

Water-use characteristics of Palmiet (*Prionium serratum*), an endemic South African wetland plant

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Palmiet, *Prionium serratum*, is an endemic wetland plant which dominates oligotrophic wetlands throughout the Cape Floristic Region, South Africa. Palmiet is often perceived as undesirable by landowners, in part because it is thought to have high water-use, although little is known about the water-use of this important wetland species. We estimated the water-use dynamics of Palmiet at the leaf scale, using stomatal conductance measurements, and at the wetland scale, by modelling evapotranspiration using remote sensing and an energy-balance model. Factors that influenced Palmiet water-use were also considered, and seasonal variations were analysed. The aim was to estimate Palmiet wetland water-use, and to develop a set of crop factors (K_c) for use in hydrological modelling of catchments containing Palmiet wetlands. Results show that Palmiet has a comparatively low stomatal conductance (11–152 mmol·m⁻²·s⁻¹), which was lower in summer than winter, and moderate evapotranspiration for a riparian species (1 220 mm·a⁻¹ compared to a local reference evapotranspiration of 1 302 mm·a⁻¹ and A-Pan evaporation of 2 809 mm·a⁻¹), which was higher in summer (more energy to drive evapotranspiration and higher vapour pressure deficits). Morphological and physiological adaptations to nutrient poverty or periodic drought are suggested theories which may explain the controls on transpiration for Palmiet.

INTRODUCTION

Palmiet (*Prionium serratum*, Thurniaceae) is a common and prominent riparian wetland plant, endemic to river floodplains and fringes from Gifberg in the Western Cape, through the Eastern Cape to southern KwaZulu-Natal, South Africa (Boucher and Withers, 2004). Palmiet grows in dense stands of what appear to be separate plants but are often clonal systems (Boucher and Withers, 2004). These Palmiet wetlands are typically underlain by peat and accumulated sediments, built up over thousands of years (Haigh et al., 2002). Palmiet grows throughout the year, with flowering in spring and summer and fruit appearing in March (Boucher and Withers, 2004). Palmiet is intolerant of saline water and full shade, is fire adapted, and characterizes oligotrophic rivers and wetlands (Boucher and Withers, 2004). Palmiet is perceived by many landowners to be a nuisance, causing blockages in rivers and depletion of water resources, as it is thought to be a high water-user (Rebelo, 2012). Palmiet is therefore often removed to ‘unblock the river’ (Rebelo, 2012) or so that floodplain sediments can be cultivated.

Fynbos is the main vegetation type in which Palmiet wetlands occur, and, similarly to other Mediterranean-climate vegetation, Fynbos species tend to have conservative water-use with relatively low stomatal conductance and photosynthetic capacity (Von Willert et al., 1989; Mooney et al., 1983; Dzikiti et al., 2014; Meijninger and Jarman, 2014). However, Fynbos riparian plants with permanent access to water in the root zone generally have higher evapotranspiration rates than their terrestrial counterparts, though not as high as invasive alien riparian trees (Everson et al., 1998; Scott, 1999; Dye et al., 2001; Everson et al., 2007; Everson et al., 2009; Clulow, 2011). The limited research conducted on South African wetlands has shown that wetland species (e.g. reeds: *Phragmites mauritianus*) are generally high water-users (Seyhan et al., 1983; Birkhead et al., 1997; Everson et al., 2001; Dye et al., 2008; Clulow et al., 2012).

There have been many studies internationally attempting to estimate the water-savings of clearing invasive alien trees with concomitant recovery of indigenous species (Doody et al., 2011; Doody et al., 2014; Le Maitre et al., 2016). There have also been many studies and much debate about wetland evapotranspiration globally, and whether it is similar, lower, or higher than evaporation from an open water surface (Mohamed et al., 2012). The pan coefficient (the ratio of mean evapotranspiration to mean pan evaporation) has been a useful technique to compare potential water savings across different climates (Mohamed et al., 2012; Doody et al., 2014). In a review of selected wetlands around the globe, the mean ± standard deviation of pan coefficients was 0.87 ± 0.26, suggesting that most wetlands markedly reduce evaporation efficiency compared to open water (Mohamed et al., 2012). There has been very little research on the water-use of wetlands in South Africa, presenting a knowledge gap, especially for the parametrisation of hydrological models in studies which seek to compare scenarios of invasion in wetlands or riparian zones (Rebelo et al., 2015; Mander et al., 2017).

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DATES

Received: 1 August 2018

Accepted: 17 August 2020

KEYWORDS

wetland evapotranspiration
substomatal chambers
crop factor
SEBAL Model
porometry

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It is widely accepted in the literature that protecting Palmiet wetlands is beneficial in terms of habitat provision, sediment stabilisation and accretion, which creates storage capacity for water and increases the ability of the floodplain to absorb floodwaters and retain water to sustain dry-season flows (Job, 2014; Rebelo, 2017). However, it is also critical to understand the water-use of such an important and dominant wetland species to determine whether its presence constitutes a gain, in terms of water preserved in the ecosystem (where Palmiet wetland evapotranspiration is less than or equal to an equivalent area of open water) or a loss (where it exceeds evaporation) (Mohamed et al. 2012; Doody et al., 2014). Catchments containing Palmiet wetlands are currently being extensively modelled using ACRU and MIKE-SHE hydrological models to examine the benefits of rehabilitation or to compare climate or habitat scenarios (Rebelo et al., 2015; Mander et al., 2017). Evapotranspiration of various vegetation types is typically modelled by applying different sets of crop factors to a grass reference evapotranspiration (Schulze, 1995; Savage et al., 2010; Jovanovic and Israel, 2012). Therefore, it is essential to have a realistic crop factor to accurately represent the water-use of Palmiet in these hydrological models.

We aimed to develop an understanding of Palmiet water-use by quantifying: (i) factors influencing Palmiet water-use; (ii) seasonal variations in Palmiet plant and wetland water-use, (iii) an annual estimate of Palmiet wetland evapotranspiration, and (iv) a set of crop factors (K_c) for Palmiet wetlands. Many methods have been developed to measure the water-use of plants at the leaf, plant, and ecosystem scale. At the leaf scale, stomatal conductance can be used as an indicator for water-use, as it measures the passage

of carbon dioxide or water vapour exiting stomata (a measure of the degree of stomatal opening). At the stand or landscape scale, the Surface Energy Balance Algorithm for Land (SEBAL) model uses the energy balance to model evapotranspiration using inputs from remote sensing and climatic variables (Bastiaanssen et al., 1998; Meijninger and Jarman, 2014). We used morphology measurements and porometry to understand factors influencing water-use, and a combination of porometry and energy-balance modelling at the landscape scale using remote-sensing inputs to investigate seasonal variations. The results were also used to estimate annual evapotranspiration, the pan coefficient and a crop factor for Palmiet wetlands.

METHODS

Study sites

Two Palmiet wetlands were selected as study sites: one in the Jonkershoek valley (33°58'38" S, 18°56'48" E) and another near the Theewaterskloof Dam (33°57'50" S, 19°10'00" E) in the Western Cape (Fig. 1). The Jonkershoek valley has a mean annual precipitation of $\pm 1\ 427$ mm (Scott, 1999), whereas that of the Theewaterskloof wetland is around $\pm 1\ 241$ mm (Kotze, 2015). Porometry measurements of stomatal conductance were collected in the field from the Jonkershoek wetland, whereas the SEBAL model was used to estimate the surface energy balance and evapotranspiration from the Theewaterskloof wetland. The reason that two different wetlands were used in this study is that the SEBAL data were available from other studies done by Meijninger and Jarman (2014) and Klaasse et al. (2008).

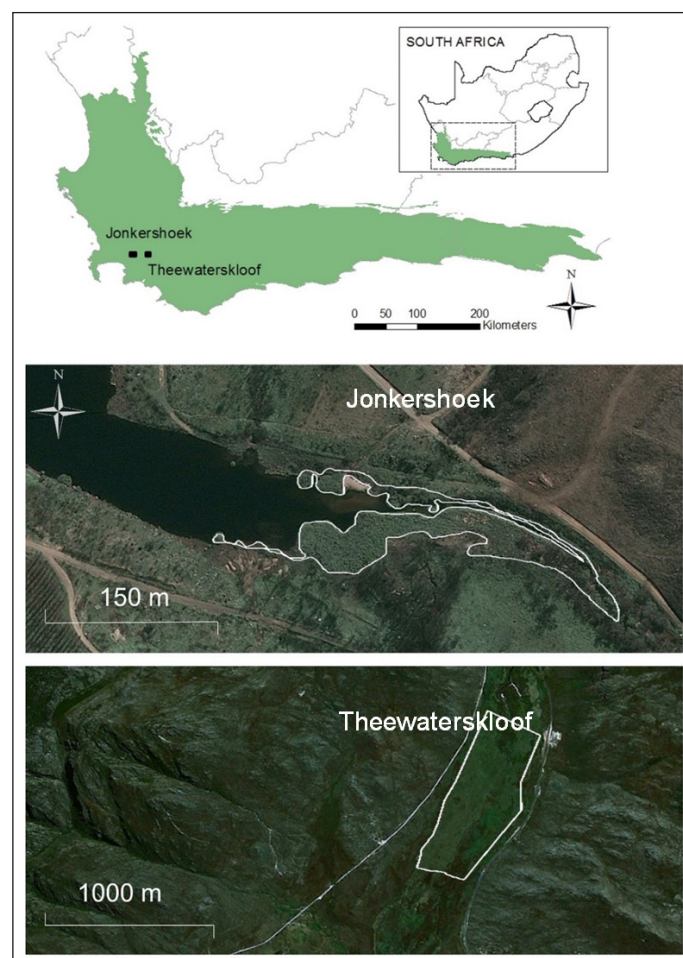


Figure 1. The location of the Jonkershoek and Theewaterskloof Palmiet wetlands within the Cape Floristic Region of South Africa (green area on the map inset). The gray lines in the maps indicate the provinces on the map inset. The approximate wetland area is indicated by white polygons in the satellite imagery which was dated 9/11/2009, obtained from Google Earth

Plant-scale field measurements

In the Jonkershoek Palmiet wetland, a stand of Palmiet (*Prionium serratum*) was selected for sampling. The number of plants in ten 1 m² plots were counted, as well as the number of dead and living leaves per plant for 10 plants. The length of 50 Palmiet leaves was also measured. Leaf area index was measured using an ACCUPAR LP-80 Leaf Area Index Meter (Decagon Devices, 2010) on a cloudy day in autumn. Leaf area index is a measure of the area of leaves of a plant per unit of ground area, and is used as an index for biomass, canopy cover, transpiration and productivity (Jarvis and Leverenz, 1983; Decagon Devices, 2010). Additionally, a leaf was collected from this Palmiet stand, and an epidermal peel made of both adaxial and abaxial surfaces using clear enamel. This epidermal peel was examined under a light microscope at 4x, 10x and 40x magnifications and the number of stomata compared between both surfaces. Cross-sections through the Palmiet leaf were made and these were examined and photographed at various magnifications under a light microscope.

Stomatal conductance (mmol·m⁻²·s⁻¹) and leaf temperature (°C) of Palmiet were measured on 6 plants at Jonkershoek wetland over 2 to 3 days in 3 different seasons: late spring 2010 (3 and 10 November 2010), late summer 2011 (26–27 February and 2 March 2011) and early winter 2011 (10 and 11 June 2011). Measurements were taken hourly, starting from 07:00 and ending by 19:00 (depending on the daylight hours for each season) using a SC1 Leaf Porometer (Decagon Devices, 2012), ensuring light levels were adequate and leaves were dry (i.e. no rainfall). Three Palmiet plants were selected along the water's edge, and three were selected inland. Two leaves were sampled per plant and both the adaxial and abaxial surface of each leaf was sampled, yielding 4 measurements per plant per hour. Light conditions of each reading were recorded: whether the leaf was positioned in the shade or sun, whether conditions were cloudy, or whether the sun had set. A pilot study revealed that leaf age and aspect did not significantly affect stomatal conductance, therefore these factors were excluded in the final sampling design (Rebelo, 2012).

The range of stomatal conductance of Palmiet used for comparison with other species in other studies was calculated by taking the mean of the daily minimum and maximum values obtained during fieldwork. For comparison with other studies, all literature values of stomatal conductance were converted to mmol·m⁻²·s⁻¹. Von Willert et al. (1989) reported stomatal conductance values in mmol·m⁻²·s⁻¹ and therefore results didn't need conversion, whereas Miller et al. (1984) reported values as mm·s⁻¹ and therefore all results had to be converted into molar values. This was done using the molar density of air (mol·m⁻³), which was calculated taking into account local atmospheric pressure and temperature using the following formula:

$$\rho = 44.6 \times (P_{\text{atm}}/101.3) \times (273.15/(273.15 + T)) \quad (1)$$

where ρ is the molar density of air (mol·m⁻³), P_{atm} is atmospheric pressure (kPa), and T is local temperature (°C). Local atmospheric pressure (P_{atm}) was calculated using the following formula:

$$P_{\text{atm}} = 101.3 \times \text{EXP}(-\alpha / 8200) \quad (2)$$

where α is the local elevation (in m above mean sea level; m amsl). Temperatures and elevations used for each location were: Algeria (18°C, 500 m amsl), Jonkershoek (16°C, 282 m amsl), Jakkalsrivier (15°C, 960 m amsl) and Pella (16°C, 300 m amsl), yielding molar densities of air of 39.4, 40.7, 37.6, and 40.6 mol·m⁻³, respectively. Meteorological data for the plant-scale field measurements were obtained from the closest local South African Weather Service station at Swartboskloof.

Wetland-scale field measurements

Scaling stomatal conductance up to plant or stand-level has high error associated with it (Whitehead, 1997), so it was not undertaken here. Rather, stomatal conductance results were compared with literature for other Fynbos species. To estimate annual evapotranspiration of Palmiet, we used a dataset where evapotranspiration and the energy balance from a Palmiet wetland had been modelled. This dataset was made available to support this analysis (Jarmain, 2009). We also calculated a set of crop factors (K_c) for use in hydrological modelling studies.

Wetland scale energy balance modelling using remote sensing inputs

SEBAL was used to model the energy balance and evapotranspiration around the region of the Theewaterskloof wetland as part of research by Meijninger and Jarmain (2014) and Klaasse et al. (2008). Remote-sensing data from two sensors of different spatial and spectral resolutions were used as input into the SEBAL Model. Firstly, the Moderate Resolution Imaging Spectroradiometer (MODIS; Meijninger and Jarmain, 2014) and, secondly, Landsat7-ETM+ (Klaasse et al., 2008). The data from these projects were made available for this research. The data for the Theewaterskloof Palmiet wetland were extracted from the full dataset using a polygon of the extent of the wetland (following the method described in Singels et al., 2018). The resolution at which SEBAL outputs were provided was 250 m – 1 km for MODIS outputs and 30–60 m for Landsat7. For this analysis, the mean monthly evapotranspiration for the entire Palmiet wetland was calculated for each scene, resulting in a mean and standard deviation value (mm/month) for each scene (Tables A1, A2). Meteorological data used in the model were obtained from local weather stations at Franschoek and Villiersdorp, managed by the South African Weather Service. Monthly rainfall data are presented in Fig. A1 (Appendix).

Details on the SEBAL modelling using the MODIS imagery are described in Meijninger and Jarmain (2014). One MODIS scene per month was selected from 3 hydrological years (July to June inclusive) (2000–2001, 2002–2003, 2006–2007). Scenes obscured by cloud cover were excluded from analysis, resulting in 6 months of missing data over the 36 months sampled (Table A1; Appendix). Crop resistance (s·m⁻¹) was also calculated and extracted from the SEBAL outputs, and therefore stomatal conductance, the inverse, could also be estimated (m·s⁻¹). Details on the SEBAL modelling using Landsat7 imagery are described in Klaasse et al. (2008). One Landsat7 scene per month (or 2 for 2 months combined) were selected over the growing season (September to April) of 3 hydrological years (2004–2005, 2005–2006, 2006–2007) (Table A2; Appendix). Evapotranspiration rates were calculated from instantaneous and daily energy balance results from the SEBAL model, and extrapolated to a monthly sum using meteorological data (Klaasse et al., 2008).

Crop factor calculations

Crop factors are used as a multiplying factor to estimate actual evapotranspiration rates for various types of vegetation cover, applied to a grass reference evapotranspiration rate (Allen et al., 1998; Savage et al., 2010). Therefore, the crop factor distinguishes different vegetation types from a grass reference crop with no water or nutrient stress (Allen et al., 1998). Grass reference evapotranspiration rates are usually calculated at an automatic weather station using the Penman-Monteith approach based on various atmospheric measurements (Savage et al., 2010). Crop factors are calculated by the quotient of evapotranspiration and reference evapotranspiration. A crop factor for Palmiet wetlands was calculated in this way, using the estimated evapotranspiration

from the SEBAL outputs (using MODIS- and Landsat7 data) and reference evapotranspiration which was obtained from the local weather stations described above. The caveat of this approach is that it is not known whether Palmiet in the Theewaterskloof wetland was water-stressed in any of the monthly scenes over the three hydrological years of measurement. However, Palmiet wetlands are highly connected to fluvial systems, and it is thought that they are fed to some extent by groundwater; therefore they are less likely to experience water-stress than terrestrial vegetation-types (Job, 2014; Rebelo, 2017). Therefore, this crop factor for Palmiet wetlands is useful as a first estimate, but further research is needed.

Data analysis

All field-measured stomatal conductance data were screened and found to be normally distributed. A mixed model repeated measures analysis of variance (ANOVA) was used to determine the significance of the difference between stomatal conductance measurements for three variables (level of inundation of the soil, abaxial/adaxial leaf surface, whether the leaf was positioned in the shade or the sun) at different times of day and in different seasons (Tables A3–A5; Appendix). Linear mixed models in R were used to confirm these results (lme4 package; Bates et al., 2015, Table A6; Appendix). Pearson correlations were used to investigate the relationship between measured stomatal conductance and various weather station measured climatic variables (wind speed, vapour pressure, saturated vapour pressure, temperature, vapour pressure

deficit, radiation, potential evaporation, and relative humidity) (Fig. A2; Appendix). A ‘Classification And Regression Tree’ (CART) Analysis (Breiman et al., 1984) was used to determine the relative importance of variables significantly affecting stomatal conductance (Fig. A3; Appendix).

Monthly Landsat7 SEBAL evapotranspiration values were not available for the three winter months. Therefore, to estimate annual evapotranspiration, the monthly dataset was interpolated using a linear model based on the relationship between monthly Landsat7 and MODIS SEBAL evapotranspiration (Pearson correlation: $r = 0.87$) (Fig. A4; Appendix). Comparisons between field measurements and modelled stomatal conductance and crop factors were also made using Pearson correlations.

RESULTS

In an average stand of Palmiet (*Prionium serratum*), the mean (\pm standard deviation) number of plants per m^2 ($n = 10$) is 7.0 ± 1.76 . The mean ($n = 10$) number of living leaves per plant is 48.3 ± 13.56 , and dead leaves is 8.3 ± 5.03 . The mean ($n = 50$) length of leaves is 89.7 ± 11.75 cm. The leaf area index of Palmiet is 11.2 ± 1.10 ($n = 25$). The number of stomata does not differ between adaxial and abaxial leaf surfaces of Palmiet leaves. From an epidermal peel of both surfaces, stomata do not appear to be sunken (Fig. 2a), as stomatal guard cells are located at the leaf surface. Yet, cross-sections through a Palmiet leaf reveal large substomatal chambers behind the guard cells (Fig. 2b–e).

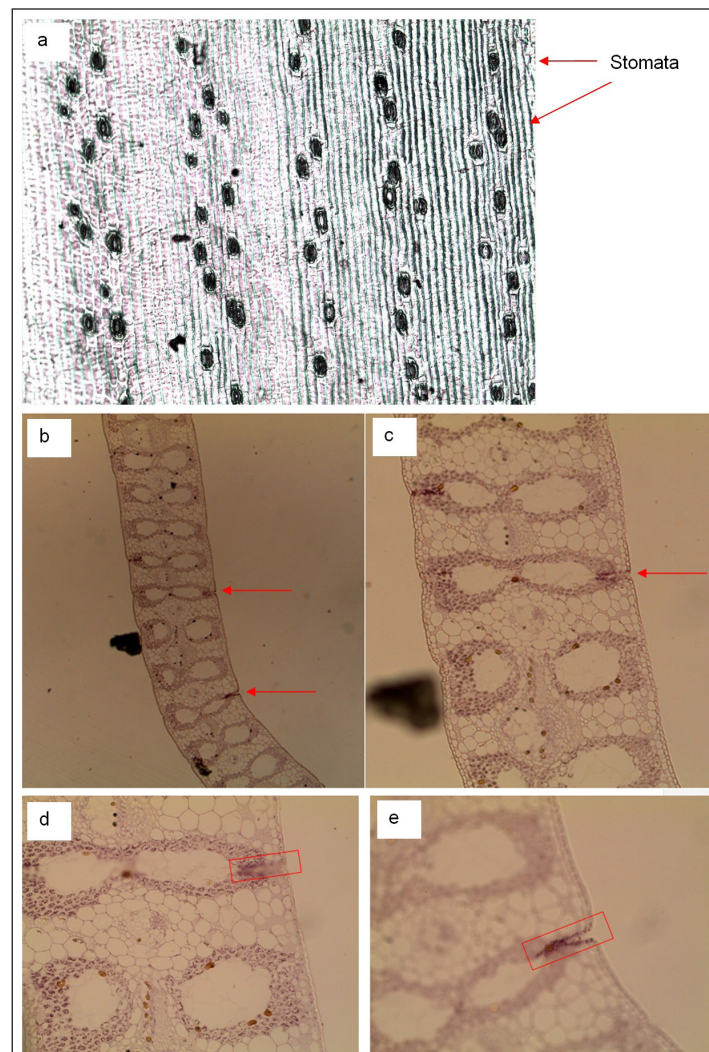


Figure 2. (a) Epidermal peel of the adaxial surface of a leaf of Palmiet (*Prionium serratum*) (10x), and cross sections through leaves at (b) 4x, (c) 10x, and (d, e) 20x. Red arrows and squares indicate the position of stomatal apertures

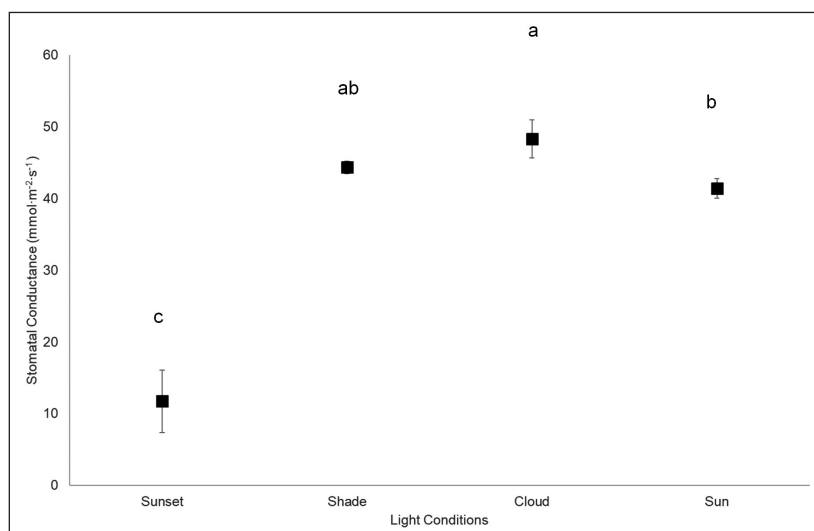


Figure 3. The effect of light conditions on stomatal conductance of Palmiet plants (*Prionium serratum*) in Jonkershoek, Western Cape. Blocks represent means and bars the 95% confidence intervals. Points with the same letters denote no significant difference

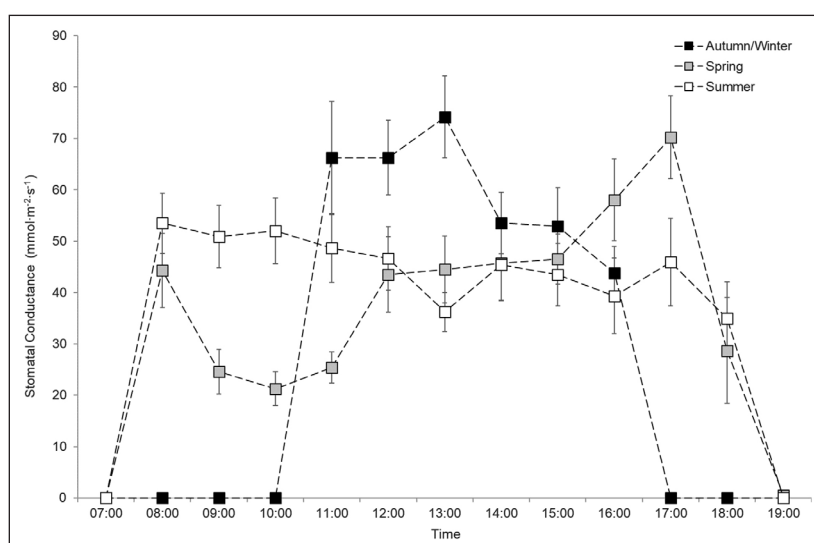


Figure 4. The effect of season and time on mean ($\pm 95\%$ confidence interval) stomatal conductance of Palmiet (*Prionium serratum*) in Jonkershoek, Western Cape

Stomatal conductance of Palmiet ranged from 11–152 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ daily and did not differ significantly with inundation, or between the abaxial and adaxial surfaces (Table A6; Appendix). Three variables were found to be important in influencing stomatal conductance in both a CART analysis (%) and using linear mixed models: light condition the leaves were exposed to (100%, Fig. 3 and Fig. A3; Appendix), the season (87%) and the time of day (82%) (Fig. 4, Table A6; Appendix). Palmiet stomatal conductance was significantly higher in cloudy compared to sunny conditions (Fig. 3, Table A4; Appendix). Before the sun rose in the morning stomatal conductance was undetectable, and after the sun set in the evening, stomatal conductance dropped significantly until it again became undetectable (Fig. 4). Wind speed, saturated vapour pressure, temperature, vapour pressure deficit, radiation, potential evaporation and relative humidity had no significant effect on the stomatal conductance of Palmiet (Fig. A2; Appendix). Vapour pressure had a significant positive effect on stomatal conductance ($p < 0.05$, $t = 1.94$).

Diurnal patterns of stomatal conductance differed significantly ($p < 0.05$) among seasons (Fig. 4, Table A5, Table A6; Appendix). In spring, stomatal conductance was low in the early morning and increased toward sunset (mean: $34.9 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). In summer, stomatal conductance was maintained at a mostly constant level throughout the day (mean: $38.2 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) whilst in winter it

was relatively high in the morning and declined towards the end of the day (mean: $27.4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

SEBAL model results using Landsat-7 as input gave the highest estimate for mean annual evapotranspiration of Palmiet, based on 7 months of data (spring, summer, autumn) over 3 hydrological years, and MODIS-SEBAL model results gave the lowest, based on 12 months of data over 3 hydrological years (Table 1). However, these estimates were reasonably well correlated ($r = 0.87$, Fig. A4; Appendix). The mean of the annual estimates calculated is $1\,220 \text{ mm}\cdot\text{a}^{-1}$. Evapotranspiration of Palmiet wetlands was higher in summer than winter (seasonal trends in Fig. A5; Appendix). The MODIS SEBAL model estimates for monthly stomatal conductance of the Theewaterskloof Palmiet wetland were somewhat lower than the stomatal conductance measured on 6 Palmiet plants at Jonkershoek, and they were poorly correlated ($r = 0.34$, Fig. A6). Stomatal conductance tended to be higher in winter (seasonal trends in Fig. A5; Appendix). The mean MODIS crop factor was slightly lower than that of Landsat7, and the monthly crop factors for the two were poorly correlated ($r = 0.47$). A-Pan evaporation was $2\,809 \text{ mm}\cdot\text{a}^{-1}$ on average from 1990–2005 according to the Villiersdorp weather station (Table A7; Appendix). Therefore, the pan coefficient (the ratio of mean evapotranspiration to mean pan evaporation) for Palmiet wetlands ranges from 0.37–0.50 (mean: 0.46) based on evapotranspiration in Table 1.

Table 1. A comparison of water-use values for Palmiet (*Prionium serratum*), in terms of evapotranspiration (Et) and stomatal conductance (cond.) across all scales, sites and methods used in this study. The (*) symbol indicates the interpolated Landsat7 values (calculated using a linear model based on the relationship between monthly Landsat7- and MODIS-SEBAL evapotranspiration ($r = 0.87$)). The crop factors (K_c) are calculated from the quotient of evapotranspiration and reference evapotranspiration. Note, the K_c values cannot be guaranteed to be stress-free values (see discussion in methods) (Allen et al. 1998)

Month	Remote sensing	Remote Sensing	Porometry	Remote sensing	Remote sensing	Remote Sensing
	SEBAL Et (based on Landsat7 inputs) (mm)	SEBAL Et (based on MODIS inputs) (mm)	Stomatal cond. ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Stomatal cond. (based on MODIS inputs) ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Landsat7 K_c	MODIS K_c
January	188.61	153.60		17.41	1.38	1.00
February	163.91	129.47	40.89	17.12	1.31	1.09
March	102.90	87.67	46.08	14.04	1.03	1.04
April	108.01*	81.27		32.85		1.20
May	51.21*	43.39		21.30		1.10
June	43.14*	38.00	59.86	25.99		1.15
July	30.53*	29.59		14.02		0.94
August	55.53*	46.27		32.18		1.01
September	132.75	73.51		29.16	1.07	1.12
October	133.95	102.23	48.50	23.77	1.00	1.07
November	166.90	110.29	36.85	28.20	1.16	1.00
December	220.21	147.65	31.86	33.69	1.48	1.01
Annual estimate (Mean)	1 397.64	1 042.94	44.01	24.15	1.20	1.06

Table 2. Ranges of leaf stomatal conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for different growth forms of Fynbos from the Cape Floristic Region, South Africa. Table adapted from Von Willert et al. (1989) and Miller et al. (1984)

Source	Location	Leaf stomatal conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)					
		Tall shrub	Mid shrub	Restioid	Geophyte	Graminoid	Palmiet
Miller et al., 1984	Cederberg (Algeria: Waboomveld)	75–217	31–665	134–339	110–146	-	-
	Cederberg (Algeria: 23 years)	43–264	71–598	283–445	-	-	-
	Jonkershoek (Waboomveld)	90–452	90–452	-	-	-	-
	Jonkershoek (Swartboskloof)	45–904	37–1 100	-	-	252–358	-
	Jonkershoek (Langrivier)	77–528	191–213	265–427	195	-	-
	Jakkalsrivier	60–143	425	350	-	105	-
	Pella	126–455	57–646	219–585	-	-	-
Von Willert et al., 1989	Cederberg	68–157	61–125	89–139	226	91	-
This study	Jonkershoek	-	-	-	-	-	11–152

DISCUSSION

The leaf area index of Palmiet measured in this study was very high relative to other vegetation types, commensurate with its high biomass and therefore possibly indicative of high transpiration. In a global synthesis of leaf area index measurements, deserts had the lowest values, with a mean \pm standard deviation of 1.3 ± 0.9 , tree plantations had the highest values (8.7 ± 4.3) followed by temperate evergreen forests (ranging from a mean of 5.1–6.7) and then wetlands (6.3 ± 2.3) (Asner et al., 2003). The leaf area index for Fynbos has been estimated as 2–3 (Miller et al., 1984).

The possibly high transpiration hinted at by Palmiet's leaf area index value is at odds with its atypical leaf morphology. Stomatal guard cells open into large cavities, or 'substomatal chambers' within the leaf, identical on both leaf surfaces, suggesting an adaptation to enhance carbon dioxide influx or minimize water vapour efflux or both (Pickard, 1982). One possible explanation for these xeromorphic adaptations could be the seasonal nature, or inter-annual variation, of water saturation in wetlands throughout the Cape Floristic Region. A second theory could be that oligotrophic soils (and groundwater) explain the extreme sclerophylly of the species (Specht, 1988; Esler et al., 2018). An excess of moisture, but shortage of phosphorus, could lead to the accumulation of

carbon, which is consequently allocated to structural phenomena, such as thicker leaves (Medina et al., 1990).

Palmiet appears to have a lower stomatal conductance than most other terrestrial Fynbos plants (Table 2). This is counter-intuitive given that Palmiet is a wetland plant and is thought to have essentially unlimited access to water in the root zone. In terms of rates of stomatal conductance, Palmiet compares most closely with that of terrestrial mid-sized shrubs and Restioids in the Cederberg; 11–152 compared to 61–125 and 89–139 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Von Willert et al., 1989). Annual evapotranspiration of riparian Fynbos (a Restioid wetland) in Jonkershoek was estimated at $1\,332\text{ mm}\cdot\text{a}^{-1}$ using the Bowen ratio energy balance technique (mean annual precipitation of $1\,324\text{ mm}$) (Dye et al., 2001). Based on the evidence that Palmiet has lower stomatal conductance than Restioid wetlands, it is likely that the annual evapotranspiration of the Palmiet wetland in Jonkershoek is lower than $1\,332\text{ mm}\cdot\text{a}^{-1}$. This corresponds well to the mean of the Landsat7 and MODIS SEBAL annual evapotranspiration estimates of $1\,220\text{ mm}\cdot\text{a}^{-1}$.

A recent study on the evapotranspiration of Palmiet wetlands found that the growing season evapotranspiration (October to April) ranged from $138\text{ mm}\cdot\text{a}^{-1}$ to $1\,204\text{ mm}\cdot\text{a}^{-1}$, depending on the

wetland size, climatic region and the model used (Ramatsabana et al., 2019). The growing season evapotranspiration (September to March) estimated by the SEBAL model using Landsat7 and MODIS in this study was 1 109.23 mm·a⁻¹ and 885.69 mm·a⁻¹, respectively. Factors contributing to the difference in monthly evapotranspiration between the Landsat7 and MODIS SEBAL models include: (i) that satellite data were from different dates (years) with different climatological conditions, (ii) the differences in spatial and temporal resolutions of the data and hence the landcover considered (e.g. more landcover adjacent to wetland included for coarser imagery), and (iii) gaps in the measurements and errors associated with the data infilling approach (e.g., simple linear mixed model for Landsat7). This range in Palmiet mean annual evapotranspiration for the different methods therefore gives an idea of associated error or possibly even of variation in annual evapotranspiration. Further research is needed to improve the measurements of water-use of this, and other, key wetland species in South Africa.

The Palmiet mean annual evapotranspiration (mean of the Landsat7 and MODIS SEBAL outputs) is lower than reference evapotranspiration for the catchment (1 302 mm·a⁻¹ on average from 2004–2007 according to the Villiersdorp weather station, Table A8; Appendix), and far lower than A-Pan evaporation (2 809 mm·a⁻¹ on average from 1990–2005 according to the Villiersdorp weather station, Table A7; Appendix). A-Pan evaporation is a theoretical indication of open water evaporation, and reference evapotranspiration indicative of a short, well-watered grass surface with no water or nutrient stress (Allen et al., 1998). Therefore, water salvage from clearing Palmiet from a wetland is highly unlikely and retaining the wetlands is likely to constitute water savings. The pan coefficient for Palmiet wetlands shows the same trend as global studies (i.e. < 1, suggesting that wetlands reduce evaporation efficiency compared to open water), but was markedly lower than the global average of 0.87 ± 0.26 for wetlands (Mohamed et al., 2012).

In south-eastern Australia this method for estimating water savings has been applied to the removal of in-stream invasive alien *Salix* species (Doody et al., 2014). Differences in the modelled (Penman–Monteith) evapotranspiration for *Salix* species and open-water evaporation (A-Pan) showed that 450 to 763 mm water could be returned to the environment per year (Doody et al., 2014). Given that Palmiet is a wetland species with moderate water-use, it must be able to exert some controls on water loss (Ramatsabana et al., 2019). For example, the mean annual evapotranspiration for an invasive alien tree (*Acacia mearnsii*) infestation in a riparian zone in the Western Cape is far higher. It is thought that annual evapotranspiration may exceed 1 500 mm·a⁻¹ where there are no soil water deficits throughout the year (Dye and Jarman, 2004).

Stomatal conductance measurements recorded higher maxima in autumn/winter than in summer and spring. However, on average, stomatal conductance was still higher in summer and spring than in winter. It may be that Palmiet responds to warmer conditions and increased radiance by reducing the size of its stomatal aperture, decreasing stomatal conductance. Again, this physiological adaptation is counter-intuitive for a wetland plant which has no shortage of water, but we hypothesize that this may be its means of persistence during interannual periods of drought (e.g. such as the 2015–2017 southwestern Cape drought). However, a second theory is that Palmiet has ‘cool climate growth’ adaptations, like most Fynbos plants (Esler et al., 2018).

Despite having higher stomatal conductance maxima in winter, evapotranspiration of Palmiet wetlands was consistently higher during the warmer months than in winter, across all methods. Winter MODIS SEBAL modelled evapotranspiration of Palmiet

wetlands was only 26% of summer modelled evapotranspiration. Spring MODIS SEBAL modelled evapotranspiration of Palmiet wetlands was 66% of the same for summer, whereas spring Landsat7 SEBAL modelled evapotranspiration was 76% of summer evapotranspiration. Another study on Palmiet wetland water-use noted similar significant seasonal variations, as well as regional variations linked to local climate (Ramatsabana et al., 2019).

The poor correlation between measured stomatal conductance and the MODIS SEBAL model stomatal conductance outputs supports the notion that it is difficult, if not impossible, to scale up from stomatal conductance to evapotranspiration, or vice versa, without complex models (Ding et al., 2014). However modelling evapotranspiration for these small wetlands using satellite imagery is not without challenges at the spatial resolutions at which that imagery is currently available. In another study on Palmiet wetlands, the relatively coarse spatial resolution of satellite imagery resulted in the interference of adjacent landcover in water-use signals of Palmiet wetlands (Ramatsabana et al., 2019). For this study, it should also be noted that local differences in climate between the Jonkershoek and Theewaterskloof valleys may also play a role in driving these slight differences in water-use by the plant Palmiet.

In conclusion, it seems that Palmiet has moderate water-use for a Fynbos riparian species (and certainly relative to invasive alien trees in riparian zones), which is an added benefit to retaining and preserving native vegetation in Palmiet wetlands. Palmiet appears to have morphological and physiological adaptations to limit water-use, despite growing exclusively in riparian areas. These adaptations may have ensured the competitiveness of Palmiet during extremely dry years, or may be linked to adaptations to oligotrophy, two possible theories explaining its dominance in valley-bottom wetlands.

ACKNOWLEDGEMENTS

The South African Weather Service is acknowledged for access to meteorological data. The authors wish to thank the following organizations for funding: ASSET Research, the Water Research Commission of South Africa, the Fynbos Forum Innovation Scholarship (Table Mountain Fund and WWF), the HB Thom Fund, Dudley D’Ewes Scholarship (Cape Tercentenary Foundation), Consolidoc (Stellenbosch University) and the Ernst and Ethel Eriksen Trust.

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APPENDIX

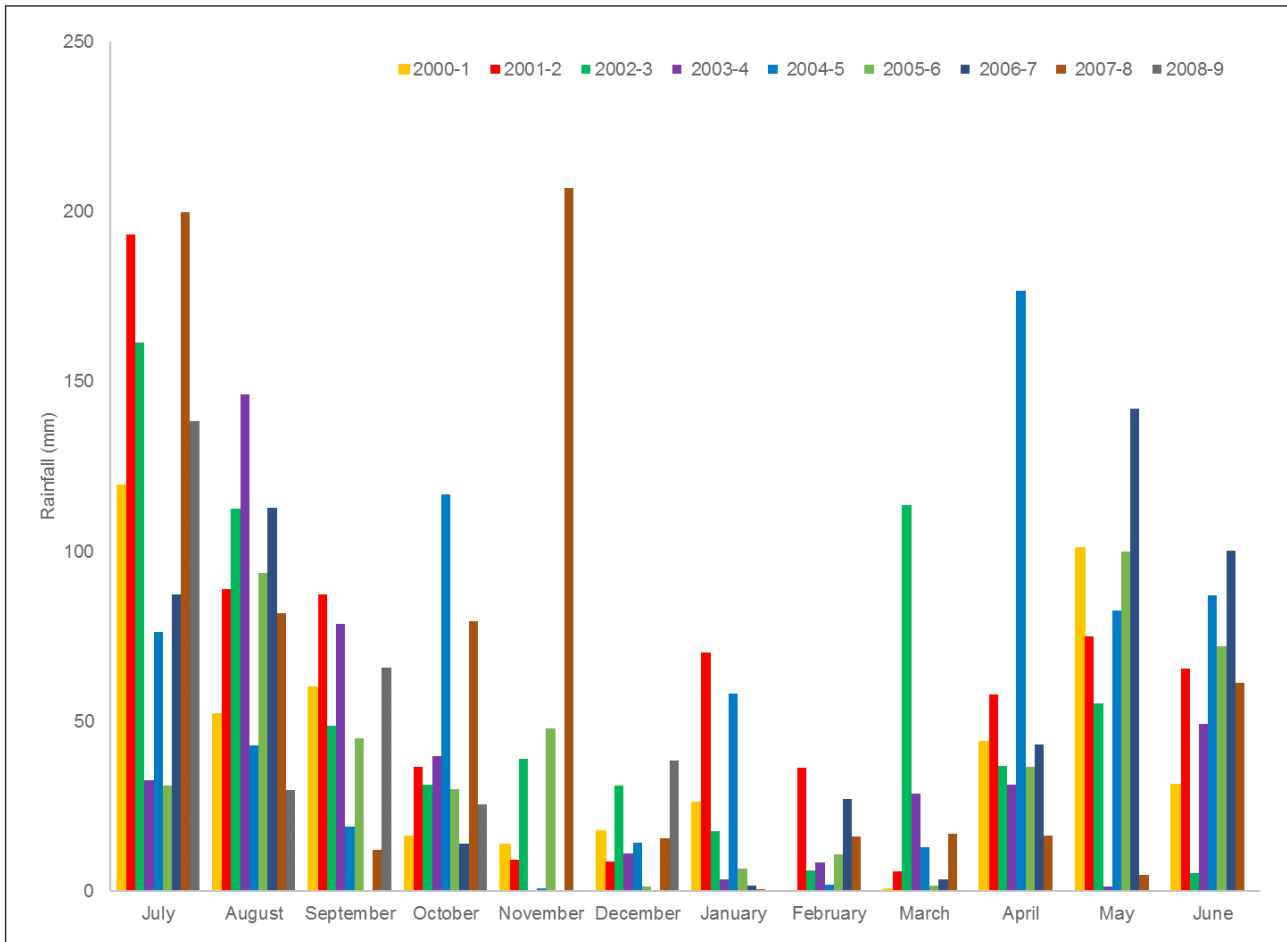


Figure A1. Mean monthly rainfall from the Villiersdorp weather station from 2000-2009, showing inter-annual variability and intra-annual patterns

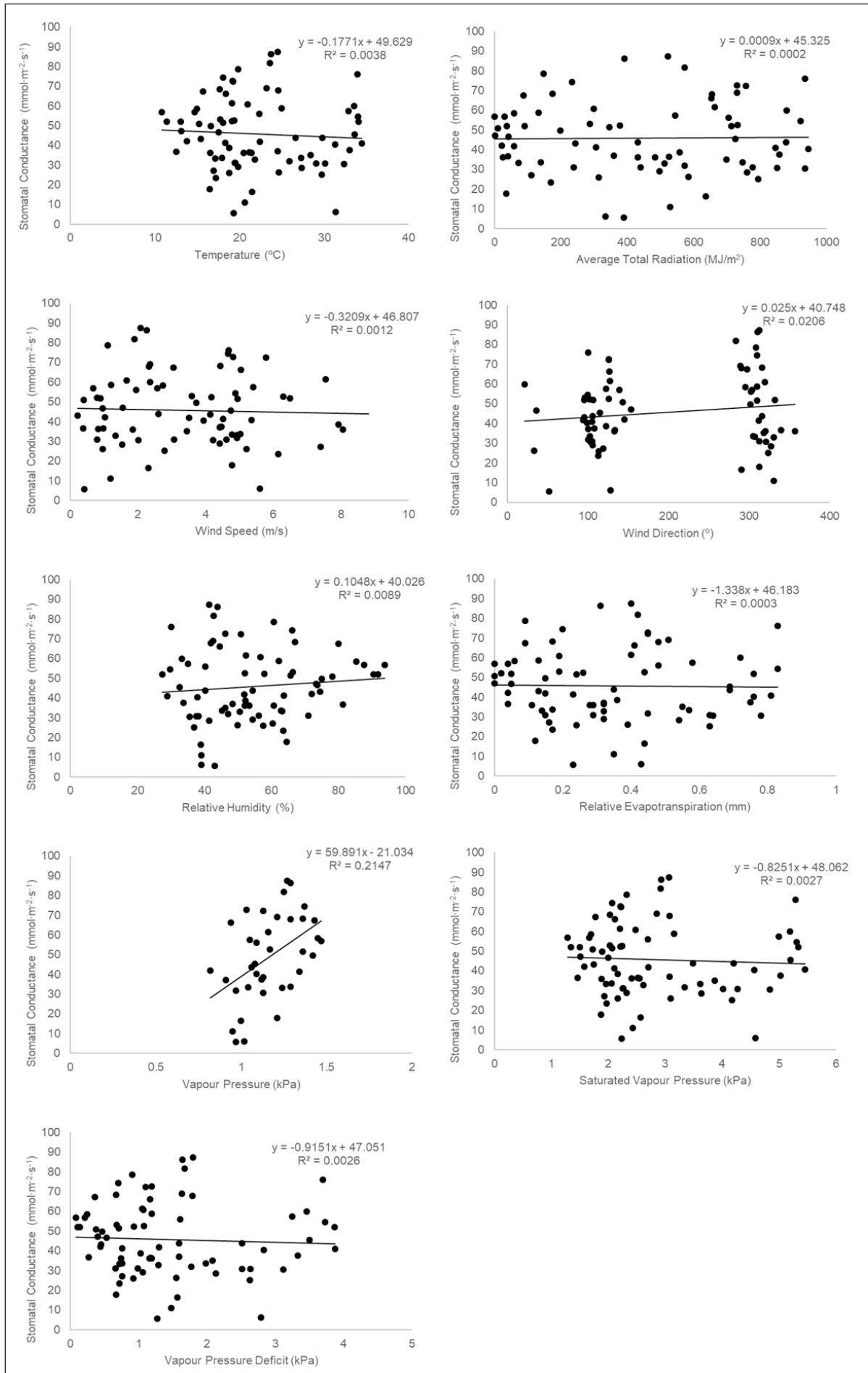


Figure A2. Correlations between field-measured stomatal conductance and climate variables taken from the South African Weather Service station at Swartboskloof

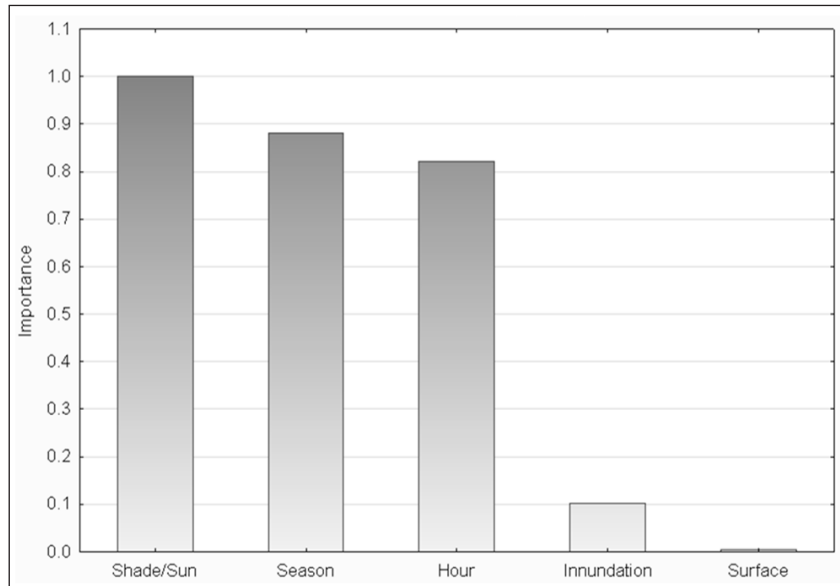


Figure A3. The relative importance of each of five variables on the stomatal conductance of Palmiet (*Prionium serratum*) in Jonkershoek, Western Cape using a CART Analysis

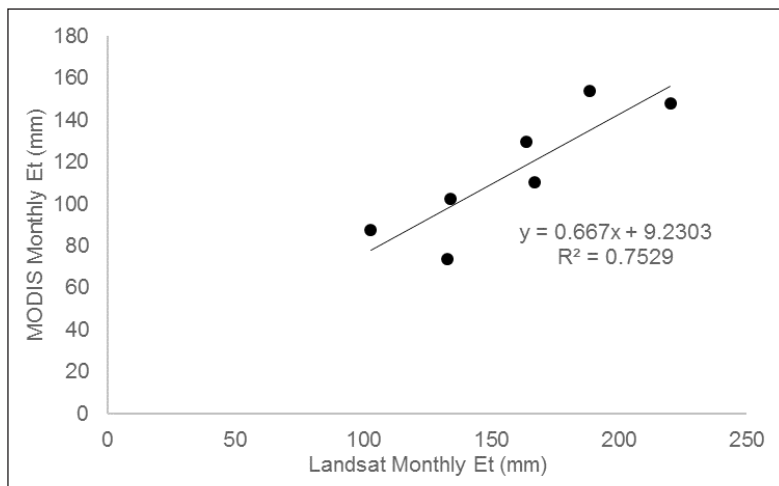


Figure A4. Correlation between the modelled monthly Landsat7-SEBAL and MODIS-SEBAL results for evapotranspiration of Palmiet: $R^2 = 0.7529$; $r = 0.8677$

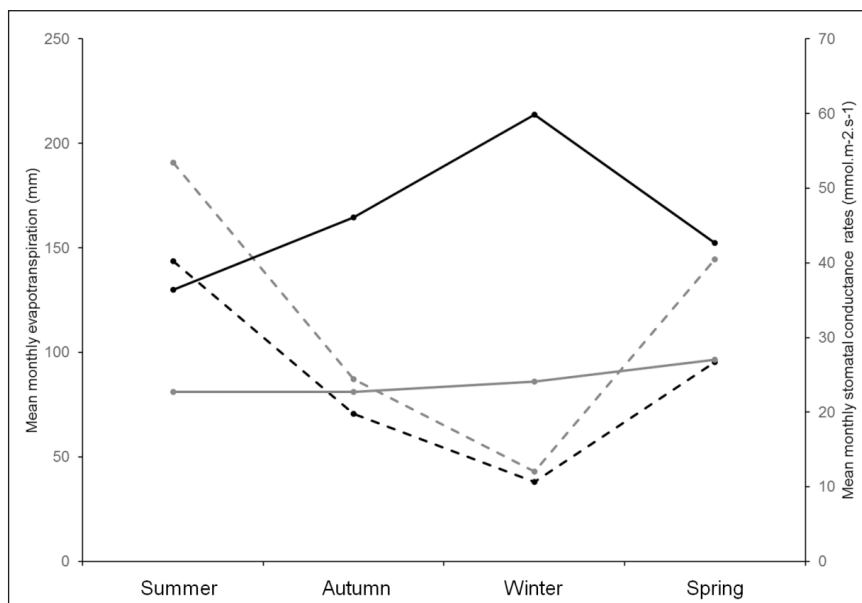


Figure A5. Seasonal trends in Landsat7 SEBAL (●) and MODIS SEBAL (●) evapotranspiration (stippled lines), and the field measured (●) and MODIS SEBAL (●) stomatal conductance (solid lines)

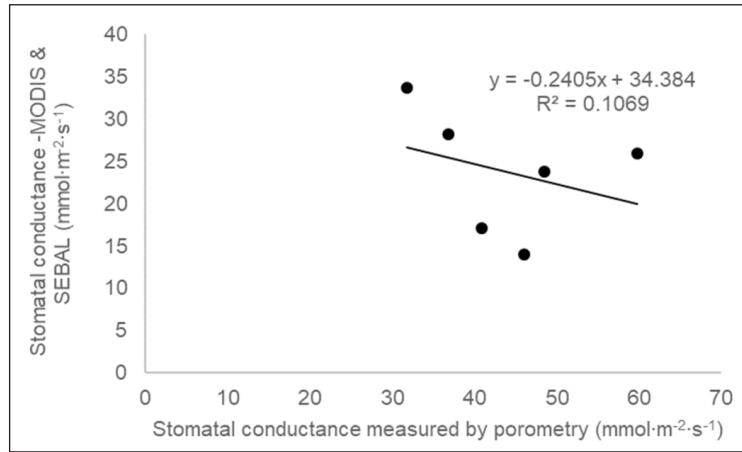


Figure A6. Correlation between monthly field measured stomatal conductance and modelled stomatal conductance from the SEBAL model (using MODIS imagery): $R^2 = 0.1069$; $r = 0.3270$

Table A1. Summary statistics for monthly MODIS SEBAL evapotranspiration (all units as mm/month) per scene showing the year, month and seasons sampled; 6 images out of 36 were excluded due to cloud cover. Data were obtained from the research by Meijninger and Jarman (2014)

Year	Month	Season	Clouds	Min	Max	Range	Mean	Std dev
2000	07	Winter	Cloud					
2000	08	Winter	Cloud					
2000	09	Spring	0	59.01	70.38	11.38	66.54	3.45
2000	10	Spring	0	134.71	154.88	20.17	147.24	6.27
2000	11	Spring	0	104.84	118.57	13.74	111.79	4.71
2000	12	Summer	0	135.97	162.91	26.94	149.14	8.75
2001	01	Summer	0	125.45	147.14	21.69	135.55	7.32
2001	02	Summer	0	110.91	122.80	11.89	116.63	3.65
2001	03	Autumn	0	81.45	99.46	18.01	91.52	5.10
2001	04	Autumn	Cloud					
2001	05	Autumn	0	25.90	37.60	11.70	32.87	3.23
2001	06	Winter	0	18.91	37.92	19.01	29.43	5.32
2002	07	Winter	0	25.66	41.05	15.39	35.58	4.40
2002	08	Winter	0	41.51	59.18	17.67	53.13	4.73
2002	09	Spring	Cloud					
2002	10	Spring	0	63.48	70.89	7.42	68.39	2.24
2002	11	Spring	0	101.94	111.50	9.56	108.78	2.85
2002	12	Summer	Cloud					
2003	01	Summer	0	146.87	165.86	18.98	160.04	5.19
2003	02	Summer	0	128.11	142.79	14.67	137.00	4.18
2003	03	Autumn	0	71.02	85.22	14.20	80.45	4.29
2003	04	Autumn	0	72.32	87.66	15.33	80.94	4.34
2003	05	Autumn	0	29.46	44.71	15.25	38.84	4.25
2003	06	Winter	0	22.01	43.30	21.29	35.12	6.08
2006	07	Winter	0	16.54	28.13	11.59	23.61	3.26
2006	08	Winter	0	33.77	43.13	9.37	39.41	2.72
2006	09	Spring	0	69.82	86.15	16.33	80.48	4.44
2006	10	Spring	0	87.94	93.26	5.32	91.07	1.77
2006	11	Spring	Cloud					
2006	12	Summer	0	139.74	150.45	10.71	146.17	3.35
2007	01	Summer	0	161.72	167.36	5.64	165.21	1.82
2007	02	Summer	0	126.31	137.67	11.36	134.79	3.48
2007	03	Autumn	0	78.69	96.50	17.81	91.03	4.93
2007	04	Autumn	0	72.78	86.13	13.36	81.60	3.89
2007	05	Autumn	0	43.11	66.73	23.62	58.45	6.24
2007	06	Winter	0	36.33	55.15	18.82	49.45	5.02

Table A2. Summary statistics for monthly Landsat7 SEBAL evapotranspiration (all units as mm/month or for 2 months depending on the number of scenes used) per scene showing the year, month and seasons sampled. Data were obtained from the research by Klaasse et al. (2008)

Image date			SEBAL period		Evapotranspiration per time period (mm)						
Year	Month	Day	Day/month	Season	Number of scenes	Min	Max	Range	Mean for all scenes	Mean	Std dev
2004	09	20	09/2004	Spring	1	65.06	127.96	62.90	104.35	104.35	13.45
2004	10	22	10/2004	Spring	1	86.72	174.80	88.08	133.95	133.95	14.94
2004	11	15	11/2004	Spring	1	170.37	234.93	64.56	204.65	204.65	8.67
2004	12	09	12/2004	Summer	1	184.07	257.48	73.41	220.20	220.20	13.43
2005	01	18	01/2005	Summer	1	121.29	228.19	106.90	192.25	192.25	15.90
2005	02	27	02/2005	Summer	1	134.07	189.06	54.99	163.91	163.91	10.94
2005	03	23	03–04/2005	Autumn	2	88.69	248.83	160.14	173.25	86.63	25.69
2005	10	09	09–10/2005	Spring	2	247.12	352.46	105.34	306.43	153.22	28.21
2005	12	04	11/2005	Spring	1	107.90	199.87	91.96	165.98	165.98	12.57
2005	12	20	12/2005	Summer	1	160.53	290.42	129.89	250.42	250.42	17.07
2006	02	06	01–02/2005	Summer	2	207.63	407.84	200.21	329.59	164.80	34.21
2006	03	10	03–04/2005	Autumn	2	166.31	310.67	144.37	262.26	131.13	17.98
2006	10	12	09–10/2006	Spring	2	231.25	319.00	87.75	281.34	140.67	15.88
2006	10	28	11/2006	Spring	1	85.75	149.36	63.61	130.07	130.07	9.26
2006	12	23	12/2006	Summer	1	154.16	206.99	52.83	190.03	190.03	8.77
2007	02	17	01–02/2007	Summer	2	366.12	451.32	85.21	417.56	208.78	15.72
2007	03	13/29	03–04/2007	Autumn	2	172.52	219.06	46.54	181.86	90.93	6.14

Table A3. One-way analysis of variance (ANOVA) Statistics. Significance is denoted by *

ANOVA	DFn	DFd	F	p	ges
Inundation	1	1 815	0.133	0.716	7.3×10^{-5}
Surface	1	1 815	0.409	0.523	0.000225
Light	3	1 813	24.892	8.81×10^{-16} *	0.04

Table A4. Posthoc analysis of variance (ANOVA) statistics to understand the significance of differences among light levels. Significance is denoted by: 0 **** 0.001 ** 0.01 * 0.05. ns: not significant

	group1	group2	n1	n2	p	P sign.	P adjusted	P adjusted sign.
1	Cloud	Shade	278	1 150	0.053	ns	0.320	ns
2	Cloud	Sun	278	382	0.004	**	0.025	*
3	Cloud	Sunset	278	56	8.44×10^{-17}	****	5.07×10^{-16}	****
4	Shade	Sun	1 150	382	0.096	ns	0.574	ns
5	Shade	Sunset	1 150	56	1.01×10^{-15}	****	6.06×10^{-15}	****
6	Sun	Sunset	382	56	2.39×10^{-12}	****	1.43×10^{-11}	****

Table A5. Statistical results of repeated-measures analysis of variance (ANOVA) in comparing the effects of season and time, as well as the interaction between them. Significance is denoted by: 0 **** 0.001 ** 0.01 * 0.05. ns: not significant

Parameter	Df	Sum sq	Mean sq	F value	Pr (>F)	Significance
Season	2	81 409	40 705	60.12	$<2 \times 10^{-16}$	***
Time	12	177 270	14 773	21.82	$<2 \times 10^{-16}$	***
Season:Time	15	130 789	8 719	12.88	$<2 \times 10^{-16}$	***
Residuals	1770	1 198 318	677			

Table A6. Statistics comparing the significance of including various fixed effects in predicting stomatal conductance. The model included fixed (season, time, light, inundation, leaf surface), random (date, plant) and interaction effects (season:time, time:light) of Palmiet wetland stomatal conductance. The F-test with Kenward-Roger approximation was used to make comparisons between models. Significance is denoted by: 0 *** 0.001 ** 0.01 * 0.05.

F Test	F Statistic	ndf	ddf	F Scaling	p value
Season	5.54	17.00	156.28	0.96	1.264 x 10 ⁻⁹ ***
Time	14.66	46.00	1 739.38	1.00	<2.2 x 10 ⁻¹⁶ ***
Light	11.25	22.00	1 476.23	1.00	<2.2 x 10 ⁻¹⁶ ***
Inundation	0.28	1.00	4.01	1.00	0.6272
Leaf surface	2.96	1.00	1 754.09	1.00	0.08549

Table A7. Total monthly A-Pan evaporation (mm) from the Villiersdorp weather station (South African Weather Service). Mean annual A-Pan evaporation for all years was 2 809 mm·a⁻¹.

	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
January	431.9	389.3	429.4	452.2	389.0	422.1	351.6	389.0	409.0	382.6	357.9	409.1	351.8	428.9	300.7	354.9
February	349.8	330.1	329.8	364.0	313.1	367.0	364.7	309.9	341.7	354.1	348.4	335.4	323.1	344.2	281.7	305.2
March	267.5	323.9	302.7	291.4	293.0	273.6	291.5	278.0	268.7	326.8	239.8	244.5	302.9	304.3	261.5	284.6
April	189.6	221.6	198.2	106.3	191.4	183.2	222.5	142.5	173.2	212.0	145.0	149.0	197.1	186.9	171.7	136.5
May	100.1	142.9	106.3	78.4	99.8	112.2	128.4	154.0	93.5	113.4	101.9	173.3	123.3	118.2	159.8	110.2
June	72.9	106.4	84.0	72.9	81.4	102.5	120.7	75.1	97.0	137.6	108.3	104.9	97.6	106.0	145.4	71.0
July	107.4	97.2	115.7	123.1	80.0	109.4	86.4	120.2	107.6	129.4	88.0	116.4	90.6	175.7	93.3	108.2
August	137.2	131.7	117.7	125.5	105.9	130.7	123.9	104.2	142.9	137.6	125.5	143.5	151.2	148.7	116.4	58.0
September	209.9	156.2	151.5	171.9	192.0	176.0	171.6	201.7	200.2	133.1	189.9	183.0	200.2	188.8	210.9	138.8
October	290.8	205.4	231.0	305.7	305.3	268.3	208.2	341.8	318.7	270.4	250.2	242.4	318.5	300.2	283.1	185.3
November	325.3	342.3	350.5	361.4	378.9	306.5	261.5	307.3	308.4	322.3	359.6	351.1	383.2	335.6	331.3	305.0
December	420.6	428.0	430.0	384.5	388.5	300.1	364.0	408.0	353.6	411.3	360.6	391.9	424.4	319.9	424.8	354.5
TOTAL	2 903.09	2 874.99	2 846.69	2 837.15	2 818.23	2 751.44	2 694.9	2 831.65	2 814.57	2 930.29	2 675.12	2 844.37	2 963.69	2 957.36	2 780.34	2 412.12

Table A8. Total monthly reference evapotranspiration (mm) from the Villiersdorp weather station (South African Weather Service). Mean annual reference evapotranspiration for all years was 1 302 mm·a⁻¹.

Month	2004	2005	2006	2007
January	139.8	131.4	122.5	166.5
February	117.3	125.4	112.8	157.9
March	92.1	106.6	103.2	142.3
April	81.0	78.3	85.8	99.3
May	75.3	73.8	74.7	90.2
June	58.8	58.5	66.3	64.2
July	67.9	61.7	74.7	75.3
August	86.2	96.4	85.6	98.3
September	116.7	122.4	123.9	124.8
October	133.6	127.1	134.2	102.9
November	145.5	150.6	133.5	136.8
December	135.8	163.4	146.9	140.7
TOTAL	1 249.97	1 295.67	1 264.17	1 399.25