegheuchte et al. (2014)
<i>Rhizophora stylosa</i>		HPV	3.5	3	6	5.9–7.8	
Species	Location	Technique ^a	Size class DBH class (cm)	n	Duration	Sap velocity/flux ^b L H ₂ O tree ⁻¹ day ⁻¹	Source
<i>Bruguiera cylindrica</i>	Phangnga Bay, Thailand	SHB	– ^c	3	24	0.7–1.23 (approx.)	Hirano et al. (1996)
<i>Avicennia germinans</i>	French Guiana	TDP	11.8–15.6	3	11–40	3.2–5.3	Muller et al. (2009)
<i>Avicennia germinans</i>		TDP	23.7–24.3	2	29	11.5–30.8	
<i>Avicennia germinans</i>		TDP	43.9–46.6	2	29	40.8–64.1	
<i>Avicennia germinans</i>	Rookery Bay, Florida, USA	TDP	5.1–15.0	5	29	0.5–2.4	Krauss et al. (2007)
<i>Avicennia germinans</i>		TDP	15.1–25.0	9	29	5.1–9.6	
<i>Avicennia germinans</i>		TDP	25.1–35.0	4	29	8.7–18.5	
<i>Laguncularia racemosa</i>		TDP	5.1–15.0	4	29	1.9–7.2	
<i>Laguncularia racemosa</i>		TDP	15.1–25.0	9	29	11.8–24.9	
<i>Laguncularia racemosa</i>		TDP	25.1–35.0	3	29	19.1–30.5	
<i>Rhizophora mangle</i>		TDP	5.1–15.0	9	29	1.0–6.8	
<i>Rhizophora mangle</i>		TDP	15.1–25.0	6	29	5.1–6.6	
<i>Ceriops tagal</i>	Mayotte Is., Indian Ocean	Isotope	6.5–8.0	3	13–15	7.5–10.0	Lambs and Saenger (2011)
<i>Rhizophora mucronata</i>		Isotope	13.0–22.0	2	13–15	10.7–17.6	
<i>Avicennia germinans</i>	Fourchon, Louisiana, USA	TDP	2.8–5.3	7	47	0.4–1.5	Krauss et al. (2014b)

Mangrove species, location of study, technique used, size class (Height, m; DBH, cm), number of individual trees sampled (*n*), duration of study (days), sap flux (velocity, cm h⁻¹; volume, L H₂O tree⁻¹ day⁻¹), and source of data.

^a SHB, Stem heat balance; HPV, Heat pulse velocity; TDP, Thermal dissipation; Isotope, injecting a deuterium (D₂O) tracer.

^b Sap flux is divided into sap velocity measures (cm H₂O h⁻¹) and sap flux density (L H₂O tree⁻¹ day⁻¹) according to original data sources.

^c DBH size class was not available, but trees were small (height, 2–3 m and leaf area, 1.0–1.4 m²).

varying in size from 2.8 to 24.3 cm *dbh* (diameter at breast height) use water at rates of 0.4–30.8 L H₂O day⁻¹ (Table 1), although one account indicated that individual tree water use for large *Avicennia germinans* (L.) Stearn. (43.9–46.6 cm *dbh*) trees was as high as 40.8–64.1 L H₂O day⁻¹ (Muller et al., 2009). Indeed higher rates might not be anomalous in some settings; point measurements of sap velocity in mangroves at specific depths can also be high (Table 1). However, overall sap flux through entire mangrove stems more often represents the lower end of what has been reported in the literature in comparison with non-mangrove trees (*mean* = 116 L H₂O day⁻¹, *n* = 92; Wullschlegel et al., 1998). Sap flux trends from mangroves also tend to be conservative when expressed on a leaf-area (Reef et al., 2012) or sapwood area basis (Krauss et al., 2007; Muller et al., 2009), establishing the need for a much broader focus on individual-tree and stand-level contributions of mangroves to regional water conservation.

Here, we apply a stand water use modeling approach (c.f., Krauss et al., 2014a) to three mangrove stands located in southwest Florida from which sap flux measurements were previously made, and where estimates of evapotranspiration (ET) and rainfall were also available either in situ or nearby. Our primary goals are to report estimates of *S*, determine the approximate *S* component of ET, and approximate the distribution of *S* versus ET over annual cycles for three mangrove forests in south Florida.

2. Materials and methods

2.1. Study sites

Sap flux data from mangroves are relatively sparse (Table 1); however, sufficient data have been collected from mangroves in the Rookery Bay National Estuarine Research Reserve, Naples, Florida, USA in order to develop a stand water use modeling approach. Rookery Bay (26°02' N) was divided into two study sites (with two,

530 m² study plots each), one adjacent to Hall Bay (see also RBF1 in Twilley and Chen, 1998) and the other along Henderson Creek (Fig. 1). Both sites contained mixed mangrove communities of *A. germinans*, *Laguncularia racemosa* (L.) Gaertn. f., and *Rhizophora mangle* L., but differed slightly in their structural composition (Table 2). Including all trees ≥5.0 cm *dbh*, stand basal area measured from the two plots per site was 22.9–27.8 m² ha⁻¹ and canopy height ranged from 10 to 11 m. Sites were located approximately 2 km apart and within 50 m of open water. Sap flux data were collected using self-manufactured, calibrated thermal dissipation probes from all three tree species (*n* = 15–18 trees species⁻¹), representing three different size classes over a period of approximately one month when sap flux was expected to be relatively high (22nd May to 21st June 2003; Krauss et al., 2007).

A third study site was located 4.1 km from the mouth of the Shark River in Everglades National Park (25°21' N), or approximately 98 km southeast of study sites in Rookery Bay (Fig. 1). This site also had two study plots (400 m² each). Dominant mangrove tree species were identical to Rookery Bay, but trees were larger with a higher percentage of *L. racemosa* (Table 2). Including all trees ≥5.0 cm *dbh*, stand basal area was 40.5 m² ha⁻¹, stand height was 19 m, and plots were within 60 m of the river (see also Barr et al., 2010). Sap flux data were collected from this site using commercially available thermal dissipation probes (TDP30 and TDP80, Dynamax, Inc., Houston, TX, USA) from all three species (*n* = 2–3 trees species⁻¹) over approximately 7.5 months (1 January to 15 July 2007; V. Engel, unpublished data), but after Hurricane Wilma impacted the site on 24 October 2005 causing significant losses in stand basal area (Smith et al., 2009).

Hall Bay and Henderson Creek sites are basin mangrove forests, which are flooded more frequently during periods of regionally higher rainfall (May–October) and experience localized ponding as ebbing tides strand surface water on occasion (Fig. 2). The Shark River site represents a riverine mangrove

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