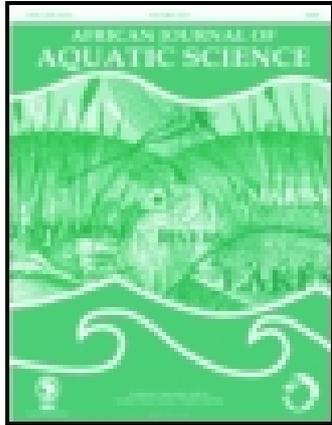


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Influence of climate variables on *Cyperus papyrus* stomatal conductance in Lubigi wetland, Kampala, Uganda

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Cyperus papyrus forms highly productive wetlands in tropical Africa, but the environmental control of transpirational water loss in wetlands is poorly understood. The influence of climate variables on papyrus stomatal conductance in dry and wet seasons of the year was investigated in a wetland in Kampala, Uganda, in June–December, 2012. *In situ* measurements were made of local climate conditions in a papyrus canopy and of bracteole stomatal conductance. Stomatal conductance was highest early in the day and declined as the day progressed, but stomata were more consistently open in the wet season than in the dry season. The daily cycle of stomatal conductance was influenced by temperature, incident radiation and vapour pressure deficit. Stomata were more sensitive to vapour pressure deficit changes during the wet season than in the dry season, closing sharply as vapour pressure deficit increased. This would seem to be a useful strategy for regulating transpiration, as it reduces water loss when the vapour pressure deficit gradient between the leaf intercellular spaces and the atmosphere is greatest.

Keywords: acclimatisation, photosynthetically active radiation, relative humidity, temperature, vapour pressure deficit

Introduction

The passage and loss of water through stomata as transpiration is a key physiological process in plants. The opening and closing of stomatal pores to allow the passage of water vapour is measured as stomatal conductance. Stomatal movement is regulated by a complex system of feed-back and feed-forward mechanisms involving both environmental and plant internal factors (Ball et al. 1987; Leuning 1995; Medlyn et al. 2011). Stomata normally open in response to increasing photosynthetically active radiation (PAR) (Meidner and Mansfield 1968) and decreasing vapour pressure deficit (VPD), but conflicting observations of stomatal response to temperature have been reported, where stomata open, close, or are not affected by increasing temperature (Meidner and Mansfield 1968; Schulze et al. 1973). Interactions between the effects of climate variables have been shown to be due to factors such as increased temperature, resulting in higher VPDs (Hall and Kaufmann 1975; Philippe 1989).

However, stomata do not always react in the same way to short-term (diurnal) variations of these environmental factors (Willmer and Fricker 1996). In addition, stomatal sensitivity can be modified over periods of days or weeks by phenology and acclimatisation to the changing environment, such as increasing water stress (Stewart 1988). Stomatal control of water loss from wetland species is relatively poorly understood, but estimates of water loss via evapotranspiration in tropical papyrus wetlands have been reported since the mid-20th century (Migahid 1952;

Penman 1963; Rijks 1969). More recently, Jones and Humphries (2002) and Saunders et al. (2007) investigated the relationship between papyrus water loss and climate factors based on eddy covariance flux measurements. *Cyperus papyrus*, the dominant species in highly productive wetlands in tropical Africa, is a C₄ sedge that uses the C₄ photosynthetic pathway (Jones 1987), but knowledge of the environmental control of stomatal movements and the consequent evapotranspiration is limited. Diurnal changes of stomatal conductance sensitivity to relative humidity (RH), air temperature, PAR and canopy transpiration have been assessed in some short-term studies (Jones and Muthuri 1984; Jones 1987), which indicated wide stomatal opening in the morning, partial closure at midday, and some wide opening during the afternoon. It was suggested that this response was to the VPD of the atmosphere, which is not, however, sufficient to cause a clear midday depression of photosynthesis (Jones 1987). Many studies have reported the direct influence of VPD on stomatal opening in a range of species in different environments (Hall and Kaufmann 1975; Black and Squire 1979; Schulze and Küppers 1979; Osonubi and Davies 1980; Mooney and Chu 1983; Jones and Muthuri 1984).

The present study was conducted during June–December 2012 to measure the diurnal patterns of papyrus stomatal conductance during dry and wet seasons in Lubigi wetland, Kampala, Uganda. It was hypothesised that differences in VPD between wet and dry seasons would influence

stomatal opening in such a way as to restrict water loss in the dry season, when VPDs are at their highest, and that the different climate conditions during wet and dry seasons would result in different daily patterns of stomatal conductance and transpiration.

Materials and methods

Study area

The study was conducted in a continuously flooded tropical monotypic *C. papyrus* wetland at Lubigi, approximately 7.5 km west of Kampala city, Uganda (Figure 1), at an altitude of approximately 1 165 m above sea level and covering geographical coordinates of 0°19' N to 0°22' N and 32°30' E to 32°32' E. The *C. papyrus* height in the wetland ranged between 5 and 6 m. The wetland forms a belt in the northern and western parts of Kampala and is surrounded by dense suburban populations. Rainy seasons in the area last from February to May and August to December, although in recent years the rainy seasons have been delayed. The shorter rainy season (February–May) sees substantially heavier rainfall per month, with April typically seeing the greatest precipitation with a monthly mean of approximately 175 mm. The lowest mean monthly temperature occurs in October, RH in January, February, July and September, and radiation in March–August and December–January (Figure 2).

Climate factors in the wetland

The air temperature, RH and PAR at the level of the canopy surface of the Lubigi wetland were monitored during the dry season of June–July 2012 and the wet season of August–November 2012 using a Skye weather station and Data Hog 2 logger (Type SDL 5260, Skye Instruments Llandrindod Wells, Powys, UK) installed 1 m above the canopy level. Climate variables were averaged at 30 min intervals and stored in the data logger. Stored data were downloaded to a computer every two weeks using Skye software. All channels for downloading climate variables were calibrated, tested and set up with the default factory settings.

The VPD in the papyrus canopy was calculated based on the formula of FAO (1998). Minimum and maximum values of temperature and RH were used in the calculations to avoid lower estimation of mean saturation vapour pressure. A standard value for the atmospheric pressure (kPa) and psychrometric constant (kPa °C⁻¹) as a function of altitude was used.

Mean saturated vapour pressure (e_s) of the air

Saturated vapour pressure (e_s) is related to air temperature and was calculated from the air temperature as follows:

$$e_s = [e^\circ(T_{\max}) + e^\circ(T_{\min})]/2$$

where T = daily air temperature (°C)

$$e^\circ(T) = 0.6108 \exp\{17.27T/(T + 237.3)\}$$

where $e^\circ(T)$ = saturated vapour pressure at air temperature T (kPa)

$\exp\{\} = 2.7183$ (base of natural logarithm) raised to the power $\{\}$

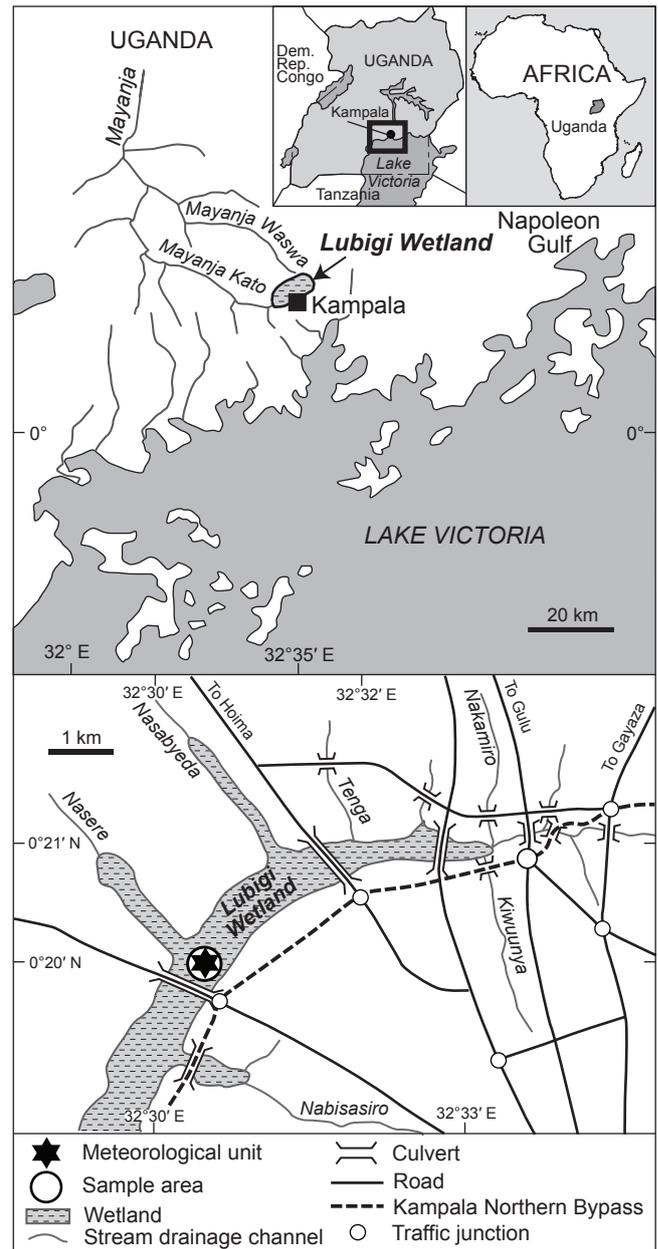


Figure 1: Map of a section of Lubigi wetland, Kampala, showing location of the weather station, the focal point of sampling

Actual vapour pressure (e_a) derived from relative humidity data of the air

Relative humidity expresses the degree of saturation of the air as a ratio of the actual (e_a) to the saturated ($e^\circ(T)$) vapour pressure at the same temperature (T). It is the ratio of the amount of water the ambient air actually holds to the amount it could hold at that temperature. Although the actual vapour pressure might be relatively constant throughout the day, the relative humidity fluctuates between a maximum near sunrise and a minimum in the early afternoon. Therefore the calculation of vapour pressure was as follows:

$$e_a = RH_{\text{mean}}/100 [(e^\circ(T_{\max}) + e^\circ(T_{\min}))]/2$$

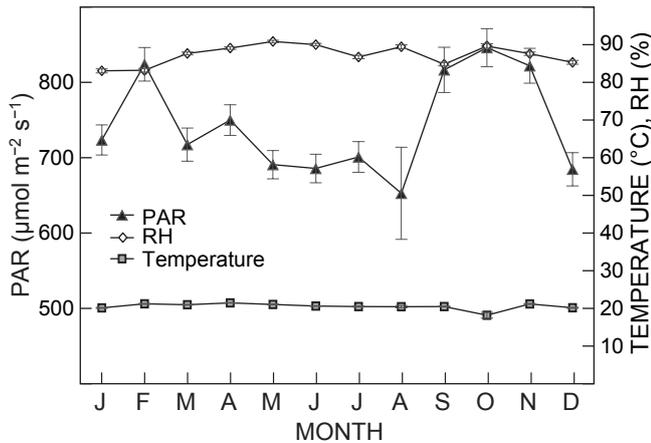


Figure 2: Mean monthly temperature, relative humidity (RH) and photosynthetically active radiation (PAR) in Lubigi *Cyperus papyrus* wetland canopy in 2012. Error bars are standard error of mean per month

where

- e_a = actual vapour pressure (kPa)
- RH_{mean} = average relative humidity, defined as the average between RH_{max} and RH_{min}
- RH_{max} = maximum relative humidity (%)
- RH_{min} = minimum relative humidity (%)
- $e^\circ(T_{\text{max}})$ = saturated vapour pressure at daily maximum temperature (kPa)
- $e^\circ(T_{\text{min}})$ = saturated vapour pressure at daily minimum temperature (kPa)

Vapour pressure deficit ($e_s - e_a$) of the air (VPD) is the difference between the saturated (e_s) and actual vapour pressure (e_a) of the air.

Bracteole stomatal conductance

The water flux through the stomata pores was measured using a steady state porometer (model AP4, Delta T Devices, Cambridge, UK) calibrated for maximum relative humidity of 60%. Calibration was done before the start of each day's measurements using a plate with six diffusion conductance settings. The calibration error rates were always less than 5%. Measurements were taken from the upper (abaxial) surface of bracteoles by inserting them into the porometer head cup. Measurements were taken every two weeks at hourly intervals during daylight (8:00–18:00) when the bracteole surface was free of dew from June 2012 to December 2012.

Five plants in the wetland, 50–300 m from the installed meteorological unit, that had similar canopy levels, were randomly selected for each day's measurements, and measurements were randomly taken from three bracteoles, with a total of 15 samples taken each hourly period.

Statistical analysis

Statistical analyses were done using Minitab software, Release 13 for Windows. The mean values of climate variables include readings over the whole month and also

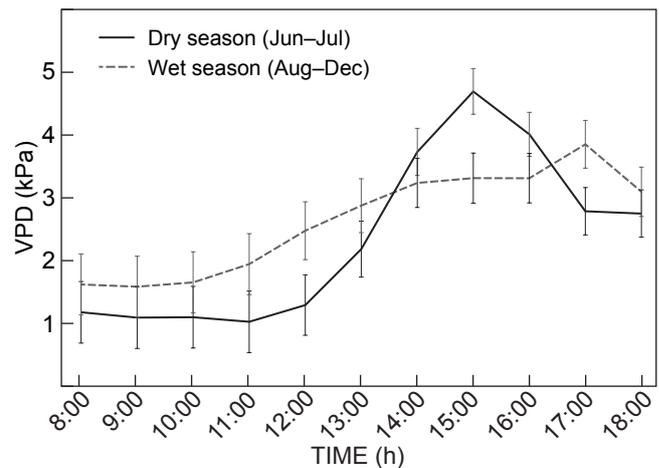


Figure 3: Temporal variation of vapour pressure deficit (VPD) in the *Cyperus papyrus* canopy of Lubigi wetland during dry and wet seasons in 2012. Error bars are standard error of mean for the different days

during when biological measurements such as stomatal conductance were taken. Multiple regression analysis was used to determine the integral effect of the climate factors on stomatal conductance, with all unmeasured inherent stomatal conductance factors represented as constants in the relationship (Mead and Curnow 1983). The coefficient of relationship or gradient of predictors was considered as the temporal sensitivity effect of the variables on stomatal conductance. Homogeneity of variance in datasets during the multiple regression analysis was automatically tested using Durbin–Watson statistics to ensure uniformity. Climate data for conductance measurement days only were selected for the correlations and the half-hourly climate data were averaged per hour to correlate to conductance measurement intervals. The Kruskal–Wallis test was used to determine differences between temporal changes of measured variables. All statistical values were considered significant at $p < 0.05$.

Results

Variation of climate variables in papyrus canopy surface

Early-morning VPD in both the dry and wet seasons was low, compared to that of the afternoon hours (Figure 3). The VPD between 14:00 and 16:00 was higher in the dry season than in the wet season but lower for the rest of the day. The maximum values of VPD during the dry and wet seasons were attained at 15:00 and 17:00, respectively.

Air temperature in the papyrus wetland canopy at midday was significantly higher in the wet season compared to the dry season ($p < 0.05$) but after 14:00 it dropped (Figure 4). Mean seasonal temperatures in the dry and wet periods were 22.89 °C (SE 0.42) and 23.21 °C (SE 0.21), respectively, and not significantly different ($p = 0.845$).

Incident PAR was maximum and higher in the morning hours in the wet season, compared to that in the dry season (Figure 5). There was a lag in the timing of maximum PAR during the dry season compared to the wet season. At 11:00 the mean wet season PAR value was significantly

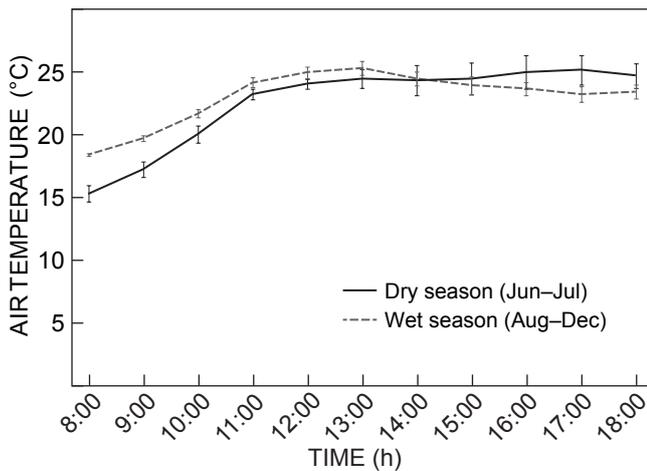


Figure 4: Temporal variation in air temperature in the surface of Lubigi *Cyperus papyrus* wetland canopy during wet and dry seasons in 2012. Error bars are standard error of mean for the different days

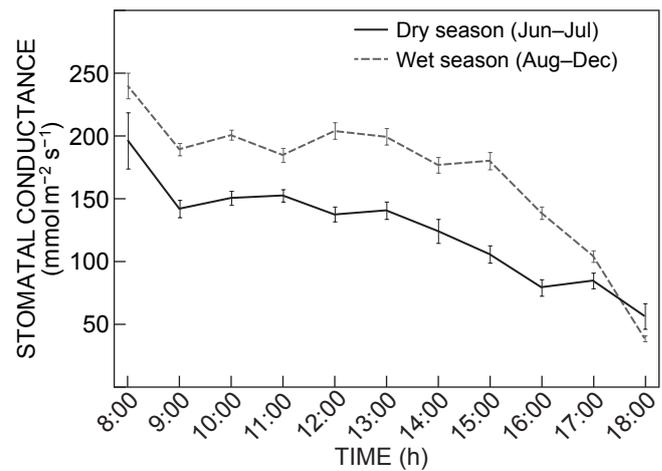


Figure 6: Temporal variation of stomatal conductance in Lubigi *Cyperus papyrus* wetland during wet and dry season in 2012. Error bars are standard error of mean for the different days

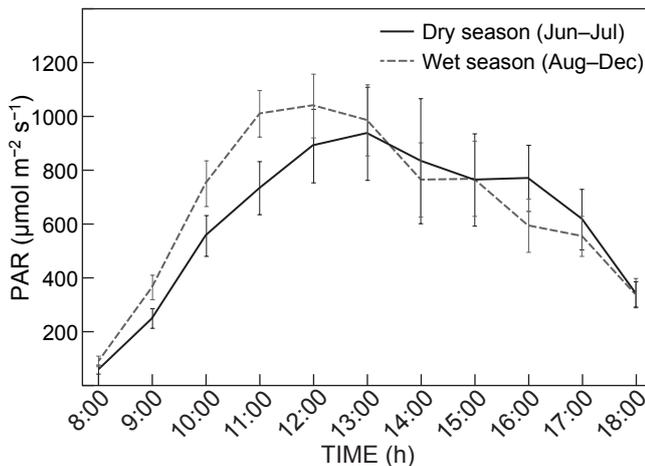


Figure 5: Temporal variation in photosynthetically active radiation (PAR) intensity at surface of Lubigi *Cyperus papyrus* wetland canopy during dry and wet seasons in 2012. Error bars are standard error of mean for the different days

higher than that in the dry season ($p = 0.035$). Mean seasonal PARs between 8:00 and 18:00 were $643 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SE 46.5) and $691 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SE 36.3) for the dry and wet periods, respectively. These values were not significantly different ($p = 0.845$).

Variation of stomatal conductance of the bracteoles

In both the wet and dry seasons, stomatal conductance was highest from 08:00 to 13:00, falling between 08:00 and 09:00, and remaining relatively stable until approximately 13:00, after which it declined (Figure 6). However, overall the stomatal conductance during the wet season was significantly higher compared to the dry season ($p = 0.00$).

The measured climate variables accounted for 69.4% and 87.5% of stomatal conductance during the wet and

Table 1: Multiple regression analysis of papyrus stomatal conductance with climate variables in the Lubigi papyrus wetland canopy in 2012

Predictor	Dry season		Wet season	
	Regression coefficient	p -value	Regression coefficient	p -value
Constant (stomatal conductance)	4.012	8.37E-05	8.84	0.023
Air temperature	-1.495	0.002	-4.04	0.071
PAR	0.122	0.006	0.28	0.037
VPD	-0.062	0.270	-0.11	0.728

dry seasons, respectively. Both PAR and air temperature had significant effects on stomatal conductance during the dry season, while in the wet season PAR was the only significant factor (Table 1). The effect of VPD on stomatal conductance at constant values of PAR and temperature indicated a significant relationship during the dry season, but not during the wet season ($F = 6.09$, $p = 0.025$; $F = 2.63$, $p = 0.132$). VPD accounted for 60.4% and 38.9% of the stomatal conductance variance during the dry and wet seasons, respectively. Figure 7a, b shows the relationship between stomatal conductance and VPD during the dry and wet seasons, respectively. During the wet season the stomata were much more responsive to changing VPD, closing sharply as VPD increased.

Discussion

The only previously published measurements of stomatal conductance in *Cyperus papyrus* under field conditions were made on Lake Naivasha, Kenya (Jones and Muthuri 1984; Jones 1987). However, these authors did not investigate seasonal changes in stomatal responses to climatic variables, and the climatic conditions were somewhat different to those during the present study. In Kampala, the early morning and evening air temperatures were

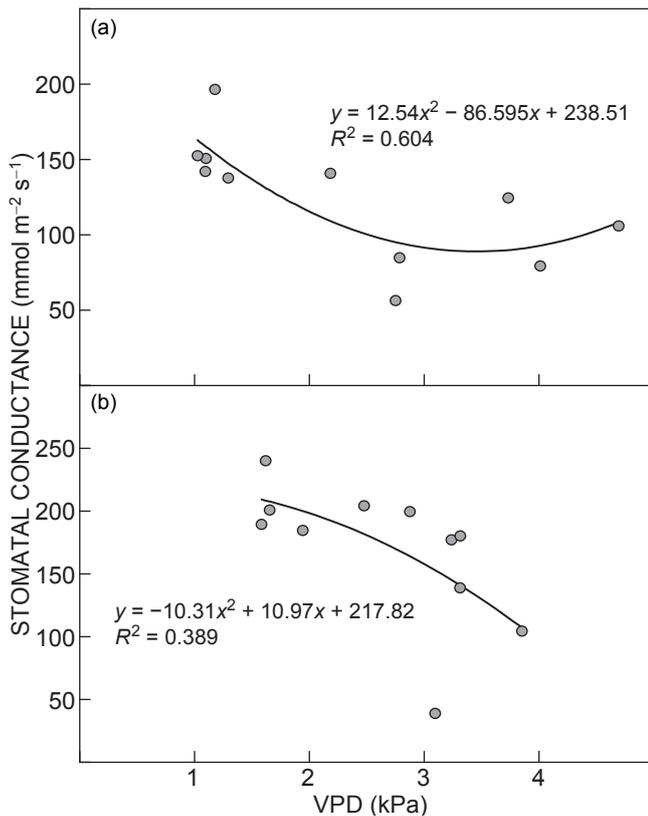


Figure 7: Relationship of stomatal conductance to vapour pressure deficit (VPD) in the canopy of Lubigi *Cyperus papyrus* wetland during (a) the dry season and (b) the wet season in 2012

higher than those at Lake Naivasha, although midday temperatures were similar. The low early-morning VPDs recorded in Kampala were similar to the values reported by Jones (1987). At both locations there is clear evidence that changes in VPD affect stomatal conductance, but the present study has shown that this sensitivity changes with season, the stomata being more sensitive in the wet season (August–November) than in the dry season (June–July). Hall and Kaufmann (1975) reported that large humidity gradients may contribute to closure of stomata at midday, and Nereu (2003) reported that, if diffusion of water from the leaves to the atmosphere increases up to a rate that cannot be supplied by the vascular structure of the plant, the leaves and the entire plant may become water-stressed. Although the response of stomatal conductance to changes in VPD has been subject of many investigations, the mechanism involved is still the subject of speculation (Jones 1987; Eamus and Jarvis 1989).

In this study, measurements of stomatal conductance throughout the day showed that the stomata of papyrus open very quickly and maximally in the early morning, which suggests a high sensitivity to the rising PAR levels at that time. Stomatal opening is stimulated in the morning, and is particularly sensitive to light when VPD is low and temperature is also relatively low. Jones and Humphries (2002) and Saunders et al. (2007), using eddy covariance to measure water vapour fluxes, also reported that water flux

from papyrus canopies increased as PAR and air temperature increased, implying that stomatal opening is mediated through increasing photosynthesis. The increasing VPD later in the day is largely a result of the temperature rise, although less stable atmospheric conditions probably also move drier air over the canopy. The result is a reduction in stomatal conductance as VPD increases, with a stronger response in the wet season than in the dry season.

The interpretation of the relationship between VPD and stomatal conductance is that there is a response to humidity in both seasons, but that in the wet season the stomata are consistently open due to the non-significant effect of VPD. This would seem to be a useful strategy, as it reduces water loss when the VPD gradient between intercellular spaces and atmosphere is greatest during the dry season. Such insights of environmental control on stomatal conductance are a focus in plant research because of the link with carbon gain and growth (Addington et al. 2004). The high morning stomatal conductance of papyrus allows early-morning carbon gain, when temperatures and VPD are low.

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References

- Addington R, Mitchell RJ, Oren R, Donovan LA. 2004. Stomatal sensitivity to vapour deficit and its relationship to hydraulic conductance in *Pinus palustris*. *Tree Physiology* 24: 561–569.
- Ball JT, Woodrow IE, Berry JA. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens J (ed.), *Progress in Photosynthesis Research*. Dordrecht: Martinus Nijhoff. pp 221–224.
- Black CR, Squire CR. 1979. Effects of atmospheric saturation deficit on stomatal conductance of pearl millet (*Pennisetum typhoides* S. and H) and groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* 118: 935–945.
- Eamus D, Jarvis PG. 1989. The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* 19: 1–55.
- FAO (Food and Agriculture Organization). 1998. *Crop evapotranspiration – guidelines for computing crop water requirements*. FAO Irrigation and Drainage Paper 56. Available at <http://www.fao.org/docrep/x0490e/x0490e00.htm> [accessed 15 February 2011].
- Hall AE, Kaufmann MR. 1975. Stomatal response to environment with *Sesamum indicum* L. *Plant Physiology* 55: 455–459.
- Jones MB, Humphries SW. 2002. Impacts of the C₄ sedge *Cyperus papyrus* L. on carbon and water fluxes in an African wetland. *Hydrobiologia* 488: 107–113.
- Jones MB, Muthuri FM. 1984. The diurnal course of plant water potential, stomatal conductance and transpiration in a papyrus (*Cyperus papyrus* L.) canopy. *Oecologia (Berlin)* 63: 252–255.
- Jones MB. 1987. The photosynthetic characteristics of papyrus in a tropical swamp. *Oecologia (Berlin)* 71: 355–359.
- Leuning R. 1995. A critical appraisal of a combined stomatal photosynthesis model for C₃ plants. *Plant, Cell and Environment* 18: 339–455.
- Mead R, Curnow RN. 1983. *Statistical methods on agricultural and experimental biology*. London: Chapman and Hall.

- Medlyn B, Duursma R, Eamus D, Ellsworth DS, Prentice IC, Barton CM et al. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology* 17: 2134–2144.
- Meidner H, Mansfield LA. 1968. *Physiology of stomata*. London: McGraw-Hill.
- Migahid AM. 1952. *Further observations on the flow and loss of water in the "Sudd" swamps of the Upper Nile*. Cairo: Cairo University Press.
- Mooney HA, Chu C. 1983. Stomatal responses to humidity of coastal and interior populations of a California shrub. *Oecologia (Berlin)* 57: 148–150.
- Nereu AS. 2003. Stomatal response to water vapour deficit; an unsolved issue. *Revista Brasileira Agrociência* 9: 317–322.
- Osonubi O, Davies WJ. 1980. The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. *Oecologia (Berlin)* 46: 1–6.
- Penman HL. 1963. *Vegetation and hydrology*. Technical Communication No. 53. Harpenden: Commonwealth Bureau of Soil Science.
- Philippe M. 1989. The significance of radiative coupling between vegetation and the atmosphere. *Agricultural and Forest Meteorology* 49: 45–53.
- Rijks DA. 1969. Evaporation from a reed swamp. *Journal of Ecology* 63: 299–309.
- Saunders JM, Jones MB, Kansiime F. 2007. Carbon and water cycles in tropical papyrus wetlands. *Wetlands Ecology and Management* 15: 489–498.
- Schulze ED, Küppers M. 1979. Short-term and long-term effects of plant water deficit on stomatal response to humidity in *Corylus avellana* L. *Planta* 146: 319–326.
- Schulze ED, Lange OL, Kappen L, Buschbom U, Evenarim M. 1973. Stomatal response to changes in temperature at increasing water stress. *Planta* 110: 29–42.
- Stewart JB. 1988. Modelling surface conductance of pine forest. *Agricultural and Forest Meteorology* 43: 19–35.
- Willmer C, Fricker M. 1996. Stomatal responses to environmental factors. In Black M, Charlwood B (eds), *Stomata: topics in plant functional biology* (2nd edn). London: Chapman & Hall. pp 126–191.